

THE DIVERSITY AND RADIATION OF HORNBILLS: HOW, WHEN, WHERE AND WHY MIGHT THEY HAVE OCCURED?

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Abstract

Thirty years ago we produced an invited paper entitled “A review of the hornbills: biology and radiation”. Now, only slightly less naïve, we try again to summarise our thoughts in a semi-popular format. In 1960, Sanft recognised 45 species of hornbills in 14 genera. Now, we include at least 60 species in a similar number but slightly different arrangement of genera. About half the species and one third of the genera still occur in sub-Saharan Africa, the rest across Asia from Pakistan east to New Guinea.

Considerable new evidence supports our assumption that hoopoes/woodhoopoes are the sister clade to hornbills, both clades well defined by apomorphies. Fossil hoopoes from the Palaeartic ~49 Ma are the earliest evidence bearing on the site and date for an origin of hornbills. Cladistic and genetic analyses so far indicate carnivorous African ground-hornbills (*Bucorvus*, 2 spp.) and small-hornbills (*Tockus*, ~16-20 spp.) as the earliest independent lineages within the family. Two extinct species of ground-hornbills, also from the Palaeartic, provide the only other fossil evidence for hornbills, but only <15 Ma which suggests that their specializations of terrestrial habits, unsealed nests and large size may be recent rather than ancestral.

All Asian hornbills (31-34 spp.) are primarily frugivorous and all but one (*Ocyrceros birostris*) occupy forest habitats. An inability to confirm relationships between hornbill genera due to their rapid radiation shown by genetic studies, especially for Asian genera, suggests some factor(s) that stimulated a rapid initial radiation of frugivorous genera. Tectonic and palaeo-botanical developments across Asia seem involved in these radiations, even within genera as species extended across Wallace’s Line into the Philippines, Indonesia and even Australasia.

Anomalous genera remain to be placed within these radiations, notably 1) the carnivorous African long-tailed *Tropicranus* and two dwarf-hornbill *Tockus* species, 2) the frugivorous wattled- and casqued-hornbills (*Ceratogymna* and *Bycanistes* (2 & 5-7 spp)), with African distributions but Asian links, and 3) *Ocyrceros* (3 spp.), small *Tockus*-like Indian species that are frugivorous and geographically pivotal. Terrestrial or arboreal ancestors, origins in Europe, Africa or Asia, emergence of frugivory only in Asia, and increases in body size remain the principal features still in need of explanation. We look forward to new information that might resolve the evolutionary history of hornbills, document their present diversity and enlighten us on the biology of the least studied species.