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Endless Skulls Most Beautiful

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The amazing disparity of living birds is self-apparent, yet immensely challenging to fully quantify. After all, birds are represented by nearly 11,000 living species, comprising a mind-boggling spectrum of shapes, sizes, and colors (1). This incredible variability manifests in an incalculable number of ways (from habitat type to diet to life history), but adequately characterizing any of these axes of variation presents distinct challenges with respect to analytical complexity and the requisite scale of data collection.

In this issue of PNAS, Felice and Goswami (2) exemplify the vanguard of comparative vertebrate morphology by taking up the challenge of characterizing and analyzing avian phenotypic disparity on a scale that was, until quite recently, unimaginable. The authors focus on the bird skull—a structure whose extreme evolutionary potential has rendered it a frequent topic of study among those interested in the tempo and mode of avian adaptive radiation (3-6).

Whereas other recent studies have focused on estimating rates of evolutionary change in the shape of that most ecologically adaptable avian feature, the beak (e.g. (4)), Felice and Goswami treat the avian skull as a cohesive whole, devising a methodology flexible enough to gather data from nearly all living bird families, yet detailed enough to (almost) completely characterize the external morphology of the skull. They accomplished this impressive feat using laser surface scanning and high-resolution computed tomography, similar to the techniques employed by Cooney *et al.* in their work on the avian bill (4), and Bright *et al.* on raptor skulls (5). This approach yielded a vast amount of anatomical data that the authors sought to marshal for quantifying cranial shape, and additional downstream parameters like rates of shape change. This demanded an approach to quantify cranial geometry in a way that would facilitate meaningful comparisons across species. To accomplish this goal, Felice and Goswami began by identifying homologous ‘key landmarks’ on each skull, as well as a hemispherical template with additional densely packed landmarks. Using an innovative shape-morphing approach (7), they then ‘morphed’ the template into the shape of each skull, using the key landmarks as anchor points. The degree to which the position of the key landmarks and additional landmarks were thereby digitally ‘stretched’ from the hemispherical starting shape allowed the authors to quantify the universe of avian cranial shapes in unprecedented detail.

From there, the authors employed a likelihood-based approach to identify regions of the avian skull that appear to evolve as reasonably autonomous entities, or modules (8). The authors identified 7 such modules, which together compose the entire skull. These include the well-studied rostrum, as well as the top of the skull, back of the skull, and palate. The recognition of substantial modularity in the avian skull challenges conflicting results from previous studies that employed more idiosyncratic taxon

sampling schemes and approaches to data collection (9, 10). This modularity is the basis for the authors' assessment of the avian skull as a classic example of 'mosaic evolution'—whereby different modules exhibit differing rates and modes of evolutionary change.

The authors were able to tackle another major analytical challenge: Discerning the tempo and mode by which rates of cranial shape change evolved throughout the phylogenetic history of living birds. They employed a recent time-scaled evolutionary tree for birds (11) to determine how quickly shape evolved among the seven cranial modules along the branches of the tree, yielding some interesting insights. For example, rates of evolutionary change in the avian rostrum were especially high along the lineage leading to (long-billed) hummingbirds following the divergence from their extant sister taxon, (short-billed) swifts. Additionally, elevated rates of change were inferred for virtually every cranial module in the immediate aftermath of the Cretaceous-Palaeogene (K-Pg) mass extinction event, 66-million-years-ago—an event that profoundly influenced avian evolutionary history (12-15). The K-Pg transition has been posited to have been a major driver of the early diversification of modern birds (11, 13, 15-17). Thus, the pulse of shape change inferred in the extinction's immediate aftermath—analytically dependent on the extremely short evolutionary branch lengths estimated by Prum *et al.* in that region of the phylogeny (11)—is consistent with a burst of phenotypic innovation and niche-filling following one of Earth history's most severe mass extinction events.

The authors convincingly illustrate that the different cranial modules evolve at different rates from one another, and at rates that are heterogeneous across avian phylogeny. But what underlies this regional variation in evolvability? Interestingly, the particular embryonic tissues that ultimately develop into the various cranial modules may shed light on this question. Felice and Goswami suggest that the cranial modules exhibiting both the highest estimated evolutionary rates, and the highest overall levels of disparity, tend to derive either from one particular embryonic source (the anterior mandibular-stream cranial neural crest), or from a mix of multiple embryonic cell populations. Those modules representing derivatives of other embryonic primordia exhibit lower estimates of evolutionary rate and overall disparity. The question of whether there are general rules governing the apparent link between embryonic origin and general evolvability awaits future insights from evolutionary-developmental perspectives.

Felice and Goswami have generated an awe-inspiring dataset, pushing frontiers in the study of vertebrate phenotypic evolution. But does their study provide the final word on the evolution of modern avian cranial disparity? While the taxonomic sample investigated is unquestionably extensive, it is worth noting that the 352 extant bird species comprising the dataset scarcely make up 1/30th of extant avian diversity, which leads to some unavoidable interpretive limitations. For example, lineages with 'unique' bill phenotypes within the context of the dataset, such as the Painted Snipe *Rostratula*, are estimated to exhibit high rates of phenotypic evolution. However, many taxa with similar bill phenotypes to *Rostratula*, such as true snipes (*Gallinago*, representing a separate avian family and a convergent acquisition of a *Rostratula*-like bill), were not included in the dataset. Thus, the apparent morphological uniqueness of *Rostratula*, and its associated high rate estimate, may be at least partly artifactual. Addressing this kind of potential over- and underestimation of evolutionary rates using the present methodology

will demand even more extensive taxon sampling than the already impressive scheme implemented here, so it is best to view the rate estimates presented in the study as basic approximations.

A greater limitation of the present study, though perhaps more challenging to overcome, is its lack of fossil data. Although it is true that incorporating fossils (which are often incomplete, broken, and otherwise distorted) into a study of this scope would present a major methodological challenge, fossils provide a uniquely valuable perspective on phenotypic evolution (18-22). As relicts of evolutionary history, fossils yield the only direct evidence that can ever be obtained of phenotypes from early representatives of living groups. Basing large-scale macroevolutionary analyses solely on data from extant organisms eliminates the potential for fossils to inform estimates of early phenotypic disparity and rates of change. This is problematic, as the exclusion of several extinct clades of crown birds such as the freakish pseudotoothed birds (Pelagornithidae (23, 24)) or monstrous terror birds (Phorusrhacidae (25)) guarantees that the authors' estimates of avian cranial morphospace are, by definition, substantially undersampled.

In the absence of fossil data bearing on the morphology of the most recent common ancestor of living birds, the authors implemented a clever approach: phylogenetic ancestral state reconstruction using their geometric dataset. Their reconstruction provides a striking and testable hypothesis (provided the future discovery of informative fossils) of what the skull of the most recent common ancestor of living birds looked like more than 70-million-years-ago. However, one does wonder whether the close geometric resemblance of the reconstruction to a living representative of the songbirds (a hyperdiverse crown clade that itself likely originated less than 50 million years ago (11)), might ultimately prove to be well off the mark. Future fossil discoveries may be able to answer this question more definitively.

Addressing all of these caveats in the context of a single study would have been prohibitive—the monumental dataset compiled by the authors, and the cutting-edge methods they employ, make this study nothing less than a major triumph in evolutionary vertebrate zoology. However, as data collection and analytical methodologies continue to improve, these critiques will ultimately need to be addressed in order to move the field, iteratively, towards a more complete and accurate picture of the tempo and mode by which avian cranial disparity, in all of its awesome variety, has evolved.

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Figure Caption

Fig. 1. Mosaic evolution produces an evolutionary mosaic: Avian diversity encompasses a spectacular variety of cranial forms. In PNAS, Felice and Goswami (2) suggest that the extreme evolvability of the avian head is a product of ‘mosaic evolution’, whereby different regions of the skull have evolved at different rates, and by different modes. Photos © Daniel J. Field.

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