

Current perspectives on the evolution of birds

Per G.P. Ericson

Department of Vertebrate Zoology, Swedish Museum of Natural History, P.O. Box 50007, SE-10405 Stockholm, Sweden, per.ericson@nrm.se

Key words: Aves, phylogeny, systematics, fossils, DNA, genetics, biogeography

Contents

| | |
|--|-----|
| Systematic relationships | 109 |
| Genome characteristics | 111 |
| A comparison with previous classifications | 112 |
| Character evolution | 113 |
| Evolutionary trends | 113 |
| Biogeography and biodiversity | 113 |
| Differentiation and speciation | 114 |
| Acknowledgements | 115 |
| References | 115 |

Abstract

The paper summarizes the current understanding of the evolution and diversification of birds. New insights into this field have mainly come from two fundamentally different, but complementary sources of information: the many newly discovered Mesozoic bird fossils and the wealth of genetic analyses of living birds at various taxonomic levels. The birds have evolved from theropod dinosaurs from which they can be defined by but a few morphological characters. The early evolutionary history of the group is characterized by the extinctions of many major clades by the end of the Cretaceous, and by several periods of rapid radiations and speciation. Recent years have seen a growing consensus about the higher-level relationships among living birds, at least as can be deduced from genetic data.

Systematic relationships

Birds (Aves) is here defined as the least inclusive clade containing the common ancestor of all living birds and the yet oldest avian fossil *Archaeopteryx*, plus all its descendants (Chiappe, 2002). Phylogenetically, the birds belong to the theropod dinosaurs, with their closest relatives being the dromaeosaurid and troodontid theropods (Hwang *et al.*, 2002, Göhlich and Chiappe, 2006). Although birds have many synapomorphic features when compared with living animals, most of these characters are also found in theropod dinosaurs. An obvious example is feathers, which also occur in several carnivorous dinosaurs

(cf. Göhlich and Chiappe, 2006), making feathers a plesiomorphy in birds. Indeed, only three synapomorphies have been proposed for Aves (Chiappe, 2002), although monophyly is never seriously questioned: 1) the caudal margin of naris nearly reaching or overlapping the rostral border of the antorbital fossa (in the primitive condition the caudal margin of naris is farther rostral than the rostral border of the antorbital fossa), 2) scapula with a prominent acromion, and 3) postacetabular process of pelvis is shallow and pointed, less than 50% of the depth of the preacetabular wing at the acetabulum.

The fossil record of birds is surprisingly rich given the often-claimed poor preservation ability of their fragile bones (but see Olson, 1985). The oldest fossil, *Archaeopteryx lithographica*, was found as early as 1860 in Late Jurassic deposits in Solnhofen, Germany. For long, *Archaeopteryx* predated the next oldest bird fossil with ca. 60-70 million years, but in the last decades numerous of Mesozoic specimens have been collected in China, Argentina, Spain and elsewhere (see Chiappe and Witmer, 2002). All living birds belong to the clade Neornithes of which the earliest finds date from Late Cretaceous. Important Mesozoic radiations of non-neornithine birds include *Confuciusornis* and *Enantiornithes*. The latter group was especially important as it exhibits a wide range of adaptations and occurred in different habitats all over the world (Chiappe and Walker, 2002). Despite the large diversity of major bird groups in the Mesozoic, only Neornithes survived the mass-extinctions at the end of the Cretaceous. The fossil record of neornithine birds increases dramatically in the early Tertiary, but it is disputed whether this reflects a true, rapid radiation of the group, or if it is caused by a geographic bias of collecting efforts (Cooper and Fortey, 1998; Cooper and Penny, 1997; Cracraft, 2001; Dyke, 2001; Feduccia, 2003). If the Mesozoic ancestors of Neornithes predominantly occurred on the southern continents (from which fewer localities with bird fossils are

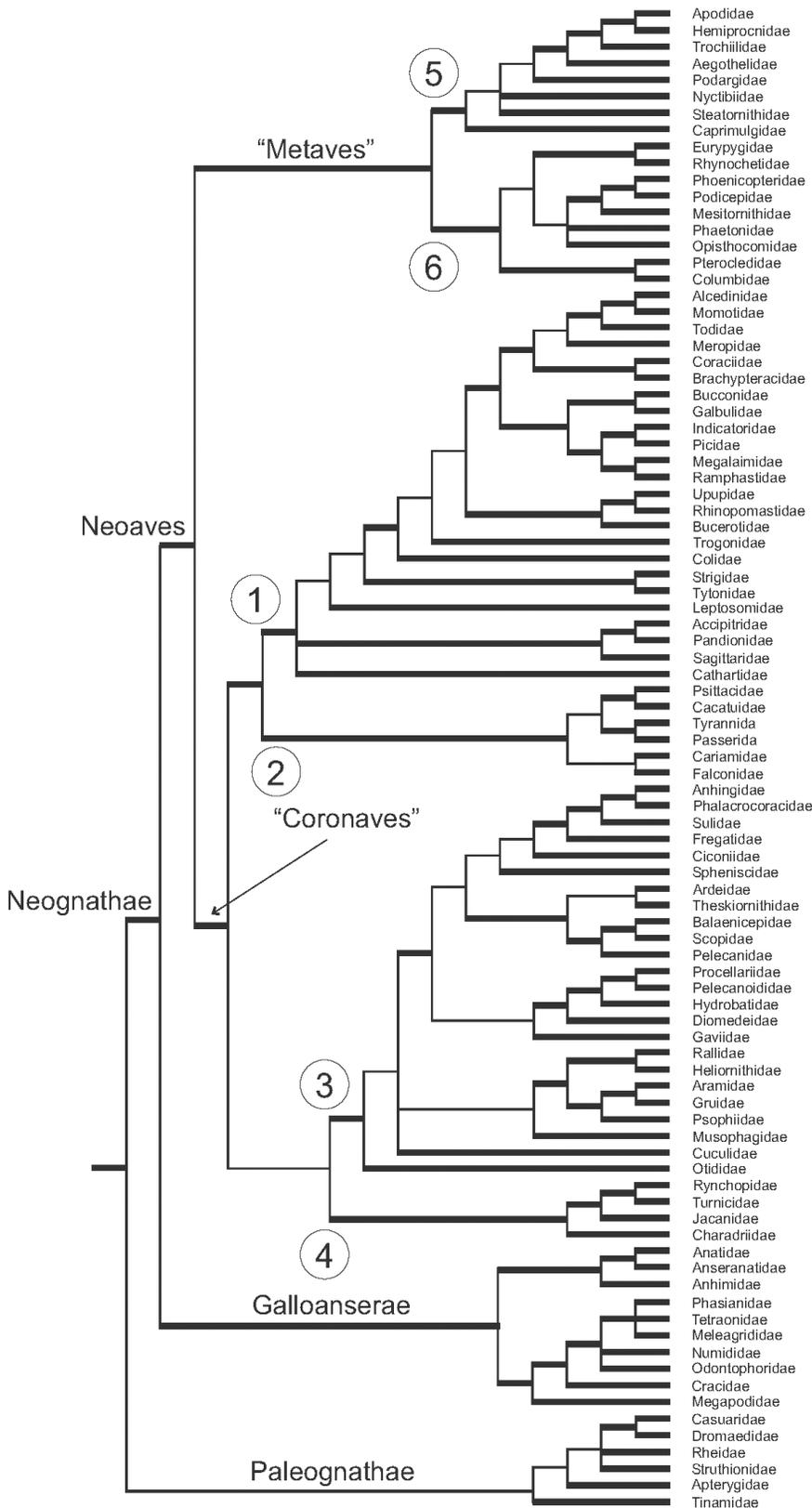


Fig. 1. A summary hypothesis for the higher level relationships in modern birds, Neornithes. Thick branches indicate clades for which monophyly is considered well supported. Relationships within Paleognathae and Galloanserae are compiled from several sources (cf. Cracraft *et al.*, 2004; Harshman, 2007). Relationships within Neoaves are from an analysis of nuclear DNA sequences (Ericson *et al.*, 2006), in which six major lineages were recovered: 1) 'landbirds clade A' (accipitrid diurnal raptors, osprey and secretarybird, rollers and allies, woodpeckers and allies, trogons, mousebirds, owls, and New World vultures), 2) 'landbirds clade B' (parrots, passerines, falcons and seriemas), 3) 'aquatic and semi-aquatic birds' (e.g., pelicans, cormorants, herons, storks, cranes, rails, loons, penguins and albatrosses, as well as the less aquatic groups cuckoos, turacos and bustards), 4) shorebirds, gulls, auks and allies (includes the buttonquails), 5) nightjars, owllet-nightjars, potoos, oilbird and frogmouths, hummingbirds and swifts, and 6) a heterogeneous assemblage of systematically enigmatic birds exhibiting many different adaptations (doves, sandgrouse, mesites, flamingos, grebes, kagu, sunbittern, hoatzin and tropicbirds).

known) they may have colonized the Northern Hemisphere only after the break-up and subsequent northward migration of Gondwana elements.

Three major clades of Neornithes have emerged from analyses of molecular data (Groth and Barrowclough, 1999; García-Moreno and Mindell, 2000; van Tuinen *et al.*, 2000; García-Moreno *et al.*, 2003), and they largely agree with hypotheses based on morphology (Cracraft and Clarke, 2001; Livezey and Zusi, 2007). The first division of Neornithes is between the ratites and tinamous (Paleognathae) and all other groups (Neognathae). Among the paleognaths, the South American, fowl-like tinamous is the sister group to the flightless ratites (ostrich, rheas, cassowaries, emu and kiwis).

The neognaths in turn are divided into two groups, Galloanserae with the galliforms (e.g., pheasants, quails, curassows) and anseriforms (e.g., ducks, geese, swans), and Neoaves, which includes the rest. Galloanserae is relatively well-studied and there is a general agreement on the higher-level relationships within both orders. In Galliformes the Australasian megapods (Megapodiidae) is the sister group to the globally distributed pheasants, grouse and their allies (Phasianidae *sensu lato*) and the Neotropical curassows (Cracidae). In Anseriformes the Neotropical screamers (Anhimidae) is sister group to the globally distributed ducks, geese and swans (Anatidae) and the Australian magpie goose (Anseranatidae).

While a general understanding of the more basal parts of the phylogenetic tree was reached in the end of the 1990s, the higher-level relationships within Neoaves has been more difficult to resolve. Numerous unsuccessful attempts have been made over the years, involving many different data types, including various molecular data sets (Johansson *et al.*, 2001; Sorenson *et al.*, 2003; Poe and Chubb, 2004). A break-through came in 2004 with the suggestion of a deep split in Neoaves into the 'Coronaves' and 'Metaves' (Fain and Houde, 2004). This unexpected result was questioned because the study was based on only one genetic marker (intron 7 in the nuclear beta-fibrinogen gene) and the statistical support for this division was weak (Fain and Houde, 2004; Ericson *et al.*, 2006; Morgan-Richards *et al.*, 2008).

A study of five nuclear genes provided the first well-supported hypothesis for basal, neoavian relationships (Ericson *et al.*, 2006). The study included representatives of all families in Neoaves (the well-studied orders of passerines and shorebirds were rep-

resented by a few families each to decrease the size of the data set). Unlike in previous studies of Neoaves, many basal (early) divergences were strongly supported. Six major lineages were identified (Fig. 1):

1. 'Landbirds clade A' (with three subclades: i; accipitrid diurnal raptors, osprey and secretarybird, ii; rollers and allies, woodpeckers and allies, trogons, mousebirds and owls, iii; New World vultures).
2. 'Landbirds clade B' (with two subclades: i; parrots and passerines, ii; falcons and seriemas).
3. 'Aquatic and semi-aquatic birds' (e.g., pelicans, cormorants, herons, storks, cranes, rails, loons, penguins, albatrosses). Cuckoos, turacos and bustards also belong to this lineage.
4. Shorebirds, gulls, auks and allies (shorebirds, gulls and auks, including buttonquails).
5. Nightjars, owlet-nightjars, potooes, oilbird and frogmouths, hummingbirds and swifts.
6. A heterogeneous assemblage of systematically enigmatic birds exhibiting many different adaptations (doves, sandgrouse, mesites, flamingos, grebes, kagu, sunbittern, hoatzin and tropic birds).

These six lineages were further grouped into two, reciprocally monophyletic clades corresponding to the clades 'Coronaves' (lineages 1, 2, 3, 4) and 'Metaves' (nos. 5, 6) postulated by Fain and Houde (2004). However, this finding does not provide independent support for this dichotomy of Neoaves, since the new study included the same beta-fibrinogen gene region on which this hypothesis was first based. Indeed, excluding beta-fibrinogen from the analysis collapses 'Coronaves' and 'Metaves' (Ericson *et al.*, 2006) and their postulated monophyly remains to be investigated. Also, the relationships between the six lineages above will certainly be disputed a long time yet. Still, the recent identification of *subgroups* of Neoaves is itself a great step towards understanding the evolution of this large clade of birds.

Genome characteristics

The average avian genome size is ca 1.45 billion base pairs, which is less than in most other vertebrates (Gregory, 2005). As genome size mostly varies with the amount of non-coding DNA, notably the incidence of repeat elements, it has little to do with the complexity of the genome. The observations that

bats also have small genomes and that the non-flying ratites have the largest avian genomes suggest that short genome size is associated with flight (Hughes, 1999). However, recent studies suggest that the genome size had already decreased in saurischian dinosaurs (from which the birds descend) some 250 to 230 million years ago (Organ *et al.*, 2007). As small genomes may correlate with higher metabolic rate (Gregory, 2002; Waltari and Edwards, 2002) it is hypothesised that this was required to provide energy for carnivorous dinosaurs to catch their prey, and later enabling birds to evolve flight. Small genomes thus become yet another bird characteristic that was inherited by birds from their dinosaur ancestors, like e.g. feathers, nesting behaviour, and, possibly, homeothermy.

As in other animals DNA is present both in the cell nucleus and in the mitochondria. In birds (unlike in mammals) also the blood cells have a nucleus, which has the consequence of allowing access to large quantities of DNA from blood. The avian mitochondrial DNA is a maternally inherited, small (typically 16-18 kilobases), circular molecule that has 37 genes. Four different mitochondrial gene orders have so far been reported in birds (Gibb *et al.*, 2007).

To date only the chicken (*Gallus gallus*) genome has been completely sequenced, but one more species is soon completed; the zebra finch (*Taeniopygia guttata*) (Zebra Finch Genome Consortium, 2006). The avian karyotype is characterised by large number of chromosomes (usually 10 pairs of so-called macrochromosomes and about 30 pairs of microchromosomes). Besides representing two distinct chromosomal size classes, the two chromosome types differ in their GC content, repeat content, gene density and recombination rate (Axelsson *et al.*, 2005). The microchromosomes are an essential component of the avian genome, as they encode 50% of the genes while representing only 25% of the genome. The diploid count in birds is rather constant with ca. 2/3 of all studied species exhibiting $2n = 74-86$, while most of the remaining have $2n = 66-74$ (Griffin *et al.*, 2007). The avian karyotype is also characterised of female heterogamety with sex chromosomes Z and W in females, and Z and Z in males. It is not yet conclusively shown that sex determination is based on a dominant role of the female-specific W chromosome, or if also a 'dosage mechanism' is involved, i.e. that the sex of the individual may be determined by the ratio of Z chromosomes to autosomes (Smith, 2007).

A comparison with previous classifications

The present understanding of the systematics of birds in many respects agree with previous hypotheses, although none of these agree in all aspects. A basal division of birds into paleognaths and neognaths, respectively, according to their palatal structure has been recognized since first described by Thomas Huxley (1867). This division has not been universally accepted and especially the monophyly of the flightless and most often large ratites (the extant ostrich, rheas, cassowaries, emu and kiwis, plus the extinct moas and elephantbird) has been questioned (Olson, 1985). It is known that flightlessness may lead to gigantism and neoteny (Feduccia, 1985; Olson, 1985; Dawson *et al.*, 1994; Dawson, 1996), and this has led to the assumption that the morphological similarities observed between ratites are convergently evolved. Although ratite monophyly does not reject this, a more parsimonious explanation is that flightlessness first evolved in their common ancestor.

Morphological and other data in support for monophyly of galliforms and anseriforms have been published for almost 50 years (Simonetta, 1963; Bock, 1970; Dzerzhinsky, 1982, 1995; Cracraft and Clarke, 2001; Mayr and Clarke, 2003; Livezey and Zusi, 2007). However, the clade Galloanserae yielded widespread acceptance only after studies of genetic data, and particular the work on DNA-DNA hybridizations summarized in Sibley and Ahlquist (1990). These results have later been corroborated by analyses of nuclear DNA (Groth and Barrowclough, 1999; van Tuinen *et al.*, 2000, and others).

In ornithology the taxonomic entity 'family' most often refers to birds whose close relationships are easily recognized. For example, all grebes are placed in the family Podicipedidae, all kingfishers in Alcedinidae, and all woodpeckers in Picidae, and so on. Families of neognathous birds are thus often easy to recognize and many of the 'families' in early classifications have been confirmed as monophyletic by recent studies. Only in passerines is it difficult to group species into families due to the widespread occurrence of convergent evolution within this order. Classifications of passerines therefore are often subjective and taxonomic changes are common following analyses of molecular data.

While individual families often are natural it has proven immensely difficult to group families into higher categorical units, as orders (Olson, 1985).

This has been true regardless of which type of data is analysed. A recently published phylogeny based on nuclear DNA suggests phylogenetic relationships that often differ from traditional opinions (Ericson *et al.*, 2006). Among other things, it refutes monophyly of several orders: Pelecaniformes, Ciconiiformes, Falconiformes, Gruiformes, Coraciiformes and Caprimulgiformes.

The hierarchy of birds above the ordinal level has never been strongly supported by data (except the paleognath/neognath division), and no relevant comparisons can be made with the recently suggested subgroups of Neoaves.

It should be pointed out that the widespread classification of birds published by Charles Sibley and colleagues (Sibley and Ahlquist, 1990; Sibley and Monroe, 1990), rests on the severely criticized and now abandoned DNA-DNA hybridization method (Cracraft, 1987; Houde, 1987; Sarich *et al.*, 1989). Furthermore, the trees were constructed from these questionable, phenetic data by using highly subjective methods (Cracraft, 1987; Houde, 1987; Sarich *et al.*, 1989). These shortcomings have resulted in a well-deserved scepticism of Sibley's classification, although some of the results have been confirmed by other methods. Furthermore, the controversial DNA-DNA hybridization studies undeniably have sparked a considerably research interest in avian systematics.

Character evolution

Being constrained by the adaptation to flight, the avian anatomy is conservative and rather uniform across taxa. Possibly, the low level of anatomical variation in recent birds is also due to a 'morphological bottleneck' event early in their evolution. Despite that the Mesozoic radiation of birds was large and morphologically diverse (see Chiappe and Witmer, 2002), all extant birds derive from a common ancestor, that may have lived in mid Cretaceous. Today, most morphological differences between bird groups are found in those anatomical regions that are directly involved in feeding and locomotion.

Regardless of the final resolution of the six lineages described above, it is clear that Neoaves exhibits many examples of parallel evolution in locomotory and feeding adaptations. Several ecomorphological counterparts can be identified when comparing groups in 'Coronaves' and

'Metaves', like grebes vs. divers, hummingbirds vs. sunbirds, tropicbirds vs. gannets (Fain and Houde, 2004). Similar examples can also be found when comparing the major groups within the 'terrestrial clade' of 'Coronaves'. For example, the two radiations of diurnal raptors belong to separate lineages within 'Coronaves' (falcons vs. hawks, eagles, buzzards and allies), and as sister to both of them is a small group of cursorial raptors adapted to an open landscape (seriemas vs. secretarybird).

Evolutionary trends

At a geological time-scale birds benefited greatly from the extinction of the dinosaurs and pterosaurs, with which they may have competed for food. Although the decline of several animal groups, including dinosaurs, had begun already during the late Cretaceous, the mass-extinction at the K/T-border left many food niches empty. Doubtless this has facilitated adaptive radiations in many lineages of birds, regardless if some of these had evolved already in the Cretaceous. One of the most successful avian radiations overall involves the switch to granivory, seed eating, in a few groups. The plesiomorphic diet in many (most) bird groups most probably is insect eating, and most of the specialised seed eaters belong to only a few evolutionary lineages. The most successful of these in terms of number of species are the weavers (Ploceidae), sparrows (Emberizidae), finches (Fringillidae), which all radiated rather rapidly in the Tertiary, probably following the documented dramatic increase in the diversity of angiosperm seed and fruit features at this time (Ericson *et al.*, 2003).

The most important factors today that influence the life of birds, as well as of all other organisms, relate to human activities in general, and to habitat destruction and climate change in particular (Collar *et al.*, 1994). However, these factors mostly act on a time-scale that is far too fast to allow birds to evolve necessary adaptations through natural selection. As a consequence, BirdLife International estimated that about 20% of all bird species were threatened by extinction in 2005.

Biogeography and biodiversity

The largest number of bird species occurs in tropical regions, where also the largest diversity (in terms

of number of families) is found. It may be argued that geographic patterns in birds are not to be expected due to their high ability to disperse, but this has been shown empirically to be wrong. Indeed, the geographic history can be reconstructed for most groups and species, not least by analyses of their genetic variation. Based on their phylogenetic relationships, age of clades, and current distributions it is evident that groups like the ratites, galliforms and anseriforms began to radiate in the former, southern supercontinent Gondwana (Cracraft, 2001). Also other groups have distinct Gondwanan signatures, for example the passerines and caprimulgiforms (Barker *et al.*, 2002; Ericson *et al.*, 2002). Ongoing analyses of the biogeography of Neoaves indicate that the large 'Landbirds clade A' (lineage 1 in Fig. 1) consisting of, e.g., diurnal raptors, kingfishers, rollers, woodpeckers, trogons, mousebirds and owls, originates in the Afrotropical region. It is likely their ancestor reached Africa from Antarctica, possibly through stepping-stone dispersal using the now submerged Kerguelen Plateau and Madagascar. Within the other large clade of terrestrial and arboreal birds ('Landbirds clade B', lineage 2 in Fig. 1), the falcons and seriemas diversified in South America and the passerines and parrots in Australasia. The ancestors of all these groups were once distributed in Gondwana and later became isolated in different continents in the Late Cretaceous. It remains to be studied how important the break-up of Gondwana has been to the diversification also of other groups. An indirect evidence of long-time separation between groups of birds comes from the many cases of convergently evolved morphologies following adaptation to similar life-styles in different groups of birds (as exemplified above). It can safely be assumed that some of these adaptations have evolved during long time in isolation and thus may have occurred in different continents, or even Hemispheres.

Major geological events also explain other distributional patterns in birds. For example, the avifaunas of Asia and Australia are separated through Wallace's Line, which runs between Borneo and Sulawesi (Celebes) and through the Lombok Strait. This biogeographic pattern reflects the geological history of the region, including both plate tectonics and fluctuations in ancient sea levels. It may be surprising to find that relatively few species have dispersed across Wallace's Line, even though most geological events occurred many million years ago.

Many bird species also exhibit biogeographic patterns observable between populations, and molecular data have been especially important to discover the details of these (Avice, 2000). Such patterns are also commonly found in species breeding in high-latitudes, even in cases of long-distance migrants (Wenink *et al.*, 1996). In ecologically more stable areas of the world, as the tropics, it has been shown that the phylogeography of one taxon often is paralleled in others (Aleixo and de Fatima Rossetti, 2007). This suggests that speciation can be attributed to large-scale changes in the geology and/or climate.

Differentiation and speciation

Birds are arguably the most important model-organism in studies of speciation in sexually reproducing organisms. For example, the hypothesis of allopatric speciation was inspired by Ernst Mayr's observations of the bird diversity on islands in the Southwest Pacific (cf. Mayr and Diamond, 2001). Today essentially all speciation in birds is considered to be allopatric, i.e. reproductive isolation evolves after a population has become isolated from the parent population. Isolation may occur as consequence of either geographic isolation or differences in behaviour. Speciation without geographic barriers to gene flow (sympatric speciation) is very rare in vertebrates. There are a few reported cases in birds that involve brood parasitic species in which speciation is initiated by a host switch. The offspring imprints the song of the new host and becomes reproductively isolated from the parent population (Sorenson *et al.*, 2003). As brood parasitism is assumed to have evolved only a handful of times in birds (e.g., in cuckoos, honeyguides and cowbirds), this mode of speciation is also very uncommon. Another mechanism that may lead to sympatric speciation is allochrony – separation of populations by breeding time. Among birds, this has only been reported from a single species of oceanic storm-petrels (Friesen *et al.*, 2007).

Phylogenetic analyses of tropical birds have shown that the largest number of old species is found in the lowlands, while younger species are more common in montane areas (Roy, 1997). It has thus been hypothesized that speciation largely occurs in montane tropical areas from where the species later disperse to the lowlands (Fjeldså, 1994),

but other scenarios should be considered and tested (Aleixo and de Fátima Rossetti, 2007). In temperate regions speciation and intraspecific genetic variation in birds is commonly assumed to follow from contractions and expansions of distribution ranges during glacial times (Rand, 1948; Selander, 1971; Hewitt, 1996). This view has been challenged by observations that in several phylogenetic lineages, many species seem to have originated well before the Pleistocene (Klicka and Zink, 1997).

Many bird species exhibit an extraordinary sexual dimorphism, especially in plumage characters but also in behavior. In groups as the quetzals and peacocks the strong selection force has led to the development of some truly spectacular male plumages, which in many cases even risk to be hazardous to the bearer because of the problem to avoid predation (Darwin, 1871).

Acknowledgements

I want to thank the organizers Ronald Vonk and Vincent Nijman for their invitation to the symposium 'Biogeography - explaining and predicting species distribution in space and time' held at Amsterdam University on 25 October 2007. Hans Ellegren, Ulf Johansson and Jan Ohlson kindly commented on the manuscript.

References

- Aleixo A, de Fátima Rossetti D. 2007. Avian gene trees, landscape evolution, and geology: towards a modern synthesis of Amazonian historical biogeography? *Journal of Ornithology* 148 (Suppl 2): S443-S453.
- Axelsson E, Webster MT, Smith NGC, Burt DW, Ellegren H. 2005. Comparison of the chicken and turkey genomes reveals a higher rate of nucleotide divergence on microchromosomes than macrochromosomes. *Genome Research* 15: 120-125.
- Avice JC. 2000. *Phylogeography: The History and Formation of Species*. Cambridge, Mass.: Harvard University Press.
- Bock W J. 1970. Secondary articulation of the avian mandible. *Auk* 77: 19-55.
- Chiappe LM. 2002 Basal bird phylogeny: Problems and solutions. In: Chiappe LM, Witmer LM eds. *Mesozoic Birds. Above the Heads of the Dinosaurs*. Berkeley: University of California Press, 448-472.
- Chiappe LM, Walker CA. 2002. Skeletal morphology and systematics of the Cretaceous Euenantiornithes (Ornithothoraces: Enantiornithes). In: Chiappe LM, Witmer LM eds. *Mesozoic Birds. Above the Heads of the Dinosaurs*. Berkeley: University of California Press, 240-267.
- Chiappe LM, Witmer LM eds. 2002. *Mesozoic Birds. Above the Heads of the Dinosaurs*. Berkeley: University of California Press.
- Collar NJ, Crosby MJ, Stattersfield AJ. 1994. *Birds to Watch 2. The World List of Threatened Birds*. Cambridge: Birdlife International.
- Cooper A, Penny D. 1997. Mass survival of birds across the Cretaceous-Tertiary boundary: molecular evidence. *Science* 275: 1109-1113.
- Cooper A, Fortey R. 1998. Evolutionary explosions and the phylogenetic fuse. *Trends in Ecology & Evolution* 13: 151-156.
- Cracraft J. 1987. DNA hybridization and avian phylogenetics. *Evolutionary Biology* 21: 47-96.
- Cracraft J. 2001. Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proceedings of the Royal Society of London B*, 268: 459-469.
- Cracraft J, Barker FK, Braun M, Harshman J, Dyke GJ, Feinstein J, Stanley S, Cibois A, Schikler P, Beresford P, García-Moreno J, Sorenson MD, Yuri T, Mindell DP. 2004. Phylogenetic relationships among modern birds (Neornithes): toward an avian tree of life. In: Cracraft J, Donoghue MJ eds. *Assembling the Tree of Life*. Oxford: Oxford University Press, 468-489.
- Cracraft J, Clarke J. 2001. The basal clades of modern birds. In: Gauthier J, Gall LF eds. *New perspectives on the origin and early evolution of birds*. New Haven, CT: Yale University Press, 143-156.
- Darwin C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- Dawson A, McNaughton FJ, Goldsmith AR, Degen AA. 1994. Ratitelike neoteny induced by neonatal thyroidectomy of European starlings, *Sturnus vulgaris*. *Journal of Zoology* 232: 633-639.
- Dawson A. 1996. Neoteny and the thyroid in ratites. *Reviews of Reproduction* 1: 78-81.
- Dyke GJ. 2001. The evolutionary radiation of modern birds: systematics and patterns of diversification. *Geology Journal* 36: 305-315.
- Dzerzhinsky FYa. 1982. Adaptive features in the structure of the maxillary system in some Anseriformes and probable ways of evolution of the order. *Zoologicheskij Zhurnal* 61: 1031-1041 (in Russian with English summary).
- Dzerzhinsky FYa. 1995. Evidence for common ancestry of the Galliformes and Anseriformes. *Courier Forschungsinstitut Senckenberg* 181: 325-336.
- Ericson PGP, Anderson CL, Britton T, Elzanowski A, Johansson US, Källersjö M, Ohlson JI, Parsons TJ, Zuccon D, Mayr G. 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. *Biology Letters* 2: 543-547.
- Ericson PGP, Irestedt M, Johansson US. 2003. Evolution, biogeography, and patterns of diversification in passerine birds. *Journal of Avian Biology* 34: 3-15.
- Fain MG, Houde P. 2004. Parallel radiations in the primary clades of birds. *Evolution* 58: 2558-2573.
- Feduccia A. 1985. The morphological evidence for ratite monophyly. Fact or fiction? In: Ilyichev VD, Gavrilov VM eds. *Acta XVIII Congressus Internationalis Ornithologici, Vol. 1*. Moscow: Academy of Science, 184-190.
- Feduccia A. 2003. Big bang' for tertiary birds? *Trends in Ecology & Evolution* 18: 172-176.
- Fjeldså J. 1994. Geographical patterns of relict and young species of birds in Africa and South America and implica-

- tions for conservation priorities. *Biodiversity Conservation* 3: 107-226.
- Friesen VL, Smith AL, Gómez-Díaz E, Bolton M, Furness RW, González-Solís J, Monteiro LR. 2007. Sympatric speciation by allochrony in a seabird. *Proceedings of the National Academy of Sciences U.S.A.*, 104: 18589-18594.
- García-Moreno J, Mindell DP. 2000. Rooting a phylogeny with homologous genes on opposite sex chromosomes (gametologs): a case study using avian CHD. *Molecular Biology and Evolution* 17: 1826-1832.
- García-Moreno J, Sorenson MD, Mindell DP. 2003. Congruent avian phylogenies inferred from mitochondrial and nuclear DNA sequences. *Journal of Molecular Evolution*, 57: 27-37.
- Gibb GC, Kardailsky O, Kimball RT, Braun EL, Penny D. 2007. Mitochondrial genomes and avian phylogeny: Complex characters and resolvability without explosive radiations. *Molecular Biology and Evolution* 24: 269-280.
- Göhlich UB, Chiappe LM. 2006. A new carnivorous dinosaur from the Late Jurassic Solnhofen archipelago. *Nature* 440: 329-332.
- Gregory TR. 2002. A bird's-eye view of the C-value enigma: genome size, cell size, and metabolic rate in the class Aves. *Evolution* 56: 121-130.
- Gregory TR. 2005. Animal Genome Size Database. <http://www.genomesize.com>.
- Griffin DK, Robertson LBW, Tempest HG, Skinner BM. 2007. The evolution of the avian genome as revealed by comparative molecular cytogenetics. *Cytogenetic & Genome Research* 117: 64-77.
- Groth JG, Barrowclough GF. 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution* 12: 115-123.
- Harshman J. 2007. Classification and phylogeny of birds. In: Jamieson BGM ed. *Reproductive Biology and Phylogeny of Birds*. Enfield, NH: Science Publishers, 1-35.
- Hewitt GM. 1996. Some genetic consequences of ice ages and their role in divergence and speciation. *Biological Journal of the Linnean Society* 58: 247-276.
- Houde P. 1987. Critical evaluation of DNA hybridization studies in avian systematics. *Auk* 104: 17-32.
- Hughes AL. 1999. *Adaptive Evolution of Genes and Genomes*. Oxford: Oxford University Press.
- Hwang SH, Norell MA, Ji Q, Gao K. 2002. New Specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from Northeastern China. *American Museum Novitates*, no 3381.
- Johansson US, Parsons TJ, Irestedt M, Ericson PGP. 2001. Clades within the 'higher land birds', evaluated by nuclear DNA sequences. *Journal of Zoological Systematics and Evolutionary Research* 39: 37-51.
- Livezey BC, Zusi RL. 2007. Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy: II. – Analysis and discussion. *Zoological Journal of the Linnean Society* 149: 1-94.
- Mayr E, Diamond J. 2001. *The Birds of Northern Melanesia: Speciation, Ecology and Biogeography*. Oxford: Oxford University Press.
- Mayr G, Clarke J. 2003. The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. *Cladistics* 19: 527-553.
- Morgan-Richards M, Trewick SA, Bartosch-Härlid A, Kardailsky O, Phillips MJ, McLenachan PA, Penny D. 2008. Bird evolution: testing the Metaves clade with six new mitochondrial genomes. *BMC Evolutionary Biology* 8: 20.
- Olson SL. 1985. The fossil record of birds. In: Farner DS, King JR, Parkes KC eds. *Avian Biology, Vol. 8*. New York: Academic Press, 79-238.
- Organ CL, Shedlock AM, Meade A, Pagel M, Edwards SV. 2007. Origin of avian genome size and structure in non-avian dinosaurs. *Nature* 446: 180-184.
- Poe S, Chubb AL. 2004. Birds in a bush: five genes indicate explosive evolution of avian orders. *Evolution* 58: 404-415.
- Rand AL. 1948. Glaciation, an isolating factor in speciation. *Evolution* 2: 314-321.
- Roy MS. 1997. Recent diversification in African greenbuls (Pycnonotidae: *Andropadus*) supports a montane speciation model. *Proceedings of the Royal Society of London B*, 264: 1337-1344.
- Sarich VM, Schmid CW, Marks J. 1989. DNA hybridization as a guide to phylogenies: a critical analysis. *Cladistics* 5: 3-32.
- Selander RK. 1971. Systematics and speciation in birds. In: Farner DS, King JR eds. *Avian Biology, Vol. 1*. New York: Academic Press, 57-147.
- Sibley CG, Ahlquist JE. 1990. *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. New Haven/London: Yale University Press.
- Sibley CG, Monroe BL Jr. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven/London: Yale University Press.
- Simonetta AM. 1963. Cines e morfologia del cranio negli uccelli non-passeriformi: Studio su varie tendenze evolutive, parte I. *Archivio Zoologico Italiano*, 48: 53-135.
- Smith CA. 2007. Sex determination in birds: HINTs from the W sex chromosome? *Sexual Development* 1: 279-285.
- Sorenson MD, Oneal E, García-Moreno J, Mindell DP. 2003. More taxa, more characters: The hoatzin problem is still unresolved. *Molecular Biology and Evolution* 20: 1484-1498.
- Sorenson MD, Sefc KM, Payne RB. 2003. Speciation by host switch in brood parasitic indigobirds. *Nature* 424: 928-931.
- van Tuinen M, Sibley CG, Hedges SB. 2000. The early history of modern birds inferred from DNA sequences of nuclear and mitochondrial ribosomal genes. *Molecular Biology and Evolution* 17: 451-457.
- Waltari E, Edwards SV. 2002. Evolutionary dynamics of intron size, genome size, and physiological correlates in archosaurs. *American Naturalist* 160: 539-552.
- Wenink PW, Baker AJ, Rösner H-U, Tilanus MGJ. 1996. Global mitochondrial DNA phylogeography of holarctic breeding dunlins, *Calidris alpina*. *Evolution* 50: 318-330.
- Zebra Finch Genome Consortium. 2006. <http://www.songbirdgenome.org>.

Received: 7 March 2008

Accepted: 16 May 2008