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Avian skull morphological evolution: exploring exo- and endocranial covariation with two-block partial least squares

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Abstract

While rostral variation has been the subject of detailed avian evolutionary research, avian skull organization, characterized by a flexed or extended appearance of the skull, has eventually become neglected by mainstream evolutionary inquiries. This study aims to recapture its significance, evaluating possible functional, phylogenetic and developmental factors that may be underlying it. In order to estimate which, and how, elements of the skull intervene in patterning the skull we tested the statistical interplay between a series of old mid-sagittal angular measurements (mostly endocranial) in combination with newly obtained skull metrics based on landmark superimposition methods (exclusively exocranial shape), by means of the statistic-morphometric technique of two-block partial least squares. As classic literature anticipated, we found that the external appearance of the skull corresponds to the way in which the plane of the caudal cranial base is oriented, in connection with the orientations of the plane of the foramen magnum and of the lateral semicircular canal. The pattern of covariation found between metrics conveys flexed or extended appearances of the skull implicitly within a single and statistically significant dimension of covariation. Marked shape changes with which angles covary concentrate at the supraoccipital bone, the cranial base and the antorbital window, whereas the plane measuring the orientation of the anterior portion of the rostrum does not intervene. Statistical covariance between elements of the caudal cranial base and the occiput inplies that morphological integration underlies avian skull macroevolutionary organization as a by-product of the regional concordance of such correlated elements within the early embryonic chordal domain of mesodermic origin.

Keywords: Birds; Cranium; Morphological integration; Geometric morphometrics; Macroevolution

Introduction

The avian skull is structurally and functionally composed of the rostrum, the orbits and the braincase. Historically, comparative morphologists have described two marked avian skull configurations, extended or flexed, depending on the way in which such structural units are arranged (Marinelli, 1928; Van der Klaauw, 1948). When the skull is viewed laterally, an extended skull type has the rostrum, the orbit and the braincase all aligned consecutively in the same plane. In this condition, the foramen magnum opens caudally (i.e., the plane defined by the foramen magnum is vertical with respect to the horizon), and thus, the medullar axis is also oriented caudally (Fig. 1a). In the flexed condition, the alignment of the rostrum, the orbit and the braincase is decoupled thereby giving the whole skull a "bent" or

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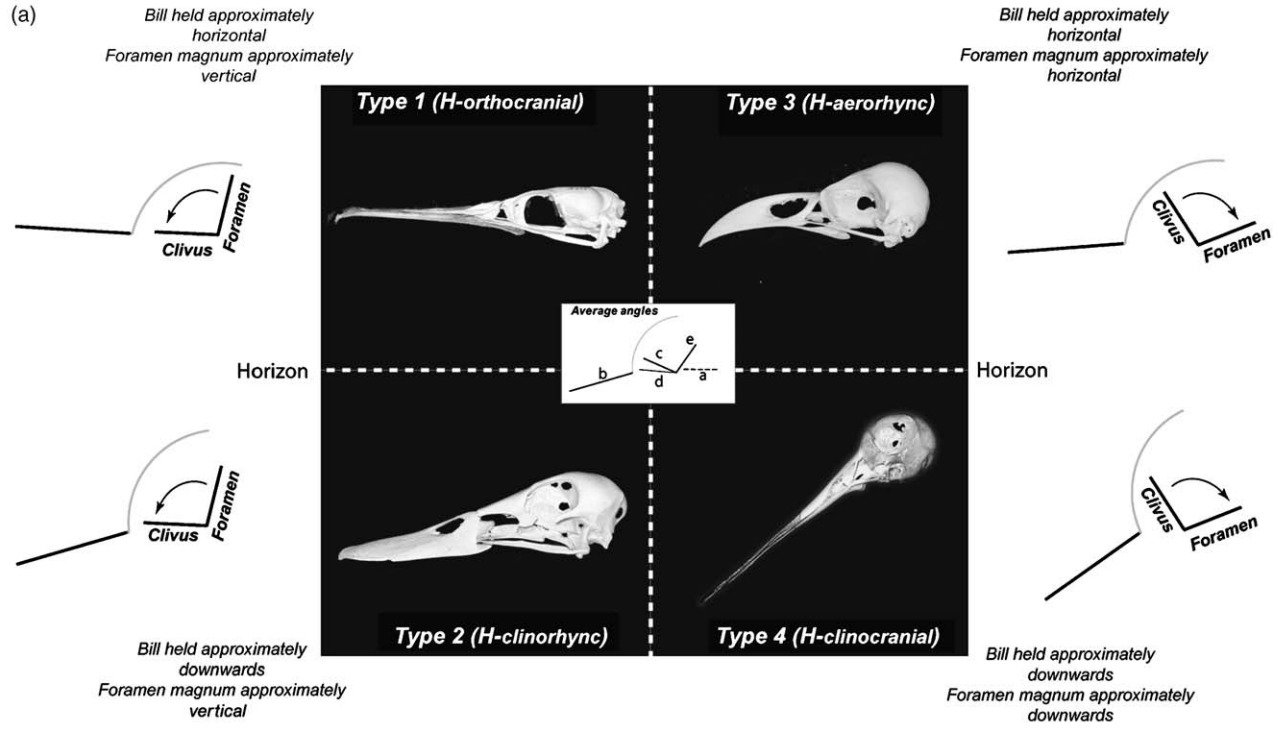

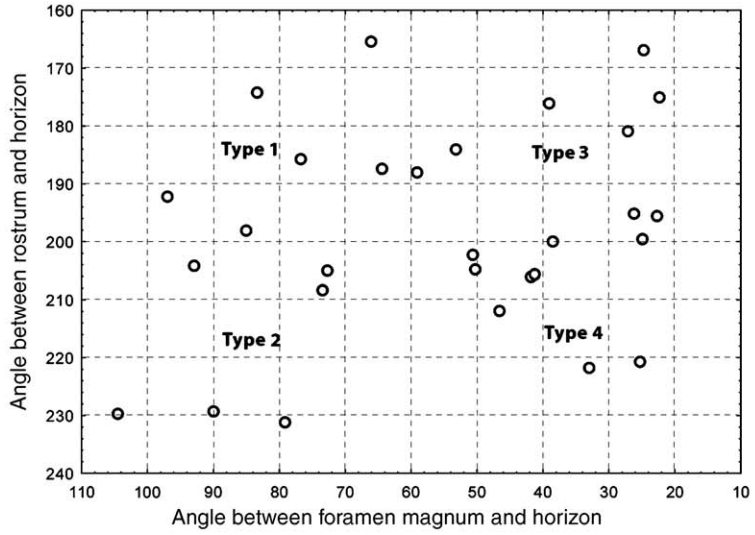

Fig. 1. Evolutionary skull typologies across modern birds (Neognathae). (a) Skull typologies after Duijm (1951): cormorant (Type 1), duck (Type 2), crow (Type 3) and woodcock (Type 4). Types are also labelled according to Hofer (1952) (in brackets), to show the analogies between both studies, even though they were conceptually different. Schematics at the sides show how measurements were depicted in the original paper; schematic in the centre portrays mean angular values of the full data set, with letters corresponding to the measured anatomical parts (see Fig. 2 and text). Horizon was the system reference (white horizontal dashed line), skulls pose in the ''natural'' posture when in alert. Sketches and text on the sides explain the structural meaning and match how measurements were depicted in Duijm (1951) (instead of scalars). (b) Scatter-plot of measured angles corresponding exactly to Duijm (1951, Fig. 5, p. 211). Distribution of points in the quadrants corresponds to types depicted in (a) (in the same order).

flexed appearance (Fig. 1a). In this latter situation the plane of the foramen magnum is declined (i.e., opens ventrally), and therefore, the medullar axis points ventrally. A typical example of an extended skull type would be a cormorant, of a flexed one, either a woodcock or a pigeon.

Comparative studies aiming to understand the evolutionary meaning of this type of structural variation of the avian skull received particular attention in the middle of the 20th century. Several studies attempted to outline what type of structural changes could underlie such phenotypic variants. Although this phenotypic