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Scientific and Artistic Representations in avian evolution

Representaciones Científicas y Artísticas en la evolución aviar

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Abstract: This essay explores the relationship between artistic and scientific perspectives in the depiction of birds' formal organization. It highlights how both fields converge in fundamental questions that shape the identity of avian organisms. Historically, early approaches to avian evolution focused on functional characters, which represented complex adaptations. Birds were later linked to archosaurian reptiles from around 200 million years ago, and their evolution was seen as gradual, emerging from terrestrial organisms. Recent palaeontological discoveries, particularly from the Maniraptora group, have provided well-preserved fossils, supporting the theory that birds are descendants of dinosaurs. These findings suggest that the emergence of birds from their maniraptoriform ancestors occurred in less than 50 million years. Phylogenetic systematics has helped to map out evolutionary transformations based on homologous traits, but discrepancies in these patterns have led to inconsistencies in cladograms. Meanwhile, studies in morphometrics, genetics, and developmental biology have focused on morphological units, interpreting these units through the lens of modularity and evolutionary integration—concepts also explored in art—to understand the new avian Bauplan.

Resumen: Este ensayo explora la interrelación entre el arte y la ciencia en la representación de la organización formal de las aves. Ambas disciplinas coinciden en comprender a las aves como animales de cuerpos singulares y biomecánica única, lo que ha influido en su comprensión evolutiva. Los primeros estudios sobre la evolución aviar se centraron en características funcionales, valorando sus adaptaciones complejas. Más tarde su origen se situó hace unos 200 millones de años a partir de arcosaurios basales. Esta evolución fue interpretada como un proceso gradual desde organismos terrestres. En el siglo XXI, los descubrimientos de fósiles completos, especialmente dentro de Maniraptora, han robustecido la hipótesis de que las aves descienden de los dinosaurios. Estos hallazgos indican que las aves modernas se diferenciaron de sus ancestros maniraptoriformes en menos de 50 millones de años. La sistemática filogenética ha ayudado a reconstruir la evolución de las aves, pero aún existen discrepancias en los caracteres evolutivos que generan incongruencias. Por otro lado, los estudios morfométricos, genéticos y del desarrollo enfocan la evolución de las unidades morfológicas, relacionándola con la modularidad y con un modelo de integración evolutiva, conceptos también explorados en el arte, para entender el nuevo Bauplan de las aves modernas.

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INTRODUCTION

This essay reflects on the historical and conflictual representations on the origin of birds. In this reflection, in homage to Professor Miquel De Renzi, I propose to examine some analogies between the scientific and the artistic mindsets when apprehending the meanings of the natural world. The concept of representation as an intellectual undertaking has been a driving force throughout my professional career. I have increasingly come to see parallels between the artistic vision, as proposed by the French philosopher Henri Lefebvre (1980), and the way scientists collectively engage in the practice of scientific knowledge. Lefebvre posits the existence of two distinct forms of nature: a first nature, comprising the objects that constitute "reality", and a second nature, which is shaped sifting these objects through intellectual spheres such as the artist's creativity or the scientific methods. In fact, the professional practice of scientists tends to be all-inclusive when they can produce, visualize, and better transmit this second nature. The filter applied is of particular interest to me, as it contains the ideas, metaphors, analogies, and prejudices used in every scientific and artistic work. The set of primary questions, axioms, criteria, objectives, and their bases is what scientists and artists share. I have chosen birds because they are one of the creatures that have given rise to the utmost scientific and

fictional productions. The dinosaur-avian transition and the emergence of the Bauplan Neornithes involve an extraordinary casuistry of morphological organization, evolutionary mechanisms, and biomechanics.

A CONFLICTIVE EVOLUTIONARY TRANSITION

Positively the fascination that birds exert in humans, based on key features of the avian anatomy, has encouraged researchers to study and assess continuous hypotheses and speculations to grasp their origination and evolution. It cannot be denied that the scientific method, as proposed by Francis Bacon [1561–1626], involved the observation of particulars with the aim of treating each object as something unique to facilitate the construction of theories. These particulars mostly include vital functions necessary to define the autonomy of living beings, and they were early defined as the capability of change, elimination, assimilation, growth, movement, multiplication, and inheritance (Cassirer, 1932). Such a *vital* paradigm has grown while addressing detailed descriptions on similarities and dissimilarities among beings and has become a powerful tool to recognize special traits for every organism, based on the principle that "nature never works in vain". Thus, a substantial volume of valuable studies has been accumulated since, projecting the formula of partializing individuals from their main adaptive features. This phenomenon has been used also in artistic representations.

Similarly, the interest in birds among Western societies until the 18th century was largely confined to their representation as food or decorative elements (Fig. 1A). However, with the advent of the natural sciences during the Victorian era, birds became the subject of much more rigorous studies by naturalists and artists. Attention to birds increased further during the Darwinian era, with studies focusing on their distinct shapes, colors, and behaviors (Lederer, 2019). In these representations functional adaptive traits were recurrently exacerbated as the "true" (*i.e.*, vital) attributes. It is a relatively easy task to identify work arts exhibiting distinctive avian characteristics. In such examples, some attributes of the species are exaggerated (Fig. 1B), while in others the objective is to remark peculiarities that are genuine curiosities. In yet others, the aim is to glorify the most extraordinary behaviors for survival that birds may exhibit (Fig. 1C–1D). It is worth noting that in the naturalistic bird art, at least until the 19th century, the animals are shown standing still, occupying a terrestrial space and niche. In none of them is the animal shown in flight, although the details on feathers, tails, heads, and beaks are highlighted.

From the scientist's part, several attributes had been identified as key features, to grasp the origin and transformations in birds. For example, Jean Baptiste Lamarck [1744–1829] placed birds as one of the most complex zoological groups below mammals in his *Philosophie Zoologique* (Lamarck, 1809). He did so because of their heart, brains and encephalon, and in addition, he took the beak (rhamphoteca) as a key vital feature for linking turtles and birds, with sea turtles and penguins representing transitional forms. It is now known that although the beaks of turtles and birds are cornified structures (Alibardi, 2021), beaks are also present in many other groups. The fossil record of beaks is extensive, with at least nine independent evolutionary origins over the past 300 million years in cephalopods, some actinopterygian fishes, early reptiles, dinosaurs such as the oviraptorosaur *Citipati*, as well as crocodile and mammal relatives (Hieronymus & Witmer, 2010; Wynd *et al.*, 2020). One of the most astonishing phylogenetic groups, which has been much debated because of the use of functionally convergent characters, was proposed by Gardiner (1998) when analyzing the Amniotes. Birds and mammals were sister groups based on their common renal systems, circulation, metabolic regulation, sensory organs, as well as parasites and molecular evidence. The clade was denominated Haematothermia (the warm blooded-amniotes) and included (Pterosauria + (Dinosauria + Aves)) as a sister taxon of Mammalia plus its stem-groups.

Aves are archosaur reptiles

Many emergent functional hypotheses concerning flight have been proposed to illustrate the distinctive nature of an aerial way of life. The presence of presumed feathers, in conjunction with a bulky skull and large orbits, as observed in the mid Triassic *Cosesaurus aviceps* from Montral-Alcover (Tarragona province), were identified as critical factors linking birds to gracile arboreal and running reptiles (Sanz, 1999, 2023), a hypothesis previously formulated by Nopcsa (1907). Such an early origin of birds would be accurate for the encompassing successive flying adaptations. Hence, a common origin for birds and pterosaurs, highlighting the occurrence of similar developments, was defended by Harry G. Seeley (1901). Seeley was convinced that pterosaurs had a high metabolic level and bird-like physiology, including the lungs, the heart, and the brain structure, and also a similar mode of locomotion on the ground (Wellnhofer, 2008). Despite the presence of hollow bones and epithelial feather-like structures in multiple pycnofibres from pterosaur specimens in the Middle–Late Jurassic Yanliao Biota pterosaur specimens from Inner Mongolia (Yang *et al.*, 2019), nowadays it is evident that pterosaurs did not possess the characteristics typically associated with Aves. However, the debate about the origin of pterosaurs has recently included a group of Triassic animals with slender bodies and outstanding and unique sensory features, such as the shape and size of the brain and inner ear. The unique neurosensory features found in these Triassic basal diapsids suggest that the evolution of sensory and nervous systems would predate an active flight. These form part of a clade denominated

Avemetatarsalia (with bird-like tarsi), which in turn is defined by Pterosauria and Dinosauria (Nesbitt *et al.*, 2017). The aphanosaurs and lagerpetids (with an important record in the Triassic of Argentina and Brazil) are not flying organisms but ancestral archosaurs close to Pterosauria, and even some authors also include the bizarre *Cosesaurus aviceps* (Peters, 2000). Hence, early phylogenetic proposals come time and again into the scene.

As depicted in Figure 2 there are many other hypotheses on the origin of Aves. The disparate origins of birds lead to several considerations. Early proposals aimed to demonstrate that, despite being flying animals, birds share universal life traits with other vertebrate groups. Lamarck's proposal used a set of independently evolved convergent traits to trace the origin of birds. The second lesson is that interpretations of the origin of birds have been replete with assumptions, assertions, and inferences about the recognition of these supposedly evolutionary decisive traits. Specifically, most of the hypothetical ancestors shown in Figure 2 fall within the archosaurian reptiles, or within the pseudosuchians (the crocodile hypothesis), or within the early avemetatarsians, or ornithodirans (pterosaurs, dinosaurs and birds). This distortion is quite interesting because it could be said that the characters used for each hypothesis are indeed due to the presence of a common ancestor within these reptiles (deep homologies). Such discrepancies depend on the level of similarity and relatedness: the more distant the ancestor, the more likely traits may be a set of homoplasies (Hall, 2007; Livezey & Zusi, 2007). If shared homologies are defined by the presence of these traits in any ancestor, no matter how

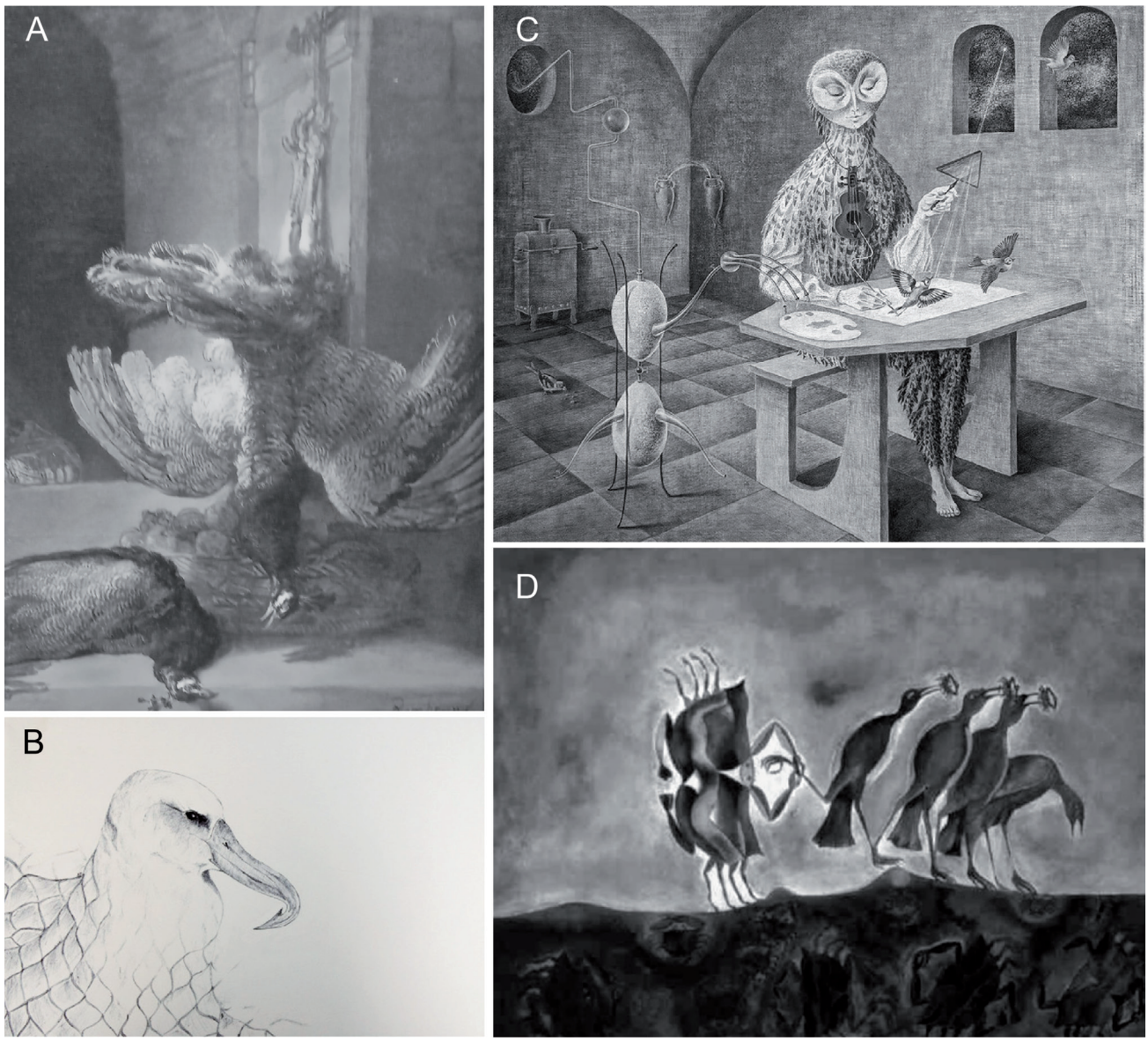

Figure 1. Figurative mode in bird representations. **A,** Birds as food. Detail from *Still Life with Peacocks* (1630), Rijksmuseum or National Museum of Amsterdam, Rembrandt van Rijn; **B,** the beak as exuberant feature. Detail of *Dodo* by Alicia Hayden; **C,** vitalistic essences of birds. Detail of *The Creation of the Birds* (1957) by Remedios Varo (Noticias de Totenart, 2024); **D,** unusual behaviors. *The Giant Crab After the Birds* by Francisco Toledo (Artnet Worldwide, 2024).

distant, then homoplastic traits would be homologous. That is, Haematothermia (evolutionary relationship of Aves and Mammals) is a case point: instead of talking about the recent origin of Aves, the resulting phylogeny is capturing other recurrent similarities, namely hypothesizing a set of shared developmental mechanisms underlining the warm-blooded condition of amniotes as a homoplastic parallelism, which should have appeared deep in time. Parallel evolution has been defined as the development of similar characters separately in two or more lineages sharing common ancestry, and many of them are grouped as developmental constraints (Willmer, 2000).

Because of birds' singular body organization and biomechanics, their origin and relationships were historically conflictive. They were explained by taking into account mere functional convergences that turned out to be evolutionarily independent, or they were approached as reptiles through simplesiomorphies, clustering them with almost every archosaurian clade (Fig. 2).

Aves are theropods

The phylogenetic analyses of Aves have led to the intriguing hypothesis that they are the descendants of theropod dinosaurs. This proposal, which is not entirely modern as it had its precedents in Huxley (1868) and Williston (1879), came to seduce society and scientists at a time when dinosaurs were at their second peak of fame. The first peak was associated with the emergence of modern natural history museums, such as the New York Natural History Museum during the 1920s and 1940s, whereas the second peak was related to the Dinosaur Renaissance, which occurred between 1960 and 1970 (Sanz, 2023). The theropod-bird origin appealed to the grotesque, the monstrous, and the mythical, not because of the dinosaur´s appearance but because of their connection with Aves. It is remarkable how delicate animals like birds emerge from a terrestrial carnivorous, carrion-eating beast.

A substantial body of fossil evidence now supports the hypothesis that theropods and birds are close relatives.

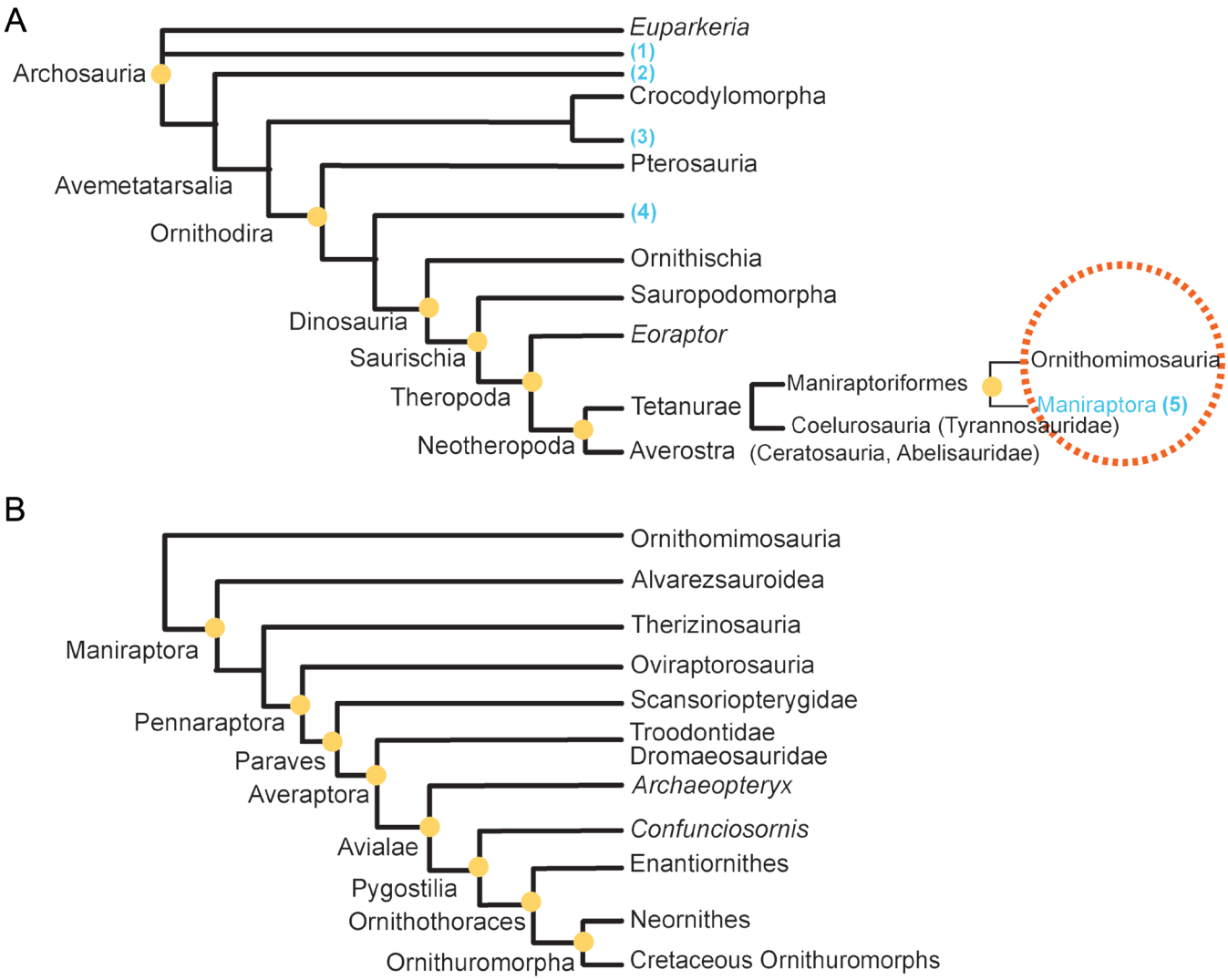

Figure 2. History of the phylogenetic positions proposed for Aves within Archosauria, and cladogram showing the clades mentioned in the text. **A,** Proposals: (1) by Heilmann, 1926; (2) by Feduccia, 1980; (3) by Walker, 1972; (4) as sister taxon of Dinosauria; (5) current view within Maniraptora; **B,** detail of the current view within Maniraptora.

The discovery of significant fossil deposits in Argentina and Brazil, specifically the Ischigualasto Formation and the Hyperodapedon Assemblage Zone, provides evidence of the early origin of theropods, which can be traced back to the Triassic period. *Eodromeus* and *Eoraptor* are acknowledged as the most basal relatives of Saurischia or within Theropoda, and Aves shares with them several traits, including modifications of the hands and feet with respect to sauropodomorphs. These include the presence of three main fingers on the manus (hand), the reduction of the fourth and fifth digits, and the presence of three main (weight-bearing) toes on the pes (foot), with the first and fifth digits also reduced. Most theropods possessed sharp, recurved teeth, which were useful consuming flesh. Additionally, claws were present on the ends of all fingers and toes (Novas *et al.*, 2021).

But why must we accept this conclusion? The significance of the origin of birds has reached the philosophy of science, due to the intense scientific debate, and it is used as a basis for contrasting or predicting scientific programs using the ideas of the philosopher Imre Lakatos [1922-1974]. Havstad and Smith (2019) in their publication schematized the two alternative hypotheses diagrammed as the **BAND**—Birds-Are-Not-Dinosaurs—against **BADM**—Birds-Are-Dinosaur-Movement. The earliest proponent of the BAND curiously was the "father of Dinosauria" Owen (1875), and the program was activated by Feduccia (1980), who suggested that the birds come from more basal groups of pseudosuchian archosaurs, echoing Heilmann's (1926) proposal. The BAND hypothesis sustains birds surely originated within the great Mesozoic radiation of the archosaurian or so-called "ruling" reptiles, which include the dinosaurs, pterosaurs, and crocodilians. Aves exhibit remarkable similarity to both the dinosaurs and to the immediate ancestors of the dinosaurs, the thecodont reptiles. Thus, the similarities between birds and dinosaurs should be understood as a mix of ancient plesiomorphies within Archosauria, and the impulse of selective forces that channeled their bipedal designs in a manner independent of that of birds (Ruben & Feduccia, 1997). The BAND proposal was backed using negative evidence, never recommended in scientific arguments, "no feathered dinosaurs ever existed" (it was so by the date of the debate), and "there is a failure of digit identity between the avian and dinosaurian hand".

Let us say that Ostrom´s (1974) research on *Deinonychus*, was decisive in assuming that birds are maniraptoran theropods, a proposal confirmed by other palaeontological and embryological evidence supporting the BADM hypothesis (Brusatte *et al.*, 2015). In fact, Ostrom´s own arguments for the BADM become scientific belts when further research programs—the origin of feathers, the shifting of the digits in the avian hand, the theropod furcula—confirmed the BADM hypothesis. In the lakatosian test for the evaluation of research programs, when the original empirical postulate has been confirmed, a protective belt around the core idea is added, and new postulates should be considered for testing the next scientific belt (Havstad & Smith, 2019).

A substantial number of scientific studies are currently engaged in testing the BAMD hypothesis through multidisciplinary research in key areas, namely embryonic experimentation and molecular mechanisms. A pertinent example is the beak and the premaxilla bone in birds, which have been tested in experiments using their living relatives, the crocodiles (Bhullar *et al.*, 2015). In birds, the premaxillae are extended posteriorly and welded medially. This extension is more pronounced in birds than in dinosaurs and crocodiles. To elucidate the premaxillary extension in the rostrum, the genetic pathways of the fronto-nasal ectodermal zone (**FEZ**) and the later midfacial Wnt-region (Wnt is a signaling pathway essential in the regulation of bone remodeling) were altered using inhibitors in two distinct routes. The morphological features of the experimentally transformed individuals show coincidences between dinosaurs and birds shapes. The experiment permitted the identification of common developmental paths within extant archosaurs (*i.e.*, crocodiles) along with the emergence of autapomorphic gene expression in Aves. The conclusion is that the premaxillary region is a key evolutionary innovation, and its flexibility has permitted birds to diversify into a range of disparate ecological niches.

THE AVIAN FOSSIL RECORD

The esteemed palaeornithologist Joel Cracraft from the American Museum of Natural History proposed a pluralistic approach to avian evolution several decades ago (Cracraft *et al.*, 2004). Holistic approaches to avian evolution seek to advance our understanding of the entire avian system, rather than focusing on the analysis or dissection of its constituent parts. These approaches integrate insights into the definition of the avian body modules and on how modules change, offering a comprehension of the character transformations from their ancestors, a group of the theropod dinosaurs denominated Maniraptora. Moreover, the discovery of an exceptional Mesozoic fossil record is challenging and have prompted the modification of previous hypotheses about avian evolution. It is evident that a scarce fossil record will introduce a significant bias in any analysis of ancestry and of character change rate through time.

Notably, due to its delicate nature, the avian record has long been suspected of being incomplete. The Chicago Palaeontological School, under the direction of Jack John Sepkoski [1948–1999], was a pioneer in the quantitative valuation of the fossil record, with the aim of understanding the origination, diversification and extinction of animal groups and their potential biases. In this regard, the contributions of the British palaeontologist Michael Benton and his colleagues

have been pivotal in assessing the adequacy of the avian fossil record during the Mesozoic for elucidating the early evolution and subsequent diversification of birds (Fountaine *et al.*, 2005). The quality of the avian fossil record has increased in several specimens following an exponential curve up to 2005. The curve is primarily driven by the discoveries made in China between 1990 and 2010. In turn, the resolution of the avian fossil record, that is the finest temporal or spatial bins, is concentrated in two periods, the Lower and Upper Cretaceous, whereas there is a huge gap of knowledge for 30 million years towards the mid-Cretaceous.

Are these numbers enough? Recent clever and original contributions provide the answer. Cashmore and Butler (2019) assess representativeness using a new metric based on specific-level data to assess variation in information content of fossil taxa and the entire record of a group. This has been denominated "skeletal completeness metric" and summarizes the percentage of preserved elements per anatomical parts of the skeleton of a particular species (Mannion & Upchurch, 2010). For instance, in the theropod *Allosaurus fragilis*, when worldwide specimens collected are considered, the metric completeness of the dorsal vertebrae represents 7.8% of the total skeletal parts discovered, and it is known the 97% of the whole skeleton using all known individuals (Cashmore & Butler, 2019). One of the best known theropods are the compsognathans (with a median of skeleton completeness ~90), placed at the base of the maniraptorans. This ranking is because they conform to a group, lasting a short interval of 25 million years, of small-sized theropods, such as *Sinosauropteryx*, with complete skeletons. This fossil reaches up to 1.07 meters in length, with an estimated weight of 0.55 kilograms. If we focus on the completeness of the theropod lineages close to Aves (Therizinosauria median of such representativeness ~20; Oviraptorosauria ~40; Dromaeosauria ~20; and Troodontidae ~10), the group of Paraves (~60) is by far the most demonstrative, showing that its fossils are less incomplete. Paraves maintain their diversity over time, but this is not correlated with the values of their representativeness over time. In fact, the Late Jurassic (Oxfordian–Kimmeridgian) and Early Cretaceous (Barremian–Aptian) show prominent peaks of representativeness associated with exceptional deposits (Cashmore & Butler, 2019).

The Early Cretaceous avian record from Iberia comes from two exceptional sites of laminated limestones: the Las Hoyas site in the Iberian Basin, and the Montsec in the Tremp Basin. Enantiornithine birds are diverse in both deposits with different morphological organizations (Sanz *et al.*, 1997, 2016; Nebreda *et al.*, 2023). In the Montsec, one of these small birds was described as a juvenile form, but recently revised as a subadult, estimating their proportions of short humeri, large radii, and short carpometacarpi (Cambra-Moo *et al.*, 2006).

Thus, enough is known about Paraves to hypothesize not only morphological patterns, even of the tail, but to discuss, for example, whether the tail feather played a role in sexual dimorphism, sexual selection, communication, or even the nature of flight, given the rectrices (Wang *et al.*, 2021). The recent discoveries of avian specimens have allowed accurate reconstruction of their relationships (Fig. 2B). Aves, or Avialae, includes the fossils that John Ostrom considered crucial to establishing similarities with theropods, the archaeopterygids, a clade that includes the genera related to *Archaeopteryx*. The Pygostylia clade is diagnosed by the bony structure that supports the tail feathers and musculature, which is shared with other parabirds, the Ornithothoraces, diagnosed by the presence of a keeled sternal plate. Ornithothoraces defines the differentiation between Enantiornithes and Ornithuromorpha each with a distinct pectoral solution based on the shape of the articulation between the coracoid and scapula: a concave facet on the coracoid accepts a convex boss from the scapula in ornithuromorphs, and the opposite in enantiornithines (Kurochkin & Walker, 1999).

THE AVIAN SYSTEM

Homology, and patterns of character transformations

It is essential to acknowledge the emergence of phylogenetics, which incorporates ontogeny and genetics in the search for a rational reference for diversity based on the origination of evolutionary novelties. Phylogenetic results are strengthened throughout the concept of taxic homology, but also on transformational homology tracing the history of character-states denoting the persistence of similarity with varying degrees of modifications in evolution (de Pinna, 1991; Hall, 2007). However, still now, a consensus about the phylogenetic relationships of paravians is still far from being reached. For this reason, knowledge of the steps toward the acquisition of anatomical and behavioral traits contributing to the origin of avian flight is still uncertain and in a state of flux. This sentence forms part of the conclusions offered by Agnolin *et al.* (2019) that analyze the evolutionary character transformations approaching the conflicts in the Maniraptora and Paraves relationships through a proper phylogenetic practice matching all the requisites suggested by Mooi and Gill (2010): examine data quality, character distribution, and evidence, plot characters to identify character conflict, and weigh evidence for homology and its functional integration.

The current state of phylogenetic systematics, which has lost control over the biological meaning of homology in pursuit of metric algorithms, has led to characters and character states being reduced to bits of phenotypic information (Freudenstein, 2005). This makes it challenging to evaluate which characters

are incongruent or incompatible. In the Systematic of Compatibility erected by Meacham and Estabrook (1985), if two hypotheses (*i.e.*, character trees) are logically inconsistent, they cannot be combined without first modifying one or both to render them compatible. Thus, part of the results was the identification of incompatibilities, and it was necessary to examine the subsets of trees where these conflicts occurred. In the avian evolution such incongruences concern: (1) characters that were not precisely defined or explored, (2) those that should be placed at the root of the tree but that are not shared by all the descendants, and (3) incompatible characters that apparently fail the *test of conjunction*.

Starting with the last item, the conjunction test was formulated to falsify homology in the same individual, so that two structures cannot be in the same organism (Patterson, 1982). If the wings of birds are a modification of the forelimb of theropods, could there be an animal with four wings? Some species of microraptorans, unenlagids, scansoriopterygids, which form the stem group of Avialae, present four wings (two located at the hind limbs). One of the wings of these dromaeosaurid dinosaurs with the body covered by feathers (Agnolin *et al.*, 2019) cannot be taken as an equivalent (homologous) structure, and therefore the modification of the hindlimb as a wing should be considered an anatomical singular (apomorphic trait). Calling the hindlimb as wings is a way to mistake structure for function. If both attributes are found in the same organism, they cannot be part of a single character transformation, instead one should be an independent feature, or a mistaken homology assessment. Therefore, the presence of feathered hindlimbs might bring about a set of homoplasies, acquired by independent mechanisms and should be discarded from the same interpretation as flying forelimbs evolutionary trend. The best question to answer is how do body feathered dinosaurs appear? Have these feathers a homologous configuration, or do they represent new lines of independent transformations? In fact, new discoveries on paravians indicate that aerodynamics was not the driving force in the evolution of feathered hindlimbs, proposing them, as a means of visual communication that would have played a very important role in the evolution of the plumage (O'Connor & Chang, 2015).

Novelties that might be placed as close to the root as possible, diagnose a more inclusive clade. These complex characters might be optimized as **ACCTRAN** (*i.e.*, accelerated transformations). ACCTRAN minimizes the parallel independent origin of complex traits, if these are really homologous for all the taxa, favoring the reversals. The phylogenetic study for the theropod-bird transition shows that many characters thought to be restricted to birds were already present in basal forms of dinosaurs, not uniformly, but in very diverse evolutionary positions. The Tetanura clade (including birds) already contains important physiological features such as: a rib cage indicating a sophisticated ventilated pulmonary system and pneumatic bones with air sacs like modern birds. The existence of air sacs connected to certain parts of the skeleton is physiologically relevant in performing an efficient double circulation of the respiration, where the air passes through the sacs, the lungs, reaches the posterior sacs and passes again through the lungs. This feature may have been accompanied by a modified circulatory system (Brusatte *et al.*, 2015).

Another interesting example of features that may be placed close to the phylogenetic root is the propatagium, which is a key in the configuration of the wing. The flexibility of the wrist and elbow depends on the configuration of the propatagium, which is arranged as *musculus propatagialis* or as a tendon on the anterior margin of the forelimb in maniraptorans, extending from the shoulder to the wrist. In its functional capacity, it maintains elbow flexion while extending the wrist joint, facilitating the sliding movement of the ulna and radius, which enables the bending and folding of the hand and the entire wing in an integrated triple joint. Interestingly, the propatagium may be observed in maniraptorans, such as *Microraptor* and *Caudipteryx*. According to the flexion that exerts the propatagial muscle, the angles of the elbow and wrist have been estimated and compared between basal maniraptorans and neornithid birds (Uno & Hirasawa, 2023). The angle of the hand folding is about 50º in Ornithothoraces and 90º in *Microraptor* (Agnolin *et al.*, 2019). Uno and Hirasawa (2023) suggest that the skeletal interlocking wing-folding system seen in the crown birds, would have been absent in an "intermediate" morphotype, such as *Deinonychus*. The intermediates, while possessing the propatagium, would extend the wrist joint toward the radial side when grasping items such as prey, whereas among pygostylians, the grasping capability was not supported.

The propatagium is an impressive piece of skin that delimits the wing surface with an aerodynamical shape for the anterior margin. Embryologically, it is linked to the cellular apoptosis in the wing bud, and to the elimination of tissues between the digits, and the process is spatiotemporally correlated with a coordinated expression to shoot the signals that establish the flight feather positions: alula, primary, secondary and tertiary (Saunders *et al.*, 1962). Flight feather morphogenesis are developmentally of an advanced type, which changes drastically since the beginning of the embryogenesis, with the feather calamus connected with specific muscles to coordinate wing movements (Kondo *et al.*, 2018). Birds possess two regions with flight feathers: the posterior edges of the wings (remiges) and the tail (rectrices). Plumed dinosaurs with various types of feathers indicate that flight feathers have their origin in Paraves (dromaeosaurs, troodontids, unenlagids, anchiornithids, microraptorids and birds) and in their stem-group oviraptorosaurs. It is postulated that an evolutionary event occurred approximately 170 million

years ago, at which point the genetic mechanisms of flight feather development in the wing and tail were already present (Seki *et al.*, 2017).

In this scenario, the development of the propatagium and the ability to acutely flex the wrist would constitute a deep homology at least for maniraptorans. Thus, a hierarchy in the definition of homologous character-states, from a more general condition to more exclusive ones, merges determining the pattern of the wing evolution. The corresponding scientific belt demands new predictions, such as the covariation of the wing configuration, the flight feathers and the avian hand. Geometric morphometrics exploring the divergence between the size configuration of the phalanges in digits I-II and III of Maniraptora (Nebreda *et al.*, 2020), show three plausible hand configurations: basal maniraptorans with long phalanges, enantiornithines with longer fingers than modern birds, and finally the modern birds with fingers I and III (alula and minor) modified by loss or shortening of phalanges. Apparently, the wing shape seems to be congruent with the hand configuration, since in the Archeopterygidae, the wing shape is long and broad, with short remiges, a rounded wing outline and a convex forewing margin; whereas in the enantiornithines, the remigial feathers are elongated (Xu *et al.*, 2014; Xing *et al.*, 2020).

Modularity: the morphological unit scale behind the modern avian Bauplan

Nevertheless, the concept of homology and homoplasy is not merely concerned with the succession of ancestors and sister groups; it continues to exert considerable influence on morphological organization (Müller, 2003a). The genesis of homology can be traced back to the rational morphology of the Enlightenment, which sought to elucidate the organization of living things and the manifestations of change. The materialistic and mechanistic view of the 18th century, advanced by the influential arguments of the philosopher Emanuel Kant (Cassirer, 1932; Ochoa, 2017), sought causal explanations for the composition of living beings and the relationship between their structure and function. One of the key fictional works of the era, which contributed to the development of the scientific paradigm of the period, is *Frankenstein* by Mary Shelley (1818). The capacity to create a living being by combining the parts of deceased corpses represents a means of asserting our ability to harness the fundamental forces of nature and to understand the correspondence between each component and the entire system. The concept of homology, as postulated by Richard Owen [1804–1892], along with the unity of plan put forth by Johann Wolfgang von Goethe [1749–1832] and the correspondence between parts proposed by Georges Cuvier [1769–1832], all seek to identify the phenotypic invariances of morphological organization, the structural and functional relationships that are common to a set of organisms.

Exemplified by the vertebrate archetype of Owen, the skull in Goethe, and the meaning of the modern Phyla in Curvier, homology is employed to delineate the identity of morphological units and biological groups (Cassirer, 1932). In fact, the owenian archetype is clearly pointing to what we later called modularity. Modularity directly results from processes (genetic, developmental, and ontogenetic) underlying the morphological organization shared by organisms that are not necessarily closely related. It concerns a set of mutually connected parts, ensuing a topographic order, and such connectivity follows a semi-independent organization implemented by a functional integrity (Buscalioni *et al.*, 2005; Eble, 2005; Rasskin-Gutman, 2005). The connectivity pattern of every morphological unit provides what is called organizational modularity (Eble, 2005). The property of being semi-independent or that parts of the constituent morphological units might be autonomous (the *autonomization* property by Müller, 2003a), confers to the modular organization the capability of variation, which is studied as variational modularity (Eble, 2005). Therefore, I present modularity as an equivalent definition of the organizational homology concept of Müller (2003a), avoiding the conflict of treating homology as an isolated character, as used in Systematics, that deprives of any casual explanation of its origin and modification. It is therefore necessary to understand modularity as the spatial occupation of the elements that make it up, whose connectivity give rise to a whole and whose construction and capabilities are regulated by rules and limitations. This section provides examples of changes in the modular organization of birds.

Complex modularity by addition. Models on feather evolution predicted in 1999 the presence of simple and seriated monofilaments appendages in theropods, such as those in the Jurassic *Sciurumimus albersdoerferi*, later confirmed by the fossil record (Prum, 2005). The feather modular architectural design comprises a simple module determined by the feather germ—a tubular appendage—which incorporates the formation of the shaft and vanes, and that grows out and in from the skin to the bone (in primary feathers). The feather germ differentiates over multiple spatial axes following a hierarchical morphological sequence that is transformed by a chain of molecular signaling. Hence, the feather is a perfect example of modular organization because, as a model, it displays a spatial disposition, has a geometric growth of branching, and is functionally integrated. The complexity is produced by the innovations introduced derived from the regulatory molecules that act as generators of new geometrical and developmental patterns within the constrained spatial parameters of the modular feather model. These changes appear to accommodate diverse eco-spaces, at least in the case of the primary feathers (Prum, 2005; Kondo et al., 2018; Chang *et al.*, 2019).

The feather distribution is related to skin pterylae, and they follow a spatial patterning, which is formed by a

periodic sequence of cell-to cell interaction by a reaction of an activator-inhibitor pair in a morphogenetic 2D field, according to a Turing model (Tseng *et al.*, 2024). The pterylae signature of the avian skin determines the appearance of every feather bud through a gap junction that mediates exchanges of ions and small molecules to build the skin tracts (*i.e.*, regions of body pterylae) separated by apteric regions. Although down and contour feathers already existed in maniraptorans, the symmetrical and asymmetrical feathers (the narrower edge towards the external part of the body) were already present at the pennaraptoran node.

Evolutionary teratology. The evolution of the forelimb in Theropoda over time has been investigated by Huntington (2013) using techniques including Bayesian ancestral state reconstruction (**ASR**), which plots the forelimb/femur ratio estimating its value for every node, starting at *Herrerasaurus* as the root. She incorporated a phylogenetic hypothesis, expressed in a network over the estimation of the ratios, showing a general tendency of forelimb shortening with respect to the root. However, the most intriguing pattern occurs at the coelurosaurian Tetanurae node, which clearly delineates two distinct evolutionary paths: (1) a lineage characterized by a pronounced reduction in forelimb length in relation to the femur (the entire forelimb became half the length of the femur) toward Tyrannosauridae, and (2) a lineage that displays a proclivity towards ancestral proportions, exhibiting a relative increase in forelimb total length (including the hands) toward Maniraptora.

In the first case, the proportions of the forelimb, with a modular organization, show an extraordinary modification becoming reduced to the extent of micromelia. This alteration concerns changes in the differential forelimbs/hindlimbs developmental growth rates, characterized by slower growth of forelimbs—secondarily associated with post-natal growth rates as occurred in the gigantic sizes of Tyrannosauridae and Carcharodontosauridae (Guinard, 2020). Micromelia is a malformation that corresponds to mutations exerted primarily during the initial stages of development (possibly involving the bone morphogenetic protein, **BMP**s, the fibroblast growth factor **FGF**s, and the sonic hedgehog Shh signaling), and that can give rise to significant phenotypic outcomes. This is specifically a teratological phenomenon, expressed in different ways regarding the outcome of the internal proportions of the stylopod (micromelia), zeugopod (rhizomelia) and hand (acromelia). This new forelimb pattern can be associated with other anatomical changes, such as rigidity of the limb elements or the loss of digits and phalanges, among others. Guinard (2020) posits that only those changes that can be registered as an alteration in development without producing mortality could be susceptible to study within the context of what he terms teratological evolution. In cases where developmental pathologies occur and the results have determined as natural mutants with new body organizations, a new macroevolutionary context may emerge (Diogo, 2020). The study of these malformations necessitates the identification of patterns within the developmental system that could display teratological characteristics, such as proportion, number, and position among skeletal elements on a morphological unit. This developmental alteration increases structural variations or designs of the limb, which frequently encompass new muscular and biomechanical conditions. These alterations are often associated with changes in other morphological units. One interesting case is the Carcharodontosaur *Concavenator corcovatus* from Las Hoyas (Cuesta *et al.*, 2016). How can an animal six mts long with micromelia compensate for its trophic function? *Concavenator* is an excellent example to prove how the biomechanics of predation—linking the technique of biting without using the hands—is related to a rigid axial skeleton (with imbricate and hypertrophied neurapophyses), and likewise, how its bipedal terrestrial locomotion is exercised without the balance of the forelimbs. In fact, the more significant number of autapomorphies in *Concavenator* have been determined in the axial skeleton (Ortega *et al.*, 2010). Briefly, although teratologies as malformations are transpecific (succeeding transversely in clades), it is not the case of ratites, in which comparative genomic studies have recently examined whether the independent loss of flight is accompanied by convergent protein and/or cis-regulatory changes (Newton & Smith, 2021).

The second case comprises the divergent lineage toward maniraptorans, a developmental shift in the control of arm and leg lengths, driven by a scaling to smaller body sizes, occurred (Huntington, 2013). Hence, it can be said that Aves present a different modular organization in fore-hindlimb proportion and in the hand length: a negative correlation of the humerus regarding the body length, a significant reduction in hindlimbs with a limited size range compared with theropods of similar body sizes, and with a constrained disparity of the hands. It has been demonstrated that the low disparity of hand shapes in birds is also independent of size (Nebreda *et al.*, 2020; Dececchi & Larsson, 2023).

Modularity in bird arts. The search for “pure” identity of beings has been a recurrent obsession in the artworks throughout modern art. In this, the identity is engaged with the geometric and constructive movements of the 20th century (Sedlmayr, 1955). The bird art series in web pages are not rare (*e.g.*, Maeght, 2020), and the sample evidences that the representations of the bird identity need abstractions, in an equivalent mode to the owenian vertebrate archetype. These abstractions reflect the modular building of the avian Bauplan, and I have selected three artistic visions as examples (Fig. 3):

(1) Eye-Beak module. In these representations the bird identity is composed of the eye-encephalon and

the beak, both topographically connected but do not form a solid unit because necks may or may not be considered (Fig. 3A). It is fabulous that a vertebrate skull can be simply represented by a triangle (beak) in front of a sphere (eye-encephalon). For the artist Wassily Kandinsky, the sense of the two geometrical figures has in turn spiritual meanings: violence, aggressiveness and action for the triangle, and the cosmic and spiritual for the circle (Kandisky, 1952). Science has checked this perception, revealing that among the neuroanatomical regions of modern birds (crown-group), the acquisition of an optic lobe and cerebellum evolved first among non-avialan dinosaurs (Watanabe *et al.*, 2021). In addition, the beak lengths must fall within the blind area of a binocular vision (Tyrrel & Fernández-Juricic, 2017). Second, although raptors and owls have enlarged eyes (with eye masses 1.4 and 2.2 times greater than average birds of the same weight), the scaling of the eye to the body mass in birds is not different to that of amphibians and small mammals (Brooke *et al.*, 1999).

(2) Wings-Tail module. The module is represented as a single surface, with the wings and tail aligned along an axis directed towards the head, forming an arrow (Fig. 3B). The animal is depicted as being in flight, with both its wings and tail extended. Alternatively, in instances

Figure 3. Abstract mode, exploring modularity and identity in birds. **A,** Eye and beak Module. Left, *Birds*, in antiquariat-rohlmann.de, uploaded by Enrique Tajes to Pinterest from https://es.pinterest.com/pin/1024428246476252132/ Right, *Yellow Birds* crane print, Japanese Oriental canvas prints for wall produced by Xuanhhao from https://www.amazon.es/XUANHHAO-Impresi%C3%B3n-amarillos-impresiones-decoraci%C3%B3n/dp/B0CG527CX8; **B,** wing and tail Module. Detail of *Two Birds* (1955) by George Braque, Tel Aviv Museum of Art; from WahooArt.com, from https://es.wahooart.com/@@/D4875U-Georges%20Braque-Dos%20p%C3%A1jaros. The corresponding modular schema is an arrow; **C,** intersecting Modules. Left, detail from *The Comedy of Birds* (1919) by Paul Klee, in Neon-Art.com from https://neron-art.com/es/klee-hand-painted-reproduction-oil-paintings-bird-comedy-1919-120x80cm.html. Right, *Bird in a Tree* (1928) by Pablo Picasso, Guggenheim, New York City, in Arthive.com from https://arthive.com/es/pablopicasso/works/484573~Pjaro_en_el_arbol#google_vignette; **D,** functional Integrity. Left, *Birds Flying before a Storm* by Pablo Risso, in Artelista, from https://www.artelista.com/obra/3691813234556624-pajarosvolandoantesdeunatormenta.html. Right, Iberian schematic art, *Stork of Cantos de la Visera*, uploaded by Jose-Manuel Benito Álvarez (Locutus Borg); **E,** modular interconnections. Interpretation of the connectivity among wings, tail and head of the work arts in C; 1, head; 2, tail; and 3 are wings. The hindlimb has no number.

where birds are depicted in a terrestrial or perching position, the module incorporates the head and hind limbs. In some instances, both the wings and the tail are represented by feathers, highlighting their flying functions (Fig. 3C). The composition in those cases plays with the center of the body as the geometrical place where all the structures intersect (Fig. 3E). The bird figures serve to illustrate the tense relationships that exist between various body parts. The correlation between forelimbs and hindlimbs has been scientifically demonstrated in data from 10,000 living bird species (Heers & Dial, 2014). This evidence indicates that flightless birds tend to have robust hindlimbs and reduced forelimbs, whereas hyperaerial birds move almost exclusively with wings and tend to have robust forelimbs and reduced hindlimbs.

(3) Feathered-Bodies module. This modular representation comprises a serial arrangement of feathers of varying lengths, collectively contributing to the formation of the animal body (Fig. 3D). The most significant feathers are the rectrices and remiges. The repetition of highly connected feathers illustrates their spatial pattern on the body, which is indicative of the aerodynamic capacity of the bird, as demonstrated by the diverging curves drawn in a harmonious balance. From a scientific perspective, the remarkable versatility observed in bird locomotion has been determined.

DISCUSSION: MACROEVOLUTION IN AVES

All the current avian research confirms the significant anatomical organization that has occurred during the theropod-bird transition. Several authors have proposed a stepped sequence to explain the morphological transition from dinosaurs to birds (Chiappe, 2009; Brusatte *et al.*, 2015; Chiappe & Qingjin, 2016). Therefore, one should expect a unique narrative to explain the macroevolutionary model of the transition: a sequence in which Enantiornithes precede the Neornithe organization, accompanied by an increase in generative processes that would lead to high disparity and diversity throughout. This seems to be strengthened because the transition was continued, with elevated rates of evolution along the stem of theropod evolution towards *Archaeopteryx*, and because all the classic 'bird' characters were acquired piecemeal over that long span of time (Benton, 2015). The macroevolutionary scenario is supported by the temporal context that states three distinct episodes occurred over a period of approximately 94 million years: (1) the Jurassic troodontids, the closest relatives of Aves, exhibiting certain flapping capabilities, known as **WAIR** (wing-assisted incline running, Tobalske & Dial, 2007) locomotion, in which the flap of forelimbs wings would aid hindlimbs in climbing. (2) the Early Cretaceous period with the emergence of enantiornithines, a group of birds with gliding and intermittent flight capabilities; and (3) the explosion of modern ornithuromorpha, which experienced a period of intense adaptive radiation. Although the earliest ornithuromorpha is from the Early Cretaceous of China (Barremian–Aptian) 130 Ma of the Huajiying Formation (Wang *et al.*, 2015), it is widely accepted that modern birds radiated at the end of the Late Cretaceous, approximately 66 million years ago. The earliest Late Cretaceous ornithuromorpha clades were curiously linked to marine and coastal environments, for instance, the Ichthyornithiformes were a group of birds that exhibited similarities to flying seabirds. It is hypothesized that *Ichthyornis* was the Cretaceous ecological equivalent to gulls, petrels and skimmers. The origin of the Euornithes, which includes modern birds, can be traced back to 66.7 million years ago, at the limit of the Cretaceous–Paleogene extinction event. The earliest euornithes were small, terrestrial galloanseres (a clade that included hens and ducks), such as *Asteriornis maastrichtensis* (Field *et al.*, 2024). This galloanser is thought to have been equipped with thin beaks, enabling it to forage for seeds and worms on the ground at the seaside. Consequently, the presented macroevolutionary scenario matches with the *Ecospace Model* in which Aves underwent a rapid increase in the number of species and in family diversity since the Late Cretaceous, accompanied by a rise in functional versatility. The expected adaptive peaks for this adaptive radiation would be characterized by convergent morphologies or by new ones due to cladogenetic events, upon environmental and functional parameters (McGhee, 2012). This pattern would be driven by key adaptations enabling the conquer of new geographic areas, and unexploited ecospaces through a process of intense specialization (Benton, 2015).

However, as far as the subsequent generative processes are explored genetically and developmentally, the origin of Aves accounted for a set of multilevel processes mediated by different evolutionary mechanisms affecting isolated characters or complex groups within and among morphological units that experienced a variety of dynamics (Tab. 1). For instance, it was expected that the trophic apparatus of birds (beak) would vary with the diet. Instead morphofunctional metrics in an ample sample demonstrate that beak shape and diet do not covary, while every diet may be picked by many types of beaks (Navalón *et al.*, 2019; Miller *et al.*, 2023). Therefore, new macroevolutionary scenarios and questions are being posed. In these approaches a parcellation model (the liaison between the beak and diet) is tested against an integration model (eating with the whole skull). Parcellation enhances a major independence, favoring a lesser constraint for those characters to conform to morphological units in the context of the genotypic-phenotypic map (Wagner & Altenberg, 1996). Nonetheless, quantitative and experimental analyses in living archosaurs suggest the new Bauplan exerted a decrease in the number of modules with more integrated morphological units, instead of parcellation. In fact, there is a high degree

of bone fusion in birds; cervical centra and ribs, dorsal neural spines in the notarium; the synsacrum, the pygostyle, the scapulo-coracoid, the carpo-metacarpus, the pelvic bones, the tarsometatarsus (Plateau & Forth, 2003).

The avian Bauplan has a distinct modular organization from that of their theropod relatives; the loss of the tail is a classic example of the avian reconfiguration underpinning a new functional locomotor module (Gatesy & Dial, 1996). Palaeobiological hypotheses suggest that the avian Bauplan—wings and even encephalization—is related to the evolutionary reduction of body size (Balanoff *et al.*, 2013). Crown-birds shows an encephalization index six to ten times greater for their body size than any other vertebrate group (including hominids). This encephalization is achieved through the organization of the skull, as the adult bird retains the shape of the juvenile, which in turn has a pattern similar to that of the adult ancestor (Plateau & Forth, 2003; Bhullar *et al.*, 2012; Balanoff *et al.*, 2013). Tracking embryonic changes—bone condensation, bone connection, and fusion—of the ontogenetic trajectory in parrots, using network analysis, Carril *et al.* (2020) show that the pelvic girdle, the vertebral column and the hindlimbs are connected earlier than the pectoral girdle and forelimbs. Such a sequence in connectivity might play a significant role in the controlling of leg and arm lengths, driven by a scaling to smaller body sizes (Dececchi & Larsson, 2023). The avian forelimb is very constrained morphologically with a low rate of evolutionary change, and the proportion between humerus-radius and metacarpus shows a high density in the morphospace, conforming to a reduced area of disparity (Benson & Choiniere, 2013). "Wings *versus* legs" was the title of the Heers and Dial article (2014) to test their tradeoffs during development, investment, and performance in crown birds. The fore-hindlimb tradeoff reveals that birds with high ratios of forelimb investment should have reduced mass-specific hindlimb performance and rely on more forelimb-dominated locomotor behaviors (hyperaerial condition). Similarly, birds with low ratios of forelimb investment should have reduced mass-specific forelimb performance and rely on more hindlimb-dominated locomotor behaviors (flightless condition). Therefore, the fore-hindlimb tradeoff reflects a modular covariation and morphological integration in the new Bauplan and suggests a process of stabilizing selection and evolutionary channeling, enabling phenotypic evolvability of isolated characters. An excellent example is the length of the coastal uncinate processes in hyperaerial birds; these processes act as levers and improve the mechanical advantage for the forward rotation of the dorsal ribs and therefore lowering of the sternum during respiration. The length of these processes is functionally crucial because longer uncinate processes increase the mechanical advantage of the appendicocostales muscle during inspiration (Tickle *et al.*, 2007).

Hence, it can be posited that the novel Avian Bauplan is structured according to mechanisms that exert an influence on its modularity (both variational and organizational, see Table 1), operating within an evolutionary integration model that assumes covariational patterns over macroevolutionary timescales.

CONCLUSION

This essay presents two contrasting perspectives on the role of the arts in the visual representation of birds. In the figurative mode, birds are depicted as creatures that are typically regarded as land animals. In these examples, the value ascribed to birds is based on their most outstanding features and behaviors, which are perceived as enigmatic. In the abstract mode, the artists have explored the geometry of their bodily organizations in order to gain insight into the connectivity of their different parts and the reasons behind their ability to fly. Thus, the artistic works of avian geometry seek to integrate form and function. It is noteworthy that these geometric representations

Table 1. Examples of multilevel processes driven by different evolutionary mechanisms in avian evolution. Sources in examples: [1] Cava *et al.*, (2019); [2] Bhullar *et al.*, (2015); [3] Varricchio & Jackson, (2016); [4] Müller, (2003b); [5] Uno & Hirasawa, (2023); [6] Plateau & Forth, (2023); [7] Watanabe *et al.*, (2021); [8] Xu & Mackem, (2013); [9] Chakraborty & Javis, (2015); [10] Dececchi & Larsson, (2023).

EVOLUTIONARY Mechanisms	PHYLOGENETIC Characters	MACROEVOLUTION Morphological Units	AVIAN EXAMPLES
Evolvability	Convergence	Eco-model	Tarsus length[1]
New developmental paths	Autapomorphy and homology	Key innovations	Beak origin[2], Egg organization[3]
Epigenetic factors	Autapomorphy	Novelties	Fibular crest[4]
Developmental constraints	Parallelism and homoplasy	Variational modularity	Propatagium[5], Skull heterochrony[6], Brain mosaicism[7]
Developmental shifts	Autapomorphy	Organizational modularity	Hand digits[8], Brain pathways[9]
Macromutations	Synapomorphy and homology	Organizational modularity	Limbs and hand proportions[10]

align with the evolutionary integration and modularity model, which posits that the reduction in the number of modules and the reconfiguration of anatomical connectivity are pivotal.

Considering all the previous examples, I would like to conclude with a question. Once the new pattern of modularity in avian organization was channeled through developmental processes related to scaling and miniaturization, did the evolution of isolated characters (such as the uncinate processes of the ribs) play a key role in the evolvability and adaptations for flight and aerodynamics? If this were the case, adaptation to different types of flight would be the evolutionary key to the radiation of modern birds. Following the same argument, could a new macroevolutionary narrative explore whether the Enantiornithes and Euornithes were a case of iterative evolution, rather than interpreting the Enantiornithes as part of the transition? Did the Enantiornithes, like the Euornithes, develop isolated characters linked to flight capabilities in parallel?

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REFERENCES

Agnolin, F. L., Motta, M. J., Egli, F. B, Coco, G. L., & Novas, F. E. (2019). Paravian Phylogeny and the Dinosaur-Bird Transition: An Overview. *Frontiers in Earth Science*, *6*, 252. doi: 10.3389/feart.2018.00252

Alibardi, L. (2021). Development, structure, and protein composition of the corneous beak in turtles. *The Anatomical Record*, *304*(12), 2703–2725. doi: 10.1002/ar.24604

Artnet Worldwide (2024). *La jaiba gigante*. https://www.artnet.com/artists/francisco-toledo/la-jaiba-gigante-tras-los-pájaros-c2nFJb6b8VkWSPcJ9I9k4A2

Balanoff, A., Bever, G., Rowe, T., & Norell, M. A. (2013). Evolutionary origins of the avian brain. *Nature*, *501*, 93–96. doi: 10.1038/nature12424

Benton, M. J. (2015). Exploring macroevolution using modern and fossil data. *Proceedings Royal Society B*, *282*, 20150569. doi: 10.1098/rspb.2015.0569

Benson, R. B., & Choiniere, J. N. (2013). Rates of dinosaur limb evolution provide evidence for exceptional radiation in Mesozoic birds. *Proceeding Biological Science*, *280*(1768), 20131780. doi: 10.1098/rspb.2013.1780

Bhullar, B-A., Marugán-Lobón, J., Racimo, F., Bever, G. S., Rowe, T. B., Norell, M. A., & Abzhanov, A. (2012). Birds have paedomorphic dinosaur skulls. *Nature*, *487*(7406), 223–226. doi: 10.1038/nature11146. PMID: 22722850

Bhullar, B-A., Morris, Z., Sefton, E., Tok, A., Tokita, M., Namkoong, B., Camacho, J., Burnham, D., & Abzhanov, A. (2015). A molecular mechanism for the origin of a key evolutionary innovation, the bird beak and palate, revealed by an integrative approach to major transitions in vertebrate history. *Evolution*, *69*(7), 1665–1677. doi: 10.1111/evo.12684

Brooke, M. de L., Hanley, S., & Laughlin, S. B. (1999). The scaling of eye size with body mass in birds. *Proceedings Royal Society London*, *266*(1417), 405–412. doi: 10.1098/rspb.1999.0652

Brusatte, S. L., O`Connor, J. K., & Javis, E. D. (2015). The origin and diversification of birds. *Cell Press. Current Biology Review, 25*(19), R888-R898. doi: 10.1016/j.cub.2015.08.003

Buscalioni, A. D., de la Iglesia, A., Delgado-Buscalioni, R., & Dejoan, A. (2005). Modularity at the boundary between art and science. In W. Callebaut, & D. Rasskin-Gutman (Eds.), *Modularity* (pp. 283–304). The MIT Press.

Cambra-Moo, O., Chamero, B., Marugán-Lobón, J., Delclós, X., Poyato-Ariza, F. J., & Buscalioni, A. D. (2006). Estimating the ontogenetic status of an enantiornithine bird from the Lower Barremian of El Montsec, Central Pyrenees, Spain. *Estudios Geológicos*, *62*(1), 241–248.

Cassirer, E. (1932). *La filosofía de la ilustración*. Edición de 1997. EFE, Fondo de Cultura Económica, México.

Cashmore, D. D., & Butler, R. J. (2019). Skeletal completeness of the non-avian theropod dinosaur fossil record. *Palaeontology*, *62*(6), 951–981.doi: 10.1111/pala.12436

Carril, J., Tambussi, C. P., & Rasskin-Gutman, D. (2020). The network ontogeny of the parrot: altriciality, aynamic skeletal assemblages, and the Avian Body Plan. *Evolutionary Biology*, *48*, 41–53.doi: 10.1007/s11692-020-09522-w

Cava, J. A., Perlut, N. G., & Travis, S. E. (2019). Heritability and evolvability of morphological traits of Savannah sparrows (*Passerculus sandwichensis*) breeding in agricultural grasslands. *PLoS ONE*, *14*(1), e0210472. doi: 10.1371/journal.pone.0210472

Chakraborty, M., & Jarvis, E. D. (2015). Brain evolution by brain pathway duplication. *Philosophical Transactions Royal Society B*, *370*, 20150056. doi: 10.1098/rstb.2015.0056

Chang, W-L., Wu, H.,Chiu, Y-K., Wang, S., Jiang, T-X., Luo, Z-L., Lin, Y-Ch., Li, A., Hsu, J-T., Gu, H-J., Lin, T-Y., Yang, S-M., Lee, T-T., Lai, Y-Ch., Lei, M., Shie, M-Y., Yao, C-T., Chen, Y-W., Tsai, J. C., Shieh, S-J., Hwu, Y-K., Cheng, H-Ch., Tang, P-Ch., Hung, S-Ch., Chen, Ch-F., Habib,

M., Widelitz, R. B., Wu, P., Juan, W-T., & Chuong, Ch-M. (2019). The making of a flight feather: Bio-architectural principles and adaptation. *Cell*, *179*, 1409–1423. doi: 10.1016/j.cell.2019.11.008

Chiappe, L. M. (2009). Downsized Dinosaurs. The evolutionary transition to modern birds. *Evolution: Education and outreach*, *2*, 248–256. doi: 10.1007/s12052-009-0133-4

Chiappe, L. M., & Qingjin, X. (2016). *Birds of stone*. John Hopkins University Press.

Cracraft, J., Barker, F. K., Braun, M., Harshman, J., Dyke, G. J., Feinstein, J., Stanley, S., Cibois, A., Schikler, P., Beresford, P., Garcia-Moreno, J., Sorenson, M. D., Yuir, T., & Mindell, D. P. (2004). Phylogenetic relationships among modern birds (Neornithes). In J. Cracraft, & M. J. Donoghue (Eds.), *Assembling the tree of life* (pp. 468–489). Oxford University Press.

Cuesta, E., Ortega, F., & Sanz, J. L. (2016). Phylogenetic distribution of morphological features of the *Concavenator corcovatus* forelimb (Carcharodontosauria. Lower Cretaceous, Spain). In F. Torcida Fernández-Baldor, J. I. Canudo, P. Huerta, & X. Pereda (Eds.), *Abstracts book of the VII International Symposium about Dinosaurs Palaeontology and their Environment* (pp. 61–63). Burgos.

Dececchi, T. A., & Larsson, H. C. E. (2023). Body and limb size dissociation at the origin of birds: uncoupling allometric constraints across a macroevolutionary transition. *Evolution*, *67*(9), 2741–2752. doi: 10.1111/evo.12150

de Pinna, M. C. C. (1991). Concepts and test of homology in the cladistic paradigm. *Cladistics*, *7*, 367–394. doi: 10.1111/j.1096-0031.1991.tb00045.x

Diogo, R. (2020). Introduction to evolutionary developmental pathology, or Evo-Devo-Path: on Neodarwinism, natural mutants, hopeful monsters, syndromes, genomics, variations, humans, apes, chameleons, and dinosaurs. *Current Molecular Biology Reports*, *6*(2), 11–15. doi: 10.1007/s40610-020-00133-0

Eble, G. J. (2005). Morphological modularity and macro-evolution: conceptual and empirical aspects, In W. Callebaut, & D. Rasskin-Gutman (Eds.), *Modularity* (pp. 221–238). MIT Press.

Feduccia, A. (1980). *The age of birds*. Harvard University Press.

Field, D. J., Benito, J., Werning, S., Chen, A., Kuo, P-C., Crane, A., Widrig, K. E., Ksepka, D. T., & Jagt, J. W. M. (2024). Remarkable insights into modern bird origins from the Maastrichtian type area (north-east Belgium, south-east Netherlands). *Netherlands Journal of Geosciences*, *103*, e15. doi: 10.1017/njg.2024.11

Fountaine, T. M. R., Benton, M. J., Dyke, G. J., & Nudds, R. L. (2005). The quality of the fossil record of Mesozoic birds. *Proceeding of the Royal Society B*, 272, 289–294. doi: 10.1098/rspb.2004.2923

Freudenstein, J. V. C. (2005). Character, states and homology. *Systematic Biology*, *54*(6), 973–983. doi: 10.1080/10635150500354654

Gardiner, B. G. (1998). Haematothermia: warm-blooded amniotes. *Cladistics*, *9*, 369–395. doi: 10.1006/clad.1993.1026

Gatesy, S. M., & Dial, K. P. (1996). Locomotor modules and the evolution of avian flight. *Evolution*, *50*(1), 331–340. doi: 10.1111/j.1558-5646.1996.tb04496.x

Guinard, G. (2020). Evolutionary teratology and the path to break through the mould of the Synthesis Paradigm. *Current Molecular Biology Reports*, *6*, 51–61. doi: 10.1007/s40610-020-00130-3

Hall, B. K. (2007). Homoplasy and homology: Dichotomy or continuum? *Journal of Human Evolution*, *52*(5),1–7. doi: 10.1016/j.jhevol.2006.11.010

Havstad, J. C., & Smith, N. A. (2019). Fossils with feathers and philosophy of science. *Systematic Biology*, *68*(5), 840–851. doi: 10.1093/sysbio/syz010

Heers, A. M., & Dial, K. P. (2014). Wings versus legs in the avian bauplan: development and evolution of alternative locomotor strategies. *Evolution*, *69*(2), 305–320. doi: 10.1111/evo.12576

Heilmann, G. (1926). *The origin of birds.* Appleton.

Hieronymus, T. L., & Witmer, L. M. (2010). Homology and evolution of avian compound rhamphothecae, *The Auk*, *127*(3), 1, 590–604. doi: 10.1525/auk.2010.09122

Huntington, S. (2013). *Osteological, myological, and phylogenetic trends of forelimb reduction in nonavian theropod dinosaurs*. (PhD Thesis, Stony Brook University, New York). Available in [http://hdl.handle.net/11401/77132]

Huxley, T. H. (1868). On the animals which are most nearly intermediate between birds and reptiles. *Popular Science Review*, *7*, 237–247.

Kandisky, W. (1952). *De lo espiritual en el arte*. Barral Editores.

Kondo, M., Sekine, T., Miyakoshi, T., Kitajima, K., Egawa, S., Seki, R., Abe, G., & Tamura, K. (2018). Flight feather development: its early specialization during embryogenesis. *Zoological Letters*, *4*, 2. doi: 10.1186/s40851-017-0085-4

Kurochkin, E. N., & Walker, C. A. (1999). What were the Enantiornithes? In N. J. Adams, & R. H. Slotow (Eds.), *Proceedings 22 International Ornithological Congress Durban* (pp. 3219–3222). Johannesburg.

Lamarck, J. B. (1809). *Philosophie Zoologique*. Satanic mil. https://ia801004.us.archive.org/28/items/LamarckPZ/Lamarck_PZ.pdf

Lederer, R. L. (2019). *The art of the bird the history of ornithological art through forty artists*. The University of Chicago Press.

Lefebvre, H. (1980). *La presencia y la Ausencia*. Edición 1983. Fondo de Cultura Económica. México.

Livezey, B. C., & Zusi, R. L. (2007). Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the Linnean Society*, *149*, 1–95. doi: 10.1111/j.1096-3642.2006.00293.x

Maeght, Y. (2020). *Les oiseaux dans l'art.* https://maeght.myshopify.com/blogs/series/oiseaux?shpxid=0eb90da2-1410-4cc5-a72f-180a000481de

Mannion, P. D., & Upchurch, P. (2010). Completeness metric and the quality of the sauropodomorph fossil record through geological and historical time. *Paleobiology*, *36*(2), 283–302. doi: 10.1666/09008.1

Meacham, C. A., & Estabrook, G. F. (1985). Compatibility Methods in Systematics. *Annual Review of Ecology and Systematics*, *16*, 431–46. http://www.jstor.org/stable/2097055

McGhee, G. R. (2012). *The geometry of evolution*. Cambridge University Press.

Mooi, R. D., & Gill, A. C. (2010). Phylogenies without synapomorphies-a crisis in fish systematics: time to show some character. *Zootaxa*, *2450*, 26–40.

Miller, C. V., Bright, J. A., Wang, X., & Zheng, X. (2023). Synthetic analysis of trophic diversity and evolution in Enantiornithes with new insights from Bohaiornithidae. *ELife*, *12*, RP89871. doi: 10.7554/eLife.89871

Müller, G. (2003a). Homology: the evolution of morphological organization. In G. B. Müller, & S. A. Newman (Eds.), *Origination of Organismal Form* (pp. 31–71). The MIT Press.

Müller, G. (2003b). Embryonic motility: environmental influences and evolutionary innovation. *Evolution & Development*, *5*(1), 56–60. doi: 10.1046/j.1525-142X.2003.03009.x

Navalón, G., Bright, J. A., Marugán-Lobón, J., & Rayfield, E. J. (2019). The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution, International Journal of Organic Evolution*, *73*, 422–435. doi: 10.1111/evo.13655, PMID: 30537045

Nebreda, S. M., Navalón, G., Menéndez, I., Sigurdsen, T., Chiappe, L. M., & Marugán-Lobón, J. (2020). Disparity and macroevolutionary transformation of the maniraptoran manus. *Bulletin American Museum Natural History*, *440*, 184–203.

Nebreda, S. M., Chiappe, L. M., Navalón, G., Chinsamy, A., Sanz, J. L., Buscalioni, A. D., & Marugán-Lobón, J. (2023). A new enantiornithine specimen from the Lower Cretaceous of Las Hoyas: avifaunal diversity and life-history of a wetland Mesozoic bird. *Spanish Journal of Palaeontology, 38*(2), 123–136. doi: 10.7203/sjp.26504

Nesbitt, S. M., Butler, R., Ezcurra, M. D., Barrett, P. M., Stocker, M. R., Angielczyk, K. D., Smith, R. M. H., Sidor, C. A., Niedźwiedzki, G., Senniko, A. G., & Charig, A. J. (2017). The earliest bird-line archosaurs and the assembly of the dinosaur body plan. *Nature*, *544*(7651), 484-487. doi: 10.1038/nature22037

Newton, A. H., & Smith, C. A. (2021). Regulation of vertebrate forelimb development and wing reduction in the flightless emu. *Developmental Dynamics*, *250*, 1248–1263. doi: 10.1002/dvdy.288

Novas, F. E., Agnolin, F. L., Excurra, M. D., Miller, R. T., Martinelli, A., & Langer, M. (2021). Review of the fossil record or early dinosaurs from South America, and its phylogenetic implications. *Journal of South American Earth Sciences*, *110*, 103341. doi: 10.1016/j.jsames.2021.103341

Nopcsa, F. (1907). Ideas on the origin of flight. *Proceedings Zoological Society London*, *1907*, 223–236.

Noticias de Toteart (2024). *Diez cuadros importantes de Remedio Varo*. https://totenart.com/noticias/cuadros-importantes-remedios-varo/

O'Connor, J. K., & Chang, H. (2015). Hindlimb feathers in paravians: Primarily "wings" or ornaments? *Biology Bulletin Russian Academia Science*, *42*, 616–621. doi: 10.1134/S106235901507007

Ochoa, C. (2017). *El eclipse del antidarwinismo*. Centro de estudios filosóficos, políticos y sociales Vicente Lombardo Toledano. México.

Ortega, F., Escaso, F., & Sanz, J. L. (2010). A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. *Nature*, *467*(7312), 203–206. doi: 10.1038/nature09181

Ostrom, J. H. (1974). *Archaeopteryx* and the origin of flight. *The Quarterly Review Biology*, *49*, 27–47.

Owen, R. (1875). Monographs of the British fossil Reptilia of the Mesozoic Formations. Part II. (Genera *Bothriospondylus*, *Cetiosaurus*, *Omosaurus*). *Monograph of the Palaeontographical Society*, *29*, 15–93.

Patterson, C. (1982). Morphological characters and homology. In K. A. Joysey, & A. E. Friday (Eds.), *Problems of Phylogenetic Reconstruction* (pp. 21–74). Academic Press.

Peters, D. (2000). A reexamination of four prolacertiforms with implications for pterosaur phylogenesis. *Rivista Italiana di Paleontologia e Stratigrafia*, *106*(3), 293–336. doi: 10.13130/2039-4942/6148

Plateau, O., & Forth, C. (2003). Birds have peramorphic skulls. *Communications in Biology*, *3*, 195. doi: 10.1038/s42003-020-0914-4

Prum, R. O. (2005). Evolution of the morphological innovations of feathers. *Journal of Experimental Zoology (Molecular Developmental Evolution)*, *304B*, 570–579. doi: 10.1002/jez.b.21073

Rasskin-Gutman, D. (2005). Modularity: jumping forms within morphospace. In W. Callebaut, & D. Rasskin-Gutman (Eds.), *Modularity* (pp. 207–220). The MIT Press.

Ruben, J. A., & Feduccia, A. (1997). The fuss over feathers. *BioScience*, *47*(6), 392–394. doi: 10.2307/1313154

Saunders, J. W., Gasseling, M. T., & Saunders, L. C. (1962). Cellular death in morphogenesis of the avian wing. *Developmental Biology*, *5*(1), 147–178. doi: 10.1016/0012-1606(62)90008-8

Sanz, J. L. (1999). *Los dinosaurios voladores*. Mundo vivo. Ediciones Libertarias.

Sanz, J. L. (2023). *Dinosaurios y otros animales*. Editorial Crítica.

Sanz, J. L., Chamero, B., Chiappe, L., Marugán-Lobón, J., O´Connor, J. K., Ortega, F., & Escaso, F. (2016). Aves. In F. J. Poyato-Ariza, & A. D. Buscalioni (Eds.), *Las Hoyas: a Cretaceous wetland* (pp. 183–189). Verlag Dr. Friedrich Pfeil.

Sanz, J. L., Chiappe, L. M., Pérez-Moreno, B. P., Moratalla, J. J., Hernández-Carrasquilla, F., Buscalioni, A. D., Ortega, F., Poyato-Ariza, F. J., Rasskin-Gutman, D., & Martínez-Delclós, X. (1997). A nestling Bird from the Lower Cretaceous of Spain. Implications for Avian Skull and Neck Evolution. *Science*, *276*, 1543–1546.

Sedlmayr, H. (1955). *La revolución del arte moderno*. Edición 2008. Acantilado.

Seeley, H. G. (1901). *Dragons of the air. An account of extinct flying reptiles*. Reprint 1967. Dover paperback.

Seki, R., Li, C., Fang, Q., Hayashi, S., Egawa, S., Hu, J., Xu, L., Pan, H., Kondo, M., Sato, T., Matsubara, H., Kamiyama, N., Kitajima, K., Saito, D., Liu, Y., Gilbert, M. T. P., Zhou, Q., Xu, X., Shiroishi, T., Irie, N., Tamura, K., & Zhang, G. (2017). Functional roles of Aves class-specific cis-regulatory elements on macroevolution of bird-specific features. *Nature Communications*, *8*, 14229. doi: 10.1038/ncomms14229

Shelley, M. (1818). *Frankenstein*. Editorial Algar.

Tickle, P. G., Ennos, R. A., Lennox, L. E., Perry, S. F. & Codd, J. R. (2007). Functional significance of the uncinate processes in birds. *Journal of Experimental Biology*, *201*(22), 3955–3961. doi: 10.1242/jeb.008953

Tobalske, B. W., & Dial, K. P. (2007). Aerodynamics of wing-assisted incline running in birds. *Journal of Experimental Biology*, *210*(10), 1742–1751. doi: 10.1242/jeb.001701. PMID: 1748893

Tseng, C-C., Woolley, T. E., Jiang, T-X., Wu, P., Maini, P. K., Widelitz, R. B., & Chuong, C-M. (2024). Gap junctions in Turing-type periodic feather pattern formation.

*PLoS Bi*ology, *22*(5), e3002636. doi: 10.1371/journal.pbio.3002636

Tyrrell, L. P., & Fernández-Juricic, E. (2017). Avian binocular vision: It's not just about what birds can see, it's also about what they can't. *PLoS ONE*, *12*(3), e0173235. doi: 10.1371/journal.pone.0173235

Uno, Y., & Hirasawa, T. (2023). Origin of the propatagium in non-avian dinosaurs. *Zoological Letters*, *9*, 4. doi: 10.1186/s40851-023-00204-x

Varricchio, D. S., & Jackson, F. D. (2016). Reproduction in Mesozoic birds and the evolution of the modern avian reproductive mode. *The Auk*, *133*(4), 654–684. doi: 10.1642/AUK-15-216.1

Wagner, P., & Altenberg, L. (1996). Perspectives: complex adaptations and evolution of evolvability. *Evolution*, *50*(3), 967–976. doi: 10.1111/j.1558-5646.1996.tb02339.x

Wang, M., O'Connor, J. K., Zhao, T., Pan, Y., Zheng, X., Wang, X., & Zhou, Z. (2021). An Early Cretaceous enantiornithine bird with a pintail. *Current Biology, 31*, 4845–4852. doi: 10.1016/j.cub.(2021).08.044

Wang, M., Zheng, X., & Zhou, Z. (2015). The oldest record of ornithuromorpha from the Early Cretaceous of China. *Nature Communications*, *6*, 6987. doi: 10.1038/ncomms7987

Walker, A. (1972). New light on the Origin of Birds and Crocodiles. *Nature*, *237*, 257–263. doi: 10.1038/237257a0

Watanabe, A., Balanoff, A. M., Gignac, P. M., Gold, E. L., & Norell, M. A. (2021). Novel neuroanatomical integration and scaling define avian brain shape evolution and development. *eLife*, *10*, e68809. doi: 10.7554/eLife.68809

Wellnhofer, P. A. (2008). A short history of pterosaur research. *Zitteliana*, *28*, 7–19.

Williston, S. W. (1879). Are birds derived from dinosaurs? *The Kansas City Review of Science*, 3, 457–460.

Willmer, P. (2000). Convergence and homoplasy in the evolution of organismal form. In G. Müller, & S. A. Newman (Eds.), *Origination and Organismal Form* (pp. 33–50). The MIT Press.

Wynd, B. M., Martinez, R. N., Colombi, C., & Alcober, O. (2020). A review of vertebrate beak morphologies in the Triassic: a framework to characterize an enigmatic beak from the Ischigualasto Formation, San Juan, Argentina. *Ameghiniana*, *57*(4), 370–387. doi: 10.5710/AMGH.13.05.2020.3313

Xing, L., O'Connor, J. K., Niu, K., Cockx, P., Mai, H., & McKellar, R. C. (2020). A new Enantiornithine (Aves) preserved in Mid-Cretaceous Burmese amber contributes to growing diversity of Cretaceous plumage patterns. F*rontiers in Earth Science*, *8*, 264. doi: 10.3389/feart.2020.00264

Xu, X., Zhonghe, Z., Dudley, R., Mackem, S., C. M., Erickson, G., & Varricchio, D. (2014). An integrative approach to understanding bird origins. *Science*, *346*, 1253293. doi: 10.1126/science.1253293

Xu, X., & Mackem, S. (2013). Tracing the evolution of avian wing digits. *Current Biology*, *23*(12), 538–544. doi: 10.1016/j.cub.2013.04.071

Yang, Z., Jiang, B., McNamara, M. E., Kearns, S. L., Pittman, M., Kaye, T. G., Orr, P. J., Xu, X., & Benton, M. J. (2019). Pterosaur integumentary structures with complex feather-like branching. *Nature Ecology and Evolution*, *3*, 24–30. doi: 10.1038/s41559-018-0728-7