A 3D geometric morphometric dataset quantifying skeletal variation in birds

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Abstract

Macroevolution is integral to understanding the patterns of the diversification of life. As the life sciences increasingly use big data approaches, large multivariate datasets are required to test fundamental macroevolutionary hypotheses. In vertebrate evolution, large datasets have been created to quantify morphological variation, largely focusing on particular areas of the skeleton. We provide a landmarking protocol to quantify morphological variation in skeletal elements across the head, trunk, hindlimb and forelimb using 3-dimensional landmarks and semilandmarks, and present a large pan-skeletal database of bird morphology for 149 taxa across avian phylogeny using CT scan data. This large collection of 3D models and geometric morphometric data is open access and can be used in the future for new research, teaching and outreach.

Keywords: birds, geometric morphometrics, macroevolution, morphology, skeleton

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INTRODUCTION

Evolution can be studied from two perspectives: microevolution, the processes that create biological variation at the intraspecific level, and macroevolution, the patterns of variation between groups at the interspecific level (Hautmann, 2020). In the broadest sense, macroevolution concerns the evolution of differences between groups, in species richness and phenotypic disparity. These evolved through extended spans of deep-time, and gave rise to the diversity of life on Earth. Macroevolution encompasses areas of research at the intersection of ecology, genetics, developmental biology and palaeobiology.

Key macroevolutionary questions seek to address variation in the tempo (rate) and mode (pattern) of evolution along lineages (Simpson, 1944; Gingerich, 1983; Schluter, 2000), and the extent to which patterns of taxonomic and phenotypic diversity are explained by speciation, extinction (Jablonski, 2005; Ezard *et al.*, 2011), competition (e.g. Jablonski, 2008; Silvestro et al., 2015; Ezard and Purvis, 2016) and opportunity (e.g. Etienne and Haegeman, 2012). Macroevolutionary theory encompasses inter-disciplinary hypotheses in the biological sciences, such as adaptive radiations (Simpson, 1953; Harmon et al., 2003, 2010; Losos and Mahler, 2010; Yoder et al., 2010), functional adaptation (e.g. Vrba, 1983; Hansen, 1997, 2012), patterns of integration and modularity (Olson and Miller, 1952; Cheverud, 1982; Goswami, 2006; Klingenberg, 2010; Klingenberg and Marugán-Lobón, 2013), innovation and evolvability (Vermeij, 1973). Considerable recent progress on these topics results from the development of powerful quantitative approaches, particularly in geometric morphometrics and phylogenetic comparative methods (e.g. Pennell and Harmon, 2013; Garamszegi, 2014; Adams and Collyer, 2019).

Model Id.	Description
FMNH336751_M3#562	mandible
FMNH336751_M3#563	right coracoid
FMNH336751_M3#564	right scapula
FMNH336751_M3#561	left carpometacarpus*
FMNH336751_M3#565	right tarsometatarsus
FMNH336751_M3#566	sternum
FMNH336751_M3#567	left femur*
FMNH336751_M3#568	skull
FMNH336751_M3#569	left humerus*
FMNH336751_M3#570	synsacrum
FMNH336751_M3#571	left radius *
FMNH336751_M3#572	left tibiotarsus*
FMNH336751_M3#573	left ulna*

Table 1. One of the specimens, FMNH 336751 (*Menura novaehollandiae*, the superb lyrebird), is presented here. Sets of 3D landmarks and semi-landmarks have been digitized on the different bones listed. Collection: Field Museum of Natural History, Chicago, USA. The 3D models and CT scans of the 149 specimens related to this project can be downloaded at MorphoSource (https://www.morphosource.org/projects/00000C420). *: these 3D models are displayed as mirror images in MorphoMuseuM 3D viewer.

The life sciences have entered an era of big data, in which fundamental questions can increasingly be addressed with large datasets. This is also true of phenotypic macroevolution (e.g. Wilman et al., 2014 [ecological traits]; Pigot et al., 2020 [external traits]), an area that was traditionally approached from a qualitative standpoint or using limited characterisations of the traits of organisms such as linear measurements, body mass estimates, or studies of skeletal parts such as the skull or mandible (e.g. Alroy, 1998; Livezey and Zusi, 2007; Nudds et al., 2007;

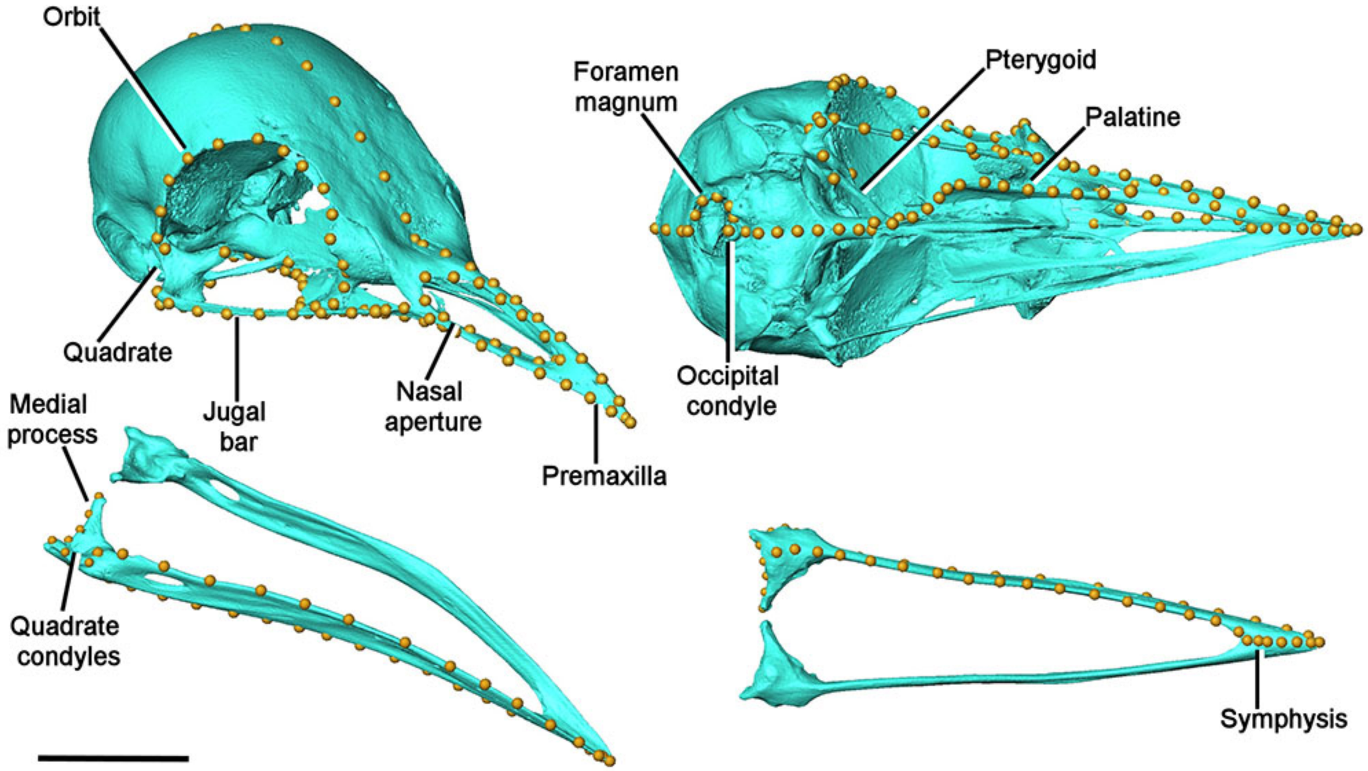

Figure 1. Head landmarks and semilandmarks shown on the skull and mandible of *Menura novaehollandiae* (FMNH 336751). The skull (A) in dorsolateral (left) and ventral (right) views, and mandible (B) in dorsolateral (left) and ventral (right) views. Scale bar equals 20 mm.

Cooper and Purvis, 2010; Venditti et al., 2011). Phenotypic data assembly has been accelerated by technologies that allow rapid 3D digitisation of morphology (e.g. Davies et al. 2017). Improved access to CT scanning and high-resolution handheld scanners means researchers can make accurate 3-dimensional (3D) models of external morphology, including study skins allowing for example quantification of the head in snakes and rhamphotheca in birds (Fabre *et al.*, 2016; Segall *et al.*, 2016; Cooney *et al.*, 2017; Segall, Herrel and Godoy-Diana, 2019) and hard tissues such as vertebrate bones (Felice and Goswami, 2018; Watanabe *et al.*, 2019; Bardua *et al.*, 2020; Coombs *et al.*, 2020; Fabre *et al.*, 2020; Fischer *et al.*, 2020). High resolution scans can be used to make large morphological datasets quantifying variation with geometric morphometric methods, providing opportunities for large, quantitative datasets to address central macroevolutionary questions and push the frontier of macroevolutionary research (e.g. Corfield et al., 2015; Cooney et al., 2017; Felice and Goswami, 2018; Watanabe et al., 2019; Bardua et al., 2020; Navalón et al., 2020; Paluh et al., 2020). Macroevolutionary studies have so far enriched our understanding of vertebrate cranial evolution (e.g. Bhullar et al., 2012; Felice and Goswami, 2018; Arbour et al., 2019; Paluh et al., 2020) and that of other anatomical units (e.g. Botelho et al., 2014; Arnold et al., 2017; Shatkovska et al., 2018; Serrano et al., 2020). However, organisms are generally complex, comprising multiple interacting parts, and few studies have quantified wider aspects of skeletal variation beyond studies of integration (e.g. Bell et al., 2011; Dececchi and Larsson, 2013; Fabre *et al.*, 2014; Heers and Dial, 2015; Martín-Serra et al., 2015; Botton-Divet *et al.*, 2016; Wright et al., 2016; Hanot *et al.*, 2018; Randau and Goswami, 2018; Michaud *et al.*, 2020).

Until recently, the expense and difficulty of accessing CT scanning and relative lack of postcranial material in natural history collections has created gaps in our understanding of skeletal macroevolution that leads to key questions: How universal are evolutionary patterns inferred from single bones to the whole organism? How does functional or developmental integration among the components of organisms structure macroevolutionary patterns? And how does the influence of ecomorphological adaptation vary among parts of the organism?

We quantified morphology across 13 skeletal units using a novel geometric morphometric landmarking scheme (see Supplementary 1-3, available at https://doi.org/10.18563/journal.m3.125.supp.data; see also Table 1.): the head (skull and mandible; see Fig. 1), trunk (scapula, coracoid, sternum and synsacrum; see Fig. 2), forelimb (humerus, ulna, radius, carpometacarpus; see Fig. 3) and hindlimb (femur, tibiotarsus and tarsometatarsushumerus; see Fig. 4). We present a pan-skeletal database of birds (Aves) skeletal morphology comprising CT scans of the entire skeleton of 149 species, of broad phylogenetic scope (https://www.morphosource.org/projects/00000C420). This is the basis of our in-preparation macroevolutionary investigations, and we anticipate that our 3D datasets will be of value to other researchers. Birds are one of the most speciose vertebrate groups with over 10,000 extant species (Gill et al. 2020). They are feathered, have lightweight bills and no teeth, small

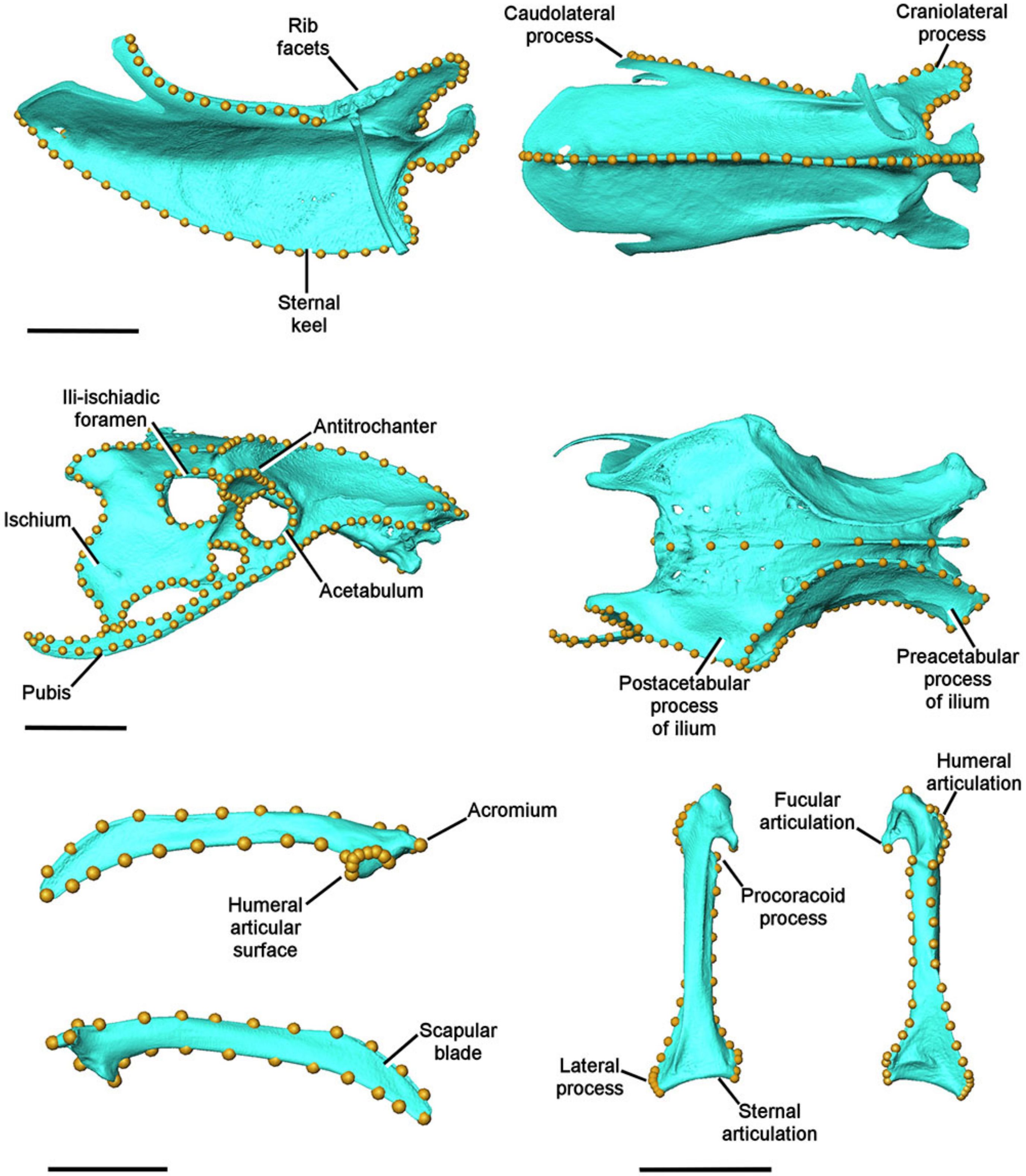

Figure 2. Trunk landmarks and semilandmarks shown on the synsacrum, scapula and coracoid of *Menura novaehollandiae* (FMNH 336751). The sternum (A) in lateral (left) and ventral (right) views, synsacrum (B) in lateral (left) and dorsal (right) views, scapula (C) in lateral right (top) and lateral left (bottom) views, and coracoid (D) in ventral (left) and dorsal (right) views. Scale bars equal to 20 mm.

Skeletal element	Number of points for minimum "min" configuration	Number of points for "mean" configuration
Skull	158	420
Mandible	43	109
Sternum	67	383
Synsacrum	208	510
Scapula	31	71
Coracoid	33	71
Humerus	79	145
Radius	10	20
Ulna	28	54
Carpometacarpus	77	166
Femur	62	128
Tibiotarsus	52	97
Tarsometatarsus	57	118

Table 2. Number of resampled landmark points for each skeletal element showing the number of points for the minimum ("min") configuration (left) and "mean" configuration (right).

body sizes, pneumatised bones and highly fused skeletons, are mostly capable of flight, and are adapted for a wide range of environments with large variation in morphology, behaviour and ecology (Proctor and Lynch, 1993; Wilman et al. 2014). The past decade has seen major advances in our understanding of avian macroevolution (e.g. Jetz et al., 2012; Jarvis et al., 2014; Prum et al., 2015; Bright et al., 2016; Cooney et al., 2017; Felice and Goswami, 2018; Felice et al., 2019; Oliveros et al., 2019; Navalón et al., 2020; Pigot et al., 2020), and future investigations of skeletal morphology using CT scan data will go far beyond what we have been able to achieve so far.

METHODS

Our dataset includes 149 genera belonging to 106 families and 33 orders, representing most major avian groups (Supplementary 1). These taxa, or close relatives that can be used as proxies, are all present in the Prum et al. (2015) avian molecular phylogeny, which provides a framework for phylogenetic comparative methods of our dataset (Supplementary 1). Our dataset was assembled by lab-based micro-CT scanning of specimens from major museum collections: Natural History Museum of London, bird collection, Tring, UK (NHMUK); University of Cambridge Museum of Zoology, Cambridge, UK (UMZC); University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA (UMMZ); Field Museum of Natural History, Chicago, USA (FMNH); University of Oxford Museum of Natural History, Oxford, UK (OUMNH); and Yale Peabody Museum, New Haven, Connecticut, USA (YPM). We also used multiple CT scanning facilities: including Nikon Metrology XT H 225 ST High Resolution CT Scanner systems at (A) School of Life Sciences, University of Bristol, Bristol UK; (B) Computed Tomography facility, Natural History Museum, London, UK (C) Cambridge Biotomography Centre, Cambridge, UK; and (D) Earth and Environmental Sciences CT facility, University of Michigan, Ann Arbor, USA; and (E) Yale University's Chemical and Biophysical Instrumentation Centre (CBIC); and custom-built dual tube CT scanner from General Electric (phoenix v—tome—x s) at the PaleoCT facility of University of Chicago, Chicago, USA. Metadata for each scan including specimen repository, CT facility, and scan settings are available at the Morphosource page associated with this publication. CT scans were initially reconstructed as 16-bit tomograms. Pre-processing steps including stitching of multiple scan volumes to single image volumes, cropping image volume, and conversion of image volumes from 16-bit to 8-bit were carried out using ImageJ 1.5 (Schneider et al., 2012). Volume data were imported into Avizo 9.3 (Thermo Fisher Scientific, Zuse Institute Berlin) for segmentation and exported as PLY files. The resulting 8-bit image volumes, 3D surfaces and scan metadata are available via Morphosource (https://www.morphosource.org/projects/00000C420).

Procrustes-based geometric morphometric data was collected in Avizo 9.3, using anatomical landmarks and semi-landmark series ((Gower, 1975; Rohlf and Slice, 1990; Rohlf and Marcus, 1993; Adams, Rohlf and Slice, 2004, 2013; Bhullar *et al.*, 2012), Figs 1–4). Detailed landmark descriptions and figures are provided in Supplementary 2. Anatomical consideration leading to landmark specification was based on multiple studies of avian morphology (Baumel and Witmer, 1993; Zusi, 1993; Livezey and Zusi, 2006; Kulemeyer *et al.*, 2009; Tokita *et al.*, 2017) and our own observations. Anatomical terms of orientation follow Clark (1993) using cranial (or rostral when referring to the head) and caudal rather than anterior or posterior. Summary landmark and semi-landmark configurations with major anatomical structures labelled are shown here using *Menura novaehollandiae* (FMNH 336751) for the head (Fig. 1), trunk (Fig. 2), forelimb (Fig. 3) and hindlimb (Fig. 4). Semi-landmarks were used to characterise curves, but not surfaces, and curves were initially characterised using variable numbers of points, according to structural complexity. They were then resampled to equal numbers of evenly spaced points in the data presented here for morphometric analysis. Resampling was conducted according to two different criteria: (1) The minimum ("min") criterion, in which semilandmarks were resampled so that each curve contained the same number of points equal to that of the specimen with the fewest number of points for that series; and (2) The "mean" criterion, in which semilandmarks were resampled so that each contained the mean number of points across all specimens (Table 2). Due to the frequency of specimens having damage to either the left or right part of a skeletal element, our overall dataset samples a mix of left- and right-side elements, with all left sided landmarks reflected to simulate right-sided elements prior to Generalized Procrustes Analysis (GPA). Just one of each skeletal element was landmarked per specimen to maximise the number of taxa that were sampled during the data collection phase of our project, and this one-sided landmarking approach is accurate at quantifying size and shape at the macroevolutionary scale (Cardini 2016, 2017). Due to expediency and maximising our time for data

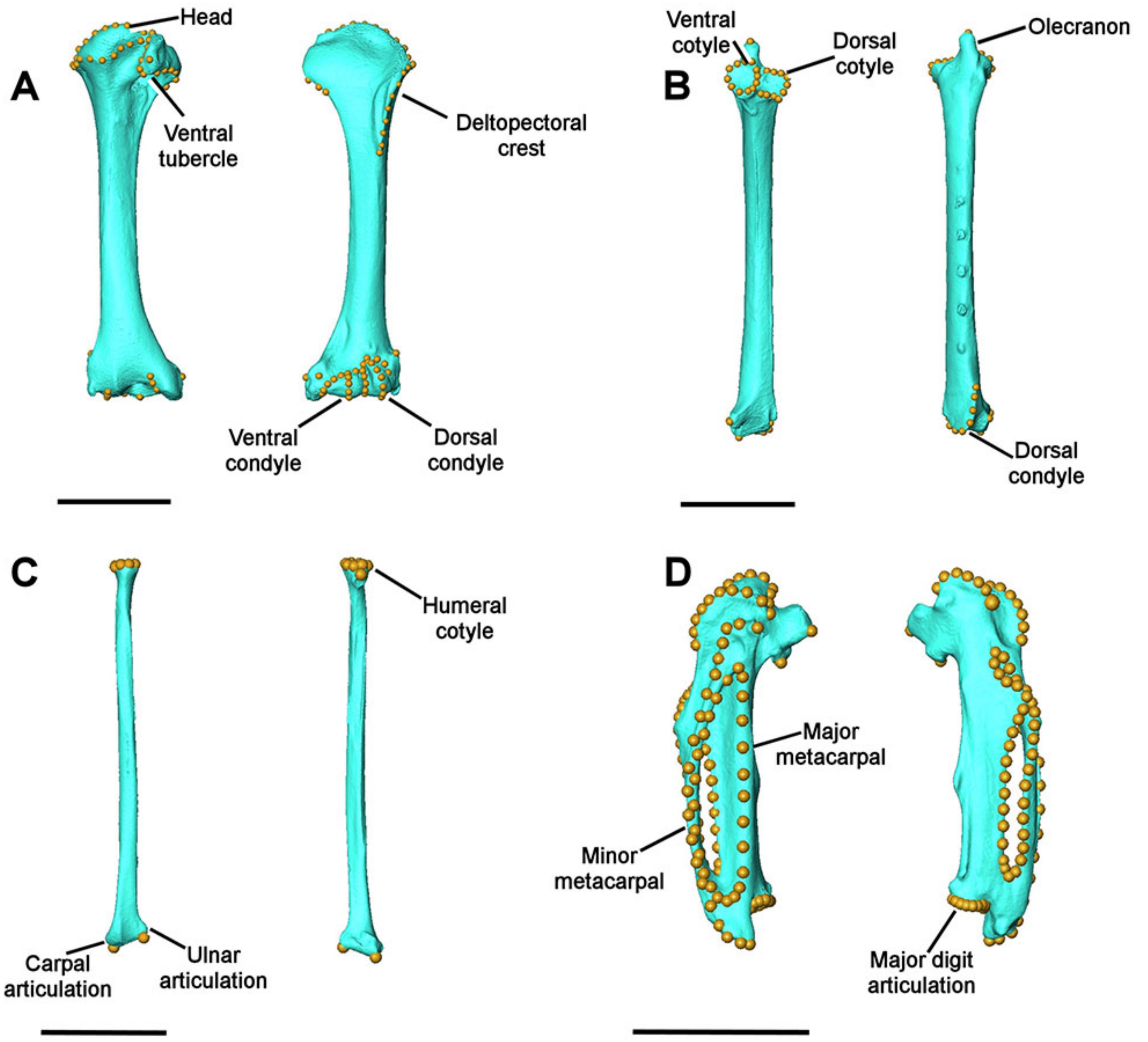

Figure 3. Forelimb landmarks and semilandmarks shown on the humerus, ulna, radius and carpometacarpus of *Menura novaehollandiae* (FMNH 336751). The humerus (A) in caudal (left) and cranial (right) views, ulna (B) in cranial (left) and caudal (right) views, radius (C) in cranial (left) and caudal (right) views, and carpometacarpus (D) in ventral (left) and dorsal (right) views. Scale bars equal 20 mm.

collection, we also landmarked only one side of each bilaterally-symmetrical element. Our data are therefore appropriate only for analyses that do not seek to analyse bilateral symmetry. Cardini (2016, 2017) noted that when sampling one half of a bilaterally symmetrical skeletal element with midline landmarks, it is advisable to mirror the missing landmarked side prior to GPA for increased accuracy, as landmarks perpendicular to the midline can be erroneously misplaced during the GPA. As a result, for bilaterally symmetrical skeletal regions of the skull, sternum and synsacrum, one half of the structure was landmarked, including along the midline, in each specimen and the collected bilateral landmarks were mirror reflected for use in the GPA. These reflected elements should not be considered for analysis of bilateral symmetry.

Data files containing our landmarks are presented in CSV and TPS formats in Supplementary 3, in a form that is readily analysable using functions in geomorph version 3.2.1 (Adams et al. 2020) and can be read into alternative geometric morphometric software such as MorphoJ. This includes relevant metadata such as matrices specifying tangent vectors for sliding semilandmarks, vectors of point colours specifying membership to semilandmark series, and original input data (i.e. with variable numbers of semilandmark points among specimens).

DISCUSSION

We present a large, broad-scope, multi-element geometric morphometric dataset of avian skeletal morphology. This dataset can be used to investigate some of the major questions in vertebrate and avian macroevolution including patterns of evolution across the skeleton, the contribution of modularity and integration to skeletal variation, and the relationship between size and shape (allometry) among and within parts of the skeleton. The large 3D database will be useful for studies of functional morphology and anatomy, including comparative osteology and phylogenetics, and complements other publically available avian databases including those on Phenome10k (https://www.phenome10k.org/), Aves 3D (https://www.aves3d.org/) and the major oVert scanning project housed on morphosource (https://www.morphosource.org/). Our CT scan data is also available to be used for investigating aspects of morphology we have not included in our data collection, such as finite element analysis, cross-sectional analysis of bone structure and microstructure, musculoskeletal and range of motion models, bioinspiration, bilateral symmetry, cranial endocasts and inner ear morphology. Our landmark and semi-landmark configurations should be considered as an initial proposal that is useful for investigating large-scale aspects of avian skeletal evolution. More detailed schemes, including surface semilandmarks or high-density landmarking (e.g. Felice and Goswami, 2018; Bardua et al., 2019b, 2019a; Goswami et al., 2019; Watanabe et al., 2019) may add further to our understanding of this topic in future, or in detailed studies of local regions of the avian skeleton.

As recently recommended (Davies et al., 2017), our data is open access in order to improve reproducibility and encourage the reuse of data and models in new studies. Bird morphology is fascinating to researchers and the 3D models associated with our dataset have clear utility in new avenues of research, and we also hope they can also be used in teaching and outreach.

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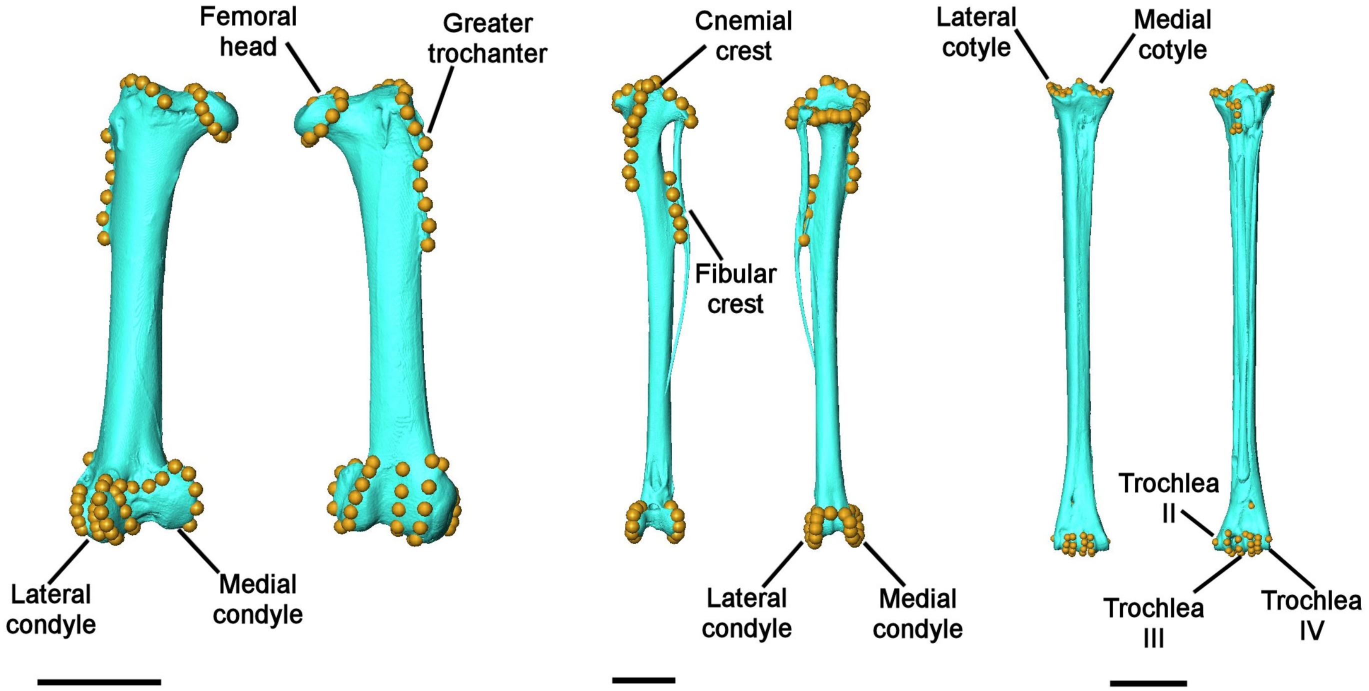

Figure 4. Hindlimb landmarks, semilandmarks shown on the femur, tibiotarsus and tarsometatarsus of *Menura novaehollandiae* (FMNH 336751). The femur (A) in caudal (left) and cranial (right) views, tibiotarsus (B) in cranial (left) and caudal (right) views, and tarsometatarsus (C) in dorsal (left) and plantar (right) views. Scale bars equal 20 mm.

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