From Dinosaurs to Modern Birds - What is the Connection?

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Dinosaurs have captured the imagination of people ever since fossil bones were first described. Images of giant lizard-like creatures such as *Tyrannosaurus rex* roaming the earth are not only frequently described in picture books for kids, but have made their way to become stars of modern day movies. The popularity of dinosaurs from their size, diversity and imagined activities is undeniable. However, one question has been looming in the scientific community for years and that is “did the dinosaurs simply disappear or are modern versions still roaming the earth today?”

While most of the dinosaur evidence is limited to fossilised structures (primarily bones), other clues about the lives of dinosaurs that link them to birds have been popping up recently. For example, fossils of Cretaceous theropod dinosaurs (*Oviraptor*) were found buried while atop and seemingly protecting eggs in a ‘bird-like fashion’. Even the shells of Oviraptor eggs show features only found in bird eggs.[1] In Thailand, remarkably fossilised eggs, one of which contained a theropod dinosaur embryo, were found and contained structures currently known only in extant and fossil eggs associated with birds.[2]

The bird fossil record is well recognised as 134 of the 153 living avian families have fossil representatives. There are 77 extinct avian families.[3] Some of the recently extinct modern species were the most spectacular such as the Madagascar elephant birds (*Aepyornis* and *Mullerornis*), Mauritius Island Dodos (*Raphus cucullatus*) and New Zealand Moas (*Dinornis*). There were at least ten species of moas that ranged in size from that of a turkey to over three meters in height.[3] Prior to human settlement over 700 years ago, the extinct New Zealand giant eagle (*Harpagornis moorei*) weighed up to 15 kg and had up to a 3 metre wingspan and was the moa’s only predator.[4]

Recent findings are strongly supporting the theory that birds are modern day dinosaurs. With improved paleontologic recovery techniques and the incredible influx of new fossil discoveries, especially from the Liaoning province in northeast China, the dinosaur-bird connection is being supported at an ever increasing rate. The bulk of the current scientific literature proposes that the primitive and derived features present in many theropod dinosaurs indisputably relate these extinct creatures with modern day birds.[5]

Time Basics

The middle era of Earth is divided into three major divisions of the Phanerozoic Eon; the Paleozoic, Mesozoic, and Cenozoic Eras.[6, 7] The Paleozoic Era spanned approximately 542 to 251 million years ago. The Mesozoic Era was known as the 'age of the dinosaurs' and spanned 245-65 million years ago. The Mesozoic was made up of the Triassic (~251-200 million years ago), Jurassic (~200-146 million years ago) and Cretaceous (~146-66 million years ago) Periods. The Cenozoic Era spans from ~66 million years ago to current time. The Cenozoic is further divided into the Tertiary (~66-1.8 million years ago) and the Quarternary (~1.8 million years ago to present.[7]

Dinosaur Basics

Archosaurs are basal diapsids (four legged vertebrates that developed two holes or temporal fenestra on each side of the skull) that first appeared somewhere around the Early Triassic (~251 million years ago). Archosaurs evolved into crocodilians, birds, pterosaurs and the most dominant and successful land vertebrates of the group, the dinosaurs.[8] The Late Triassic period (approximately 215 million years ago) marked the emergence of dinosaurs.[9]

The fossil records show that dinosaurs dominated the earth for 150 million years. During the Triassic, two dinosaur clades (similar to families) emerged; the Ornithischia and the Saurischia. The Saurischia later gave rise to the theropods, the proposed ancestors of birds. Towards the end of the Triassic, the theropods branched into the tetanurans out of which came the coelurosaurs. Out of the coelurosaurs, maniraptorans evolved and gave rise to the bird clade Aves in the Late Jurassic (159-146 million years ago). The Aves then gave rise to the Ornithothroaces which branched into the Enantiornithes ('opposite birds') and Euornithes ('true birds). In the Late Cretaceous (66-100 million years ago), the Euornithes gave rise to the Neornithes which became modern birds.[9]

Theropods are the basal dinosaurs frequently linked to birds. In general, the theropods were carnivorous, terrestrial, bipedal dinosaurs with small forelimbs and specialised predatory features such as long hands with three digits capable of scratching or catching prey.[9] Some of the 'non-avian' theropods had simple filament-like appendages and others had complex modern asymmetric feathers.[9] More commonly recognised theropods include Allosaurus, Oviraptor and Velociraptor that have been popularised in books and movies. Ultimately, the 'avian-type' theropods evolved into modern birds.

What is a Bird?

Perhaps the best way to understand the dinosaur-bird connection is to understand what a 'bird' truly is. As you will see below, the definition of 'bird' is variable:

- 'any of the class Aves of warm-blooded, egg-laying, feathered vertebrates with forelimbs modified to form wings.'[10]

- ‘a creature whose body is covered with feathers, a kind of skin outgrowth no other animals possess; the blood is hot; the heart is perfectly four chambered. The lungs are fixed and molded to the cavity of the chest, and some of the air passages run through them to admit air to other parts of the body, as under the skin and in various bones. Reproduction is oviparous. There are always four limbs, of which the fore or pectoral pair are strongly distinguished from the hind or pelvic pair, being modified into wings, fitted for flying, if at all, by means of feathers’.[11]

- ‘a warm-blooded vertebrate of the class *Aves*, covered with feathers except for the legs and feet, which are scaly, and having the forelimbs converted into wings’.[12]

Even our understanding of extant birds would bring these modern definitions into question. What about ‘wings’? Most think of modern birds as using wings for flying as with the blue and gold macaw (*Ara ararauna*) while some have no apparent use as with the flightless cormorant (*Nannopterum harrisi*) which has stubby vestigial appendages. Feather patterns are also highly variable among birds. Of course featherless flight is noted in tetrapods, pterosaurs and modern day bats that are all non-avian.[13] Feathers vary from highly ornate for mating rituals in the birds of paradise (Paradisaeidae) to the rigid dense feathers of the emperor penguin (*Aptenodytes forsteri*) that help this Antarctic bird conserve heat and energy during intense cold, prolonged and dark winters. What about many of the owl species, such as the great horned owl (*Bubo virginianus*), that have feathers on both legs and feet. According to the last definition, many raptors would not fit as ‘birds’.

These simple examples only point out superficial differences between extant birds. These examples also demonstrate just how complex and different birds are between species. Similar examples of variations and ties to modern day birds can be found within fossil records of dinosaurs.

Specific characteristics help us further define birds

Birds, by the physical characteristics of their skulls, belong to the diapsid clade (meaning they have upper and lower temporal openings).[14] Within the diapsid clade, birds have an antorbital opening and belong to archosaurs. However, birds don’t resemble other living archosaurs (crocodiles or other living members) - at least from external appearances.[14]

Characters of Aves can be further defined.[13] Aves have 23 or less caudal vertebrae and their tails have been reduced to a fused pygostyle (which is present in a few non-avian dinosaurs). The forearm is greater than 90% the length of the humerus while the fore limb is more than 120% the length of the hindlimb, which all shows a tendency towards flight. The foot is anisodactyl with three forward directed toes (digits II though IV) and a rear facing digit I or hallux.[13]

Until recently, the bird digits arising from the manus were labeled digits II-IV.[15] This was actually a barrier to the theropod dinosaur-bird link as homologous digits on theropods, which also have a three fingered hand, are numbered I-III.[16] Recent molecular studies in chickens have shown that the last two digits are lost and digits I-III truly make up the distal end of the avian wing further supporting the theropod-avian link.[16, 17]

Modern birds have an elongated cochlea duct to enhance hearing ability likely related to the role of sound in feeding, mating and territorial behavioral responses. This anatomic variation is much more pronounced than in many other vertebrates. Avian optic lobes and other structures are also modified to integrate special senses involved with flying.[18]

Feathers are present on all living birds. All feathers are made of keratin and composed with a central hollow shaft that decreases in diameter toward the tip.[14] Barbs radiate off the central shaft and hook together in a neat pattern via barbules (small hooks) to make the feather 'vane'. Those feathers with well developed asymmetrical vanes are primarily used for flights (aka flight feathers). Those feathers with undeveloped or absent barbules and poorly developed vanes are fluffy and are termed down or downy feathers and tend to serve as insulation.[14]

Extant birds do not possess teeth. Modern day birds therefore do not chew food as do mammals but rather process food in the gut.[14] The loss of teeth and formation of the cornified beak likely evolved with a more aerodynamic and streamlined body, a characteristic for avian flight.[9] Interestingly, molecular and morphologic studies have shown that the oral mucosa of modern chickens forms a dental lamina which soon degenerates suggesting the ancestral mechanisms for tooth growth may still exist in the DNA of extant birds.[9]

Extant birds do not have a tail. Most, but not all, birds have a vestigial structure of fused bones called the pygostyle.[14]

Bird skeletons have multiple modifications that allow for flight. The strong sternum, or breast plate, has a deep keel that allows for the attachment of the pectoral flight muscles. The semi-rigid pectoral girdle is completed with the coracoid, scapulae and furcula where the flight muscles also attach. Birds are the only living organism with a furcula (wishbone).[14] However, a few theropods (such as some maniraptors) had a furcula.[13] The downstroke of flight is completed by the powerful pectoral muscles. Flighted birds have a well developed deep keel and large pectoral muscles. The recovery upward stroke is carried out by the supracoracoideus muscle that originates at the keel, runs along the coracoid and forms a tendinous attachment at the top of the humerus after going through the triosseous canal formed by the coracoid, scapula and furcula. This supracoracoideus muscle/tendon and triosseous canal is unique to modern birds and their particular type of flight. However, a similar pulley-like system is seen in pterosaurs which were featherless flying archosaurs that had no common relationship to birds other than very basal dinosaurs.[3, 19]

Archaeopteryx - The First Bird

The first *Archaeopteryx* feather impression was found in 1860 in southern Germany. The deposits came from the Late Jurassic era in a poorly oxygenated, stagnant lagoon. The fine-grained carbonate mud created beautiful specimens, some with exquisite detail. Since 1860 numerous several full bodied specimens have been found.[14] *Archaeopteryx* is still the only undoubted bird from the Late Jurassic (146-161 million years ago).[13]

The cause for all the excitement came when the full bodied specimens, which were the size of modern day magpies, showed both bird and reptilian features.[14] *Archaeopteryx* has nasal, antorbital and ocular eye openings. Upper and lower temporal openings are highly suggested based on current fossils. As noted above, this puts *Archaeopteryx* in with archosaurs. The large round eye has a sclerotic ring. The sternum and keel are relatively small. However a strong furcula is present. The well preserved feathers have asymmetrical vanes.

Pnuematicity in the skull, cervical and thoracic vertebrae and pelvis is also characteristic of modern flying birds.[20] Foramina in the cervical and thoracic vertebra and pubis indicate the presence of at least two of the five air sac systems found in modern birds.[3] Computerised-tomography examinations of fossil skulls has shown that while more primitive than modern birds, Archaeopteryx's brain had the neurological and structural adaptations necessary for flight.[21,21a] *Archaeopteryx* probably could fly but likely could not engage in slow, agile or highly maneuverable flight.[3]

Archaeopteryx's non-avian features include recurved teeth, 'reptilian' pelvis (no synsacrum) and a well developed tail (complete with feathers). Archaeopteryx also has no trace of a horny beak.[3] The *Archaeopteryx* specimens quickly became a potential link between dinosaurs and birds.[14] *Archaeopteryx* is a transition fossil and while not considered the common ancestor of all birds, it is considered the most basal bird known.[13]

Where Do Feathers Come From?

Feathers are likely the most commonly recognised feature of modern birds. Their diversity in form and function are awe-inspiring. However, modern day birds are not the only creatures to have possessed 'feathers'.

While most birds require feathers for flight, not all of the class *Aves* fly. There is now evidence that modern type feathers evolved in dinosaurs before flight.[22] In fact, 'feathers' have been found on multiple non-avian dinosaurs such as the oviraptorosaur *Caudipteryx*, the coleurosaur *Protarchaeopteryx* and a dromaeosaur termed BPM. The feathers identified on BPM are considered 'identical to those of modern birds'.[22, 23] Additionally, multiple non-avian theropods including *Protarchaeopteryx*, *Sinornithosarus*, *Sinosauropteryx*, *Caudipteryx*, *Beipiaosaurus*, *Microraptor* and more (all from Early Cretaceous China) were feathered.[13]

While members of the class *Aves* are not the only modern animals that can fly, the question of feathered flight in dinosaurs has been examined. The 'four-winged dinosaur' *Microraptor gui* had extremely long leg feathers complete with an unambiguous asymmetric vane and curvature characteristic of flight feathers.[24] In general flight of early extinct birds is accepted, although they were likely not strong flyers as with modern *Aves*.[24]

So how does skin or scales evolve into feathers? The original theories that 'reptilian' scales evolved into feathers has been highly disputed based on new theories and supporting fossil, morphologic and molecular evidence. Current findings support that feathers are homologous with scales at a very primitive stage.[25] However, the feather bud and its subsequent ‘feather structures’ are novel and not homologous with a scale in any way.[25] Further, while feathers originate and grow as tubes of epidermis they are also very different from hair.[5] Feathers are in fact, a unique evolutionary design.

The proposed evolution of feathers is based on a five stage process starting with skin and not scales.[5, 14] The first is the outgrowth of simple, cylindrical, hollow, hair-like filaments. Second, multiple elongated filaments attached at one end develop. Third, the filament tufts align in a single plane (a) and/or develop barbs and barbules (b). Out of these evolutionary changes (a + b), a vaned and barbed feather emerges (at this stage the barbules are not yet connected). Fourth, a semi-closed vane forms as the barbules hook on to adjacent barbs. At this stage, air flow through the feather is limited. In the fifth and last evolutionary step, the vane become asymmetrical and is consistent with modern day feathers.[14] Only the highly evolved feather shapes, which represent stage five feathers, could be used for flight.[5, 26]

The above feather evolution theory is even seen in action in extant birds.[5] Modern day stage one feathers are found on the entire crown of the Bornean bristlehead (*Pityriasis gymnocephala*) and the central crown patch of male African peafowl (*Afropavo congensis*). Certain display plumes in birds of paradise (*Paradisaea*) and egrets (*Egretta*) correspond well to stage two feathers. Open pennaceous contour feathers and semiplumes of many modern birds correspond to stage three a + b feathers.[5]

Discoveries of feather theropod dinosaurs, especially coming from the Lower Cretaceous Yixian Formation in the Liaoning Province of China, have supported this five step feather evolution.[5, 14] In 1997 a non-flying, chicken-sized theropod called *Sinosauropteryx* had feather impressions of a primitive downy coat and first-second stage feathers. Shortly later, the turkey-sized oviraptorisaurian *Caudipteryx* emerged with stage four feathers that had well-developed barbs, barbules and a symmetric vane. Next the large, flightless ostrich sized, thereizinosauroid *Beipiasaurus* was found with primitive second-third stage feathers with barbules that is believe to have served as insulation only. A non-flying deinonychosaur, *Sinornithosaurus*, have stage five feathers comparable with modern birds. Later another deinonychosaur, *Microraptor gui*, was revealed to have stage five feathers on its wings and legs. In fact, the recent fossil finds keep adding support to this five stage feather development hypothesis. [5, 9, 14]

These findings of feather evolution also lead to other hypotheses and conclusions.[27] The first is that feathers were likely present long before flight was used. Also, the development of feathers covering the body could have provided the insulation necessary for endothermy which could eventually allow theropods to maintain high levels of activity for extended periods of times (a characteristic of warm blooded animals).[14]

Also, feathers may have been used for display, tactile organs, defense and water repellency.[5] The flightless *Caudipteryx* had fossilised tail feathers with evident color banding and is the only known direct evidence of coloration in dinosaurs.[13] Half of the *Confuciusornis* specimens (presumably males) have extremely long tail feathers forming dramatic pennants that may have been used for display.[3] *Confuciusornis* (127-121 million years ago) is the oldest known toothless bird that had primitive (dinosaur-like) and advanced (modern bird-like) features.[19, 28]

How Did Endothermy Evolve?

Endothermy is among the most significant features that distinguishes living birds and mammals from amphibians, fish and reptiles and represents a major evolutionary milestone of vertebrates.[8] While extant reptiles are capable of spectacular bursts of intense exercise, ectotherms are generally limited to unsustainable anaerobic metabolism for activities beyond slow movements. Endothermy allows the elevated rates of aerobiosis required for high levels of sustained activity. Endothermy is what allows modern birds and mammals to maintain large territories, migrate and forage widely. One presumed requisite for powered and sustained flight is endothermy. The question ultimately leads back to dinosaurs - were they endo or ectotherms?[29]

The above question is highly debatable. However several clues in certain fossilised dinosaur remains help support the theory that some of these extinct species had developed endothermy - or were at least heading in that direction. Understanding the origins of endothermy also help solidify the notion that dinosaurs were the ancestors of birds.

Considering the generally warm climates of the Mesozoic Era, it is possible that thermal inertia and behavioral regulation were enough to keep large bodied dinosaurs at a relatively high and stable body temperature for prolonged periods of time regardless of whether or not they were endo or ectotherms.[8] Some large modern tropical lizards such as monitors (*Varanus* sp) are similarly capable of some aerobic metabolic capabilities that allow more endotherm-like activity. However, modern birds and mammals have increased lung ventilation rates, separated pulmonary and circulatory systems and expanded cardiac output that are distinctly different from ectotherms.[8]

Bone type can give some suggestion as to the metabolic status of animals.[8, 29] The primary bone type of extant amphibians and most reptiles is lamellarzonal which is poorly vascularised, often has a layered appearance, contains relatively few primary osteons, forms comparatively slowly and is associated with low growth rates and ectothermy. Fibrolamellar bone is well vascularised, has numerous primary osteons, has a woven and fibrous appearance and is deposited during the initial rapid growth phase of extant juvenile birds and mammals and is associated with endothermy. However, extant reptiles are capable of forming fibrolamellar bone and some small endotherms (shrews, small birds, rodents and bats) can form simple lamellated bone. The widespread presence of fibrolamellar bone in dinosaurs is supportive of endothermic (or at least an intermediate step) metabolism.[29]

A recently discovered single ornithischian (66 million year old, small, plant eating dinosaur), *Thescelosaurus* fossil, has what appears to be a fossilised four chambered heart complete with a fully partitioned ventricle and single aortic arch.[29, 30] This provides further support of endothermic-like metabolism for at least one dinosaur. Of course if the fossil interpretation is true, this feature alone does not define metabolic rates as fully partitioned ventricles are present in both birds and crocodilians.[29] However after a detailed computerised tomography scan of the fossil heart, a team of cardiologists concluded the 'heart's anatomy is more like that of birds and mammals than crocodiles or other reptiles'.[31]

The presence of feathers also suggests a trend toward endothermy. Theoretically, feathers would provide insulation and allow an animal to retain heat. A large variety of feather-like integumentary structures on numerous recently discovered theropod (including non-avian) dinosaurs from the Early Cretaceous deposits (China) suggests a trend toward feather evolution. These partially feathered ancestral species may very well been 'intermediates' in terms of metabolism. Even some modern birds utilise behavioral thermoregulation to absorb radiant heat even though they have feathers. For example, the body temperature of the roadrunner (*Geococcyx californicus*) declines by 4°C during the night in low ambient temperatures. After sunrise the roadrunner exposes his apteria to solar radiation to warm ectothermally to normal body temperature.[29]

Features of the respiratory turbinates also give clues as to metabolic activity.[8] The respiratory turbinates of endotherms absorb a substantial portion of heat and moisture in respiratory air via a mechanism of intermittent countercurrent exchange. Otherwise, the high rate of persistent lung ventilation of mammals and birds would result in significant loss of heat and water as warm humid air is expelled from the lungs.[29] The nearly ubiquitous presence of nasal turbinates in endotherms are entirely absent in living ectotherms. In fact, there are no other nasal cavity modifications in exant ectotherms that are designed for respiratory water vapor recovery. Based on fossil records and knowledge of current species, it seems that respiratory turbinates evolved in conjunction with persistent and high lung ventilation and metabolic rates and endothermy.[29]

The Triassic cynodonts, which gave rise to the earliest mammals, have attachment scars of respiratory turbinates suggesting these animals had elevated resting lung ventilation and metabolic rates.[29] The nasal turbinate ridges in the earliest mammals (those related to the cynodonts) are almost identical to those of modern mammals suggesting that persistent respiration and endothermy had evolved by the end of the Triassic. [29]

In contrast, many early theropod dinosaurs had a nasal cavity that was restricted to a narrow, tubular passage with little evidence of respiratory turbinates much as is seen in extant ectotherms.[29] However, pneumatisation of the skull was taking place in advanced theropods in which fenestrae or openings in the rostral portion of the antorbital fossa, open into an expansive maxillary antrum and promaxillary sinus. In other words, pneumatised spaces within the skull opened into sinuses. Similar fenestrae, sinuses and a probable lack of complex respiratory turbinates are identified in basal birds such as *Archaeopteryx* and Early Cretaceous enantiornithine (a now extinct lineage of early birds).

However, the ornithurine (precursors to modern avian species) birds have caudally pushed sinuses and obliterated fenestrae that allowed for the expansion of the nasal passage and subsequent development of respiratory turbinates. The skull changes probably in part allowed for a change in metabolic status to a more endothermic state. It is now recognised the nasal cavity of Late Cretaceous ornithurines likely had fully functional respiratory turbinates and are nearly indistinguishable from that of extant birds.[29]

The seemingly 'late' evolution of avian endothermy (at least compared to mammals) is also evident in the specialised ventilatory mechanisms associated with the lung air sac system of modern birds that first appeared in ornithurine species.[29] Because of the lack of clear evidence of soft tissue lungs and air sacs in fossils it is difficult to infer more detailed information on ancient avian and dinosaur respiration and respiratory physiology.

However, some changes obvious in the fossil records suggest trends towards 'modern' avian specialization. Hinged thoracic and sternal ribs and specialised sternal-costal joints, characteristic of extant birds, are present in Late Cretaceous ornithurines but not so in more primitive relatives.[29] Pneumatised bones with foramina that likely correlate with air sacs are also well-recognised in the theropod fossil record. In-depth analysis of well-preserved fossils supports that even the most basal avians (including *Archaeopteryx*) had a bird-like, flow through septate lung and at least two of the five air sac systems present in Aves.[32] Many of the enantiornithine birds and some theropod dinosaurs retain gastralia ('belly ribs') that probably reflects an association with more primitive forms of lung ventilation and breathing.[29]

As mentioned above, endothermy is likely needed for sustained flight.[29] The development of the keel is generally associated with larger pectoral muscle attachments and more powerful flight. It is generally believed that *Archaeopteryx* and most enantiortnithines and confuciusornithines were capable of flight despite their poorly developed keel. The latter two, and 'younger' extinct bird groups, had a more developed keel. Progressing forward in time, the ornithurine birds had an even better developed keel. Finally, modern flighted birds have well developed pectoral muscles and a deep keel. The exceptions having a poorly developed or absent keel include the flightless birds such as extant and extinct ratite birds, flightless ornithurines and hesperonithids. Even with these observations, it is not clear if endothermy developed before or after initial flight as the first fliers may have produced short bursts of ectothermally powered flight.[29]

How Did Bird First Start Flying?

The origin of flight is explained in one of three hypotheses: arboreal (tree down), cursorial (ground up) and wing-assisted incline running. [3, 13, 14] The arboreal hypothesis proposes that a prehistoric bird climbed a tree and then glided down. Through time, the gliding range was increased by flapping and ultimately powered flight. A quadrupedal ancestor is usually implicated. That is one, like *Archaeopteryx*, that used both feet and wings to climb a tree and had a foot structure that allowed grasping tree limbs and perching. The modern day hoatzin (*Opisthocomus hoazin*) has claws on its wings (in juveniles only as adults have fused digits in their manus as with other modern birds) that are adapted for climbing trees. Some feel the hoatzin is modern day evidence supporting the arboreal hypothesis.[13]

In the cursorial hypothesis, a winged dinosaur running along the ground used flapping motions to avoid obstacles and briefly become airborne. Over time, the brief flapping became sustained powered flight originating from the ground.[14] *Archaeopteryx* with its short hallux (making perching less ideal) and legs adapted for bipedal running has also been suspected as a cursorial flyer. [13]

Wing-assisted incline running is a synthesis of the arboreal and cursorial hypotheses and is based on studies of extant birds. [13, 33] Studies completed on partridges showed that birds running up a steep incline benefitted from energetic wing flapping. Theoretically, this wing-assisted incline running gives birds an advantage to either escape predators or possibly catch prey. In a study, birds had feathers trimmed to varying degrees and were then run up an incline. Unfeathered (severely trimmed) birds could not run up steep slopes (>60^{o}). However, half feathered birds performed significantly better than unfeathered but not as well as fully feathered cohorts. The theory then extends to 'half-feathered' extinct theropods having an evolutionary advantage over non-winged species.

Where Do We Go from *Archaeopteryx*?

While *Archaeopteryx* is bird-like, it is not a modern bird. Archaeopteryx possessed a tail, unfused hand, teeth, gastralia ('abdominal ribs'), and no synsacrum all of which are different from extant birds. [34] *Rahonavis*, a Late Cretaceous (66-100 million years ago) Madagascar theropod, was 25 million years younger than Archaeopteryx and displayed more modern day bird-like qualities. *Rahonavis* pneumatic foramina going from the internal cavities to the thoracic vertebrae, fusion of six sacral vertebrae into a synsacrum, shortened fibula and quill knobs along its forelimbs suggesting the animal had feathered wings and could fly were all changes that were more like our modern birds. [34]

Other fossils show continued progression from the primitive dinosaur-birds to modern day *Aves*. [34] Flight appears to have strongly driven avian evolution. More recent fossils show increasing to seven vertebrae to form the synsacrum, shortening of the tail to form the pygostyle, reinforcement of the shoulder and lengthening of the coracoid. The Confuciusornithidae, including *Confuciusornis* and *Changchengornis* from the Early Cretaceous (100-146 million years ago) of China, display these features. Following the time line, fossil dinosaur-birds reduced their thoracic vertebrae, began to form the carpometacarpus from fused digits, evolved an alula (bastard-wing), altered the shoulder joint, developed three to four quill-like feathers on the small and highly modified first digit of the carpus allowing low speed flight and maneuverability, and progressively lost teeth and formed a beak. [9, 34]

The progression of earlier fossils shows continued reduction of primitive features and development of modern day structures into birds as we currently know them. [34] The Enantiornithes, the most diverse clade of now extinct Mesozoic (245-65 million years ago) small sparrow-sized birds gained perching feet and well developed flight. [33] The enantiornithes, or 'opposite birds' named for their unique anatomical features, are well represented in the fossil records compared to their successors the Ornithurae which includes the modern birds. [35, 36]

Hesperornithiform birds from the Late Cretaceous were large, long-necked, flightless diving birds had no gastralia, a completely fused tarsometatarsus, a shortened trunk, carpometacarpus and pygostyle and a synsacrum composed of at least 10 vertebrae. [34] Closer yet to modern Aves are the ichthyornithiformes from the Late Cretaceous. These long-necked, gull-like toothed birds had many of the changes noted in hesperornithiforms plus a massive keel and deltoid crest indicative of powerful flight. [34]

No enantiornithines, including hesperonithiforms and ichthyornithiformes are known to have survived the Cretaceous/Tertiary (K/T) boundary. [37] The K/T period was likely devastating for birds and the surviving species are considered the ancestors of modern birds. [37] Ornithurine birds are the only group of Mesozoic birds known to have survived the K/T extinction. [33] The truly modern toothless birds began appearing approximately 65 million years ago (beginning of the Cenozoic Era). [19]

The fossil records clearly show evolutionary development from dinosaurs to birds - even with the large gaps still present. All bird-like lineages except the neornithines (modern birds) went extinct before or at the end of the Cretaceous Period. [13] The survival of neornithines (of which 60% are Passeriformes) has shaped our current world. Passerine birds occupied most terrestrial environments and due to their intimate relationship with fruits and seeds likely were integral in the dispersal of flowering plants. [13]

Even recent fossil finds are starting to show what prehistoric birds ate and how avian species began to shape the flora of earth. A *Jeholornis prima* (large extinct bird) fossil from the Early Cretaceous period had no teeth and had numerous unidentified seeds in the stomach position providing direct evidence of seed eating in Mesozoic birds. [20, 38] Fossils of other Mesozoic birds have also provided direct evidence for arthropod-based, fish-based and even possibly sap-based diets supporting the idea that birds were occupying multiple feeding strategies and foraging habits. [33, 39, 40]

While China has produced more of the theropod-avian fossils, Europe has the best fossil records of birds from the more recent Paleocene, Eocene and Oligocene (aka the Paleogene; ~65-23 million years ago). [41] Based on fossil records, most of the relatives of modern birds (neornithines) experienced an explosive radiation during the Paleogene. [41] Even the oldest confidently identified members of Psittaciformes (parrots) come from the Eocene (~55 to 34 million years ago) deposits of Europe. [3]

Despite their large numbers today, Passeriformes are completely absent from pre-Oligocene Europe and only first appear in the early Oligocene (30-34 million years ago). [41] Molecular studies show that all European and most Old World passerine birds originally dispersed from the Australian continental plate. [42] Passerine evolution has also been attributed to their unique vocalizations linked to reproductive cycles which likely changed the sounds of prehistoric to modern day earth. [13]

Summary

The rapidly expanding fossil record combined with new forensic techniques (highly detailed imaging, molecular analysis, genetic probes, etc) has given the scientific community a much better idea as to 'what a bird is' and how they are related to dinosaurs. Understanding how various anatomical and physiological features developed, also gives a better appreciation for the purpose, form and function of birds. The recent discoveries and enthusiasm coming from fossil finds worldwide will likely shape our understanding of the origins of birds.

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