The impact of allometry on vomer shape and its implications for the taxonomy and cranial kinesis of crown-group birds

Olivia Plateau[1]*, Christian Foth[1]

[1]Department of Geosciences, University of Fribourg, Chemin du Musée 6, CH-1700 Fribourg, Switzerland

*e-mail: olivia.plateau@unifr.ch

O.P. (ORCID: 0000-0002-8321-2687)

C.F. (ORCID: 0000-0002-9410-4569)

Abstract

Crown birds are subdivided into two main groups, Palaeognathae and Neognathae, that can be distinguished, among other means, by the organization of the bones in their pterygoid-palatine complex (PPC). Shape variation of the vomer, which is the most anterior part of the PPC, was recently analysed with help of geometric morphometrics to discover morphological differences between palaeognath and neognath birds. Based on this study, the vomer was identified as sufficient to distinguish the two main groups (and even some inclusive neognath groups) and their cranial kinetic system. As there are notable size differences between the skulls of Palaeognathae and Neognathae, we here investigate the impact of allometry on vomeral shape and its implication for taxonomic classification by re-analysing the data of the previous study. Different types of multivariate statistical analyses reveal that taxonomic identification based on vomeral shape is strongly impaired by allometry, as the error of correct identification is high when shape data is corrected for size. This finding is evidenced by a great overlap between palaeognath and neognath subclades in morphospace. Correct

taxonomic identification is further impeded by the convergent presence of a flattened vomeral morphotype in multiple neognath subclades. As the evolution of cranial kinesis has been linked to vomeral shape in the original study, the correlation between shape and size of the vomer across different bird groups found in the present study questions this conclusion. In fact, cranial kinesis in crown birds results from the loss of the jugal-postorbital bar in the temporal region and ectopterygoid in the PPC and the combination of a mobilized quadrate-zygomatic arch complex and a flexible PPC. Therefore, we can conclude that vomer shape itself is not a suitable proxy for exploring the evolution of cranial kinesis in crown birds and their ancestors. In contrast, the evolution of cranial kinesis needs to be viewed in context of the braincase, quadrate-zygomatic arch and the whole pterygoid-palatine complex.

Introduction

The pterygoid-palatine complex (PPC) of crown birds is mainly formed by five bones: the unpaired vomer that results from the fusion of the originally paired vomer elements, and the paired pterygoids and palatines. The general morphology of the PPC was first studied by Huxley (1867), who distinguished the clade Palaeognathae from all other birds on the basis of palatal morphology. Although the PPC of Palaeognathae is quite variable (McDowell 1948), it is characterized by a large vomer that is only partly fused. The pterygoids and palatines are highly connected, forming a rigid unit that articulates with the braincase via well-developed basipterygoid processes, while a contact with the parasphenoid is not present (see Bellairs & Jenkin 1960; Zusi 1993; Gussekloo et al. 2001, Mayr 2017; Fig. 1A). In contrast, neognath birds possess a movable joint between pterygoid and palatine, which plays an important role in the kinematic movement of the upper jaw. Here, the pterygoid articulates with the parasphenoid, while the basipterygoid processes are often reduced. The vomer is highly variable in size and shape and often has no connection with the upper jaw beyond an

association with the nasal septum and the palatine. In some neognaths, the vomer is greatly reduced or even absent (see Bellairs & Jenkin 1960; Bock 1964; Zusi 1993; Mayr 2017, Fig. 1A).

In a recent paper, Hu et al. (2019) investigated palate evolution in crown birds and their stem, focusing on the morphology of the vomer. Using 3D geometric morphometrics, the study found that the vomeral shape of neognaths is clearly distinguishable from Palaeognathae, in that the latter group has a stronger similarity with their non-avian ancestors. Linking vomer shape with the kinetic abilities of the skull, the authors concluded that cranial kinesis represents an innovation of Neognathae. Furthermore, the authors concluded that vomeral morphology allows for a taxonomic differentiation between the major groups of Neognathae, namely Aequorlitornithes, Galloanserae, Gruiformes, and Inopinaves. However, according to their PCA results, all groups strongly overlap each other within PC1, while a taxonomic differentiation is only noticeable within PC2 (other principal components are not shown). Taking the great size variation of the vomer of neognath birds into account (Zusi 1993), we wonder if the reported taxonomic differentiation between palaeognaths and the neognath subclades could alternatively be related to allometry, i.e. the dependence of shape on size (Klingenberg 1998), rather than pure shape variation. In order to test this hypothesis, we re-analysed the dataset of Hu et al. (2019), comparing allometric shape data with non-allometric residuals, and re-evaluating the role of the vomer in the evolution of cranial kinesis in crown birds.

Materials and Methods

The published 3D models and landmarks data of 41 specimens including 36 species were downloaded from Hu et al. 2019 (https://doi.org/10.6084/m9.figshare.7769279.v2). This dataset contains five extinct species (two stem line representatives: the troodontid

Sinovenator changii, the Avialae *Sapeornis chaoyangensis*; and three fossil palaeognath crown birds from the clade Dinornithiformes: *Pachyornis australis*, *Megalapteryx didinus* and *Diornis robustus*), five extant Paleognathae and 27 extant Neognathae representing the two major clades of crown birds.

The original landmark data (Dataset A) is composed of five anatomical landmarks and 43 semi-landmarks (see Hu et al. 2019). The landmark data were imported into the software *R v.3.5.2* (R Core Team, 2018). Using the *plotAllSpecimens* function of *Geomorph v.3.2.1* (Adams *et al*. 2013) in *R*, we notice great variability for each anatomical landmark, resulting from two main shapes of the vomer. The majority of bird possesses a fused vomer that is bilaterally symmetric and roof-shaped in transection, with a horizontal orientation within the pterygoid-palatine complex (Fig. 1B). In contrast, some members of Aequorlitornithes (e.g., *Podiceps nigricollis*, and *Podilymbus podiceps*), Galloanserae (e.g., *Anas crecca*, *Anseranas semipalmata*, and *Cairina moschata*) and Inopinaves (e.g., *Aquila audax*, *Falco cenchroides*, and *Haliastur sphenurus*) possess a fused vomer that is completely mediolaterally flattened in transection and vertically orientated within the pterygoid-palatine complex (Fig. 1B). Therefore, we created a second dataset (Dataset B), where species with this latter, flat vomer morphology were excluded. Furthermore, the palaeognath birds *Struthio camelus* and *Dromaieus novaehollandiae* of the original Dataset A were represented by both juvenile and adult specimens. Because ontogenetic variation could, however, potentially affect size and position of the palaeognath morphospace, we removed the juvenile and subadult specimens of *Struthio camelus* and *Dromaieus novaehollandiae* in order to reran the analysis just with adult semaphoronts (Dataset C). Finally, we created a fourth dataset, where both juvenile/subadult specimens and species with flat vomers were removed from the sample (Dataset D).

For superposition of the 3D landmark data, we followed Hu et al. (2019) by performing a *Generalized Procrustes Analysis* (*GPA*). The *GPA* was done with the help of the *gpagen* function in *Geomorph*. Afterward, we performed a *principal component analysis* (*PCA*) in order to visualize the shape variability of the vomer and the variance of morphospace for two groupings: (1) Paleognathae versus Neoganthae and (2) Paleognathae, Inopinaves, Galloanserae, Gruiformes and Aequorlitornithes. This was done with the *plotTangentSpace* function from *Geomorph*.

Because the vomer showed great variation in centroid size after superimposition, ranging from 14.60 (*Manorina melanocephala*) to 168.32 (*Dromaieus novehollandia*), we tested if there is a significant correlation between Procrustes coordinates and log-transformed centroid size (Goodall 1991) using the function *procD.lm* in *Geomorph*. This function performs a multivariate regression between the shape and size with a permutation of 10,000 iterations. A significant relationship between both parameters indicates that the superimposed shape still contains an allometric signal. Based on this correlation we estimated non-allometric residuals of the Procrustes coordinates and repeated the *PCA*. In addition, we tested each of the first eleven PCs that together describe more than 95 of total variation for allometric signals.

A set of 1,000 relaxed-clock molecular trees, which follow the topology of Hackett et al. (2008) and summarize the range of uncertainties in terms of time calibration of ancestral nodes, were downloaded from birdtree (http://birdtree.org) (Jetz et al. 2012, 2014) including all extant bird species in the dataset (Supplementary Data S1). Due to uncertainties in the taxonomic identification of *Aquila sp*., this specimen was removed from the sample as we could not include it in the phylogeny. Because the specimen occupies almost the same position as *Aquilla audax*, we consider this deletion to have a negligible effect on the outcome of the analyses. Furthermore, the species *Sterna bergii* and *Grus rubincunda* used in

the analysis from Hu et al. (2019) are junior synonyms of *Thalasseus bergii* (Bridge et al. 2005) and *Antigone rubicunda* (Krajewski et al. 2010). Using the function *consensus.edges* in the *R* package *phytools v.0.7-20*, we computed a temporal consensus. The extinct dinornithiform species were placed as sister-group to Tinamidae following Mitchell et al. (2014). Because of their recent extinction (Holdaway & Jacomb 2000; Turvey & Holdaway 2005), the age was set to zero, similar to the other crown birds. The stem line representatives *Sinovenator changii* and *Sapeornis chaoyangensis* were added following the time-calibrated phylogeny of Rauhut et al. (2019). Because of the presence of juvenile specimens in dataset A and B, we added the juvenile specimens by splitting OTU (operational taxonomic unit) of *Struthio camelus* and *Dromaieus novehollandia* into a polytomy with each sub-OTU having a branch length of one year (this value had to be standardized, as *pFDA* requires an isometric tree). The impact of phylogeny on shape and centroid size (log-transformed) was tested using the function *physignal* in *Geomorph*. Based on *K*-statistics, this method evaluates the impact of phylogeny on a multivariate dataset relative to what is expected, if evolution is simulated under a Brownian motion model (Blomberg et al. 2003).

To explore the size of the single morphospaces of each taxon, we computed the morphological disparity using *morphol.disparity* in *Geomorph*. This analysis uses the Procrustes variance as disparity metric, which is the sum of all diagonal elements of a group covariance matrix divided by the number of observations within the group (Zelditch et al. 2012). Statistical comparisons of group sizes were executed with help of a permutation test with 999 iterations. To test for potential overlap in morphospace of vomer shapes in different clades of crown bird (see grouping 1 and 2) and their relation to the stem line representatives *Sinovenator changii* and *Sapeornis chaoyangensis*, we applied three different multivariate statistical methods, using the first eleven PCs as input data. We first applied a nonparametric multivariate analysis of variance (*perMANOVA*). This method evaluates the potential

overlapping of groups in morphospace by testing the significance of their distribution on the basis of permutation (10,000 replications) and Euclidean distance (as one of several possible distance measures), not requiring normal distribution of the data (Anderson, 2001; Hammer & Harper, 2006). The spatial relationship of groups relative to each other is expressed by an *F* value and *p* value. For the five-group comparison, the *p* values were Bonferroni-corrected by multiplying the value with the number of comparisons. Next, we ran a discriminant analysis (*DA*), which reduces a multivariate data set to a smaller set of dimensions by maximizing the separation between two or more groups using Mahalanobis distances. This distance measure is estimated from the pooled within-group covariance matrix, resulting in a linear discriminant classifier and an estimated group assignment for each species. The results were cross-validated using Jackknife resampling (Hammer & Harper, 2006; Hammer 2020). Both multivariate tests were done with the program *PAST v.4.03* (Hammer et al. 2001). Finally, we performed a phylogenetic flexible discriminant analysis (*pFDA*) (Schmitz & Motani, 2011; Motani & Schmitz, 2011) in *R*. This method removes the phylogenetic bias from the categorical variables before the actual discriminant analysis is unertaken by estimating Pagel's lambda, which tests how the grouping correlates with phylogeny. This was done for all allometric and non-allometric datasets.

The error of correct identification from the resulting confusion matrices was compared between allometric and non-allometric data. For these comparisons, we used non-parametric *Mann-Whitney U* and *Kruskal-Wallis* tests, which both estimates, whether or not two univariate samples were taken from populations with equal medians, being more robust against small sample sizes and data without normal distribution than parametric tests (Hammer & Harper 2006). Both tests were carried out with *PAST*.

Finally, we applied an ordinary least square regression analysis to 19 species test the correlation between log-transformed vomer size and the skull size using a log-transformed

box volume (Height x Width x Length). The measurements of the skull box volume were taken from skullsite (https://skullsite.com).

Results

Based on the *PCA* of the original dataset, the first two PCs explain over 52% (Fig. 2A) of total shape variation (PC1: 27.5%; PC2:25.1%). The morphospace of Palaeognathae and Neognathae is almost equal in size. Taking the small sample size of Palaeognathae into account, the size of their morphospace indicates relatively great shape variation. This is supported by the Procrustes variances, which indicates a larger shape disparity in Palaeognathae. Both Palaeognathae and Neognathae show a strong overlap along PC1 and a partial overlap along PC2. When comparing neognath subclades, Aequorlitornithes show strong overlap along both PCs with the palaeognath morphospace. Gruiformes lie in the overlapping area of both groups. The morphospace of Inopinaves and Galloanserae overlap with each other on both axes, but are separated from Palaeognathae, Aequorlitornithes and Gruiformes along PC2. Within Neognathae, Galloanserae have the largest shape disparity, becoming successively smaller in Inopinaves, Aequorlitornithes and Gruiformes (Supplementary Data S2; S3: Fig. S1; S4: Table S1).

Allometry summarizes about 6.4% of total shape variation. Using non-allometric residuals PC1 explains 29.3% and PC2 22.9% (Fig 2.B). While the general distribution of the single bird clades does not change along PC1, the groups are less separated along PC2, which contains the major allometric signal within the principal components (slope: -0.523; R^2: 0.185; p: 0.005; predicted variation: 19.5%), which is 4.9% of total shape variation in the original dataset. Here, the palaeognath morphospace overlaps fully with Aequorlitornithes and Gruiformes, partly with Inopinaves and marginally with Galloanserae. For the three other datasets, we observe more or less similar general trends before and after size correction,

although the single morphospaces are partly shrunk. In all cases, the two stem line representatives *Sinovenator changii* and *Sapeornis chaoyangensis* lie within the marginal area of the palaeognaths/aequorlitornithines morphospace. Here, vomer morphology of the troodontid *Sinovenator changii* is more bird-like than that of the avialian *Sapeornis chaoyangensis*. The exclusion of the allometric shape variation has only a minor impact on disparity. Thus, all disparity trends found in the original dataset persist in the non-allometric datasets (Supplementary Data S2; S3: Fig. S1; S4: Table S1).

As previously detected by Hu et al. (2019), vomer shape is impacted by phylogeny. Neither the modification of the sampling nor the exclusion of allometry changes this relationship. In contrast, log centroid size does not contain a phylogenetic signal (Supplementary Data S4: Table S2).

In all studied datasets, the *perMANOVA* found a significant separation between palaeognath and neognath birds, showing no impact of allometry. For the five-group comparison of the original dataset (A), the overall results still indicate significant separation between clades for both allometric and non-allometric data. However, group-by-group comparison of allometric data indicates an overlap in morphospace of Gruiformes with Aequorlitornithes, Inopinaves, Galloanserae and Palaeognathae. These overlaps of Gruiformes with other bird clades persist when allometry is removed from shape, but in addition, Aequorlitornithes cannot be distinguished from Palaeognathae anymore, as indicated by the *PCA* results (Fig. 2 A, B). The overlap between clades increases with the exclusion of species with flat vomers and non-adult semaphoronts (Supplementary Data S4: Table S3, S4).

For the original dataset (A) with allometry included, the *DA* identifies all species correctly as Palaeognathae or Neognathae. The error of false identification increases to 2.6% if the data are jackknifed. When allometry is removed, the error increases to 13.2% before

and 36.8% after jackknife resampling. In the former case, the misidentifications are restricted to neognath birds, which are wrongly classified as Palaeognathae, while jackknifing leads to identification errors in both groups. For the five-group comparison, all species of dataset (A) are correctly identified, when allometry is still present. The error is 18.4% after jackknife resampling, showing minor mismatches in all clades. Excluding allometry, the error increases to 10.5% before and 47.4% after jackknifing. While in the former case, a few Aequorlitornithes (2) and Inopinaves (1) species are wrongly identified as Palaeognathae (Fig. 2 C, D), Palaeognathae cannot be separated from the neognath subclades anymore after resampling. The exclusion of species with flat vomers and non-adult semaphoronts leads to an increase of error (Supplementary Data S4: Table S3-S6).

The *pFDA* found 15.8% of incorrect identifications when Palaeognathae are compared with neognaths in the original dataset (A). This error increases to 31.6% if shape is corrected for allometry. In both cases, error is primarily based on the incorrect identification of palaeognath specimens as neognaths. When Palaeognathae are compared with neognath subclades, the error of correct identification is 10.5% before and 26.3% after allometry is removed from the data. For the allometric data, the misidentifications result from the overlap between Paleognathae, Aequorlitornithes and Gruiformes. The misidentifications between these three groups are increased when shape is corrected for allometry, while Inopinaves are in part also wrongly identified as Palaeognathae. The exclusion of species with a flat vomer and/or non-adult semaphoronts usually causes a decrease of false identifications. However, the non-allometric dataset shows an increase in error for the two-group comparison, when species with flat vomers are excluded, and for the five-group comparison, when only adult semaphoronts are taken into account (Fig. 2 E, F). Nevertheless, for all four datasets, the error of correct identification is significantly higher for non-allometric vomer shapes (Fig 3A, Supplementary Data S4: Table S3-S6).

Discussion

The skull of crown birds possesses a complex kinetic system that includes a mobilized quadrate, the zygomatic arch (= jugal bar) and the pterygoid-palatine complex (PPC) that allows for the simultaneous, but restricted motion of both jaws (Bock 1964; Zusi 1984). According to Zusi (1984), the kinetic system can be differentiated into three main types: (1) prokinesis describes the rotation of the whole beak around the nasal-frontal hinge; (2) amphikinesis is derived from prokinesis, including the rotation of the beak around the nasal-frontal hinge plus an additional flexion of the anterior portion of the beak; and (3) rhynchokinesis, which in contrast includes a simple flexion of the beak around one or several bending zones rostral to the nasal-frontal suture, lacking a true hinge. Depending on the position of the bending zones, rhynchokinesis can be further differentiated into five subtypes (Zusi 1984). Most palaeognath birds possess central rhynchokinesis, while neognaths have realized all types of cranial kinesis (Zusi 1984), including some taxa with akinetic skulls (Reid 1835; Sims 1955; Degrange et al. 2010). In the past, several authors (Hofer 1954; Simonetta 1960; Bock 1963) suggested a close relationship between the morphology of the PPC and type of cranial kinesis. However, Gussekloo et al. (2001) demonstrated that all types of kinesis present in crown birds have similar movements of the quadrate, zygomatic arch and PPC. Palaeognathae and Neognathae only differ in the magnitude of kinetic movements in that Palaeognathae have slightly more restricted movement due to their rigid palate missing a movable joint between the pterygoid and palatine (Gussekloo et al. 2005).

Thus, although the results of geometric morphometric analysis of the vomer shape by Hu et al. (2019) imply at first glance a distinct separation between Palaeognathae and Neognathae, this separation does not necessarily reflect their conclusions regarding the evolution of cranial kinesis in crown birds, i.e., that cranial kinesis represents an innovation

of Neognathae. As indicated by the *PCA*, Palaeognathae occupy an enormous vomeral morphospace (Hu et al. 2019), which mirrors their generally large palatal disparity (see McDowell 1948) and partly overlaps with Gruiformes and Aequorlitornithes. In all cases tested, however, the exclusion of allometric shape variation generally increases the error of misidentification between all groups (Fig. 3A; Supplementary Data S4: Table S7), indicating that the taxonomic distinctions of shape found by Hu et al. (2019) are at least partly an artefact of size. This primarily concerns PC2, which according to Hu et al. (2019) separates Palaeognathae from Neognathae, but also contains the major part of allometric information. According to shape variation explained by PC2, larger birds tend to evolve vomers that are more dorsoventrally compressed. Only members of the Galloanserae could be still identified with a high amount of certainty when allometry is excluded.

Thus, our finding supports previous studies that demonstrated a relevant impact of allometry on skull shape evolution in birds (Klingenberg & Marugán-Lobón 2013; Bright et al. 2016; Linde-Medina 2016; Tokita et al. 2016, Bright et al. 2019). By modifying the dataset, it becomes further clear that both the homoplastic presence of flat vomers in Aequorlitornithes, Inopinaves, Galloanserae (Dataset B) and ontogenetic variation (Dataset C) affects the accuracy of taxonomic identification. In addition, Palaeognathae and Neognathae do not differ in vomer size when compared to the head size (Fig. 3B). Consequently, vomer shape is not practical for taxonomic identification and should not be used as a proxy to infer the presence or absence of cranial kinesis in crown birds or their stem. As the manifold shape diversity of crown bird's skulls is impaired by a tessellated evolution with multiple convergent events (e.g., Zusi 1993; Felice & Goswami 2018), the use of isolated elements for taxonomic identification and/or biomechanical implications should be treated generally with some caution.

In fact, *DA* and *pFDA* frequently identified the troodontid *Sinovenator changii* and avialan *Sapeornis chaoyangensis* as neognaths or neognath subclades when allometry is excluded, while the original dataset implied a referral to Palaeognathae (see also Hu et al. 2019). However, the skull anatomy of both species indicates no cranial kinesis (Xu et al. 2002; Wang et al. 2017; Yin et al. 2018; Hu et al. 2020).

The origin and evolution of cranial kinesis in the stem line of birds is still not well understood due to the rarity of complete three-dimensional skulls. However, skull material from the ornithurines *Ichthyornis dispars* and *Hesperornis regalis* indicates a certain degree of rhynchokinesis (Bühler et al. 1988; Field et al. 2018) that might be comparable to that of extant Palaeognathae or some Aequorlitornithes, but further shows that this functional character was already present before the origin of the crown. Their kinesis is indicated by the loss of the jugal-postorbital bar and the ectopterygoid (resulting in a loss of contact in the jugal with the skull roof and the palate), the presence of a mobile bicondylar quadrate and a mobile joint between quadrate and quadratojugal. Recently, Plateau & Foth (2020) speculated that the peramorphic bone fusion in the braincase could be also related to cranial kinesis, in which the fusion-induced immobility constrains a controlled kinetic dorsoventral flexion of the avian beak during biting/picking. Based on these characters, most Mesozoic Avialae (including *Sapeornis chaoyangensis*) still had akinetic skulls, although some Enantiornithes possessing a reduced jugal-postorbital bar might have evolved primitive kinesis convergently to Ornithurae (O'Connor & Chiappe 2011).

Allometry describes the relationship between size and shape, which is one of the key concepts in biology to explain variation of shape in organisms (Klingenberg 1998), and is crucial for studying taxonomy, ontogeny and functional morphology. Investigating the effect of allometry on the vomer shape in crown birds with help of multiple multivariate statistical methods, indicates that this bone is not a good proxy for taxonomy. Shape differences

between Palaeognathae and Neoganthae are clearly affected by size and can neither be used to differentiate between different types of cranial kinesis nor to explain the evolution of cranial kinesis within crown birds. In contrast, the evolution of cranial kinesis in birds needs to be studied in context of the whole pterygoid-palatine complex and its contacts with the braincase and quadrate-zygomatic arch.

Acknowledgements

We thank Walter Joyce Roland Sookias and Sergio Martínez Nebreda for their critical comments on previous versions of the manuscript. The Swiss National Science Foundation is thanked for its financial support (PZ00P2_174040 to C.F.).

Additional information

Funding

This study was funded by the Swiss National Science Foundation (PZ00P2_174040).

Conflict of interest disclosure

The authors of this article declare that they have no financial conflict of interest with the content of this article. None of the authors is a *PCIPaleo* recommender.

Author Approvals

All authors have seen and approved the manuscript. The manuscript has not been accepted or published elsewhere.

Author contributions

O.P. and C.F. designed the research project and analysed the data; and O.P. and C.F. wrote the paper and prepared all figures.

Data availability

The 3D models and landmarks data of Hu et al. (2019) are available at Figshare (DOI: https://doi.org/10.6084/m9.figshare.7769279.v2).

Supplementary information

- Data S1: Phylogenetic trees used for *pFDA.*
- Data S2: PCA results of all dataset before and after correction for allometry.
- Data S3: PCA plots of Dataset B-D before and after correction for allometry.
- Data S4: Results of npMANOVA, DA and pFDA.
- Data S5: R Code including all statistical analyses.

References

Adams DC, Otárola-Castillo E. 2013. *geomorph*: an *R* package for the collection and analysis of geometricmorphometric shape data. *Methods in Ecology and Evolution* 4:393–399.

Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46.

Bellairs ADA, Jenkin CR. 1960. The skeleton of birds. In: Marshall AJ ed. *Biology and Comparative Physiology of Birds, Vol. 1*. New York: Academic Press, 241–300.

Blomberg SP, Garland TJ, Ives AR. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57:717–745.

Bock WJ. 1963. The cranial evidence for ratite affinities. *Proceedings of the 13th International Ornithological Congress* 1:39–54.

373 Bock WJ. 1964. Kinetics of the avian skull. *Journal of Morphology* 114:1–42.
374 Bridge ES, Jones AW, Baker AJ. 2005. A phylogenetic framework for the terns (Sternini)
375 inferred from mtDNA sequences: implications for taxonomy and plumage evolution.
376 *Molecular Phylogenetics and Evolution* 35:459–469.
377 Bright JA, Marugán-Lobón J, Cobb SN, Rayfield J. 2016. The shapes of bird beaks are highly
378 controlled by nondietary factors. *Proceedings of the National Academy of Sciences,*
379 *U.S.A.* 113:5352–5357.
380 Bright JA, Marugán-Lobón J, Rayfield J, Cobb SN. 2019. The multifactorial nature of beak
381 and skull shape evolution in parrots and cockatoos (Psittaciformes). *BMC Evolutionary*
382 *Biology* 19:1–9.
383 Bühler P, Martin LD, Witmer LM. 1988. Cranial kinesis in the Late Cretaceous birds
384 *Hesperornis* and *Parahesperornis*. *The Auk* 105:111–122.
385 Degrange F, Tambussi C, Moreno K, Witmer L, Wroe S. 2010. Mechanical analysis of
386 feeding behavior in the extinct "Terror Bird" *Andalgalornis steulleti* (Gruiformes:
387 Phorusrhacidae). *PLoS ONE* 5:e11856.
388 Felice RN, Goswami A. 2018. Developmental origins of mosaic evolution in the avian
389 cranium. *Proceedings of the National Academy of Sciences, U.S.A.* 115:555–560.
390 Field DJ, Hanson M, Burnham DA, Wilson LE, Super K, Ehret D, Ebersole JA, Bhullar B-
391 AS. 2018. Complete *Ichthyornis* skull illuminates mosaic assembly of the avian head.
392 *Nature* 557:96–100.
393 Goodall C. 1991. Prorustes methods in the statistical analysis of shape. *Journal of the Royal*
394 *Statistical Society: Series B (Methodological)* 53:285–321.
395 Gussekloo SWS, Bout RG. 2005. The kinematics of feeding and drinking in palaeognathous
396 birds in relation to cranial morphology. *The Journal of Experimental Biology* 208:3395–
397 3407.

Gussekloo SWS, Vosselman MG, Bout RG. 2001. Three-dimensional kinematics of skeletal elements in avian prokinetic and rhynchokinetic skull determined by roentgen stereophotogrammetrics. *The Journal of Experimental Biology* 204:1735–1744.

Hackett SJ, Kimball RT, Reddy S, Browie RCK, Braun EL, Chojnowski JL, Cox A, Han K, Harshman J, Huddleston CJ, Marks BD, Miglia KJ, Moore WS, Sheldon FH, Steadman DW, Witt CC, Yuri T. 2008. A phylogenomic study of birds reveals their evolutionary history. *Science* 320:1763–1768.

Hammer O, Harper DAT. 2006. *Paleontological Data Analysis*. Malden: Blackwell Publishing, 351 pp.

Hammer O, Harper DAT, Ryan PD. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4:1–9.

Hammer O. 2020. *PAST Paleontological Statistics v.4.03. Reference Manual.* Oslo: University of Oslo, 283 pp.

Hofer H. 1954. Neuere Untersuchungen zur Kopfmorphologie der Vögel. *Acta XI Congressus Internationalis Ornithologici*:104–137.

Holdaway RN, Jacomb C. 2000. Rapid extinction of the moas (Aves: Dinornithiformes): model, test, and implications. *Science* 287:2250–2254.

Hu H, O'Connor J, McDonald P, Wroe S. 2020. Cranial osteology of the Early Cretaceous *Sapeornis chaoyangensis* (Aves: Pygostylia). *Cretaceous Research* 113:104496.

Hu H, Sansalone G, Wroe S, McDonald PG, O'Connor JK, Li Z, Xu X, Zhou Z. 2019. Evolution of the vomer and its implications for cranial kinesis in Paraves. *Proceedings of the National Academy of Sciences, U.S.A.* 116:19571–19578.

Huxley TH. 1867. On the classification of birds; and on the taxonomic value of the modifications of certain cranial bones observable in the class. *Proceedings of the Zoological Society of London* 27:415–472.

423 Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in
424 space and time. *Nature* 491:444–448.
425 Jetz W, Thomas GH, Joy JB, Redding DW, Hartmann K, Mooers AO. 2014. Global
426 distribution and conservation of evolutionary distinctness in birds. *Current Biology*
427 24:1–12.
428 Klingenberg CP. 1998. Heterochrony and allometry: the analysis of evolutionary change in
429 ontogeny. *Biological Reviews* 73:79–123.
430 Klingenberg CP, Marugán-Lobón J. 2013. Evolutionary covariation in geometric
431 morphometric data: analyzing integration, modularity, and allometry in phylogenetic
432 context. *Systematic Biology* 62:591–610.
433 Krajewski C, Sipiorski JT, Anderson FE. 2010. Complete mitochondrial genome sequences
434 and the phylogeny of cranes (Gruiformes: Gruidae). *The Auk* 127:440–452.
435 Linde-Medina M. 2016. Testing the cranial evolutionary allometric "rule" in Galliformes.
436 *Journal of Evolutionary Biology* 29:1873–1878.
437 Mayr G. 2017. *Avian evolution*. Chichester: John Wiley, 293 pp.
438 McDowell S. 1948. The bony palate of birds. Part I. The Palaeognathae. *The Auk* 65:520–
439 549.
440 Mitchell K, Llamas B, Soubrier J, Rawlence N, Worthy T, Wood J, Lee M, Cooper A. 2014.
441 Ancient DNA reveals elephant birds and kiwi are sister taxa and clarifies ratite bird
442 evolution. *Science* 344:898–900.
443 Motani R, Schmitz L. 2011. Phylogenetic versus functional signals in the evolution of form-
444 function relationships in terrestrial vision. *Evolution* 65:2245–2257.
445 O'Connor JK, Chiappe LM. 2011. A revision of enantiornithine (Aves: Ornithothoraces)
446 skull morphology. *Journal of Systematic Palaeontology* 9:135–157.
447 Plateau O, Foth C. 2020. Birds have peramorphic skulls, too: anatomical network analyses

reveal oppositional heterochronies in avian skull evolution. *Communications Biology* 3.

R Development Core Team. 2011. *R*: a language and environment for statistical computing. *http://www.r-project.org*.

Rauhut OWM, Tischlinger H, Foth C. 2019. A non-archaeopterygid avialan theropod from the Late Jurassic of southern Germany. *eLife* 8:e43789.

Reid J. 1835. Anatomical description of the Patagonian penguin. *Proceedings of the Zoological Society of London* 3:132–148.

Revell LJ. 2012. *phytools*: an *R* package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3:217–223.

Schmitz L, Motani R. 2011. Nocturnality in dinosaurs inferred from scleral ring and orbit morphology. *Science* 332:705–708.

Simonetta A. 1960. On the mechanical implications of the avian skull and their bearing on the evolution and classification of birds. *The Quaterly Review of Biology* 35:206–220.

Sims S. 1955. The morphology of the head of the hawfinch (*Coccothraustes coccothraustes*). *Bulletin of the British Museum* 2:371–393.

Tokita M, Yano W, James H, Abzhanov A. 2016. Cranial shape evolution in adaptive radiations of birds: comparative morphometrics of Darwin's finches and Hawaiian honeycreepers. *Philosophical Transactions of the Royal Society B* 372:20150481.

Turvey ST, Holdaway RN. 2005. Postnatal ontogeny, population structure, and extinction of the giant moa *Dinornis*. *Journal of Morphology* 265:70–86.

Wang Y, Hu H, O'Connor JK, Wang M, Xu X, Zhou Z, Wang X, Zheng X. 2017. A previously undescribed specimen reveals new information on the dentition of *Sapeornis chaoyangensis*. *Cretaceous Research* 74:1–10

Xu X, Norell MA, Wang X, Makovicky PJ, Wu X. 2002. A basal troodontid from the Early Cretaceous of China. *Nature* 415:780–784.

Yin Y, Pei R, Zhou C. 2018. Cranial morphology of *Sinovenator changii* (Theropoda: Troodontidae) on the new material from the Yixian Formation of western Liaoning, China. *PeerJ* 6:e4977.

Zelditch ML, Swiderski DL, Sheets HD. 2012. *Geometric morphometrics for biologists: a primer*. Amsterdam: Elsevier Academic Press, 488 pp.

Zusi RL. 1984. A functional and evolutionary analysis of rhynchokinesis in birds. *Smithsonian Contributions to Zoology* 395:1-40.

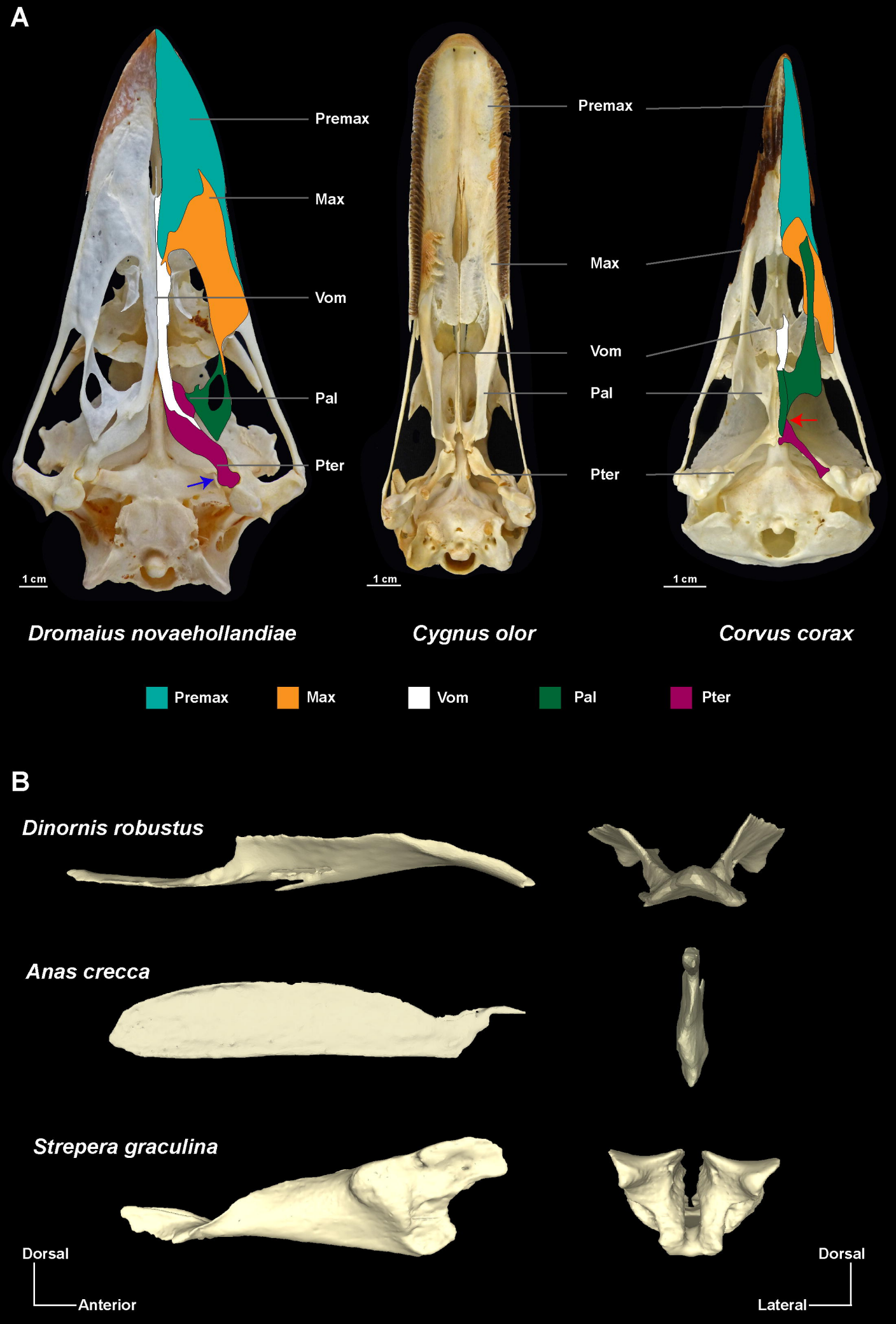
Zusi RL. 1993. Patterns of diversity in the avian skull. In: Hanken J, Hall BK eds. *The skull. Vol. 2. Patterns of structural and systematic diversity*. Chicago: University of Chicago Press, 391–437.

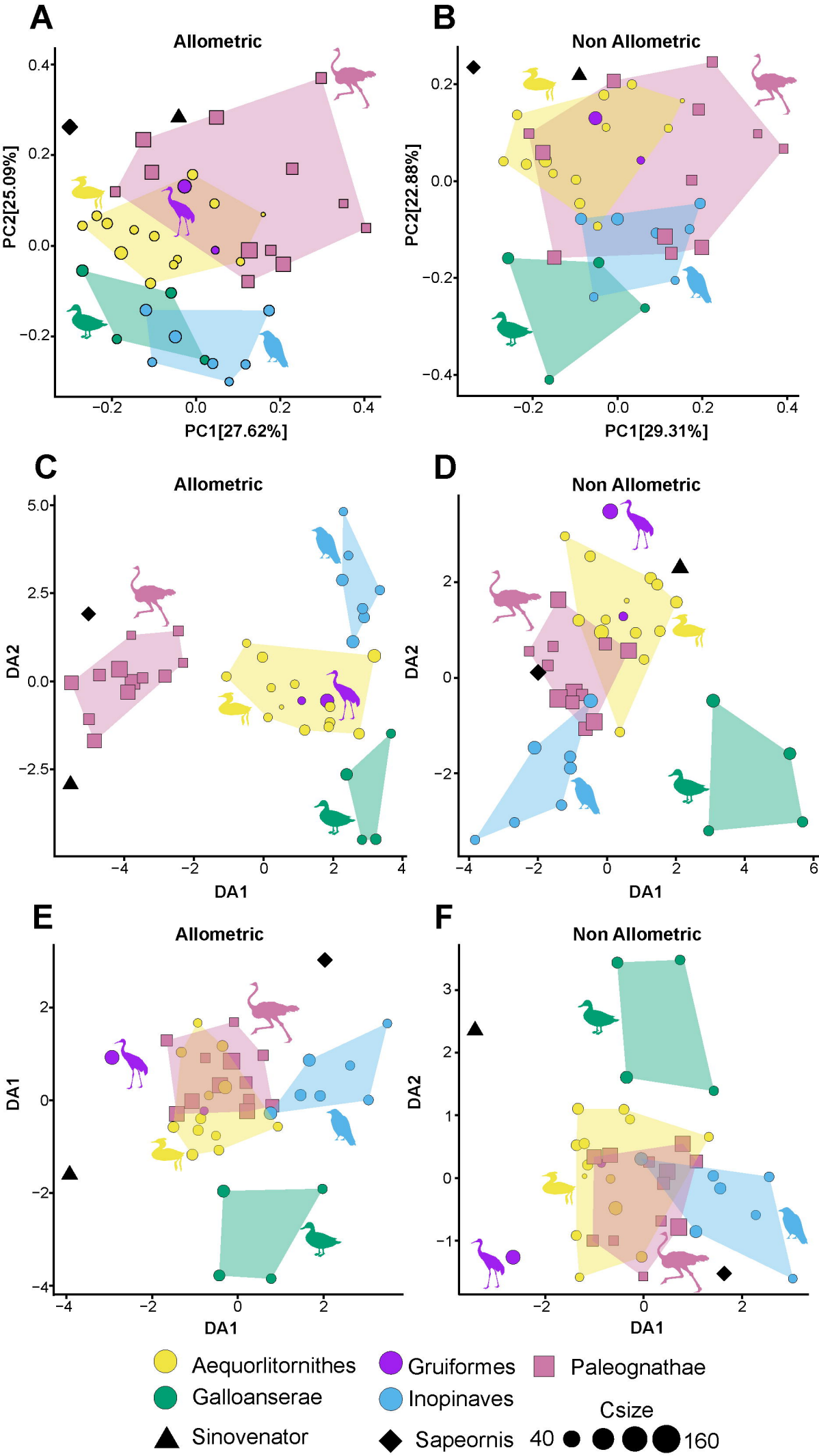
Figure legends

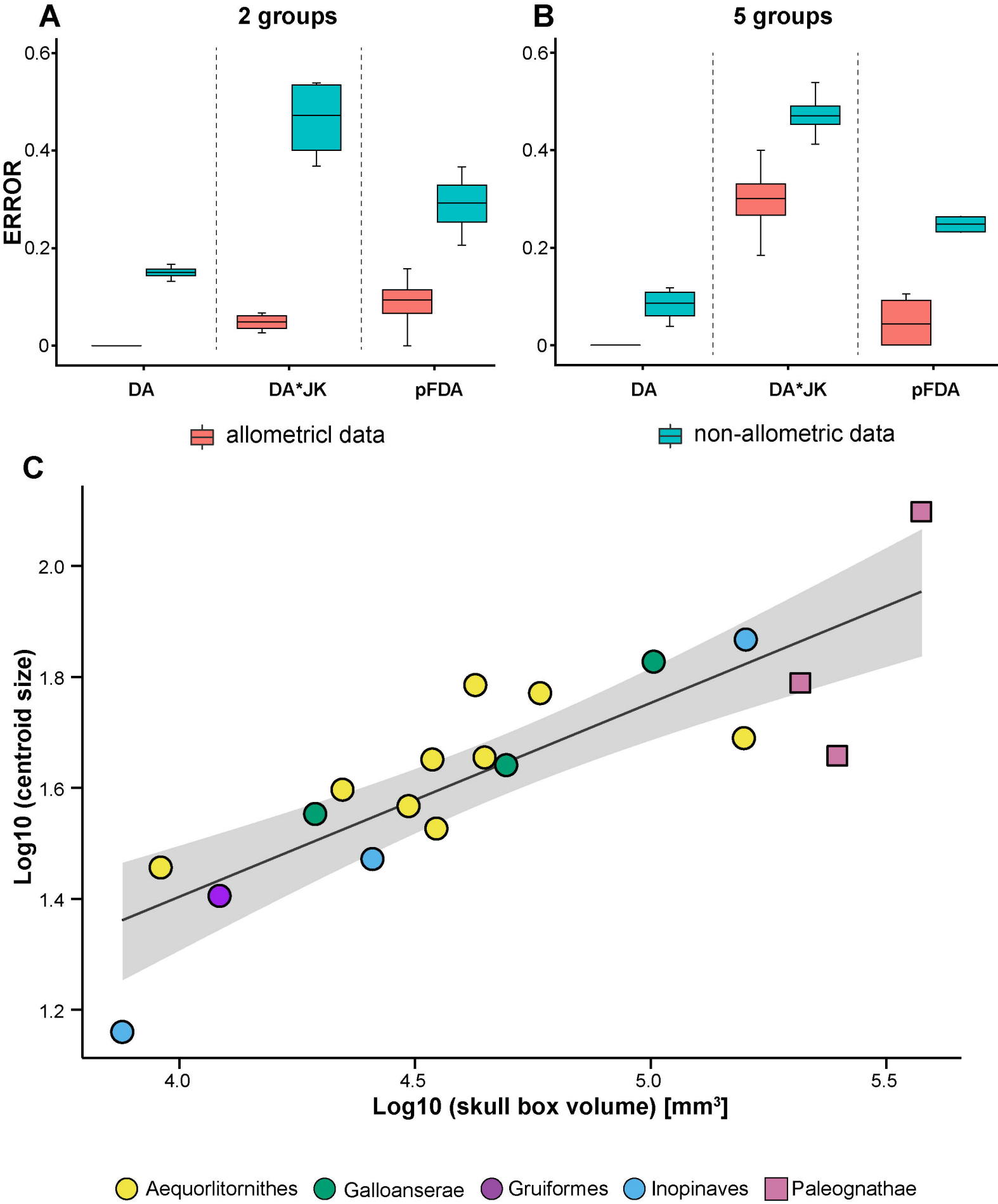
Fig. 1. Anatomical organization of the pterygoid-palatine complex (PPC) and shape variability of the vomer in palaeognath and neognath birds. (A) Palates of *Dromaius novaehollandia* (left), *Cygnus olor* (middle) and *Corvus corax* (right) in ventral view (all specimens form the Natural History Museum of Fribourg/University of Fribourg). For *Dromaius novaehollandiae* and *Corvus corax* the main organization of palate morphology is highlighted in a coloured scheme. The blue arrow in *Dromaius novaehollandiae* indicates the contact between the basipterygoid process and the pterygoid. The red arrow in *Corvus corax* indicates the mobile joint between pterygoid and palatine. **(B)** 3D models of the vomer of *Dinornis robustus*, *Anas crecca* and *Strepera graculina* in lateral view (left) and anterior view (right) from (not at scale) (3D models from Hu et al. 2019). Abbreviations: Max, Maxillary; Pal, Palatine; Premax, Premaxilary; Pter, Pterygoid; Vom, Vomer.

Fig. 2. Differences between allometric and non-allometric morphospaces of the vomer (Dataset A) in palaeognath and neognath birds. (A) PCA *(Principal Component Analysis)* results of allometric data. **(B)** *PCA* results of non-allometric data. **(C)** *DA (Discriminante Analysis)* results of allometric data. **(D)** *DA* results of non-allometric data. **(E)** *pFDA* (*phylogenetic Flexible Discriminant Analysis*) results of allometric data. **(F)** *pFDA* results of non-allometric data. Centroid sizes (Csize) are indicated by the size of the symbols. All silhouettes are taken from http://www.phylopic.org/.

Fig. 3. Errors of correct taxonomic identification for all comparisons of Dataset A-D. (A) Two-group identification (Palaeognathae and Neognathae) before (red) and after (green) correction for allometry. *DA*, Discriminant analysis; *DA*JK*, Discriminant Analysis with jackknife resampling; *pFDA*, phylogenetic Flexible Discriminant Analysis. **(B)** Five-group identification (Palaeognathae, Aequorlitornithes, Galloanserae, Gruiformes and Inopinaves). **(C)** *OLS* regression (black line) between log-transformed skull box volume and log-transformed centroid size of the vomer. Grey shadow marks the area of the 95% confidence interval.


A
Premax
Max
Vom
Pal
Pter
1 cm
Premax
Max
Vom
Pal
Pter
1 cm
Premax
Max
Vom
Pal
Pter
1 cm
Dromaius novaehollandiae
Cygnus olor
Corvus corax
Premax
Max
Vom
Pal
Pter
B
Dinornis robustus
Anas crecca
Strepera graculina
Dorsal
Anterior
Dorsal
Lateral


A
Allometric
PC2[25.09%]
PC1[27.62%]
B
Non Allometric
PC2[22.88%]
PC1[29.31%]
C
Allometric
DA2
DA1
D
Non Allometric
DA2
DA1
E
Allometric
DA1
DA1
F
Non Allometric
DA2
DA1
Aequorlitornithes
Galloanserae
Sinovenator
Gruiformes
Inopinaves
Sapeornis
Paleognathae
Csize
40
160


A
2 groups
B
5 groups
ERROR
0.6
0.4
0.2
0
DA
DA*JK
pFDA
allometricl data
non-allometric data
C
Log10 (centroid size)
2.0
1.8
1.6
1.4
1.2
4.0
4.5
5.0
5.5
Log10 (skull box volume) [mm³]
Aequorlitornithes
Galloanserae
Gruiformes
Inopinaves
Paleognathae