The Mona Lisa of Ornithology: a short history of *Archaeopteryx lithographica*

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I. The Death of a Bird

A very, very long time ago, during an age so remotely gone from us as to be counted in millions of years past, the period classified as the Jurassic,[2] a fascinating and beautiful bird died. Although the cause or causes of the feathered creature's death are unknown and doubtless will ever be, its final resting place has been uncovered. Such a find is not ordinarily the case with light-boned and fragile beings such as birds. Birds perish in enormous numbers from starvation, cold, exhaustion, accident or disease, and often become meals for stalking or soaring predators. To know the location of any among their last stops is considered most fortuitous.

In addition to the location of bird's burial, we possess a few other facts about the little vertebrate's demise. At its end it was not dismembered or eaten by another animal. Rather, it died whole after having somehow flapped, run, or perhaps even having been blown by storms into the waters of an ancient and hyper-saline tropical lagoon. As it succumbed, its intact body rapidly sank, bones and feathers neither disintegrating nor scattering during the descent to the lagoon's anoxic bottom. There the corpse came to rest in an accumulating, calcareous muck slowly filling the briny depths, to be interred within a viscous, ever-deepening tomb.

In the larger scheme of things the passing of one primitive bird would hardly seem a major historical event considering the vast time scale we're dealing with. Others of its kith and kin soon occupied its place in the species' preferred niches. Life continued and expanded. New days dawned. Time moved on. Deep time. Monumental time. Time of such an extent that the course of its inexorable flow saw whole mountain ranges grow and weather away, saw floating continents reorient the world, and panoplies of new life forms arise and flourish while others faded into extinction.

As the ages came and went, as millennia adding to millennia ticked away, astounding forces acted upon the buried ooze and silts containing the body of the long-deceased Jurassic bird. The now-dried salty lagoon, the bird's cemetery, was compressed, hardened and layered until, in the amazing fashion by which geologic powers combine and prevail, there were created

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[2] Geologic time is divided first into eras, then subdivided into periods. The Jurassic period, the period in which the bird died, marks the middle period of the Mesozoic era (the Mesozoic is the second among the four vast geologic eras: the Pre-Cambrian, the Paleozoic, the Mesozoic and the Cenozoic). The Jurassic period lasted from about 213 million years ago to approximately 144 million years ago, give or take a few scores of dozens of millennia. See the geologic time scale in Podulka, et al., (2004)

expanses of limestone within which was fixed the stony accounting of a seemingly insignificant early flying being.

More than the fossilized remains of a departed feathered species was conserved within the densely hardened sediments. Cast within those vast limestone sheets was a record of inestimable value to biology and to all of science, a Darwinian bridge marking the adapting transformation of one group of animals into another. The encased vertebrate would one day be named *Archaeopteryx lithographica*. Its feather impressions, the detailed remnants of its bones, its graceful structures, to our good fortune, have glided down through the eons to furnish a truly magnificent page in the great illuminated manuscripts recounting the history of life on our planet.

The strata holding the mineralized bones and feathers are fine-grained, Middle Jurassic deposits named the Solnhofen formation, accessible today in a region of Western Europe called German Bavaria. The Solnhofen are massive *plattenkalk* sheets, measuring fifty miles long by nineteen miles wide. In many places the sheets are nearly three hundred feet thick, and underpinning a land presently experiencing a continental climate of moderate precipitation, warm summers and cold winters.

The Bavaria of the Jurassic was far different in its meteorological makeup than today's Bavaria. In those ancient times it was a monsoon place, with drier periods alternating with lengthy rainy seasons, where plants and animals thrived in great and varied profusion. The conditions of temperature, sunshine and rainfall may be compared, according to those who study paleoclimates, to the environs of the Gulf of Cariaco along today's northern coast of modern Venezuela.

The Solnhofen region of the Jurassic was probably not a bad place in which to make a living for the expanding diversity of crawling, creeping, burrowing, running, jumping, swimming, slithering, pouncing, dashing, leaping or flying creatures of the time. Paleologic evidence clearly reveals a vibrant and busy scene. Besides a multitude of different plants to dine upon, there were vertebrate and invertebrate organisms of unimaginable shapes and sizes to capture and swallow, whether these latter were sedentary, or moving by any means of locomotion imaginable. Denizens had water to drink, bushes and trees to hide or nest in, and good air to breathe. These plants, animal or otherwise organisms formed a web of being that fed on the soils, the minerals, plants and each other. There were new and developing habitats to explore and exploit, and of course there were the more skilled hunters to avoid while in quest of one's own sustenance.

Not just the lands and waters teemed with life – could we have been there to look into the sky we would have seen, flying above the fray or gliding down to join in as the need occurred, a varied and complex volant fauna – plethoras of mayflies, dragonflies, wasps, crickets, beetles, cicadas, or flying cockroaches to list just a few. And because the Jurassic

marks the great age of dinosaurs, there were the airborne of that heterogeneous tribe, skin-winged and long-jawed terrors called pterosaurs, ranging from the sparrow-sized to far beyond the proportions of even today's Andean Condors (one species of pterosaur, *Pteranodon*, had a twenty-three foot wingspan). These extraordinary flyers spent their days patrolling from and through the air, in search of each other for mating or a good meal, or for the two combined.

Living alongside and among that ancient flying menagerie was another host of animals neither insect nor pterosaur, an elegant family that fluttered and sailed on feathered wings, that journeyed from bush to bush or from tree to tree using extended forelimbs turned to wings. We would have wanted to call them birds. The little feathered animal engulfed into the muck of that old Bavarian lagoon that eventually turned to limestone was one among them. While it and its fellow avian wonders were more than somewhat reptilian, leather-winged pterosaurs or gossamer invertebrates they were not. Beside body and wing feathers, they sported tails with rectrices, tail feathers, for steering, braking, and balancing; and well-developed beaks. They had hollow-boned skeletons evolved for lightness, wishbone arrangements to anchor flight muscles and although it has not yet been proven, almost certainly warm-blooded circulatory systems to fuel the rigors of taking and keeping to the air. Much, much later in the span of their record, as they became known to science, our German colleagues would designate these first as-much-birds-as-reptiles "Urvogels." The word Urvogel translates as "ultimate" or "original bird."

The title of ultimate or original bird, Urvogel, might seem to fall somewhat on the windy side of hyperbole, but the tribute has long been accepted in the scientific community. The rich and varied trove of evidence we possess today does permit the creatures to be called the first birds. In their assemblage they form an elaborate divergence in the complex transition from reptiles through to the class Aves.

Were there a goodly number of these Urvogels, moving from one place to another, spreading over the world, searching for food, building nests, mating, laying eggs, teaching young to fly or run like the wind, taking dinner from among the myriad organisms with which they lived, or on occasion serving as snack or dinner for others of their neighbors? Because *Archaeopteryx* fossils are relatively rare, we cannot be sure. The dense rocks of Solnhofen and vicinity have yielded only a few specimens.

II. Urvogels

It was not long ago, not until the mid-nineteenth century, that unequivocal evidence of Urvogels came to light. The first startling hint came in 1860; a fossilized feather showing asymmetrical vanes and a clearly defined rachis (a feather shaft) was discovered in a quarry near the town of Solnhofen, after which the great limestone deposits had been named. The feather was a bird's flight feather, unquestionably dating from the Jurassic. News of a

paleofeather older than anyone had believed possible (and by extension the bird that had worn it) set the world of natural science a-buzz. Many who saw the fossil or studied its drawings and descriptions realized it was a harbinger, a long awaited herald bringing tidings announcing that somewhere within those great Solnhofen archives lay evidence of an ancient bird species.

Only a year later, in 1861, the gem that had been anticipated, the fossilized skeleton of a potential bird, was reported. Although the fossil was nearly headless, it showed distinct feather impressions emanating from its limbs and body. The quarryman who made the find took his prize to a local physician and well-known specimen-accumulator named Karl Häberlein, who had purchased the feather uncovered the year before. When Dr. Häberlein examined the new relic, when he saw the feather impressions with clear evidence of a bird's wishbone, he did not hesitate. He happily accepted it in exchange for a medical debt the stoneworker had earlier incurred.

To ascertain the fossil's authenticity and value, Dr. Häberlein brought his treasure to Germany's preeminent paleontologist of the day, Herr Doctor Professor Hermann von Meyer. After studying the specimen, after assuring himself the animal had feathers and could doubtless fly, von Meyer declared it to be the long-hoped-for Urvogel. He assigned to both the fossil and the earlier 1860 feather a genus and a species name: *Archaeopteryx lithographica*; '*Archaeo-*' meaning of ancient age, '*-pteryx*' meaning winged; and '*lithographica*' meaning from lithographic stone.[3]

Physician Häberlein was not a paleontologist. Neither was he a sentimental collector. He immediately put the fossil feather and skeleton on the market. Offers to buy poured in. But to the dismay of many among his compatriots, powerful anti-evolutionists of the day fought tooth and claw to keep the *Archaeopteryx* specimens out of Germany's museums. And they were able to. No institution in the country could touch either piece. Dr. Häberlein was left little choice but to sell to the highest foreign bidder, which turned out to be the British Museum of London, which handed over 700 pounds for the feather and the skeleton. No trivial sum – seven hundred pounds represented two entire years' budget for museum acquisitions, so much as to require payment to be made in two installments.

A few years passed without a new quarry find. In the meanwhile heated and acrimonious debates raged between those who subscribed to Charles Darwin's new and exciting theory of evolution (*On the Origin of Species by Means of Natural Selection* had been published in 1859) and those who rejected the work as anathema. Along with Darwin's theories, the importance and meaning of *Archaeopteryx lithographica* was the subject of bitter controversy. Scientists such as the brilliant British naturalist T.H. Huxley saw *Archaeopteryx* as proof positive of Darwin's breathtaking proposals. In the opposing camp, one German scientist, in his hands-

[3] The Solnhofen limestone slabs were long known for their high quality in the printing process called lithography.

down rejection of the entire Darwinian ethos, went so far as to craftily disparage *Archaeopteryx* with a different name entirely – the reptilian title of *Griphosauros* (*gryps*, mythical beast; *sauros*, lizard).

In the spring of 1877 another worker in another quarry not far from the town of Solnhofen cleaved free a lithographic slab containing a complete crow-sized bird fossil, showing a head, legs, clear outlines of feathered wings, clawed feet and an easily-seen wishbone. The workman informed quarry owner who, on the spot, generously rewarded his employee for his good work, and gave him the rest of the day off. The owner then communicated with one Ernst Häberlein, son of the physician-collector who, fifteen years earlier, had acquired by barter the first complete *Archaeopteryx* specimens. This next-generation Häberlein also knew his stuff when it came to trading in paleontology. Upon seeing the stunning new fossil, he bought it from the quarryman for 140 deutsche marks.

Like his father, Häberlein the younger was a good businessman. He put out word that he had a most amazing bird fossil in his possession, and that it was for sale. As the news and description of this second *Archaeopteryx* spread, a frenzy of bidding began. Learned professors, collectors, and museum curators from several countries went after it. The Dutch wanted the fossil. The English wanted the fossil. The French wanted it. So did the Danes, the Swedes and the Italians. Even the Americans, in the person of Professor Othniel Charles Marsh of Yale University, were parties to the escalating rounds of bids and counter-offers. But this time the Germans were not going to let their bird in hand escape to the bush as they had done earlier. After months upon months of haggling, price increases and endless negotiating, the wealthy industrialist, Werner von Siemens, founder of the Siemens Corporation that thrives to this day, paid the junior Häberlein the princely sum of 20,000 marks for his *Archaeopteryx* slab and its counterslab.

But Baron von Siemens was not in the game for profit. In 1881 he resold the *Archaeopteryx* to the Prussian ministry for the same amount he paid for it, 20,000 marks, thus permitting its two imprints, the slab and counterslab, to go to Berlin's Humboldt Museum für Naturkunde. The 1877 *Archaeopteryx* has been housed there ever since. It has come to be referred to as the "Berlin specimen." The earlier but less complete *Archaeopteryx* in the British museum is known as the "London specimen."

The London and the Berlin specimens were the only ones publicly and academically known for nearly a century to follow. Then, in 1959, a third example of an *Archaeopteryx* was reported from the same quarry that produced the London specimen. The fossil was apparently found in 1955 and sold to a man named Eduard Opitsch, who allowed it to be displayed for a time in the local museum, then removed it to keep in his home to which he refused public access. When Opitsch's estate was being settled after his death, the fossil could not be located. To this day it is missing.

A fourth specimen was identified in 1970 when Professor John Ostrum of Yale University realized a fragmented Solnhofen fossil in a Dutch museum, earlier classified as a pterosaur, was in fact a poorly preserved *Archaeopteryx*. The fossilized remains Ostrum recognized as Urvogel are referred to as the Teylers specimen, after the Haarlem Museum in which it was and still is displayed. A fifth Urvogel came to light in 1973 when a fossil in the Eichstätt City Museum in Bavaria thought to be a diminutive dinosaur was reclassified as an *Archaeopteryx*. It was again the alert Professor Ostrum who pointed out its barely faintly feather impressions.

Archaeopteryx fossil number six appeared in 1987, located among the holdings in a private collection of a former mayor of Solnhofen. That fossil resides to this day in Solnhofen's Bürgermeister-Müller Museum. In 1992, a very much smaller *Archaeopteryx*, in good condition but which the German paleontologist Peter Wellnhofer considers a different species, was found in the same quarry that had furnished the London specimen over 130 years earlier. Wellnhofer named this seventh fossil *Archaeopteryx bavarica*, although it may well be a juvenile *Archaeopteryx lithographica*. It is owned by the Bavarian State Collection of Paleontology and Historical Geology in Munich, and called the Munich specimen.

In 1997 an eighth *Archaeopteryx* was reported, the specimen consisting of a damaged skull and portions of forelimbs. The exciting aspect of this fossil is that it dates from rocks laid down in the late Jurassic called the Mörnsheim Formation, meaning the Archaeopterygidae spanned many hundreds of thousands of years more than originally thought. Unfortunately, as the fossil remains in private hands, it has not enjoyed direct and exacting scientific scrutiny. Only a cast has been released by its owner.

A ninth specimen, the right wing of an *Archaeopteryx*, was discovered in 2004. It too is privately owned but is currently on loan to Solnhofen's Bürgermeister-Müller Museum. Chiappe (2006) describes the wing as three-dimensionally preserved, with feathers still attached.

Finally, a tenth Solnhofen *Archaeopteryx* of unknown provenance was reported in 2005 (Mayr et al., 2005). It was purchased by and is now displayed at the Wyoming Dinosaur Center in Thermopolis, Wyoming. It is referred to as the Thermopolis specimen. The skull and feet are in particularly good condition. The toe structure shows evidence of a running animal, as were the theropod dinosaurs, the ancestors of birds (Mayr et al., 2007). Those who have studied the fossil prefer it be named *Archaeopteryx siemensii*, in other words a distinct species from *Archaeopteryx lithographica* (Hartman, 2008).

The Urvogel *Archaeopteryx*, the first bird, is thus represented, in addition to the feather found in 1860, by only ten skeletons or partial skeletons of which one has gone missing (number three), by another yet to be studied (number eight), and by another that is a wing only (the ninth). Among that small number the Berlin *Archaeopteryx* is considered the typal because of its superb state of preservation and clarity of features. One of America's premier paleornithologists, Alan Feduccia, has written that the Berlin *Archaeopteryx* "may well be the

most important natural history specimen in existence, comparable perhaps in scientific and even monetary value to the Rosetta stone…."

III. Art and Science, Science and Art

Likening *Archaeopteryx lithographica* to the Rosetta stone emphasizes its scientific importance, and that is good. The fossil is truly a keystone in the bridge toward understanding the complexities of natural selection and avian evolution. On the other hand, comparing the delicate *Archaeopteryx* to cold, carved rock is somewhat dissatisfying because we cannot forget that *Archaeopteryx* was once a living, moving and agile form of life able to make itself lighter than air. While the species no longer inhabits this earth, we nevertheless owe this marvelous antecedent its due as our earliest representative among the several forerunners to today's multitudes of birds.

Happily, another of our great avian paleontologists, Dr. Luis Chiappe, adeptly softens the stone analogy by referring to *Archaeopteryx* as a kind of "Mona Lisa,[4] a comparison that nicely stresses the scientific importance of *Archaeopteryx* as well as conveys the iconic value of this ephemeral creature from a long-past and mysteriously fascinating time. Still, while characterizing *Archaeopteryx lithographica* as a Mona Lisa might be both efficient and emotionally appealing, it could also be seen as frankly anthropomorphic if not downright precious. If we really want to get down to brass tacks, how does all of this paleontology and grandiose reference to one of the Western world's greatest paintings meaningfully relate to the occupation and pleasures of birding?

After all, we can list none of the *Archaeopteryx's* field marks – the color of its feathers, its posture, its flight style or how it folded its wings. Nor do we know if the bird sang, called, squawked or croaked. What was its preferred habitat or niche? Did it soar or glide? Did its feathered legs function as lift-generating secondary wings as has been postulated by Canadian paleontologist Nick Longrich? Did it confine itself to the trees, either perching on branches and limbs or clinging to trunks, or did it hop or scamper along the ground?[5] Was it shy or curiously aggressive? Were there ritualized social behaviors? Were there well-fashioned nests? Did it live in flocks or was it inclined to the solitary? We don't know what it ate, if it migrated or not, if it was monogamous or polygynous, if it molted, if the female of the species or her mate, or both,

[4] See the chapter entitled "*Archaeopteryx*: The Earliest Bird," in Chiappe (2006).

[5] A number of scientists have suggested *Archaeopteryx's* principal means of locomotion was sprinting along the ground, Roadrunner style, and flying or sailing only when necessary. This view is well supported in at least one specimen (the tenth *Archaeopteryx),* where the hallux is not fully reversed and the second toe could hyperextend, as in ground-based dinosaurs known as maniraptoran theropods. On the other hand, there are many scientists who believe *Archaeopteryx* evolved from tree-dwelling dinosaurs by using emerging and requisite flight structures to sail about and eventually, with added adaptations, to acquire full, powered flight. This view is supported in specimens where the sharp, gripping claw structures show no blunting wear from ground contact, but more resemble a perching or perhaps clinging foot complex.

incubated their clutches, if the hatchlings were precocial or altricial. Since we know so little about its appearance, habits and it cohorts, why not just say, “How interesting,” and return to our living birds, an occupation which keep us busy enough? Why not leave a dead bird lie? In fact, there are good reasons to look and consider more deeply.

All species that exist or existed have, or had, immediate and more distant precursors. The immediate precursors were of course parents, which in turn have had parents, which themselves had parents, and so on back farther and father in time such that we speak of the preceding forms that lived as ancestors. Ancestors and decedents, particularly when separated by large expanses of time, are not the same. If we examine the status of a species at various points along an historical line, if we look at a species separated by many dozens of generations let us say, we will find the conspecifics living or having lived at a later period to be different, sometimes very different, from the earlier assemblages of interbreeding individuals.

The changes that occurred between the two distant points can be quantified, and those changes, when compared, whether the changes be large, small or incredibly complicated, are a measure of evolution. The younger generations may be bigger, more streamlined, have developed new physical features or behavioral capacities, have gained or lost attributes and skills, or even have gone through an entire change of appearance. Whales are such an example.

Evolution occurs because some among the diverse genetic mutations that alter characteristics, behaviors and features are those advantageous enough to carry forward, while those mutations providing for reduced survival and reproductive advantages are left by the wayside as innovations that didn’t pay off. This is the process underlying evolution. It is called natural selection. Natural selection is the interacting dynamic that amplifies advantageous traits and culls out disadvantageous traits, both of which occur sporadically in the genetic machinery of a group capable of interbreeding. What is called evolution is the sum total of descent by modification through natural selection.

As already pointed out, *Archaeopteryx lithographica* represents a transitional species. The creature was not a reptile. It was a good part bird. While it had upper and lower bills containing pointed teeth, those bills were formed into a beak. It had feet with the curved toes resembling the gripping claws of a passerine. Admittedly there was a jointed boney tail consistent with reptiles as well as with a group of contemporaneous, cursorial dinosaurs called theropods. But the tail had well-developed feathers, organized biserially and symmetrically along the horizontal plane, an airfoil arrangement predicting the rectrices of modern birds. On *Archaeopteryx lithographica’s* body were overlapping contour feathers. Its wings had interlocking aerodynamic flight feathers, remiges, and the wings could be widely extended to reach for air. The skeleton had evolved weight-reducing hollow bones that included a wishbone, the fundamental anchor for flight muscles that flap the wings that render a bird airborne.

Here was structure become more avian than anything earlier in the record, a product of the selective pressures moving precursors along their paths into and through the Jurassic, precursors whose offspring evolved into a unique species showing the earliest integrated complex of avian traits. *Archaeopteryx lithographica* represents an astounding biological synthesis, a coming together of adaptations assembled up until that distant moment.

When we find ourselves fascinated and moved before Leonardo da Vinci's graceful Mona Lisa, we soon realize we are not merely experiencing an astounding work of art. The portrait is a powerful cultural synthesis of the highest forms of beauty, nobility and humility of the Renaissance. The painting is a great work of human achievement due not to its technical power alone but because it is a perfected example of a moment in time. Gazing at it permits us to look back to what was a momentous portion in human history. In the Mona Lisa we recognize a cultural precursor to our own value systems and concepts of the beautiful. Leonardo's Mona Lisa helps us to locate the signposts along path along by which we came. Precursors such as she tell us much about what we once were in our intellectual and social development. Yet her emblematic and enigmatic smile only hints at, but does not easily reveal, the countless complexities of the past that were selected, recombined, carried forward or discarded as time when on. She engages our search for those ever-changing aggregations of preferences, mores and clusters of ideas that eventually brought us to our own so very fleeting moments on this earth.

In this respect, human cultural selection and biologic or natural selection have similarities. Both lead on to something else. But the works and workings of selection, cultural or biologic, can only be recognized after the fact, when we examine their respective artifacts. In the case of art and culture those artifacts are the paintings, the sculptures, the books and the myriad other products of creative minds coupled to skill. In biology, the artifacts are fossils. Biology, like art, leaves us to consider remains.

If human cultural selection and biologic selection share commonalities as they go about generating outcomes, their respective selective mechanisms do not function at the same levels. Human achievements are the product of a creators, or groups of creators, with ability. Those creators consciously interpret and manipulate materials available to them according to their ideas and the surrounding ideas that are in play. They have a goal in mind. By contrast natural selection is devoid of a purposeful creator. Within the natural sciences, a family, a genus, a species and the individuals comprising that hierarchy are the result of processes absent a centralizing, overarching agent. Natural selection has no foresight.

This distinction between cultural and biologic selection suggests that we use a modicum of caution when applying the Mona Lisa mantel to one of our most important fossils, lest we unconsciously, or perhaps even consciously, assume the bird to have been the work of an omnipotent, talented creator, thereby facilitating our anthropometric biases and further tricking

us into designating that creator as either evolution with a purpose, or a chosen deity. There is no reason, of course, if we keep this caveat in mind, that we cannot honor *Archaeopteryx* as the Mona Lisa of ornithology, a title that justifiably elevates the bird to a deserved high status. We just need to keep our self-aggrandizing, romantic inclinations in check, because it is perennially tempting to consider ourselves and our present century as the apogee of perfection and progress. But neither the ancestral bird forms on which we focus our microscopes nor the contemporary birds toward which we aim our binoculars, spotting scopes or cameras were the product of a creative genius having the present avian glory in mind, and most surely not our personal satisfactions. Natural selection is just that – natural. It has no favorite species. It is not divine. It does not plan for an ultimate future nor compose for a grand finale. I just keeps chugging haphazardly along.

When the earliest humans of Africa began their world-wide expansion out from their changing savannah homelands, it is difficult to imagine they had our twenty-first century in mind as they trekked along meeting new environments, then either adapting or perishing. So let us admire *Archaeopteryx* for what the species represents: a momentous interlude within the history of avian life. In the great pantheon of biology *Archaeopteryx* was a creature that fortuitously, fortunately, and to our unintended delight, traveled part way along the broad flyways leading to the airborne creatures we admire each day as we take to the field. It is for this reason, because *Archaeopteryx* reveals this wonderfully expansive historical perspective onto our natural world, that we can fittingly honor the fossil, a once-living living bird, as the Mona Lisa of ornithology, whether our avocations flow to birding or to the others of those diverse and noble pursuits which search to understand the intricate pageant of life.

References and Works Consulted:

Bakker, Robert T. ((1986). *The Dinosaur Heresies*. Kensington Publishing Corporation, New York.

Chiappe, Luis M. (2006). *Glorified Dinosaurs: The Origin and Early Evolution of Birds*. John Wiley and Sons, Hoboken, N.J.

Darwin, Charles (1859). *The Origin of Species by Means of Natural Selection*. Barnes and Noble Classics Edition, 2004. Introduction and notes by George Levine. Barnes and Noble, New York.

Feduccia, Alan (1999). *The Origin and Evolution of Birds*. Yale University Press, New Haven. Second Edition.

Gill, Frank B. (2007). *Ornithology*. Third Edition. W.H. Freeman and Co., New York.

Hartman, Scott (2008). Personal Communication.

Longrich, Nick (2006). "Structure and function of hindlimb feathers in Archaeopteryx lithographica," *Paleobiology* 32 (3): 417-431.

Mayr, Gerald, Pohl, Burkhard and D Stefan Peters (2005). "A Well-Preserved Archaeopteryx Specimen with Theropod Features," Science 310: 1483-1486.

Mayr, Gerald., Pohl, Burkhard., Hartman, Scott and D. Stefan Peters (2007). "The tenth skeletal specimen of Archaeopteryx," *Zoological Journal of the Linnean Society* 149: 97-116.

Podulka, S., Rohrbaught, R.W., Jr. and Bonney, R. (2004). *Handbook of Bird Biology*. Cornell Laboratory of Ornithology, Ithaca, N.Y.

Shipman, Pat (1998). *Taking Wing: Archaeopteryx and the Evolution of Bird Flight*. Simon and Schuster, New York.