DISPATCH

Bird Evolution: Convergence Fits the Bill

New fossils help pinpoint when some birds started relying on a seed-based diet and reveal that disparate bill shapes evolved repeatedly throughout bird evolutionary history.

Daniel J. Field[1*]

Here in the UK, birdwatching is big business. Studies suggest that up to one third of Britons feed birds on their properties — good news for the birdseed industry. Many backyard birds, including finches, sparrows and tits, find birdseed irresistible. And why not? Seeds, after all, are bursting with energy. The trick, however, is being able crack through a seed's hard exterior. A new study in this issue of *Current Biology* by Daniel Ksepka and colleagues [1] sheds light on when this skill arose, revealing the earliest evidence of specialized seed-eating birds.

Without the benefit of hands or teeth, accessing the interior of a well-protected seed presents a 'tough nut to crack' for small birds. As a result, many living seed-eating birds have acquired strong, deep bills that are ideally suited for this task (Figure 1). Most avian seed-eating specialists belong to a large group called the passerines (otherwise known as 'perching birds'). Passerines comprise over 6,000 living species — more than half of living bird diversity.

Long-term ecological studies [2, 3] of Darwin's famous finches demonstrate that selection for enhanced seed-cracking ability can rapidly drive the evolution of beak size and shape, yielding general insights into the adaptability of the passerine beak. This adaptability has given rise to an impressive variety of additional specialized passerine bill shapes, including elongated, curved bills for nectar-feeding seen in sunbirds, large mouths optimized for enhanced gape size in many aerial insectivores and even sharply hooked bills for nectar robbing in the aptly-named flowerpiercers (Figure 1).

What makes the new ~52-million-year-old fossils described by Ksepka and colleagues [1] remarkable is their discovery that this seed-cracking morphology, and indeed a wide variety of additional bill morphotypes, first arose among stem-passerines, a mysterious suite of extinct early Cenozoic birds that branched off the tree of life before modern-type passerines had arisen. This means that these features arose independently from their subsequent origins among extant passerines.

Early passerine phylogeny and evolution

Recent phylogenetic work drawing on massive genomic datasets has greatly clarified the relationships among the major groups of living passerines [4-6]. Until now, however, the early fossil record of passerines has been sparse, clouding how and when the extraordinary diversity of living passerines, and their penchant for exploring the far corners of beak morphospace, arose [7]. Careful anatomical work has allowed Ksepka and colleagues [1] to reconstruct the most compelling picture to date of stem-passerine phylogeny, revealing that early Cenozoic avian fossils that were previously allied with several distantly related bird groups (e.g. shorebirds, parrots, and cuckoos) are, in fact, stem-passerines. Some of these extinct taxa exhibit moderately elongated bills, similar to those of living generalist thrushes (Turdidae). Others exhibit slender, recurved bills, resembling living nectar-feeding sunbirds (Nectariniidae). The new fossils, described by Ksepka and colleagues [1] for the first time, display short, conical bills, similar to those of living seed-eating finches (Fringillidae). The authors name their new finch-billed fossils *Eofringillirostrum* ("Dawn Finch Beak") — apropos both because the fossils reveal the earliest evidence of this morphology to date, but also because the authors' careful systematic work heralds a new dawn in our understanding of early passerine evolution.

The last several years have witnessed major advances in our understanding of the evolution of the avian skull. Unanticipated fossil discoveries have shed light on the origin of the modern bird skull itself [8]; insights from development have revealed the gene expression patterns responsible for yielding a variety of bill shapes [9]; and, massive efforts to quantify the variation of avian cranial form have evaluated the interplay of ecological and developmental factors on the acquisition of beak shape [10-13]. The work of Ksepka and colleagues [1] reminds us of the power of the fossil record to shed light on the unforeseeable complexity of evolutionary history [14]: although modern techniques allow us to study phenotypic evolution with vast comparative anatomical datasets, without fossils we would never know that the spectacular disparity of living passerines was independently presaged by a Palaeogene radiation of stem-passerines.

Disappearance of stem-passerines

Our gradually accumulating appreciation of stem-passerine diversity (and their surprising ecological disparity) raises important questions about the extinction of these erstwhile successful birds. Why did stem-passerines disappear, when the extant passerine radiation has produced over 6,000 living representatives? Little in the skeleton reveals obvious evidence for competitive superiority of crown-passerines over stem-passerines. As such, whatever differences may have existed among stem and crown-passerines may have had limited potential for fossilization. Ksepka and colleagues [1] offer a potential explanation for this uneven survivorship, namely that stem-passerines may have lacked their crown group relatives' amazing penchant for sophisticated nest construction.

The variety of crown-passerine nests is spectacular, and their striking ability to construct a home in virtually any environment is presumably related in some way to their present-day ecological dominance [15, 16]. However, even if stem-passerines were confined to nesting in cavities, as Ksepka and colleagues [1] hypothesize, this idea does little to explain why stem-passerines may have gone extinct; after all, numerous highly diverse extant groups such as parrots, kingfishers and indeed many extant passerines nest in cavities. It may simply be that a more complete understanding of the factors responsible for stem-passerine extinction awaits the discovery of additional fossils, and a clearer picture of the crown-passerine evolutionary timeline from molecular divergence time analyses. At least the latter of these factors will hopefully be addressed in the near-term.

Given the sensational diversity of living passerines, their numerical dominance in virtually every region of the modern world [17] and their fairly sparse fossil record, untangling the early branches of the perching bird tree of life is undoubtedly one of the most pressing ornithological research subjects at the moment. The thought-provoking study by Ksepka and colleagues [1] substantially advances our understanding of early passerine evolution by revealing the unforeseen ecological disparity of stem group passerines. While important questions about stem-passerine extinction remain unanswered, Ksepka and colleagues [1] reveal, beyond any doubt, that these early birds had the hardware for getting the worm, the seeds and almost anything in-between.

[1]Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB1 3AS, UK
***E-mail:** djf70@cam.ac.uk

References

1. Ksepka, D.T., Grande, L., and Mayr, G. (2019). Oldest finch-beaked birds reveal striking parallel ecological radiations in the earliest evolution of passerines. Curr. Biol.
2. Boag, P.T., and Grant, P.R. (1981). Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. Science *214*, 82-85.
3. Grant, B.R., and Grant, P.R. (1993). Evolution of Darwin's finches caused by a rare climatic event. Proc. Roy. Soc. B *251*, 111-117.
4. Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M., and Lemmon, A.R. (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature *526*, 569-573.
5. Moyle, R.G., Oliveros, C.H., Andersen, M.J., Hosner, P.A., Benz, B.W., Manthey, J.D., Travers, S.L., Brown, R.M., and Faircloth, B.C. (2016). Tectonic collision and uplift of Wallacea triggered the global songbird radiation. Nat. Comm. *7*, 12709.
6. Ericson, P., Klopfstein, S., Irestedt, M., Nguyen, J., and Nylander, J. (2014). Dating the diversification of the major lineages of Passeriformes (Aves). BMC Evol. Biol. *14*, 8.
7. Mayr, G. (2013). The age of the crown group of passerine birds and its evolutionary significance - molecular calibrations versus the fossil record. Syst. Biodiv. *11*, 7 - 13.
8. Field, D.J., Hanson, M., Burnham, D., Wilson, L.E., Super, K., Ehret, D., Ebersole, J.A., and Bhullar, B.-A.S. (2018). Complete Ichthyornis skull illuminates mosaic assembly of the avian head. Nature *557*, 96-100.
9. Abzhanov, A., Kuo, W.P., Hartmann, C., Grant, B.R., Grant, P.R., and Tabin, C.J. (2006). The calmodulin pathway and evolution of elongated beak morphology in Darwin's finches. Nature *442*, 563.
10. Cooney, C.R., Bright, J.A., Capp, E.J.R., Chira, A.M., Hughes, E.C., Moody, C.J.A., Nouri, L.O., Varley, Z.K., and Thomas, G.H. (2017). Mega-evolutionary dynamics of the adaptive radiation of birds. Nature *542*, 344-347.
11. Bright, J.A., Marugán-Lobón, J., Cobb, S.N., and Rayfield, E.J. (2016). The shapes of bird beaks are highly controlled by nondietary factors. PNAS *113*, 5352-5357.
12. Felice, R.N., and Goswami, A. (2018). Developmental origins of mosaic evolution in the avian cranium. PNAS *115*, 555-560.
13. Navalón, G., Bright, J.A., Marugán-Lobón, J., and Rayfield, E.J. (2018). The evolutionary relationship between beak shape, mechanical advantage, and feeding ecology in modern birds. Evolution. doi:10.1111/evo.13655
14. Field, D.J. (2018). Endless skulls most beautiful. PNAS *115*, 448-450.
15. Irwin, M. (1962). The adaptive significance of nest construction in the evolution and radiation of the Passeres. In Proceedings of the First Federal Science Congress (Harare, Rhodesia). pp. 217-219.
16. Collias, N.E. (1997). On the origin and evolution of nest building by passerine birds. The Condor *99*, 253-270.
17. Olson, S.L. (2001). Why so many kinds of passerine birds? BioScience *51*, 268-269.
18. Mayr, G., and Wilde, V. (2014). Eocene fossil is earliest evidence of flower-visiting by birds. Biol. Lett. *10*.

Figure 1. Passerine bill disparity.

Top left: the seed-eating habits of living finches, such as this house finch, may echo similar habits of the Eocene fossil *Eofringillirostrum* [1]. Top tight: the nectar-feeding specializations of sunbirds, such as the streaked spiderhunter, may recapitulate those of the Eocene *Pumiliornis* [18]. Additional passerine bill morphologies include broad gapes in aerial insectivores (e.g. Western wood-pewee, bottom left) and hooked bills for nectar robbing (e.g. cinnamon-bellied flowerpiercer, bottom right). Photos: Daniel J. Field.