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Authors: Wood, Jamie R., and De Pietri, Vanesa L.

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PERSPECTIVE

Next-generation paleornithology: Technological and methodological advances allow new insights into the evolutionary and ecological histories of living birds

Jamie R. Wood[1]* and Vanesa L. De Pietri[2]

[1] Long-Term Ecology Lab, Landcare Research, Lincoln, Canterbury, New Zealand
[2] School of Biological Sciences, Flinders University, Adelaide, South Australia, Australia
* Corresponding author: woodj@landcareresearch.co.nz

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ABSTRACT

Paleornithology, the study of fossil or ancient bird remains, provides an important context for understanding the biology, evolutionary history, and ecology of living birds. Recent technological and methodological advances in the field of paleornithology have opened up the potential to extract new pools of information from fossil bird remains, and hence provide new insights into the histories of living birds. Here we review some of these advances, covering aspects of ancient DNA and protein analyses, sedimentary proxies for birds, stable isotope analyses, coprolite analyses, high-resolution computed tomography, paleoneurology, finite elements analysis, and paleohistology. These new advances offer exciting prospects for the future of paleornithology, but also reaffirm the importance of basic fieldwork, exploration and the discovery of new fossil specimens, museum archives in which to curate the specimens, and traditional morphological approaches to studying the fossil remains.

Keywords: computed tomography, DNA, histology, paleornithology, proxies, sediments, stable isotopes, techniques

Paleornitología de nueva generación: Avances tecnológicos y metodológicos permiten nuevas perspectivas sobre las historias evolutivas y ecológicas de las aves vivientes

RESUMEN

La paleornitología, el estudio de los restos de aves fósiles o antiguas, provee un contexto importante para entender la biología, historia evolutiva y ecología de las aves vivientes. Los recientes avances tecnológicos y metodológicos en el campo de la paleornitología han creado el potencial para extraer nuevos conjuntos de información de los restos fósiles de aves y así proveer nuevas perspectivas sobre las historias de las aves vivientes. Aquí revisamos algunos de estos avances cubriendo aspectos del análisis de ADN y proteínas antiguas, aproximaciones de sedimentación para aves, análisis de isótopos estables, análisis de coprolitos, tomografía computarizada de alta resolución, paleoneurología, análisis de elementos finitos y paleohistología. Estos nuevos avances ofrecen perspectivas emocionantes para el futuro de la paleornitología, pero también reafirman la importancia del trabajo de campo básico, la exploración y el descubrimiento de nuevos especímenes fósiles, los archivos de museo en donde se puedan curar los especímenes y las aproximaciones morfológicas tradicionales para el estudio de los restos fósiles.

Palabras clave: ADN, aproximaciones, extinciones, fósiles, histología, isótopos estables, paleornitología, sedimentos, técnicas, tomografía computarizada

Modern birds (Neornithes; Gadow 1893; used here in reference to crown group Aves) include over 10,000 extant species (Gill and Donsker 2014), which occupy a diverse array of ecological niches and occur in almost all environments and habitats on Earth. Their widespread distribution, varied and often beautiful plumages and songs, and diverse array of life histories have long attracted the interest of scientists and amateur enthusiasts alike. As a result, birds have been widely studied for at least several hundred years (Bircham 2007). The development of ornithology as a science continues to this day, with the application of rapidly developing technologies, such as molecular tools and satellite tracking systems, providing new insights into many aspects of avian biology (Bircham 2007). However, a complete understanding of many aspects of the biology and ecology of living birds requires a broader temporal context than studies of extant individuals or populations can provide. Paleornithology (the scientific study of fossil, extinct, or prehistoric bird remains) plays an important role in providing this

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extended temporal view. Through the study of ancient bird remains we can gain further insights into avian biology, a broader perspective on the evolutionary pathways of birds, and a better understanding of how living bird taxa might respond in the face of future environmental change.

Fascination with fossil birds goes back centuries; a report of a fossilized bird's nest was published as early as the 13th century (see Lambrecht 1916, 1933). Yet the field of paleornithology perhaps has its true origins in the scientific debate around fossilized bird remains (at the time referred to as 'ornitholites') discovered during the 18th and 19th centuries (e.g., Scheuchzer 1708, Lamanon 1782, Cuvier 1800, 1807). With the subsequent development of comparative osteology of living birds (e.g., Huxley 1867, Fürbringer 1888, Newton 1893) and evolutionary theory (Darwin 1859) in the 19th century, the study of fossil birds began to shed new light on the evolutionary and ecological histories of extant avian lineages (e.g., Milne-Edwards 1867–1871, Owen 1879, Lambrecht 1933). Although the total number of extinct neornithine species that are known to science has not been totaled, the relative significance of fossil birds for understanding avian biology and ecology soon becomes apparent when one considers just a few of the figures published for discrete geographic regions or time periods. For example, ~500 species-level taxa have been described from Paleogene (66–23 Ma) deposits around the world (Mayr 2009), >800 species are represented in the Cenozoic fossil record of Europe alone (Mlíkovský 2002), and some researchers have estimated that more than 1,000 nonpasserine bird species may have gone extinct on Pacific islands during the Late Holocene (as a result of human impacts following island colonisations; Duncan et al. 2013).

For most of its history, the field of paleornithology has been largely centered on comparative osteology, and this approach still plays a dominant role in understanding the taxonomic relationships and paleobiology of fossil birds. Perhaps for more than any other group of living vertebrates, ecological adaptations to specific modes of life are reflected in the skeletons of birds (Cheneval 1989), and because these adaptations are, for the most part, well-understood in extant birds, osteological comparisons have been useful for inferring the biology and ecology of fossil taxa (Lambrecht 1933, Feduccia 1999). However, paleornithology is now expanding rapidly in regard to the analytical techniques being used. Technological and methodological advances during the past couple of decades in several areas of science relevant to this field have brought about a revolution in the types and amount of data that can be generated by studying the remains of fossil and extinct bird taxa. In this paper we outline some of the key recent (21st century) advances in the field of paleornithology, focusing specifically on those that have aided our understanding of the evolutionary and ecological histories of living birds (Table 1). We also provide perspectives on the current state of the field and the directions in which we see it moving in the future.

Ancient DNA and Proteins

Perhaps the greatest technological and methodological advances relevant to paleornithology that have been made during the 21st century are those related to the field of ancient DNA (aDNA) research. While molecular studies of living birds have played a key role in developing our understanding of the phylogenetic relationships among bird taxa, aDNA has taken this a step further by allowing extinct taxa to be placed within molecular phylogenetic frameworks, permitting a 'real-time' view of temporal genetic change and providing unique insights into the biology and ecology of extinct bird species.

Ancient DNA research is a field still in its relative infancy (see Rizzi et al. 2013 for a recent review). However, due to the rapid technological advances being made in genetic sciences, current methods and techniques are almost unrecognizable compared with those that produced the first aDNA sequences from ancient specimens during the mid-1980s. A key recent advance in aDNA research has been the adoption of high-throughput DNA sequencing platforms (the development of which has been driven largely by medical research), meaning that genomic-scale sequencing is now possible for extinct and ancient specimens (Huynen et al. 2012, Meyer et al. 2012, Orlando et al. 2013, Prüfer et al. 2014). Such technology continues to become more cost-efficient, in terms of the number of bases sequenced per dollar (Shendure and Ji 2008, Kircher and Kelso 2010), as well as reducing the amount of time required to sequence genomes. New protocols also continue to be developed for increasing the efficiency of aDNA recovery from ancient specimens (e.g., Gnirke et al. 2009, Mertes et al. 2011, Gansauge and Meyer 2013), and in future such methods may potentially increase the temporal range of aDNA studies. It has been shown that early reports of aDNA having been extracted from geologically ancient fossils (e.g., Golenberg et al. 1990, Cano et al. 1992, Woodward et al. 1994) were erroneous and were a result of contamination of samples by modern DNA (Zischler et al. 1995, Austin et al. 1997, Willerslev and Cooper 2005), an issue that is now better understood and routinely controlled for in aDNA research (Cooper and Poinar 2000, Hebsgaard et al. 2005). Currently, the oldest authentic aDNA sequence retrieved from a fossil bone (from a horse) stands at 560–780 thousand years (Orlando et al. 2013), but theoretical evidence suggests that DNA molecules may persist in such remains for up to 6.8 million years under optimal conditions (Allentoft et al. 2012). Moreover, the types of ancient bird remains from which aDNA has been successfully extracted continues to grow (Huynen et al. 2012). In addition to bone (e.g.,

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TABLE 1. Summary of key paleornithological techniques that have undergone recent advances as discussed in the text. The age of avian remains or sediments to which they are applicable, and what they can tell us about the evolutionary and ecological history of living birds, are also shown.

Technique or method	Temporal range	Potential insights for understanding living bird species	Examples
Ancient DNA analyses of avian remains	Theoretical upper limit 6.8 Ma. Oldest vertebrate aDNA currently 560–780 ka. Most studies focus on past 20 ka.	Phylogenetic relationships between living and extinct avian taxa.	Mitchell et al. (2014a, 2014b)
		Establishing baselines of past levels of genetic diversity within avian species.	Bouzat et al. (1998)
		Past population dynamics of avian species (allowing prediction of responses to future environmental or anthropogenic drivers).	Hung et al. (2014)
Ancient proteomics	Undetermined. Current oldest accepted record is 1.5 Ma. Possibly as old as the Cretaceous, although the authenticity of pre-Pleistocene records remains debated.	Phylogenetic relationships between living and extinct avian taxa, using remains beyond the limits of aDNA preservation.	Not tested on birds. For mammals: Wadsworth and Buckley (2013)
		Identification of avian bone fragments or associated remains (e.g., eggshell).	Stewart et al. (2013)
Geochemical proxies for birds (trace elements, rare-earth elements, stable isotopes)	In paleornithology have been used mainly on Holocene sediments, but could be applicable to older sediments as well.	Past distribution of marine bird colonies.	Hawke et al. (1999), Yuan et al. (2010)
		Longevity of marine bird colonies.	Hawke (2004)
		Past population dynamics of marine bird species (allowing prediction of responses to future environmental or anthropogenic drivers).	Huang et al. (2009, 2011)
Biomolecule proxies for birds (e.g., aDNA, cholesterol, cholestanol)	Pleistocene and Holocene sediments.	Reconstructing past distributions of living avian taxa.	Willerslev et al. (2003), Huang et al. (2010)
Coprophilous fungi proxies for birds (e.g., *Sporormiella*)	Used widely on Pleistocene and Holocene sediments, but likely to be applicable to older sediments as well.	Past population dynamics of insular avian-dominated herbivore communities; especially useful in establishing the timing of major extinction events.	Wood et al. (2011)
Stable isotope analyses of avian remains	Varies between isotopes, but largely depends on preservation conditions rather than time. Have been used on bird bones as old as Paleocene.	Trophic levels.	Angst et al. (2014)
		Species' responses to climate change.	Rawlence et al. (2012)
		Changes in migration patterns through time.	Untested in fossil bird remains; for example using living birds see Font et al. (2007)

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TABLE 1. Continued.

Technique or method	Temporal range	Potential insights for understanding living bird species	Examples
Avian coprolite analyses	Avian coprolites exist for a wide range of time periods. Most information can be gained from those within the range of aDNA analyses (i.e. particularly last 20 ka).	Reconstructing habitat use and diets of bird species in undisturbed (prehuman) ecosystems.	Horrocks et al. (2008), Wood et al. (2013a)
		Identifying ecological links between certain bird and plant taxa (e.g., pollination, seed dispersal), which may no longer co-occur.	Wood et al. (2012)
		Changes in parasite faunas through time, which may relate to population declines in the host bird species.	Wood et al. (2013b)
		Characterizing natural gut microbiotas (bacterial and microscopic eukaryotes).	Untested on avian coprolites, but for example using human coprolites see Tito et al. (2012)
High-resolution CT technology	Unrestricted.	Brain and sensory organ evolution.	Ashwell and Scofield (2008), Scofield and Ashwell (2009), Ksepka et al. (2012)
Finite element analysis	Unrestricted.	Evolution of feeding ecology within a group.	Degrange et al. (2010)
Paleohistology	Unrestricted.	Evolution of life history traits within a group.	Turvey et al. (2005), Bourdon et al. (2009)
		Ecological and functional adaptations through time.	Smith and Clarke (2014), Cerda et al. (2014)
		Phylogenetic relationships.	Legendre et al. (2014)

Cooper et al. 2001), aDNA has now also been extracted from ancient feathers (Rawlence et al. 2009, Olsen et al. 2012), eggshells (Oskam et al. 2010, 2011), coprolites (Wood et al. 2008, 2012), and sediments (Willerslev et al. 2003); coprolitic and sedimentary aDNA are discussed in more detail in the 'Coprolite Analyses' and 'Sedimentary Proxies for Birds' sections below, respectively.

Due to their large size, relatively recent extinction date, and abundance of fossil remains, the ratite moa (Dinornithiformes) of New Zealand have long been the poster-children for aDNA studies of birds. More specimens from moa have been studied using DNA techniques than from any other extinct taxon (Allentoft and Rawlence 2012). The first aDNA sequences obtained for birds were from moa bones (Cooper et al. 1992), as were the first complete ancient avian mitochondrial (mt) genomes (Cooper et al. 2001, Haddrath and Baker 2001), ancient avian microsatellite markers (Allentoft et al. 2009), and the first sex-linked nuclear DNA sequences from an extinct species (Bunce et al. 2003, Huynen et al. 2003; Figure 1). Since the 1990s, a raft of studies on moa tissues have highlighted the breadth of information that aDNA can reveal about extinct bird species, including aspects of phylogenetic relationships, evolution, physical appearance, sensory capabilities, and population dynamics (e.g., Aidala et al. 2012, Rawlence et al. 2012, Allentoft et al. 2014, Huynen et al. 2014, with earlier work reviewed by Allentoft and Rawlence 2012 and Worthy and Scofield 2012). Moreover, molecular analyses of associated remains have provided insights into the biology of moa and their ultimate demise. For example, ancient DNA analysis of moa eggshells has provided insights into the moa-hunting strategies of early settlers and subsequent extinction dynamics (Oskam et al. 2011). Recently, aDNA has also been used in the analysis of moa coprolites, providing unequivocal identification of the depositor (important when there were several sympatric species at a site), and thus allowing niche partitioning and broken ecological links to be examined (Wood et al. 2013a), as well as allowing the gastrointestinal parasite communities associated with these extinct birds to be

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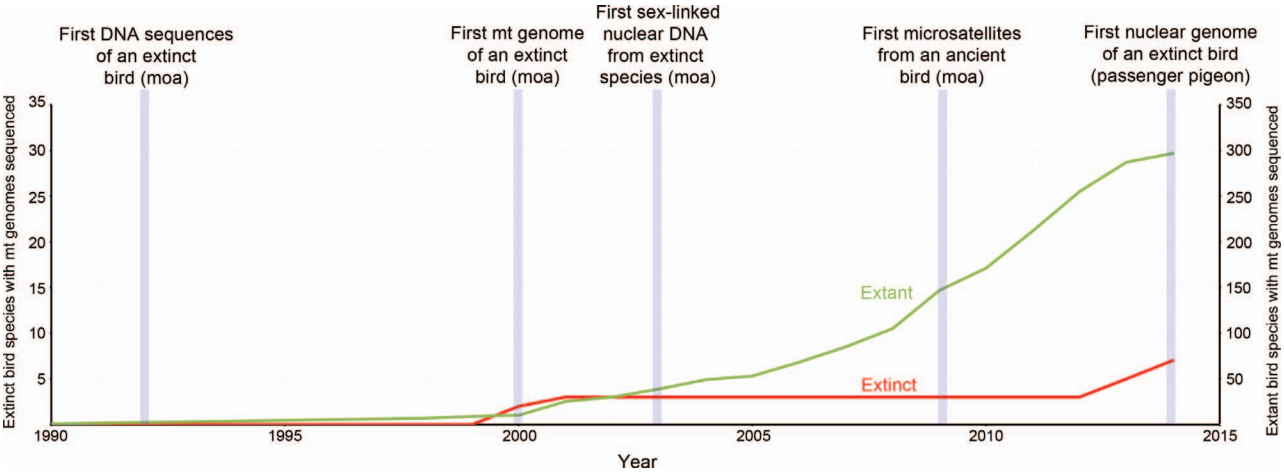


FIGURE 1. Cumulative number of avian species (extant vs. extinct) for which mitochondrial (mt) genomes have been sequenced, with key milestones in the genetic analysis of extinct bird species.

characterized (Wood et al. 2013b). Coprolite analyses are discussed in more detail in a later section of this paper.

However, apart from moa, the application of aDNA to avian studies has lagged behind that of mammals. Complete (or near-complete, i.e. >15,000 base pairs) mt genomes for just seven extinct bird species have been published at the time of writing (*Emeus crassus*, *Dinornis robustus*, *Anomalopteryx didiformis*, *Ectopistes migratorius*, *Anas chathamica*, *Mullerornis agilis*, and *Aepyornis hildebrandti*; Cooper et al. 2001, Haddrath and Baker 2001, Hung et al. 2013, Mitchell et al. 2014a, 2014b), representing only 2.3% of the 304 bird species for which mt genomes were available on GenBank in July 2014. Eight ancient mitogenomes have also been sequenced from the extant Adelie Penguin (*Pygoscelis adeliae*; Subramanian et al. 2009). Just recently, the first large portions of nuclear genomes from an extinct bird species were sequenced from the Passenger Pigeon (*Ectopistes migratorius*; Hung et al. 2014). But, overall, this is relatively few compared with the number of mt genomes and nuclear genomes that have now been produced for ancient humans and other mammal species (>124 reported by Paijmans et al. 2013).

One potential application of aDNA research on ancient bird remains is 'de-extinction,' a topic that has gained much attention recently. The basis of de-extinction is to re-create extinct species, with the ultimate goal of taking the concept of rewilding to the next level by restoring the ecosystem functions once provided by extinct species (Seddon et al. 2014). However, whether the re-created species will exhibit any of the behavioral and ecological traits of the original species is a matter of debate, and there are a large number of ethical (Sandler 2014) and legal (Carlin et al. 2014) considerations involved with the de-extinction process. Two of the main methods proposed for de-extinction, somatic cell nuclear transfer and genetic engineering (Carlin et al. 2014), both rely heavily on aDNA techniques. The latter is the method currently being used in a project aiming to re-create the Passenger Pigeon, through splicing key genes from the Passenger Pigeon into the genome of a near relative, the Band-tailed Pigeon (*Patagioenas fasciata*; Revive & Restore 2014). A similar technology has recently been used in a study in which genes related to wing formation from the extinct moa were re-created and studied in vivo through splicing into chicken embryos (Huynen et al. 2014).

Without going to the extreme of reconstituting extinct species, there is also the potential for aDNA analyses to help inform the conservation management of currently rare and threatened bird taxa. A key conservation concern for small, fragmented populations is the loss of genetic diversity. DNA analysis of prehistoric bones can help to determine the natural level of genetic diversity within a species prior to its decline, thus providing a baseline against which to compare current populations (e.g., Bouzat et al. 1998, Shapiro et al. 2004, Chan et al. 2005). This may, in future, lead to the reintroduction of lost genetic diversity into extant species using gene splicing technologies. Recent analyses of archaeological chicken bones have also highlighted the potential for aDNA to explore issues of human-mediated dispersal and domestication processes (Flink et al. 2014, Thomson et al. 2014, Xiang et al. 2014).

Proteins may persist for longer than DNA molecules (Buckley and Collins 2011), and therefore might extend the temporal limits of molecular phylogenetic signals from fossil bird remains. Techniques for sequencing ancient proteins have undergone major developments recently (see Hofreiter et al. 2012 for a review). As a result, authentic

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protein sequences with meaningful phylogenetic signals have now been obtained from bones up to 1.5 million years old (Wadsworth and Buckley 2013). Proteins have also been reported from Cretaceous dinosaur bones (e.g., Schweitzer et al. 2007). Although this is certainly an exciting prospect, as the ability to examine proteins in fossil bird bones that are tens of millions of years old would undoubtedly provide major new insights into avian evolution and the taxonomic relationships between fossil and living birds, significant scientific debate remains regarding the authenticity of these results (Service 2009). The true temporal limits of protein preservation in fossils remain to be tested.

Presently, the broadest application of ancient proteins lies in providing a molecular 'barcode' with which to identify bones and eggshell fragments, a technique named ZooMS (Zooarchaeology by Mass Spectrometry; e.g., Stewart et al. 2013). This has been most widely applied in archaeology, but also has potential applications for paleontology. Current methods can routinely identify remains to family or genus, but require further refinement to attain species-level taxonomic resolution (Hofreiter et al. 2012).

It is also worth noting that the past decade has seen important advances in the way that molecular (and morphological) data can be used to infer relationships among taxa. In particular, new approaches to combining molecular data and morphological characters have helped to improve our understanding of the evolutionary histories of birds (e.g., Bertelli and Giannini 2005, Mitchell et al. 2014b). The development of new statistical techniques for examining phylogenies and the application of preexisting phylogenetic techniques to new areas have also helped resolve issues around equivocal relationships within fossil birds (e.g., Lee and Worthy 2011).

Sedimentary Proxies for Birds

Historically, the study of ancient birds has largely relied on visible physical or trace remains, such as bones or footprints. However, a range of sedimentary proxies for birds are now routinely used, and new ones continue to be developed. These proxies provide information on ancient bird populations based solely on the biological or chemical traces of their presence preserved in sediments. Many of these proxies are semiquantitative, and can therefore provide useful insights into the responses of bird populations to past environmental changes (especially during the Pleistocene and Holocene epochs). Such data have clear implications for predicting the potential impacts of future climatic and environmental change on avian species.

The most widely used sedimentary proxies for birds are geochemical, and can be classified as either trace element (Liu et al. 2006a, 2006b, 2007, 2011, 2013, Xie and Sun 2008, Brimble et al. 2009, Huang et al. 2009, 2011, Nie et al. 2014a) or stable isotope (Hawke 2004, Sun et al. 2005, Yuan et al. 2010, Keatley et al. 2011, Liu et al. 2013, Nie et al. 2014b) proxies. A key strength of geochemical proxies is their ability to record marine inputs into terrestrial ecosystems, and therefore their main utility has been for inferring the past distribution (e.g., Hawke et al. 1999, Yuan et al. 2010), colony longevity (Hawke 2004), and population trends (e.g., Sun et al. 2005, Liu et al. 2006a, 2007, Huang et al. 2009, 2011) of marine birds such as procellariiforms and penguins. Important trace element indicators of seabird guano in terrestrial sediments include As, Cd, Cu, Se, Zn, P, F, and Ni (Liu et al. 2006a, 2007, 2013, Brimble et al. 2009). More recently, rare-earth elements have also been proven to be an effective avian proxy (Liu et al. 2011, Nie et al. 2014a). Isotopic proxies for seabirds include $\delta^{15}N$ (although recently it has been suggested that $\Delta^{15}N$ may be more useful in some circumstances; Liu et al. 2006, Nie et al. 2014b), $\delta^{13}C$ (Liu et al. 2006, 2013), and $^{87}Sr/^{86}Sr$ ratios (Sun et al. 2005). Geochemical proxies have been applied at a local scale (to ornithogenic sediments, i.e. those that form on the site of a breeding colony; e.g., Nie et al, 2014a) and at a catchment scale (to sediments from lakes near breeding colonies; Liu et al. 2011). Recently, much focus has been placed on using geochemical proxies to understand Holocene penguin population dynamics in Antarctica (Sun et al. 2005, Liu et al. 2006b, 2007, Huang et al. 2009, 2011), but they have also been used successfully in Arctic (Brimble et al. 2009, Keatley et al. 2011) and low-latitude sites (Liu et al. 2006a). Once normalized to account for terrestrial inputs, changes in the concentrations of these elements within sediments through time appear to accurately reflect local seabird population trends, which in turn can be correlated with past changes in the environment, such as climate (Liu et al. 2007, Huang et al. 2009, 2011) or sea surface temperatures (Liu et al. 2006a). In addition to sediments, stable isotope analyses can also be performed on avian remains themselves, and this is described in a following section.

Biological proxies, such as fungal spores (Wood et al. 2011), sedimentary aDNA (Willerslev et al. 2003, Haile et al. 2007, Epp et al. 2012), and other biomolecules (e.g., cholesterol and cholestanol; Huang et al. 2010), have also undergone major development this century, and are becoming routinely used tools. Unlike geochemical proxies, their use is not limited to marine birds. One of these biological proxies, coprophilous fungal spores, is an example of a preexisting proxy that has recently been adapted for use in paleornithology. The fungal genus *Sporormiella*, in particular, lives almost exclusively on herbivore dung and produces robust, morphologically distinctive spores that preserve in sediments. Since the 1980s, *Sporormiella* spores in sediment cores have been

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quantified to examine the timing of Pleistocene and Holocene extinction events in mammalian-dominated faunas, such as those of North America (Davis 1987, Robinson et al. 2005, Gill et al. 2009), Australia (Rule et al. 2012), and Madagascar (Burney et al. 2003). However, Wood et al. (2011) showed that *Sporormiella* spores could also be found in sediments on islands with avian-dominated faunas, and therefore were a useful proxy for prehistoric changes in herbivorous bird populations. The benefit of a stratigraphic approach such as this is that it allows changes in avian herbivore abundance to be directly compared with concomitant changes in other proxies (such as pollen, reflecting the local vegetation, or charcoal abundance, reflecting fires; e.g., Rule et al. 2012) without the need for absolute dating. Future work, potentially involving a combination of spore morphology and aDNA, may resolve vertebrate-taxon-specific species of *Sporormiella*, thereby allowing populations of mammals and birds to be independently traced on landmasses where they co-occur.

With new developments in high-throughput sequencing technologies, ancient DNA analysis of Pleistocene and Holocene sediments is likely to become an increasingly powerful tool for detecting the former presence of avian species when no macrofossils are preserved. Typically, a 'barcoding' approach is used, whereby short, variable (i.e. taxonomically informative) sequences are amplified from a sediment-DNA extract using PCR primers specific to birds (e.g., Epp et al. 2012). Willerslev et al. (2003) presented one of the earliest studies to use avian primers on sedimentary aDNA, detecting the DNA of three extinct moa species and a parakeet in Holocene rock shelter sediments from New Zealand. Haile et al. (2007) also successfully obtained ancient bird DNA by using avian-specific primers on sediments from a New Zealand rock shelter, but also highlighted a potentially complicating factor associated with this proxy, that of vertical DNA leaching through sediment layers; e.g., sheep (*Ovis aries*) DNA was recovered from sediments thousands of years older than the time of their introduction to New Zealand. Further research into the dynamics of DNA leaching would greatly improve the utility of sedimentary aDNA as a proxy for birds in temperate, wet sites. Although there is some evidence to suggest that leaching may be less of an issue in sites with dry (e.g., Willerslev et al. 2003) or permanently frozen soils (e.g., Epp et al. 2012), there is still some potential for leaching in these areas via mammals urinating at a site. Beyond avian-specific primers, we can see future potential for the development of new soil DNA markers of avian presence. Examples may include detection of aDNA from coprophilous fungi related to birds (as discussed above) or in bacterial taxa and/or communities in sediments associated with birds (e.g., Aislabie et al. 2009).

It is also worth noting that, in some instances, avian remains themselves can be used as proxies for the ancient environmental conditions in which the birds lived. Isotopic analyses of preserved tissues, such as bones and feathers, and eggshell fragments have provided insights into past dietary or habitat shifts of certain bird taxa, reflecting changing climatic conditions (Johnson et al. 1999, Segalen et al. 2002, Emslie and Patterson 2007, Lorenzini et al. 2010, Rawlence et al. 2012, Huang et al. 2013, Yanes et al. 2013). Mercury levels in ancient eggshell, and copper in seabird excrement, have been used as proxies for anthropogenic activities such as industrialization and smelting (Yan et al. 2010, Xu et al. 2011).

Stable Isotope Analyses

Stable isotope analyses of faunal tissues have been used extensively for several decades, in modern biology and ecology, archaeology, and paleontology. A large number of reviews and textbooks exist on the use of stable isotopes in these fields (e.g., Kelly 2000, Katzenberg 2007, Clementz 2012), as well as for modern bird ecology (Inger and Bearhop 2008), and so we refer readers interested in the background of the methods and assumptions used to these texts. With regard to their relevance to paleornithology, stable isotopes in soils and sediments can serve as indicators for the former location of bird colonies, as discussed in the previous section on 'Sedimentary Proxies for Birds.' However, the stable isotope composition of actual fossil remains, such as bones and eggshells, can also provide useful insights into the diet, biology, environment, and habitat preferences of ancient birds. Therefore, isotope analyses can provide one of the few ways to trace behavioral changes through the fossil record (Lister 2014). Proteins and minerals are the two main sources of stable isotopes in fossil remains that are frequently analyzed. The isotopic analysis of proteins, such as collagen, is mostly applicable to samples that are $<$100 ka in age (or older if preservation is remarkable), whereas isotopic analysis of minerals such as calcite or bioapatite can be applied to much older fossil remains (Clementz 2012). The isotopic composition in each of these sources can be affected by contamination or postburial modification, so several tests have been developed to ensure the reliability of samples being analyzed (Kohn and Cerling 2002, Clementz 2012).

While stable isotope analyses have been applied widely in mammalian paleontology, the application of isotopic techniques to the study of fossil birds has been more limited. In fossil mammals, tooth enamel is most often used in isotope studies, as its composition of dense, large apatite crystals with relatively low organic content lessens the potential for diagenetic modification (Blyth 2011). The inorganic fraction of bird bones is likely less stable than that of mammalian tooth enamel (Steadman 2005), and

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therefore the isotopic composition of bird fossils may be more prone to contamination and modification. Accordingly, most fossil avian isotope studies have been performed on geologically young (i.e. Pleistocene or Holocene) material, or on relatively stable substrates such as eggshell. For example, Clarke et al. (2006) examined isotopic values for Late-Quaternary eggshells of elephant birds (*Aepyornis* sp.) and demonstrated that these birds mainly browsed C_3 vegetation and utilized drinking water from groundwater-fed wetlands. Wiley et al. (2013) analyzed carbon and nitrogen isotopes in Late-Holocene bones of the Hawaiian Petrel (*Pterodroma sandwichensis*) to show that prolonged dietary stability within this species had been disrupted by a relatively recent trophic decline related to the fishing industry.

However, there are a few examples of isotopic studies that were performed on older remains. For example, Angst et al. (2014) used $\delta^{13}C$ values of Early Cenozoic *Gastornis* eggshell and bone apatite to infer an herbivorous diet for these large birds, and Patnaik et al. (2009) used $\delta^{13}C$ of Miocene ratite eggshells to infer that these birds had a diet of mainly C_3 plants. These examples show that, given the right preservation conditions, the original isotopic composition of fossilized bird remains may be preserved. However, the overall proportion of avian fossil remains that preserve their original isotopic composition, and the prevalence of situations in which this occurs, remain to be determined.

Clementz (2012) highlighted several areas in which new techniques and methodological advances in isotopic analyses are currently being applied to the study of fossil mammals, however these also have potential future applications for the study of fossil birds. The first of these, laser ablation, has only recently been applied in paleontology (Clementz 2012), but provides isotopic analyses using only minute amounts of material (producing holes a fraction of a mm in diameter). This is useful for rare or small fossil specimens. In addition, it allows linear sampling across a specimen at fine spatial scales (e.g., Benson et al. 2013). One possible application of this technique may be to explore aspects of seasonality, such as migration, in extinct or fossil birds that retain multiple cyclical cortical growth marks (e.g., moa; Turvey et al. 2005). Another of the recent advances discussed by Clementz (2012) is the development of analyses of clumped isotopes, which have proven to be accurate body thermometers for both living and fossil species (Eagle et al. 2010).

Coprolite Analyses

The analysis of coprolites (ancient dung) is not strictly a single technique. It usually requires a multidisciplinary approach, including several of the techniques mentioned above. However, it is of relevance to the scope of this paper, as avian 'coproecology' has undergone major advances within the past decade (due largely to progress in the field of aDNA research), and can now provide detailed insights into the past diets, ecological functions, parasites, and gut microbiotas of birds that are unattainable by other methods. Such information can have important implications for the restoration of broken ecological links, and for understanding the ecology of rare or threatened bird species (Wood et al. 2012).

The development of aDNA research has been a key factor in allowing the bird species that deposited a coprolite to be identified. Prior to this, coprolites were often assigned to species based on their size, shape, collection locality, and associated osteological remains (e.g., James and Burney 1997, Horrocks et al. 2004). However, aDNA analyses have revealed that avian coprolite deposits can often contain specimens from multiple species, and that these cannot always be distinguished based on size and shape (Wood and Wilmshurst 2014). The ability to assign coprolites to bird species with a high degree of certainty has allowed the diets of these species (which may be determined using aDNA or conventional microscopic analyses of coprolite content) to be compared and contrasted, providing the potential to study the structure of prehistoric avian communities (Wood et al. 2013a).

Coprolites also provide excellent records of the prehistoric parasite faunas (especially gastrointestinal parasites) associated with birds. Although the parasites can be studied using conventional microscopic techniques, aDNA analysis has provided the ability to identify them with increased taxonomic resolution, as well as a way to identify parasites that are less readily preserved or difficult to identify visually (Wood et al. 2013b). The study of parasite communities using the coprolites of rare or threatened bird species may provide interesting insights into how the parasite communities of a species changed through time and how they responded as their hosts declined in abundance and populations became fragmented, and may reveal parallel extinctions for different endemic lineages (Wood et al. 2013b).

There is an ever-increasing awareness about the important role that microbiotas (including parasites, but especially bacterial communities) can play in nutrition, metabolism, the immune system, and reducing the risk of certain diseases (Lee and Mazmanian 2010, Tlaskalová-Hogenová et al. 2011, Flint et al. 2012). Gastrointestinal microbiotas are readily characterized using molecular analysis of dung, including those of birds (e.g., Waite et al. 2012, Waite and Taylor 2014). Characterizing microbiotas from coprolites could therefore potentially provide insights into the natural microbiotas associated with species that, due to their extreme rarity, now exist only in intensively managed populations. Individuals, and

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indeed whole populations, of such species (e.g., the New Zealand Kakapo [*Strigops habroptilus*]) may have significantly altered microbiotas due to hand-rearing or the administration of antibiotics (Waite et al. 2012, 2014), and coprolites could be key to providing baseline information that could, in future, be used to help to restore natural microbial communities (and therefore the health benefits that they provide) in these birds.

From an ecological perspective, coprolites provide an important window into the interactions among species within ancient ecosystems. This can have direct implications for living birds. For example, pollen from the bizarre subterranean root-parasite plant *Dactylanthus taylorii* was recently discovered in the coprolite of a Kakapo, providing evidence for a former link between two species that, due to population declines and range contractions, no longer co-occur (Wood et al. 2012). Understanding such links is an important part of ecosystem restoration, and is part of the developing practice of 'conservation paleobiology,' which focuses on using evidence from the past to inform current conservation management (Dietl and Flessa 2011).

High-Resolution Computed Tomography

Following the trend for other groups of vertebrates (e.g., Donoghue et al. 2006, Wu and Schepartz 2009, Schilling et al. 2013), new descriptions and redescriptions of fossil birds are beginning to incorporate data obtained from high-resolution computed tomography (CT) scanning of specimens, as well as details of bone microstructure and histological descriptions (e.g., Clarke et al. 2005, de Ricqlès 2011, Houssaye 2014). Both X-ray tube–based high-resolution CT systems and synchrotron radiation source μCT imaging are widely used in paleontological research, and their applications are numerous. Medical CT scanning is still popular, particularly for large specimens, but, despite the resolution of commercial scanners having improved, it remains of limited use in resolving very small structures in detail (e.g., Wu and Schepartz 2009). The three-dimensional information obtained from CT data allows for an integral examination of specimens, fossil and extant, in a nondestructive manner, enabling the visualization of slices in sectional views (to a few microns) and revealing internal structures in astounding detail.

The insights into various aspects of the ecology and paleobiology of extinct taxa gained from surveying the internal structures of fossil birds, at the micro- and macro-anatomical level, are tightly linked to our understanding of the biological processes, morphology, and phylogenetic relationships of living birds. The implementation of these techniques in avian paleobiology ultimately allows for the reconstruction of fossil birds as biological entities, and therefore these techniques are becoming more and more attractive for paleornithologists.

Applications of CT in paleoneurology. One of the most common uses for the volumetric information obtained from CT data is the virtual rendering of internal structures that are not preserved in fossil specimens, such as nervous tissue and blood vessels. In the past, the anatomy of the brain of fossil birds could only be examined with rarely preserved natural endocasts (i.e. where sediment replaced the neural tissue and filled up the neurocranium, forming a natural cast), or with plaster casts of the endocranial cavity (Edinger 1928), which is a partially destructive technique. Now, however, it is possible to virtually reconstruct the brain and sensory organs accurately through 3D imaging techniques (Figure 2). As with the preparation of plaster endocasts, this is possible because, in birds, the brain fills almost the entire cranial cavity, so that the braincase closely conforms to the shape of the brain (Iwaniuk and Nelson 2002). Virtual endocasts therefore represent a satisfactory record of the morphology and size of the organ (Witmer et al. 2008).

Paleoneurology is the study of brain evolution in fossil taxa. Avian (paleo)-neurological research is centered around the question of whether evolutionary changes, in the form of adaptations to a specific mode of life, are reflected in the avian brain, and, if so, what patterns can be identified across higher-level taxa, and what level of variation is identifiable at lower taxonomic levels. Behavior and sensory ecology can have profound effects in shaping the brain structure of birds (e.g., Winkler et al. 2004, Smith and Clarke 2012), but the presence of a phylogenetic signal in brain volume and morphology has also been examined in other vertebrates (e.g., Rojas et al. 2013, Racicot and Rowe 2014). So far, research within this field has been mostly aimed at understanding the early stages of brain evolution in different groups of vertebrates, and emphasis has been placed on taxonomic groups that are central to answering key evolutionary questions (e.g., Domínguez Alonso et al. 2004). Studies within Neornithes are fewer than those in other vertebrates, the greatest limitations being the restricted availability of well-preserved fossil cranial material, and a lack of extensive sampling of comparative material of extant taxa.

Virtual reconstructions of sensory and neural structures, such as the inner ear, optic nerve, and olfactory bulb, have provided information on the sensory capabilities of living and extinct birds (e.g., Sipla 2007, Walsh et al. 2009, Walsh and Milner 2011, Zelenitsky et al. 2011, Walsh et al. 2014, Degrange et al. in press). For instance, it has been shown through correlations with known hearing sensitivity in living birds that the dimensions of the cochlear duct are likely to predict mean hearing frequency and range in fossil taxa, and that these measurements can potentially be used to predict social and vocalization complexity, as well as habitat selection (Walsh et al. 2009). Predictions of sensory capabilities have been obtained for some Late Paleocene

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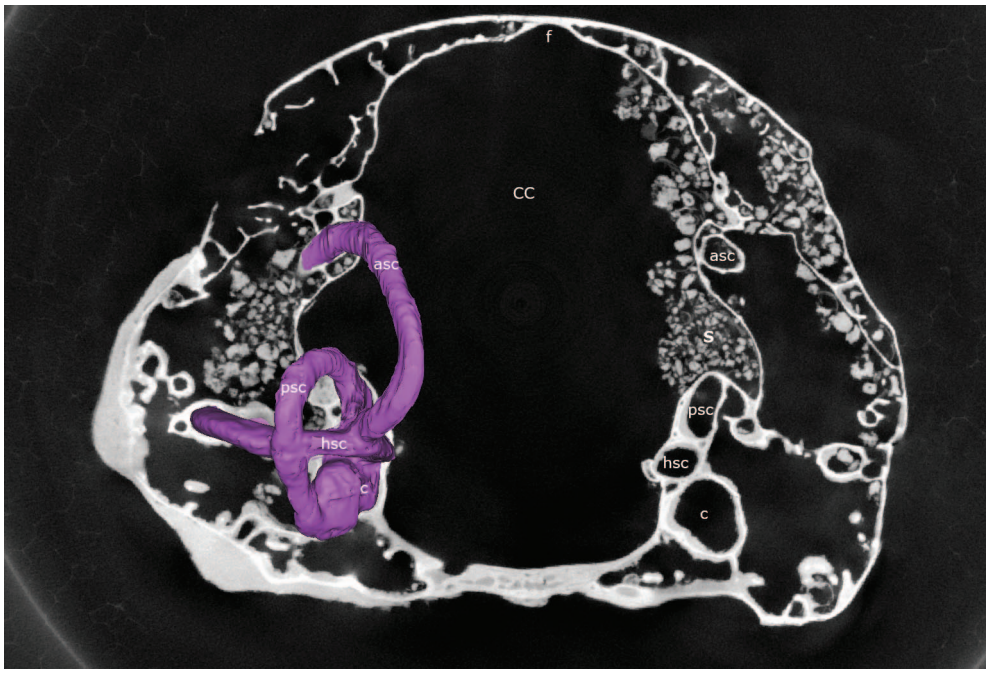


FIGURE 2. Coronal slice through the skull of the Late Oligocene–Early Miocene gull-like or tern-like charadriiform *Laricola elegans*, obtained by high-resolution CT scanning. Left side shows the reconstruction of the inner ear. Abbreviations: asc, anterior semicircular canal; c, cochlea; CC, cranial cavity; f, frontal bone; hsc, horizontal semicircular canal; psc, posterior semicircular canal; S, sediment. Image courtesy of P. Scofield.

and Early Eocene (ca. 60–50 Ma) birds (Walsh et al. 2009, Walsh and Milner 2011, Zelenitsky et al. 2011), but more data from extant species is required to explore these relationships in further detail. However, it is worth noting that data from living taxa is gradually being made available in recent studies on avian endocranial anatomy (e.g., Ksepka et al. 2012, Smith and Clarke 2012, Kawabe et al. 2013).

Inferring the behavior of an extinct bird based on brain morphology is not always straightforward. An understanding of the relationship between behavior and neural function, gleaned from observations of living taxa, is pivotal for neuroanatomical research to assist in the prediction of behavior in extinct birds. However, this is only possible if differences in neural function are causally related to perceptible changes in the volume and morphology of certain regions of the brain (Walsh et al. 2013). It has been reported, for instance, that the relative size of the cerebellar flocculus, a structure that processes reflexes involved in gaze stabilization, is not (contrary to previous hypotheses) a reliable indicator of the flying ability of extant birds (Walsh et al. 2013). Similarly, encephalization quotients in birds (the ratio of actual to expected brain size for an animal of a given body size; Kawabe et al. 2013) have been linked to environmental adaptability and certain life-history traits, but results obtained from studies of some neornithine clades, some of which have included fossil taxa, have not been able to explain these observations (Scofield and Ashwell 2009, Smith and Clarke 2012).

The study of brain and sensory organ evolution in extinct avian taxa within Neornithes is obviously tightly linked to our understanding of brain morphology and neural function in living birds. For this reason, recent research has focused on ecological, behavioral, and phylogenetic aspects of brain morphology in the context of a broad taxonomic sampling of extant forms, although few clades have been looked at (Ashwell and Scofield 2008, Scofield and Ashwell 2009, Ksepka et al. 2012, Smith and Clarke 2012, Kawabe et al. 2014, Paulina-Carabajal et al. 2014, Tambussi et al. in press). These studies appear to indicate that a phylogenetic signal in brain morphology, especially at lower taxonomic levels, may be lost to homoplasy. Furthermore, the amount of neuroanatomical variation at different taxonomic levels (including intraspecific variation) has not been ascertained for most groups within Neornithes.

Finite Element Analysis

Originally developed as an engineering tool, finite element analysis (FEA) is one technique used in biomechanical modeling to understand the functions of complex morphological features (Young et al. 2012). The FEA approach allows the visualization and modeling of stress

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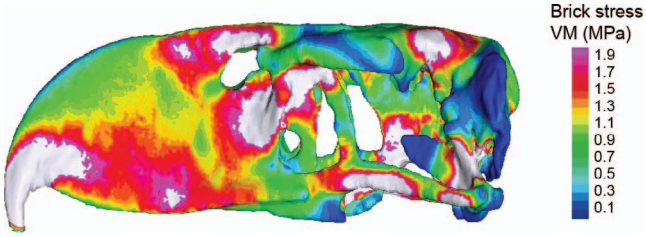


FIGURE 3. Stress distribution of a Finite Element model applied to the skull of the phorusrhacid *Andalgalornis steulleti* under lateral shake load simulation. Abbreviations: VM, Von Misels; MPa, mega pascals. White areas represent stress loads greater than 2 MPa. Image courtesy of F. Degrange.

and strain distributions within complex and irregular shapes, such as animal skeletons, by subdividing the object into a mesh of plates, bricks, elements, and nodes, so as to approximate the complex structure with an object of simpler geometry (e.g., Rayfield 2007). This method, which is based on 3D models, has been applied with increasing frequency in vertebrate paleontology (e.g., Rayfield 2005, Tseng 2009, Young et al. 2012) to predict the mechanical behavior of fossilized biological structures under varying simulated conditions of loading profiles and magnitudes (Figure 3). The interpretation of results often relies on correlating the intensity of areas of functional stress, strain, and/or deformation with morphological features, with the purpose of assessing functionality and inferring aspects of the paleobiology of the extinct taxon (Wroe 2008, Oldfield et al. 2012, Young et al. 2012, Wroe et al. 2013, Attard et al. 2014), thus establishing a relationship between form and function.

Most studies of vertebrate paleontology that have used FEA have focused on the biomechanics of the skull (e.g., Tseng 2009, Oldfield et al. 2012, Young et al. 2012). Cranial biomechanical modeling, in combination with knowledge of morphology (i.e. bone thickness, muscle organization; e.g., Tambussi et al. 2012) and bite force analysis (e.g., Wroe et al. 2005), represents an interesting prospect for assessing the functional adaptations of extinct taxa in terms of feeding ecology and predatory behavior (e.g., Oldfield et al. 2012). However, in the absence of validation studies based on extant taxa, results obtained from FEA methods can only be used in a comparative context (i.e. changes in shape as functional adaptations), rather than in an absolute numerical context (see Bright and Rayfield 2011, Bright 2014). This is because a number of initial conditions that need to be specified in the model, such as the material properties of the skull, may be unknown for a fossil taxon (Bright 2014, but see also Degrange and Tambussi 2009).

Functional analyses based on FEA focusing on living taxa within Neornithes are few (e.g., Degrange et al. 2010, Soons et al. 2010, 2012, Rayfield 2011). Regarding extinct representatives of Neornithes, at present, the phorusrhacid *Andalgalornis steulleti* (Kraglievich 1931) and the New Zealand moa are the only fossil birds for which FEA has been applied to the skull (Degrange et al. 2010, Attard et al. 2014). Phorusrhacids, or 'terror birds,' were giant, predatory, flightless birds that inhabited predominantly South America from reportedly the Late Paleocene (ca. 62–59 Ma) to the Late Pleistocene (<0.5 Ma; Mayr 2009, Alvarenga et al. 2010), although both the youngest and oldest records have been challenged (Agnolin 2013, Tambussi and Degrange 2013). FEA indicates that the skull of *Andalgalornis steulleti* (Figure 3) was best adapted to endure dorsoventral (i.e. sagittal) and rostrocaudal (i.e. as in 'pullback' motions) loadings, but displayed high stress when lateral loadings were applied (Degrange et al. 2010). This suggests that *A. steulleti* was unlikely to engage in behavior that required lateral head shaking (as for subduing large, struggling prey), and was therefore more likely to consume small prey or to administer repeated, targeted sagittal strikes with the beak. The loss of cranial kinesis in phorusrhacid birds, which contributes to enhanced craniofacial rigidity, further explains the reduced stress capacity during sagittal loading (Degrange et al. 2010).

Although the paucity of cranial material from modern birds preserved in the fossil record may somewhat explain the limited number of functional analyses based on FEA for Neornithes, using this method to infer the paleobiology of extinct birds that do not differ considerably in morphology from modern representatives of their lineages, and therefore presumably in feeding strategy, may prove impractical. For that reason, FEA is probably better suited to elucidating the ecology and behavior of 'odd' taxa, especially when this information cannot be inferred with confidence otherwise. Within Neornithes, the unusual cranial morphology of the adzebills (Aptornithidae) makes these birds likely candidates for this approach. Lastly, it is also important to note that paleoecological conclusions drawn from FEA and other forms of biomechanical modeling of the skull (e.g., Witmer and Rose 1991) should not ignore the overall morphology of the taxon when this information is available.

Paleohistology

Another area of vertebrate paleontology to have benefited from recent technological advances is paleohistology: the study of the microanatomical organization of mineralized tissue (mostly bone, but also calcified cartilage, dentine, and enamel) in fossil organisms (e.g., Houssaye 2014). Progress made within this field over the past 80 years has been outlined by de Ricqlès (2011) and Padian (2011). This discipline relies on comparative histology with extant taxa to infer a correlation between bone microstructure and various biological traits of fossil taxa (paleobiology), such

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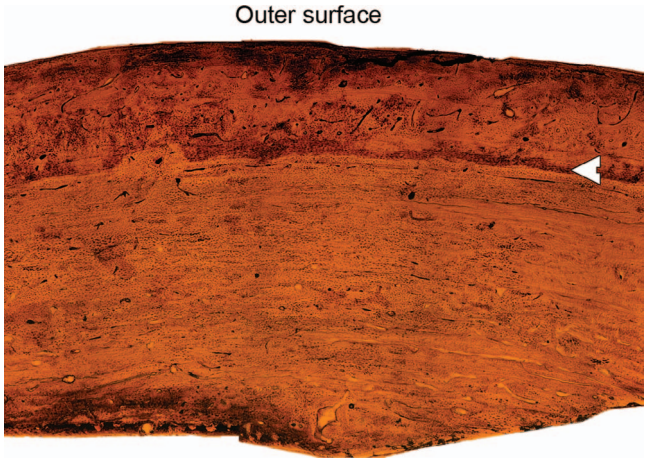


FIGURE 4. Transverse section of the left femur of the moa *Dinornis robustus* (MNHN Av. 8470), showing a line of arrested growth (LAG). Image courtesy of L. Legendre.

as rates of growth, physiology, and functional morphology (e.g., Houssaye 2014, Wilson and Chin 2014).

Currently, 3D virtual imaging complements traditional histological techniques (i.e. preparation of thin sections that are observed in either ordinary or polarized light; e.g., Padian and Lamm 2013), producing virtual tomographic slices that offer a 3D rendering of structures without the need for destructive sampling (i.e. serial sectioning) of specimens (de Ricqlès 2011). New developments within this field also encompass advances in computer science and statistical methods that aid in discerning the different signals present in microanatomy and histology (Cubo et al. 2008, de Ricqlès 2011 and references therein, Legendre et al. 2013). This is because the structure of bone tissue is constrained by a range of different factors, including ontogeny, phylogeny, mechanical adaptations to a specific mode of life, and the environment (Padian 2011, Padian and Lamm 2013), all of which have been investigated in some groups of fossil birds and their living relatives. Despite the potential benefits of this approach, there are currently few studies that have used paleohistology to elucidate ecological and biological aspects of fossil taxa within Neornithes.

Life-history traits of extinct bird taxa can be inferred from paleohistological data. It has been shown, for instance, that some species of moa attained skeletal maturity at ~10 yr, suggesting a *K*-selected life-history strategy that is not uncommon in insular environments (Turvey et al. 2005; see also Chinsamy et al. 2014). Cortical bones of most species of moa display lines of arrested growth (LAGs; Figure 4), which reflect decreased rates of growth in response to seasonal periodicity before an individual reaches skeletal maturity (Turvey et al. 2005). Although LAGs have been reported for a few neornithine birds (Bourdon et al. 2009), with the exception of kiwi (*Apteryx* spp.) this condition is absent in other ratites (Bourdon et al. 2009), and indeed in most other ornithurine birds as well, such as the Mesozoic *Hesperornis* and *Ichthyornis*, and the early-diverging neornithine bird *Vegavis iaai* (e.g., Chinsamy et al. 1998, de Ricqles et al. 2001, Clarke et al. 2005, Bourdon et al. 2009). This is because, as evidenced in extant birds, maturity is reached within 1 yr, i.e. too quickly for annual growth marks to be deposited in the bone cortex (Turvey et al. 2005).

A further recent example of how paleohistology may provide information on life-history traits, and also on evolutionary development in extinct birds, was reported for the so-called 'bony-toothed birds' (Odontopterygiformes), an extinct group of marine birds of uncertain affinities known from the latest Paleocene to the Plio-Pleistocene (ca. 56.0–2.6 Ma; Owen 1873, Mayr 2009, 2011). On the basis of histological thin slices and X-ray microtomography, Louchart et al. (2013; but see also Howard 1957) evaluated hypotheses on how the pseudo-teeth (bony excrescences of the jaw that give the group their name) developed in the Plio-Pleistocene *Pelagornis mauretanicus*. The high degree of vascularization and the parallel-fibred tissue forming the walls of the hollow teeth seem to have posed a functional constraint (i.e. risk of hemorrhage and breakage), which, in addition to the absence of wear observed on the teeth, suggests that these structures must have been covered by a rhamphotheca in life. The rhamphotheca could only have become hardened after growth of the teeth was complete, indicating that this taxon must have been altricial (Louchart et al. 2013).

Histological comparisons of fossil and extant taxa have been performed on a limited number of other neornithine lineages. Smith and Clarke (2014) analyzed bone microstructure in fossil wing-propelled diving charadriiforms (Alcidae) to assess microstructural variation within the group and compared with other taxa. As expected, the cortical thickness of some bones differed from that of the closely related Long-tailed Skua (*Stercorarius longicaudus*: Stercorariidae), and the wall thickness of limb bones varied between volant and nonvolant alcid species. It is therefore possible to discern volant from flightless wing-propelled divers based on fragmentary fossil remains (Smith and Clarke 2014). In an example of how microhistology can also disclose the evolution of physical appearance in bird groups, Clarke et al. (2010) examined melanosomes preserved within a giant fossil penguin from Peru to show that the plumage was likely gray or reddish brown.

It is also noteworthy that the amount of histological variation at different taxonomic ranks, especially at the intra- and inter-specific level, has not been ascertained for most lineages of living birds. Microanatomical variation in the compactness of the internal architecture of the bone at the interspecific level has been documented for Eocene penguins from Antarctica (Cerda et al. 2014), in which

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larger taxa had more massive bones, which is likely to be due to mechanical (larger taxa need more compact bones) or functional (variations in diving behavior) factors. However, the overall paucity of studies dealing with variation at different taxonomic levels makes it difficult to assess the phylogenetic distribution of histological characters. It has been noted that the separation of the phylogenetic component that influences bone microstructure from ontogenic, biomechanical, and environmental signals may prove difficult because these are often linked to phylogeny (Padian and Lamm 2013). Legendre et al. (2014), however, in a study that included the extinct moa and elephant birds, showed that bone size and bone vascular density carry a strong phylogenetic signal within the clade of palaeognathous birds (Palaeognathae). Although a phylogenetic signal of some features has been found to be relevant at higher taxonomic ranks within amniotes (Cubo et al. 2008), it remains to be tested whether this is consistent at lower taxonomic levels (e.g., family-level taxa).

Presently, the implementation of paleohistological techniques on fossil neornithine birds is constrained by the monumental task of assembling comparative data from extant taxa, in order to provide a biological context for making inferences about the paleobiology of fossil taxa. Application of these new methods to a larger number of extant species would help to determine which constraints act on mineralized tissues, and would therefore allow for a more detailed understanding of the paleobiology of fossil birds (Houssaye 2014).

Future Prospects

As the above examples show, the field of paleornithology is experiencing a period of rapid technological and methodological development at the beginning of the 21st century. This is largely being driven by the adoption of techniques developed in other fields for application to fossil remains. If this trend continues, then the future is bright with respect to the amount of new data that will be retrievable from fossil bird remains over the next few decades, and the degree to which this will inform us about living birds. As with most biological sciences, paleornithology is now entering an era of 'big data.'

However, it is important to acknowledge the caveats associated with many of these newly developed techniques. In particular, most (excluding CT imaging) are destructive. Although the amount of material required for different analyses has tended to decrease as techniques are refined, preference should be given in the meantime to the preservation of morphologically important features of fossil bones. This is perhaps less crucial for large fossils (e.g., moa leg bones), where much more material is available for destructive analyses, than for small specimens. We should also not lose sight of the importance of traditional approaches, as the new techniques should only serve to complement, not replace, these. For example, the combination of new genetic techniques and traditional morphological analyses can provide increased resolution around the evolutionary history of extant lineages than either would provide alone (e.g., Mitchell et al. 2014b). Moreover, many of the techniques described in this paper are relevant only to geologically young or relatively complete fossil specimens, and so morphology-based studies will always be key to paleornithology.

It is also essential to acknowledge the vital role of museum and palaeontology department collections as repositories of specimens for continued study. As new analytical methods become available, the ability to apply them to fossils that have previously been analyzed using different methods provides increased scientific value to these specimens.

Additionally, it is worth noting that fieldwork, exploration, and the discovery of new fossil specimens on which to use these techniques remain vital to the field of paleornithology. For example, since the year 2000, remarkable new fossil discoveries have been key to shedding new light on, among other things, the origins of birds (Zhou and Zhang 2007, Feduccia 2013), the diets of ancient birds (e.g., Mayr 2004), the evolution of avian digestive tracts (e.g., Zheng et al. 2011), the origins of plant–bird mutualisms (e.g., Mayr and Wilde 2014), and the evolution of behavior and nesting strategies (Naish 2014). However, such exploratory work can often be difficult to fund. With many major science-funding bodies around the world anecdotally shifting more toward funding projects with a high chance of guaranteed results, as well as more applied (end user–relevant) research, the number of avenues available for funding fieldwork or exploratory (proof-of-concept) projects appear to be diminishing. However, some sources do still exist, through organizations such as National Geographic, or even new initiatives such as crowd-sourcing sites (e.g., www.petridish.org or www.kickstarter.com).

As regards the potential for increased linkages between paleornithology and ornithology in the future, we also see several ways in which this can be nurtured. Although there are some key philosophical differences in the approaches of disciplines focused on historical (e.g., paleornithology) and modern (e.g., ornithology) organisms—the latter are classically driven by empirical testing of a priori hypotheses, whereas the former rely heavily on the discovery and description of specimens and the generation of a posteriori hypotheses to explain them—technological and methodological advances continue to close the gaps by enabling greater analytical and quantitative power in the study of ancient remains and the ability to answer more targeted questions about fossil remains (e.g., regarding diets, breeding biology, and phylogenetic relationships). The

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incorporation of evolutionary- or paleontological-focused symposia at ornithological conferences is also a means by which the two fields can foster integration and increased collaboration. An excellent example of this was achieved at the last (2014) International Ornithological Congress, where 14 of the 48 session themes (29%) focused on aspects of evolutionary history, phylogeographic history, and palaeontology.

There are also likely to be more practical linkages between the past and the present that could be promoted in the future. One way in which paleornithology (at least at the more recent end of its temporal spectrum) could be useful in more applied situations is through the increased implementation of conservation paleobiology, particularly in guiding the restoration of the natural roles of lost birds in ecosystems. To some extent this is already being undertaken on some islands, for example, in Hawaii, where grazing tortoises are being used as ecological surrogates for the extinct flightless moa nalos (*Chelychelynechen*, *Thambetochen*, and *Ptaiochen*; Hansen 2010). However, with the current rate of advances in the field of paleornithology, it may not be too long before extinct species are able to be resurrected, and rock hammers can be replaced by binoculars!

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