

## **Research Statement**

**Summary:** Extensive molecular and morphological studies are beginning to reveal the large-scale architecture of avian evolutionary relationships<sup>1-7</sup> but exhibit conflicting relationships at the base of Neoaves, a group comprising approximately ninety percent of all extant bird lineages.<sup>3</sup> Results indicate that the stem-lineages of modern bird lineages, especially Neoaves, diversified within a 5-8 million year window of time around the K-Pg boundary; however, these findings are almost entirely shaped by molecular data and there remains a vacuum of understanding regarding early phenotypic evolution during this explosive radiation. Furthermore, fossils that are key to uncovering these transitions as well as better resolving divergence timing, biogeographic history and evolutionary relationships have either not been recovered or confidently placed. Better resolving the relationships of such fossils is especially critical to reconcile divergence timing, as recently recovered relationships of early Paleogene fossils (e.g. Musser et al. 2019<sup>8</sup>) suggest that recent nuclear gene and genomic-level molecular studies may be underestimating the divergence timing of basal neoavian groups.

Although a small number of studies have looked at the large-scale relationships of birds using morphology,<sup>4,9-10</sup> each has suffered from either limited taxon sampling or preconceptions about avian taxonomic relationships. Morphological study of extinct and extant avian taxa is thus critical for resolving conflicting basal clade relationships and providing a framework for reconstructing biogeographic history, divergence timing of key groups, and early neoavian phenotypic transitions. My research incorporates morphological, molecular, and combined data along with integrative methods to provide better solutions to these issues within Neoaves and other paravian clades.

### **Research questions:**

- 1) New frontiers in dinosaur phylogenetics
  - a) What is the contribution of morphological characters to resolving avian evolutionary relationships?
  - b) How can we best combine different morphological data types with large-scale molecular phylogenetic data?
  - c) How can combined data inform questions regarding the genetic underpinnings of morphological traits of interest in both avian and non-avian dinosaurs? (e.g. better understanding convergent evolution; locating phenotypic proxies for molecular information such as correlation between bone-cell size and genome size in avian and non-avian dinosaurs<sup>11</sup>)
  - d) How can evolutionary models for morphological data be improved and applied to integrative datasets?
  - e) How can we reconcile conflicting phylogenetic relationships and differing results from downstream analyses? (e.g. ancestral state reconstructions, divergence timing, biogeographic history)
  - f) What can studying avian dinosaur evolution across the K-Pg boundary tell us about better resolving relationships in other groups that evolved rapidly, especially in those that evolved across mass extinction events?

- g) How can phylogenetic datasets including extinct taxa inform conservation strategies (e.g. through elucidating diversity dynamics, past climatic interactions, and combined data results)?
- 2) Evolution and biogeography of Paraves and non-avian theropods
  - a) What are the major phenotypic patterns that characterize early avian and neoavian diversification, and how did they arise?
  - b) When and how did the phenotypic diversity of Neoaves arise?
  - c) How and when did key avian features arise, and what can recovery of specimens from new international field initiatives in understudied areas reveal about paravian and non-avian theropod biogeography?
  - d) When did each paravian group diverge?
  - e) How did paravian taxa disperse across the globe?
- 3) Comparative anatomy
  - a) How can we improve visualization and description of anatomical structures in dinosaurs, especially in fossil Aves?
  - b) What can cutting edge visualizations (e.g. micro x-ray computed tomography or micro-CT, scanning electron microscopy or SEM) tell us about skeletal and soft tissue function, development and evolution?
  - c) What additional proxies in avian and non-avian dinosaurs can be located to better elucidate the behavior, paleobiology, ecology, biogeography and evolution of these taxa and how can we best locate these proxies?
  - d) What preparation techniques are best for locating additional anatomical structures such as syringes, feathers, and other soft tissue?

**Ongoing research and future directions:** To address these research questions I am in the process of building a new, more comprehensive morphological dataset for Aves that will include more exemplars of extinct and extant basal neoavian taxa than any previous data matrix (see results from preliminary data in Figure 1; Musser et al in prep.). This dataset will provide a foundation for reconstructing morphological transformations, biogeographic history, and divergence timing, and will be combined with large-scale molecular data for further elucidation of relationships with the potential for linking molecular and phenotypic traits. This research is supported by funding from various institutions, including the National Science Foundation Graduate Research Fellowship Program and the Smithsonian Institution Fellowship Program. The initial morphological matrix framework is detailed in Musser and Cracraft (2019)<sup>12</sup>, which focused on placement of the extinct *Adzebill* of New Zealand and combined nuclear gene sequences with large-scale morphological data. The matrix has grown immensely since that publication and currently contains over 150 taxa and 800 characters.

Initial taxon sampling focuses on taxa historically included in the "Gruiformes" (e.g. Kagu, bustards, mesites, and turacos) and their putative relatives, which are now distributed across the base of Neoavian molecular trees.<sup>2,3</sup> Core-Gruiformes (rails, cranes and allies) are also an important focus-group as their affinities to basal neoavian lineages are similarly uncertain; thus resolving patterns in their phenotypic evolution in the context of other basal lineages is important for reconstructing phenotypic evolution in all of Neoaves. Morphological analysis of core-Gruiformes also has important implications for neoavian temporal history as many have a rich Paleogene fossil record<sup>10,13-16</sup> and are of global significance for Neoavian biogeographic history, especially for resolving the uncertain role of the Northern Hemisphere in early avian

biogeographic history.<sup>13-15</sup> This was most recently demonstrated in Musser et al. (2019)<sup>8</sup>, in which we confirmed the extinct Paleogene-Eocene *Pellornis mikkelsenii* of the Fur Formation of Denmark to be within Gruiformes. The age of this fossil alone suggests that recent molecular studies using genomic and nuclear gene-based data are underestimating the divergence date of Gruiformes, and perhaps other neoavian groups.

This basal neoavian dataset will include many more key fossils with important implications for Neoaves like *P. mikkelsenii*, with a focus on Paleogene gruiform-like fossils from the Eocene Green River Formation<sup>15</sup> (Figure 1). This includes many Green River fossils within the collections of the Field Museum that I am currently describing through phylogenetic analysis, SEM, and micro-CT (See Figure 2 for an example of several visualizations, Musser et al. in prep). The morphological dataset primarily comprises skeletal characters but also includes characters detailing soft tissue that are being imaged using micro-CT (e.g. syringes, tracheas, and endocasts), egg anatomy, development, and life history traits. Once complete, I will work with my collaborators to combine this morphological dataset with the B10K large-scale genomic data soon to be available (<https://b10k.genomics.cn>) and future available genomic data from collaborators at OpenWings (<https://www.openwings.org>) to explore interactive data effects and resulting relationships. I will then create a calibrated time-tree as well as reconstructions of biogeographic history and ancestral states. Building this dataset begins to address several of the research questions I am interested in and provides a foundation of integrative data to address others described above.

My research questions as outlined above are impacted by and inclusive of questions regarding the origin and evolution of archosaurs and dinosaurs, especially theropods and paravian dinosaurs. Thus I am keenly-interested in working with students who are motivated to answer research questions regarding non-avian dinosaurs. I would welcome the opportunity to co-supervise both undergraduate and graduate students obtaining degrees at institutions such as the University of Chicago and other institutions affiliated with the Field Museum. I am also interested in working with undergraduate and graduate students along with postdoctoral researchers through additional programming such as the Research Experiences for Undergraduates Program.

### **Fieldwork initiatives and collection expansion:**

- 1) Domestic: The Field Museum has an extensive North American paleontological collection and further collection and phylogenetic analysis of fossils from this region is critical to better resolving avian relationships. I plan to continue to focus on collection of avian fossils from Green River in addition to locating new Paleogene sites that yield avian fossil remains, while continuing to collect avian and non-avian dinosaurs from older sites within North America.
- 2) International: As a Ph.D. candidate within Dr. Clarke's Lab, I am currently collaborating with several universities and museums in Chile and China, which includes co-coordinating and participating in joint fieldwork initiatives. At Cretaceous and Paleogene sites in Chile I was able to recover avian remains along with the remains of several non-avian dinosaurs, including a titanosaur, several ornithopods, and theropod teeth. Dinosaur field work initiatives in South America are especially critical, as fossil recovery efforts have thus far largely focused on Northern Hemisphere localities.<sup>13-17</sup> In China, fieldwork has focused on Eocene and other Cenozoic sites in which I recovered avian and non-avian remains (Musser et al. in review<sup>18</sup>, Musser et al. in prep). I am currently working on several gruiform-like fossils from Eocene and Miocene sites in China along with Dr. Zhiheng Li at the Institute of

Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing that are similar in preservation to those of the Green River Formation (Musser et al. in prep). I plan to search for a Paleogene avian laagerstaten site in China, which is critical for better understanding the interactions of taxa across Eurasia and North America during this time. I am also interested in collaborating with additional researchers at IVPP and the China University of Geosciences to work in Cretaceous sites in China to locate both non-avian dinosaur and paravian remains.

### **Outreach initiatives:**

- 1) Museum exhibitions: I have considerable experience in the creation of museum exhibitions and related programming and have researched the history of natural history museum exhibitions extensively, especially the lives of Carl and Delia Akeley. I have always admired natural history museum dioramas and their critical historic and educational roles, and began researching the artists who created them as an undergraduate. During this time I received an Elizabeth Greenshields Foundation Grant for the Visual Arts (\$15,000.00) and used it to visit exhibition artists' living family members, friends and colleagues in order to collect stories and peer through their personal belongings. I then used this information and access to related research materials at the American Museum of Natural History (AMNH) to make large oil paintings that incorporated diorama scenes with themes from my research. I also completed two internships in the Exhibition Department of AMNH where I aided in the design and construction of several dioramas and outreach programming for two traveling exhibits: "Our Global Kitchen: Food, Nature, and Culture" and "The Power of Poison." Both are currently being shown at various institutions worldwide and were viewed by over five million visitors at AMNH alone. The creation of each diorama comprised many hours of scientific research, consulting with AMNH executive staff and curators, collaborating with a team of artists, and employing my own visual arts skills to create a scientifically accurate and aesthetically intriguing exhibition piece. I am currently continuing to participate in museum exhibition design and creation at the University of Texas at Austin (UT Austin), where I am creating an exhibition on a new crane-like fossil (Musser et al. in review<sup>18</sup>). I am passionate about museum exhibition and scientific outreach and want to continue aiding in designing compelling exhibits that engage, educate and inspire the public.
- 2) Additional outreach: I have led and participated in scientific outreach initiatives while attending UT Austin, Columbia University, and the College of Charleston (C of C). At C of C, I led the Literacy Outreach Initiative Program in which I created and taught biological curricula to 4th and 5th grade students from several Charleston County Title 1 schools, coordinated weekly undergraduate student visits to each school during which undergraduates taught literacy courses, and organized C of C campus and Mace Brown Museum of Natural History visits for the students throughout each semester. My personal highlight of the program involved completing a large campus visit in which students designed and conducted their own biological experiments at C of C and watched fossil preparation take place at the Mace Brown Museum. It was moving to see such incredible gratitude in each student and watch the activities spark their curiosity about the biological and paleontological sciences. As a Master's student at Columbia University, I coordinated and participated in similar campus visits for diverse female K-12 students and was a mentor to a female undergraduate student through the Research Experiences for Undergraduates program at AMNH. UT Austin has allowed me to continue to organize and participate in scientific outreach programs that serve the general public and students of all ages. This includes the GeoFORCE program, during

which I have been able to mentor an underprivileged female undergraduate who aspires to a career in medical research. Working with her and watching her grow and thrive academically has clarified for me the impact of outreach and mentorship, especially for diverse students from different socioeconomic backgrounds.

I believe that outreach beyond the walls of the Museum is critical, especially for engaging underserved youth, college students, and educators. Some examples of outreach initiatives that I believe are important include digitization of collections, heightened social media campaigns, further professional development for educators, application of Museum knowledge to real-world challenges, and partnerships with volunteers, universities and local schools to bring Museum knowledge to a diverse range of communities.

[1] P. G. Ericson et al. *Biol. Lett.* 2, 543–547 (2006). [2] E. D. Jarvis et al. *Science*. 346, 1320-1331(2014). [3] R. O. Prum et al. *Nature*. (2015). [4] B. C. Livesey, R. L. Zusi. *Zool. J. Linn. Soc.* 149, 1-95 (2007). [5] C. P. Renae et al. *Mol. Biol. Evol.* 26(2), 313-326 (2009). [6] S. Reddy et al. *Sys. Biol.* 66(5), 857-879 (2017). [7] R. T. Kimball et al. *Diversity* 11(7): 10.3390/d11070109 (2019). [8] G. Musser et al. *Diversity* 11(7): 10.3390/d11070102 (2019). [9] G. Mayr, J. Clarke. *Cladistics*. 19(6), 527-553 (2003). [10] B. C. Livezey. *Phil. Trans. Roy. Soc. B.* 353(1378), 2077-2151 (1998). [11] C. L. Organ et al. *Nat. Lett.* 446(8), 180-184 (2007). [12] G. Musser, J. Cracraft. *Novitates* 3927(69), 1-69 (2019). [13] G. Mayr. *Paleogene Fossil Birds* (Springer; 2009). [14] G. Mayr. *Avian Evolution: The Fossil Record of Birds and Its Paleobio. Sig.* (Wiley-Blackwell, 2016). [15] L. Grande. *The Lost World of Fossil Lake: Snapshots from Deep Time* (The University of Chicago Press, 2013). [16] A. Hesse. In *Papers in Avian Paleo. Honoring Pierce Brodkorb*, ed. K. E. Campell, Science Series of the Nat. Hist. Mus. of L. A. County 36, 171–178 (1992). [17] D. D. Cashmore, R. J. Butler. *Paleo.*, 1-31: 10.1111/pala.12436 (2019). [18] Musser et al. (in review, 2019): A new species of Eogruidae (Aves, Gruiformes) from the Miocene of the Linxia Basin, Gansu, China: *Evol. and Climatic Implications*.