

Correlated evolution of sternal keel length and ilium length in birds

Tao Zhao¹, Di Liu^{2,3,4} and Zhiheng Li³

¹ School of Earth Sciences and Engineering, Nanjing University, Nanjing, China

² University of Chinese Academy of Sciences, Beijing, China

³ Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China

⁴ Beijing Museum of Natural History, Beijing, China

ABSTRACT

The interplay between the pectoral module (the pectoral girdle and limbs) and the pelvic module (the pelvic girdle and limbs) plays a key role in shaping avian evolution, but prior empirical studies on trait covariation between the two modules are limited. Here we empirically test whether (size-corrected) sternal keel length and ilium length are correlated during avian evolution using phylogenetic comparative methods. Our analyses on extant birds and Mesozoic birds both recover a significantly positive correlation. The results provide new evidence regarding the integration between the pelvic and pectoral modules. The correlated evolution of sternal keel length and ilium length may serve as a mechanism to cope with the effect on performance caused by a tradeoff in muscle mass between the pectoral and pelvic modules, via changing moment arms of muscles that function in flight and in terrestrial locomotion.

Subjects Evolutionary Studies, Paleontology, Zoology

Keywords Birds, Correlated evolution, Sternal keel length, Ilium length, Early birds

INTRODUCTION

Although the pectoral module (the pectoral girdle and limbs) and the pelvic module (the pelvic girdle and limbs) of birds are specialized for different functions, they are likely to be linked during evolution (Allen *et al.*, 2013; Gatesy & Dial, 1996; Heers & Dial, 2015). This linkage could be a result of developmental and functional constraints (Allen *et al.*, 2013; Young, Hallgrímsson & Janis, 2005), as the pectoral and pelvic limbs share a broad range of development pathways, though they acquire distinct identity in adults in tetrapods (Young, Hallgrímsson & Janis, 2005). Restricted by overall resources availability, pectoral and pelvic modules are negatively correlated in skeletal mass and muscle mass (Heers & Dial, 2015). In addition to simple resource partitioning, changes to one of the two modules, for example, an elongation of the forelimb, have implications for shifts in the position of center of mass, which can further alter the hindlimb posture and functions (Allen *et al.*, 2013; Dececchi & Larsson, 2013; Hutchinson & Allen, 2009). But the functional specialization could also weaken the integration between the pectoral and pelvic limbs, as suggested by morphometric analyses of avian and mammalian limbs (Bell, Andres & Goswami, 2011; Schmidt & Fischer, 2009; Young, Hallgrímsson & Janis, 2005). This conflict

Submitted 20 April 2017

Accepted 7 July 2017

Published 26 July 2017

Corresponding authors

Tao Zhao, zhaotao@smail.nju.edu.cn,

zhaotao_nju@126.com

Zhiheng Li, lizhiheng@ivpp.ac.cn

Academic editor

Virginia Abdala

Additional Information and
Declarations can be found on
page 7

DOI 10.7717/peerj.3622

© Copyright
2017 Zhao et al.

Distributed under
Creative Commons CC-BY 4.0

OPEN ACCESS

between drivers of limb evolution necessitates empirical studies to understand whether and how traits of pectoral and pelvic modules co-vary.

Along the theropod to avian lineage leading to the origin of crown birds, a series of morphological changes in the pectoral and pelvic girdles have previously been identified (*Brusatte Stephen, O'Connor Jingmai & Jarvis Erich, 2015; Makovicky & Zanno, 2011*). In the pectoral girdle, the changes include the enlargement of the sternum and keel (*O'Connor et al., 2015; Zheng et al., 2014; Zheng et al., 2012*), the elongation of the coracoid (*Zheng et al., 2014*), the origin of an acrocoracoid process and the triosseal canal (*Baier, Gatesy & Jenkins, 2007; Longrich, 2009*), the reorientation of the glenoid fossa from laterally directed to dorsolaterally directed (*Jenkins, 1993*), and the transformation of the furcula from boomerang-shaped to U-shaped (*Nesbitt et al., 2009; Zhou & Zhang, 2002*). In the pelvic girdle we find the elongation of the ilium and the loss of the pubic symphysis (*Hutchinson, 2001*). Of these changes, two major derived features that characterize derived birds are the larger sternal keel and the longer ilium (*Hutchinson, 2001; O'Connor et al., 2015*). This pattern of similar first appearances of these two key features could result from the correlated evolution between the sternal keel and the ilium, since pectoral and pelvic modules are suggested to be integrated in evolution (*Allen et al., 2013; Heers & Dial, 2015*). Here we compile morphometric data on extant birds and Mesozoic birds to empirically test this hypothesis based on sternal keel length and ilium length.

MATERIAL AND METHODS

Data collection on extant birds

We sampled 224 skeleton specimens with body mass data of 137 volant bird species from 45 families of 19 orders. All the specimens are housed in the collection of Beijing Museum of Natural History ([Table S1](#)). Sternal keel length and ilium length were taken with a digital caliper (± 0.01 mm) ([Fig. 1](#)). When multiple specimens were measured for a species, the mean values of those specimens were used. These variables were log₁₀-transformed before subsequent analyses.

Phylogenetic comparative methods

All analyses were carried out in R 3.3.3 (*R Core Team, 2017*) using packages “ape” (*Paradis, Claude & Strimmer, 2004*), “phytools” (*Revell, 2012*) and “paleotree” (*Bapst, 2012*). [Figure 2](#) was created using “ggplot2” (*Wickham, 2009*) and RColorBrewer (*Neuwirth, 2014*).

Phylogeny and size-correction

We used 1,000 time-calibrated phylogenetic trees for the 137 species included in our study from [birdtree.org](#) (*Jetz et al., 2012*). Phylogenetic size-correction of log₁₀-transformed ilium length and keel length was conducted using the function `phyl.resid` in the “phytools” (*Revell, 2012*).

Evolutionary rate matrix

Under the assumption of Brownian motion model, the variance of a trait at a given time interval is equal to the length of the time interval times the Brownian motion rate parameter, σ^2 . The multivariate Brownian motion is governed by the evolutionary rate matrix, which

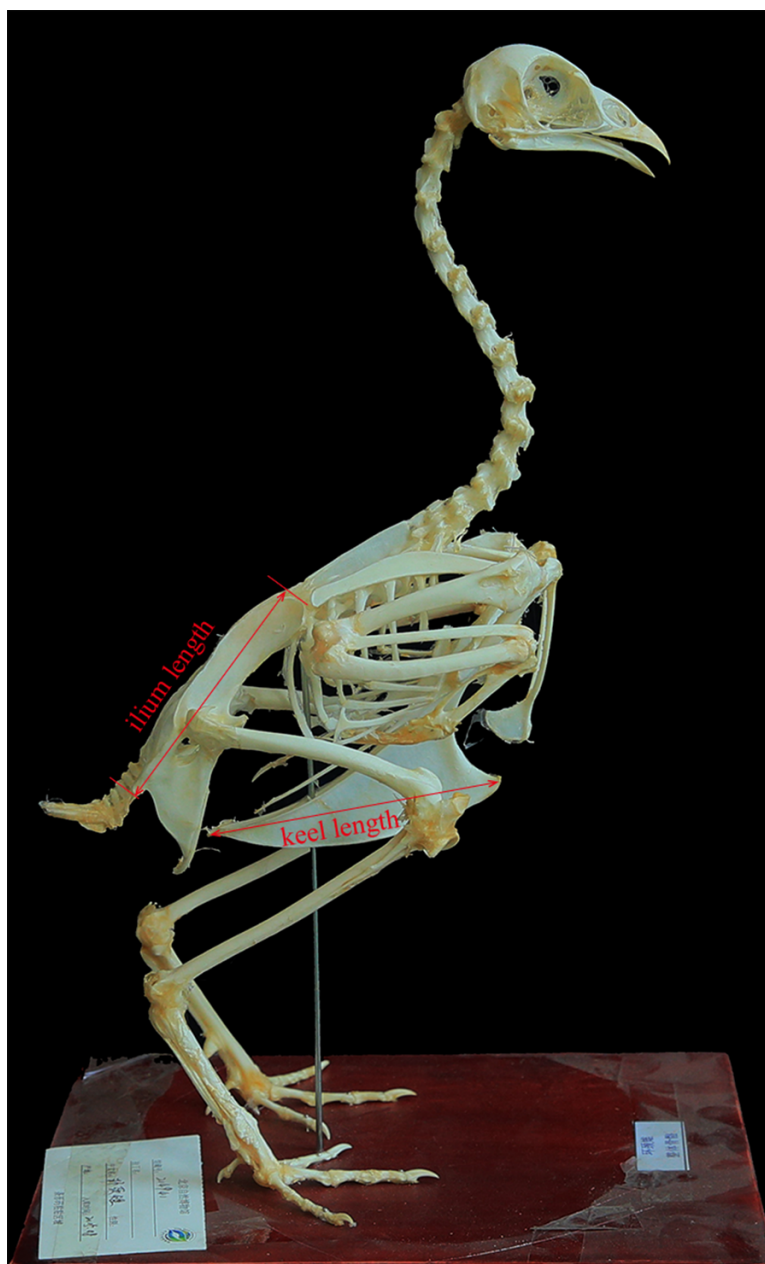


Figure 1 Measurements used in this study (*Phasianus colchicus*, BMNH 214941, in lateral view).
Photo credit: Qiong Wang.

contains the evolutionary variances or rates (σ^2) for individual characters on its diagonals and the evolutionary covariances on its off-diagonals (Revell & Collar, 2009; Revell & Harmon, 2008). The Pearson correlation coefficient (r) can be calculated based on these values. This analysis was implemented using the function `evol.vcv` in the “phytools” (Revell, 2012). The Pearson correlation coefficients from iterations across the 1,000 trees were averaged, weighted by their Akaike weights based on AICc (Burnham & Anderson, 2002).

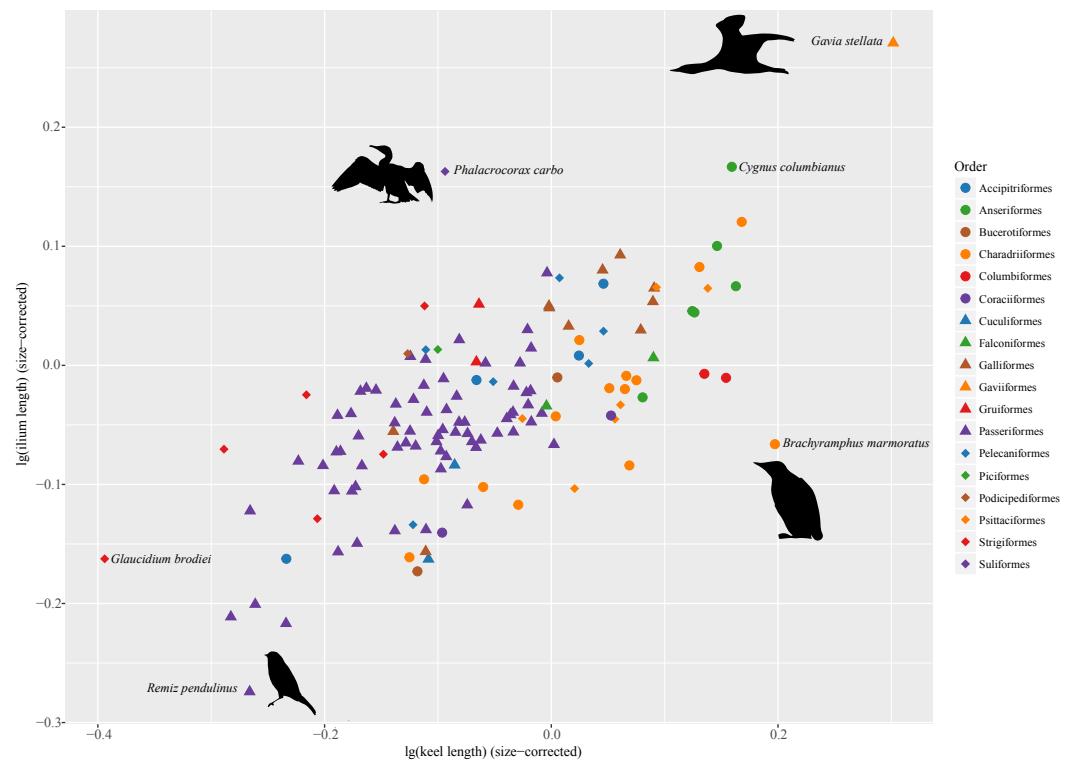


Figure 2 Morphospace defined by sternal keel length and ilium length showing distribution of extant birds. Silhouettes were modified from images licensed under creative commons: *Gavia stellata* (Tony Morris, <https://www.flickr.com/photos/tonymorris/429265757/>); *Phalacrocorax carbo* (Tony Morris, <https://www.flickr.com/photos/tonymorris/6102041629/>); *Remiz pendulinus* (Michele Lamberti, <https://www.flickr.com/photos/60740813@N04/8360911825/>); *Brachyramphus marmoratus* (J. J. Audubon, <http://www.faculty.ucr.edu/~legnerref/birds/jpg/avex178.jpg>).

As the Pearson correlation coefficient does not follow a normal distribution, Fisher transformation was used during the process.

Mesozoic birds

To determine whether keel length and ilium length are correlated during early evolution of birds, we sampled 10 Mesozoic avian species housed in the collection of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. Sternal keel length, ilium length and femur length were measured (Table S1). They were log₁₀-transformed before subsequent analyses. Calibration dates for these taxa were adapted from Wang & Lloyd (2016a) and Wang & Lloyd (2016b). A phylogenetic tree including these 10 species was constructed manually based on a recent phylogenetic analysis (Wang & Zhou, 2017). The fossil bird tree was time-calibrated using the function timePaleoPhy with the “equal” method in the “paleotree” (Bapst, 2012), with tip dates drawn randomly from a uniform distribution between the maximum and minimum dates, producing 1,000 trees. The estimate of the evolutionary rate matrix was iterated across these 1,000 trees to account for the uncertainty in time-calibration. The estimated correlation coefficients from 1,000 iterations were averaged, weighted by Akaike weights.

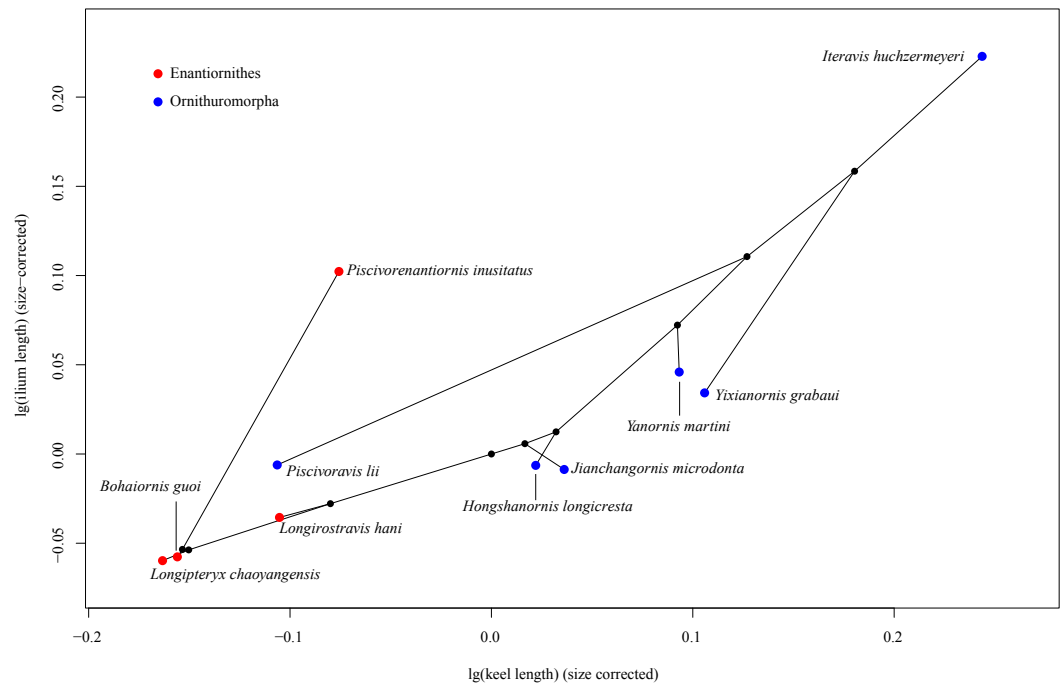


Figure 3 Phylomorphospace depicting a Mesozoic bird tree in shape space defined by sternal keel length and ilium length.

RESULTS

In extant birds, the correlation between sternal keel length and ilium length is 0.77 (95% CI [0.69–0.84]). Similarly, the correlation is 0.90 in Mesozoic birds (95% CI [0.61–0.98]). Both are positive and statistically significant, as their 95% confidence intervals do not include 0.

In the morphospace defined by sternal keel length and ilium length (Fig. 2), several outliers are identifiable in these extant birds. *Phalacrocorax carbo* deviates from other taxa by entering the upper-left space, indicating that it has relatively long ilia but a relatively short keel. By contrast, *Brachyramphus marmoratus* enters the lower right space, by having a relatively long keel but relatively short ilia. *Gavia stellata* also deviates from others, but it largely follows the pattern of a positive correlation between sternal keel length and ilium length.

In the phylomorphospace defined by sternal keel length and ilium length of Mesozoic birds (Fig. 3), the enantiornithines are located in the lower left part, while the ornithuromorphs in the upper right part, indicating that the ornithuromorphs have a longer keel and longer ilia than the contemporary enantiornithines. An exception is a recent described enantiornithine bird, *Piscivorenantioornis inusitatus*, which has relatively longer ilia than most ornithuromorphs except *Iteravis huchzermeyeri*. *Piscivoravis lii* differs from other ornithuromorphs in having a comparatively shorter keel and shorter ilia.

DISCUSSION

Our results support the hypothesis that ilium length and sternal keel length are correlated during avian evolution and further provide quantitative support of the integration between pelvic and pectoral modules (Allen *et al.*, 2013; Gatesy & Dial, 1996; Heers & Dial, 2015). Among basal birds, an ossified sternal keel is absent in *Archaeopteryx*, *Jeholornis* and *Sapeornis*, and only a faint keel is present in *Confuciusornis* (Chiappe, Ji & Ji, 1999; O'Connor *et al.*, 2015; Zheng *et al.*, 2014). The keel is small and restricted to the caudal part of the sternum in Early Cretaceous enantiornithines (O'Connor *et al.*, 2011; Wang & Zhou, 2017; Zheng *et al.*, 2012), while comparatively larger in ornithuromorphs (e.g., Zhou & Zhang, 2001; Zhou & Zhang, 2006). Despite these differences, the recovered positive correlation between the sternal keel length and ilium length based on data of enantiornithines and ornithuromorphs suggests that this pattern appears very early in avian evolution.

Heers & Dial (2015) showed that the pectoral and pelvic modules are negatively correlated in muscle mass and skeletal mass and suggested the tradeoff in investment is associated with a tradeoff in performance. In other words, the less-invested module has to cope with a larger burden. The correlated evolution of sternal keel length and ilium length may serve as a mechanism to offset, to some extent, the effect on performance caused by the tradeoff in muscle mass via changing moment arms of pectoral muscles and hindlimb muscles, because the torque produced by a muscle is determined by its mass and moment arm and the effect caused by a decrease in the muscle mass can be offset by an increase in the muscle moment arm. This requires that the mass and moment arm of a muscle can be modified independently to some extent. The sternal keel provides a surface for the attachment of muscles essential for flight, i.e., *m. supracoracoideus* and *m. pectoralis*; therefore, their moment arms can be directly affected by changes of sternal keel length. Though sternal keel length is correlated with the mass of these muscles ($R^2 = 0.47$; Wright, Steadman & Witt, 2016), parts of their variances cannot be statistically explained by each other. These facts imply that during evolution of flight, birds have the potential to modify masses and moment arms of pectoral muscles independently. Indeed, long-distance migratory birds can adjust the mass of pectoral muscles during their lifetime (Dietz *et al.*, 2007; Lindstrom *et al.*, 2000). Similarly, evolution of hindlimb functions may be achieved through changing the masses or moment arms of hindlimb muscles, though their relationship has not been empirically estimated. These inferences need to be tested in future studies.

In the sampled extant birds, two birds, i.e., *Brachyramphus marmoratus* and *Phalacrocorax carbo*, are major outliers from other taxa in the morphospace defined by sternal keel length and ilium length (Fig. 2). As a wing-propelled diver, *Brachyramphus marmoratus* has an elongated keel which accommodates the enlarged *m. supracoracoideus* and the elongated *m. pectoralis* to flap the wing in the water, which is about 800 times as dense as air (Kovacs & Meyers, 2000; Spear & Ainley, 1997). To adapt to this situation, the pelvic girdle of *B. marmoratus* shifts to an upright posture rather than acquires an elongated ilium as in other birds (Fig. 2) (Storer, 1945). The relatively long ilium in *Phalacrocorax carbo* is an adaptation of foot-propelled diving (Hinić-Frlog & Motani, 2010). Its comparatively

shorter sternal keel than that of other foot-propelled divers, for example, *Gavia stellata*, is associated with its weak flight ability; it can only slope soar in strong winds (Norberg, 1990). *Phalacrocorax carbo* is an example of the evolution towards flightlessness with the pelvic module enhanced and the pectoral module reduced (Wright, Steadman & Witt, 2016), which is seen in some flightless birds such as the Galápagos cormorant (*Phalacrocorax harrisi*) (Livezey, 1992) and ratites (Cracraft, 1974).

Among our sampled Mesozoic birds, *Piscivorenantornis inusitatus*, a fish-eating enantiornithine (Wang & Zhou, 2017; Wang, Zhou & Sullivan, 2016), differs from other enantiornithines (*Longipteryx chaoyangensis*, *Bohaiornis guoi* and *Longirostravis hani*) in that it has relatively longer ilia (Fig. 3). The functional significance of this feature in *P. inusitatus* is unclear, but in extant birds it is associated with an aquatic lifestyle (Hinić-Frlog & Motani, 2010; Stoessel, Kilbourne & Fischer, 2013). This provides additional evidence of its ecology besides the pellet found associated with the holotype skeleton (Wang, Zhou & Sullivan, 2016).

In summary, pectoral and pelvic modules are linked in a more complicated way than just negatively correlated in overall investment. Besides modifying moment arms of muscles, birds may change behaviors to cope with the effect caused by tradeoff in investment. Moreover, these two modules may be linked through avian eggs, the shape of which is suggested to be correlated with both the pelvic shape (Dyke & Kaiser, 2010; Mayr, 2017) and flight ability (Stoddard et al., 2017). More integrative studies in the future can provide more insight into the relationship between pectoral and pelvic modules.

ACKNOWLEDGEMENTS

We thank Mr. Zhaohui Zeng for access to specimens housed in Beijing Museum of Natural History and Mr. Qiong Wang for taking the photo for Fig. 1. Comments from Jonathan Mitchell and T. Alexander Dececchi improved the manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

The research was supported by the National Natural Science Foundation of China (91514302, 41688103). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
National Natural Science Foundation of China: 91514302, 41688103.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Tao Zhao conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Di Liu performed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, reviewed drafts of the paper.
- Zhiheng Li performed the experiments, wrote the paper, reviewed drafts of the paper.

Data Availability

The following information was supplied regarding data availability:

The raw data and code have been provided as [Supplemental Files](#).

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.3622#supplemental-information>.

REFERENCES

- Allen V, Bates KT, Li Z, Hutchinson JR. 2013. Linking the evolution of body shape and locomotor biomechanics in bird-line archosaurs. *Nature* 497:104–107 DOI 10.1038/nature12059.
- Baier DB, Gatesy SM, Jenkins FA. 2007. A critical ligamentous mechanism in the evolution of avian flight. *Nature* 445:307–310 DOI 10.1038/nature05435.
- Bapst DW. 2012. paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods in Ecology and Evolution* 3:803–807 DOI 10.1111/j.2041-210X.2012.00223.x.
- Bell E, Andres B, Goswami A. 2011. Integration and dissociation of limb elements in flying vertebrates: a comparison of pterosaurs, birds and bats. *Journal of Evolutionary Biology* 24:2586–2599 DOI 10.1111/j.1420-9101.2011.02381.x.
- Brusatte Stephen L, O'Connor Jingmai K, Jarvis Erich D. 2015. The origin and diversification of birds. *Current Biology* 25:R888–R898 DOI 10.1016/j.cub.2015.08.003.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer-Verlag.
- Chiappe LM, Ji S, Ji Q. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the late mesozoic of northeastern China. *Bulletin of the American Museum of Natural History* 242:1–89.
- Cracraft J. 1974. Phylogeny and evolution of the ratite birds. *Ibis* 116:494–521 DOI 10.1111/j.1474-919X.1974.tb07648.x.
- Dececchi TA, Larsson HCE. 2013. Body and limb size dissociation at the origin of birds: uncoupling allometric constraints across a macroevolutionary transition. *Evolution* 67:2741–2752 DOI 10.1111/evo.12150.
- Dietz MW, Piersma T, Hedenström A, Brugge M. 2007. Intraspecific variation in avian pectoral muscle mass: constraints on maintaining manoeuvrability with increasing body mass. *Functional Ecology* 21:317–326 DOI 10.1111/j.1365-2435.2006.01234.x.

- Dyke GJ, Kaiser GW. 2010.** Cracking a developmental constraint: egg size and bird evolution. *Records of the Australian Museum* **62**:207–216
DOI [10.3853/j.0067-1975.62.2010.1547](https://doi.org/10.3853/j.0067-1975.62.2010.1547).
- Gatesy SM, Dial KP. 1996.** Locomotor modules and the evolution of avian flight. *Evolution* **50**:331–340 DOI [10.2307/2410804](https://doi.org/10.2307/2410804).
- Heers AM, Dial KP. 2015.** Wings versus legs in the avian bauplan: development and evolution of alternative locomotor strategies. *Evolution* **69**:305–320
DOI [10.1111/evo.12576](https://doi.org/10.1111/evo.12576).
- Hinić-Frlog S, Motani R. 2010.** Relationship between osteology and aquatic locomotion in birds: determining modes of locomotion in extinct Ornithurae. *Journal of Evolutionary Biology* **23**:372–385 DOI [10.1111/j.1420-9101.2009.01909.x](https://doi.org/10.1111/j.1420-9101.2009.01909.x).
- Hutchinson JR. 2001.** The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* **131**:123–168
DOI [10.1111/j.1096-3642.2001.tb01313.x](https://doi.org/10.1111/j.1096-3642.2001.tb01313.x).
- Hutchinson JR, Allen V. 2009.** The evolutionary continuum of limb function from early theropods to birds. *Naturwissenschaften* **96**:423–448
DOI [10.1007/s00114-008-0488-3](https://doi.org/10.1007/s00114-008-0488-3).
- Jenkins FA. 1993.** The evolution of the avian shoulder joint. *American Journal of Science* **293**:253–267 DOI [10.2475/ajs.293.A.253](https://doi.org/10.2475/ajs.293.A.253).
- Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012.** The global diversity of birds in space and time. *Nature* **491**:444–448 DOI [10.1038/nature11631](https://doi.org/10.1038/nature11631).
- Kovacs CE, Meyers RA. 2000.** Anatomy and histochemistry of flight muscles in a wing-propelled diving bird, the Atlantic puffin, *Fratercula arctica*. *Journal of Morphology* **244**:109–125
DOI [10.1002/\(SICI\)1097-4687\(200005\)244:2<109::AID-JMOR2>3.0.CO;2-0](https://doi.org/10.1002/(SICI)1097-4687(200005)244:2<109::AID-JMOR2>3.0.CO;2-0).
- Lindstrom A, Kvist A, Piersma T, Dekinga A, Dietz MW. 2000.** Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fuelling. *Journal of Experimental Biology* **203**:913–919.
- Livezey BC. 1992.** Flightlessness in the Galápagos cormorant (*Compsohalieu* [*Nannopterum*] *harrisi*): heterochrony, giantism and specialization. *Zoological Journal of the Linnean Society* **105**:155–224 DOI [10.1111/j.1096-3642.1992.tb01229.x](https://doi.org/10.1111/j.1096-3642.1992.tb01229.x).
- Longrich N. 2009.** An ornithurine-dominated avifauna from the Belly River Group (Campanian, Upper Cretaceous) of Alberta, Canada. *Cretaceous Research* **30**:161–177 DOI [10.1016/j.cretres.2008.06.007](https://doi.org/10.1016/j.cretres.2008.06.007).
- Makovicky PJ, Zanno LE. 2011.** Theropod diversity and the refinement of avian characteristics. In: *Living Dinosaurs*. Hoboken: John Wiley & Sons, Ltd, 9–29.
- Mayr G. 2017.** Evolution of avian breeding strategies and its relation to the habitat preferences of Mesozoic birds. *Evolutionary Ecology* **31**:131–141
DOI [10.1007/s10682-016-9872-1](https://doi.org/10.1007/s10682-016-9872-1).
- Nesbitt SJ, Turner AH, Spaulding M, Conrad JL, Norell MA. 2009.** The theropod furcula. *Journal of Morphology* **270**:856–879 DOI [10.1002/jmor.10724](https://doi.org/10.1002/jmor.10724).
- Neuwirth E. 2014.** RColorBrewer: colorBrewer palettes. R package version 1.1-2. Available at <https://cran.r-project.org/web/packages/RColorBrewer/index.html>.

- Norberg U. 1990. *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. Berlin: Springer-Verlag.
- O'Connor JK, Chiappe LM, Gao C, Zhao B. 2011. Anatomy of the early cretaceous enantiornithine bird *Rapaxavis pani*. *Acta Palaeontologica Polonica* **56**:463–475 DOI 10.4202/app.2010.0047.
- O'Connor JK, Zheng XT, Sullivan C, Chuong CM, Wang XL, Li A, Wang Y, Zhang XM, Zhou ZH. 2015. Evolution and functional significance of derived sternal ossification patterns in ornithothoracine birds. *Journal of Evolutionary Biology* **28**:1550–1567 DOI 10.1111/jeb.12675.
- Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**:289–290 DOI 10.1093/bioinformatics/btg412.
- R Core Team. 2017. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at <https://www.R-project.org/>.
- Revell LJ. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**:217–223 DOI 10.1111/j.2041-210X.2011.00169.x.
- Revell LJ, Collar DC. 2009. Phylogenetic analysis of the evolutionary correlation using likelihood. *Evolution* **63**:1090–1100 DOI 10.1111/j.1558-5646.2009.00616.x.
- Revell LJ, Harmon LJ. 2008. Testing quantitative genetic hypotheses about the evolutionary rate matrix for continuous characters. *Evolutionary Ecology Research* **10**:311–331.
- Schmidt M, Fischer MS. 2009. Morphological integration in mammalian limb proportions: dissociation between function and development. *Evolution* **63**:749–766 DOI 10.1111/j.1558-5646.2008.00583.x.
- Spear LB, Ainley DG. 1997. Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis* **139**:221–233.
- Stoddard MC, Yong EH, Akkaynak D, Sheard C, Tobias JA, Mahadevan L. 2017. Avian egg shape: form, function, and evolution. *Science* **356**:1249–1254 DOI 10.1126/science.aaj1945.
- Stoessel A, Kilbourne BM, Fischer MS. 2013. Morphological integration versus ecological plasticity in the avian pelvic limb skeleton. *Journal of Morphology* **274**:483–495 DOI 10.1002/jmor.20109.
- Storer RW. 1945. Structural modifications in the hind limb in the alcidae. *Ibis* **87**:433–456 DOI 10.1111/j.1474-919X.1945.tb01375.x.
- Wang M, Lloyd GT. 2016a. Data from: rates of morphological evolution are heterogeneous in early cretaceous birds. *Dryad Data Repository*. Available at <http://dx.doi.org/10.5061/dryad.c128h>.
- Wang M, Lloyd GT. 2016b. Rates of morphological evolution are heterogeneous in early cretaceous birds. *Proceedings of the Royal Society B: Biological Sciences* **283**: 20160214.
- Wang M, Zhou Z. 2017. A morphological study of the first known piscivorous enantiornithine bird from the early cretaceous of China. *Journal of Vertebrate Paleontology* **37**:e1278702.

- Wang M, Zhou Z, Sullivan C. 2016.** A fish-eating enantiornithine bird from the early cretaceous of China provides evidence of modern avian digestive features. *Current Biology* **26**:1170–1176 DOI [10.1016/j.cub.2016.02.055](https://doi.org/10.1016/j.cub.2016.02.055).
- Wickham H. 2009.** *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.
- Wright NA, Steadman DW, Witt CC. 2016.** Predictable evolution toward flightlessness in volant island birds. *Proceedings of the National Academy of Sciences of the United States of America* **113**:4765–4770 DOI [10.1073/pnas.1522931113](https://doi.org/10.1073/pnas.1522931113).
- Young NM, Hallgrímsson B, Janis C. 2005.** Serial homology and the evolution of mammalian limb covariation structure. *Evolution* **59**:2691–2704 DOI [10.1111/j.0014-3820.2005.tb00980.x](https://doi.org/10.1111/j.0014-3820.2005.tb00980.x).
- Zheng X, O'Connor J, Wang X, Wang M, Zhang X, Zhou Z. 2014.** On the absence of sternal elements in Anchiornis (Paraves) and Sapeornis (Aves) and the complex early evolution of the avian sternum. *Proceedings of the National Academy of Sciences of the United States of America* **111**:13900–13905 DOI [10.1073/pnas.1411070111](https://doi.org/10.1073/pnas.1411070111).
- Zheng X, Wang X, O'Connor J, Zhou Z. 2012.** Insight into the early evolution of the avian sternum from juvenile enantiornithines. *Nature Communications* **3**:1116 DOI [10.1038/ncomms2104](https://doi.org/10.1038/ncomms2104).
- Zhou Z, Zhang F. 2001.** Two new ornithurine birds from the early cretaceous of western Liaoning, China. *Chinese Science Bulletin* **46**:1258–1264 DOI [10.1007/BF03184320](https://doi.org/10.1007/BF03184320).
- Zhou Z, Zhang F. 2002.** A long-tailed, seed-eating bird from the early cretaceous of China. *Nature* **418**:405–409 DOI [10.1038/nature00923](https://doi.org/10.1038/nature00923).
- Zhou Z, Zhang F. 2006.** A beaked basal ornithurine bird (Aves, Ornithurae) from the lower cretaceous of China. *Zoologica Scripta* **35**:363–373 DOI [10.1111/j.1463-6409.2006.00234.x](https://doi.org/10.1111/j.1463-6409.2006.00234.x).