ORNITHOLOGY
Lecture 2: Evolutionary history of birds

Relevant chapters in Gill:
Chapter 2: History
Chapter 3: Systematics

-Fossil birds, and other fossils with bird-like features, allow us to determine the age of birds, the ancestors of birds, the series of changes that birds underwent in evolution, whether modern birds are related to the radiation of fossil birds in the Mesozoic, and what makes a bird a bird.
-Evolution proceeds when a new heritable trait emerges in some organism and is passed genetically to its descendants. The idea indicates that two groups of animals that share a set of these new or "derived" traits are more closely related to each other than they are to groups that display only the original traits but not the derived ones. Of course these traits can be lost subsequently, and similar traits can evolve more than once, but tracking these traits is the best way to work out the phylogenetic relationships among organisms. May track more than one trait, such as both feathers and skeletons. Results of these analytical tracks is a "cladogram," a treelike diagram that describe the order in which new traits and new creature evolves. Each branching point reflects the emergence of a ancestor that founded a group having derived characters that were not present in the group from which it evolved. The ancestor and its descendants constitute a branch in the tree; root word "clade" = branch. This style of reasoning is cladistics. The groups are hierarchial in a historical sense, a branch includes all animals that shared a recent common ancestor. "What is a bird" is a historical question.
-Two theories of the age of diversity of modern bird orders. (1) orders may date from Eocene, 65 million years ago, massive extinction of earlier kinds of birds was associated with global changes brought about when an asteroid storm hit the earth from outer space. This idea is based on fossil birds, which show no clear match between the older fossils and the kinds of bird groups now on earth, all the major groups radiated around the Eocene (Feduccia, Science, 267:637, 1995). (2) molecular genetics studies, based on extrapolation of rates of 1-2% change / million years, as calibrated from a few fossil forms, suggest the major groups of birds go back even earlier, to > 80 million years ago, and there was no strong evidence for a K-T extinction (Padian & Chiappe 1998). The same debate has affected mammal paleontology. We need to work on gathering fossils and developing molecular techniques to narrow down this 15my discrepancy.

A. Birds and bird relatives of the Mesozoic (Triassic, Jurassic, Cretaceous)
-Since 1995 there have been so many discoveries of fossils that our knowledge of the evolutionary history of birds and their ancestors is filling out more quickly than it ever has. For instance, we now know that the ancestors of modern birds had feathers long before they could fly-- a few large reptiles had feathers but no other flight-related adaptations. E.g. A fossil from China, *Sinosauropteryx*, has a row of "down" along back and on flanks. So we might be able to call a bird a bird because it has feathers today, but an evolutionary biologist or paleontologist would quibble with that description-- there were feathers before there were birds, unless we want to call a loping dinosaur with a few feathers a bird. It's all a matter of semantics anyway, when we decide to call animals particular names, because they are always changing. The closest relatives of the earliest birds were the running dinosaurs (dromaeosaurid theropods) like *Deinonychus* (like the velociraptor of Jurassic Park). Dinosaurs had many features that birds show today: fused furcula, elongated forearm, laterally flexing wrist, long hollow bones, nesting behavior, and of course, feathers.
-A fossil from Texas, discovered in 1983 by dinosaur paleontologist Chatterjee, dates to 225 mya, late Triassic (before Jurassic), 80my earlier than the earliest known bird fossil. He named it *Protoavis texensis* "first bird from Texas," in Phil. Trans. Roy. Soc. London, 1991. The skull was described there, later in 1995 rest of fossil was described. It is a reptile that has a few characteristics that are similar to those of birds, but it is apparently more reptilian than bird-like.
-Jurassic, ca 140 mya. *Archaeopteryx*, Greek for "ancient wing," is the oldest known fossil with enough bird-like characteristics for paleontologists to more or less unanimously call it a bird. For this reason it is considered "the link" between birds and reptiles, although most people overestimate what "links" mean because they don't understand evolution. *Archaeopteryx* looked like a small dinosaur with feathers, and is remarkably well preserved in fine-grained limestone. Several fossils have been discovered in Germany, and possibly the same kind in Korea. Crow-sized, had a snout with teeth like reptile, also wings and tail

with long feathers. Feathers were much like modern feathers in having barbs, present on wings and tail as flight feathers, also on body, asymmetrical as are flight feathers of flying birds. Probably also had downy feathers, as base of modern vane feathers are downy. Because it has modern feathers, it doesn't tell us much about the early origin of feathers. We'd have to go even earlier than 140mya for that. Most famous fossils are in BMNH in London and in Berlin Museum, where popular displays. *Archaeopteryx* was contemporary in Jurassic with the dinosaurs, had gliding flight. Similarities with modern birds: its feathers, furculum or fused wishbone, fused sclerotic ring, wing digits 1-3 with phalangeal formula 2,3,4 (number of bones in each digit) partway to modern birds with its partly fused tarsometatarsus, and in having 4 toes, with 2-3-4-5 phalanges. More like dinosaurs and other reptiles in other characteristics: teeth in jaw, curved backward. Snout rather than a bill. Small braincase (intermediate in relative body size between modern reptiles and modern birds) with large olfactory lobes. Abdominal ribs or gastralia. Tail vertebrae are unfused, n=23 in London specimen, sternum shows no keel (vs modern flying birds), also no foramen triosseum (a hole between coracoid, sternum and clavicles where these bones come together and a pulley tendon runs through, for breast muscles to pull up the wing) (vs modern flying birds). So it did not have powered flight. Unfused carpals (hand bones) and metacarpals (foot bones). Most of these traits are same as in the dinosaur ancestors of birds. They evolved from thecodont reptiles, the common ancestor of dinosaurs and birds. There is still a single notable ornithologist (Alan Feduccia) who still believes that other reptiles outside of the dinosaur clade were the ancestors of birds, but he is basically sticking to a stand he took decades ago before we had intervening embryological, fossil, molecular, and other evidence that makes his opinion incredible today.

-Late Jurassic or early Cretaceous, over 120 million years old, fossil bird: *Confuciusornis*, from China. Chicken-size, feathers, toothless beak, ability to fly well, lighter bones, shorter tail than *Archaeopteryx*, claws on wing. The oldest evidence for a beaked, toothless bird.

-Early Cretaceous: ca 135-100 mya. *Sinornis*, sparrow-sized bird from an old lake bed in China, described in 1992 Science. Coracoid buttress to sternum, would resist compressive forces by the flight muscles, skeletal support for primaries and secondaries. Transition from the primitive wing of *Archaeopteryx* to a specialized wing and tail more like that of modern birds, well on its way to flight. Modern avian flight and perching therefore evolved in small-bodied birds in inland habitats not long after *Archaeopteryx*.

-*Ambiortus* from Mongolia, incomplete, Early Cretaceous. Small, first bird that looks like a modern bird.

-*Eoalulavis*, Spain, earliest known "alula," a tuft of feathers attached to the thumb, as in modern birds, the alula gives good control at low flying speeds, in takeoffs and landings. 115 mya.

-In summary, by Early Cretaceous birds, flight has taken over. Fossil birds were small, sparrow- to pigeon-sized, they could fly, they looked like birds, with feathers, sustained flight ability, and could perch (reversible first toe or hallux).

-Mid-Cretaceous fossils *Hesperornis* and *Ichthyornis* were marine, toothed, large birds. *Hesperornis* includes 13 species of diving seabird ranging in size from a chicken to a large penguin, foot-propelled, superficially resembled modern loons, flightless. No keel on sternum, large crest on tarsometatarsus for swimming muscles like loon and grebe, vertebrae looked like those of modern birds. *Ichthyornis* was a flying, tern-like bird, anterior keel on sternum. Apparently off the main lineage of bird evolution, vertebrae amphicoelous like primitive reptile, they left no living descendants. Both Hesperornis and Ichthyornis are closely related to modern birds, in Ornithurae.

-Late Cretaceous, 70-80 mya, Mongolia, *Apsaravi*, together with *Ichthyornis*, basal to modern birds Aves. There were other birds around at the time which did not give rise to modern birds, but whose descendents have died out (look at evolutionary history like a tree. E.g. large group *Enantiornithines***,** nearly worldwide, known in Argentina, then in Spain, central Asia, China and Mongolia, and in Montana, Utah and Alabama. Several genera and species. Wing and leg differs in construction from modern birds, the direction of fusion of the legs (cf. anatomy lecture) is the opposite; they are on a different evolutionary trajectory than modern birds, and have died out, despite the fact that their wings were more advanced than the ancestors of modern birds at the time.

-As in all studies of evolutionary history, we should not see things as a line, but a tree. Just as the most recently evolved floral forms are the bilaterally symmetrical flowers like orchids and irises, we still have the older, simpler radially symmetrical daisies and sunflowers with us. In the same way, at any particular time in the evolutionary history of birds there are fossils with more primitive traits than the new traits that are most interesting to bird paleontologists. I am presenting the developments as a line simply because that is the order of the origination of novelty in the history of birds.

B. Birds in the Cenozoic

-Whether modern birds diversified largely before the K-T mass extinction, or after it (as most believe, because of the fossil record), is still debated. Few fossils from before the mass extinction are clearly from existing orders of birds-- most, on the other hand, seem to have gone extinct. The most widely accepted order that almost certainly existed from before the extinction is waterfowl. But there are fossils from many orders by the Oligocene, and several are even in the Eocene (about 55mya). The question is whether they radiated earlier than that, and we just haven't found the fossils. The molecular evidence suggests that this might be the case, but we haven't enough evidence yet to distinguish the hypotheses with confidence.

-Oldest known possible fossil songbirds were in Australia, in the Eocene period, 55 mya (Boles, 2 March 1995, Nature). This evolutionary radiation of songbirds started about same time as the origin of many other groups of birds.

-Eocene, 60-40 mya. Most modern orders of birds, including waterbirds such as loons, cranes, ducks, petrels, well established. Greatest diversity of Eocene birds and mammals in oil shale deposits at Messel, in Germany. Displays of fossils in museum in Frankfurt, Germany, many modern orders first appear in fossil record in Eocene.

-Large flightless big-billed birds *Diatryma* are known from this epoch, from W North America and Europe; they were perhaps predators, scavengers or herbivores (Anders 1992). Also big wading birds with duck-like heads (or carnivores) *Presbyornis*.

-Large flightless carnivores in South America, the Phorarhacids, large flightless carnivores where no mammals had this niche (lower Oligocene through Pliocene). There is one species known from Florida (How did it get there?)

-Oligocene: The largest known sea bird was found at an airport site in South Carolina in 1987, dating about 30 mya. It had bony teeth, a wingspan 18-19 feet!, weight is estimated at about 90 pounds. Compare this to the largest today, the albatross, wingspan only 11 feet and much lighter at 20 pounds! (But some pterosaurs had 40-foot wingspans-- they died out and left no descendants).

-Old World vultures found in the New World, and New World vultures in the Old World; shows that not all groups were as restricted in distribution as they are today.

-Pleistocene (last million years): Fossils are easier and easier to find and identify as time gets more recent. Just one story here: huge New World vultures existed during the last ice age. *Teratornis meriami* had a 4 m wingspan in southern California, in La Brea tarpits in Los Angeles, which have > 85,000 bird fossils of 133 species of birds (see Novacek 2002). Another species *T. incredibilis* in Nevada had a wing span of 5-6 m, fed on the megafauna of the time (mammoth), the California Condor is similarly adapted for an earlier time.

C. Bird systematics

-Relationships among modern groups of birds: 1- paleognathous birds (ratites and tinamous), 2- ducks and chickens, 3 - others. There is good agreement among ornithologists about these groups, but not about other orders. This lack of information is remarkable compared with the better data that some other animal groups have. Birds have radiated in so many environments so quickly, and have changed so much, converging on each other in similar habitats so that distantly related species look similar morphologically, that it is a mess to untangle all that history. With new molecular techniques, together with morphological evidence and a rapidly accumulating fossil record, the next decade or so will see a proliferation of phylogenetic work. For instance, just this year will be published the first comprehensive phylogenetic analysis of the cuckoos (Cuculiformes) by UMMZ researchers, and currently in process at the UMMZ are equally comprehensive phylogenetic analyses of three families of finches (Ploceidae, Estrilidae, Viduidae), and the order of hawks and eagles (Falconiformes), both for the first time.

-We are in a remarkable time of discovery of fossils. What we know now is but a stage in our ultimate understanding of the origin of birds, feathers, and flight.

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