Citation for published version:
Field, D 2017, 'Big-time insights from a tiny bird fossil', *Proceedings of the National Academy of Sciences of the United States of America (PNAS)*, vol. 114, no. 30, pp. 7750-7752. https://doi.org/10.1073/pnas.1710941114

DOI:
10.1073/pnas.1710941114

Publication date:
2017

Document Version
Peer reviewed version

Big-time insights from a tiny bird fossil

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Birds are among the most diverse and widely distributed groups of vertebrate animals. There are well over 10,000 recognized species alive today, occupying virtually every subaerial ecosystem (1). The amazing breadth of extant bird diversity is manifested in dizzying varieties of forms, colors, and lifestyles—ranging from iridescent, hovering, nectar-feeding hummingbirds, to nocturnal, flightless, worm-eating kiwis. But how, when, and why has this spectacular diversity arisen? The only direct evidence informing such questions can be obtained from the fossil record of the modern bird radiation, but the early fossil record of modern birds is exceedingly sparse. In this issue of PNAS, Ksepka et al. (2) help improve our understanding of this pivotal interval of bird evolutionary history by reporting the discovery of a new fossil bird filling an important temporal gap.

The fossil, *Tsidiiyazhi abini* (derived from the Navajo Diné Bizaad language for “little morning bird”) is indeed little—the specimen was collected within a 25cmx25cm grid from fossil beds in the San Juan basin of New Mexico. In fact, *Tsidiiyazhi*’s broad evolutionary implications are far from obvious from a casual glance at its broken and incomplete skeleton. However, thanks to careful and detailed anatomical work, the authors demonstrate that this tiny fossil bird punches well above its weight in helping to elucidate the nature and timing of the modern bird radiation.

Attempts to correlate the geological timescale with important events early in modern bird evolutionary history are often controversial (3-5). Still, recent studies integrating the fossil record and molecular clock techniques suggest an extremely rapid radiation of the major avian subclade Neoaves in the aftermath of the Cretaceous-Paleogene (K-Pg) extinction that wiped out the non-avian dinosaurs, 66 million years ago (Ma) (6, 7).

Today, Neoaves comprise over 90% of living bird diversity, but bird fossils from the first few million years after the extinction are exceedingly rare. In fact, the earliest-known definitive representative of Neoaves (the giant extinct penguin, *Waimanu manneringi*, from New Zealand) is ~60.5Ma (8). What happened in neoavian evolution between the K-Pg extinction event and the earliest record of *Waimanu*? At ~62.5Ma, *Tsidiiyazhi* exceeds *Waimanu* in age, and appears to be an early stem group representative of a living group of birds called mousebirds (sometimes also known as colies).

Tsidiiyazhi’s age implies not only that the lineage leading to mousebirds had diverged from its closest living relatives by 62.5Ma, but also that a host of other deep divergences within the neoavian tree of life had taken place by this early time as well. If the neoavian radiation was stimulated by the mass extinction of non-avian dinosaurs as has been suggested (6, 7, 9-11), its pace must have been amazingly rapid.

But the evolutionary insights yielded by *Tsidiiyazhi* do not end there—this discovery also enhances our understanding of the biogeographic history of mousebirds, and is part of a broader evolutionary picture. Living mousebirds comprise a small group of only six species, endemic to sub-Saharan Africa (12). Mousebirds are classified in their own taxonomic order, Coliiformes, owing to the fact that they share no particularly close affinities with other groups of living birds. While their phylogenetic position within the broader bird tree of life was debated for decades, we now believe that they represent an early offshoot of the lineage ultimately giving rise to groups like kingfishers, woodpeckers, and hornbills (6, 7). Considering the geographic distribution of living mousebirds, it is easy to assume that the group simply arose in Africa and never left. However, the discovery of *Tsidiiyazhi* in the southwestern USA illustrates that the past distribution of total group mousebirds was likely more widespread than that of the group's living representatives. Indeed, an impressive diversity of early stem group mousebirds are known from the Paleogene of North America and Europe (13). Mousebirds are in good company—many living bird groups with restricted modern-day distributions, such as the seriemas of today's South American planes, hummingbirds from the New World, and Amazonian hoatzins have early fossil representatives known from very different regions of the world (14). Such observations plainly illustrate the value of fossils to historical biogeography: only the direct evidence of the fossil record can definitively show us where groups of birds were formerly distributed, since avian biogeography is vastly more complex than can be understood on the basis of modern geographic distributions alone.

Future efforts to refine our understanding of how modern birds obtained their characteristic geographic distributions will therefore need to accommodate the presence of stem mousebirds in the early Paleocene of North America (15). This kind of integrative biogeographic work may have implications for our ability to predict the future; in determining the extent to which climatic changes throughout Cenozoic Earth history were responsible for driving such dramatic biogeographic changes, we may gain insight into how bird biogeography may evolve in response to our planet's current climatic trajectory.

Of course, the new fossil discovery also provides us with important insights into the evolution of modern mousebird biology. Living mousebirds are distinctive (Fig. 1a): they are smallish, arboreal birds with short conical bills, very long tails, feathered crests on their heads, and specialized toes that can be directed backwards to assist with perching (16). Ksepka et al. confirm the presence of this flexible foot condition in *Tsidiiyazhi*, illustrating that this specialization evolved early in mousebird evolutionary history. Surprisingly, however, the authors illustrate that such 'semi-zygodactyly', although present in several living neoavian families including owls and the Madagascan endemic courol, likely evolved independently in these different groups. This inference is only supported in analyses that incorporate fossil information, providing another example of the potential for fossils to reveal unforeseen complexity in the evolutionary history of birds.

Despite the largely uniform structure of living mousebirds, the fossil record reveals a surprising menagerie of highly divergent stem group forms, suggesting a considerable amount of ecological experimentation throughout their evolutionary history.

For example, *Chascacocolius cacicirostris*, from the early Eocene of Germany, exhibits bizarrely enlarged posteriorly-directed extensions of its lower jaws—thought to assist in prying into tough fruits (17) or probing in the ground for invertebrates (18). In contrast, the Oligocene *Oligocolius*, also known from German sediments, exhibited a short, deep, superficially parrot-like beak, and may have fed on tougher food items as evinced by a jumble of large seeds found in the presumed area of its crop (19).

Why should a bird as tiny as *Tsidiiyazhi* make such a big paleontological impact? How can the early Cenozoic fossil record of modern birds be sufficiently patchy that a single bird fossil can tell us so much? It is true that *Tsidiiyazhi* represents only a single data point, and future refinements of the avian evolutionary timescale, models of biogeographic change, and anatomical evolution must await additional fossil discoveries.

But the question of *why* the early Cenozoic avian fossil record is so poor is one that is in need of attention. Detailed paleontological surveys of fossil avifaunas from the latest Cretaceous and the earliest Paleocene suggest that Mesozoic bird-like forms, including close relatives of living birds like enantiornithines ('Mesozoic opposite birds') and hesperornithines (toothed marine forms), flourished up to the very latest stages of the Mesozoic before falling victim to the asteroid-induced K-Pg mass extinction (10). The extinction event likely would have decimated population sizes among the handful of surviving bird lineages, and limited resources in the extinction's aftermath may even have driven transient selection for reduced body size (3). The dual influence of reduced population size and preservational factors that conspire against the fossilization and discovery of small birds may together help to explain the conspicuous rarity of fossils documenting the earliest stages of the neoavian radiation. The value of tiny *Tsidiiyazhi* is underscored considering this general lack of evolutionary information from such an important stage in the history of bird life.

The work of Ksepka et al. affirms the immense value of new fossil discoveries that are at once well constrained with respect to both their geological age and their phylogenetic position. One hopes that the discovery of this "little morning bird" will usher in the dawn of a new phase of fossil bird discoveries from the early Paleocene that will help clarify the earliest stages of bird life in the Cenozoic. Our understanding of the origin of modern birds—as well as our understanding of Earth's recovery from the devastation of the end-Cretaceous mass extinction—will depend on it.

Acknowledgements

The author is supported by a 50th Anniversary Prize Fellowship at the University of Bath, and thanks L. Field, T. Field, J. Hanna, A. Hsiang, and E. Saupe for editorial assistance.

Figure Caption

Fig. 1: A) The extant Speckled Mousebird (*Colius striatus*), which is widespread across sub-Saharan Africa. Photo © Daniel J. Field. B) Simplified representation of the time-scaled interrelationships among living bird groups, following a recent phylogenomic study (6). The root of the tree is estimated at roughly 73 million-years-ago (Ma), and the dotted circle represents the approximate position of the Cretaceous-Paleogene (K-Pg) mass extinction event, ~66Ma. The approximate age (~62.5Ma) and phylogenetic position of *Tsidiiyazhi abini*, the new fossil described by Ksepka et al., is denoted by the black arrow, and the phylogenetic position of living mousebirds (Aves: Coliidae) is

represented by the letter ‘M’.

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