

Symposium on ‘Evolving approaches for studying the anatomy of the avian brain’: introduction

Birds have long been recognized as the only vertebrates that approach the level of brain expansion observed in mammals, yet until recently avian brain evolution has garnered only a fraction of the research effort devoted to mammals. Avian neuroanatomical research is rapidly expanding in scope, fueled by advances in imaging techniques, gene expression studies, and the discovery of new fossils bridging the transition from non-avian dinosaurs to birds. The six contributions presented here provide a glimpse of the variety of studies that characterize current avian neuroanatomical research: research that frequently combines observations from the fossil record with those for extant species and that analyses these data in ever more sophisticated ways.

The studies contained in this volume are largely the result of collaborations conceived at a catalysis meeting on the avian brain that we held at The National Evolutionary Synthesis Center (NESCent) in Durham, NC, in May of 2014. The meeting, entitled ‘A Deeper Look into the Avian Brain: Using Modern Imaging to Unlock Ancient Endocasts’, brought together neurobiologists studying the structural evolution of the avian brain at tissue and cellular levels, anatomists utilizing endocasts to compare the anatomy of the brain and sensory organs of both living and extinct birds, and paleontologists studying the neuroanatomy of derived non-avian theropod dinosaurs (https://www.nescent.org/cal/calendar_detail.php?id=1070.html). Our goal was to establish the limits of inference that can be attained with these data in living and extinct taxa and to generate exciting new ideas for collaboration between senior experts, early career scientists, and graduate students, an assemblage that might not be realized elsewhere.

Arguably, one of the most important products of the NESCent meeting was an agreement between the more than 30 participants regarding ‘best practices’ for constructing endocasts. Balanoff et al. address challenges and opportunities facing the field of avian neuroanatomy and evolution as it relates to endocast construction. The use of digital endocasts to study neuroanatomical patterns in the deep history of vertebrates has become pervasive in the past several years; however, what might be considered ‘best practices’ for digitally constructing these casts has yet to be articulated. The contribution by Balanoff et al. represents collaboration by a large number of researchers actively working on comparative neurological studies involving endocasts and an attempt to standardize such techniques. It is our hope that this will stimulate discussion and empirical

testing of methods so that scientific consistency can be achieved throughout this research community.

Studies of living birds benefit from a wealth of ecological and behavioral knowledge and information regarding species diversity that is often not available to paleontologists. By combining the use of digitally rendered endocasts with geometric morphometric approaches, investigations by Carril et al. and Marguán-Lobón et al. highlight the ability of these modern methods to quantify the changes in avian brain shape, a relatively unexplored facet of avian neuroanatomy.

Although the differences in gross brain morphology across Aves have been well documented for decades, few studies have investigated the fine-scale variation within extant clades of birds. Carril et al. provide an in-depth look at the morphology of 14 species of Neotropical parrots, a group of birds characterized by advanced cognitive abilities and derived locomotor and feeding behavior. Carril et al. document marked differences in the neuroanatomy of neotropical parrot species, a finding with implications for interpreting the total degree of variation across birds. The interspecific-based results of Carril et al. provide a complementary comparison to those of Marguán-Lobón et al., who sampled 61 species of extant birds representing 22 of 23 ordinal level clades of extant birds. The exploration of geometric morphometric techniques to assess the relationship of encephalization and allometry hints at the potential for these methods to greatly expand our understanding of how the avian brain forms and functions.

Studies of fossil endocasts from two critical sectors of the avian tree of life are also represented. Walsh et al. revisit a crucial specimen with a complicated history. Endocasts from Mesozoic birds are vanishingly rare, and so the reappraisal of *Cerebavis cenomanica* adds a critical data point. Ironically, *Cerebavis* was originally described as a natural endocast of an enantiornithine bird, but Walsh et al. demonstrate the specimen is actually a worn braincase. They utilize CT scanning to render a new virtual endocast from this braincase and thus demonstrate the specimen belongs to an ornithurine bird that retained primitive features such as the lack of a Wulst. Proffitt et al. explore another important fossil, belonging to the oldest known penguin taxon *Waimanu*. Despite its age, *Waimanu* already shows many of the features that are typical for penguin brains such as widening of the cerebellum, and the lack of any impressions of cerebellar folds on the endocast. On the other hand, *Waimanu* is primitive in showing weak

development of the Wulst, which expands later in penguin evolution. Finally, Balanoff et al. undertake an explicit test of whether the acquisition of powered flight is the most likely evolutionary scenario responsible for the variation in endocranial volumes present among birds and their non-avian relatives. Using statistical models, Balanoff and co-authors suggest that flight plays only a minor role in the origin of bird-like endocranial volumes, and the modular changes observed in different brain regions (i.e. cerebrum and cerebellum) suggests a much more complex evolutionary history.

Investigations into the evolution of the avian brain provide relatively unexplored research territory and hold the promise to reveal tantalizing new directions for future anatomical study.

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