

# Morphometric analysis of the cervical vertebral series in extant birds with implications for Mesozoic avialan feeding ecology

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**Abstract** The inference of Mesozoic avialan bird diets previously relied on traditional methods such as morphological comparisons among taxa and direct evidence such as identifiable stomach contents. However, the application of these approaches has been limited because of uncommon preservation of relevant fossil evidence. We searched for additional informative characteristics to help develop new methods to assess the diet of fossil birds. In particular, the morphology of the avialan neck is highly modularized and plays roles in multiple functions including food acquisition. The structure of and variation among the cervical vertebrae likely reflects the demands of feeding ecology in fossil and extant birds because the avialan neck evolved to, at least in part, replace the forelimbs by assisting with activities such as cranioinertial feeding and other ecological functions. Here, we utilize morphometric and statistical analyses to establish an initial quantitative relationship between cervical morphology and dietary modes in both extant and extinct birds. This morphometric framework derived from the cervical morphology of living birds is used as a basis to estimate the diet categories of five taxa of Mesozoic birds. The results indicate that there is a quantitative correlation between cervical morphology differentiation and their interrelated feeding modes. The enantiornithine taxa examined exhibit cervical morphologies similar to extant insectivorous or carnivorous birds. The ornithurine species show cervical morphologies that are more aligned with generalist or herbivorous birds, and exhibit preliminary morphological features tied to aquatic adaptations. These findings are consistent in part with other direct fossil evidence, as well as hypotheses developed from other skeletal comparisons. Therefore, the cervical vertebral series, as a skeletal system closely linked to food acquisition, can serve as one of the valuable metrics to provide information for inferring the diet of long extinct Mesozoic birds.

**Key words** Mesozoic birds, cervical morphology, diet, ecological variation

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## 1 Introduction

Crown group birds are characterized by having elongated and extremely flexible ‘S’-shaped necks, supported by an extended series of cervical vertebrae that are articulated with heterocoelous contacts. This combination of cervical morphological features along with an increased number of cervical vertebrae helps to provide a greater freedom of movement in comparison to other vertebrate clades (Tambussi et al., 2012; Kardong, 2012). The unique morphology of bird neck has been linked to its novel function in assisting the avian head to accomplish multifunctional roles in stabilizing, feeding, and preening (Kardong, 2012; Böhmer et al., 2019). Bird evolution marks one of the great transitions in tetrapod evolution with the origin of wings and powered flight among feathered bipedal theropod dinosaurs. Concomitantly with the change in function of the forelimb for flight, the head and neck must have altered their utility in relation to foraging and other roles as they took to the air and lost or reduced the use of the forelimb for its ancestral functions. The large diversity present in the crown avian neck and their cervical vertebral column likely arose during Mesozoic niche diversification and expansion. Morphological variation in their cervical morphology and number have been linked to their adaptative roles in crown avian feeding or foraging strategies (van der Leeuw et al., 2015; Terray et al., 2020). For example, wading birds tend to have longer and more flexible necks for acquiring food items, but birds of prey typically have more robust and tightly articulated cervical vertebrae assisting live prey capture and processing (Wilkinson and Ruxton, 2012; Rico-Guevara et al., 2019; Marek et al., 2021). Given this diversity of form and function in a single body region, we have conducted a morphometric investigation to elucidate the potential linkage between the form and function of avialan cervical vertebral system, particularly in relation to their foraging modes.

A large number of Early Cretaceous bird fossils, representing a great diversity of taxa and lineages, have been recovered from the Jehol Group in North China over the last two decades (Xu et al., 2020). Those discoveries have dramatically enriched our understanding of the ecological and morphological disparity and diversity during the early portion of bird diversification. These Mesozoic stem birds display a great diversity in both skeletal and integumentary morphologies (including features absent among crown birds), along with documentation of dietary diversification associated with their inferred foraging modes. The published diversity in Jehol bird dietary preferences include insectivore, herbivore, and piscivore, demonstrating an evolutionarily rapid occupation of various ecological niches resembling those of their crown counterparts in the early Cenozoic (Zhou and Zhang, 2007).

Direct evidence of diets among Cretaceous birds remains limited to relatively few taxa, including *Jeholornis* (Zhou and Zhang, 2002), *Piscivoravis* (Zhou et al., 2014b), and *Yanornis* (Zheng et al., 2014), most of which are associated with the preservation of stomach contents *in*

*situ* or extrinsic evidence preserved along with the fossil skeletons. Other hypotheses of dietary diversity derive mostly from indirect evidence, and were proposed based on examination of the morphology of the feeding apparatus (e.g., a specialized rostrum morphology), and functions related to the jaws and their dentition (O'Connor, 2019; O'Connor and Chiappe, 2011; Miller and Pittman, 2021). For example, among stem enantiornithine birds with longer rostra, *Longipteryx* has been hypothesized to be piscivorous or carnivorous, and a shortened rostrum in *Brevirostruavis* was considered as likely linked to an insectivorous diet (Wang et al., 2015; Li et al., 2022). In addition, the presence of gastroliths or gizzard stones used in digestion has been considered an indicator of at least seasonal herbivory, in a few Cretaceous avialan taxa (O'Connor, 2019). Those direct and indirect data supporting dietary diversification have been used as the basis for hypothesizing several intriguing feeding adaptations among Mesozoic birds, linking various feeding niches and specialized morphologies.

The long cervical vertebral column of Mesozoic birds evolved gradually with the initial indication of heterocoelous articulations among early enantiornithines, like *Pengornis* (Chiappe and Walker, 2002; Zhou et al., 2008; Hu et al., 2014). Given the wide documented and hypothesized diversity of stem bird diets, the cervical vertebral system of bird taxa from the Jehol Biota likely evolved equally variable ecological and morphological functions comparable with those of crown birds. However, given the complexity of dexterous and multifarious functions and phylogenetic constraints, the pattern of the early evolution of the bird neck and its potential ecological adaptations remains relatively unknown. The morphological comparison of the cervical vertebral system and its implication for neck flexibility and foraging behavior have been made in a few extinct clades of sauropods (Upchurch and Barrett, 2000; Copley et al., 2013) and extinct birds (Tambussi et al., 2012; Zelenkov and Averianov, 2016). More recent studies further demonstrate the quantitative relationships of cervical morphology with neck flexibility, mobility, and regionalization (Krings et al., 2017; Kambic et al., 2017; Terray et al., 2020; Marek et al., 2021). Those studies have divided the cervical system into between three to nine subregions based on the morphology and mobility of the necks of crown birds (Krings et al., 2014; Kambic et al., 2017; Terray et al., 2020). Other investigations have limited the subregions to five, deriving from geometric morphometrics analysis and phylogenetic comparative methods (Böhmer et al., 2015; Marek et al., 2021). Although the bird neck is highly conserved in its regionalization, cervical vertebral morphologies within the subregions display indications of various degrees of ecological adaptation (Marek et al., 2021).

Like crown birds, morphological variation within and among cervical vertebral series have also been elaborated in various Mesozoic stem birds, although the degree of neck flexibility and regional modularity in the fossils remains unclear. Prior morphological comparisons of cervical characters across different extinct taxa have been rather simple, with a focus on the number of vertebrae, their pattern of articulation, and the aspect ratio of the

centra (which indicates the shape of the vertebra). Some affiliated structures also have been considered, such as the articulation with the cervical rib (Zhang et al., 2001; O'Connor et al., 2009; Zhou et al., 2014b; Wang, 2023). To our knowledge, no quantitative studies have been done in using a morphometric approach to examine cervical morphology and its potential relationship to various ecological adaptations and functions among Mesozoic birds.

Most recent studies attempting to link skeletal morphometrics with ecological adaptations among early birds commonly focus on other skeletal regions, not the cervical vertebrae. For instance, hind limb and foot morphometrics have been used as continuous traits to bridge ecological gaps between extant and extinct taxa (Falk et al., 2021). A similar approach also was applied to the skull and appendicular skeletal regions (Li and Clarke, 2016; Miller and Pittman, 2021). In comparison, fewer studies have been published that focus on the cervical vertebrae and neck system, through which morphological similarities and ecological convergence could be identified between extant and extinct birds. The lack of detail in our understanding regarding the evolutionary change in the bird neck has been a hurdle to reaching a greater understanding of the potential link between cervical morphology and function in Early Mesozoic birds and their adaptive variation.

Here, we attempt to apply a morphometric approach to disentangle the cervical vertebral morphology and functional flexibility of crown birds with related ecological/functional adaptations within cervical vertebral series subregions, and apply insights into a better understanding of the variation in major Mesozoic avialan clades. By using statistical, morphometric, and phylogenetic comparative methods, we have collected cervical vertebral data and applied a combination of quantitative approaches to understanding cervical morphology and dietary modes in both extant and extinct birds. In present study, dietary hypotheses for five Cretaceous birds from the Jehol Biota resulted from our analyses. They either supported or contradicted prior hypotheses regarding the individual species. These data and results help to build a framework for better understanding and interpreting the dietary inferences of Mesozoic birds, to improve knowledge of the morphometric relationship between cervical morphology and dietary mode, and to provide a new perspective for evaluating the feeding ecology of early birds.

## 2 Materials and methods

### 2.1 Sampling for extant and extinct bird specimens

**Specimens** Extant bird bodies from a total of 23 species (distributed across 16 families in 11 orders, Supplementary file 1: Table S1) were acquired after their natural decease from Nature Reserve of Snake Island-Laotie Mountain, Dalian, Liaoning Province in northeast China. Carcasses used in this study were collected by staff in the Nature Reserve and preserved in the frozen storage during 2020–2021. The sampled set of extant bird taxa

is aimed at recovering the relationship between dietary modes and cervical morphological signals. The feeding mode categories for the extant Chinese birds mainly follow data compiled in comprehensive published guides (Liu and Chen, 2021). The selection of taxa was based primarily on their feeding ecologies, in addition to consideration of their phylogenetic diversity. As a result, carnivory, insectivore, herbivore, piscivore, and generalist diets are all represented in our sample set.

Mesozoic fossil bird specimens were selected from the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences (IVPP) in Beijing collections, including three enantiornithines (*Bohaiornis* IVPP V31156, *Longipteryx* V31371, *Brevirostruavis* V13266) and two ornithurines (*Yanornis* V31692, and *Iteravis* V18688). All of those fossil skeletons are from the Jiufotang and Yixian Formations with an approximate age of between 120 Ma and 126 Ma (Zhou et al., 2021).

**CT-scanning** All of the deceased extant avian specimens were frozen (−20 °C), and remained in a frozen state during the CT-scanning process. Scanning was performed in the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences in the IVPP and in the Institute of Geology, Chinese Academy of Geological Sciences (CAGS). CT-Scanning equipment included an XT H 225 (in CAGS) and GE Phoenix v|tome|x m (in IVPP) in Beijing.

The scanning of the fossil bird specimens focused on the neck region. Further segmentation and measurements were completed using Software VG-Studio MAX 3.0, Avizo 9.2, focused on the cervical vertebrae reconstruction. All of the measurements were acquired in the three-dimensional models by using the measuring tools in Avizo 9.2. CT data is stored and accessible online (<http://admorph.ivpp.ac.cn/shouye.html>).

**Cervical measurements** In order to quantify the morphological variation across species, three linear variables, one angle, and one ratio (centrum length to width) were obtained and compiled from the 12 individual cervical vertebrae present in each bird specimen. To be precise and consistent, linear measurements using digital rendering of the CT scan, including the centrum length, width, relative length of post zygapophyseal process (i.e., zygapophyseal protrusion), and the angle formed by the diverging left and right outlines of the left and right post zygapophyses (Fig. 1).

These measurements were selected because they emphasized features that could be examined in both the fossils and modern skeletons. Since most available Jehol bird fossils are compressed in flat rock slabs, three-dimensional measurements were excluded from this study, including the diameter of the neural canal and pitching angle (Krings et al., 2014). In addition, the atlas and axis were excluded because of their special morphology compared to other cervical vertebrae.

The morphometric data collected are described and illustrated as follows (Fig. 1):

Variable 1 – centrum length (CL): the centrum length is measured in ventral view, and is determined by the distance between the midline center of cranial and caudal articular surfaces of the centrum (Fig. 1A).

Variable 2 – centrum width (CW): the centrum mediolateral width is determined by the minimum width of the centrum (Fig. 1B).

Variable 3 – zygapophyseal angle (ZA): the zygapophyseal angle is measured using 3D angle tools in Avizo 9.2, and is an angle formed by lines from both caudal end points of the postzygapophyses to the dorsal caudal end of the neural arch (Fig. 1C).

Variable 4 – zygapophyseal protrusion (ZP, Krings et al., 2014): this measurement is used to quantify the relative extension of the postzygapophyseal processes. The zygapophyseal protrusion is determined by connecting the caudal end points of the postzygapophyses with a line, drawing a perpendicular line intersecting it at a midpoint, and then measuring the distance between the caudal end of the neural arch and the intersection point (Krings et al., 2014). The distance was measured in two dimensions in dorsal view (Fig. 1B).

Variable 5 – ratio of centrum length to width: the ratio is calculated by using the obtained craniocaudal centrum length and mediolateral width from variable 1 and 2.

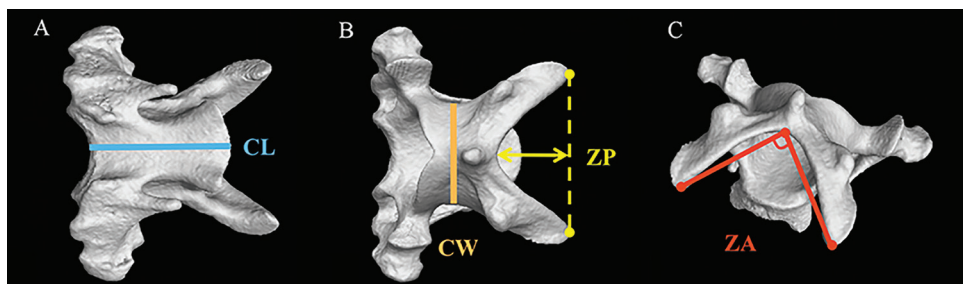


Fig. 1 Measurements acquired for individual cervical vertebrae

The fifth cervical vertebra of *Falco subbuteo* was used as an exemplar here as showing in ventral (A), dorsal (B), and dorsal-caudal (C) views with measurement axes and angles

Abbreviations: CL. centrum length; CW. centrum width; ZA. zygapophyseal angle;

ZP. zygapophyseal protrusion

## 2.2 Morphometric analysis

**Principal component analyses (PCA)** Principal component analyses on the measurement data of extant birds were performed in ‘R’ (Venables and Ripley, 2002), the grouping of diet and ecology categories for extant taxa follows that of Liu and Chen (2021). Similar analyses were completed with the inclusion of extinct taxa.

Twenty-three extant bird species were classified into five dietary categories (Supplementary file 1: Table S1): 1) carnivory; 2) insectivore; 3) herbivore; 4) piscivore; and 5) dietary generalist. In total, 50 variables on the 3rd to 12th cervical vertebrae (abbreviated as ‘C3’ to ‘C12’ here, and in following text) are used in the principal component analysis of



extant species. For analysis including the five fossil taxa, only 30 variables are available (C3 to C8) and used for PCA because of missing data (Li and Clarke, 2016) due to the incomplete preservation of fossil specimens. Details of measurements and their values can be found in the Supplementary file 2.

**Phylogenetic signal test** Phylogenetic relatedness can place constraints on the evolutionary and similarity of the species' cervical vertebral series. Therefore, it is necessary to test how big of an influence and to what degree the phylogenetic signal impacts each measured trait. Blomberg's K is used to estimate the phylogenetic signal of the 30 measurements recorded for C3 to C8 across all birds (Freckleton et al., 2002; Blomberg et al., 2003; Kamilar and Cooper, 2013).

The phylogenetic tree used here including extant and extinct birds is based on previous analyses (Wang and Lloyd, 2016; Cooney et al., 2017). A strict consensus tree was built based on those two recently published datasets in R version 4.2.2 using the '*ape*' package (Paradis et al., 2004). Since the published trees do not include two of the fossil taxa used in this study, *Iteravis* and *Brevirostruavis* (Wang and Lloyd, 2016), the phylogenetic position of the two extinct taxa was inferred, and they were placed by the phylogenetically closest known taxa in other phylogenetic studies in order to build our final phylogenetic tree for analyses (Zhou et al., 2014a, b; Wang and Lloyd, 2016; Li et al., 2022).

In addition, the phylogenetic signal was calculated using the '*ape*', '*picante*', '*geiger*', and '*phytools*' packages in R version 4.2.2 (Paradis et al., 2004; Harmon et al., 2007; Kembel et al., 2010; Revell, 2012). The variables with significant phylogenetically correlated signals were screened out of further phylogenetic principal component analyses. The results were compared with a regular PCA as well. R codes for all the phylogenetic analysis and principal component analyses can be found in the Supplementary file 3.

**Phylogenetic principal component analyses (PPCA)** Principal component analyses are used typically for preliminary data transformations and dimension reduction in statistical analyses. However, a phylogenetic influence on our data cannot be ignored since most biological data are not independent given their shared evolutionary history (Revell, 2009). Therefore, we calculated the degree of phylogenetic signal for each variable, and we retained those variables that exhibited statistical significance in their phylogenetic signal. Phylogenetic principal component analyses (pPCA) were applied to remove phylogenetic signals. The analysis was used to correct for the nonindependence among the morphological variables for closely related species (Revell, 2009), and to help verify the assessment of associations between measurements and ecological groups based on our cervical measurement data, diet categories, and phylogenetic tree. The pPCA also was performed using '*ape*' and '*phytools*' packages in R (Paradis et al., 2004; Revell, 2012).

## 3 Results

### 3.1 Raw measurement comparison

Mesozoic fossil birds usually have a smaller number (less than 12 in total) of cervical vertebrae than extant birds, and sometimes it is hard to count the number of vertebrae in some fossil specimens because of incomplete preservation. Our analyses with both extant and extinct birds included covered cervical series ranging from C3 to C8 because available cervical measurements in extinct taxa are limited to this region. Therefore, the raw measurement comparison also only focuses on the region of C3 to C8 between the extant and extinct birds (Fig. 2).

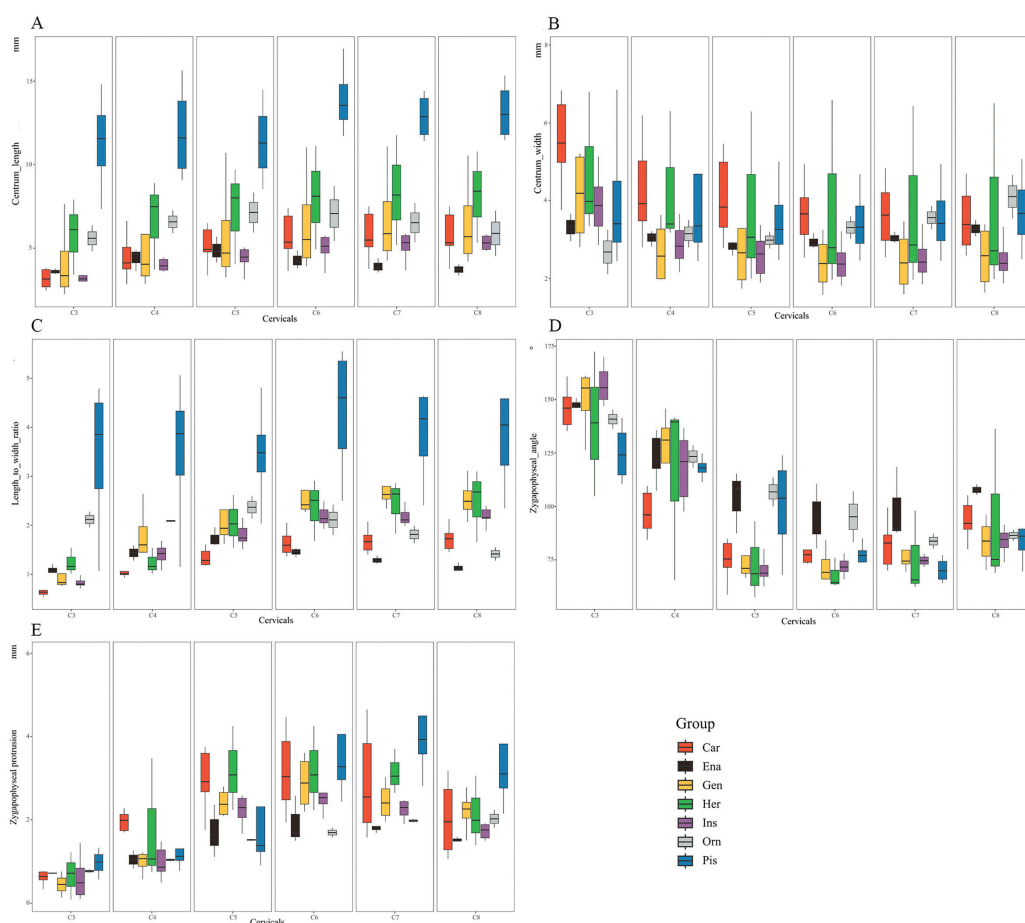


Fig. 2 Comparison of raw measurements from sampled birds

The data covers cervical vertebra from C3 to C8. Box plots showing the comparison of cervical change in length (A), width (B), ratio of centrum length to width (C), zygapophyseal angle (D), and zygapophyseal protrusion (E). The black line in the box represents the median value of the measurements for given group, and the endpoint of the upper and lower whiskers represent the maximum and minimum values, respectively

Abbreviations: Car. carnivory (red); Ena. enantiornithine (black); Gen. generalist (yellow); Her. herbivore (green); Ins. insectivore (purple); Orn. ornithurine (gray); Pis. piscivore (blue)

More comparison is available in online Supplementary file 1, for the comparison of C3 to C12 among extant birds (Fig. S1a–e)



**Centrum length** (Fig. 2A) The change in centrum length in the cervical vertebral series demonstrates a similar pattern across all birds examined (Supplementary file 1: Fig. S1a). The centra of the more cranially positioned cervical vertebrae (C3–C4) are the shortest. The maximum centrum length is among in the middle part of the series (C5–C8), and there is a decrease in centrum length among the more caudal part of the series, such as C9–C12 (Supplementary file 1: Fig. S1a). The longest cervical vertebrae occur in C6–C8 for most extant birds, as opposed to the C5 or C6 in the sampled extinct birds. Dietary categories can be distinguished by the variation in centrum length changes in living birds. For example, the carnivorous birds exhibit similar lengths from C6–C9, indicating a stable unit in the middle region of cervical vertebral series. Interestingly, piscivorous birds display the most specialized variation over their centrum lengths, as demonstrated by the presence of dual peaks at length of C3–C7 and C8–C12 respectively (Supplementary file 1: Fig. S1a).

**Centrum width** (Fig. 2B) The centrum width shows a similar tendency across all extant taxa examined. The cervical vertebrae tend to become mediolaterally narrower in the cranial region, and then broaden gradually caudally. Among fossil birds, the enantiornithines exhibit the same variation as the pattern shown in extant birds, but the ornithurine taxa exhibit an overall increasing tendency in the region of C3–C8.

**Centrum length-to-width ratio** (Fig. 2C) A similar pattern is consistently present in both extant and extinct taxa regarding the changes of centrum ratio over all of the cervical vertebrae (Supplementary file 1: Fig. S1c). The extant carnivorous and insectivorous birds have the lowest range of the ratio, varying from 0.5–2.5, as compared to 0.8–3.4 in herbivores and generalists, and 1.1–5.6 in wading birds. As for the sampled fossils, range of the ratio is rather small in the enantiornithines (1.0–2.0), and only slightly larger in the ornithurines (1.2–2.6).

**Zygapophyseal angle** (Fig. 2D) The postzygapophyseal angle is proposed to be related to the mobility and flexibility of the avian neck (Kambic et al., 2017). The postzygapophyseal angle of extant and extinct birds are compared here with a focus on the range of variation and occurrence of a minimum value. All of the stem and crown birds share a similar tendency regarding variation of the postzygapophyseal angle change along the cervical vertebral series. The smallest angle occurs at C5 or C6 in most extant birds, but at C7 in wading birds. The smallest angle among the fossil specimens also is located at C5 or C6. The range of angle variation is between 80°–150° for stem birds, and is larger in extant taxa, with values between 50°–180°.

**Zygapophyseal protrusion** (Fig. 2E) Zygapophyseal protrusion tends to be negatively correlated with the zygapophyseal angle. The smaller the angle of the two processes formed usually coincides with a greater postzygapophyseal protrusion. The pattern is similar across both extant and extinct birds but with a different range in zygapophyseal extension. The fossil birds tend to have a shorter zygapophyseal protrusion with a maximum length of 2.6 mm, and extant birds have a larger range of 4–6 mm.

### 3.2 Phylogenetic signal of cervical traits

Calculation of Blomberg's K reveals 19 variables (out of 30) with statistically significant of phylogenetic signal (Fig. 3; Supplementary file 1: Table S2,  $p < 0.05$ ). Eleven variables did not exhibit significant phylogenetic signal (Supplementary file 1: Table S2,  $p > 0.05$ ), including centrum length of C4 and C5, centrum width of C4 to C8, zygapophyseal angle of C3 and C4, zygapophyseal protrusion of C3 and C4.

Within the 19 traits with statistically significant phylogenetic signal, the K-value of most traits range from 0.435 to 0.772, with three traits over than 1, including the ratio (centrum length to width) of C7 and C8, and the zygapophyseal angle of C5 (Fig. 3). The high values for these three traits indicate that they are phylogenetically conserved with a Brownian motion (Kamilar and Cooper, 2013). By contrast, the K-value of the 11 variables without statistically significant signals ( $p > 0.05$ ) are quite lower than these 19 traits (Supplementary file 1: Table S2), meaning that those traits have evolutionary lability and were more subject to change under environmental and functional pressures (Kamilar and Cooper, 2013). The greater phylogenetic signal for the zygapophyseal angle and the centrum ratio suggest similar cervical shape shared with more closely related species. Among different cervical vertebrae, the third and fourth cervical exhibit a lower level of phylogenetic signal than the other cervical vertebrae, implying that the phylogenetic influence on the neck region is not equal with some parts conserved and others not.

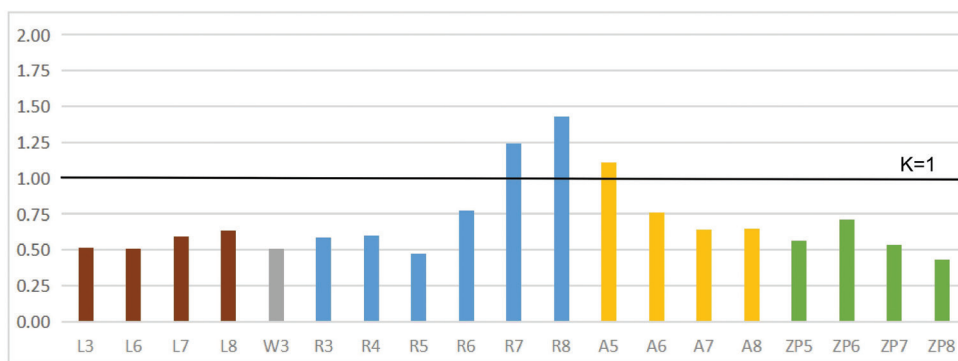


Fig. 3 Significant phylogenetic signal detected in cervical vertebral traits using Blomberg's K. Traits with K-value over or equal one indicates strong phylogenetic signal as following brownian motion and are phylogenetically conserved. Traits with a K-value smaller than one indicate a departure from Brownian motion. Different categories of measurements are labeled with different colors  
Abbreviations: A. zygapophyseal angle; L. centrum length; R. ratio of centrum length to width; W. centrum width; ZP. zygapophyseal protrusion

### 3.3 Principal component analyses (PCA)

The PCAs were performed twice, exclusively with data from extant taxa and with the incorporation of data from extinct taxa. Different cervical vertebral regions were used for the

two analyses: C3 to C12 for extant birds only; and C3 to C8 for incorporation of the extinct taxa.

With total data included (Fig. 4), the first two major principal components (PC1 and PC2) explained 47% and 27% of the total variance respectively. Most variables are correlated with each other and loaded positively on PC1 (Supplementary file 1: Fig. S2), and the centrum length is the most influential factor. The aspect ratio of centrum (length to width) and zygapophyseal protrusion of most cervical vertebrae also load positively on PC1, except for C4 and C5, which have a negative loading on PC2 for their zygapophyseal protrusion. Regarding PC2, almost all of the variables are loaded negatively, and the centrum width influences the most of the variation.

In the morphospace formed by the PC axes, the separation of species by different diet categories can be discerned partially. This separation is particularly clear for carnivory and piscivore (Fig. 4), but the other dietary groups are distributed relatively closely in the plots. Among the two separated diet categories, the piscivorous bird is separated clearly from all others along the PC1, and the carnivorous taxa are separated from most non-

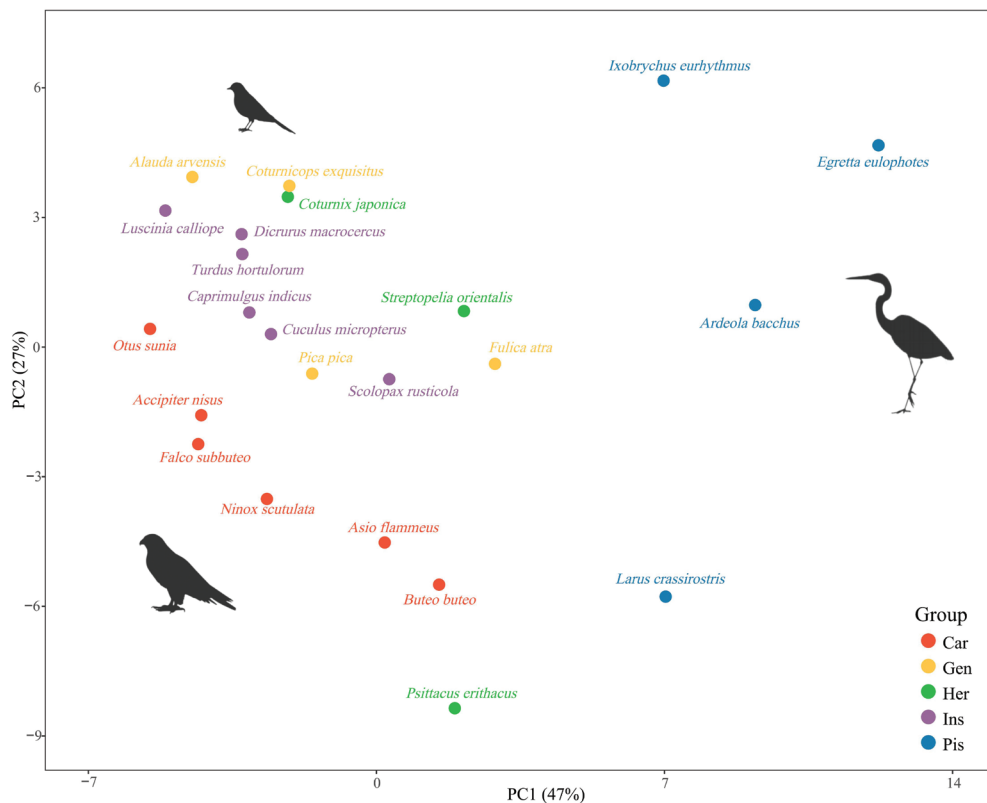


Fig. 4 PCA of the cervical measurements for extant birds only, C3 to C12 covered. Abbreviations see Fig. 2. See online supplementary file 1 for details on loadings and percentages of variance explained (Fig. S2)

raptorial insectivorous, generalist, and herbivorous birds along PC2. The piscivorous birds are characterized typically by having long necks, and our results further supported the proportionally longer cervical column in them as compared to other groups of birds in our sample set. Among the carnivorous birds, the group (except *Otus sunia*) has a negative loading along PC2, while most of the other birds tend to load relative positively (except the piscivorous *Larus crassirostris* and *Psittacus erithacus*, which have a climbing behavior distinguished from most herbivorous birds). Overall, this indicates that the cervical vertebrae of the carnivorous bird tend to have a wider centrum and a larger postzygapophyseal angle than other diet categories.

For PCA with the incorporation of extinct birds (Fig. 5), the PC1 axis explains 41% of the variance, and the PC2 axis explains 27%. The variables are loaded largely negatively along PC1 (Supplementary file 1: Fig. S3), and this pattern is most obvious for the centrum length. Regarding PC2, the ratio of centrum length to width is associated with positive loading values, while the centrum width, and part of zygapophyseal protrusion, are associated with negative loading values.

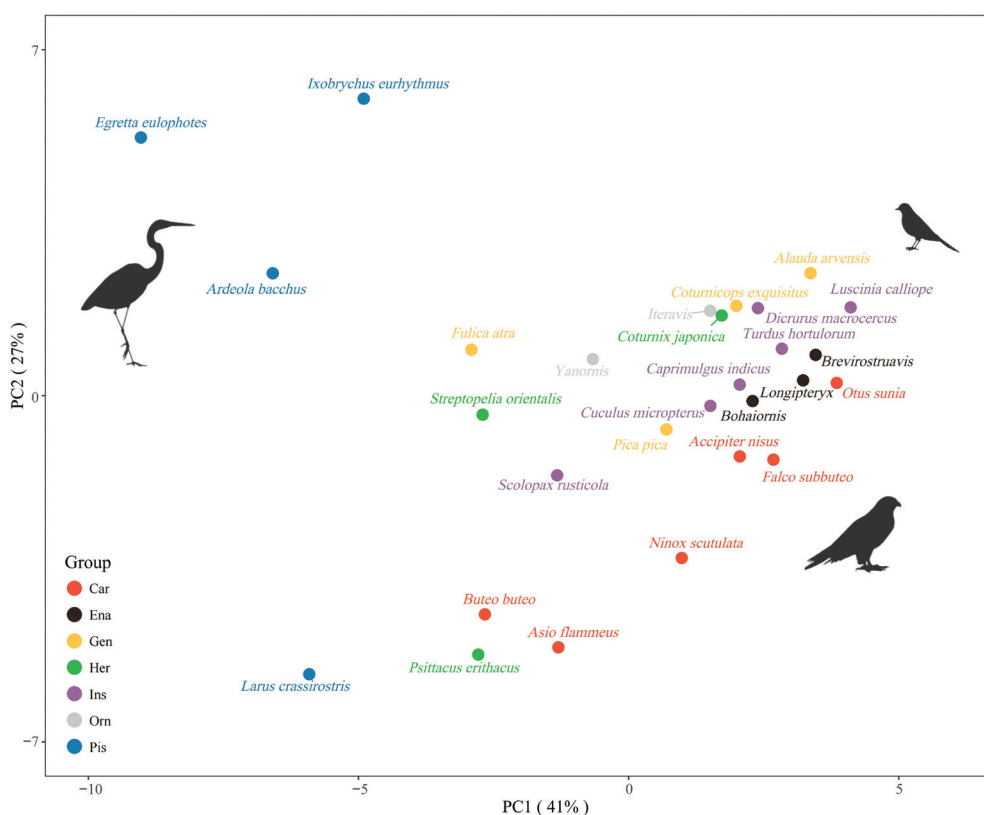


Fig. 5 PCA results with both extant and extinct birds, C3 to C8 covered  
Abbreviations see Fig. 2. See online supplementary file 1 for details on loadings  
and percent variance explained (Fig. S3)

With the inclusion of extinct birds, the partial cervical vertebral series dataset (C3–C8) was used. In comparison with the results of analyses of the total data set (C3–C12), the morphospace of the extant bird plots became more concentrated. The clustering result of all extant birds is similar to the result of the full dataset, but the separation among different dietary categories, except the piscivorous birds, exhibits less disparity when the cervical series is reduced.

Based around the dietary clusters formed by extant birds, the dietary mode of the five extinct birds can be inferred. The three enantiornithines plot in the morphospace at the gap between the insectivorous and carnivorous taxa. Compared with the other two enantiornithines, *Brevirostruavis* is more likely to be classified as insectivorous, based on its positive loading on PC 2 which has a higher value than all of the extant carnivorous birds. The two ornithurines (*Yanornis* and *Iteravis*) are placed in the morphospace close to the generalist and herbivorous feeders, which are both relatively negatively loaded on PC1 and positively loaded on PC2 compared to the enantiornithines. The results suggest that compared to the three enantiornithines, ornithurines have longer and thinner cervical vertebrae. Further examination of cervical morphology should be completed with these taxa to determine any potential phylogenetic informative traits related to this increased length and narrowed width.

### 3.4 Phylogenetic principal component analyses (PPCA)

PPCA were performed with those variables exhibiting a statistical significance of phylogenetic signal (Fig. 3; Supplementary file 1: Table S2,  $p < 0.05$ ). The first and second principal component axes (pPCs) account for over 80% of the total variation. The first PC axis (pPC1) explains 64% of the variance and the second PC axis (pPC2), explains 17% of the total variation. Most variables pertaining to length (i.e., CL and R) are loaded positively on pPC2 (Supplementary file 1: Fig. S4) in contrast to the centrum width which is loaded negatively. Regarding pPC1, the zygapophyseal angle is associated with negative loading values, and the zygapophyseal protrusion is associated with positive loading values.

In the morphospace of PPCA (Fig. 6), the extinct and extant groups are separated along pPC1. Most extinct birds are placed relatively negatively along pPC1 compared with the extant groups, showing a specific distinction in zygapophyseal angle and protrusion between the early and living birds. The enantiornithine and stem ornithurine birds can be distinguished along pPC2, and they exhibit a difference in centrum length and aspect ratio of centrum (length to width). This separation is consistent with the PCA results above, and indicates that the shape of the cervical vertebrae in ornithurines is more elongate than those of enantiornithines. In addition, in the PPCA, only the two ornithurines and *Bohaiornis* plot near the extant groups. The two ornithurines are close to the morphospace of extant piscivorous birds, and the *Bohaiornis* is in the region of the carnivores. The diet inference of *Iteravis* is different from the PCA result, but for *Yanornis* and *Bohaiornis*, the result is consistent with their prior dietary

inferences as piscivorous for *Yanornis* (Zheng et al., 2014), and carnivorous for *Bohaiornis* (Li et al., 2014).

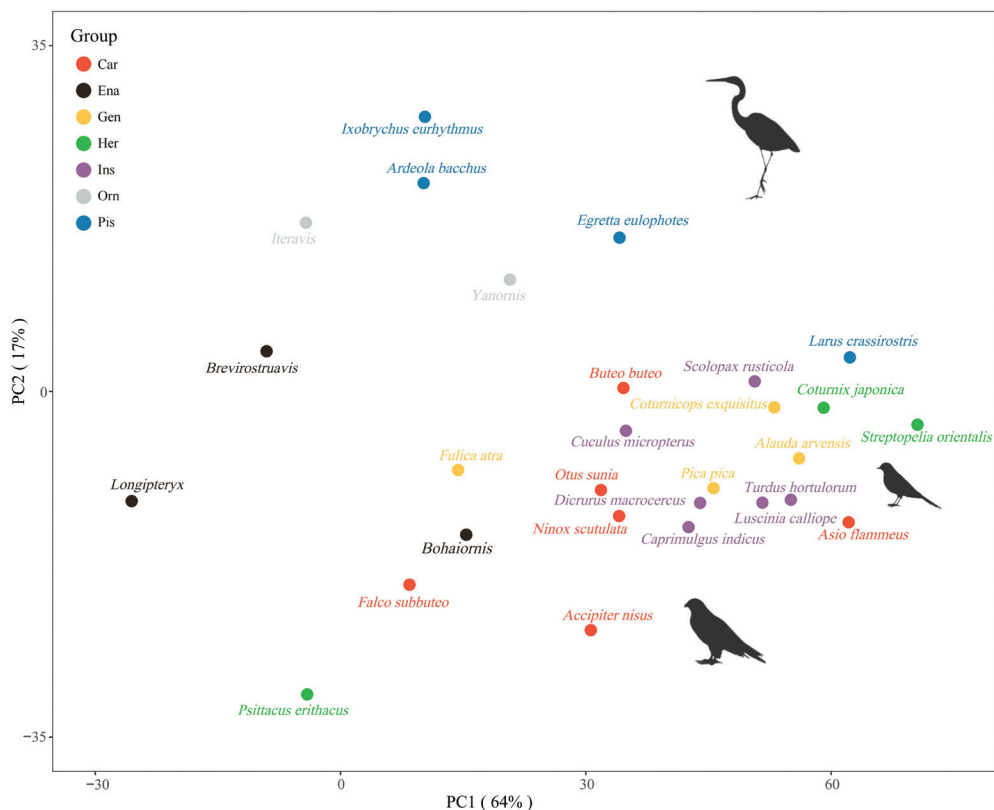


Fig. 6 Phylogenetic PCA for extant and extinct birds with data for vertebrae C3 to C8

Variables in Fig. 3 were involved with this pPCA analysis. Abbreviations see Fig. 2

See online supplementary file 1 for details on loadings and percent variance explained (Fig. S4)

## 4 Discussion

### 4.1 Cervical morphology differentiation reflects avian feeding diversity

The vertebral series raw measurements, as well as morphometric analyses of cervical vertebrae shape, show that the avialan neck displays varying degrees of dietary associated adaptations. Principal components analysis of cervical morphometric data demonstrates the separation of extant birds among different dietary strategies in morphospace, particularly for those taxa with piscivorous and carnivorous diets (Fig. 5). Regional modularity of the avialan neck appears to be differentiated between carnivores and insectivores based on previous analysis of inter-regional morphology (Marek et al., 2021). However, in our analyses, these morphological variations tend to exhibit less disparity as the morphometric variables are limited to two-dimensional geometric measurements, in addition to the analyses with reduced numbers of vertebrae included. The cervical vertebral system is directly linked to the range of

head motion and swallowing (Heidweiller, 1989; van der Leeuw et al., 2015; Zelenkov, 2017), and it is influenced further by the adaptations for different ecologies, leading to variation in cervical vertebral morphology among different species (Marek, 2023). For example, wading birds utilize their long necks (which are composed of numerous gracile cervical vertebrae; Fig. 2A, C) to catch animal prey like fish underwater (Wilkinson and Ruxton, 2012). Raptorial birds tend to develop rather wide and robust cervical vertebrae to support the extensive motion of tearing a prey item apart (Fig. 2B, C). Therefore, birds with specialized feeding modes are characterized by derived cervical morphologies, and consequently occupy the unique morphospaces in the PCA and pPCA results. In addition, it is worth noticing that most herbivorous, insectivorous, and generalist birds have a relatively close positioning in morphospace of both PCA and pPCA, indicating the similarity of cervical morphology among these birds. This result may lend some support to previous studies that suggested that avian cervical morphology may only be modified significantly by mechanical demands of entirely different ecological adaptations (van der Leeuw et al., 2015; Marek et al., 2021; Marek, 2023), such as the distinct foraging requirements between aquatic and terrestrial ecologies.

Moreover, even the specialized morphological adaptations of the avialan neck are probably rather conservative among early birds. Compared with extant birds, the five avialan species examined here occupied a rather low diversity in the cervical morphospace of the PCA results (Fig. 5). The diet categories of major Mesozoic avialan clades (enantiornithines and ornithurines) could be distinguished through the cervical shape determined by morphometric variables, particularly the aspect ratio of the centrum (Supplementary file 1: Fig. S1c). The two ornithurines have a higher ratio than that of the enantiornithines (Fig. 2C), indicating a more elongated shape of individual cervical vertebrae. In extant groups, statistical comparison indicates that herbivorous, generalist, and insectivorous birds have a higher aspect ratio of their cervical centrum than those carnivores, and highly elongated cervical vertebrae are present in piscivorous birds. The two ornithurines in our study have a similar ratio with most herbivorous and generalist birds (Fig. 2C), and the PCA classified them as herbivorous or generalist as well. However, fossil evidence such as fish bones have been recovered in the oophagous region of *Yanornis* specimens providing a clear indication of their piscivorous diet (Zheng et al., 2014; O'Connor, 2019), and only the pPCA result coincided this direct diet record (Fig. 6). We suggest that the different classification obtained in the PCA and pPCA may result from an incomplete aquatic adaptation or an omnivorous diet for *Yanornis* (Zhou et al., 2004). Since most variables related to centrum width were excluded in the pPCA (Fig. 4), the dominant variables along pPC2 were excessively influenced by length-related variables, leading to an over assessment of morphological similarity between the ornithurines and extant piscivorous birds in pPCA. Although the cervical vertebrae of *Yanornis* exhibit a possible convergence with extant aquatic birds, ecological adaptation in neck elongation remains conservative



in fossil ornithurines. The cervical vertebrae of these early aquatic ornithurines maintain a relatively short and wide shape, but in comparison with most arboreal and insectivorous enantiornithines, early ornithurines have obvious neck elongation.

## 4.2 Implications for the feeding ecology of fossil birds

Based on the ecological framework established with crown birds, we estimated the diet category of five extinct birds. Morphological analysis using quantitative data partly supports previous hypotheses of the trophic pattern in Mesozoic birds. In our analyses, the three enantiornithines converged into feeding niches quite close to each other, resembling extant insectivorous or raptorial birds. Similar hypotheses have been proposed with different lines of evidence, like analysis of cranial and appendicular skeletal morphology (Li et al., 2014, 2022; Miller and Pittman, 2021). In addition, raptorial behavior proposed for *Longipteryx* was recently supported by other quantitative analysis, including ungual claw morphometrics (Miller and Pittman, 2021).

The Mesozoic birds are inferred as having occupied relatively low trophic levels with largely herbivorous, insectivorous, and piscivorous diets (O'Connor, 2019; Wu, 2021). However, there are several taxa are hypothesized still with a particular hypercarnivorous diet, like *Bohaiornis* (Li et al., 2014), *Longipteryx* (Wang et al., 2015), and pengornithids (Miller et al., 2023). The placements of *Bohaiornis* and *Longipteryx* in the PCA results fall in the gap between insectivores and carnivores, and the pPCA results further separate *Bohaiornis* from *Brevirostruavis* and *Longipteryx* along pPC2 and pPC1 respectively. This places *Bohaiornis* closer to the carnivores. Although this division is not clear enough to determine the diet category of each enantiornithine taxon, the cervical vertebrae of *Bohaiornis* exhibit a morphological potential to support a carnivorous function like living raptorial birds, or at least a raptor-like behavior in capturing live prey and feeding on them. Our results may provide new quantitative evidence supporting presence of a carnivorous ecology among early Mesozoic birds.

Differing from the arboreal enantiornithines, most stem-ward Early Cretaceous ornithurines already exhibit certain morphological adaptations for wading or semi-aquatic behavior (Zhou and Zhang, 2007), with more derived taxa being recognized as piscivores based on direct association of the digestive system with fossilized fish fragments including *Jianchangornis*, *Piscivoravis*, *Yanornis*, and others (Zhou et al., 2009; Zhou et al., 2014b; Zheng et al., 2014). The two ornithurines sampled here, *Yanornis* and *Iteravis*, have dietary records of fish bones (O'Connor, 2019) and gastroliths (Zhou et al., 2014a) respectively. In our analysis, the two Early Cretaceous ornithurines seem to share the feeding ecology with generalists or herbivores in the PCA, falling into the ecological niches of aquatic or semi-aquatic birds (Supplementary file 1: Fig. S5a, b) in both the PCA and pPCA. This inference of ecological category has been hypothesized previously for these two ornithurines, indicating

that the neck of *Yanornis* and *Iteravis* exhibit some morphological change related to aquatic adaptations. Moreover, the dietary inference for *Yanornis* in our PCA analysis is different from previous studies where it was regarded as piscivorous based direct evidence (Zheng et al., 2014). However, its neck morphology is closer to extant generalist or herbivorous birds. We suggest that this result also may be the result of an incomplete specialization to aquatic habits, and lead to the morphological difference present between *Yanornis* and extant piscivorous birds, particularly with respect to the centrum length and width. In addition, compared with most insectivorous enantiornithines, the ornithurines appear to have a broader feeding niche incorporating both forest and lacustrine environments. The expansion of feeding ecology and habitat away from forests might have played a role in their overall survival across the K-Pg Boundary (Zhou and Zhang, 2005).

In conclusion, our initial analyses show that cervical vertebral morphology can be used for assessing the possible diet or ecological preference of fossil birds. However concrete information about feeding ecology still needs more metrics to capture the neck morphological variation among different dietary adaptations. The framework established with living birds can be used as an ecological reference for the extinct taxa as well, but the links among morphology, phylogeny, and ecology is complicated, requiring more sampling to unveil evolutionary pattern in avialan neck. Therefore, this study represents a preliminary investigation to uncover a quantitative relationship between cervical morphology and ecological inference for fossil birds. That relationship would have major implications for the reconstruction of the ecological evolution in Cretaceous birds. We hope that this approach can be improved further by expanding the sample size in living birds, as well as incorporating more traits from fossil birds.

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## 现生鸟类颈椎形态测定分析及其对中生代鸟类饮食生态的启示

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**摘要:** 中生代鸟类的食性推断往往依赖于传统的形态对比和直接的化石证据, 但不完整的化石记录和特异埋藏的稀缺性使得我们需要寻找更多有用特征和方法来对化石鸟类进行食性评估。鸟类颈部结构是一个高度模块化、形态和功能密切关联的系统; 在恐龙向鸟类演化的过程中, 前肢由于飞行适应独立出来, 使得颈部需要更多地帮助鸟类实现捕食及其他生态功能。因此, 颈部有可能成为鸟类食性推断的显著特征之一。利用形态测定和统计分析, 建立起现生鸟类和中生代灭绝鸟类的颈椎形态和食性模式之间的量化关系。基于现生鸟类构建了形态-功能框架, 评估了早白垩世热河生物群中发现的5种鸟类的食性模式。结果表明, 颈椎形态分异与鸟类取食多样性量化相关, 3种反鸟表现出了食虫或食肉鸟类的颈椎形态特征, 两种今鸟型类则表现出杂食性或植食性, 以及原始的水生适应形态特征。新的分析结果与之前发现的化石直接证据以及其他相关的形态研究基本一致, 因此, 颈椎作为与取食功能密切相关的骨骼系统, 可以为中生代鸟类取食生态的推断提供一定信息。

**关键词:** 中生代鸟类, 颈椎形态, 食性, 生态分异

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