Untangling the *Illadopsis* family tree

Africa's lowland rainforests blanket a swathe of the continent from Sierra Leone eastwards to the Rift Valley. These forests are rather uniform, and ornithologists have long been puzzled by the unexpectedly high number of bird species occurring in this biome. One hypothesis that has been advanced to explain the diverse avifauna centres on the cyclical climate changes that occurred in Africa during the Pleistocene epoch, which lasted from about 1.8 million years ago (mya) until 10 000 years ago. During this era, ice ages that saw much of the northern hemisphere periodically covered by glaciers caused Africa's climate to enter drier, cooler phases. The dry phases alternated with periods of warm and humid conditions, prompting rainforests to undergo cycles of contraction and expansion.

According to this hypothesis, bird species that evolved in isolated forest fragments during drier glacial periods dispersed throughout the biome during wetter interglacial phases. The high present-day avian diversity is thought to reflect these successive waves of birds dispersing outwards from isolated rainforest refugia that existed during each ice age.

The genus *Illadopsis*, or African jungle babblers, is a group of seven nondescript, thrush-like birds that forage in the understorey of lowland rainforests. In terms of morphology and appearance, they are remarkably similar to each other and would thus seem to be a group of closely related species that diverged recently in evolutionary history. A recent study by Fitztitute research associate Rauri Bowie and colleagues, however, suggests that the reality is quite different. By analysing four regions of illadopsis DNA that have changed at different rates through evolutionary time, the team was able not only to tease apart the relationships between the species, but to establish when each split in the illadopsis family tree occurred.

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Novel genetic analyses indicate that what is currently known as the Brown Illadopsis of West and Central Africa may in fact be more than one species.

The analysis suggests that there are three clades (taxonomic groups, each of which contains a single common ancestor and its descendants) within the genus *Illadopsis*. The largest clade contains four extant species, namely Rufous-winged (*rufescens*), Puvel's (*puveli*), Blackcap (*cleaveri*) and Scaly-breasted (*albipectus*). Within this clade, the Rufous-winged/Puvel's lineage diverged from that of the Blackcap/Scaly-breasted some 3.5 mya. Rufous-winged and Puvel's then diverged about 2.3 mya, while Blackcap and Scaly-breasted diverged slightly later at 2.2 mya.

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The second *Illadopsis* clade contains Pale-breasted (*rufipennis*) and Mountain (*pyrrhoptera*). However, Pale-breasted Illadopsises from Liberia are genetically distinct from those from Cameroon and the Central African Republic, raising the possibility that there may in fact be more than two species in the clade.

The third clade contains what is presently considered a single species, the Brown Illadopsis (*fulvescens*). However, it turns out that there are considerable genetic differences between populations. Brown Illadopsises from Liberia diverged from other *fulvescens* populations about 3.1 mya, while the genetic differences between populations from three widely separated sites, namely Tanzania's Mahale Mountains, Angola's Kumbira Forest and the Central African Republic, suggest that they split about 2.2 mya.

It is apparent that there is considerably more genetic diversity among the illadopsises than previously thought, and that some of the currently recognised species underwent genetic divergence millions of years ago, suggesting that there are more than seven species of illadopsis in Africa. However, the most intriguing finding of this study is that many of the major splits within the genus occurred more than two million years ago, well before the Pleistocene epoch. There is also evidence for major pre-Pleistocene splits in other groups, including *Andropadus* greenbuls and *Sheppardia* forest akalats. This new evidence for ancient genetic divergence events flies in the face of the hypothesis that Pleistocene climate cycles were the major force driving the evolution of the remarkable bird diversity of Africa's lowland rainforests. □

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