

ARCHAEOPTERYX

ARCHAEOPTERYX: THE FOSSIL

Contrary to Wells's subtitle, *Archaeopteryx* is not a "missing link." The term "missing link" is an outdated term that does not accurately reflect the way biologists and paleontologists think about fossils. We prefer not to talk about "missing links" or "intermediate forms," but rather intermediate *features*. *Archaeopteryx* has features intermediate between those of living birds and ancient reptiles; along with many other fossils, it preserves ancestral features while it shows descendant novelties. *Archaeopteryx* retains the ancestral "reptilian" features of a long bony tail, clawed hands, teeth, and many others. It also has the derived "avian" features of feathers and powered flight. *Archaeopteryx*, along with other dinosaur fossils, shows the evolution of avian features and flight. These fossils show that many features thought of as unique to a certain group of animals were also shared by some of their ancestors; this helps paleontologists to reconstruct the evolutionary history of living animals. When many fossils are looked at in their genealogical context, they blur the lines between the normally recognized taxonomic groups (most of which were based originally only on living forms). *Archaeopteryx* is frequently used for pedagogical purposes because it is easy to recognize its mixture of "bird" and "reptile" features and because it played an historical role in helping to cement Darwin's theory (it was discovered 2 years after publication of the *Origin*). Textbook authors like *Archaeopteryx* for these reasons and often illustrate their discussions with pictures of the Berlin specimen, one of the most beautiful fossils ever discovered, and remarkably complete. Textbooks also use *Archaeopteryx* as an exam-

ple of how fossils are important for showing transitional features of evolution, and how the fossil record is good evidence that evolution has occurred.

WELLS MISSES MORE THAN THE LINKS

Wells objects to textbook treatments of *Archaeopteryx* as a transitional form or as an "ancestor" of birds. Wells wants textbooks to say that *Archaeopteryx* was not an "ancestor" because modern birds are not descended from it and that its transitional status is "controversial." Wells claims that *Archaeopteryx* has been "quietly shelved" by paleontologists and that the search for a "missing link" between dinosaurs and birds goes hopelessly on "as though *Archaeopteryx* had never been found" (Wells, 2000:138). Paleontologists would find this surprising. By making such claims, Wells exposes the depths of his ignorance of phylogenetic methodology, paleontology, and avian evolution.

Wells is clearly confused by *Archaeopteryx*, "transitional forms," and ancestors. First of all, Wells asserts that *Archaeopteryx* is no longer considered a transitional form or an "ancestor." Wells is correct, but only in a specialized sense, not appropriate in the context of his generalized discussion. We cannot — and do not — say for certain that the animal that we call *Archaeopteryx* was *actually genetically transitional* to living birds, or that it was a *direct genetic ancestor* of living birds. However, in a less strict sense (that appropriate to Wells's discussion), *Archaeopteryx* has a great many transitional *features* between living birds and Mesozoic dinosaurs: if it was not a *direct* ancestor, it was surely a close *collateral* ancestor (see below).

Second, there is no such thing as a "missing link," and paleontologists are not looking for

them. Paleontologists collect, survey, and reconstruct past forms of life. Some of these fossil organisms have features that illustrate the path evolution took to reach the forms we see today. We can think of these organisms as showing transitional or ancestral features. Paleontologists are also not looking for ancestors, but rather features of ancestors. Paleontologists distinguish between *lineal* and *collateral* ancestors. Lineal ancestors are those that are directly ancestral to living organisms: your lineal ancestors are your father and mother, grandfathers and grandmothers, and so on. Collateral ancestors are those organisms that share an ancestor with living organisms: your collateral ancestors are your uncles, great-uncles, cousins, second cousins, and so on. Paleontologists do not claim to be able to identify lineal ancestors. Without observational or genetic evidence, how could you ever know that a fossil organism left any offspring? It is not the ancestry that is important to paleontologists, but rather the *ability* to reconstruct the *features* of those ancestors. This is a powerful and important concept, one completely lost on Wells.

To illustrate this powerful approach, let's say you wanted to know something about your own ancestors. If you knew your ancestors came from a certain small village in France in the 1600s, you could return to that village and, even if you can't locate their graves, you might find those of many of their contemporaries in the churchyard. A collection of artifacts from any of those people would give you a perfectly adequate idea of the characteristics, culture, possessions, and daily life of your direct ancestors (Padian and Angielczyk, 1999). Using similar methods for similar reasons, paleontologists try to uncover features of ancestors, not the ancestors themselves.

Even Wells's claim that paleontologists do not think *Archaeopteryx* is "ancestral" is incor-

rect. *Archaeopteryx* has no features that would actually disbar it from being a direct ancestor of living birds. Whether it was a direct ancestor of today's birds or not is irrelevant: *Archaeopteryx* exhibits unique features of the last ancestor it shared with birds, so, regardless whether it is a *lineal* ancestor, it still preserves features that indicate what the last ancestor of *Archaeopteryx* and birds may have been like. In other words, *Archaeopteryx* has many features intermediate between those of its dinosaurian ancestors and its avian descendants, which is exactly what would be predicted by evolution. No amount of stridency on Wells's part can change that.

When paleontologists reconstruct relationships of living and fossil organisms, they use the features of both living and fossil organisms. This allows them to reconstruct the features of the ancestors and get a pretty good picture of what the ancestors were like. Phylogenetic systematics, commonly called "cladistics," is the method that nearly all biologists use to determine relationships, whether they work on dinosaurs or dinoflagellates, and whether they use molecules or morphology. Its simplicity, objectivity, testability, repeatability, utility, and firm rooting in the principle of descent has led to its near-universal application. Contrary to Wells's characterization, cladistics is not a search for "missing links" or direct ancestors, but for shared evolutionary features. The basic idea behind cladistics is that when novel features arise, they are passed on to descendants. Therefore, these "derived features" should be more informative in reconstructing relationships than those that are present across a larger group. For example, if a population of animals evolve stripes on their backs and all their descendants continue to sport stripes, then all the members of that species that have stripes are probably more closely related to each other than they are to

those without stripes. It is that simple, yet Wells's discussion of cladistics reveals that he either does not grasp the method or has no interest in explaining it properly.

In the nearly two pages devoted by Wells to a discussion of cladistics (Wells, 2000:118–119), he states that cladistics is based on overall similarity. Yet as stated above, cladistics is not based on mere similarity, but instead focuses on a special kind of similarity — features that are *derived*, or evolutionary novelties. Evolutionary novelties help to show relationships and thus are “phylogenetically informative.” In contrast, similarities that are not evolutionary novelties are “ancestral” features and are not phylogenetically informative. For example, a derived feature of primates is an opposable thumb; this feature is phylogenetically informative because it allows us to group all primates together to the exclusion of other mammals. On the other hand, a five-fingered hand is an ancestral feature and not phylogenetically informative because we would not group all animals possessing a five-fingered hand together to the exclusion of those that do not. For example, we do not propose that all five-fingered mammals are more closely related to each other than they are to three-fingered, two-fingered, or one-fingered mammals. So cladistics *is not* based on mere similarity. Further, paleontologists who apply cladistic methods to the problem of avian evolution do not think that how flight evolved is “irrelevant”; in fact we specifically use cladograms to inform our models of how flight (and other things) evolved. By rooting our explanations in phylogenies, we can move beyond subjective models, and constrain our hypotheses (e.g., Witmer, 1995; Padian, 1995). These explanations can also serve as yet another independent test of our phylogenies (Padian, 2001a, 2001b).

Wells then accuses cladistics of “rearrang-

ing” the evidence, stating that the supposed “ancestors” of *Archaeopteryx* are millions of years younger. First of all, none of these more “recent” avian-like dinosaurs thought to be closely related to *Archaeopteryx* (e.g., troodontids and dromaeosaurs) are considered “ancestors”; rather, they retain ancestral features that show us what the ancestors of *Archaeopteryx* were like. Here again Wells mistakes lineal for collateral ancestry. Second, the statement that there are no fossils of these close cousins of *Archaeopteryx* until “millions of years” later is false. Fossils of non-avian maniraptor dinosaurs, which are closely related to the ancestors of *Archaeopteryx*, have been found in rocks dating to the same age as those in which *Archaeopteryx* has been found (Jensen and Padian, 1989); this discovery was reported over 10 years ago. Wells apparently has not done his homework very well.

Despite Wells's claims to the contrary, *Archaeopteryx* is still an important contributor to our knowledge of transitional features, and it clearly shows the dinosaurian ancestry of birds (Figure 12). To confirm this, all one has to do is peruse any piece of literature on the origin of birds. Papers on *Archaeopteryx* and bird evolution appear in many journals each year, and there is even an entire journal (called *Archaeopteryx*) devoted to the study of *Archaeopteryx* and its environment. Rather than consult the vast body of literature on the origin of birds, Wells appears to base much of his discussion on two popular works, one technical — *The Mistaken Extinction* by Lowell Dingus and Tim Rowe (1998) — and the second non-technical — *Taking Wing*, by Pat Shipman (1998). Both are excellent books. However, during the same period when Wells apparently wrote *Icons* (1998–1999), well over 50 papers were published that in some way dealt with *Archaeopteryx* and the dinosaurian origin of birds. A number of these were very

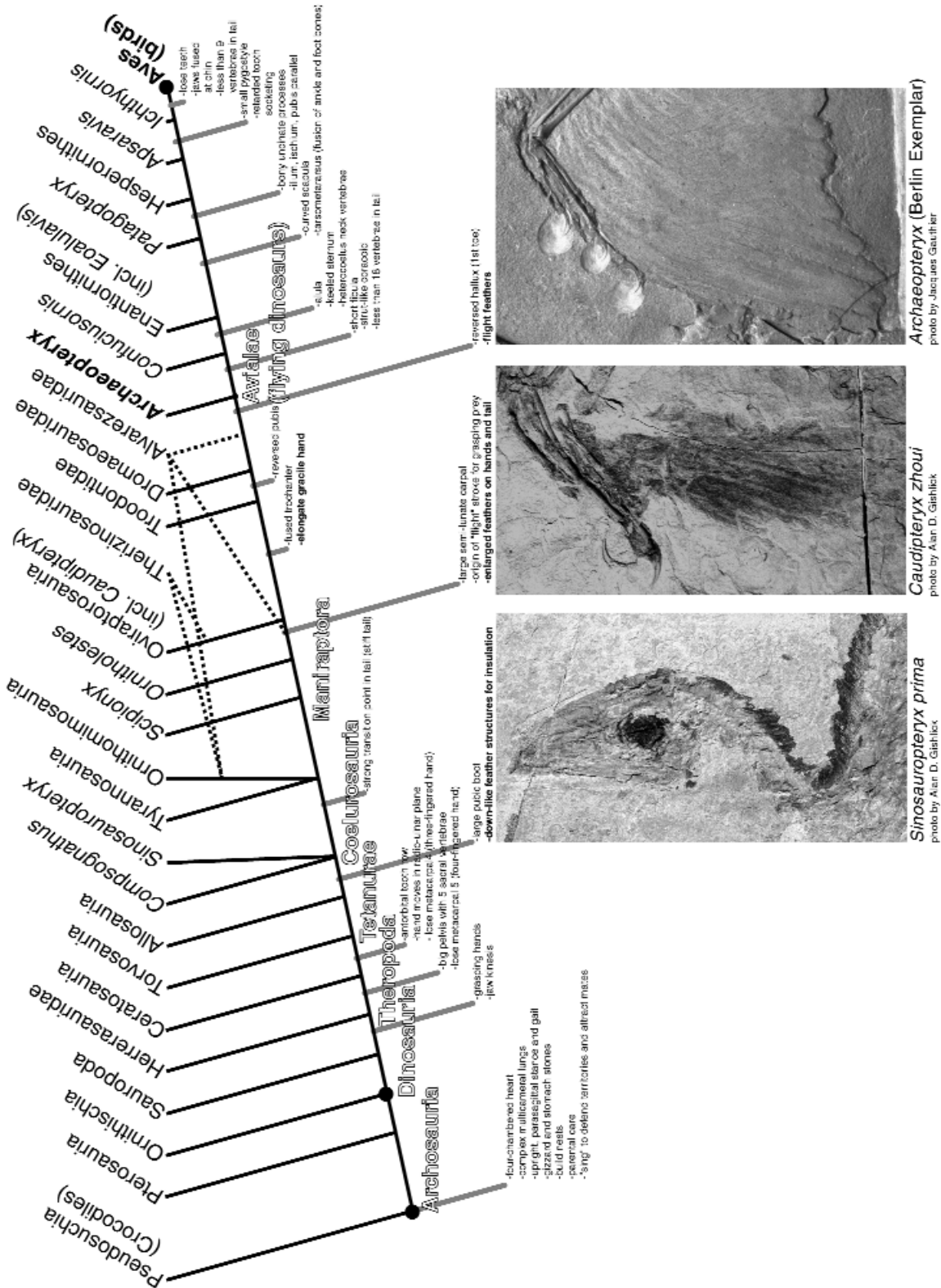


Figure 12. Archaeopteryx (bold) shown in evolutionary context with respect to crocodylians, non-avian dinosaurs, and birds. Some relevant features plotted.

important (e.g., Britt et al., 1998; Padian and Chiappe, 1998; Forster et al., 1998; Ji et al., 1998; Burgers and Chiappe 1999; Chiappe et al. 1999; Clark et al., 1999; Garner et al., 1999; Norell and Makovicky, 1999; Ostrom et al., 1999; Wagner and Gauthier, 1999; Xu et al., 1999), yet Wells cites none of them.

Wells also ignores the many fossil discoveries of feathered non-avian dinosaurs from Liaoning, China (see Figure 13), which should play an important role in *any* discussion of avian origins, save for one notable exception. In an attempt to discredit the entire field, Wells brings up “Archaeoraptor,” which he regards as a “hoax” and indicative of the sloppy science that paleontologists do. In fact Wells spends the remaining third of the chapter trying to use “Archaeoraptor” in an attempt to slander the field of paleontology. Here too, he gets most of the facts wrong.

“Archaeoraptor” was a fossil bought at the Tucson Gem and Mineral Show for Steve Czerkas, a knowledgeable dinosaur enthusiast and skilled sculptor and artist. Its remains came from the Liaoning area of China, which has produced numerous beautifully preserved fossils of fish, mammals, lizards, and both avian and non-avian dinosaurs. Many of these were preserved with their body coverings, such as fur or feathers, intact. So it was not unexpected to see an allegedly new find from there that combined features of fossil birds and closely related dromaeosaurid dinosaurs, especially given the large body of evidence suggesting that birds evolved from these dinosaurs. The fossils of Liaoning are collected by local villagers and farmers who know that “complete” specimens, particularly those with feathers, are preferred by scientists and collectors. Therefore, a cottage industry has sprung up around using parts to enhance or make “whole” specimens (Chiappe et al., 1999). These constructed specimens are very

well done and can fool an untrained eye, which is more or less what happened with “Archaeoraptor.” The first paleontologists to see the specimen were immediately suspicious because the prevalence of composite specimens was already known, and its distribution of features were not what would be expected in an avian-like dinosaur. We would not expect it to have the arms of a primitive bird and the legs of a non-avian theropod. Even though a number of paleontologists were skeptical, *National Geographic* went ahead with an article that featured this specimen along with two others. This became an embarrassment for *National Geographic* when, at nearly the same time it ran its article, computerized axial tomography (CAT) scanning of the specimen showed it to be a composite. As it turns out, the legs of the specimen belong to the counterslab of a tiny non-avian theropod called *Microraptor* (Xu et al., 2001); a full description of the composite was published by Rowe et al. (2001). To view the scans of the composite, visit the UT Austin CT lab website (www.ctlab.geo.utexas.edu/pubs/nature2000).

Wells concludes that this sorry episode occurred because of “the cladists’ desire to prove their theory. Just as the need for a missing link between apes and humans led to Piltdown man, so the need for a missing link between dinosaurs and birds paved the way for the ‘Piltdown bird.’” (Wells, 2000:125). Not so. The people who bought and promoted the specimen weren’t cladists, and they never performed a cladistic analysis or attempted to place the specimen in a phylogeny. Piltdown man was an intentional hoax played on scientists, and the hoax was revealed by scientists when the specimen was studied. The forgery of “Archaeoraptor” was discovered by scientific investigation as well, and it was *cladists* Tim Rowe, Xu Xing, and Phil Currie who uncovered it. The name “Archaeoraptor” was never

formally published as a scientific name, and has no scientific standing — the animal never existed. This doesn't prevent Wells from italicizing the name as if it *were* a real species. Further, the specimen was never considered important to our understanding of avian evolution. This doesn't stop Wells from pretending otherwise, as if it were somehow important, even crucial, to the idea that birds are descended from dinosaurs.

Returning to *Archaeopteryx*, Wells then resorts to a classic creationist taxonomy game. In this game, the creationist says that scientists have to choose whether a fossil belongs to one taxonomic group or another. So, in the case of *Archaeopteryx*, it has to be a bird *or* a reptile. Then the creationist says that because it has feathers it is a bird, and therefore because it is a "bird" it cannot be a transitional form. In effect the transitional features of the fossil are defined out of existence. This is a classic creationist ploy, and nothing new; it is what we have seen for decades from Duane Gish and Henry Morris. Wells uses a slightly different approach, claiming that if *Archaeopteryx* and birds are just dinosaurs, then humans are just fish, which — he implies — is absurd. But this is another case of Wells trying to use semantics to negate the evidence of evolution, just as he did with the Cambrian Explosion.

Here Wells exploits the systematic practice by which all groups of organisms must be "monophyletic," that is, consist of an ancestor and *all* of its descendants. In Wells's rather naïve example, "fish" must be taken to include hagfishes, lampreys, sharks, goldfish and other rayfins, coelocanth, and lungfishes. If "fish" were defined that way, then tetrapods (all animals that have four limbs) would indeed be "fish" and "fish" would become another name for "vertebrate." But "fish" is not a taxonomic name; it is a colloquial term, and as a Ph.D. biologist, Wells should know that. Real sys-

tematists don't use the term "fish" except in a restricted sense referring either to a subgroup that is monophyletic such as Actinopterygia or to "rayfins" (things like goldfish, trout, swordfish, etc.) — the vast majority of living "fishes." Humans are vertebrates; so are fishes. Birds, by phylogenetic relationship, are dinosaurs. Just as dogs are canids, and also mammals, and also tetrapods and vertebrates. Consider a mailing address: just because you live on 1010 Main Street does not mean that you don't live in Peoria or in Illinois, or that someone living on 411 South Street *doesn't* live in the same town or state.

Wells's most ridiculous treatment of "science" in this chapter is when he takes childish shots at paleontologists. This is another popular creationist tactic: attacking the character of a prominent scientist or scientific field. In fact, he devotes six pages to making fun of paleontologists at a Florida symposium without appearing to understand what they were saying. Worse yet, Wells completely misrepresents the proceedings. For example, he claims that a "cladistic analysis" showed a specimen presented there, called "*Bambiraptor*," to be an ancestor of *Archaeopteryx*, yet no "cladistic analysis" was mentioned in either the description (Burnham et al., 2000) or the conference proceedings. To my knowledge, no cladistic analysis has ever been performed on that specimen. Wells then claims to be appalled that in the reconstruction, "*Bambiraptor*" was shown covered in feathers even though none were found fossilized with it. But other fossilized dromaeosaurid dinosaurs are found covered in feathers (e.g. Xu et al., 1999; Ji et al., 2001; Norell et al., 2002) and so are the more basal Oviraptorids (Ji et al., 1998). The even more basal Compsognathids are found with down-like feathers as well (Chen et al., 1998; see Figures 12, and 13). So it is conservative to reconstruct "*Bambiraptor*" with a covering of

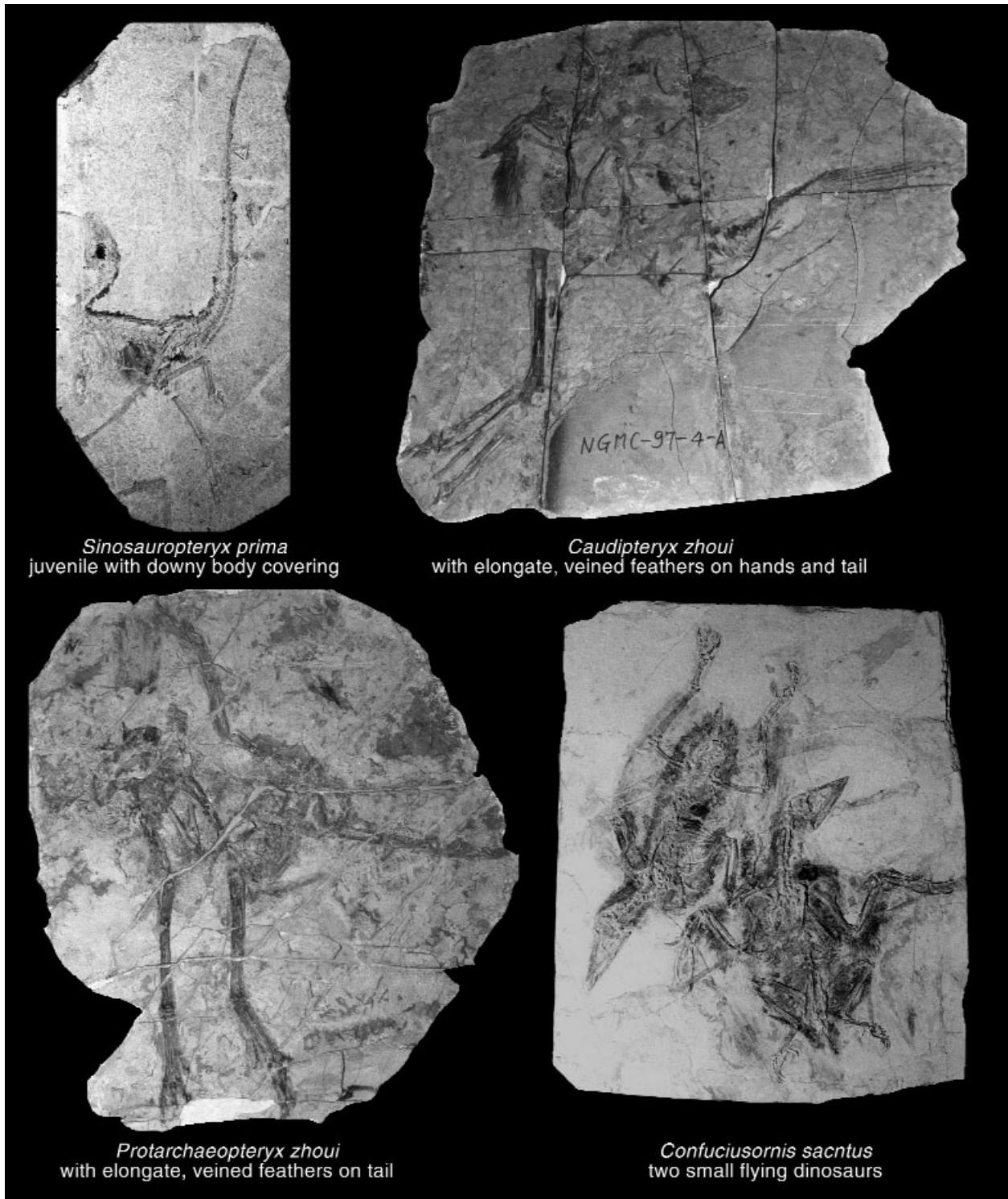


Figure 13. Some examples of feathered dinosaurs discovered in Laioning, China.

feathers. Besides, the reconstruction is a picture, not scientific evidence — a confusion of Wells’s revealed further in the peppered moths chapter. By Wells’s logic, we shouldn’t accept the likelihood of fur on a fossil sabertooth cat. Is this the kind of “critical thinking” Wells wants us to teach our students?

Finally, Wells caricatures the conference presentation of Kevin Padian, who not only is a respected paleontologist but also happens to be the president of NCSE. Padian’s talk was a critique of the hypothesis that birds evolved from something *other* than dinosaurs. Wells likens Padian’s talk to an “old lawyers’ joke” about a “cracked kettle.” Wells even says that Padian was not trying to be funny, and that it would be unkind to compare his talk to the joke, yet he continues the *ad hominem* attack summarizing Padian’s talk as a joke. Wells’s summary, however, looks nothing like either the abstract that Padian submitted, which Wells (as a conference attendee) received, or the text of the talk he gave. In particular, Padian never called the *critics* of the dinosaurian origin of birds “unscientific,” just their *criticisms*. He never accused them of “selective interpretation” of the evidence; he just said that they did not use accepted methodologies to evaluate the evidence. He never said that scientists reject their methodology regardless of the evidence; he said that we cannot evaluate their methodology because they do not provide one. Finally, Padian’s conclusion was not that there was no controversy, but that the controversy over bird origins was journalistic, not scientific (Padian, pers. comm.). If Wells was taking notes at the conference, he didn’t do a very good job.

Although Wells smugly chides paleontologists for their supposed views about bird evolution, he has not attended any meetings of the Society of Vertebrate Paleontology or the Ostrom Symposium on the origin of birds. He

has no training or expertise in the field. Instead, he relies on caricatures of paleontology and paleontologists, and lampoons the entire field, treating scientists as if they were a bunch of dinosaur-loving buffoons who are easily fooled and misled. This is not science or scholarship; this is tabloid journalism.

WHAT THE TEXTBOOKS SAY

Textbooks cover *Archaeopteryx* with varying degrees of brevity, frequently giving only a paragraph to *Archaeopteryx*, usually in the section on reptiles or birds or in the history of life section. The lengths of the paragraphs vary from 54 words to well over 500 (Figure 14), and the average length falls around 200 words. *Archaeopteryx* is frequently used as an example of a transitional form between reptiles (dinosaurs) and birds. Eight of the books treat it as showing a dinosaurian ancestry for birds, while two state that the ancestry is simply reptilian (Figure 14). Few of these books treat *Archaeopteryx* well and most of these discussions are garbled and contain factual errors about *Archaeopteryx*. For example, Guttman contains numerous errors, even suggesting that it could not fly. Wells apparently does not even know enough about the topic to point this out. Wells only singles out the two books that use the word “link” in their descriptions, Mader and Schraer and Stolze. The most accurate discussions can be found in Raven and Johnson, Campbell et al., and Johnson. *Archaeopteryx* is sometimes used as an example of how fossils can elucidate evolutionary relationships. Few books use *Archaeopteryx* as direct evidence for evolution; some books (e.g., Johnson) instead use the origin of whales as the principal example of a transitional sequence.

Book	<i>Archaeopteryx</i>					
	#pages	#words	evolution chapter	diversity chapters	dinosaur link	Wells's grade
Schraer, W. D. and H. J. Stolze. 1999. <i>Biology: The Study of Life</i> , seventh edition. Prentice-Hall, Upper Saddle River, NJ. 944p.	1/8	54	No	Yes	No	F
Johnson, G. B. 1998. <i>Biology: Visualizing Life</i> . Holt, Rinehart & Winston, Orlando. 895p.	1/3	112	No	Yes	Yes	D ¹
Biggs, A., C. Kapinka, and L. Lundgren. 1998. <i>Dynamics of life</i> . Glencoe/McGraw Hill, Westerville, OH. 1119p.	1/2 1/3	164 +61	Yes	Yes	No	C
Miller, K. R. and J. Levine. 2000. <i>Biology</i> , fifth edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	1/3 +1	160 +420	No	Yes	Yes	D
Starr, C. and R. Taggart. 1998. <i>Biology: The Unity and Diversity of Life</i> , eighth edition. Wadsworth Publishing Company, Belmont CA. 920p.	1 +1/8	>500 +46	Yes	Yes	Yes	F
Guttman, B. S. 1999. <i>Biology</i> . WCB/McGraw-Hill, Boston. 1175p.	1/2 +1/4	298 +129	Yes ²	Yes	Yes	D
Mader, S. 1998. <i>Biology</i> , sixth edition. WCB/McGraw-Hill, Boston. 944p.	1/4 +1/8 +	58 +52 +11	Yes	No	Yes (but not strongly)	F
Raven, P. H. and G. B. Johnson. 1999. <i>Biology</i> , fifth edition. WCB/McGraw-Hill Boston. 1284p.	1	466	No	Yes	Yes	F
Campbell, N. A., J. B. Reese, and M. G. Mitchell. 1999. <i>Biology</i> , fifth edition. Benjamin Cummings, Menlo Park, CA. 1175p.	3/4 +1/4	256 +79	No ³	Yes	Yes	B ⁴
Futuyma, D. 1998. <i>Evolutionary Biology</i> . Sinauer Associates, Sunderland, MA. 761p.	1.5	>600	Na ⁵	Na ⁵	Yes	D

1. Discusses *Archaeopteryx* as an example of a genetic modification in evolution (scales – feathers); however, the discussion contains numerous errors.
2. Johnson does not “hint” at a controversy over *Archaeopteryx*'s transitional status. An “F” would be a more appropriate grade.
3. *Archaeopteryx* is discussed in the introduction chapter of the book under the topic of evolution with a picture of the Berlin specimen.
4. Wells gives a “B”; however, this makes little sense given that the book clearly presents *Archaeopteryx* as a transitional form, and plugs the “dinosaur” hypothesis, in all but the last 2 sentences. A “C” or “D” may be more appropriate on Wells's scale.
5. Futuyma is entirely about evolution so there is no “diversity of life” chapters. *Archaeopteryx* is discussed under “evolving lineages in the fossil record” section, which catalogues many fossil examples of evolution.

Figure 14. Textbooks' treatment of and Wells's grades for *Archaeopteryx*.

WELLS'S EVALUATION

In grading textbooks on *Archaeopteryx*, the grading scheme, as usual, seems skewed to fail the books. Any book that does not describe the transitional status of *Archaeopteryx* between reptiles and birds as “controversial” gets a D. As mentioned above, there is no controversy about whether it is *transitional*, i.e., possesses structural features both of its reptilian ancestors and of birds. To get better than a D, a book would have to pres-

ent scientifically incorrect data. What is most puzzling is that some books are given rather high grades compared to those given for other “icons.” Close examination of these books suggests that Wells misgraded them (Figure 14). For example, Wells gives Campbell, Reese, and Mitchell a B, yet they clearly state that *Archaeopteryx* is a transitional form between dinosaurs and birds, for which a C or D would have been a more accurate grade given Wells's criteria. This negligent application of his own criteria calls into question the

rigor of Wells's evaluation and the value of his grades whether or not one accepts his idiosyncratic criteria.

WHY *ARCHAEOPTERYX* STILL FLIES IN TEXTBOOKS

If anything, the value of *Archaeopteryx* as a pedagogical tool is increasing with all the new discoveries of feathered dinosaurs from China. Literally every new fossil discovery has added to the utility of *Archaeopteryx*. *Archaeopteryx* is still one of our best examples of a fossil that preserves ancestral features while showing descendant novelties. *Archaeopteryx* is but one of many fossils showing a clear genealogical connection between dinosaurs and birds (Figure 12). Much like Mark Twain's, the reports of its death are greatly exaggerated.

HOW TEXTBOOKS COULD IMPROVE THE USE OF *ARCHAEOPTERYX* AND TRANSITIONAL FORMS

Textbooks could improve their explanations of transitions in evolution by focusing on *transitional features* (not forms or individual animals) that are borne by a series of closely related organisms. Further, textbooks should be clear in presenting the idea that in general fossils are not considered to be direct ancestors, but as records of ancestral features. Finally, in discussions of *Archaeopteryx*, textbooks need to tighten up their descriptions and check their facts about the history of both *Archaeopteryx* and the dinosaur–bird relationship. Textbooks should be clear that birds are descendants of dinosaurs and that there are no other credible potential ancestral groups; they should also augment their rather short discussions of avian evolution with some of the new fossil evidence from China where non-avian dinosaurs have been found with feathers (Figure 13). Wells's claims

about *Archaeopteryx* are simply inaccurate. To follow his lead would mislead students into thinking that fossils tell us nothing about evolutionary relationships. Considering the fact that Wells doesn't understand ancestry or phylogenetic reconstruction, and he isn't even aware of *Archaeopteryx*'s status in paleontology, should we really be inclined to trust anything he says on these topics?

References

- Britt, B. B., P. J. Makovickey, J. A. Gauthier, and N. Bonde. 1998. Postcranial pneumaticity in *Archaeopteryx*. *Nature* 395:374–376.
- Burnham D. A., K. L. Derstler, P. J. Currie, R. T. Bakker, Z. Zhou and J. H. Ostrom. 2000. Remarkable new bird-like dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. *University of Kansas Paleontological Contributions* 13:1–14.
- Burgers, P., and L. M. Chiappe 1999. The wing of *Archaeopteryx* as a primary thrust generator. *Nature* 399:60–62.
- Chen, P.-J., Z.-M. Dong, and S.-M. Zhen. 1998. An exceptionally preserved theropod dinosaur from the Yixian formation of China. *Nature* 391:147–152.
- Chiappe, L. M., S.-A. Ji, Q. Ji, and M. A. Norell. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the late Mesozoic of northeastern China. *Bulletin of the American Museum of Natural History*. 242:1–86.
- Clark, J. M., M. A. Norell, and L. M. Chiappe. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. *American Museum Novitates* 3265:1–36.
- Dingus, L. and T. Rowe. 1998. *The mistaken extinction: dinosaur evolution and the origin of birds*. W. H. Freeman and Company, New York 332p.
- Forster, C. A., S. D. Sampson, L. M. Chiappe, and D. W. Krause. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279:1915–1922.
- Garner, J. P., G. K. Taylor, A. L. R. Thomas. 1999. On the origins of birds: The sequence of character acquisition in the evolution of avian flight. *Proceedings of the*

- Royal Society of London, Biological Sciences Series B* 266:1259–1266.
- Jensen, J. A., and Padian, K. 1989. Small pterosaurs and dinosaurs from the Uncompahgre fauna (Brushy Basin Member, Morrison Formation: ?Tithonian), Late Jurassic, western Colorado. *Journal of Paleontology*. 63:364–373.
- Ji, Q., P. J. Currie, M. A. Norell, and S.-A. Ji. 1998. Two feathered dinosaurs from northeastern China. *Nature* 393:753–761.
- Ji, Q., M. A. Norell, K.-Q. Gao, S.-A. Ji, and D. Ren. 2001. The distribution of integumentary structures in a feathered dinosaur. *Nature* 410:1084–1088.
- Norell, M., Q. Ji, K. Gao, C. Yuan, Y. Zhao, L. Wang. 2002. ‘Modern’ feathers on a non-avian dinosaur. *Nature* 416:36–37.
- Norell, M. A., and P. J. Makovicky. 1999. Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. *American Museum Novitates* 3282:1–45.
- Ostrom, J. H., S. O. Poore, and G.E. Goslow. 1999. Humeral rotation and wrist supination: Important functional complex for the evolution of powered flight in birds? *Smithsonian Contributions in Paleobiology* 89:301–309.
- Padian, K. 1995b. Form and Function: The evolution of a dialectic. In J.J. Thomason ed. *Functional Morphology and Vertebrate Paleontology* Cambridge University Press p. 264–277.
- Padian, K. 2001a. Cross-testing adaptive hypotheses: phylogenetic analysis and the origin of bird flight. *American Zoologist* 41:598–607.
- Padian, K. 2001b. Stages in the origin of bird flight: beyond the arboreal–cursorial dichotomy. In J.A. Gauthier and L. M. Gall eds. *New Perspectives on the Origin and Early Evolution of Birds*. Yale University Press, New Haven p.255–273.
- Padian, K., and K. D. Angielczyk. 1999. Are there transitional forms in the fossil record? In P.H. Kelley, J.R. Bryan, and T.A. Hansen eds. *The Evolution–Creation Controversy II: Perspectives on science, religion, and geological education*. Paleontological Society Papers 5:47–82.
- Padian, K. and L. M. Chiappe. 1998. The origin and early evolution of birds. *Biological Reviews of the Cambridge Philosophical Society* 73:1–42.
- Rowe, T., R. A. Ketcham, C. Denison, M. Colbert, X. Xu, and P. J. Currie. 2001. Forensic paleontology: the Archaeoraptor forgery. *Nature* 410:539–540.
- Shipman, P. 1998. *Taking wing: Archaeopteryx and the evolution of bird flight*. Simon and Schuster, New York 336p.
- Wagner, G. P., and J. A. Gauthier. 1999. 1,2,3 = 2,3,4: a solution to the problem of the homology of the digits in the avian hand. *Proceedings of the National Academy of Science* 96:5111–5116.
- Wells, J. 2000. *Icons of evolution: science or myth?: why much of what we teach about evolution is wrong*. Regnery, Washington DC, 338p.
- Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft issues in fossils. In J.J. Thomason ed. *Functional Morphology and Vertebrate Paleontology* Cambridge University Press p. 19–33.
- Xu, X., X.-L. Wang, and X.-C. Wu. 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* 401: 262–266.
- Xu, X., Z. Zhou, and X. Wang. 2001. The smallest known non-avian theropod dinosaur. *Nature* 408:705–708.