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SYMPOSIUM

Evolutionary Integration and Modularity in the Archosaur Cranium

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Synopsis Complex structures, like the vertebrate skull, are composed of numerous elements or traits that must develop and evolve in a coordinated manner to achieve multiple functions. The strength of association among phenotypic traits (i.e., integration), and their organization into highly-correlated, semi-independent subunits termed modules, is a result of the pleiotropic and genetic correlations that generate traits. As such, patterns of integration and modularity are thought to be key factors constraining or facilitating the evolution of phenotypic disparity by influencing the patterns of variation upon which selection can act. It is often hypothesized that selection can reshape patterns of integration, parceling single structures into multiple modules or merging ancestrally semi-independent traits into a strongly correlated unit. However, evolutionary shifts in patterns of trait integration are seldom assessed in a unified quantitative framework. Here, we quantify patterns of evolutionary integration among regions of the archosaur skull to investigate whether patterns of cranial integration are conserved or variable across this diverse group. Using high-dimensional geometric morphometric data from 3D surface scans and computed tomography scans of modern birds ($n = 352$), fossil non-avian dinosaurs ($n = 27$), and modern and fossil mesoeucrocodylians ($n = 38$), we demonstrate that some aspects of cranial integration are conserved across these taxonomic groups, despite their major differences in cranial form, function, and development. All three groups are highly modular and consistently exhibit high integration within the occipital region. However, there are also substantial divergences in correlation patterns. Birds uniquely exhibit high correlation between the pterygoid and quadrate, components of the cranial kinesis apparatus, whereas the non-avian dinosaur quadrate is more closely associated with the jugal and quadratojugal. Mesoeucrocodylians exhibit a slightly more integrated facial skeleton overall than the other grades. Overall, patterns of trait integration are shown to be stable among archosaurs, which is surprising given the cranial diversity exhibited by the clade. At the same time, evolutionary innovations such as cranial kinesis that reorganize the structure and function of complex traits can result in modifications of trait correlations and modularity.

Introduction

The evolution of multi-functional structures requires that the associations among and within complex traits can shift in response to natural selection, gaining new phenotypes and functions. This is exemplified by the evolution of the vertebrate skull. For example, the exaptation of pharyngeal arches to form the jaw (Miyashita 2016) and the evolution

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of the mammalian middle ear from post-dentary mandibular bones (Urban et al. 2017) illustrate qualitatively how patterns of correlations among traits can shift as new functions evolve. These types of shifting associations among traits are possible because of both the integration of traits and the modular nature of complex phenotypes. Morphological integration describes the strength and patterns of correlation among traits, while modularity describes the degree to which clusters of highly-integrated traits form semi-independent subunits (Olson and Miller 1958). Patterns of integration and modularity among phenotypic traits reflect the underlying developmental and genetic systems that generate the traits (Wagner and Altenberg 1996; Klingenberg 2008; Goswami et al. 2009; Hallgrímsson et al. 2009; Wagner and Zhang 2011). Thus, by quantifying the strength and pattern of phenotypic modularity, it is possible to gain insight into the systems generating variation and, in turn, the evolution of the structures in question (Hansen and Houle 2008; Klingenberg and Marugán-Lobón 2013; Goswami et al. 2014; Felice et al. 2018).

The effect of trait correlation on macroevolution can vary, either facilitating or constraining phenotypic evolution, depending on the direction of selection on correlated traits (Goswami et al. 2014; Felice et al. 2018). Trait correlation determines the axes of variation and thus the “lines of least resistance” upon which selection can act. When selection is aligned with the major axis of variation, integrated traits can promote higher morphological disparity than unintegrated structures (Goswami et al. 2014). In contrast, when there is discordant selection on the sub-units comprising an integrated whole, the evolutionary response may be constrained. Patterns of integration and modularity are thought to evolve (Wagner and Altenberg 1996; Goswami et al. 2015). However, most studies of evolutionary modularity have focused on single clades and do not assess shifting patterns of trait correlation (although see Goswami 2006; Piras et al. 2014; Haber 2015; Anderson et al. 2016; Heck et al. 2018). The tetrapod skull has been one of the most common structures used to studying phenotypic modularity. Most analyses have focused on testing simple or single hypotheses of modularity. Typically, this involves quantifying the strength of correlation between the face and braincase regions of the skull (Marugán-Lobón and Buscalioni 2003; Kulemeyer et al. 2009; Klingenberg and Marugán-Lobón 2013; Piras et al. 2014; Bright et al. 2016). However, evidence from mammals (Cheverud 1982, 1995, 1996; Marroig and Cheverud 2001; Goswami 2006; Porto et al. 2009; Santana and Lofgren 2013; Goswami and Finarelli 2016; Parr et al. 2016), lizards (Sanger et al. 2012), birds (Felice and Goswami 2018), and caecilians (Bardua et al. 2019; Marshall et al. 2019) indicate that the patterns of trait covariation in the skull are much more complex than can be accurately summarized with these two-module hypotheses based on a limited sampling of anatomical landmarks.

Recent advances in geometric morphometric techniques have allowed complex phenotypes to be quantified with higher detail than before (Botton-Divet et al. 2015; Parr et al. 2016; Fabre et al. 2018; Felice and Goswami 2018; Martınez-Abadıas et al. 2018; Bardua et al. 2019). At the same time, new approaches for testing hypotheses of modularity have allowed for more complex hypotheses of modularity to be evaluated using these data (Márquez 2008; Adams 2016; Goswami and Finarelli 2016; Larouche et al. 2018). Using high-dimensional geometric morphometrics, we recently quantified the strength of correlation among the components of the avian skull, demonstrating that the avian cranium is highly modular (Felice and Goswami 2018). All skull regions exhibit relatively weak correlations with each other except for the jaw joint and pterygoid, which show a high level of integration. Our approach revealed that each cranial module evolves with a unique tempo and mode and are variably associated with trophic ecology (Felice and Goswami 2018; Felice et al. 2019). However, it is unclear whether the particular pattern of trait correlations in the avian skull represents a pattern unique to birds or if this pattern was inherited from their non-avian dinosaur ancestors. In addition, the highly fused nature of the avian skull obscures the boundaries between many of the cranial elements (e.g., nasal and premaxilla, frontal, and parietal). This fusion limits the potential to further subdivide landmark configurations quantifying the avian skull into smaller units for testing more complex hypotheses of modularity, like those that can be tested in many other vertebrates (Cheverud 1982; Goswami and Finarelli 2016; Bardua et al. 2019). For example, examining shape correlations between different bones, let alone the individual ossifications, that make up the cranial vault would be impossible. However, we can examine patterns of modularity in the close bird relatives that exhibit more distinct boundaries between cranial elements, including their closest living relatives, Crocodylia, and extinct non-avian dinosaurs.

Crocodylomorpha (crocodylians and their extinct relatives) represents the only extant archosaurs other than birds. Although much maligned for their apparent lack of ecological and morphological disparity, more recent studies have highlighted the previously underappreciated craniofacial and ecomorphological variation in Crocodylomorpha (Pierce et al. 2008; Stubbs et al. 2013; Wilberg et al. 2019). This is especially true of fossil forms like notosuchians and peirosaurids which exhibit more diverse dentition and trophic ecology than modern forms (e.g., Pierce et al. 2009; Sereno and Larsson 2009). Did crocodylomorphs achieve their high cranial diversity under the same pattern of integration and modularity as birds? Or have differences in skull function and development forged different trait organization in these taxa? Using 3D morphometrics, it has been shown that the face and braincase of extant crocodylians are strongly integrated, with stronger integration in Alligatoridae than Crocodylidae (Piras et al. 2014). However, these analyses have never before been extended to include the broader crocodylomorph or archosaur clades, nor have more complex modularity patterns been assessed.

Non-avian dinosaur skulls exhibit even larger cranial disparity than crocodylomorphs, exemplified by wide range of cranial ornaments, dentitions, and feeding systems. As the sole extant clade of dinosaurs, neornithine birds have undergone major developmental and structural reorganization of the skull, including restructuring of the face and vault (Bhullar et al. 2012, 2015; Maddin et al. 2016; Fabbri et al. 2017; Smith-Paredes et al. 2018). These types of developmental shifts are expected to change patterns of cranial integration and modularity. However, very little is known about cranial integration in non-avian dinosaurs. Data from linear measurements have suggested that the face, orbit, and braincase are independently evolving modules in dinosaurs (Marugán-Lobón and Buscalioni 2003), but this has yet to be tested with modern morphometric approaches.

Here, we quantify the cranial integration and modularity across archosaur groups using unprecedented 3D geometric morphometric data and unprecedented taxonomic sampling. By comparing the patterns of trait covariation observed across Dinosauria and in Crocodylomorpha, we evaluate whether patterns of cranial integration have remained static through the nearly 250-million-year history of archosaurs or evolved with changes in skull structure, function, and development.

Methods

Morphometric data

We quantified skull morphology across archosaurs using 3D digital models derived from surface scans and computed tomography scans of modern and fossil specimens. For fossil specimens, we selected only those that were highly complete, articulated, and undeformed or had the ability to be retrodeformed (i.e., taphonomic deformation removed by editing digital model of the specimen). Although this requirement constrains our overall taxonomic sampling, it limits the effects of taphonomy and missing data on the results. Our dataset is composed of 352 extant bird species, 24 extant and 14 extinct mesoeucrocodylian crocodylomorph species, and 27 extinct non-avian dinosaurs (Electronic Supplementary Data 1). We focus on evolutionary (i.e., interspecific) modularity and integration rather than static (i.e. intraspecific variation within a growth stage) modularity and integration as few extinct archosaurs are known from enough cranial specimens for rigorous morphometric analysis at this resolution. Furthermore, studying evolutionary integration and modularity with broad taxonomic sampling and fossil data, as in the present dataset, allows for the study of shifts in trait correlation patterns in deep time (Klingenberg 2014; Goswami et al. 2015). For each group, we established a landmarking scheme allowing for the maximum number of anatomically distinct regions to be partitioned given the presence of visible sutures in the digitized data (Electronic Supplementary Data 2). For mesoeucrocodylians and non-avian dinosaurs, the premaxilla, maxilla, nasal, frontal, parietal, squamosal, prefrontal+lacrimal, jugal+quadratojugal, postorbital, supraoccipital/exoccipital/otoccipital, occipital condyle, basioccipital, and articular surface of the quadrate are preserved in all specimens. In mesoeucrocodylians, the pterygoid, ectopterygoid, pterygoid flange, palatine, ventral surface of the maxilla and premaxilla were also quantified. However, the ventral surface of the skull is preserved and accessible in fewer than 30% (9 of 27 species) of the non-avian dinosaur specimens. Thus, these regions were excluded from the non-avian dinosaur dataset. Furthermore, many of the non-avian dinosaur species are preserved with the cervical vertebrae and/or mandible in articulation with the skull, obscuring the occipital and jaw joint regions. For this reason, we divided the dinosaur dataset into two groups. One that contains 27 species which preserve nine regions on the lateral and dorsal elements of the skull (premaxilla, maxilla, nasal, frontal, prefrontal+lacrimal, parietal, squamosal, jugal+quadratojugal, and postorbital). The second dataset is made up of the 19 of these 27 specimens which also preserve the anatomy of the occipital region (supraoccipital, occipital condyle, basioccipital) and the articular surface of the quadrate. These datasets (the 9-region dataset and 13-region dataset, respectively) represent our effort to optimize specimen number and anatomical sampling.

Compared to mesoeucrocodylians and non-avian dinosaurs, crown birds have highly fused skulls with fewer visible cranial sutures present in adults (Baumel and Witmer 1993; Bhullar et al. 2015; Maddin et al. 2016; Fabbri et al. 2017). Therefore, anatomical landmarks at the sutural boundaries of all the regions present in the other groups are difficult to discern. We employed a previously described landmarking scheme for the bird dataset that divides the skull into the rostrum, palate, vault, occipital, basisphenoid, pterygoid, naris, and articular surface of the quadrate (Felice and Goswami 2018).

Whereas anatomical landmarks and boundaries marked by semilandmarks can provide a robust characterization of anatomical structures (Gunz et al. 2005), these points are largely limited to the contact between, or midlines of, elements. Hence, this approach thus excludes large portions of anatomical variation that exist within complex cranial regions. For example, many pachycephalosaurs exhibit ornamental horns on the squamosal which would not be captured by simple semilandmark curves around the margins of the squamosal (Goodwin and Evans 2016). In this study, we used a semi-automated procedure, implemented in the R package “Morpho” to project surface semilandmarks from a template on to each specimen (Schlager 2017). This results in a high-dimensional morphometric characterization of surficial shape of the skull (Fig. 1).

Anatomical landmarks were digitized on the left and right sides, but semilandmark curves and surface semilandmarks were digitized on the right side due to the frequency of incompletely preserved fossil specimens. Digital models of specimens that show better preservation on the left side were mirrored before landmarking. Finally, for each group, right-side semilandmarks were mirrored to the left side to mitigate artifacts related to Procrustes alignment of unilateral points on symmetrical structures (Cardini 2016). After subjecting each dataset to Procrustes alignment, all left-side landmarks were removed to reduce the dimensionality of the data and remove redundancy in shape information due to bilateral symmetry. The final datasets consist of 757 landmarks and semi-landmarks in birds, 1515 landmarks and semi-landmarks in non-avian dinosaurs, and 1291 landmarks and semi-landmarks for mesoeucrocodylians.

Phylogenetic hypotheses

To evaluate the strength of correlation between skull regions, we employed phylogenetically informed analysis of modularity by calculating the independent contrasts of shape and calculating trait correlations on these data (Felsenstein 1985). For the bird dataset, we utilized a phylogenetic hypothesis that combines the backbone topology of a recent molecular sequence dataset (Prum et al. 2015) to which the fine-scale relationships of an older species-level topology (Jetz et al. 2012) were grafted. This topology was generated following published procedures (Cooney et al. 2017) and has been used extensively to study avian macroevolution in recent years (Chira et al. 2018; Felice and Goswami 2018; Felice et al. 2019).

The relationships among non-avian dinosaurs are currently debated, with the uncertainty focused on the branching of Theropoda, Sauropodomorpha, and Ornithischia. Traditionally, Theropoda and Sauropodomorpha form a monophyletic clade (Saurischia) (Steeley 1887; Langer and Benton 2006; Nesbitt 2011; Langer et al. 2017). In contrast, some recent hypotheses have placed Ornithischia as the sister clade to Theropoda (forming Ornithoscelida) (Baron et al. 2017; Müller and Dias-da-Silva 2017; Parry et al. 2017). We performed analyses on non-avian dinosaurs with two phylogenetic trees—a “traditional” topology with Theropoda and Sauropodomorpha as Saurischia and another with “Ornithoscelida.” The time-calibrated “traditional” topology was generated using first and last appearance data to calibrate the phylogeny in the R package “paleotree” (Bapst 2012), generating a posterior distribution of dated tree (e.g., Benson and Choiniere 2013). We then used TreeAnnotator to create a maximum clade credibility tree from this distribution (Drummond et al. 2012). To create the Ornithoscelida topology, we manually manipulated the basal branches from the “traditional” topology to match the published undated phylogenies originally reported for the hypothesis (Baron et al. 2017).

There are two main areas of uncertainty in the phylogenetic relationships of Crocodylomorpha. These relate to the affinities of the false gharial (*Tomistoma schlegelii*) and the marine thalattosuchians. *Tomistoma* has been reconstructed as either a sister to *Gavialis gangeticus* (Gatesy et al. 2003; Willis et al. 2007) or as a member of Crocodylidae (Brochu 1997, 2003), whereas Thalattosuchia may be nested within Neosuchia (Pol and Gasparini 2009) or basal to Crocodyliformes (Benton and Clark 1988; Wilberg 2015). Because of these debated

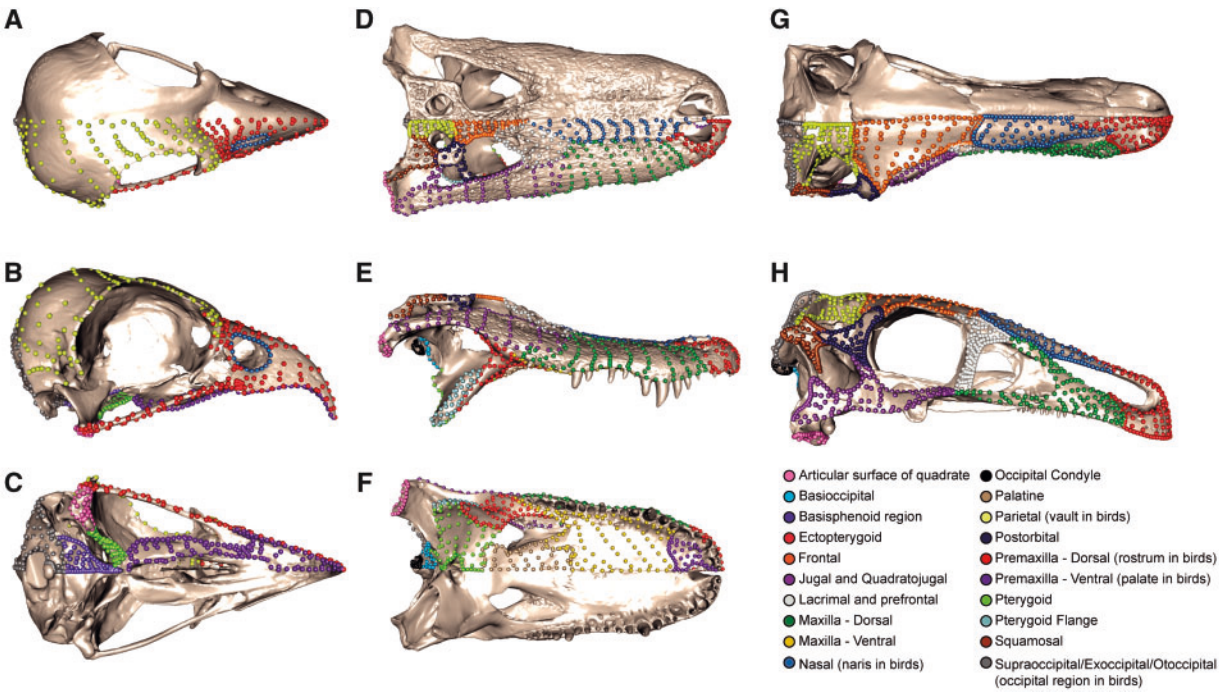

Fig. 1 Cranial regions in birds (dorsal, **A**; lateral, **B**; ventral, **C**), mesoeucrocodylians (dorsal, **D**; lateral, **E**; ventral, **F**), and non-avian dinosaurs (dorsal, **G**; lateral, **H**) characterized in this study. The 3D surface semilandmarks were placed on digital skull models using the "Morpho" R package (Schlager 2017). Colors of landmarks indicate the cranial region based on the most parameterized model of modularity for that group. Landmarks are illustrated on *Pandion haliaetus* (USNM 623422, A–C), *Alligator mississippiensis* (AMNH R-40582, D–F), and *Erlikosaurus andrewsi* (IGM 100/111, G–H).

relationships, we conducted all analyses of mesoeucrocodylians with four different topologies, representing the four possible combinations of these hypotheses. Trees were time calibrated applying the same methods used for non-avian dinosaurs (Electronic Supplementary Data 3).

Modularity

We evaluated the strength of correlation among cranial regions using two methods. First, we used the EMMLi method, a likelihood-based approach which allows multiple hypotheses of modular organization to be compared (Goswami and Finarelli 2016). This is achieved by calculating model likelihood from the within- and between-module correlations (ρ) for alternative hypotheses. For each dataset, we tested multiple hypotheses of cranial organization (Electronic Supplementary Data Table S4), ranging from the entire skull as a single module, to two modules (face and neurocranium) to all cranial elements as modules (19 modules in mesoeucrocodylians, 13 modules in non-avian dinosaurs, and 8 modules in birds, Fig. 1). Second, we used covariance ratio (CR) analysis implemented in the "geomorph" R package (Adams and Otárola-Castillo 2013) to quantify the strength of association between modules with a measure derived from the covariance matrix of the traits and to evaluate significance using a permutation procedure (Adams 2016). Both analyses were conducted in a phylogenetically-informed context with each of the topologies described above by performing the analyses on the phylogenetic independent contrasts of shape, calculated using the "ape" R package (Felsenstein 1985; Paradis et al. 2004).

To test whether allometric effects significantly affect skull shape and integration patterns, we conducted a Procrustes linear regression against log-transformed centroid size (Collyer et al. 2015). In birds ($R^2 = 0.18$, $P < 0.001$) and mesoeucrocodylians ($R^2 = 0.22$, $P < 0.001$), allometry has a small but significant effect on shape, but the effects of allometry are non-significant in non-avian dinosaurs (13 region dataset: $R^2 = 0.07$, $P = 0.299$; nine-region dataset: $R^2 = 0.06$, $P = 0.127$). Following this result, we carried out EMMLi analyses on the size-corrected shape data derived from the residuals of the linear regression for the bird and mesoeucrocodylian datasets.

We repeated the phylogenetically-informed EMMLi analysis on the mesoeucrocodylian data with landmarks partitioned into just seven regions corresponding to the regions present in the bird dataset to allow direct comparability between analyses of these clades. To ensure that differences in pattern of modularity were not due to differences in dimensionality of the landmark configurations, we randomly subsampled the mesoeucrocodylian data to contain the same number of landmarks as the bird data using the subsampleEMMLi function in the "EMMLiv2" R package (www.github.com/hferg/EMMLiv2). Subsampling was repeated for 100 iterations. The basisphenoid has little to no exposure on the external cranial surface in mesoeucrocodylians and was thus excluded from this analysis.

Results

In all EMMLi analyses, the hypothesis with the highest number of regions had the highest likelihood (Electronic Supplementary Data 5 A-N). These modularity hypotheses are also supported by CR analysis (Electronic Supplementary Data 5 O-R). The choice of phylogenetic topology does not appreciably alter the patterns of modularity and integration. Thus, we present the results using the traditional Dinosauria phylogenetic topology and Crocodylomorpha hypothesis 1 (thalattosuchians as neosuchians and *Tomistoma* as Crocodylidae) here and the results for all other topologies in the Electronic Supplemental Data 5. In birds, non-avian dinosaurs, and mesoeucrocodylians, all regions in the most-parameterized modularity hypothesis are significantly modular (CR < 1, $P < 0.001$). Examination of the correlations among regions demonstrated that birds exhibit weak correlation between all cranial regions except for the articular part of the quadrate and the pterygoid (Fig. 2A, Electronic Supplementary Data 5E). The correlation between these two elements ($\rho = 0.63$) is greater than the maximum within-region correlation of any of the eight regions present (basisphenoid, $\rho = 0.62$). In contrast, the pterygoid and quadrate are weakly correlated in mesoeucrocodylians ($\rho = 0.18$, Fig. 2C, Electronic Supplementary Data 5 F-I) relative to within-region correlation in these structures (pterygoid: $\rho = 0.69$, quadrate: $\rho = 0.95$). Instead, mesoeucrocodylians exhibit the highest correlations between occipital components (occipital condyle to supraoccipital: $\rho = 0.57$, occipital condyle to basioccipital: $\rho = 0.60$) and the dorsal and ventral sides of the premaxilla ($\rho = 0.74$). The frontal and prefrontal/lacrimal complex also exhibit high correlation in mesoeucrocodylians ($\rho = 0.56$).

When EMMLi is applied to the mesoeucrocodylian dataset with the same modularity hypothesis observed in birds, some important similarities and differences between these clades are observed (Fig. 2C). In both birds and mesoeucrocodylians, the vault and occipital region exhibit weak correlations with each other and with all other regions (Electronic Supplementary Data 5 J-M). Unlike birds, mesoeucrocodylians exhibit the highest correlation between the anterior and ventral elements of the skull (rostrum, palate, naris, pterygoid, and articular part of the quadrate). However, all between-module correlations ($\rho = 0.23$–0.35) are much lower than the lowest within-module correlation value (naris, $\rho = 0.50$), indicating relative decoupling of these skull regions with respect to shape variation.

In non-avian dinosaurs, the correlations between elements of the occipital region are high ($\rho = 0.59$–0.82), as in mesoeucrocodylians (Fig. 2D, Electronic Supplementary Data 5). Unlike mesoeucrocodylians, however, the quadrate is strongly correlated with the jugal+quadratojugal region ($\rho = 0.72$) in non-avian dinosaurs. All other pairwise comparisons of skull regions show relatively low correlations ($\rho < 0.50$). In the nine-region dataset that excludes the quadrate and occipital region, there is high within-region correlation ($\rho = 0.69$–0.82, Electronic Supplemental Data 5 A-D) and relatively low between-module correlation. The strongest between-region correlation are observed between the premaxilla and maxilla ($\rho = 0.43$), premaxilla and nasal ($\rho = 0.47$), parietal and frontal ($\rho = 0.46$), and the postorbital with the squamosal and lacrimal/prefontal ($\rho = 0.43$). This result suggests that rostral elements (premaxilla, maxilla, nasal) and the neurocranium (parietal, frontal, postorbital, squamosal) are highly integrated, and these are in fact fused structures in birds.

Effects of allometry

Evolutionary (interspecfic) allometry has been proposed as a significant factor shaping phenotypic integration in the avian skull (Bright et al. 2016). Our analysis shows that allometry has relatively minor effects on patterns of trait correlations. In birds, within- and between-region correlations are reduced by as much as 52% when allometric size is removed from the shape data (Electronic Supplementary Data 5E). However, relative patterns of correlation remain the same, with the highest within-region correlation in the pterygoid, basisphenoid, and quadrate and the highest between-region correlation between the pterygoid and quadrate. This finding indicates that allometric size is a significant factor driving the magnitude of, but not overall patterns of, modularity and integration in birds. Whereas allometry contributes to stronger trait correlation in birds, the effect of allometry is more complex in mesoeucrocodylians (Electronic Supplementary Data 5E). Allometry tends

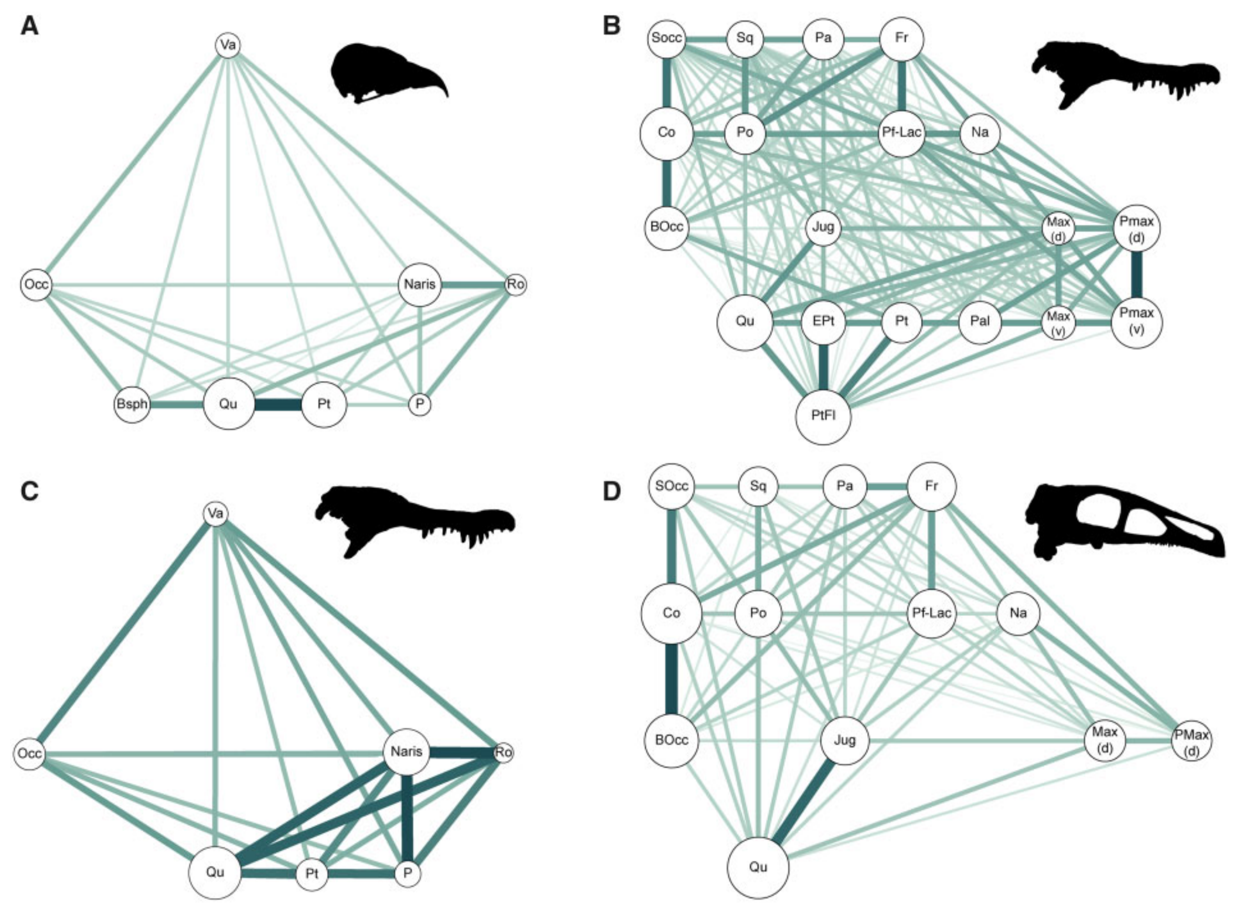

Fig. 2 Networks diagrams illustrating the results of phylogenetically-informed EMMLi analyses. Nodes represent cranial regions, with the size of the circle scaled to the magnitude of within-region correlation. Lines connecting nodes represent the strength of correlation between regions, with darker, thicker lines representing higher correlation. Network plots are illustrated for birds (**A**), mesoeucrocodylians (**B**), mesoeucrocodylians with landmarks partitioned according to the regions present in birds (**C**), and non-avian dinosaurs (**D**). BOcc: basioccipital, Bsph: basisphenoid region, Co: occipital condyle, Ept: ectopterygoid, Fr: frontal, Jug: jugal and quadratojugal, Pf-Lac: lacrimal and prefrontal, Max(d): dorsolateral side of the maxilla, Max(v): ventral surface of maxilla, Na: nasal, Occ: occipital region, Pa: Parietal, Pal: palatine, P: palate region, PMax(d): dorsolateral side of the premaxilla, PMax(v): ventral surface of premaxilla, Po: postorbital, Pt: pterygoid, PtFl: pterygoid flange, Qu: articular surface of the quadrate, Ro: rostrum region, SOcc: superior occipital region including supraoccipital and otoccipital, Sq: squamosal.

to contribute to stronger correlation between the occipital condyle and the lacrimal/prefrontal regions with other regions of the cranium. Conversely, the ectopterygoid, pterygoid, pterygoid flange, and jugal+quadratojugal are less strongly correlated with other skull regions as a result of allometry. Taken together, the overall pattern of modularity is similar with and without the effects of allometric size, with the highest correlations between the parts of the premaxilla and between the ectopterygoid and pterygoid flange. However, occipital elements are not strongly correlated when the effect of allometry on shape is statistically removed. This finding indicates that size drives the integration of the basicranium in mesoeucrocodylians, which reflect the scaling of biomechanical forces related to the loads produced by larger heads.

Discussion

Birds and their relatives show distinct patterns of trait correlation across the skull. In birds, the strongest correlations are between the quadrate and pterygoid, articulated elements that contribute to cranial kinesis (Bock 1964). Within-region correlation is highest in neurocranial and basicranial elements compared to the face and palate. If this pattern of modularity were inherited from non-avian dinosaurs, we expect the non-avian dinosaurs to exhibit high between-element correlation in these bones. Indeed, the supraoccipital, basioccipital, and occipital condyle are strongly correlated in non-avian dinosaurs, as well as in the mesoeucrocodylian dataset. This shared pattern suggests that a highly integrated occipital is an ancestral feature of archosaurs. The occipital is a highly multifunctional skull region as a site of articulation of the skull to the vertebral column, attachment area for the cervical musculature, and transmission of the spinal cord. Tightly correlated evolution of this region may be essential to properly maintaining its many functions. Furthermore, the observation that occipital integration is partially related to allometric effects suggests that high integration is related to biomechanical function (i.e., supporting loads at the craniocervical junction). This is also consistent with the observation that the basicranium experiences slow or conserved evolutionary patterns in some clades (Polly et al. 2006).

Although assessing patterns of integration and modularity in the palate or pterygoid in non-avian dinosaurs is challenging with the current sample, we observe notable differences in palatal integration when comparing mesoeucrocodylians and birds. The premaxilla in mesoeucrocodylians exhibits high integration among its skull regions, but the maxilla does not. This correlation among the premaxillary regions is enough to generate relatively strong rostrum–palate correlation in mesoeucrocodylians, when landmarks are binned according to the regions present in birds. Notably in mesoeucrocodylians, the palatal surface of the pterygoid, the pterygoid flange, and the ectopterygoid are strongly correlated. This region not only forms the bony secondary palate but also forms an "open joint" which buttresses the mandibles (Ferguson 1981; Walmsley et al. 2013). As such, shifts in the integration of the pterygoid with other adjacent elements may be driven by divergence in pterygoid function. Data from early branching archosauromorphs and dinosauromorphs, as well as non-neornithine paravians, are needed to track palate and pterygoid shape evolution across Archosauria to determine whether birds or mesoeucrocodylians (or both) represent a deviation from the ancestral patterns of association in this cranial region.

One area where avian and non-avian dinosaurs diverge is in the strength of correlation between the quadrate and other elements. In non-avian dinosaurs, we recover a high correlation between the articular surface of the quadrate and the jugal+quadratojugal region. The quadratojugal is articulated posteriorly with the quadrate and both elements contribute to the shape of the inferior temporal fenestra. Consequently, the position of the articular surface of the quadrate is expected to show correlated evolution with the jugal region. Because of a lack of a clear suture between the maxilla and jugal in extant birds, the jugal and quadratojugal were included as part of the "rostrum" module of the skull. As a result, we cannot test whether the avian jugal bar is more correlated with the quadrate or with the anterior face given the current bird landmark configuration. The anatomy of the jugal and quadratojugal underwent massive changes through avian evolution, becoming a slender bar associated with the cranial kinesis system (Bock 1964; Wang and Hu 2017). Indeed, avian cranial kinesis is a multi-bar linkage system that incorporates articulation of the beak, jugal, pterygoid, quadrate, and squamosal (Bock 1964; Olsen and Westneat 2016). However, because of the fusion of sutures in the neurocranium and rostrum in crown birds, it was only possible to isolate the quadrate and pterygoid, which show high integration. It is not currently possible to test whether functional and anatomical changes among the other elements of this system resulted in changes in trait correlations (or vice versa). Answering this question will necessitate focused study on these specific elements in early birds and paravians.

The observed patterns of modularity and integration are detectable due to the high-dimensional geometric morphometric data used to quantify skull shape. This robust morphological characterization of each cranial element allows the strength of correlation between and within individual skull elements to be measured more accurately than with only Type I landmarks (Bookstein 1991). Critically, regional analysis in non-avian dinosaurs allowed for the detection of quadratojugal–quadrate integration, a deviation from previous findings in avian dinosaurs (Felice and Goswami 2018). This demonstrates how increasingly fine-scale partitioning of hypotheses for cranial organization can lead to the discovery of new patterns and drive new hypotheses. Moreover, the fused regions present in birds (e.g., rostrum, vault, occipital region) are composed of bones which exhibit high between-region correlations in non-avian dinosaurs. Therefore, the fusion observed in bird skulls are likely the result of enhancing existing patterns of trait correlation already present in non-avian dinosaurs.

Taken together, these findings illustrate that evolutionary grades within Archosauria exhibit largely congruent patterns of trait correlations across the skull. The differences across these groups in patterns of integration and modularity and integration are largely concentrated on the structures that form the palate and cranio-mandibular joint(s). This result adds to the growing body of evidence that patterns of integration are largely conserved within major clades but they are not immutable and can evolve (Goswami 2006; Piras et al. 2014; Haber 2015;

Anderson et al. 2016; Heck et al. 2018). Because these groups differ so greatly in cranial disparity, geometry, mechanics, and development, a key next step is to investigate the causes of these shifts in trait correlations. The differences in craniofacial development that control modularity differences between birds and mesoeucrocrocodylians are only beginning to be understood (Bhullar et al. 2015; Maddin et al. 2016; Fabbri et al. 2017). Nonetheless, some major insights into craniofacial development in these clades are emerging as potential candidates for explaining integration patterns. For example, the evolution of the avian beak and palate phenotypes were achieved through shifts in the expression domains of the genes *FGF* and *WNT* in the frontonasal prominence during embryonic development (Bhullar et al. 2015). These evolutionary and developmental changes correspond with differences in phenotypic integration in the facial skeleton between birds and mesoeucrocodylians (low integration and high integration, respectively). As such, this restructuring of the developmental genetics and anatomy of the avian face and palate may have been responsible for the observed difference in integration. Similarly, superficially major differences in skull roof development and phenotype between birds and other tetrapods appear to be result of the morphogenic primacy of the brain over skull development (Fabbri et al. 2017). The relatively high within-neurocranium integration observed in birds, non-avian dinosaurs, and mesoeucrocodylians may be a consequence of underlying neuroanatomical integration patterns shaping the neurocranial elements examined in this study. The genetic and developmental underpinning of the pterygoid–quadrate correlation, however, remains to be seen.

Furthermore, understanding the macroevolutionary consequences of differences in cranial integration necessitates evolutionary model fitting using these data. In birds, integration constrains the evolution of disparity, as skull regions with higher within-module integration evolve at slower rates (Felice and Goswami 2018). Whether shifts in modularity across these three grades contribute to differences in evolutionary rates and disparity remains to be established. However, identifying differences in the patterns of cranial modularity across archosaurs is a critical step to investigating how modularity has shaped the evolution of diversity though deep time in this clade.

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Author contributions

Analyses were designed by R.N.F., A.W., and A.G., and carried out by R.N.F. and A.G. All authors collected data and contributed to the writing of the manuscript.

Supplementary data

Supplementary data available at *ICB* online.

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