h17 The descent of birds < neornithines, *Archaeopteryx*, Solnhofen Lms >

Alfred, Lord Tennyson / once solved an enigma: When is an / eider [a seaduck] most like a merganser [a lake and river duck]? / He lived long enough to forget the answer. —*an anonymous clerihew*.[1]

All eighteen species of penguin live in the Southern Hemisphere. ... The descendants of a common ancestor, sharing common ground. ... 'This bond, on my [Darwin's] theory, is simple inheritance.'[2]

Bird evolution during the Cenozoic has been varied and rapid in the beak but not in the body. For example, Hawaiian Island bird arrivals beginning 5 Ma (million years ago) have evolved to new species with beaks specialized to feed on various flowers and seeds but their bodies have changed so little that the various pioneer-bird stocks are easy to identify. With that perspective, bird varieties distinctive in the beak as owls, hawks, penguins, ducks, flamingos, and parrots, are likely to have diverged in very ancient times. Ducks, albeit primitive ones such as web footed *Presbyornis*, which could wade but not paddle, already existed in the bird diversity of the Eocene when giant "terror birds," such as *Diatrema*, patrolled the ground.

Feathers are made mostly of beta keratin, a strong light-weight material. Bird feathers are modified scales which extrude from cells that line skin follicles. The shape and color of the feather so formed can change during the birds growth (say, a downy feather in youth and a stiff feather in adulthood) and by seasonal molts (say, a white feather in the winter and a colored feather for times of courting).[3]

All birds of the Cenozoic (30 orders) are characterized by toothless jaws and have a pair of elongated foot bones that are partially fused from the bottom up.

Living birds are taxonomically split into neognathes (modern birds) that have a palate more derived than in palaeognathes—which primitive skull structure persists as a character of ratites (flightless birds from the Southern Hemisphere) and the tinamous (their flighted sister taxa).

Ratites (L. *ratite* means raft), called so for their flat (raft-like) breastbone, include the rhea (*Rhea americana, Rhea pennata*, South America), ostrich (*Struthio camelus*, Africa and formerly Eurasia), emu (*Dromaius novaehollandiae*, Australia), cassowary *(Casuarius casuarius, Casuarius bennetti, Casuarius unappendiculatus*, Australasia), and kiwi (*Apteryx mantelli, Apteryx owenii, Apteryx haasti*, New Zealand), as well as the recently extinct moa (11 spp., New Zealand) and elephant-bird (3 spp., Madagascar). Palaeontological data are that emu and cassowary lineages separated sometime before 25 Ma and possibly 30-35 Ma which molecular estimates yeilding 33-39 Ma also indicate.

The ancestors of modern birds were survivors of the end-Mesozoic extinctions. But did the varieties diverge after or before the beginning of the Cenozoic? Since 1990, much evidence, according to Joel Cracraft, has been forthcoming that terrestrial ecosystems on the southern continents were not as badly disrupted or subject to as much extinction as were their Northern Hemisphere counterparts. This allows him to speculate that "many of the early lineages of modern birds may have escaped the K-T [E-K] asteroid calamity because they [occupied far southern continental regions]."[4]

Mesozoic birds are famous for the rareness of their fossils. Their known variety is biased by fossilization favoring shore and sea-going birds. So, modern birds may turn out to have ancestral roots in addition to palaeognathes.

The only Mesozoic birds that had decidedly modern features, according to Alan Feduccia, were Neornithes. These birds looked similar to today's curlews and their fossils occur in sediments that suggests they too were shore birds.

Well known from Late Cretaceous marine sediments in Kansas is the diversification of two sea-going birds: *Hesperornis*, has only vestigial wings with powerful legs for swimming and diving, and *Ichthyornis*, gull-like, with well-developed wings for flying. Of these, neither has a tail (a condition for all known birds of the Cenozoic) nor do their bills have teeth. For flighted birds, a light beak instead of bony teeth confers an advantage. A Late Cretaceous flighted bird *Apsaravis ukhaana*, described by Mark A. Norell and Julia A. Clarke in 2001, is from continental (not near-shore or marine) deposits near Ukhaa Tolgod, Mongolia.[5] 115 million year old, finch-sized *Eoalulavis* ("early bird with alula") by the evidence of its alula (a small tuft of feathers, also called a *bastard wing*, attached to the thumb) was a fine-tuned flyer.[6]

Conventional wisdom is that diversification of Neornithes was well underway before the end of the Mesozoic. Only this would easily account for the distribution of ratites (order Struthioniformes), which are birds that never had the ability to fly.

Ratite fossils are found on all the Southern continents formed by the Cretaceous break-up of the Gondwanaland realm of Pangea, and are commonly used as an example of vicariant speciation:

For the kiwi, Alan Cooper in 2001 found molecular phylogeny and biogeographic evidence of land-based dispersals between Australia, New Caledonia and New Zealand, presumably along the Norfolk Ridge or Lord Howe Rise.[7]

For the moa (remarkable for possessing no wing bones whatsoever),[8] molecular divergence dates its basal separation from the other ratite taxa to have been around 82-85 Ma, and so relates it to the geological split between New Zealand and Australia/Antarctica. The vicariant speciation of ratite taxa could thus post-date the separation of South America and Africa around 90 Ma.

For the ostrich, two hypotheses are:

The ostrich evolved in Eurasia before entering Africa—the evidence being skeletal and putative eggshell ostrich fossils in Paleogene deposits in Europe, India and Mongolia.

The ostrich arrived in Eurasia from India when that subcontinent joined—the speculation being that it and the elephant-bird entered Indo-Madagascar 80 Ma from Australia/Antarctica via the Kerguelan Plateau (of which Kerguelan island is yet emergent) that formed 110-115 Ma and was (dredging has found) tropical forest covered.

The common condition for birds before 75 Ma, were small teeth in the jaws, except in the premaxilla (front upper-jaw bone). However, the oldest example of a bird with a toothless bill is *Confuciusornis sanetus* which died in a forest lake, the sediments of which date older than 132 million years old (Early Cretaceous).[9]

Mesozoic birds include enantiornithines (means "opposite bird"), which have foot bones partially fused from the top down. In addition to teeth, distinctive of these are fat, fleshy, tails.

The truly great diversity of Mesozoic birds has been revealed by a rash of finds beginning in the 1980s *and* because some well known Cretaceous reptile taxa, the Enantiornithae (*Confusiusornis*, *Sinornis*, *Cathayornis*) and the Alvarezsauridae (misidentified as dinosaurs) belong to the class Aves (birds).[10]

Lius M. Chiappe (committed to focusing exclusively on fossils and cladistics—scientists who do otherwise "belong to the arm-waving school of envisioning and speculating and looking for what is intuitively pleasing")[11] has recently reviewed the eighty million years of bird evolution known for the Mesozoic (***Figure h17.1***). During the Late Cretaceous (66-100 Ma), bird lineages range to large size and are variously specialized to flightless land-birds, tree dwellers, waders, and foot-propelled divers that stem from ancestral 112 million year old *Gansus yumenensis*.[12] The fossil birds known from the Early Cretaceous (100-146 Ma) are small-sized and have the specialized perching feet of arboreal birds.[13] In the Liaoning province of northeastern China, many of these are well preserved. Amidst them in the entombing sediments was found a 1-meter-long dinosaur with impressions of what appears to have been a cloak of short feathers. Is this a hold over from a transitional stock of reptiles-to-birds?

The oldest known creature that was certainly a bird is *Archaeopteryx* ("ancient wing"). Its fossils are preserved, part and counterpart, in the finest detail in a bedded, almost clay free, lithographic limestone that accumulated some 150 Ma. Like modern birds, *Archaeopteryx* had feathered wings but different was its long, feathered, reptilian tail. In 1860, a single *Archaeopteryx* feather had been found in the Upper Jurassic Solnhofen stone quarries, Bavaria. There, later in that year, a complete *Archaeopteryx* skeleton was found with feather impressions in their life arrangement. The skeleton had the appearance of a bipedal saurischian dinosaur and would have been so classified, were it not for the feathers. "He is certainly a wise man who today can tell a bird from a reptile, with only the fragments of an ancient form before him" declared Othniel C. Marsh in 1890.[14] In 1973, John Ostrom published detailed anatomical comparisons of *Archaeopteryx* and small carnivorous bipedal ceolurosaurs; specifically, *Deinonychus*.[15] His proposal then that birds evolved from such dinosaurs is now disputed or is restated correctly with the same as clade sisters. A seventh specimen discovered near Solnhofen in 1992, described as a new species, *Archaeopteryx bavarica Wellnhofer*, was valued in 1993 for sale at US$1.2 million by its owner a private stone company in Solnhofen. From Solnhofen limestone, a tenth, and most complete, skeleton (now owned by the Wyoming Dinosaur Center, Thermopolis, WY) has feet with second toes that could be hyperextended as in dromaeosaurs and troodontids, and first toes pointing (as preserved) sideways as does a human thumb and not backward as in perching birds.[16]

Powered-flight adaptations in *Archaeopteryx* are as in modern birds:[17] flight feathers strongly curved for passive rotation of the feather about its axis through its base (so that on the upstroke of the wing the air slips through), and vane asymmetry in primary forward wing feathers held (so that the separated tips would provide automatic pitch control).[18] However, the flat sternum of *Archaeopteryx* does not suggests powered flight. (Modern birds have a keel on the sternum as an extra surface of attachment for their thick breast muscles.) Nevertheless, *Archaeopteryx* had flown, for it had died far from land. It had probably taken off from the ground as the Solnhofen lagoons were not surrounded by forests (K. W. Barthel, in 1999, determined) but by open ground and a scattering of small plants that offered no adequate perches. The Caicos Platform, according to the editors, K. W. Barthel, N. M. H. Swinburne, and S. Conway Morris, of *Solnhofen: A study in Mesozoic paleontology*, 1990, is a present example of the warm, shallow, carbonate lagoon in which the Solnhofen limestone formed.[19] Limestone deposition is because dissolved carbon dioxide degases as seawater that flows in warms and because, in shallow sunlit waters, algae encrust with calcium carbonate as they remove carbon dioxide from the seawater.

Birds first appear in the Triassic if *Protoavis* (yet to be fully described) is indeed one. Although no feather impressions are preserved with its one known fossil, its "wing" hand has an elongated second finger and the same persisted in *Archaeopteryx*.[20] Tracks of "birds" of this age are genus *Anomoepus*.

According to most descriptions, birds diverged from small, bipedal when running, theropod dinosaurs (maniraptors).[21] But the oldest fossils of these date 115 million years old, and *Archaeopteryx* is of Tithonian Age (146-151 Ma). "You can't be your own grandmother," Alan Feduccia in 2002 teases those in the camp of opinions who would have it so. In 2003, Xu Xing described from the Lower Cretaceous Jehol Group of western Liaoning, China, two small (77 cm long) *Microraptor gui*, unequivocally a dromaeosaur theropod and with feathers on arms legs and tail.[22] These fossil, 124-128 million year old, non-avian dinosaurs, are not on the line that became birds, but as Alan Brush has said, "many dinosaur traits fit neatly into a family tree branching into birds." *M. gui* has feet comparable to those of arboreal birds and forelimbs similar to those of *Archaeopteryx*. Yet a case can still be made that dinosaurs and birds are not so closely related. Are *Archaeopteryx* fingers I, II, III as in theropods, or II, III, IV that E. S. Morse's Law (1872) stipulates,[23] debatably, for birds? [24] In 1999, Gunter Wagner and Jacques Gauthier proposed that developmental signals transformed the tissue so.[25] Corroborating this in 2005, Alexander Vargas, and John Fallon find that fingers are specified by developmental genes Hoxd13 and Hoxd12 working together but only the first programs for the thumb of mice and "finger II" of chickens.[26]

In the Late Triassic Santo Domingo fm red-bed sequence, Argentina, 55 million years before *Archaeopteryx*, "bird-like" footprints, described by Ricardo N. Melchor in 2002, have the tell-tale feature of a hallux (digit I) impression at a high ~160º angle to digit III.[27] Also, feathers do not make a bird if these are what 6-8 pairs of long, narrow "feathers" are on the back of 10 inch long, Triassic lizard-like, non-dinosaur, collected (and misidentified) in 1969 by Alexander Sharov (1923-1973).[28] Described and named *Longisquama insignis* in 2000, no claim is yet that *L.i.*, which lived 75 million years before *Archaeopteryx*, gave rise to birds.[29] However, this strange 220 million year old fossil, Alan Feduccia comments, "points toward the right time to look for the ancestors of birds."[30] ❑

Figure h17.1 [31] Phylogenetic relationships in the class Aves (birds) of the best known Mesozoic taxa