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THE LAST WORD ON THE evolution OF birds

The Avian Phylogenomics Consortium was established four years ago to conduct the first genomic study across a vertebrate class. Its goal was to obtain complete gene sequences for representatives of all bird orders. When you consider that the human genome project cost US\$3-billion and lasted 14 years, this might seem an unrealistic goal. But sequencing technology has progressed in leaps and bounds since the human genome project was completed in 2003. Today a genome can be sequenced in a matter of months for around US\$100 000. The greatest challenge is managing the vast amount of data generated – the average bird genome

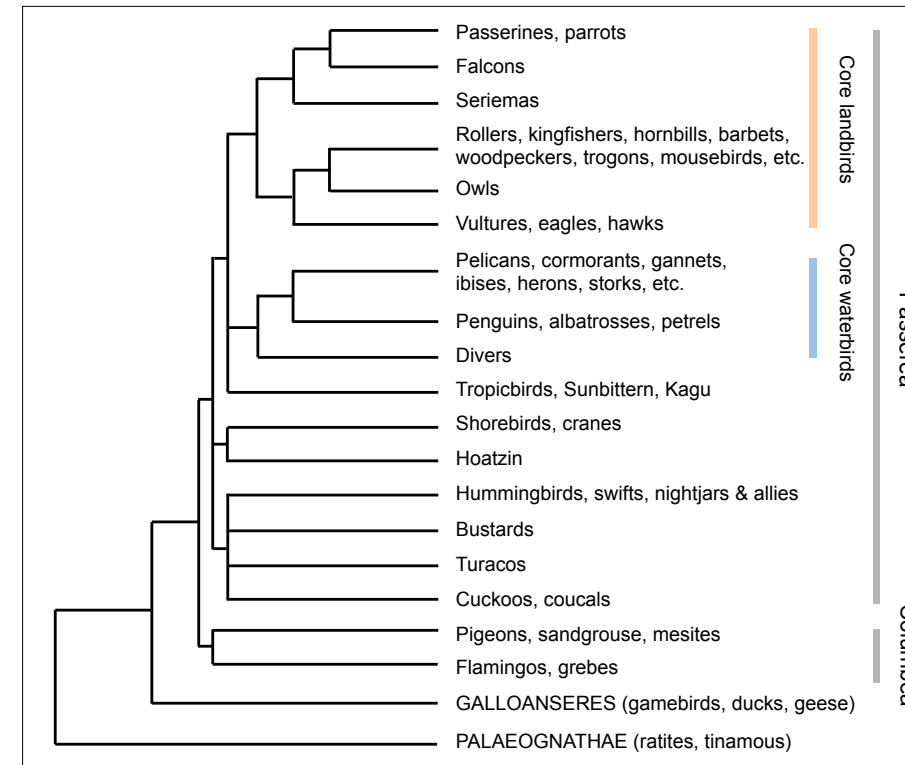
above Rüppell's Bustard. The bustards formed an unlikely alliance with the turacos, cuckoos and nightjars/swifts/hummingbirds.

comprises more than one billion base pairs!

Erich Jarvis and 103 colleagues recently published some of the findings of this vast endeavour in the leading journal *Science*. They had at their disposal the genomes of 48 birds from 36 of 40 extant bird orders (missing only storks, which are allied to the broader Pelecaniformes, and three ratite groups: rheas, kiwis and cassowaries-Emu). With such a vast amount of data to work with they had the luxury of using a variety of datasets to infer the evolutionary history of birds. What they consider to be the 'best' tree was based on a mere 41.8-million base pairs – less than five per cent of the total genome – selected because they were comparable gene sequences across all species sampled. Yet this is more than one thousand times more data than was used by Shannon Hackett and colleagues in 2008, in what

was until now the most comprehensive assessment of bird evolution.

At the largest scale there were no big surprises. Modern birds are still divided into three groups: the Palaeognathae (ratites and tinamous), Galloanseres (gamebirds and waterfowl) and Neoaves (all other birds). What was new, however, was the ability to infer the early origins of the Neoaves. This vast group, which comprises more than 10 000 species in 33 orders, underwent an explosive radiation around 60–70 million years ago, almost certainly associated with the sudden availability of new niches following the large meteor impact 66 million years ago that triggered the most recent mass extinction event (and saw the demise of all non-avian dinosaurs). Because the Neoaves radiated so quickly, it has been very hard to deduce the sequence in which they evolved.



The study found that the Neoaves are divided into two groups, dubbed the Columbea and Passerea. The former comprises two main lineages: the pigeons, sandgrouse and mesites (Columbimorphae), and the flamingos and grebes (Phoenicopterimorphae). The branching sequence among the Passerea was not resolved unequivocally, but core groups of landbirds and waterbirds were detected, as well as several miscellaneous groupings. Perhaps the more surprising groupings included the Sunbittern (and Kagu) being linked to the tropicbirds, and the enigmatic Hoatzin associated with the shorebirds and cranes. However, these relationships were lost when a smaller subset of the data was used. The bustards formed an unlikely alliance with the turacos, cuckoos and nightjars/swifts/hummingbirds.

Among the core landbirds, the parrots were again found to be sister to the passerines, together forming a group with the falcons and seriemas. The position of the mousebirds and trogons was not fully resolved, but both fall within the core landbird group. The results of the 'best' tree were broadly supported by analyses based on different subsets of the genome data, but incomplete lineage sorting (due to very

rapid radiations) resulted in plenty of conflicting gene and species trees.

Given that the entire genome was available for analysis, is this really the last word on the evolutionary history of birds? Almost certainly not at a fine scale: adding more species is likely to shuffle some of the branches around. However, the broad structure is likely to remain. Indeed, there are relatively few changes from the relationships established by Hackett's study on a much smaller amount of genetic data six years ago. I think it's safe to say that we now have a fairly good idea of how and when modern birds evolved. Adding more species is most likely to improve our understanding of where these events took place.

Jarvis's paper was just one of a suite of 23 published jointly as a 'flock of genomes', with eight papers in *Science* and 15 papers in other journals. One paper showed that the common ancestor of all modern birds lost its bony teeth about 116 million years ago. Another paper found that convergent changes in the activity of more than 50 genes are responsible for the brain structures involved in vocal learning in humans and birds, even though song learning has evolved three times in birds

Comparing the genomes of representatives of almost all bird orders provides better resolution of the relationships among the major lineages in the Neoaves (lower case groups).

(among oscine passerines, parrots and hummingbirds). However, there are also some key differences, with unique genes associated with song learning in passerines, and a peculiar 'song-within-a-song' system found in parrots, which might explain their ability to mimic human words.

Still another paper showed how the bird's sex-determining w-chromosome (which is found in females) has evolved to different degrees in different lineages, and in some birds retains many more functional genes than the y-chromosome in mammals. Another paper explored the genes that allow penguins to tolerate extreme Antarctic environments. And a more applied paper explored genetic diversity in endangered species. Not surprisingly, species such as the Crested Ibis that have experienced recent population bottlenecks had reduced diversity in their immune-system genes. However, genetic diversity was greater than expected, and there was evidence of rapid evolution in metabolic- and brain-function genes, giving some degree of hope for the long-term viability of such populations.

The studies confirmed that all modern birds have appreciably smaller, more streamlined genomes than mammals, thanks to shorter sections of non-coding DNA and about 10 times fewer contributions from viral genomes. The latter result suggests that birds either are less susceptible to viral invasions or are better able to purge viral genes than mammals. With the notable exception of woodpeckers, all lineages also have many fewer repeat genes, which might limit their rate of evolution relative to mammals. Quite why birds have smaller genomes remains open to debate, but it has been argued that it represents yet another adaptation to flight – with smaller genomes reducing the mass of each cell! What is certain is that the raw data generated by the Avian Phylogenomics Consortium – all publicly available – is set to revolutionise our understanding of avian evolution and genetics.

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