

# Why do we know that birds are living dinosaurs?

Evaluation of reasoning in anti-evolutionist treatise

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Bird-like dinosaur *Anchiornis huxleyi*  
Image: ZHAO Chuang; Courtesy of PNSO

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## A. Introduction

What is the evolutionary origin of birds? The 130-year-old controversy over which archosaur group birds descended from has been over for about 25 years. Today, the scientific consensus is that birds evolved from certain dinosaurs. Strictly speaking, this formulation is not quite correct, because birds *are* actually highly evolved dinosaurs. Taxonomists assign them to one of the many nested subgroups descending from the last common ancestor of dinosaurs (Fig. 4).

Thus, birds are members of the dinosaur subgroup Theropoda (carnivorous bipeds), of the theropod subgroup Coelurosauria (hollow-tailed lizards), and of the coelurosaur subgroup Maniraptora (“hand snatchers”). Today, only a very few dinosaur specialists and paleornithologists dispute this finding, and the few who do so seem to have ideological rather than scientific reasons (cf. PRUM 2003; SMITH et al. 2015; RAUHUT & FOTH 2020).

It is also undisputed that the most exclusive feature of this highly evolved group of dinosaurs, the pennaceous feather, did not appear suddenly. From an evolutionary perspective, biologists predicted that proto-feathers, like keratinous skin appendages derived from scales, originated among coelurosaurs or other proto-avian archosaurs before the advent of flight (cf. MADERSON 1972; MARTIN 1983).

The knowledge that modern birds (crown group birds) differ from early theropods only by graded similarities has always been a thorn in the side of religious evolution deniers (creationists). It simply does not fit well into the mould of genealogically separated lineages or “basic kinds” of life originated by supernatural acts of divine creation. Instead, graded similarities between seemingly fundamentally different groups of animals fulfill a central expectation of the theory of evolution. Hence, it is no surprise that since the discovery of the famous proto-bird *Archaeopteryx*, creationists have been running up against the theropod affiliation of birds.

A biologically skilled creationist who has tackled bird evolution for decades is Reinhard JUNKER, former managing director of the German evangelical organization WORT-UND-WISSEN. In his writings, he presents numerous empirical findings, declaring them “anomalies for evolution and indications for creation” (JUNKER 2019, p. 66). Most of his arguments are typical of anti-evolutionist reasoning and are prevalent among US creationists as well.

In this paper, we elucidate some main lines of this kind of anti-evolutionist reasoning.<sup>1</sup> We show that it draws its credibility from outdated or even clearly false ideas about evolution.

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<sup>1</sup> Many sources are originally in German; the authors translated all quotes from them without further mention.

## B. Why the descent of birds from dinosaurs is a well-established fact

Recent studies suggest that pterosaurs, which are only distantly related to birds, had feather-like structures on their skin. There is empirical evidence that these could have been *proto-feathers*, which means pennaceous feathers evolved from such structures in the ancestral lineage of birds. JUNKER (2022) remarks on this:

Beyond the evolutionary view that birds originated from dinosaurs, one would... hardly come to the idea that those structures were 'feathers'... One can certainly speak of a *confusion of terms* here. It arises from the fact that 'feathers' are ultimately defined not primarily on the basis of morphological characteristics but on the basis of presumed evolutionary relationships.

Among experts, however, these “evolutionary relationships” are not a *conjecture* but rather a corroborated and empirically well-established theory. Why is that? Already around 1870, a few years after the discovery of *Archaeopteryx*, Thomas H. HUXLEY hypothesized that birds and theropods were closely related (PADIAN & CHIAPPE 1998). In fact, the skeleton of *Archaeopteryx* is so strikingly similar to that of the predatory dinosaur *Compsognathus* that two apparently featherless specimens of the proto-bird were mistaken for this non-avian theropod for decades (SHIPMAN 1999, pp. 43 ff.).

HUXLEY’s hypothesis was temporarily sidelined, mainly due to an influential book by Dutch paleontologist Gerhard HEILMANN. He argued that theropods seem to lack clavicles, which in birds are fused to form a furcula (“wishbone”), and could therefore not possibly be the ancestors of birds (HEILMANN 1926). Today, however, we know that most theropods indeed possessed clavicles that had already been fused into wishbones (RAUHUT et al. 2020). In the 1970s, HUXLEY’s hypothesis experienced a renaissance when the paleontologist John OSTROM showed that birds share more features with theropods than with any other archosaurian group (OSTROM 1976).

OSTROM’s conclusion that birds must have descended from small theropod dinosaurs met with more and more acceptance as phylogenetic systematics (*cladistics*) became the gold standard of comparative biology.<sup>2</sup> The goal of cladistics is to classify organisms into hierarchically nested groups (called *taxa*, singular: *taxon*) defined exclusively by evolutionary novelties (*derived traits* or *apomorphies*). With maximum objectivity, hierarchical systems of natural classes are established and displayed as branched diagrams (*cladograms*). Cladograms, which we can transform into phylogenetic trees (phylogenies or evolutionary trees), reveal the common ancestry of species.

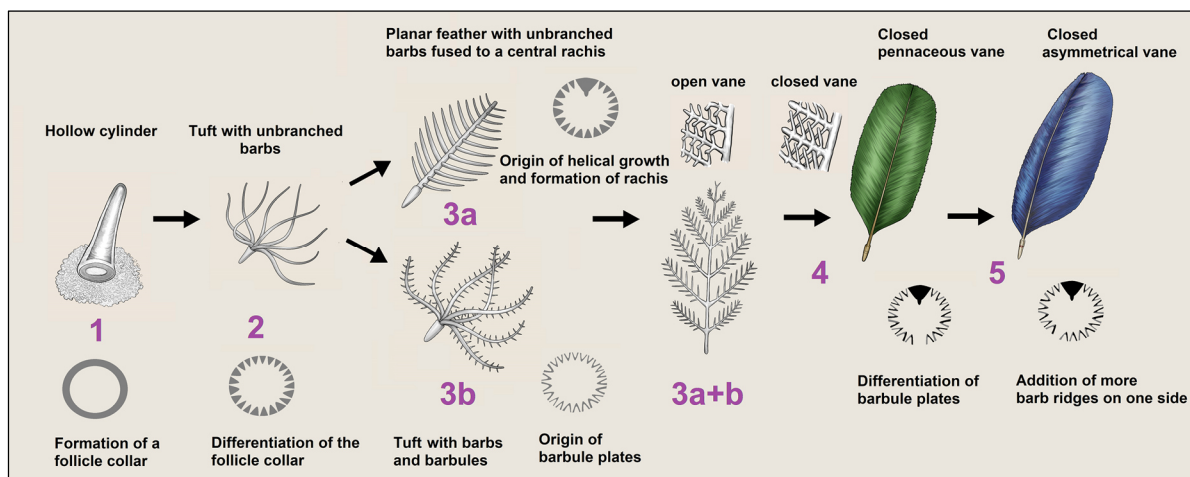
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<sup>2</sup> FEDUCCIA (2013) is one of the few in his guild to dispute the evidential value of morphological cladistics. He suggests that the respective homology assumptions are not justified due to questionable trait weightings, that the taxon samples are too small, etc. However, SMITH et al. (2015) show that cladistics is well founded and uses *additional knowledge* from almost all biological disciplines to assess plausibility. Many independent findings from disciplines such as paleontology, physiology, histology, developmental biology, and behavioral biology fit into the picture of theropod ancestry. The authors also show that FEDUCCIA himself is not consistent. He is biased by accepting a few data sets and controversial studies that allegedly support his alternative ancestry thesis.

GAUTHIER (1986) described 84 synapomorphies (shared derived characters) of Saurischian dinosaurs (which also include theropods and birds) and fully confirmed Ostrom's inference. Employing cladistics methods, he showed that birds belong to Maniraptora, these to Coelurosauria, and the latter to Theropoda. The data supporting this analysis increased considerably until today, as did the knowledge of the successive acquisition of avian traits (cf. BRUSATTE et al. 2015; SMITH et al. 2015; CAU 2018; RAUHUT & FOTH 2020). This includes morphological as well as molecular sequence-based data, studies of nesting behavior, histological data, etc.

As remarked above, in the 1970s and 1980s, biologists predicted the existence of (proto) feathers in non-avian dinosaurs because birds are related to theropods. However, they found not even one. Hence, the discovery of feathery filaments in *Sinosauropteryx* in 1996 and pennaceous feathers in *Caudipteryx* in 1998 created a sensation. Since then, scientists have found numerous other feathered non-avian dinosaurs in China.

The morphological gap between filaments and pennaceous feathers was still quite large at the time. Thus, Richard PRUM (1999) predicted a series of evolutionary intermediate feather forms on the basis of embryological differentiation processes in birds. If the theropod hypothesis is correct, then certain feather stages, which birds transiently pass through in their ontogeny, should have existed as mature feather types in adult dinosaurs (Fig. 1).

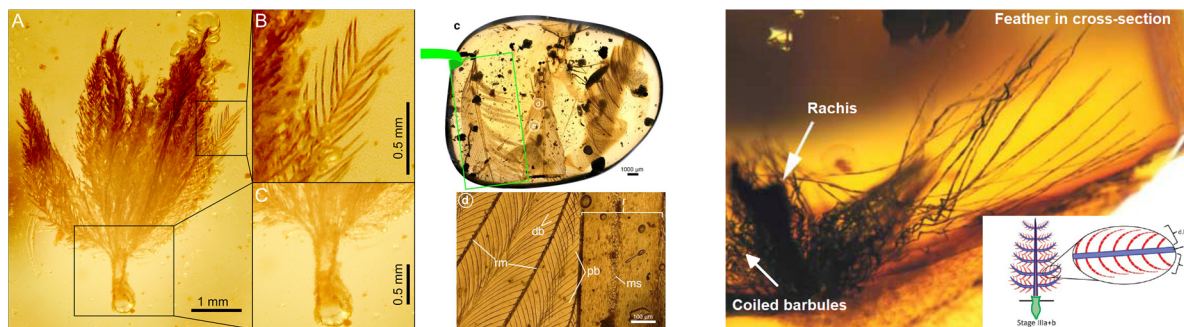


**Fig. 1.** Steps in the evolution of pennaceous feathers according to PRUM (1999). Stage 1 proposes an unbranched, hollow filament that develops from a cylindrical invagination of the epidermis around a papilla. The feather emerges at the base of the follicle through the continuous division of keratin-forming cells. The growth zone forms a follicle collar, from which the cells push out. Stage 2 involves the differentiation of the follicle collar into barb ridges; a tuft of unbranched filaments emerges. Stage 3a represents the formation of a central rachis (shaft) via fusion of barbs and the development of a planar feather with unbranched barbs. Stage 3b displays the development of barbules that branch from the tufts of barbs; this corresponds morphologically to a downy feather. In stage 3a+b, the features of stages 3a and 3b combine to produce a planar feather with a central rachis, secondary branched barbs (barbules stem from the barbs), and an open vane. In stage 4, the barbules differentiate into hooklets and bow barbules, generating a closed pennaceous vane. Finally, in stage 5, lateral displacement of the new barb locus by differential new barb ridge addition to each side of the follicle leads to the growth of a closed pennaceous feather with an asymmetrical vane resembling modern remiges. Drawing by James Paul BAELO, compiled from SUES (2001), PRUM & BRUSH (2003), and PERRICHOT et al. (2008).

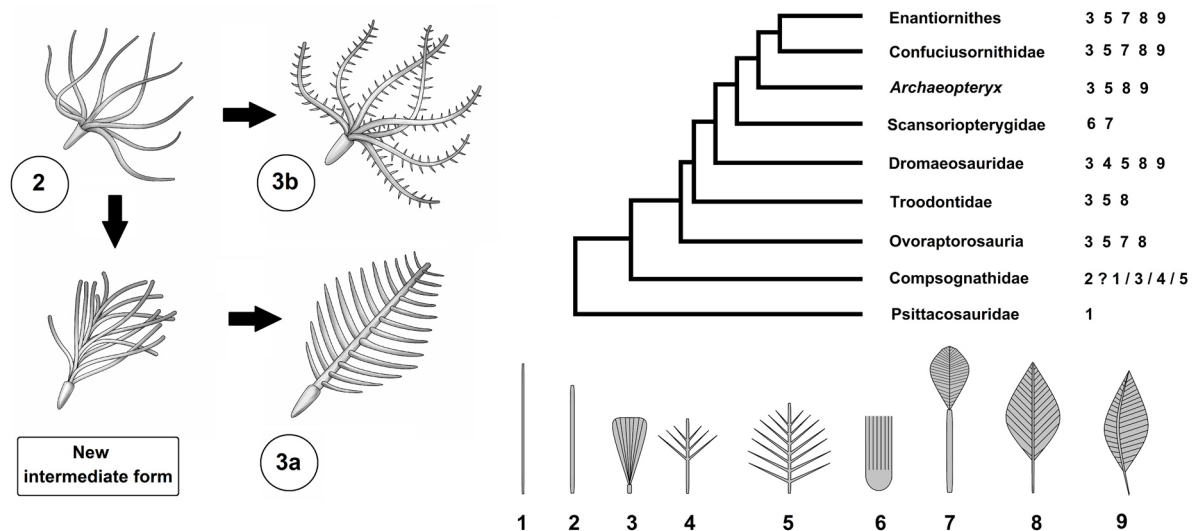


The rest, as they say, is history. Gradually, *all* of the feather subtypes predicted from PRUM's ontogenetic model have so far been discovered in theropod skeletons or in amber (Figs. 2 and 3). Another intermediate form, not explicitly predicted, even mediates between stages 2 and 3a (Fig. 3).

**In short:** The predicted feather shapes deduced from the differentiation processes of embryonic feather development are more than mere constructs. They existed! Obviously, feather follicles such as those existing in the Middle Jurassic carried the evolutionary capabilities for the development of modern feathers (ROY et al. 2020).



**Fig. 2.** Fossil feathers in amber. The morphology of the specimen on the left is consistent with stage 3b of PRUM's widely accepted model (from ROY et al. 2020). The center photo shows a stage 3a feather (from CARROLL et al. 2019). Right: stage 3a+b feather (from MCKELLAR 2011; [www.tinyurl.com/8h5edctm](http://www.tinyurl.com/8h5edctm)). Images licensed under CC BY-NC 4.0.

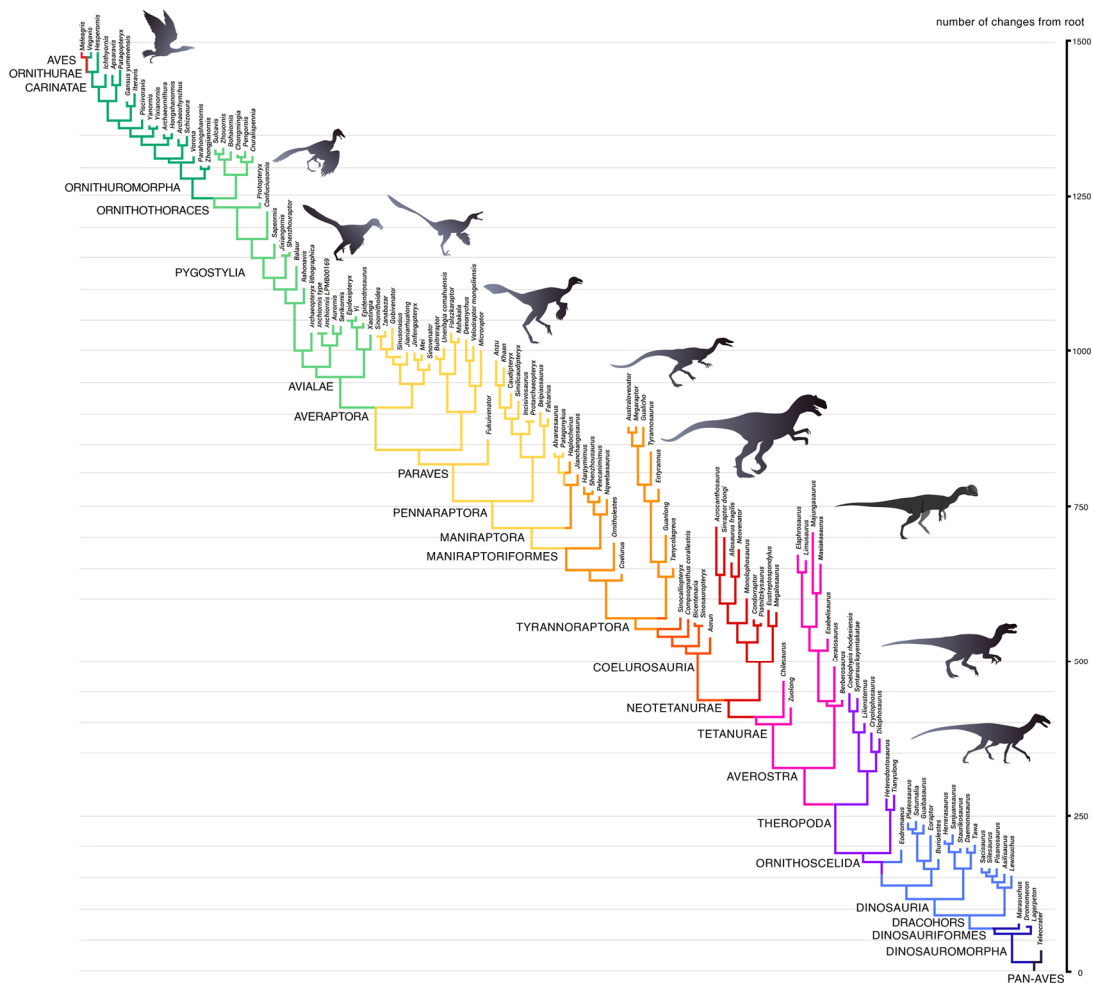


**Fig. 3.** Left: another intermediate form of the feather preserved in amber. Here, several branches are loosely connected to the shaft, which consists of secondary branches that are still incompletely fused. The flattened, bilaterally symmetrical form of modern feathers is already indicated. This stage lies between steps 2 and 3a in PRUM's model. By PERRICHOT et al. (2008, p. 1200). Right: feather types associated with theropod skeletons. Own sketch, redrawn and modified from XU et al. (2010, p. 1340). Drawing on the left by James Paul BAELO.

Thus, among experts, for the last 20 years, there has been no real controversy over the insight that birds have dinosaur ancestors. There is no way around this fact, at least if one accepts today's scientific rationality standards (cf. PRUM 2003; HAVSTAD & SMITH 2019).

As PADIAN & HORNER (2002, p. 120) put it:

Opponents to the cladistic view rely on other kinds of knowledge. The theropod dinosaurs in question were too large, too late in time, could not climb trees, lacked postulated 'key features,' could not pass through an allegedly necessary gliding phase, or were physiologically incapable of performing birdlike functions... These are all propositions that have been answered on their own terms, whether functional, stratigraphic, or metabolic... but the important point is that none was based on any evidence of relationship, so they do not really test the question of bird origins. No alternative hypothesis has withstood cladistic testing; and, in fact, there have not been any specific alternative hypotheses for >20 years. No other method of phylogenetic analysis has been proposed and argued to supplant cladistics, which is why the field, as a whole, remains unconvinced by these objections.



**Fig. 4.** Phylogenetic tree of Pan-Aves (Avemetatarsalia). This taxon (or clade) includes modern birds (Aves, top left), birds in a broader sense (basal Avialae), non-avian dinosaurs, pterosaurs, and other basal archosaurs more closely related to birds than to crocodylians. Modern birds differ from the stem species of Pan-Aves located at the base of this tree (lower right) by about 1500 morphological changes (derived traits). These acquisitions emerged successively within the ancestral lineage leading to modern birds over the last 250 million years. As expected, the groups are hierarchically nested. Thus, Dinosauria include Theropoda, Theropoda include Tetanurae, and Tetanurae include Coelurosauria. Maniraptora, in turn, is a subgroup of Coelurosauria. Pennaraptora is a subgroup of Maniraptora, and so on. Thereby, every node in this phylogenetic tree is a lineage-splitting event. The hierarchical system and the graded similarity of species contained in it are the strongest evidence for the evolution and descent of birds from early dinosaurs. Illustration by James Paul BAELLO, according to CAU (2018, p. 9). For the high-resolution image, see: <https://www.ag-evolutionsbiologie.net/bilder/kladogramm-pan-aves.jpg>.

## C. Discussion of popular objections by creationists

### C.1: Widespread convergences and conflicting phylogenetic trees

It is hard to argue against the overwhelming phylogenetic evidence discussed above. Hence, creationists often focus on alleged “anomalies” that do not fit into their flawed version of evolutionary theory. To this end, JUNKER (2019) primarily focuses on the so-called “convergence problem.” 93 times he points out that, from an evolutionary point of view, a huge number of bird characters that also occur in non-avian theropods must have arisen *convergently (independently, many times)* in different lineages:

Evolutionary convergences must be assumed more or less often for almost all of the characters examined because of their mosaic-like distributions. (p. 4)

Depending on the characters considered for tree construction, this would lead to different and mismatched phylogenetic trees. Cladists call such conflicting trees “*incongruent*.” In short, incongruent trees are due to “contradictory combinations of characters” in different species. According to JUNKER (2019), this means “that their graphical representation is more easily possible in a net-like form than in a tree-like form” (p. 53). In his view, such findings “fit better into a creation model” than into an evolutionary model.

Indeed, evolutionary convergences and conflicting trees are quite common. However, creationists ignore several elementary facts of evolutionary and developmental biology, invalidating JUNKER’s conclusion cited above:

- ✚ They ignore “... the fact that most analyses of morphology and molecules produce congruent results” (SMITH et al. 2015, p. 473). Despite widespread convergences and uncertainty about the position of some taxa in the phylogenetic tree, “...there is a remarkable consensus on the backbone structure of the family tree of the ancestors of birds and the relative hierarchical placement of almost all major clades that constitute this tree” (RAUHUT & FOTH 2020, p. 37). In short, birds are and remain deeply nested inside Theropoda on the basis of their specific (shared derived) characters.
- ✚ There are *observable* population-genetic mechanisms explaining incongruences (cf. PFENNINGER 2016, p. 29). One such mechanism is *hybrid speciation*.<sup>3</sup> Restricted gene flow is often still possible for a longer period between species that split up. Depending on the genes considered, different phylogenetic trees will result. Another mechanism is “*incomplete lineage sorting*,” described in Fig. 5.

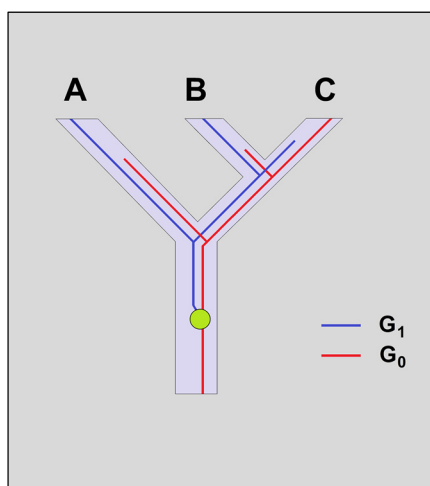
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<sup>3</sup> One example: a lineage of cottids (*Cottus*) observed in the Rhine for a few decades originates from the blending of two different parent species. Meanwhile, the parent species no longer reproduces with either daughter species (NOLTE et al. 2005). There is also evidence that hybrid speciation plays an important role in bird evolution (BRELSFORD 2011; OTTENBURGH 2018).

- + Some characters preferentially evolve *convergently* for *developmental-genetic* reasons (LUO et al. 2007; SHUBIN et al. 2009; MCGHEE 2011; HALL 2012; NARAMOTO et al. 2019). For example, modified expression of genes encoding growth factors has enabled the convergent evolution of lobed feet in waterfowl (cf. Fig. 6; TOKITA et al. 2020). Convergences occur more frequently the more species are genetically similar. This phenomenon is based on *development constraints*. For instance, ancient homologous regulatory genes can independently be switched on and off many times in evolution to produce convergent traits: “The same forms have been produced by the repeated channeling of evolution along the same developmental trajectory” (MCGHEE 2011, p. 7).

Thus, while some cases of convergence are due to the similar response of similar genomes to similar selection (= *parallelism*), others can be attributed to the loss or reversal of traits in related species. Especially the *reduction* of characters, such as the degeneration of the furcula to separate clavicles in flightless birds, is easily accomplished, e.g., by *loss-of-function mutations*. *Reversions*, i.e., the renewed emergence of phylogenetically older character states, are not difficult to explain if the developmental potential for the given trait is still present (*atavisms* are an example of reversions).

Sometimes this requires only the reactivation of an old pathway (MCGHEE 2011, p. 7), usually by a mutation. LUO et al. (2007, p. 292) explain this principle using the example of multiple independent origins of lumbar ribs in some Mesozoic mammals. Of course, old pathways can be reactivated only if the genes involved have been preserved by selection, presumably by being involved in other pathways that were not suppressed.



**Fig. 5.** Example of incomplete lineage sorting. Two speciation events are shown: first, an ancestral species splits into two species, and later, once again, into sister species B and C. Consider the phylogenetic trajectories of the gene G, which originally occurred in a single genomic copy. Therefore, the common ancestor of A, B, and C initially possessed only allele  $G_0$ . At some point, a duplication event occurred (symbolized by the green dot), and in the ancestral population, the copy  $G_1$  became fixed, and afterwards, both versions evolved independently from each other, accumulating numerous mutations. Imagine that  $G_0$  was lost in the lineage of A, whereas the ancestors of B and C retained both copies. After B and C diverged, only  $G_1$  prevailed in B, and only  $G_0$  prevailed in C. Because of the co-occurrence of  $G_1$  in species A and B, one might now think that they are sister species, although they are not. This disturbing effect is even stronger when paralogues (generated by gene duplication) arise and, much later, each lineage loses a different representative. We are dealing with an *incongruence* that does not reflect the actual relationships. Own drawing.

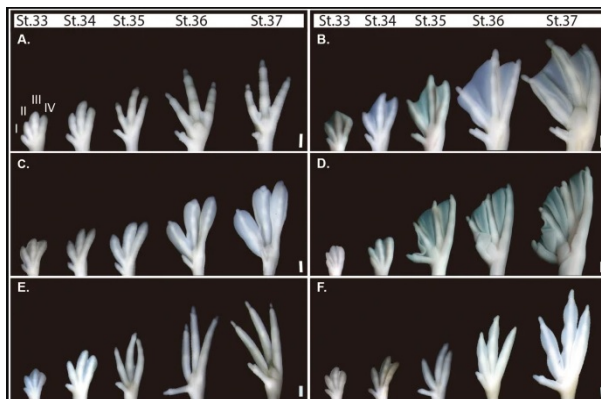
Two things follow from all this. First, for the plausibility of the descent of birds from non-avian dinosaurs, it is irrelevant that several characters arose convergently. For this reason, *individual* traits are never particularly meaningful; the *multitude* of graded similarities corroborating birds' deep hierarchical nesting within Theropoda is crucial.



In order to create the impression of “strongly interconnected or even chaotic character distributions” (JUNKER 2019, p. 65), a crucial statistical aspect is ignored: even for a small number of considered organisms, the total number of possible trees is extremely large. For instance, if we consider 11 taxa, there are already 34 million possible unrouted trees (PENNY et al. 1982). Thus, the probability of ending up with two similar trees by chance via two independent methods, or different sets of characters, is extremely small. Moreover, even “incongruent trees” mostly show a very similar hierarchical placement of their major clades and mismatch only by some branches. To quote THEOBALD (2013):

In general, phylogenetic trees may be very incongruent and still match with an extremely high degree of statistical significance... The stunning degree of match between even the most incongruent phylogenetic trees found in the biological literature is widely unappreciated, mainly because most people (including many biologists) are unaware of the mathematics involved.

In other words, if the characters of different species were chaotically distributed or even “freely combined (by creation)” as creationists often claim, it would be extremely unlikely to calculate even *similar* trees. We would have to deal with up to 34 million different trees for 10 taxa, depending on the characters we use as input. In fact, though, at worst, we end up with a few dozen alternate trees that are broadly consistent and share a very similar backbone structure. As PENNY & HENDY (1986, p. 414) calculate, this corresponds to a measurement accuracy of 99.9999%! This is a very strong phylogenetic signal indeed.



**Fig. 6.** Comparison of different stages of embryonic foot development in waterfowl. Altered expression of genes encoding certain growth factors explains convergent evolution of lobed feet in water birds such as the common coot (F) and little grebe (C). Single mutations are often sufficient for this. Such a mutation in a BMP receptor can also initiate the convergent development of duck-like webbed feet, for instance, in the great cormorant (D). Source: TOKITA et al. (2020). Image licensed under [CC BY 4.0](https://creativecommons.org/licenses/by/4.0/).

Second, considering developmental biology background knowledge, *common convergences are not anomalies* but rather an *explicit expectation* of evolutionary theory. Cladists must judge, on a case-by-case basis, how plausible convergence is. This remains uncertain without appropriate knowledge of developmental biology. However, the blanket assertion that widespread convergences speak against evolution is wrong. On the contrary, the scientific community has known for decades that

...if you are studying a closely knit group such as Hominidae you can never ignore it [convergence], because the more similar a pair of species is genetically, the more likely the same detailed morphology is to arise in parallel. (TATTERSALL 1995, pp. 167–168)



## C.2: Discontinuous, “chaotic” evolution in a zigzag course

Linked to the “convergence objection” is the anachronistic idea that evolution must proceed both linearly and continuously. Accordingly, regarding the flight ability of birds, JUNKER (2019) emphasizes that such a “linear, stepwise mode of development”—to be expected from an evolutionary point of view—is not observed (p. 9).<sup>4</sup> Rather, development has been “chaotic.” Regarding some traits, “problematic re-versions” (p. 48) must be postulated, or

...in terms of evolutionary theory, a degeneration [reduction] or some kind of evolutionary zigzag course, as in the case of the shoulder girdle, must be assumed, which is generally considered implausible. (JUNKER 2019, p. 62)

Apparently, only rectilinear, unidirectional changes in single, non-branching lineages (*anagenetic trends*) are considered for evolutionary development. However, lineage-splitting events (*cladogenesis*) give rise to *different* lines of development. Subsequently, quite separate evolutionary dynamics that unfold convey the image of a non-linear and chaotic zigzag course among lineages (see, e.g., MACFADDEN 2005).

The very insistence on “continuous changes” (JUNKER 2019, p. 40) reflects obsolete ideas concerning evolution and speciation. First, developmental constraints often cause discontinuous variations (MAYNARD SMITH 1983). For instance, continuous variation of ontogenetic parameters (e.g., morphogen gradients or biomechanical forces effecting tissue interactions) can produce discontinuous changes in phenotypic traits or, in some cases, even large-scale effects, especially when threshold values are exceeded (PETERSON & MÜLLER 2016).

Second, continuous changes are not to be expected, because of the “spatial and temporal heterogeneity of the environment with its limited resources, which requires ecological segregation to avoid competition” (MAHNER 1986, p. 68). As populations establish themselves in different adaptive zones, their traits evolve at different rates—and often in different directions (FUTUYMA 2015, p. 35).

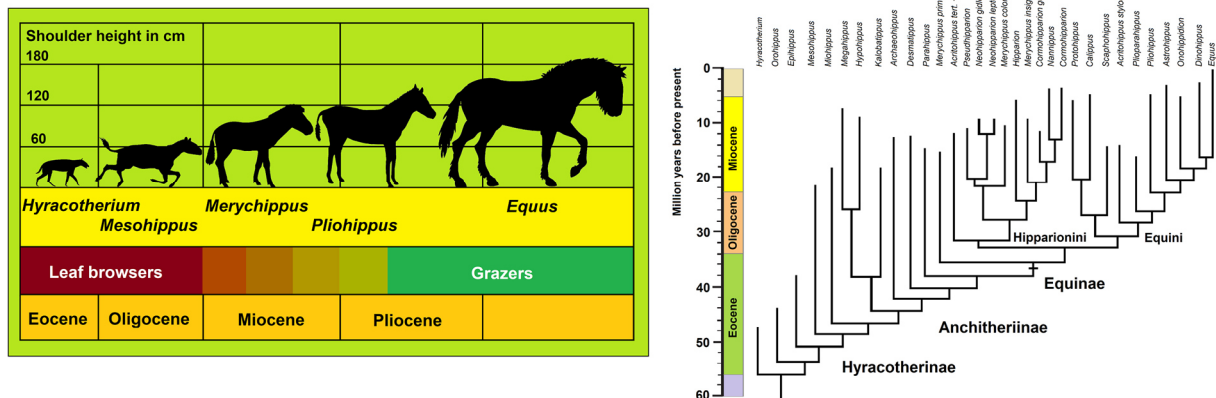
<sup>4</sup> JUNKER quotes BRUSATTE (2017) to show that “the development of flight was chaotic” (p. 792). However, nowhere in BRUSATTE’s paper is there any mention of the need for “linear, stepwise” evolution. On the contrary, BRUSATTE refutes the view that theropods developed—or even needed—feathers and wing profiles *specifically designed* for flight. Instead, numerous lineages existed that possessed various potential makeshift solutions, such as skin flaps, stiffened coverts, and membranous wings to provide semi-stable wings. For example, the wings and feathers of *Anchiornis* were anything but tailor-made for flight (PITTMAN et al. 2022a). Nevertheless, those skin membranes’ “bridge construction” at least allowed for a gliding or weak flapping flight.

On the other hand, the genus *Yi*, superficially resembling a bat and solely equipped with a skin membrane between the fingers, only barely managed even gliding flight. The center of gravity was far behind the gliding membranes, so its flight was probably very unstable (DECECCHI et al. 2020).

JUNKER’s assumption that such a *chaotic developmental path*, in which “dinosaurs *experimented* with different ways of flying” (BRUSATTE 2017, p. 792) speaks *against* evolution, is a poor straw man argument, born from the obsolete view that evolution must proceed linearly. The fact that JUNKER adds BRUSATTE’s metaphor of an “experimental field” as an argument for “creation,” although a chaos of different forms with many dead ends (such as *Yi*) fits perfectly into a non-intended natural process, is just the icing on the cake.

A well-studied example concerns the evolution of the horse and the splitting of its ancestral lineages in the Cenozoic (Fig. 7). As early as the 1950s, evolutionary biologist George Gaylord SIMPSON demonstrated that the phylogenetic tree of the horse does not reveal a simple, unilinear course of evolution (SIMPSON 1951). Instead, it has many side branches that have become extinct.<sup>5</sup> Several complex lineage-splitting events occurred in horse evolution as some of the leaf-browsing genera evolved into grazers.

Multiple lineages established themselves in each adaptive zone. While some grazers already had well-developed hooves, others retained their toes. Teeth, toes, and body size evolved at different tempos and modes, with high-rate variability among lineages depending on climate, vegetation, selection, and random genomic variations (MACFADDEN 2005; MIHLBACHLER et al. 2011). For more than 70 years, this “chaotic” evolution has been fully consistent with our knowledge of speciation processes. Behind this evolutionary zigzag course, a clear trend is recognizable only over many millions of years.



**Fig. 7.** Left: a simplified (linear) diagram emphasizing an anagenetic trend in horse evolution. Right diagram: how evolution proceeded considering lineage-splitting events. In the late Oligocene and Miocene, the branchings were so numerous that we cannot depict all of them. A trend toward increasing body size and reducing toes is visible only over very long periods and numerous lineages. Silhouettes of the horses: Scott HARTMAN (*Hyracotherium*), T. Michael KEESEY (*Meshippus*), Andrew FARKE (*Merychippus*), Julián BAYONA (*Plihippus*), and Mercedes YRAYZOZ (*Equus*). Source: [www.phylopic.org](http://www.phylopic.org) | License: CC BY 4.0. Based on a template from [www.sofatutor.com/biologie/videos/stammbaum-der-pferde](http://www.sofatutor.com/biologie/videos/stammbaum-der-pferde). Courtesy of S. KIEFER. Phylogeny of horses according to MIHLBACHLER et al. (2011), own sketch.

To sum up, morphological evolution is most commonly gradual but discontinuous, episodic, and fluctuating in direction. Most notably, evolution proceeds *on multiple tracks* due to numerous lineage-splitting events causing multiple lines of development in parallel. To put it another way, contrary to creationists’ premise, examples of unilinear phylogenetic paths are very rare. We can trace back phylogeny

...to a last common ancestor by a labyrinthine route, but no paths are straight, and all lead back by sidestepping from one event of branching speciation to another, and not by descent down a ladder of continuous change. (GOULD 2011, p. 67)

<sup>5</sup> Note that “side branches” are apparent only in retrospect. The side branches in horses’ evolution are the ones that did not lead to the extant horse (*Equus*).

### C.3: “Mismatched” mosaic forms instead of transitional forms

Creationist arguments frequently contain antiquated ideas about the nature of evolutionary transitional forms. For instance, JUNKER (2019) quotes many examples in order to show that “the mosaic of features” of the fossil in question is such that it does not fit as an evolutionary transitional form but must represent an evolutionary lineage of its own (p. 63). For instance, the bird-like theropod *Rahonavis* (Fig. 8) was

...more 'primitive' than *Archaeopteryx* with respect to some features but distinctly more birdlike with respect to others, thus not suitable as a transitional form. (p. 55)



**Fig. 8.** Depiction of *Rahonavis* (left) and *Archaeopteryx* (right). On the one hand, *Rahonavis* still has features of dromaeosaurids (Fig. 4) that proto-birds lack, such as the sickle claw on the second toe. On the other hand, in some features, it already corresponds more to the anatomy of today's birds than the proto-bird *Archaeopteryx*. For example, the shoulder girdle was already quite flexible, in contrast to the fused, rigid shoulder girdle of *Archaeopteryx*. This feature, adapted to active flight, may have evolved in birds convergently. Thus, both mosaic forms possessed different “transitional characters” “on the way” to the birds. This shows that evolution did not proceed harmoniously along *one single* track for birds. Lineage-splitting events cause characters to evolve at different rates in each organism and in each lineage (*heterobathmy*). Left graph: artwork by James Paul BAELO, all rights reserved. Right graphic: Author: DBCLS | Source: [www.doi.org/10.7875/togopic.2020.192](https://doi.org/10.7875/togopic.2020.192) | License: CC BY 4.0.

Lineage-splitting events, followed by disparate further development, contribute to the evolution of such different mosaics of “primitive” and “advanced” characters. This finding is by no means new. For instance, even MAYR (1967, p. 465 f.) says:

When migrating into another adaptive zone, a structure or a structural complex is under particularly strict selection pressure... As a result, this structure or complex evolves particularly fast, while others are left behind. The result is not a steady and harmonious change of all parts of the 'type', as idealistic biology imagines, but far more of a *mosaic evolution*. Each evolutionary type is a mosaic of primitive and advanced features, of general and specialized traits. (Emphasis added)

The fact that in *Archaeopteryx* some traits remained more “primitive” than in *Rahonavis*, while others were more advanced, is not surprising against this background: the occupation of different ecological zones is accompanied by different ways of life. As a result, different selection pressures can act on the same traits in

two related species. For instance, *Rahonavis* was an agile predator of the air with adaptations to sustained flapping flight (PITTMAN et al. 2022b). *Archaeopteryx* was rather a glider with lower flapping flight potential (LONGRICH et al. 2012; KSEPKA 2022), whose life took place more on the ground (ELŻANOWSKI 2002). In turn, the more primitive feature of the sickle claw accommodated the lifestyle of dromaeosaurids (FRASER 2014). Consequently, *Rahonavis* preserved the sickle claw.

**In short:** Different biological characters (or the same character at different periods of time) evolve at various rates both *within* and *between* species, a phenomenon called *mosaic evolution* (CARROLL 1997). Here, evolution varies from stasis to “rapid” change, depending on the selection pressures the traits are exposed to in different ecological niches, under different environmental conditions, and under different behaviors.

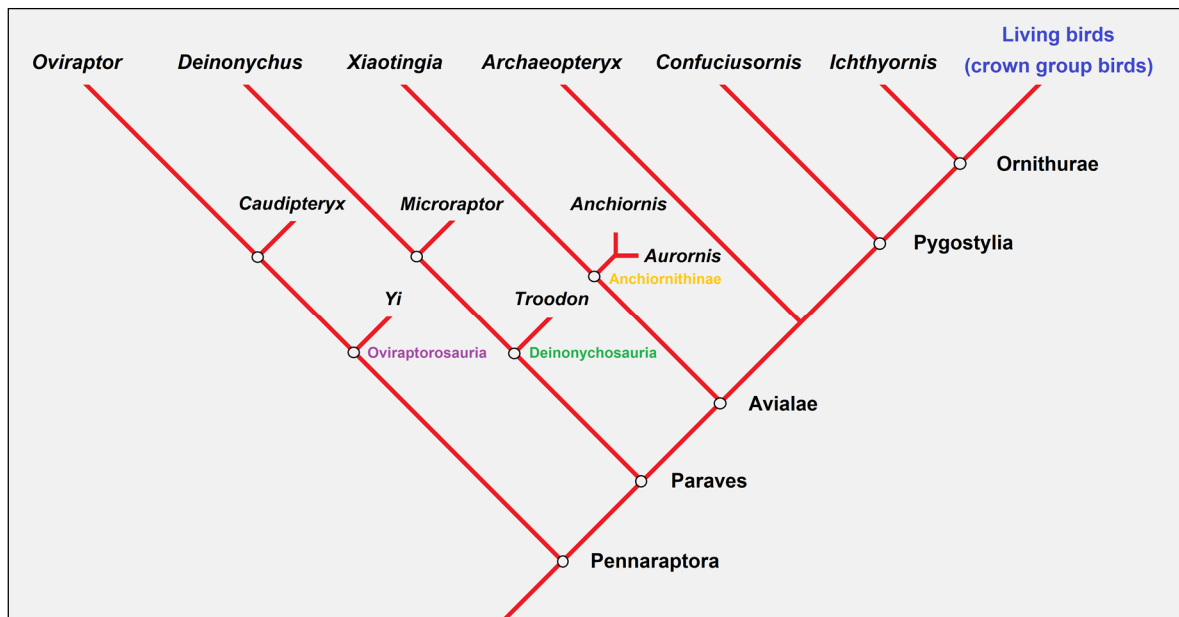
Moreover, mosaic evolution is often the result of developmental constraints or functional and genetic burdens that have their roots in the hierarchical, modular organization of traits in organisms (cf. RIEDL 2003, p. 209; FELICE & GOSWAMI 2018).<sup>6</sup> Claiming that “mosaic evolution” is a “foreign body in an evolutionary scenario” (e.g., JUNKER 2019, p. 65) clearly shows a lack of knowledge of elementary principles of evolutionary biology in creationist criticism.

Given that the mode of phylogenetic development is usually *mosaic evolution*, what do *transitional forms* look like? Early anthropologists anticipated discovering fossils of human progenitors, whose features were transforming steadily into those of current humans (PROTHERO 2017, p. 135). However, due to the mosaic mode of evolution, lineages retain “primitive” features while developing “advanced” traits in parallel. The branching (speciation) process of founding independent taxa further complicates the picture. Hence, this classical expectation of the nature of transitional forms is not tenable any more (PROTHERO 2017, *ibid.*).

For that reason, PADIAN & ANGIELCZYK (1999) recommend shifting the focus from transitional *forms* to transitional *features*. However, the concept of transitional forms is still fruitful within the realm of cladistics if the term “transitional form” experiences a semantic shift: from a cladistic point of view, transitional forms toward birds represent extinct *mosaic forms* exhibiting some derived characters of crown group birds (*avian synapomorphies*), but not yet all of them. Additionally, those fossils still possess

<sup>6</sup> In general, the phylogenetically older a biological trait or system is, the more other features rest upon its functionality and the slower it evolves. We can say that it is highly *burdened*. Therefore, it hardly evolves any more.

some ancient characters that crown group birds lack. This is the *modern* meaning of the term *transitional form* (Fig. 9).



**Fig. 9.** Simplified cladogram of Pennaraptora, that is, the theropod clade including living birds (crown group birds). All species depicted here (and many more not shown here, which may have been direct or indirect ancestors) embody the *ancestral lineage* of birds. This implies they already possessed some (but not all) of the derived traits of crown group birds while still possessing quite a few non-avian theropod characteristics that living birds lack. This is exactly what is to be expected from a *transitional form* from a cladistic perspective. Their position in the cladogram tells us the sequence of origination of derived features in living birds. Own sketch, modified from PITTMAN & XU (2020).

Quite pointless is the attempt to dismantle the status of transitional forms by pointing out that they represent a side branch:

All in all, this mosaic form with very primitive and highly derived characters can only find a place in the phylogenetic tree of birds if it is placed on a blind-ending side branch and significant convergences are assumed. (JUNKER 2019, p. 55)

Creationists often argue that many fossils exhibit progressive specialization of traits or unique distinctive characters (*autapomorphies*), ruling them out as direct ancestors of extant species. However, it is naive to demand that transitional forms can be strung like pearls on a necklace in procession from the Mesozoic ancestors to the modern species (crown groups) in a rectilinear ladder of change. Such thinking is “simplistic and inaccurate, reminiscent of the pre-evolutionary concepts of the ‘Great Chain of Being’ or *scala naturae*” (PADIAN & ANGIELCZYK 1999, p. 56).

On the one hand, evolution is a branching process with a great number of dead-end branches. At least 99% of all species that have ever lived eventually became extinct (TAYLOR 2004, p. 1). Thus, fossils usually represent “dead-end” side branches, except for those few that *directly* lead to a crown group. However, even if we found a direct ancestor, there is no way to determine *precisely* how close it is to the branching point due to the incompleteness of the fossil record (PADIAN & ANGIELCZYK 1999).



Thus, we must redefine the archaic meaning of the “transitional form”—a point that creationist arguments usually miss:

Tree-thinking shifts the focus from looking for fossils of lineal (direct) ancestors to looking for synapomorphies that link collateral (side-branch) ancestors. (MEAD 2009, p. 311)

**In short:** The exact position of mosaic forms, such as *Archaeopteryx* or *Rahonavis*, in the phylogenetic tree is irrelevant with respect to the integrity of the theory of evolution. Their probative force derives from the fact that mosaic forms fit into a system of graded similarities, so that we can put them in a sequence in which their morphology gradually takes on the shape of modern birds (Fig. 10).

Character	<i>Anchiornis</i>	<i>Archaeopteryx</i>	<i>Jeholornis</i>	<i>Confuciusornis</i>	<i>Ichthyornis</i>	Crown group birds (Neornithes)
Gastralia	+	+	+	+	+	-
Paired temporal windows (diapsid skull)	+	-	+	+	-	-
Sternal keel (Carina)	-	-	-	-	+	+
Wing claws	+	+	+	+	-	-
Pygostyle	-	-	-	+	+	+
Horn beak	-	-	-	+	+	+
Toothed jaw	+	+	+	-	+	-
Elongate, strut-like coracoid	-	-	+	+	+	+
Fused metacarpals	-	-	+	+	+	+
Ossified breastbone (sternum)	-	-	+	+	+	+
Reversed pubis	-	+	+	+	+	+
Asymmetric wing feathers	-	+	+	+	+	+
Feathers mostly composed of $\beta$ -keratins	-	+	+	+	+	+
Plumage	+	+	+	+	+	+
Clavicles fused to a furcula (wishbone)	+	+	+	+	+	+
Hollow bones	+	+	+	+	+	+

**Fig. 10.** Table of characters of some theropods. (+) means the feature is present, (-) the feature is absent, and (±) the feature is rudimentarily present. Orange boxes indicate the possession of primitive non-avian theropod characters, and green boxes indicate the presence of advanced avian characters. We observe that the number of avian features (shared derived traits or *synapomorphies* of crown group birds) *gradually increases* from *Anchiornis* via *Archaeopteryx*, *Jeholornis*, and *Confuciusornis* through to modern birds, as expected by evolutionary theory. The character distribution also suggests that some avian characters evolved *convergently* in different lineages. For example, in *Archaeopteryx*, independently of crown group birds, the diapsid skull changed in such a way that none of the temporal windows is clearly visible. In addition, the loss of teeth in *Confuciusornis* and today's birds seems to have occurred independently.

#### C.4: Abrupt appearance of characters and the “waiting time problem”

A gradual appearance of different individual characteristics... does not automatically imply that their emergence is plausible from an evolutionary perspective. Some features appear relatively abruptly. (JUNKER 2019, p. 49)

This objection is meaningless because the known fossils are not at all a representative sample of extinct forms. Each instance of a fossil theropod specimen, such as the 12 known *Archaeopteryx* individuals, is an enormous stroke of luck. In each case, only a single specimen represents half of all dinosaur genera, and 80% of all dinosaur skeletons are only fragmentarily recorded (DODSON 1990). According to estimates, fewer than one to a few percent of species have left a fossil record (RAUP 1994). Due to the incompleteness of the fossil record, the demand for finely staggered transitions is absurd.

From an evolutionary perspective, many avian traits are regarded as early established [in a bird's phylogeny]. They show abrupt fossil appearances. This situation is a challenge for evolutionary mechanisms; rapid emergence [of traits] is not expected from an evolutionary perspective. (JUNKER 2019, p. 50)

Here, JUNKER ignores the explanation of *punctuated equilibria* (cf. ELDREDGE & GOULD 1972; JUNKER & HOSSFELD 2001) as well as the ambiguity of the term “abrupt.” When a paleontologist speaks of the “abrupt” appearance of a feature, he thinks of periods of time of several tens of thousands to millions of years; creationists think of a lightning-fast emergence in the sense of a *creatio ex nihilo*.

Grossly misleading is the claim that evolutionary mechanisms are “clearly overstrained... with bringing forth a great diversity of forms relatively abruptly in geologically short periods of time” because of the “waiting time problem” (pp. 67, 93). Why is that?

Before we explain why JUNKER's claim is deceptive, we must elucidate the waiting time problem. In short, advocates of the “waiting time problem” assume that a feature with specific characteristics would take too long to evolve because evolution must wait until the complete set of responsible mutations has cumulated (HÖSSJER et al. 2021).

In essence, the “waiting time problem” is based on two premises: First, evolution must reach a “fixed and pre-specified target” (HÖSSJER et al. 2021, p. 51). Second, finding that target would require multiple “coordinated mutations” (ibid., p. 5). Given the required genetic “fine-tuning” and the fact that back mutations eliminate potentially beneficial single mutations again, the argument goes, novelties could not evolve in realistic time periods.

However, creationists such as HÖSSJER et al. are working under a misunderstanding or misrepresentation of evolutionary theory in order to make their waiting time argument.<sup>7</sup>

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<sup>7</sup> Daniel STERN-CARDINALE, Assistant Teaching Professor at Rutgers University, produced a highly instructive video on the waiting time problem on his YouTube channel ([https://www.youtube.com/watch?v=F748itCI\\_es](https://www.youtube.com/watch?v=F748itCI_es)).

Specifically, they are wrong in assuming that there are pre-specified targets or functions that evolution must have worked towards. Even if a particular function is given, there is no need for evolution to wait for pre-specified DNA or protein structures. Each functional state can be accomplished in countless and totally different ways.

Take antibiotic resistance as an example: Among others, antibiotics can be rendered ineffective by novel enzymes, modified receptors, efflux pumps, or “up-regulating” an antagonistic signaling pathway. Each of these pathways, in turn, has multiple routes open to evolution. In terms of the enzymatic route, for instance, cleavage or acetylation can inactivate a drug. For each route, evolution can in turn use numerous different options. For example, the enzyme class of beta-lactamases is highly diverse. It includes protein families that have little structural similarity to each other (HUNT 2007a). Finally, each individual protein can exhibit enormous variability while maintaining its function.

The assumption that multiple coordinated mutations are necessarily required to achieve a target also proves to be false. The emergence of enzymes with completely novel properties can often be accomplished by single mutations (DE KRAKER & GERSHENZON 2011). Analogous to this finding, YONA et al. (2018) showed that ~ **60%** of *purely random* DNA sequences containing no functional information (!) are only *one* mutation away from turning into active promoter sequences. A similar study demonstrated that a high percentage of randomized peptides (when attached to the end of a cytosolic protein) can serve as functional targeting signal for specific import into a certain cell organelle (TONKIN et al. 2008).

Even irreducibly complex systems with multiple well-matched components, like specific protein-protein binding sites or functionally rearranged genes with suitable promoters, have been shown to arise rapidly (e.g., VIGAN & NEIL 2010; NEUKAMM 2012; SAUTER et al. 2012; BEYER et al. 2022; NEUKAMM 2022).

Monte Carlo experiments show that the mechanisms of evolution would not necessarily be overstrained, even if that would require three, four, or even more “matching” mutations (TROTTER et al. 2014). This is because thousands of (cryptic) genes, signaling pathways, and co-factors imply an enormous number of candidate combinations for complex gene interactions.

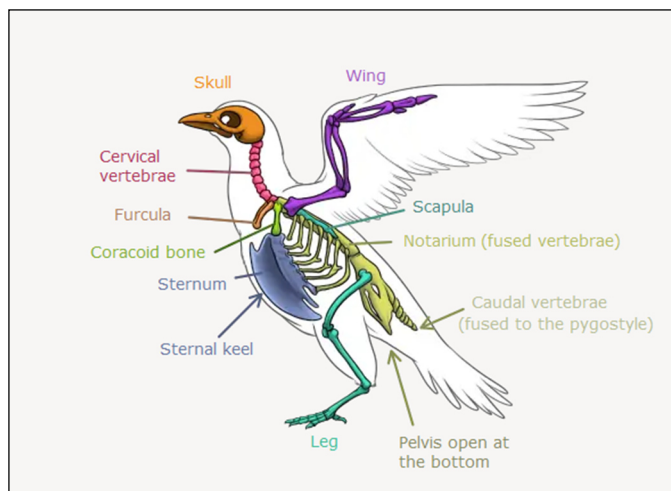
Moreover, as long as no one can demonstrate that the proportion of promising mutations and gene interactions is extremely small compared to the universe of possibilities, the waiting time problem will remain a pipe dream.

### C.5: Evo-Devo solutions for bird evolution

A major step in the evolution of birds was the conversion of limbs into functional wings. The prolongation of the extremities, reduction of the fingers, and fusion of the carpus and metacarpals accompanied this conversion, for instance. Evolution deniers like to argue that each of these changes required a complicated sequence of mutations or even the acquisition of entirely new genes. If this argument were true, such adaptations would be lengthy, and convergences would be unlikely. However, the argument is not true:

The limb-to-wing transition does not require a complete new set of genes but rather changes in the control of a few genes that promote or stop growth. These genes produce chemicals called growth and signaling factors that give directions to the cells in a growing embryo. When they are turned on and off at different times, that can drastically change the shape of an animal. (HORNER & GORMAN 2009, p. 11)

Recent research has led to entirely new insights into the emergence of new traits and body plans. There are a limited number of control genes; their products serve as *signaling molecules* and interact with promoters and enhancers of other genes. In combination with environmental conditions, they orchestrate the morphogenesis in embryonic development. Slight changes in those interactions may cause fundamental shape changes. *Evolutionary developmental biology* (or “Evo-Devo”) focuses on these mechanisms.



**Fig. 11.** Skeletal structure of birds. Skull structure, reduced digits, fused metacarpal bones, sternal keel, fused metatarsals, tarsal bones, and fused vertebrae—most adaptations in birds required changes in the regulation of genes. More explanation is in the text. Graphics: courtesy of SchuBu Systems GmbH (Stefan PROCHASKA), drawing only. Source: [www.schubu.at/p172/das-vogelskelett](http://www.schubu.at/p172/das-vogelskelett). English description: MN.

(cranial kinesis); and many others (cf. CHATTERJEE 2015, p. 275).

Many amazing adaptations rest primarily on changes in the temporal coordination of developmental processes (*heterochrony*). For instance, some mutations affect the activity of developmental genes in such a way that juvenile traits are preserved into adulthood. Such a case is called *pae-domorphosis*. These include numerous adaptations in birds such as reduction in body size; an inflated braincase; a shortened beak; reduction of teeth; loss of the metatarsal wing; thin, flexible, loosely connected skull bones

Other mutations affecting regulatory genes accelerate or prolong the growth of structures. The prolonged growth can result in structures merging, nesting, or increasing in size compared to their ancestral status. For instance, recent studies suggest prolonged growth phases as a cause of the formation of the prominent sternal keel (carina or keel bone) in birds (Fig. 11) and the convergent structure in bats (LÓPEZ-AGUIRRE et al. 2019).

Another distinctive bird feature is the pygostyle, which is a product of fused distal caudal vertebrae (cf. Fig. 12). It serves birds as a stable base for their tail feathers, which are erected by folding up the pygostyle. Comparable morphologies can be induced even experimentally (!) by ectopic overexpression of Hoxb13 or changes in the retinoic acid gradient (RASHID et al. 2014, p. 9). Retinoic acids affect gene expression and exert an influence on cell differentiation.



Fig. 12. Skeleton of a giant petrel with an erected pygostyle at the end of the tail. Author: Daiju AZUMA | Source: [Wikiwand.com](https://www.wikiwand.com) | License [CC BY-SA 4.0](https://creativecommons.org/licenses/by-sa/4.0/).

PLATEAU & FOTH (2020) showed that the final step towards highly modular, integrated skulls in modern birds is grounded in an abrupt fusion of cranial bones. Phylogenetic comparisons suggest that cranial bone fusion represents a developmental exaggeration of the ancestral adult trait. In fact, in number and distribution of modules, juvenile bird skulls resemble the adult skulls of non-avian theropods (including *Archaeopteryx*) more closely than their own adult skulls. Adults possess significantly fewer cranial modules due to ontogenetic bone fusion.

A particularly interesting case is the *evolution of bird beaks*. The beak (bill or rostrum) is the toothless jaw part of sauropsids, covered with hardened horny sheaths (rhamphothecae).<sup>8</sup> The bony base of a beak is largely formed by the premaxillary, which is greatly enlarged compared to non-avian theropods (Fig. 13). The premaxillary sits on top of a shortened face and a bulbously enlarged cranium, and it is functionally integrated into the kinetic system of the avian skull. The horny sheaths are composed of several superposed polygonal scales composed predominantly of specialized beta-keratins ( $\beta$ -keratins) and a

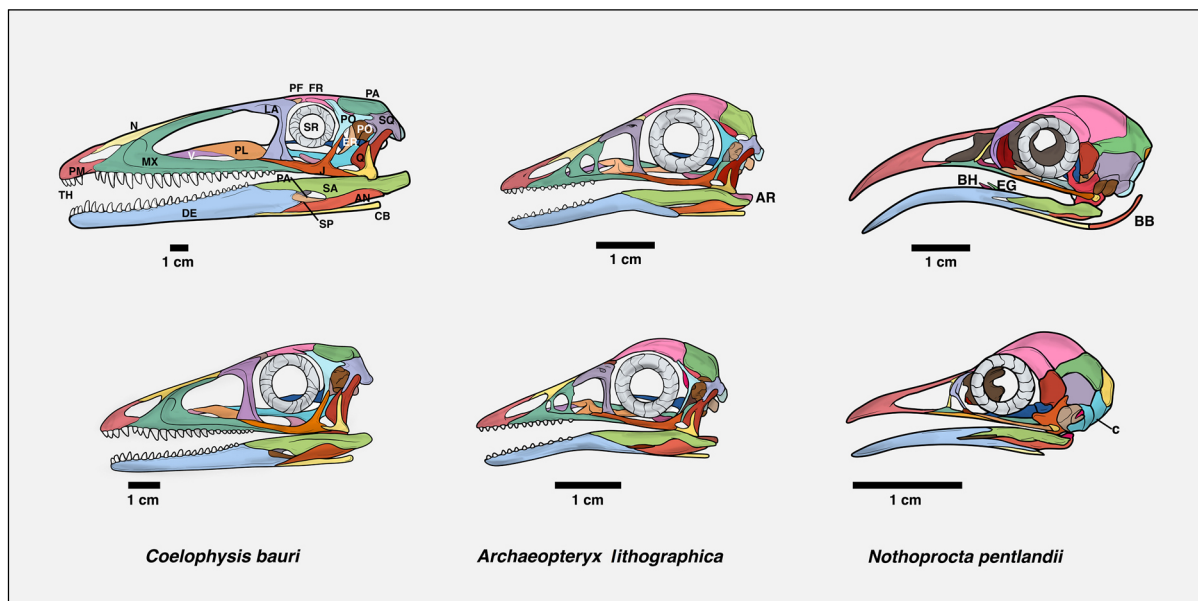
<sup>8</sup> Among extant sauropsids, beaks are only found in the crown groups of birds and turtles. In extinct sauropsids, beaks are found in various groups of theropods, e.g., oviraptorosaurs, ornithischians, and rhychososaurs. Corresponding analogs also occur in cephalopods and a few mammalian species. However, in no other animal group have horned beaks been differentiated into such unique and diverse mouthparts as in birds.



small amount of alpha-keratin ( $\alpha$ -keratin). Mixture and layer thickness vary from species to species and determine the mechanical properties of the beaks.

Transitional forms like *Archaeopteryx* and various Cretaceous birds such as *Ichthyornis* show that beaks did not develop abruptly. Their components did not evolve simultaneously but incrementally and independently from each other. First, cranial modifications caused by paedomorphosis took place, such as facial shortening, reduction of the maxilla (the upper jawbone), enlargement of the cerebral skull, and shrinkage of the bones, resulting in remarkable mobility (kinesis) of the cranial bones in birds.

Skull comparisons between juvenile non-avian theropods such as *Coelophysis* (Fig. 13 at lower left) and proto-birds like *Archaeopteryx* (Fig. 13 at upper middle) show that these modifications are results of paedomorphosis. The transition from thin, loosely connected, significantly movable skull bones to thick, overlapping, and firmly connected cranial bones happened in the ontogeny of non-avian dinosaurs and still takes place in extant crocodylians (BHULLAR et al. 2016, p. 397).



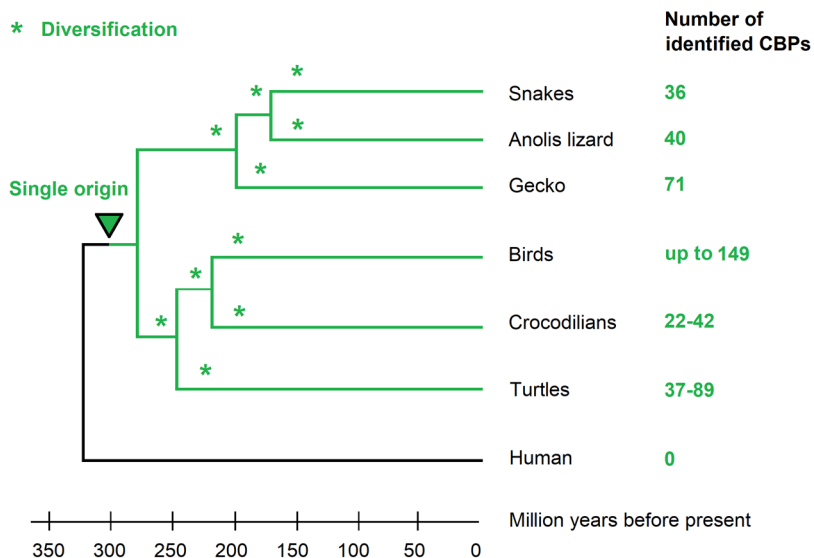
**Fig. 13.** Lateral skull view of the non-avian theropod *Coelophysis* (left column), the proto-bird *Archaeopteryx* (middle column), and the extant Andean Tinamou (right column). The skulls of adults are shown at the top, those of juveniles at the bottom. The different skull bones are color-coded. We can see that the evolution of the beak was preceded by a marked reduction of the maxilla (MX, dark green). This was the prerequisite for the subsequent enlargement of the premaxillary (PM, red), which forms the upper beak in modern birds. Drawing by James Paul BAELLO, modified from BHULLAR et al. (2016, p. 392).

In the next evolutionary step, with the appearance of crown group birds, the premaxillary was enlarged and integrated into the kinetic system of the cranial bones in a relatively short time. Recent studies suggest that functional integration of the enlarged premaxillary into the skull from a biomechanical point of view could occur only after

the paedomorphic shortening of the face and a significant reduction of the maxilla (BHULLAR et al. 2016).

Evolutionary transformations in cranial modules like the premaxillary are not complicated. Findings concerning the molecular control of beak development show that its parameters are subject to precise control mechanisms that are independent of the remainder of the snout (SCHNEIDER & HELMS 2003). Many adjusting screws can influence the development, such as changes in concentration of the transcription factor BMP4, which controls bone growth, among other things, or the BMP antagonist Noggin. Afterwards, mutations that influence the BMP signaling pathway in the maxillary bone enable “fine-tuning” of the shape and size of the beaks.

Various transitional forms provide information about another evolutionary step, namely the formation of horny sheaths on the beak. In some Cretaceous birds, only parts of the snout were covered with horny sheaths, starting from the tip of the beak. In present-day birds, formation also begins initially in the distal region of the beak primordia. *Ichthyornis*, for example, still possessed a small transitional beak with a toothless, horn-covered pincer tip that may have served as a type of grasping tool for picking up food.<sup>9</sup> However, *Ichthyornis*' beak caudally<sup>10</sup> still possessed teeth and a hornless snout (FIELD et al. 2018).



**Fig. 14.** Origin, duplication, and subsequent diversification of corneous beta-proteins (CBPs) in different sauropsids. From HOLTHAUS et al. (2019).

Where do the genes involved in the formation of horny sheaths come from? Analyses show that at least 149 different  $\beta$ -keratins are involved in the formation of horn-like structures, such as claws, beaks, and feathers in birds; they are called *corneous*

<sup>9</sup> The formation of a surrogate “hand” seems to be a key selective advantage, as the actual hands were integrated into increasingly specialized bird wings towards the end of the Cretaceous (BHULLAR et al. 2016, p. 398).

<sup>10</sup> Towards the back of the head.

*beta-proteins* (CBPs) (Fig. 14). Their genes are organized in the epidermal differentiation complex (EDC), and they are expressed in a specific temporal sequence. All EDC genes are involved in the complex differentiation process of the epidermis. The EDC contains both structural proteins and regulatory proteins of the epidermis.

However, neither the EDC nor the CBPs arose *de novo* in the avian lineage. Rather, the development potential for horny epidermal structures like claws, scales, fibrous skin appendages, and horny sheaths was already present in the genetic makeup of early dinosaurs such as *Psittacosaurus*. In birds, however, a strong expansion and differentiation of the gene cluster occurred.

A closer investigation of  $\beta$ -keratin gene evolution suggests that multiple waves of gene duplication within a single genomic locus with subsequent diversification accompanied the evolution of claws, scales, feathers, and horny scales in birds (LI et al. 2013; HOLTHAUS et al. 2019). A similar but independent process accompanied the evolution of the scales of the carapace in turtles. In other words, epidermal structures in Sauropsida share a common evolutionary origin that began with the emergence of the first CBPs more than 300 million years ago (Fig. 14). In this scenario, a growing number of new variants of CBP genes allowed for the progressive specialization of integument structures.<sup>11</sup>

As an aside, there is additional evidence that, from the viewpoint of developmental biology, scales and feathers can be considered homologous (MUSSEY et al. 2015). Thus, remarkable similarities exist in Wnt/ $\beta$ -catenin signaling during the early development of feathers and reptile scales, for instance, with respect to the localization of the transcription cofactor  $\beta$ -catenin. Expression of  $\beta$ -catenin is a reliable marker of the ability of epithelia to form feathers and scales. Essentially, feather morphogenesis differs from scale morphogenesis in that additional differentiation steps such as follicle formation and the development of an epidermal collar have been added incrementally (cf. PRUM 1999).

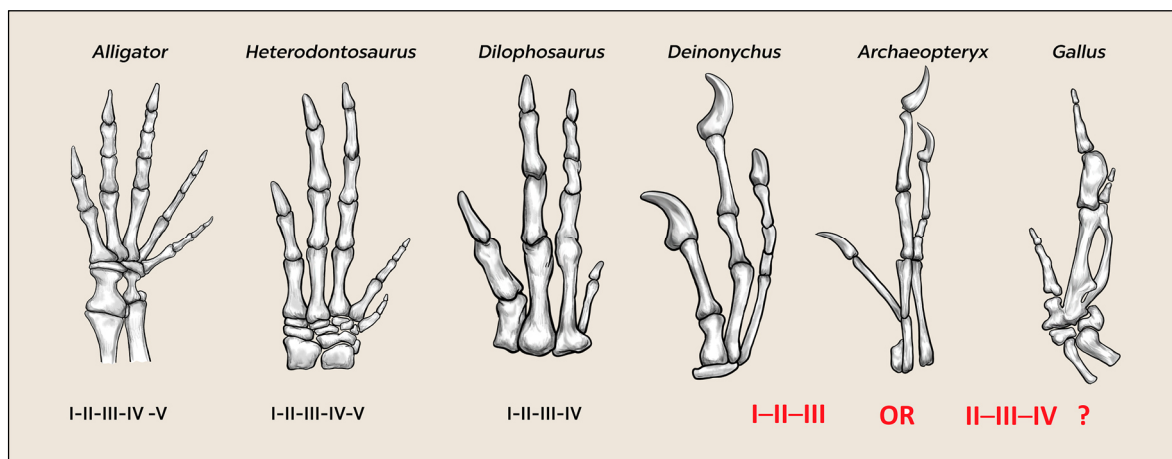
A word about the decades-old controversy over whether birds have thumbs (Fig. 15). What at first glance seems like a trivial question was a highly explosive matter in the past and occasionally led to questioning of the theropod ancestry of birds. Why? Well, in principle, terrestrial vertebrates have five fingers per hand, whereas the bird's wing has three fingers. There is evidence of a fourth digit early in

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<sup>11</sup> Work on the properties of  $\beta$ -keratins in the epidermis of various reptile species indicated a correlation between the type and amount of  $\beta$ -keratin expressed and the hardness of the epidermis. Duplicated  $\beta$ -keratin genes were possibly conserved because a greater amount of  $\beta$ -keratin increases the hardness of the epidermis and allows the emergence of different morphologies (ALIBARDI et al. 2007). Mutations, in turn, caused “fine-tuning” of traits.

ontogenesis, but it disappears again. Which digits do survive: the thumb (digit I), index finger, and middle finger (I-II-III) or the index, middle, and ring finger (II-III-IV)?

On the one hand, successive fossils show the reduction of two fingers on the posterior side (pinky side) of the hand among the ancestors of *Deinonychus* (Fig. 15). The remaining fingers resemble the three fingers of *Archaeopteryx*. This and the phalangeal formula, which is 2-3-4 in *Deinonychus*, *Archaeopteryx*, and birds, support the indexing of the fingers as thumb, index finger, and middle finger (I-II-III). Indeed, the gene expression patterns of the most anterior avian finger match those of the thumb in other animals.



**Fig. 15.** Schematic representation of finger reduction in various archosaurs. The numbering of the digits is given below each sketch, starting with the thumb (digit I), and moving to the posterior side (pinky side, digit V) of the hand. Drawing by James Paul BAELO, compiled from WELTEN et al. (2005) and ČAPEK et al. (2014).

On the other hand, in terrestrial vertebrates, the ring finger is the first to be formed in ontogenesis. In birds, it is the finger on the posterior side of the hand, which also speaks for the ring finger. Since on the anterior side (thumb side) of the hand an embryonic finger begins to develop but quickly disappears, this would have to be digit I. There are also dinosaurs, such as *Limusaurus*, that partially reduced their thumbs and missed a pinky. These data argue for an identification of the fully formed bird fingers as the index, middle, and ring fingers (II-III-IV).

The conflicting finger counts in theropods were not resolved for a long time. Recent explanations of evolutionary developmental biology (Evo-Devo) have resolved this contradiction. What is the solution?

Only a handful of general signaling factors called morphogens orchestrate the embryonic development of organisms. These include proteins of the HOX, Wnt, Hedgehog, and TGF $\beta$  families as well as their ligands, such as the growth hormone BMP4. They influence the expression of hundreds of genes in a context-dependent manner. For instance, the signaling factor *Sonic Hedgehog* (Shh) plays a key role in hand development. Its gene is activated only on one side of the hand; Shh concentration is highest

on the posterior (pinky) side of the hand and decreases toward the anterior digits. Now Shh concentration controls gene expression patterns in the different finger primordia and thus determines their development. They gain positional information from Shh, so to speak, about where they are and how they are to develop.

On the basis of this morphogenetic mechanism, ČAPEK et al. (2014) proposed that gene regulatory changes initially led to the reduction of the pinky and the partial reduction of the ring finger. However, the thumb and pinky form last, and developmental constraints require the digit primordia that form last to be reduced first. Accordingly, the index, middle, and ring fingers are retained and utilize the available space by growing further inward.

This causes the biomechanically *anteriorly* displaced fingers (II-III-IV) to leave the original Shh activity zone and adopt the gene expression pattern of the anterior digits (I-II-III) under the influence of altered morphogen gradients. In other words, they obtain anterior digit phenotypes. This concerted mechanism explains why the fingers of theropods like *Deinonychus* have the shape of the inner digits (I-II-III). Moreover, it explains why the transcriptome of the foremost bird finger corresponds to that of the thumb of other animals.

In other words, there is strong evidence that a partial homeotic frameshift of digit identity occurred. Scientists call this scenario the *axis shift hypothesis*.

### C.6: The irreducibly complex avian body plan

In order to suggest that the evolution of bird flight is extremely improbable, JUNKER & WIDENMEYER (2021) claim that evolution would have had to pass through innumerable feature changes and subtleties in the construction of plumage, skeletal structure, behavior, etc. at the *same time* in order to achieve flight ability:

In addition to suitable feather material and functionally fine-tuned structure, suitable anchoring of the feathers in the skin is also indispensable, as is a complex network of feather musculature, nerve cords, and sensory organs for the motility of the feathers. In addition, a functional plumage must be formed overall, with diverse control mechanisms and coordination of flight movements, details of the bird's body structure, and sophisticated behavior with corresponding data processing in the brain. The tasks that flight feathers must perform place special demands on the construction... First, suitable construction material is required. This consists of long fibers of a special protein, beta-keratin... The keratin must be 'built' into the feather shaft, barbs, and barbules in a very specific way so that the feathers exhibit their special properties... (p. 84)

For these reasons, many researchers point to the aspect of synorganization. The individual modules and levels (from building material to behavior) cannot be understood in isolation from each other, nor can they have evolved separately. In sum, together with



the plumage, we are facing an overall organization that seems to be irreducibly complex with respect to flight ability and represents a clear indication for design. (p. 86)

It is one thing to list the features of a highly specialized locomotor system that *extant* birds use for perfect flapping flight. However, it is another thing to conclude that all of these features are indispensable for rudimentary flight and could not have evolved separately. The weak spot in such reasoning is that this conclusion is invalid.

Consider, for example, *Anchiornis* (compare the cover picture on the title page); this airworthy theropod already possessed some (but not all) of the features listed above. However, it still lacked numerous other components. For instance, the feathers largely consisted of  $\alpha$ -keratin (PAN et al. 2019). Hence, they did not have the “special properties” of modern feathers (like flexibility and buckling resistance). Their structure also differed significantly from the “functionally fine-tuned structure” of modern feathers. For instance, there is evidence for open-vened feathers (SAITTA et al. 2017, p. 276).

In addition, compared to modern birds, *Anchiornis* possessed much shorter wing feathers in relation to the length of the humerus. The feathers were symmetrical and poorly differentiated; both the primary feathers and the secondaries were narrow and weak (LONGRICH et al. 2012), and the covert feathers of *Anchiornis* were not arranged in tracts or rows (WANG et al. 2017). The longest wing feathers were those nearest the wrist, making the wing broadest in the middle and tapering near the tip for a more rounded, less flight-adapted profile (HU et al. 2009).

*In general, creationists overrate the role of feather material, fine-tuned feather structures, and plumage for flight capability.* Experiments and computer modeling revealed that the *proptagium* (Fig. 16) produces the majority of the lift; the removal of secondary feathers, leaving six distal primaries and an intact proptagium, did not noticeably affect flapping flight in house sparrows (BROWN & COGLEY 1996). Even with the removal of all flight feathers except for the distal six primaries, the loss of approximately 50% of the proptagium's projected area and its cambered profile did not render flight impossible! Additionally, for a gliding flight, “motility of the feathers” is dispensable; it is an optimization step, too (ALEXANDER 2015).

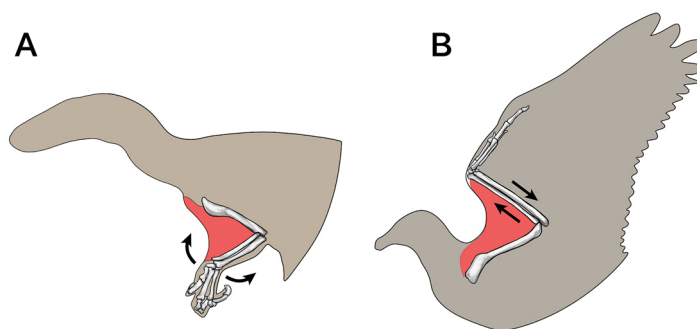
On the one hand, we can see that early flying theropods lacked or could have lacked quite a few of the properties listed above. All those “yet missing features” were subsequent, *successive* optimization steps of crown group birds. On the other hand, we can trace the evolutionary roots of countless features enabling birds to fly back to non-avian dinosaurs. Experts refer to favorable *exaptations*,<sup>12</sup> which, in retrospect, paved the way for the evolution of flight in the first place.

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<sup>12</sup> Contrary to *adaptation*, the word *exaptation* describes a trait whose function is accidentally adaptive at a given time without having been produced by selection “for” it.

To list a few examples (cf. BRUSATTE et al. 2015):

- ✚ The development of air-filled, hollow bones and a bird-like lung-air sac system began in the first Saurischia.
- ✚ The long legs and the three thin main toes typical of birds developed more than 230 million years before birds emerged. These were accompanied by the transformation of the quadruped “reptilian” body into upright-walking theropods.
- ✚ 100 million years before birds emerged, a rapid increase in metabolism and growth rates took place, as well as the development of the avian-typical air sacs and power lungs. These favorable exaptations had nothing to do with flight capability either. By means of those adaptations, birds manage their energy needs today.
- ✚ About 50 million years before the appearance of birds, the paired clavicles fused into a furcula (“wishbone”). Presumably, the wolf-sized raptors used them to stabilize the shoulder girdle when tearing apart their prey. In their flying descendants, the innovation helps to save energy when flapping.
- ✚ Most likely, maniraptorans such as *Deinonychus* possessed the propatagium before the origin of flight (UNO & HIRASAWA 2023). This structure contains a muscle connecting the shoulder with the wrist. Without this structure, birds could not fly; it gives the wing a leading edge, generates lift, and supports flapping. This was another favorable condition for the origin of flight (Fig. 16).<sup>13</sup>



**Fig. 16.** A: Propatagium (red) in *Deinonychus*, a predator. It is likely that this structure allowed for a more agile hunt. B: *Sapeornis*' wing membrane, showing the interlocking wing folding system of birds. Soft tissues are not preserved, but the elbow joint angles are good indicators for the presence or absence of the propatagium. Drawn by James Paul BAELO according to UNO & HIRASAWA (2023).

In short, the assertion that features or parts of the avian body plan could not have originated separately from each other is nonsensical. Theropod fossils can be put into a sequence in which the “irreducibly complex” “overall organization” of birds resolves in a series of stepwise trait additions. One does not find any bird that would

<sup>13</sup> Admittedly, there are a few publications advocating the unusual idea that *Deinonychus* and *Caudipteryx* were secondarily flightless birds and thus possessed volant ancestors (cf. FEDUCCIA 2020, p. 281). Currently, the fossil record does not support this assumption, and this idea requires too many unsupported prior assumptions to be scientifically respectable (QIU et al. 2019, p. 7; FOTH, pers. comm.). See also below in section C12.

differ fundamentally from dinosaurs but only graded similarities within Dinosauria.

These graded similarities indicate that the evolution of avian characteristics such as feathers and wings was initially not shaped by selection for aerodynamic properties. Rather, those structures evolved for other reasons like courtship display or brooding behavior (BRUSATTE 2017, p. 793). Thus, evolution did not care about the “irreducible complexity” of the (*not yet even existing!*) flying apparatus. Instead, one trait after another evolved in dinosaur lineages because they fit in the given, differing selective regimes. In this process, the prerequisites for a rudimentary flight emerged gradually, quite casually, without being intended or even foreseeable.

We can ask how the evolution of flight, coming as it did from non-avian theropods that had not yet crossed the threshold to flight, proceeded from this point. Doing so, we must keep in mind the exaptations already present (see above). Then the emerging picture is that of an “experimental field” combining a simple wing design with a jumping behavior for a rudimentary gliding flight (FOTH 2008).

According to FOTH (2008), already large, stiffened coverts or skin flaps can constitute a simple but functional wing construction. Sifaka lemurs on Madagascar demonstrate that it can be even simpler: long, thickened hairs on the arms and a small skin between the upper arm and the body slow down the fall when jumping from tree to tree and carry the primate up to ten meters wide (Fig. 17).



**Fig. 17.** Sifaka lemurs from Madagascar show the simplest adaptations to parachute flight in combination with jumping behavior. The arms are covered with long, stiffened hair, and there is a small flap of skin between the upper arm and the body, which increases the wing's surface area. When jumping, the Sifakas stretch out their arms and legs. Therefore, they can glide more than ten meters thanks to the enlarged “wing.” Source: © Andrey GUDKOV | Depositphotos.com.

As shown above, non-avian theropods had exaptations that were more favorable for gliding. Biomechanical studies also show that flightless representatives with pennaceous feathers can also generate dynamic lift from the ground (HEERS 2016). In this way, they were able to get over obstacles by gliding or flapping over short distances. In addition, the buoyancy allows for faster, more agile, and energy-efficient running. Over time, body size, leg-wing coordination, muscle capacity, wing length, and behavior can thus have been successively adapted to the requirements of ever more enduring flight (HEERS et al. 2018).

So far, it is an open question whether bird flight evolved from the ground up or from trees down. However, this may be a false dichotomy. At first sight, energetic considerations seemed to speak against the ground-up theory: *Archaeopteryx* would have had to run three times as fast as modern birds for liftoff. However, recent biophysical calculations show that updrafts on mountainsides or cliffs could carry small-feathered paravians from the ground up into the trees (SHAHID et al. 2019).

According to the authors, the meteorological aspect eliminates the existing problems of both scenarios and makes the virtual contradictions between *ground-up* (cursorial theory) and *trees-down* (arboreal theory) disappear: depending on wind conditions, paravians glided both upward and downward and required neither climbing aids nor distinctive running or pronounced flying muscles.

### C.7: Gliding versus flapping flight: another false dichotomy

Creationists often attempt to problematize the evolution of active flight (flapping flight) from gliding by postulating insurmountable hurdles for this transition (e.g., JUNKER 2018). JUNKER says that the “problems of the emergence of bird flight from trees” are “so numerous and severe that this path seems evolutionarily infeasible.” The reasons he gives are essentially the following:

“A transition from gliding to flapping flight is complicated and laborious because these two types of flight are very different (Padian 1982, p. 11). Gliders have comparatively few changes in their body plan apart from the possession of flight skins, whereas all active flyers are highly modified in skeletal structure and physiology.”

“There is no evidence that any group of gliding animals... is or ever has been on the path to active flight (Padian 1982, p. 12; Caple et al. 1983, 475; Paul 2002, p. 117) or that any glider would use its limbs to actively achieve forward or upward thrust (Dial et al. 2008, p. 988).”

“Selection conditions for gliders and active flyers are partly contrary to each other. A glider needs large wings—as large as possible and right from the start. The best way to get there is to stretch out all the extremities, as today's gliders do. 'In birds, however, there is nothing to indicate that their legs ever played a major role as part of the wing' (Peters 2002, p. 425).”

“Already, gliding flight is not 'gratuitous' but requires control mechanisms; this is true even for poor gliders. The selection pressure for control and stabilization in a gliding 'proto-bird' must have been high (Norberg 1985, pp. 305 ff.).”

At first, it is noticeable that JUNKER mainly uses quite old sources to underline his unusual opinions. Why? Obviously, because biomechanical studies that are more contemporary demonstrate that there is a functional continuum with gradual adaptations between gliding and elaborate flapping flight.

For example, ALEXANDER (2015, p. 55) notes under the text section *Gliding flight versus flapping flight: false dichotomy*:

Some scientists have argued that weak or poorly developed flapping would be so ineffective that it would provide no benefit to gliding animals (or might even be less effective than gliding), so gliding could not have led directly to flapping.

In fact, both theoretical modeling and experiments using flapping robots show that even low-amplitude, weak flapping can produce enough thrust to be useful, even when such flapping is too weak to maintain level flight. These results mean that we must think of gliding versus fully powered flight—flapping flight as used by living birds, bats, and insects—as two extremes on a continuum. Between these extremes, animals could use flapping with a range of effectiveness, from weak flapping to slightly extend a glide to stronger flapping that might increase glide distance by five- or tenfold.

Thus, the assertion that selection conditions for gliders and active flyers are partly contrary to each other is simply obsolete. Moreover, the “highly modified” physiology of active flyers is a gradual optimization of already existing skeletal and feather structures. *Archaeopteryx*, for instance, did not yet possess a sternal keel, where the powerful muscles for flapping flight attach in birds. In addition, the rigid shoulder girdle did not permit a persistent flapping flight. Nevertheless, there is evidence that it was no longer a pure glider but flew actively at times (VOETEN et al. 2018).

Thus, the claim that there is “no evidence that any group of gliding animals... is or ever has been on the path to active flight” is false. *Archaeopteryx* simply is to be located at a different place in the continuum between primitive gliding and ultimate flapping flight than modern birds. *Anchiornis* possessed a lower flapping flight potential than *Archaeopteryx* (PITTMAN et al. 2022a, p. 9), and *Eosinopteryx*, *Aurornis*, and *Xiaotingia* had an even lower one.

That “Mesozoic birds whose flight consisted mainly in gliding and soaring” are “not known” is at best an argument from ignorance but not an objection: just replacing “Mesozoic birds” by “basal Avialae” like *Aurornis* and *Xiaotingia*, which lived between 152 and 166 million years ago, turns this statement invalid.

Even stranger is the often-heard argument that even gliding flight requires sophisticated control mechanisms (see also JUNKER 2018). It implies that evolution had to consider every nuance of motor skills. However, this view underestimates the plasticity and learning curves of neuronal systems. Dromaeosaurids like *Velociraptor* were intelligent hunters that followed group strategies to outsmart their prey. Are we to believe that such animals were too stupid to learn how to balance their extremities for gliding? No control behavior needs to be perfect, and even nowadays, every young bird must first... yes! *learn it!* Even humans can easily learn how to operate a hang glider, and we surely are not made for flying.



Additionally, we must expect primitive flyers, such as *Archaeopteryx*, to be inherently stable (“stability configured”), whereas the highly maneuverable, inherently unstable (“control configured”) systems of crown group birds are more derived (less primitive) (MAYNARD SMITH 1952; ALEXANDER 2015). In other words, there is a trade-off between built-in stability and high maneuverability; the active stabilizing mechanisms required in modern birds’ nervous systems represent potent *specializations*, not plesiomorphies.

Interestingly, even many wingless arboreal animals without any aerodynamical adaptation, such as certain ants, are gliders or parachuters in its most rudimentary form (ALEXANDER 2015). They produce some lift, have orientation about their position, and can reliably adjust their descent during a fall. In a nutshell:

If many arboreal animals have this ability, as now seems likely, and if some of those animals experienced selection pressure to extend falls into glides, they would have a head start in evolving more effective gliding. Ironically, biologists have long considered the evolution of flight control ability to be one of the major hurdles to be overcome during the evolution of flight, but this ‘hurdle’ may already be behind many arboreal animals (ALEXANDER 2015, p. 50).



**Fig. 18.** No exception: the crash landing of an albatross (right). So much for the claim that a “landing must work from the beginning”! Source: ROYAL ALBATROSS CAM.

It is completely unclear what JUNKER wants to say with the following: “Landing must work from the beginning.” As if a botched landing were impossible! Let us think of the albatrosses, which fly with perfection but whose takeoff and landing are associated with considerable problems (Fig. 18). If it were up to JUNKER, these species would have become extinct long ago.

### C.8: Open questions about the mechanisms of evolution

[T]he question of evolutionary remodeling... [is] not answered. The presence of putative intermediates is not evidence of a sufficiently probable mechanism. For these reasons, it is essentially unresolved *how* airworthy feathers could have evolved solely by future-blind variations, selection, and other completely natural processes—and therefore, of course, *whether* they could have evolved. (JUNKER & WIDENMEYER 2021, p. 91)

The answer to the question of *whether* feathered birds are a product of evolutionary history is logically independent of the knowledge of the evolutionary *mechanisms* (the answer to the question of *how* they evolved). In analogous cases, this is indisputable: The

effectiveness of drugs is provable without knowing their mechanisms of action. The glacial theory had gained general acceptance by the end of the 19th century, even though by that time scientists knew nothing about the causes of glaciation (EHLERS 2011). Marine fossils attest to the process of mountain folding even without knowledge of the tectonic forces responsible for it (Fig. 19). The Big Bang is well confirmed, although its cause is unclear. One could extend this list of examples endlessly.

The very fossil record corroborates that birds are the product of a historical evolutionary process,<sup>14</sup> without requiring knowledge of the molecular genetic details or selection regimes of this transformation. This is even more convincing since descent, heritable variability, and speciation are *observable facts*. Therefore, even

...if we knew nothing at all about the causes, the fact of evolution would remain untouched. (REMANE et al. 1973, p. 11)



**Fig. 19.** Left: fossil ripple marks in the Bavarian Hass Mountains. Right: recent ripple marks on the beach of Borkum, North Sea. If such structures are found in mountains, often with embedded fossils of former sea dwellers, strong evidence is provided that the sea floor was uplifted thousands of meters. The evidence for mountain folding is logically independent of whether we know the forces in the Earth's mantle, the drift of the individual continental plates, etc. Left image: Author: R. KIRCHNER | Title: 'Fossile Rippelmarken' | Source: [Mineralienatlas.de](http://Mineralienatlas.de) | License: [CC BY-NC-SA 3.0](https://creativecommons.org/licenses/by-nc-sa/3.0/). Right image: Author: Amanda77 | Title: 'Strömungsrippel im Wattenmeer von Borkum bei Niedrigwasser' | Source: [Wikipedia, Rippel](https://de.wikipedia.org/wiki/Rippel) | License: [CC BY-SA 3.0](https://creativecommons.org/licenses/by-sa/3.0/). Image curtailed.

However, one point is correct: variation and selection *alone* do not provide a *sufficient* explanation for the origin of the flight apparatus of birds. This has a simple practical reason: variation and selection are *general* mechanisms. They explain evolution on a *principled* level. To explain something as *specific* as the flight apparatus of birds, evolutionary biologists must develop a specific model based on the general theory (MAHNER & BUNGE 1997, pp. 95 ff.).

Ideally, such a model would show step-by-step how mutations and developmental biological mechanisms reshaped the plesiomorphic

dinosaurian features into derived avian features under real historical conditions. In this context, it would be particularly interesting to elucidate how, in this remodeling process,

<sup>14</sup> Incidentally, the claim that fossil interpretation is "ambiguous," i.e., also open to transcendental interpretations like intelligent design, is not a reasonable objection. Transcendent things can be used for the "explanation" of everything without being testable (or, more limitedly, falsifiable). Even perfectly natural evolution can be (and is!) easily interpreted as a result of design (cf. BEHE 2008, p. 166). Such *omniexplanatory* "power," as philosophers of science call it, puts Intelligent Design outside any scientific realm (cf. MAHNER & BUNGE 1997, p. 108).

the functionality of each individual step was maintained. In short, we would need to substantiate the general theory of evolution with additional knowledge about the structural, functional, and developmental details of the species in question. In addition, the model would need to include data on historical conditions, such as Jurassic selection regimes.

The problem is that we do not have complete knowledge of all those details and we never will. We can reconstruct it only fragmentarily and hypothetically. In addition, we deal with highly diverse, individual, and complex biosystems:

It is precisely the boundary conditions, such as ecological interactions, other historical circumstances, and coincidences of all kinds, which are not only different in each individual case but also unique and consequently constitutive of the biological system under consideration... (MAHNER 1986, p. 42)

This does not preclude working with highly plausible scenarios that contain well-known developmental mechanisms (we discussed a few examples in text section C.5). However, we never know for *sure* whether these mechanisms played a role in the past. Moreover, it is easy for evolution deniers to add an endless number of unanswered questions: Which *individual mutations* triggered the developmental change? Through what adaptive intermediate steps did the gene regulatory network that created the conditions for it emerge? Where did the genes come from? Which selection pressure caused the phylogenetic change? How and why did selection regimes change? And so on.

Again, we do know in some detail which mechanisms are involved in the assembly and differentiation of gene regulatory networks.<sup>15</sup> However, analysis of individual networks is difficult, especially the reconstruction of preceding differentiation steps, since the genomes of extinct animals are decomposed and lost. Therefore, we see that doubtlessly confirmed and sufficiently detailed explanations will never be achievable. We will never get a *complete* explanation of any complex natural process, considering all its interdependencies and boundary conditions. That would be illusory!

Still, creationists believe they have an argument against the plausibility of evolutionary models by arguing this way. Thereby, they overlook the fact that practical problems in gaining knowledge do not indicate a defect in the theory of evolution. Moreover, even if the models in question contain only *parts* of the relevant mechanisms, they still provide the basis for more complete explanations. *Without* this basis, *no* explanation is possible; *with* it, at least *plausible partial explanations* exist. Plausible means that all premises and mechanisms are empirically well-founded and harmonize with background knowledge.

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<sup>15</sup> For those interested in this topic, METTERNICH (2021) is well worth reading.

**In short:** Martin MAHNER, a philosopher of science, notes the following: “What we are able to achieve in historical contexts as mechanistic explanations, we could call *mechanistic evolutionary scenarios*” (pers. comm.). Thus, plausible hypothetical explanations are sufficient because they are just what we can reach.

Incidentally, it is not only in *historical* reconstructions that we must deal with simplified, hypothetical explanations. Models for describing complex developments in the present, such as climate change, also contain quite a few idealized assumptions (VOLLMER 2000, p. 210). Premises very often do not match reality completely. Think of ideal gases and ideal populations. Although they do not exist, they are the basis for more realistic models.

Natural processes are processes within complex systems. In most cases, one can resolve and explain only single aspects or interactions and obtain only restricted knowledge on boundary conditions. This is due to the complexity of nature and, hence, a problem inherent to the scientific analysis of complex systems. Creationists misapply this fact as a reason to refuse macro-evolutionary explanations. Consequently, they would have to reject almost *all* models in *all* natural sciences for the same reason—and especially their highly speculative “intelligent design approach.”

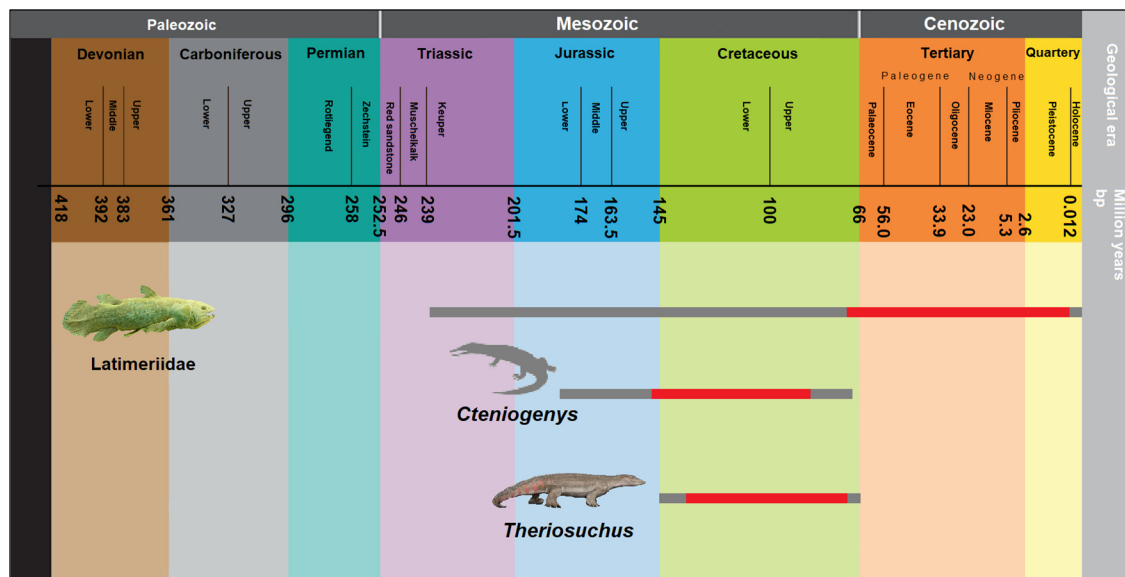
### C.9: Ghost lineages in the fossil record

Ghost lineages are ancestral lineages of species that have left no fossil evidence for some time during their existence but can be inferred to have existed because of the fossil record before and thereafter. JUNKER (2019) argues that ghost lineages pose a severe theoretical problem when they extend over long periods. In his opinion, evolutionary theory can only provide problematic *ad hoc* explanations:

It must be assumed under evolutionary theoretical premises that many lineages have left no fossils during 20–30 and possibly even more million years of their assumed existence, while fossil remains have survived from other lineages from comparable geological strata. Such a situation is problematic in evolutionary theory and in a long-term framework. (p. 65)

However, many taxa demonstrate that ghost lineages are real at this duration. Among them is the coelacanth subdivision of marine Latimeriidae (Fig. 20). Fossil genera are known from the Mesozoic, dating back to the Triassic, but disappeared from the fossil record at the end of the Cretaceous (FOREY 1998). Throughout the Cenozoic, coelacanths were no longer present in strata and were thought to be extinct. Since 1938, however, we have known that latimeriid coelacanths still populate the seas (VENTER et al. 2000). Thus, we are dealing with a ghost lineage that lasted 70 million years.





**Fig. 20.** Ghost lineages (shown as red lines) of some selected taxa whose transmission in the fossil record (grey) starts again tens of millions of years later. This shows that, contrary to JUNKER, they are not inventions. These and further examples are available at [https://en.wikipedia.org/wiki/Ghost\\_lineage](https://en.wikipedia.org/wiki/Ghost_lineage).

The ghost lineage of the atoposaurid genus *Theriosuchus* from the Late Jurassic turned out to be similarly long. The fossil record of this crocodylomorph broke off about 135 million years ago and did not resume until the uppermost Cretaceous deposits. The duration of this ghost lineage ranges between 55 and 75 million years (CSIKI et al. 2011).

**In short:** One must keep in mind that successful fossilization is extremely rare, and the rediscovery of a fossil is a fortunate coincidence. Hence, it is not a surprise that quite a few taxa remain undiscovered for time spans of various lengths.

Incidentally, one can also ask for a satisfactory explanation for ghost lineages in a creationist scenario. Why is there a gap in the fossil record? Did God create those taxa twice? Alternatively, did God prevent the fossilization of some selected taxa for a given time span in distinct geological strata?

### C.10: The “discrepancy” between stratigraphy and phylogeny

Creationists often argue that the succession of species and taxa in the fossil record is not in accordance with a phylogenetic scenario. Here, we present some examples:

Most theropod genera that have bird-like features are geologically younger than the geologically oldest birds. (JUNKER 2019)

*Cruralispennia* occupies a derived position among the opposite birds [Enantiornithes] and is not interpretable as a transitional form. Moreover, this genus is among the oldest birds after *Archaeopteryx*, [which means there is] a 'stratigraphic-phylogenetic discrepancy' (Wang et al. 2017). (JUNKER 2019, p. 52)

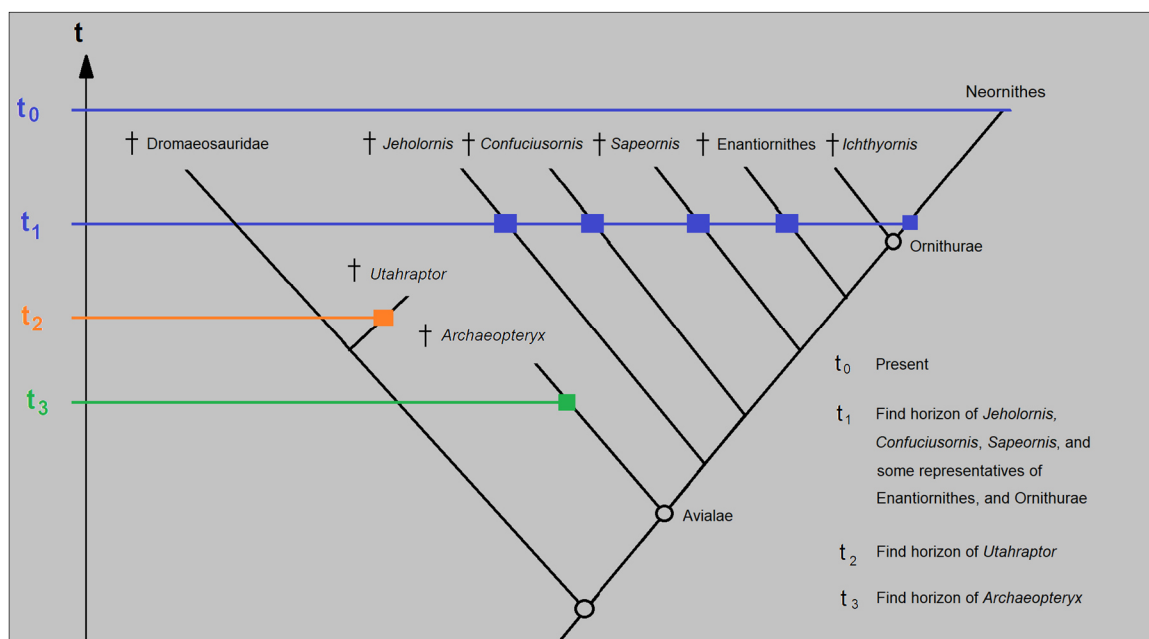


Both Enantiornithes and Ornithurae appear relatively abruptly in the fossil succession in great diversity, temporally common with forms such as *Confuciusornis*, *Jeholornis*, and *Sapeornis*, which are classified as more primitive. (JUNKER 2019, p. 65)

The dromaeosaurids, in turn, are placed in a broader ancestral context with birds (although they have been found in much younger strata than forms with true, flat, flight feathers). (JUNKER 2022)

The content of these statements is correct, but they are not suitable as an *objection* against evolution. As Fig. 21 shows, from an evolutionary perspective, taxonomists can insert all these mosaic forms into a phylogenetic scheme without any difficulty.

From a cladistic point of view, the explanation for that “stratigraphic-phylogenetic discrepancy” is simple: when more advanced avian features evolved in some evolutionary lineages (like Enantiornithes), dinosaurs displaying more primitive features (like *Sapeornis* but also *Dromaeosaurus*) did not automatically die out. Why should they? These differently evolved theropods coexisted for a very long time.<sup>16</sup> Many basal non-avian dinosaurs even evolved much later than some proto-birds. For instance, when *Utahraptor* appeared, *Archaeopteryx* was already extinct (Fig. 21). At the same time, the first opposite birds (Enantiornithes) evolved. Why not? Whoever interprets all this as problematic for the theory of evolution has not understood the basics of evolution.



**Fig. 21.** Simplified phylogenetic tree of birds (Avialae) with corresponding geological strata of different fossils (blue, orange, and green horizontal lines). The extinct bird species *Jeholornis*, *Confuciusornis*, and *Sapeornis* are older and more primitive than the extinct Enantiornithes and the oldest representatives of Ornithurae. Nevertheless, they all coexisted over a long period, so it is not surprising that we know corresponding fossils from the same time horizon (t<sub>1</sub>). The dromaeosaurids, in turn, are more primitive than birds. However, some dromaeosaurids, such as *Utahraptor*, evolved later, so they are found in younger strata (t<sub>2</sub>) than, for instance, *Archaeopteryx* (t<sub>3</sub>). Own drawing.

<sup>16</sup> Finally, “fish” still exist today, some of which belonged to the stem group of tetrapods, the ancestral lineage of all land vertebrates, 380 million years ago.

NORELL (1992) is right in emphasizing that it is the phylogenetic relationships of groups, not their stratigraphic relations, that matters. Pliocene whales, as an example, are not more closely related to Pliocene hippos than they are to modern whales.

Moreover, there are only a few rich fossil deposits in the world, which allow some sparse insights into the lives of Jurassic-Cretaceous theropods. Among these are the 150-million-year-old Solnhofen limestones from the Franconian Alb in Bavaria, where paleontologists found all (!) *Archaeopteryx* specimens. Since the layers of the former lagoon system formed within a few millions of years, they provide only spot checks. Thus, we cannot expect fossils to be representative of the duration of their existence in geological strata. The apparent patterns of fossil diversity

...are heavily distorted by uneven sampling intensity through time from geological biases that affect the temporal distribution of fossils and formations, differing preservation potential across organisms and environments, and heterogeneity in collection practice, reporting and even geopolitics. Therefore, the known fossil record is not only an incomplete sample of the total fossil record..., but that incompleteness is also inconsistent through time and across space. (FLANNERY-SUTHERLAND et al. 2022)

Nevertheless, “the succession of fossils in time does not correspond to a random sequence with respect to their morphological change” (MAHNER 1986, p. 61). With the decreasing age of the layers, we find more and more bird-like theropods.

The following two objections do not come from a creationist. Nevertheless, we must mention them because they stem from the well-known paleornithologist Professor Alan FEDUCCIA, whose arguments creationists employ for their argumentation.

### C.11: Does DOLLO's “law” argue against theropod ancestry?

Theropod dinosaurs (still lacking any meaningful morphological definition) are generally characterized by forelimbs approximately half the length of the hind limbs. If birds and flight arose from theropods, therefore, it would appear extremely unlikely for the forelimbs to elongate into avian wings. This statement relates to the generally accepted Dollo's Law (or Rule), which deals with the improbability of reversibility of a once lost or reduced part of the anatomy. S.J. Gould suggested that irreversibility forecloses certain evolutionary pathways once broad forms have emerged: '[For example], once you adopt the ordinary body plan of a reptile, hundreds of options are forever closed, and future possibilities must unfold within the limits of inherited design.'

In other words, re-elongating once greatly reduced forelimbs of dinosaurs makes it extremely unlikely that they could re-evolve elongated wings. This is exactly what we see in flightless birds, where there is no example of any of the flightless lineages re-elongating forelimbs and developing flight wings.

(A. FEDUCCIA, email of 12/30/2021 to MN. Reprinted with permission.)

We asked paleontologist Professor Oliver RAUHUT, a specialist in predatory dinosaurs (theropods), what he thinks of FEDUCCIA's argument. In the following selected parts of his answer:

FEDUCCIA's statement is problematic in so many ways that it is almost difficult to argue against it...

- 'Theropod dinosaurs (still lacking any meaningful morphological definition)...

Theropoda is a subgroup of dinosaurs recognized since the 1880s. It has been defined umpteen times on the basis of apomorphic features, including more recently by GAUTHIER (1986), OSMÓLSKA (1990), SERENO (1999), myself (RAUHUT 2003), HOLTZ & OSMÓLSKA (2004), NESBITT et al. (2009), CAU (2018), and many more. For a just-published discussion of the features that separate the various dinosaur groups at the base, see NOVAS et al. (2021, <https://doi.org/10.1016/j.jsames.2021.103341>).

However, I fear (from other writings of his) that FEDUCCIA means a *typological* characterization, which has no meaning in an evolutionary context and thus has been increasingly abandoned by most biologists over the last 50 years.

- '...are generally characterized by forelimbs approximately half the length of the hind limbs.'

This genuine typological statement dates from 80 years ago. Theropods show a very wide variation in the length of the forelimbs compared to the hind limbs, so this statement is simply wrong. There are animals with strongly reduced forelimbs, such as abelisaurids or alvarezsaurids, but also theropods with much longer arms, such as dromaeosaurids. [Quite a few early coelurosaurs, such as *Guanlong*, a progenitor of *Tyrannosaurus rex*, had relatively long arms as well; the authors].

- 'If birds and flight arose from theropods, therefore, it would appear extremely unlikely for the forelimbs to elongate into avian wings.'

I do not know any reason why forelimbs should not be able to elongate evolutionarily. Studies of contemporary animals have shown that exactly such proportions can be extremely variable and can often even change over a few generations (no matter in which direction) when a new habitat is conquered.

- 'This statement relates to the generally accepted Dollo's Law (or Rule), which deals with the improbability of reversibility of a once lost or reduced part of the anatomy.'

Several remarks on this. First, DOLLO's law targets structures that are either *completely rudimentary* (i.e., practically useless) or *completely reduced*, such as the legs of snakes. This is not the case with the arms of theropods; most theropods have relatively short but fully functional arms that were presumably used for a variety of functions. Moreover, no one has claimed that birds descended from abelisaurids.

On the other hand, DOLLO's 'law' has proved to be an often-observed rule, but it is not incontrovertible, as numerous atavisms show. Just modern genetics (of which DOLLO,

of course, could not know anything) has shown that the genetic 'programs' for many reduced or lost organs are often still present but are not called up any more. There is, however, no reason why such a thing might not sometimes be reversed (experimentally, for instance, it is possible to trigger the formation of dentition in present-day birds by adding certain hormones at a certain embryonic stage, although birds have been toothless for at least 80 million years).

- 'S.J. Gould suggested that irreversibility forecloses certain evolutionary pathways once broad forms have emerged: '[For example], once you adopt the ordinary body plan of a reptile, hundreds of options are forever closed, and future possibilities must unfold within the limits of inherited design.'

This is the school of thought of construction morphology, which was very popular in the 1960s and 1970s. There is certainly something to it: of course, evolution must always take place within the framework of physical, chemical, and genetic possibilities. Nevertheless, the statement in this form is problematic. First, what is a "reptile"? The definition of reptiles still in use until the 1990s was typological, which, as stated above, has no meaning in an evolutionary context. If I define my groups of organisms in a very narrow framework and then claim that there is no way out of this framework, then this makes evolution impossible. This quotation then also raises the question: does FEDUCCIA thus believe that birds are not descended from "reptiles" at all? Where do they come from, then?

- 'In other words, re-elongating once greatly reduced forelimbs of dinosaurs makes it extremely unlikely that they could re-evolve elongated wings.'

This is, if I may say so, nonsense based on the points made above. The forelimbs are neither 'greatly reduced' (at least not in a form that is not also the case in numerous other reptile groups), and there is no reason at all why the proportions of a functional arm cannot evolve in whatever direction under changed selection conditions.

- 'This is exactly what we see in flightless birds, where there is no example of any of the flightless lineages re-elongating forelimbs and developing flight wings.'

Perhaps, but that is an argument from ignorance. The fossil record of birds is so incomplete that I would not rule out the possibility that at some point there were flightless birds that extended their arms again (especially our modern ratites, which have an extremely poor fossil record). However, even that argument is irrelevant in the context of the origin of birds. Flightless birds descend from airworthy birds. Of course, they have the same arm and hand configuration that constitutes volant birds, and almost nowhere is the modification of anatomy in adaptation to flight as severe as in the arms. That is, modifying these extremely specialized arms again for other uses is evolutionarily difficult but not impossible, as shown, for instance, by penguins. Here, it would be interesting to see if there were not extensions of the originally reduced arms in certain evolutionary lineages of penguins.

(O. RAUHUT, e-mail of 12/30/2021 to MN. Reprinted with permission.)

## C.12: FEDUCCIA's typological classification of the species *Scansoriopteryx*

Some years ago, news broke that the feathered glider *Scansoriopteryx* had overturned the “doctrine” on the origin of birds. CZERKAS & FEDUCCIA (2014) hold this view because of the unusual skeletal anatomy of the pigeon-sized, 120- to 170-million-year-old “climbing winged creature,” which is presumably identical to *Epidendrosaurus* (Fig. 22). This maniraptoran spent much of its life in trees, possibly climbing up the trunks.



Fig. 22 Life restoration of *Epidendrosaurus*  
 Source: Wikipedia | Author: Matthew Martyniuk | License: CC BY 3.0

The authors note that certain traits, such as the anteriorly directed pubis (hipbone), its short length and proportions, the large ischium, the widely spaced ilia, and the greater relative total arm length, are all atypical for theropods. In addition, scansoriopterygids lacked a fully perforated hip socket (acetabulum):

A fully perforated acetabulum is a sine qua non for dinosaurian status associated with major changes in posture and gait, by which a more upright posture and parasagittal stance is attained. (CZERKAS & FEDUCCIA 2014, p. 846)

The authors take the mosaic of primitive skeletal traits and advanced avian characters as a starting point for a bold interpretation. They claim that *Scansoriopteryx* lacks “the salient characters necessary to be regarded as dinosaurs.” Furthermore, they postulate that birds evolved from basal avemetatarsal non-dinosaur archosaurs, such as *Scleromochlus* (Fig. 23).

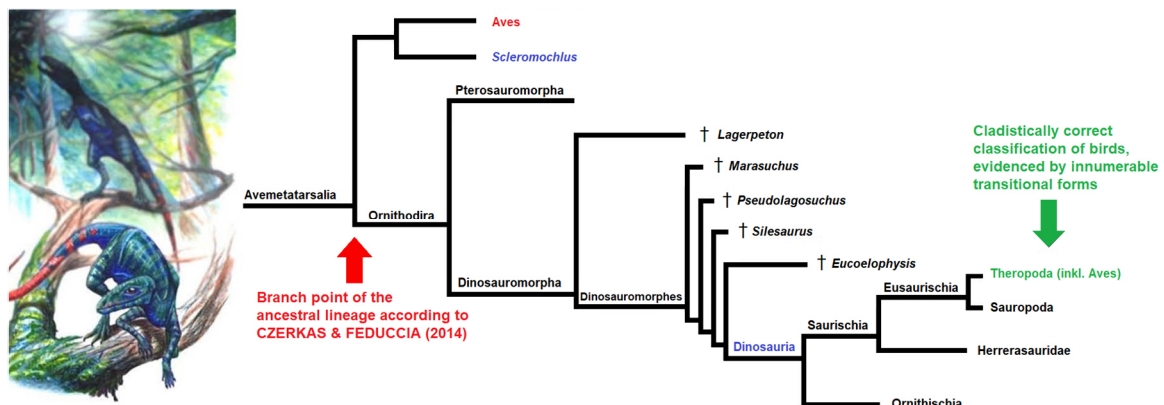
Moreover, they reinterpret the basal, still flightless, maniraptorans as *secondarily* flightless birds derived after *Scansoriopteryx* (cf. CZERKAS & FEDUCCIA 2014, p. 850), ignoring all cladistic work that unanimously identify maniraptorans as non-avian theropod dinosaurs on the basis of their synapomorphies.

When faced with the strong divergence between this odd ancestry hypothesis and the generally accepted bird phylogeny, laypeople may get the impression of complete arbitrariness and inconsistency in the reconstruction of evolutionary relationships. However, this impression is deceptive, which brings us to the reasons why an overwhelming majority of experts does not attach evolutionary significance to the authors' classification.

As RAUHUT has indicated above, the main problem is that CZERKAS & FEDUCCIA (henceforth referred to as C&F) do not refer to the *regular* Dinosauria clade, which is



consistently defined by derived traits. Instead, they choose the *traditional* but obsolete *typological category* of “dinosaurs,” which refers to an ideal-typical body plan. This approach focuses on a few “key features,” while at the same time neglecting the range of variation within the respective taxon. Real species deviate more or less from any typological scheme. Many species fall completely out of those categories, which are defined by some rigid group characteristics.



**Fig. 23.** Left: a drawing of the non-dinosaur archosaur *Scleromochlus*, quite closely related to the last common ancestor of crocodylians and birds. Right: phylogenetic tree of Avemetatarsalia showing the basal genus *Scleromochlus* and the highly diverse group of dinosaurs (including theropods) nested deep within Avemetatarsalia. Contrary to the orthodox view, CZERKAS & FEDUCCIA (2014) place birds next to *Scleromochlus* at the base of Avemetatarsalia. According to this view, the ancestral lineage of birds would have split off very early from all other archosaurs (red arrow). Thus, birds would only be distantly related to dinosaurs. A large part of the bird characters would have developed *convergently* within the dinosaur lineage. Green arrow: well-established cladistic placement of birds within Dinosauria, which is also supported by innumerable transitional forms. Artwork by Wikipedia | Author: Pavel.Ruha.CB | License: CC BY-SA 3.0. Phylogenetic tree: own drawing.

We recognize such a typological view, e.g., in C&F's assertion that only “reptiles” with a fully perforated acetabulum should be regarded as dinosaurs. The same applies to the assertion that individual traits such as “short, anteriorly directed pubic bones” or the absence of a “supra-acetabular crest” are “unequivocally non-dinosaurian” (p. 849). Due to a lack of such alleged key features, they detach *Scansoriopteryx* as well as the other maniraptorans from Theropoda. Instead, they assign *Scansoriopteryx* to primitive avemetatarsals like *Marasuchus* just because it *superficially* looks more like them with respect to a few *individual features*.

**In short:** C&F tear apart the solidly established descent community of Theropoda by focusing only on a few “key features” of a typologically defined dinosaur body plan rather than neatly using all derived characters for classification.

Ernst MAYR also advocated such a typology with his “evolutionary” classification system. However, such a classification scheme may have strange consequences, as MAHNER & BUNGE (1997, p. 250) have noted:

...cousins can be more closely related than sisters if the former are more similar to each other than the two sisters.

The considerable subjectivity of such typological considerations is the reason why, in fact, all contemporary biologists unanimously reject them. If C&F applied *phylogenetic systematics*, the supposed essential differences between *Scansoriopteryx* and dinosaurs would appear only in the form of graded similarities, between which quite a few theropods mediate. As thorough feature analyses have shown, *Scansoriopteryx*, like all maniraptorans, belongs to Coelurosauria and, consequently, to Dinosauria:

Pennaraptorans are a clade of vaned feathered coelurosaurian dinosaurs that are comprised of the Oviraptorosauria, Scansoriopterygidae, Dromaeosauridae, Troodontidae, and Avialae... They include the only dinosaurs to have evolved flight and the only ones to have persisted to the present day. (PITTMAN & XU 2020, p. 38)

C&F not only tear apart the Theropoda clade but also create an enormous gap between basal archosaurs and birds (cf. PADIAN & HORNER 2002, p. 121). The artificially created gap between Triassic archosaurs like *Scleromochlus* and bird-like forms like *Scansoriopteryx* would have to be bridged by corresponding transitional forms now. However, scientists found not even one such form among the basal Avemetatarsalia because they appear only in the highly diversified dinosaur lineage. The early maniraptorans cannot close this gap either, because C&F reinterpret them as *secondarily* flightless birds, regardless of their numerous plesiomorphic features! Phylogenetically, C&F's relationship hypothesis is thus extremely implausible.

Fatally, the phylogenetic tree favored by C&F would require a maximum of convergently developed traits: all features that evolved within Ornithodira (Fig. 23) and that are present in both non-avian dinosaurs *and* birds would have to have evolved in *parallel*. Parallelisms are always to be expected in *closely* (!) related groups, like Maniraptora (see section C.1). The assumption, however, that dozens, if not hundreds, of anatomical details arose in parallel at the base of the Avemetatarsalia phylum as well as in the phylogenetically distant dinosaur group is completely implausible. Therefore, an even more primitive archosaur in the lineage of Avesuchia, from which crocodiles descended, should have had the developmental genetic potential for such far-reaching parallel developments. Such a scenario is not compatible with our knowledge of developmental biology.

Keep in mind that we are *not* talking about the convergent emergence of superficially similar structures easily explained by functional similarity and adaptation to the same habitats. Such *analogous* features would be, for example, the wings of pterosaurs and the wings of birds. Rather, we are talking about detailed correspondences of hierarchically organized, highly derived feature *complexes*. Countless features of birds

can be traced in graded similarity back to early maniraptorans, coelurosaurs, theropods, and dinosaurs. These include dozens of details in the fine structure of the skeleton (CAU 2018, pp. 5–9), as well as the air sac system, the thin-walled, air-filled hollow bones connected to the air sacs, the long legs with three thin main toes, the ultrastructures of the feathers and feathery integuments, and many, many more.

As pointed out, there are graded similarities within Sauropsida and therefore between birds and other theropods as well. C&F dissolve this pattern of shared apomorphic characters (synapomorphies) into arbitrarily constructed convergences. Hence, it is unclear why they seek the last common ancestral species of birds and non-avian theropods precisely among archosaurs, of all things. They could just as easily seek them among basal parareptiles or synapsids and postulate even more far-reaching convergences.

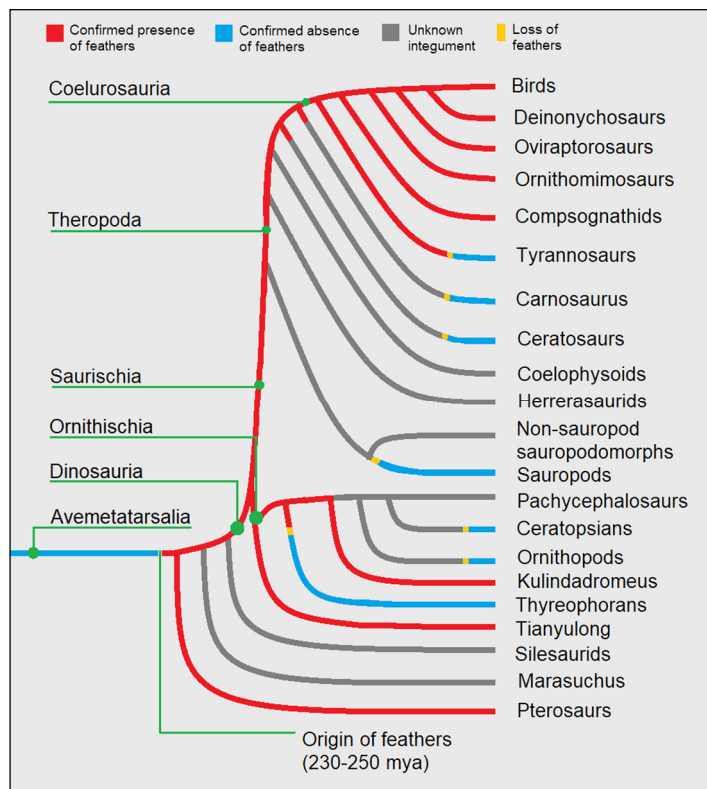
Since they apparently do not accept consistent patterns of graded similarities as good evidence for phylogenetic relationships, the question arises why they assume evolution at all.

### C.13: On the convergence of feathery integuments in pterosaurs

Let us turn back to the evolution of feathers. JUNKER (2022) points out that the interesting feather intermediate form of type 3a (Figs. 1 and 3) has been discovered in pterosaurs, which are evolutionarily more distantly related to birds. In his opinion, that questions the interpretation of type 3a as precursors of “true feathers”:

On the basis of the distribution of type 3b ‘feathers’ [this corresponds to type 3a above] on the body, one would have to assume—as also noted by Cincotta et al.—a convergent origin in pterosaurs and dromaeosaurids. Thus, even if one argues evolutionarily, just the interesting stage 3b (resembling the integument structures of *Tupandactylus*) could not be interpreted as a precursor of true feathers.

First, the presence of feathery appendages in pterosaurs has been known for many years (YANG et al. 2018; FOTH et al. 2020). Moreover, this finding entails no evolutionary problem at all. Since pterosaurs and dinosaurs are sister groups within Avemetatarsalia, it is convincing that the formation of feathery skin appendages had already been present in the developmental possibilities of their last common ancestor some 230–250 million years ago (YANG et al. 2018; Fig. 24).



**Fig. 24.** Evolutionary relationships in Avemetatarsalia, which contains pterosaurs and dinosaurs as close relatives. The diagram illustrates the single origin of feathers (better say: proto-feathers) in a common ancestor of both groups some 230–250 million years ago and multiple losses within different dinosaur species. The red branches indicate lineages with proto-feathers; the blue ones symbolize lineages with scales only; and the gray lines represent lineages without skin fossils. Own sketch, redrawn from BUCHHOLZ (2021).

In other words, the potential for the morphogenesis of proto-feathers has been preserved in the ancestral lineage of birds and was lost in some side branches (Fig. 24). Hence, there is no reason why we cannot interpret the feathery integuments of pterosaurs as precursors of avian feathers—as *true* proto-feathers.

### C.14: Were pterosaurs feathered?

Remarkably, JUNKER (2022) denies that pterosaurs possessed feathers at all by presenting the following argument:

Who does not first think of ‘feathers’ as the flat bird feathers that form part of a complex flying apparatus? Messages like ‘feathers in pterosaurs’ therefore seem misleading.

However, the notion that pterosaurs possessed feathers seems “misleading” only against the background of Carl LINNAEUS’s traditional systematics, which defined groups typologically and assumed *constancy of traits*, neglecting existing variation (see above in section C.12).

Thus, LINNAEUS’s classification still clearly demarcates birds, together with their most prominent features (the feathers), from “reptiles.”<sup>17</sup> However, we have known for a

<sup>17</sup> Contrary to birds, the traditional category of *reptiles* is not a closed descent group. Rather, it is a paraphyletic assembly of species; that is, not all of their descendant species are included in this group. To indicate that there are no reptiles in the phylogenetic system (WIESEMÜLLER et al. 2003, p.107), we put the word *reptiles* in quotation marks.

long time that birds and “reptiles” are not essentially different groups. Instead, they form the common taxon of Sauropsida, in which the formerly “great” differences between “reptiles” and birds exist only in the form of graded similarities (see above in sections B, C.1, C.7, and C12).

In addition, many bird features appear in the fossil record in a gradual and successive way, as we expect from an evolutionary point of view. This holds true also for the keratinous skin appendages of various dinosaurs, gradually leading to highly developed pennaceous feathers in maniraptorans.

As far as pterosaurs are concerned, YANG et al. (2018) concluded that the different pycnofiber types on pterosaurs and filamentous structures on non-avian dinosaurs and birds show profound morphological, ultrastructural, and chemical similarities, which confirms their homology. In that case, those structures would have had a single evolutionary origin some 230–250 million years ago, meaning that pycnofibers are (proto-) feathers. Then it is purely a matter of taste whether to call these structures “true feathers,” “feather precursors,” or whatever. Personally, we would prefer the names “pycnofibers,” “proto-feathers,” or “feathery integuments.”

### C.15: Did feathers evolve for flight?

A typical problem often encountered in public discussion concerns the “purpose” of the development of derived structures. Laypeople usually have the idea of a linear, quasi-intended line of development. Creationists reinforce this opinion by arguing in a typological way. One example is JUNKER 2022:

A consequence of the confusion of terms is the confusing statement that pterosaurs possessed feathers. One will think here spontaneously that this has something to do with their flight ability. However, what should be the purpose of feathers in a specialist that can fly excellently with a sophisticated flying skin (cf. Pittman et al. 2021)? These formations obviously contribute nothing to flying ability.

If feathers necessarily suggested flight, then *Anchiornis* would not have had any feathers either. They consisted mainly of thick, inflexible  $\alpha$ -keratins (PAN et al. 2019), and there is still dispute over what this feature could have contributed to flight since computer modeling revealed that the propatagium is the major lift-generating component of the wing (BROWN & COGLEY 1996). Similarly, the feathers of flightless oviraptorosaurs (“egg thief lizards”) and those of penguins should not be considered feathers either.

As discussed in section C6, a large part of the evolution of avian features occurred in contexts that had nothing to do with birds or avian flight. This is a principle that, in general, is typical of evolution. For instance, as discussed before, the highly efficient



lungs of birds, including their associated air sac systems, had already evolved in non-avian theropods, which thus achieved a significant increase in physical performance compared to previous performance. That is a crucial success criterion for actively hunting predators.

It was the same story with the feathers: before birds could use them for active flapping flight, they served for gliding. Before that, they were used in some other functional context, such as thermal insulation, display, camouflage, and brooding (ZHOU 2014). We know the latter thanks to an oviraptoran covered by a shifting dune; it died in brooding posture and then fossilized (CLARK et al. 1999).

### D. Summary

The finding that birds are descendants of certain dinosaurs has been a scientific consensus for over 20 years. Only a very few experts still question it. In the publications of those who deny macroevolution and want to have it replaced by an “intelligent” origin (that is, *creationists* of various stripes), such criticism is clearly overrepresented. However, unlike the scientists they cite, creationists do not primarily cast doubt on the membership of birds in particular archosaur taxa. Rather, they want to see the evolutionary development as such questioned. They achieve this only by mixing the criticism of individual scientists with antiquated and factually incorrect ideas on evolution.

One of the creationists who is concerned with criticizing avian evolution is Reinhard JUNKER, former managing director of the German evangelical association WORT-UND-WISSEN. His argumentation is typical of creationist criticism. Since such criticism relies on antiquated views of evolution, numerous findings look like serious anomalies.

In this review, we explain why birds' ancestry from Mesozoic dinosaurs is a scientifically well-established fact. Afterwards, we discuss popular objections against this thesis presented by creationists like Reinhard JUNKER and by scientists like Alan FEDUCCIA as well. We show that creationist criticism is working under a misunderstanding or misrepresentation of evolutionary theory. This line of reasoning is influential worldwide. It is representative of the whole creationist spectrum.

The ten main theses of our analysis are as follows:

- ✚ The statement **that** birds are the product of a long, evolutionary-historical process is logically completely independent of the question of **how** this evolution proceeded in detail. The same is true for other natural processes. For instance, marine fossils testify to the process of mountain folding even without knowledge of the mechanisms or forces responsible for it in the Earth's mantle.

The evolution of birds and birds' ancestry from Mesozoic dinosaurs is essentially supported by the fact that we can put theropod fossils into a sequence in which their shape gradually takes on the appearance of modern birds. Given that descent, heritable variability, and speciation are *observed facts*, bird evolution (or evolution in general) would remain untouched even if we knew nothing about its mechanisms.

- ✚ Creationists allege a “[waiting time problem](#)” causing a very slow pace of evolution. Hence, in their eyes, evolutionary mechanisms are overstrained by producing the great diversity of avian forms “abruptly” in geologically short periods. However, their reasoning is quite wrong. First, creationists do not seem to have understood how novelties arise in evolution. For instance, evolution never faced the task of waiting until a “fixed and pre-specified target” was reached. Second, the evolvability of novelties, even of [irreducibly complex systems](#), within short time periods is a well-corroborated and no longer reasonably disputable fact (see, for instance, HUNT 2007b; TONKIN et al. 2008; DE KRAKER & GERSHENZON 2011; SAUTER et al. 2012; TROTTER et al. 2014; YONA et al. 2018; RAWCLIFFE 2019; BEYER et al. 2022; NEUKAMM 2022).
- ✚ When it comes to the “[abrupt](#)” [appearance of characters](#) in the fossil record, the explanation of *punctuated equilibria* must be considered as well as the ambiguity of the term “abrupt”. When a paleontologist speaks of the “abrupt” appearance of a feature, he may still think of periods of millions of years. Here, the biased and fragmentary sedimentary record, both in time and in space, must be taken into account. Abrupt appearance may hence be a *geological artifact*.
- ✚ Creationists ignore the progress of [evolutionary developmental biology](#) (Evo-Devo) in solving specific problems. This includes, for example, the question of how the supposedly contradictory counting of fingers in some theropods (apparently, I-II-III) and birds (II-III-IV) fits together. Evo-Devo can also explain the capability for rapid and convergent evolution of numerous avian features.
- ✚ Evolution deniers portray the [convergence problem](#) as much more serious than it is. Despite widespread convergence and uncertainty about the position of some taxa, there is a remarkable consensus on the backbone structure of the family tree of the ancestors of birds and the relative hierarchical placement of almost all major clades that constitute this tree. Birds still lie in a deeply nested position within Theropoda (RAUHUT & FOTH 2020, p. 37).
- ✚ Contrary to creationists' reasoning, [widespread convergences](#) are [not anomalies](#) but rather a clear *expectation of evolutionary theory when developmental biological background knowledge is considered* (MCGHEE 2011, p. 7).

- ✚ For at least half a century, the idea that evolution must run **continuously and linearly** has not been compatible with contemporary knowledge of the processes of speciation and differentiation of species (MAHNER 1986, p. 68). Creationists do not seem to know that just these processes are accompanied by discontinuities, incongruities, and a zigzag course (such as reversions of traits in different lineages).
- ✚ Creationists place antiquated expectations on the nature of evolutionary **transitional forms** and claim to have recognized “contradictory” trait mosaics. Hence, they ignore that mosaic evolution is the result of genetic burdens (RIEDL 2003, p. 209) and lineage-splitting events (MAYR 1967, p. 465 f.).
- ✚ The claim that the features of the avian body plan could not have evolved isolated from each other is false. The theropod fossils can be placed in a sequence in which the “irreducibly complex overall organization” of birds resolves into a **series of consecutive** feature addition steps.
- ✚ Creationists seem not to understand *cladogenesis*; otherwise, they would not problematize the “**phylogenetic-stratigraphic discrepancy**,” i.e., the chronologically *later* appearance of some species with *more primitive* features in the fossil record. (For the attempt to compress the geological time scale by six orders of magnitude, see: <https://www.ag-evolutionsbiologie.net/html/2014/kreationismus-und-radiometrische-datierung.html>).

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