Salient Visionary Publications

International Journal of Genome Research
Review Article

Evaluation of Contemporary Avian-Reptilian Phylogeny

Arjavon Talebzadeh[*]

California Northstate University School of Medicine, USA

Citation: *Arjavon Talebzadeh. Evaluation of Contemporary Avian-Reptilian Phylogeny. Inter Jour Genom Res. 2023;1(1):1-5.* DOI: https://doi.org/10.5281/zenodo.7860784

Received Date: 20 April, 2023; **Accepted Date:** 24 April, 2023; **Published Date:** 25 April, 2023

[*]**Corresponding author:** Arjavon Talebzadeh. California Northstate University School of Medicine, USA

ABSTRACT

Birds are currently defined as archosaurs, a clade of reptiles including crocodilians and dinosaurs. Birds and non-avian reptiles share enough homologous adaptations to infer birds belong with the greater clade reptiles. Such adaptations include laying of eggs outside of aqueous environment, eggs with at least some calcification, and keratinized integument with the appearance of scales. Before the emergence of recent developments suggesting otherwise, *Archaeopteryx* was considered to be the common ancestral species of all birds because of its bird-like morphology and feathers. Analysis of newer *Archaeopteryx*-like specimens from China like *Xiaotingia zhengi* have served as evidence to one emerging hypothesis proposing archaeopterygids belong to a sister taxon to birds. Analysis of the four-winged, arboreal *Scanosoriopteryx* has been used to support a hypothesis going even further to discredit the dinosaur-bird hypothesis which suggests birds have evolved from theropod dinosaurs. This research study assesses the theory that birds are derived from reptiles before proceeding to investigate the current understanding of the evolution of birds from other archosaurs.

Keywords: Bird; Reptile; Phylogeny; Egg; Scales; Feather; Integument; *Archaeopteryx*; *Praeornis*; Xu; *Scanosoriopteryx*

INTRODUCTION

Phylogenetic studies and analysis of paleontological findings have been instrumental in deducing the origin of feathers in birds. It is widely accepted birds belong within the clade (a group of organisms including all known descendants of a common ancestral species) of reptiles. Birds currently belong to Archosauria, a clade of reptiles which includes crocodilians and dinosaurs. Despite decades of research investigating fossilized archosaurs with bird-like morphology, the contemporary understanding of the origin of feathers in modern avian species has been less than satisfactory. Feathers are notable for being among the most complex of three-dimensional accessory features within the integumentary system among vertebrate animals. Since its discovery in 1861, *Archaeopteryx* was believed to be the most recent common ancestor of all avian species with enough resemblance to modern birds.

Studies have emerged within the last decade to challenge this position and suggest birds are derived from more primitive archosaurs. This study seeks to re-evaluate the phylogenetic relatedness of non-avian reptiles and birds, explore the current understanding of how birds evolved from other archosaurs, and relate the significance of feathers and flight to the contemporary understanding of bird evolution.

LITERATURE REVIEW

Phylogenetics is the study of categorization of species based on the evolutionary changes of their common ancestors. Phylogenetics draws upon comparative anatomy and physiology, genetics, and the appearance of derived traits in order to explain the divergence of an ancestral organism into the species of interest. Contemporary phylogenetic studies have concluded birds belong to Archosauria, a clade consisting of crocodilians, dinosaurs, and pterosaurs.[1] This section will explore contemporary literature to compare the eggs and integument of birds and non-avian reptiles.

Laying eggs outside of an aqueous environment is a signature quality of the reptilian clade. The eggs of birds and non-avian reptiles differ in their amounts of calcification, the color of their shells, and their required conditions for successful incubation. Most reptiles have less calcified egg shells relative to birds, and crocodilian eggs are generally as calcified as those of birds.[2] In addition, reptile eggs generally exhibit an immaculate white color while the eggs of different bird species vary extensively in color.[3] A study by Wang et al. compared rates of predation between an artificial bird nest containing two pigeon eggs and another nearby with two turtle eggs that were each replenished every two days. Turtle eggs were left intact while the bird egg nest experienced increased rates of predation with each replenishing. They also observed specimens of vibrantly-colored eggs reflect ultraviolet radiation. Ultimately, the increased rates of predation were attributed to different bird species recognizing eggs of another bird species using their UV-light receptors. It is evident that calcified eggs are unique to archosaurs and some other reptiles while bright coloration and UV-reflectance are unique to some bird eggs.

Another means of comparison for birds and reptiles are the required conditions of their eggs. Birds generally lay their eggs in a nest exposed to the elements, and reptiles bury their eggs to minimize risk of overheating.[4] They examined the influence of taxonomic relatedness on the initial egg mass and incubation period of bird and reptile eggs. They also successfully expressed incubation as a function of initial egg mass. They also observed reptiles have longer incubation times attributed to the requirement of lower temperatures.

Birds and reptiles may also be compared for differences in the characteristics of their integument. Contemporary research has struggled to map the evolution from the rough, accessory-lacking integument of reptiles to the feathered integument of birds. An animal's integumentary system consists of skin and its accessory features. The reptilian integumentary system consists of an epidermis with three distinct layers and a dermis composed of connective tissue. The stratum corneous, the most superficial layer of the epidermis, is rich in keratin, providing a rough texture indicative of scales.[5] Keratin is a protein that gives superficial integument of higher vertebrates a rough texture. Alibardi et al. examined Nile crocodile skin samples to learn about crocodilian scale growth. They observed that the stratum corneous thickens with age. The texture of the most superficial integument of crocodilians was attributed to the development of keratinous epithelium.

The avian integumentary system includes scales on the lower limbs and feathers covering the rest of the body. Chickens have three types of scales that are keratin-rich and morphologically resemble those of reptiles. Chicken leg scales do not exhibit localized growth[6] like the epidermis of crocodilians. The epidermis feathers protrude from is not as keratin-rich as reptilian integument and thus not as rough. Feathers are comprised of a branching series of keratin-based shafts.[7] A series of tertiary shafts (barbules) may each have their own hooklet interweaving into a nearby barbule of an adjacent barb, providing the toughness and lightness of flight feathers; a lack of hooklets is characteristic of fluffy feathers. Since the 1860s, *Archaeopteryx* was considered by the majority of paleontologists to be the most recent common ancestor of the bird lineage. Xu et al. and others analyzed well-preserved specimens of archosaurs supporting a hypothesis that *Archaeopteryx* is not a bird and belongs to a sister taxon to birds.[8-9] Xu extracted *Xiaotingia zhengi*, an archaeopterygid. Due to its similarity to *Archaeopteryx* and theropod dinosaurs, *Xiaotingia* and other archaeopterygids were placed by Xu et al. into a new sister taxon to birds called Deinchosauria. Czerkas et al. evaluated a skeleton of *Scansoriopteryx*, a small arboreal archosaur; they concluded birds evolved from scansoriopterygids, challenging hypotheses that birds evolved from dinosaurs or *Archaeopteryx*. Dzik et al. found a fossilized protofeather specimen from *Praeornis*.[10] Comparison of the specimen to dorsum scales of *Longisquama* suggests feathers may have evolved from "isolated, flattened, elongated, reptilian scales" that were "rather robust proximally and very thin and wide at their distal ends" with functions in sexual display. With a lack of protofeathers in the fossil record, more research is needed to understand the evolution of birds.

Despite that research in protofeather evolution is still limited, analysis of modern species provides strong evidence suggesting birds have evolved from reptiles. Both birds and some non-avian reptiles lay calcified eggs outside of aqueous environments. Birds have scales on their lower limbs that are both morphologically analogous and keratinized like the integument of crocodilians. After analysis of the journals used in development of this section, it is reasonable to conclude birds are appropriately placed into the clade of reptiles.

DISCUSSION

In recent decades, many paleontological studies have focused on fossilized specimens and other findings useful in mapping the evolution of feathers in some archosaurs. Birds are relatively young clade of animals, as marked by the discovery of *Archaeopteryx* and other paravians. The dinosaur-bird hypothesis suggests birds evolved from descendants of theropod dinosaurs with feather-like, integumentary accessories. Challengers to the dinosaur-bird hypothesis suggest there are important differences in anatomical features of theropod and avian species, weakening the hypothesis. These researchers propose feathers evolved separately among theropod dinosaurs and the ancestral species of birds due to similar environmental pressures. Preserved skeletal structures are instrumental in support of new hypotheses suggesting birds are not derived from *Archaeopteryx*.

First discovered in 1861, *Archaeopteryx* was considered by archaeologists to be the earliest bird. Eleven skeletal specimens indicate *Archaeopteryx* exhibited morphological features previously thought to be unique to the avialan clade. Analysis of skeletal remains of *Xiaotingia zhengi*, an archaeopterygid, provided the information to Xu et al. required to draw the controversial conclusion that *Archaeopteryx* and other archaeopterygids are paravians with qualities warranting separate placement in Deinonychosauria, a newly proposed sister taxon to Avialae (birds). Such traits as pennaceous feathers and "long and robust forelimbs" are now accepted as characteristic of paravians, a broader clade including deinonychosaurs and birds as separate lineages. Foth et al. later analyzed a new *Archaeopteryx* skeletal specimen with great preservation of its pennaceous feathers.[11,12] Findings of symmetrical pennaceous feathers in oviraptorosaurs imply feathers are not unique to paravians. The presence of pennaceous feathers in different lineages within Pennaraptora (the least inclusive clade to include birds, archaeopterygids, and oviraptorosaurs) implies true feathers must have evolved prior to the diversification of pennaraptorians.

In evolutionary biology, convergence describes the separate evolution of analogous adaptations or anatomical features within different lineages due to the presence of similar environmental pressures. When biologists develop cladograms based on morphological features, there is risk for convergent evolution to mislead developments of phylogenetic relationships. Such a risk comes with analyses of fossilized specimens. Dzik et al. discuss a feather-like specimen believed to be from the Late Jurassic period believed to a protofeather from *Praeornis*. This protofeather has fused barb-like extensions and three vanes (in contrast to the two of modern birds) from which the "barbs" extend from. It is evident that the *Praeornis* protofeather was also rich in a tough protein like keratin or collagen. Comparison of the *Praeronis* specimen to modern feathers and a dorsal scale from *Longisquama* suggests the evolution of feathers in a common ancestor of pennaraptorian species. Examination of a *Scansoriopteryx* specimen by provides evidence scansoriopterygids may be ancestral to modern birds. *Scansoriopteryx* was likely an arboreal paravian with a wing on each limb. Like other pennaraptorians, *Scansoriopteryx* probably had feathers used for display, flight, and body incubation, similar to the pennaceous feathers of *Archaeopteryx*. Qualities of *Scansoriopteryx* match a gliding stage in the evolution of flight as hypothesized by Beebe (1915), who suggested pre-avian species would assume a "tetrapteryx" (four-winged) form before evolving into a more avian form.[13] Of the currently known scansoriopterygids, *Scansoriopteryx* is estimated to be the oldest. This suggests *Scansoriopteryx* is a strong candidate for being most recent common ancestor of avians.

CONCLUSION

The discoveries of *Archaeopteryx*, *Praeornis*, *Xiaotingia*, and *Scansoriopteryx* were each revolutionary in advancing the current understanding of avian evolution. Analyses only of archosaurs existing today would suggest feathers are unique to birds. Comparison of genomes from non-avian reptiles to those of birds would provide limited insight to the evolutionary origins of birds from within the reptilian clade. The bird-like and reptile-like qualities of *Archaeopteryx* specimens were the source of inspiration to paleontologists who first hypothesized birds are closely related to reptiles. *Praeornis* protofeathers were essential to properly map out the evolution of feathers exhibited by avian species today. *Xiaotingia* and *Scansoriopteryx* were specimens that pushed many paleontologists to reassess the placement of *Archaeopteryx* as the common ancestor of birds and consider less popular hypotheses of bird evolution. With these specimens and others, there is now considerable theoretical framework regarding how populations reptiles with elongated dorsal evolved to yield new species of feathered archosaurs like modern birds and other pennaraptorian species that are now extinct. Understanding the evolution of flight in birds requires further investigation into paravians and underappreciated features contributing to the evolution of true spontaneous flight in birds.

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