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Are Birds Dinosaurs?
A Critical Analysis of Fossil Findings

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Abstract

Birds are now considered "living dinosaurs" by evolutionary theorists. The putative descent of birds from dinosaurs has become established as one of the most popular evolutionary transitions. In recent years, apparent bird-like features have been increasingly detected in theropod dinosaurs, and a majority of apparent avian traits have been found to be represented in various dinosaur groups. Therefore, a *gradual* transition from dinosaurs to birds is considered by evolutionary theorists well supported by fossil evidence. Only a few characteristics are considered suitable to distinguish between birds and dinosaurs. Thus, one could no longer draw a line between dinosaurs and birds today according to evolutionists. The occurrence of a number of bird-typical traits in dinosaurs and Mesozoic birds is here analyzed in more detail. In which theropod groups do the traits in question occur, and what is the phylogenetic and stratigraphic position of the genera in question? Is it supported by data that the apparent avian features were added step by step? The cladistic methodology is used to test whether consistent evolutionary hypotheses can be made within an evolutionary interpretive framework in light of the fossil evidence. The following traits or trait complexes are examined: feather types and flight ability, teeth and beak, brain and encephalization quotient, furcula, gastralia, rib cage, sternum, pneumaticity, air sac system and respiration, pelvis and posteriorly oriented pubis, pygostyle, fibula, wrist, and eggs, clutch, and brood care. It was concluded that even after examining the claimed fossil evidence, there are no unequivocal evolutionary transitions. Instead, the evidence confirms the creation of a variety of original basic types (created kinds) that subsequently diversified.

Keywords: Dinosaurs, birds, fossils, opposite birds, ornithurans, convergence, creation, evolution

Summary of Findings

Assuming an evolutionary emergence the resulting analysis shows that a number of apparent bird-typical traits that occur in theropod dinosaurs would have evolved multiple times convergently and were presumably not expressed at all in phylogenies at the base of the respective groups. For almost all studied traits, convergences have to be assumed more or less frequently due to the mosaic-like distributions. In some cases, different relationships are suggested depending on the underlying trait. This manifests itself, for example, in the fact that a number of genera, measured against established phylogenies, show contradictory trait combinations that make phylogenetic classification more or less difficult. This often mosaic distribution also favors the controversial interpretation that some genera interpreted as avian precursors may be secondarily flightless birds. In this case, their features would be eliminated as evidence for a gradual transition from dinosaurs to birds. Some features continue to show significant jumps.

Based on these findings, the claim of a gradual evolutionary "buildup" of the avian assemblage based on the fossil record is strongly questioned and is not supported by the fossil record for some traits. Moreover, these and other commonly encountered findings do not conform to evolutionary theory expectations and may be considered anomalies:

(1) Based on the distributions of features in early birds and the dinosaurs close to them and their stratigraphic positions, a picture emerges of different mosaics and consequently of a network of similarity relationships.
(2) It is not clear which group is at the base of the birds.
(3) The large extent of homoplasy means that the cladograms are not stable and new finds can lead to major changes.
(4) The oldest bird groups are already strongly differentiated at the base and there are partly also "modern" characteristics in the oldest representatives of a group.
(5) Especially in plumage characteristics, the greatest degree of diversity is seen near the base of the bird groups.
(6) Most theropod dinosaur genera that have apparent bird-like features are geologically younger than the geologically oldest birds.

Some findings appear able to be interpreted well from an evolutionary point of view (which does not mean that this interpretation is correct). Some (but by far not all) mosaic forms could possibly be close to evolutionary transitional forms. In some groups, apparent trends in the change of trait expression can be traced over the course of the Cretaceous. Also, the fact that many apparent bird features appear to occur in different dinosaur groups of theropods could be interpreted to be evolutionary with certain restrictions (for example, convergence problems).

"Evolutionary Experiments"

The mosaic character of the trait distributions and especially the diversity of early established feather types and modes of flight (with four-winged forms and partly unclear flight capabilities) leads many researchers to assume a kind of "evolutionary experimentation." This terminology, however, is questionable in evolutionary hypotheses because it implies a goal orientation, which, however, is not inherent in a natural process. The talk of experimental phases in evolution conceals the evolutionary-theoretical problem of a rapidly established variety of different mosaics.

Creation

In the questions on origins in biology usually only explanations are discussed which are committed to the naturalistic paradigm. For this determination there is neither a scientific nor a philosophical justification, but it is a convention, which can also be discarded. Under the assumption of the creation of flexible, adaptable basic types (created kinds), the findings that are problematic in terms of evolutionary hypotheses can be explained:

(1) The explosive occurrence of the variety of forms reflects the existence of basic types (created kinds), which were created in finished distinct and diverse form.

(2) The numerous, most diverse mosaic forms are the expression of manifold combinations of characteristics, the expression of which is explained by the respective way of life and not by a preceding evolution.

(3) The difficulties that arise for evolutionary theoretical modeling of how the various mosaic forms arose become superfluous if the traits can be freely combined according to the requirements for particular lifestyles and habitats.

(4) The discussed problem of an "experimentation" is omitted. There are no "experiments," but an initial variety of forms, which was originally in some respects the greatest compared to today's diversity (especially with feather types and flight forms).

Introduction

It is now claimed: "Birds are living dinosaurs" (Erickson et al. 2017), and "In truth, birds *are* dinosaurs" (Brusatte 2017b, 53[1]). One may find this equation of birds and dinosaurs odd or even outlandish, but in recent decades the putative descent of birds from dinosaurs has become established as one of the most popular evolutionary transitions, at least according to the conviction of the majority of paleontologists (for example, Brusatte, O'Connor and Jarvis 2015, R888[2]). This claimed transition is defended against criticism almost as vigorously as the underlying evolutionary paradigm itself. The basis for determining the ancestral relationship here is trait comparisons of different taxa. The fact that birds are even identified as "dinosaurs" has to do with the method of cladism, which is also used almost unchallenged in evolutionary research. According to this, the system of living beings and thus the presumed ancestral relationships are brought into a bifurcated (cladistic) system on the basis of so-called derived ("advanced") characteristics, in which birds represent a branch in the "dinosaur tree"—hence the paradoxical-sounding statement that birds are not only descended from dinosaurs, but *are* even dinosaurs. Accordingly, many dinosaur genera that are placed close to birds are called "non-avian dinosaurs" (see table 1 for this term). Fig. 1 shows the most important groups of the assumed evolutionary

Table 1. Evolutionary hypothesis-laden terms and phrases and their translation into theory-free form.

Gradual evolution	Genera with an increasing number of bird-typical features have survived in geologically increasingly younger dated strata
Cretaceous birds	Birds that are recorded in the fossil record only in the Cretaceous geological system.
early birds	the geologically oldest birds
basal species	Species that are placed at the base of cladograms based on their traits or trait expressions according to cladistic analyses.
original (plesiomorphic)	also "primitive". Traits interpreted as initial in the presumed evolution (standing at the base).
derived (apomorphic)	also "progressive". Traits interpreted as occurring late in the presumed evolution (deeply nested).
already formed	Formulation expressing that a feature is geologically established early in evolutionary theory interpretation.
experimental phase	Assumption of an early evolutionary phase in which no clear evolutionary lines are yet discernible.
Non-avian dinosaurs	Dinosaurs placed in groups close to birds in cladograms. The term suggests that birds are evolved dinosaurs.

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[1] Full quote: "In truth, birds are dinosaurs—they are one of the many subgroups that can trace their heritage back to the common ancestor of dinosaurs... You can think of it this way: birds are dinosaurs in the same way that bats are an aberrant type of mammal that can fly" (Brusatte 2017b, 53).

[2] "The origin of birds is now one of the best understood major transitions in the history of life" (Brusatte, O'Connor, and Jarvis 2015, R888).

transitional range of dinosaurs and birds in a cladogram.[3]

In recent years, a number of studies have been published that purport to document a *gradual* transition from dinosaurs to birds. The main message is: The features that are characteristic of birds were essentially already formed in different frequencies in different dinosaur genera from several families of theropods. Therefore, it is no longer possible to draw a line between dinosaurs and birds today (Brusatte 2017b, 55[4]). Thus, numerous "non-avian dinosaur" genera are known to possess apparent bird-like characteristics. Foremost among these features are feathers or feather-like body appendages[5], the wishbone (furcula), a large sternum, ossified sternal plates, an enlarged encephalization quotient, long arms, the construction of the wrist (with a semilunate carpal in the carpus[6]), a three-fingered hand with a long second finger[7], pneumaticity, the air sac system, hooked, posteriorly directed projections on the anterior ribs[8], a posteriorly directed pubis, bipedal locomotion, long hind legs with a three-toed foot, a reduced fibula, fused caudal vertebrae, brood care, a significantly reduced body size, and others (Organ et al. 2007; Padian and Chiappe 1998a, 44; Xu 2006; Xu et al. 2014; see fig. 2).

Conversely, many Upper Jurassic (most notably *Archaeopteryx*) and Lower Cretaceous birds possess features that are atypical of present-day birds but seem to be developed in many theropod genera. These include the possession of teeth (widespread, with varying degrees of reduction of teeth in different genera), a long caudal spine (in *Archaeopteryx* and *Jeholornis*, instead of a short pygostyle), lack of a sternal keel, relatively few bone fusions, and other features.

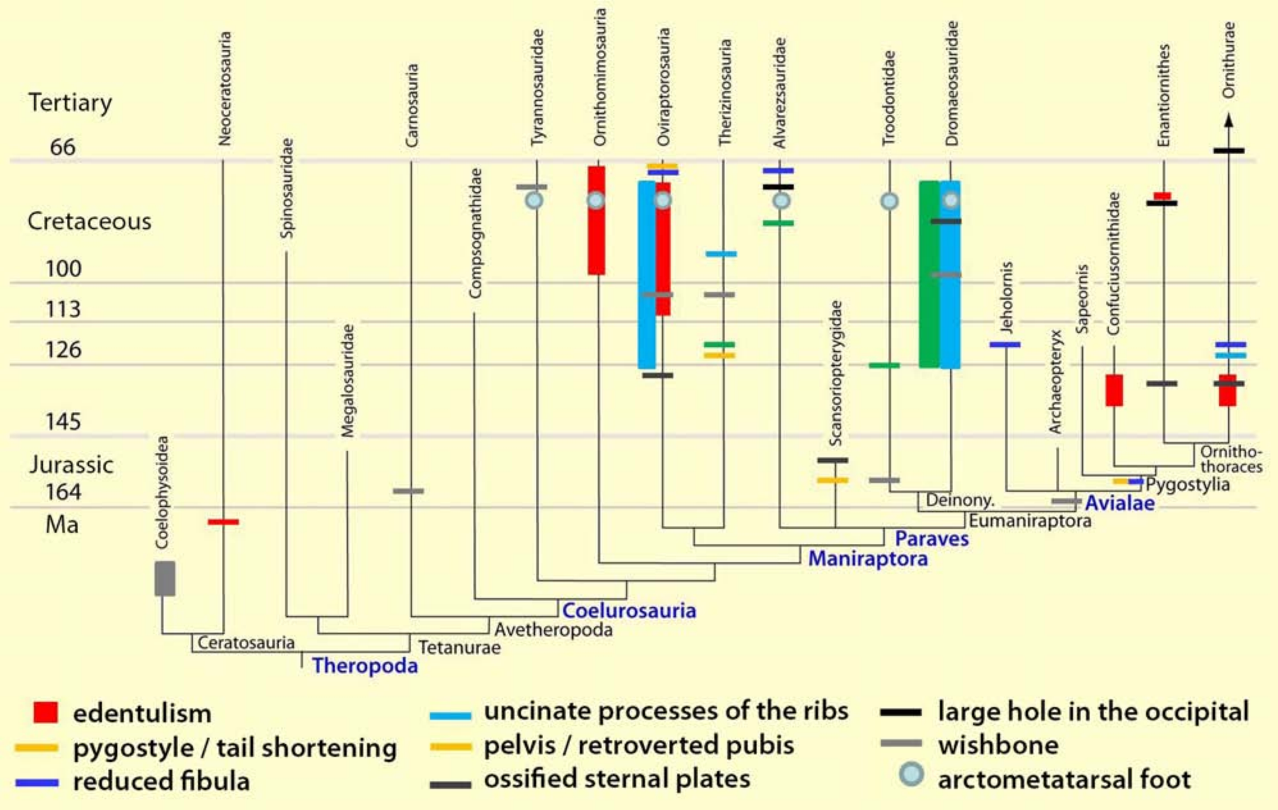

Fig. 1. Time-scaled cladogram of theropod-dinosaur groups and birds and synopsis of the convergent distribution of some bird-typical features discussed below. The phylogenetic reconstructions of different workers often yield different arrangements of individual groups. However, the various cladogram variants do not substantially change the multiple convergence. In many cases the distributions of features are so unsystematic that the assumption of numerous convergences is unavoidable. Ma: million radiometric years (according radiometric dating which is not the same as real years). (Assembled from numerous sources.)

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[3] The positioning of the groups in the cladogram is controversial (see below).

[4] "Instead the morphospace we produced was a mess: birds were interspersed among a bigger cloud of dinosaurs. There was no clear separation between them, indicating that the transition was so slow as to be imperceptible" (Brusatte 2017b, 55).

[5] However, just this significant feature is controversial in this respect: Some researchers consider forms with pennaceous feathers to be birds (possibly secondarily flightless). And whether (in other genera) hair-like appendages should be interpreted as feathers at all is strongly theory-dependent and not obvious. Compare the more detailed analysis by Junker (2017).

[6] Important for high mobility of the wrist (in flight and folding the wings on the ground).

[7] However, the homology relations are controversial here, see the review paper by Ullrich (2008).

[8] These processes stabilize the chest and play a role in inhalation. https://en.wikipedia.org/wiki/Uncinate_processes_of_ribs.

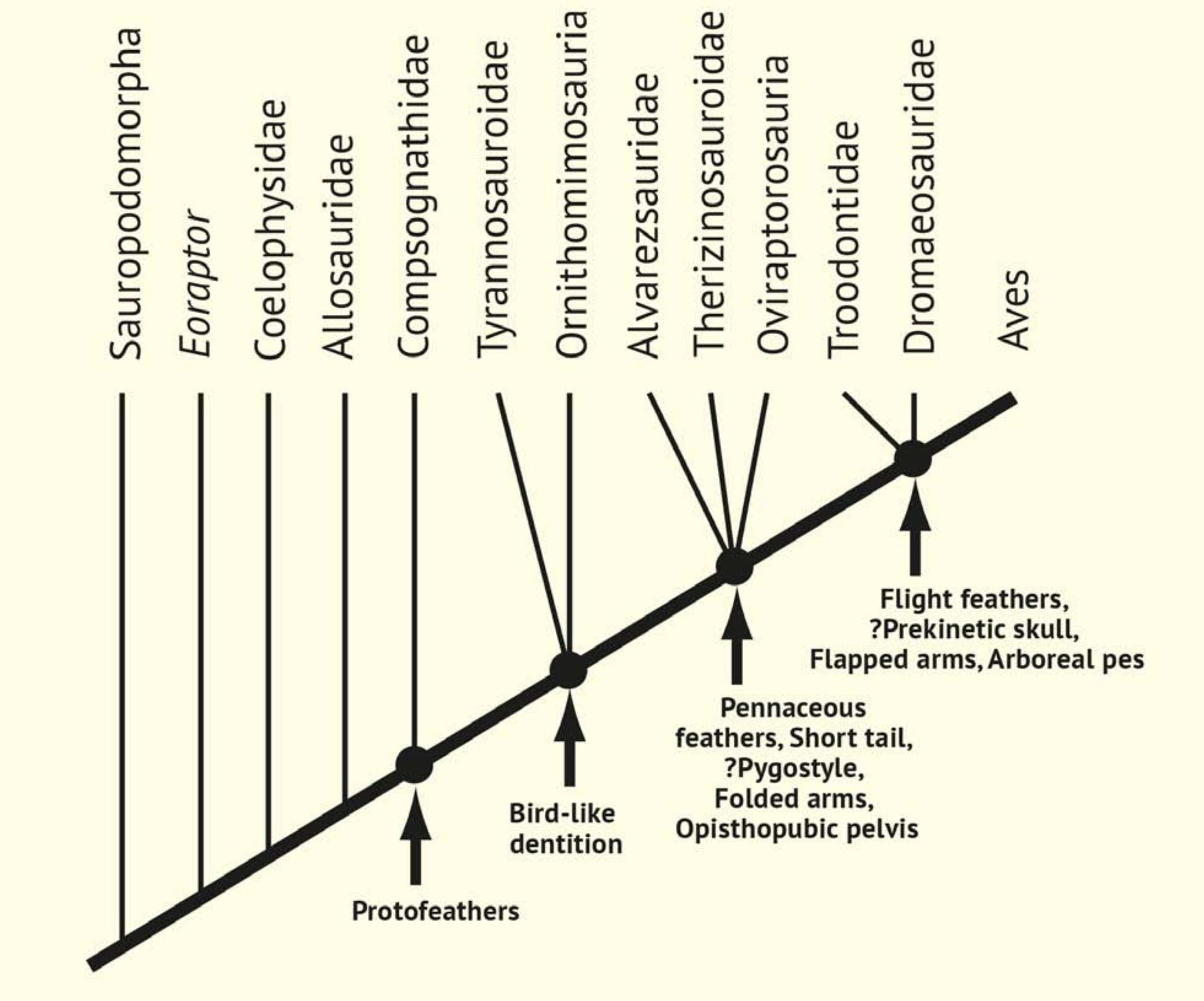

Fig. 2. Stepwise acquisition of bird traits according to Xu (2006).

Seen in this light, it seems well founded that there is an almost continuous gradual transition from theropod dinosaurs to birds. This assessment is supported by the fact that within the individual relevant features there are also still different expressions, for example, a different extent of reduction of teeth or differently expressed pygostyles (for details see below).

But, even when we closely examine the claimed fossil evidence from the evolutionists' perspective, from their own assessments of the fossils it can be shown that this picture is incomplete and more or less misleading for the following reasons:

(1) Many apparent bird features in dinosaurs occur several times independently (convergent), that is, not only in a single, but in different lineages without a supposedly common ancestor. Moreover, the individual apparent bird features are partially distributed on different branches of theropods (fig. 1).
(2) The stratigraphic positions of the dinosaur genera, which possess a different number of apparent bird-typical features, do not correspond in many cases to the evolutionary sequences to be assumed (see figs. 3–5). The increase of apparent bird-typical features is only a rough tendency when considering several lineages at the same time.
(3) The same applies to dinosaur features and their successions in Upper Jurassic and Lower Cretaceous birds.
(4) Some genera, which are interpreted as bird precursors, could be secondarily flightless birds. Their traits would in this case be eliminated as evidence for an assumed gradual transition from dinosaurs to birds.
(5) In some features there are more or less prominent gaps (where gradual reconstruction would be functionally prohibitive).
(6) A number of genera have contradictory combinations of traits that make phylogenetic classification more or less difficult.

This situation manifests itself, for example, in the fact that no specific genus can be given as the (ultimate)

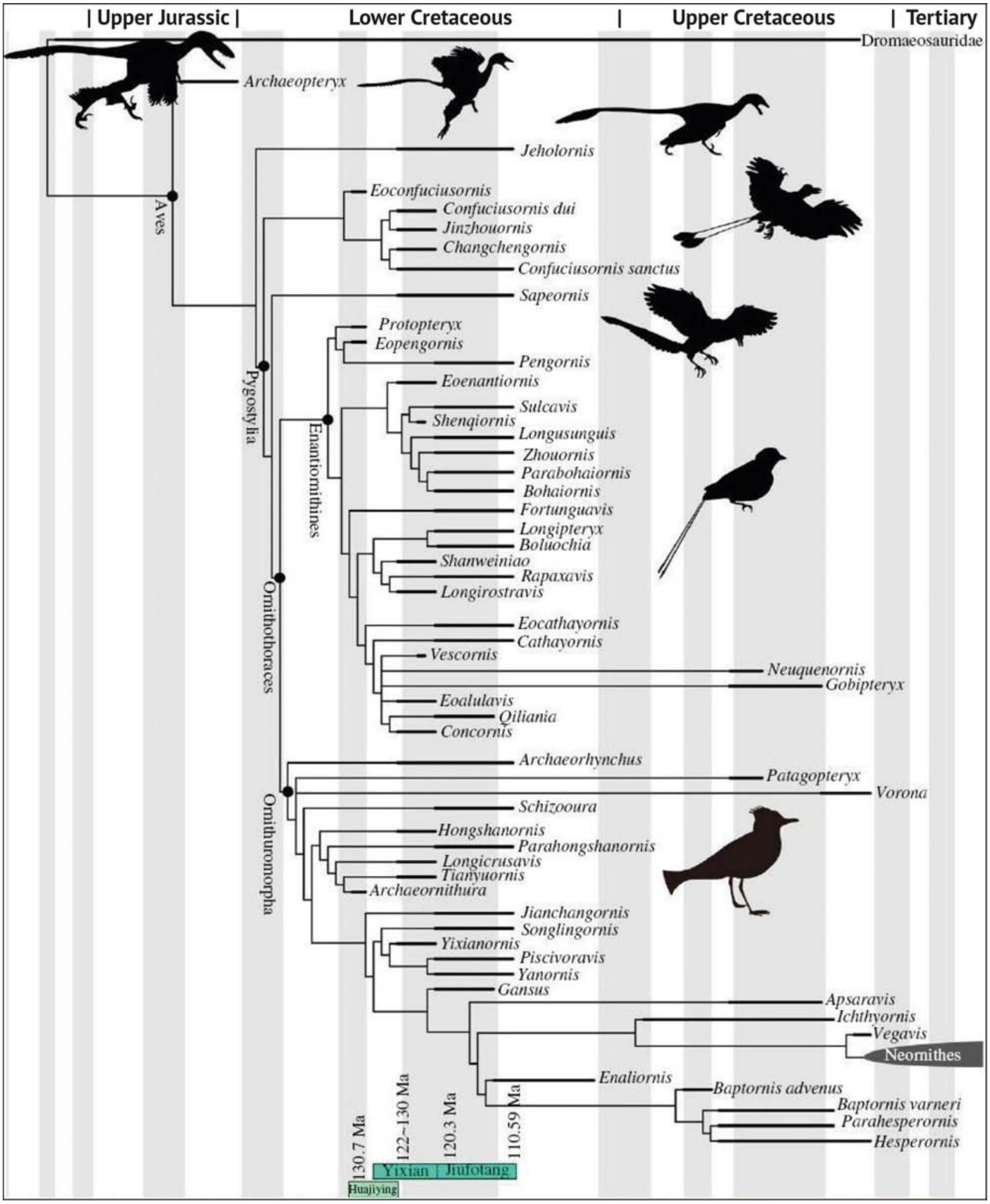

Fig. 3. Detailed time-scaled phylogeny of Mesozoic birds after Wang and Lloyd (2016). The cladogram is the consensus tree obtained from the phylogenetic analysis. The thicker lines represent the dating of the upper and lower limits of the geological strata in which the genera of interest were found. (© 2016 National Academy of Sciences)

ancestor of birds: "Although virtually all recent analyses put Dromaeosauridae or Troodontidae (or the two together as Deinonychosauria) as the sister group of Aves, neither is truly the ancestor, and hence known forms like *Deinonychus* or *Troodon* can only go so far as models for the true avian ancestor" (Witmer 2002, 16).

The points mentioned will be elaborated on in more detail below and supported by numerous examples.

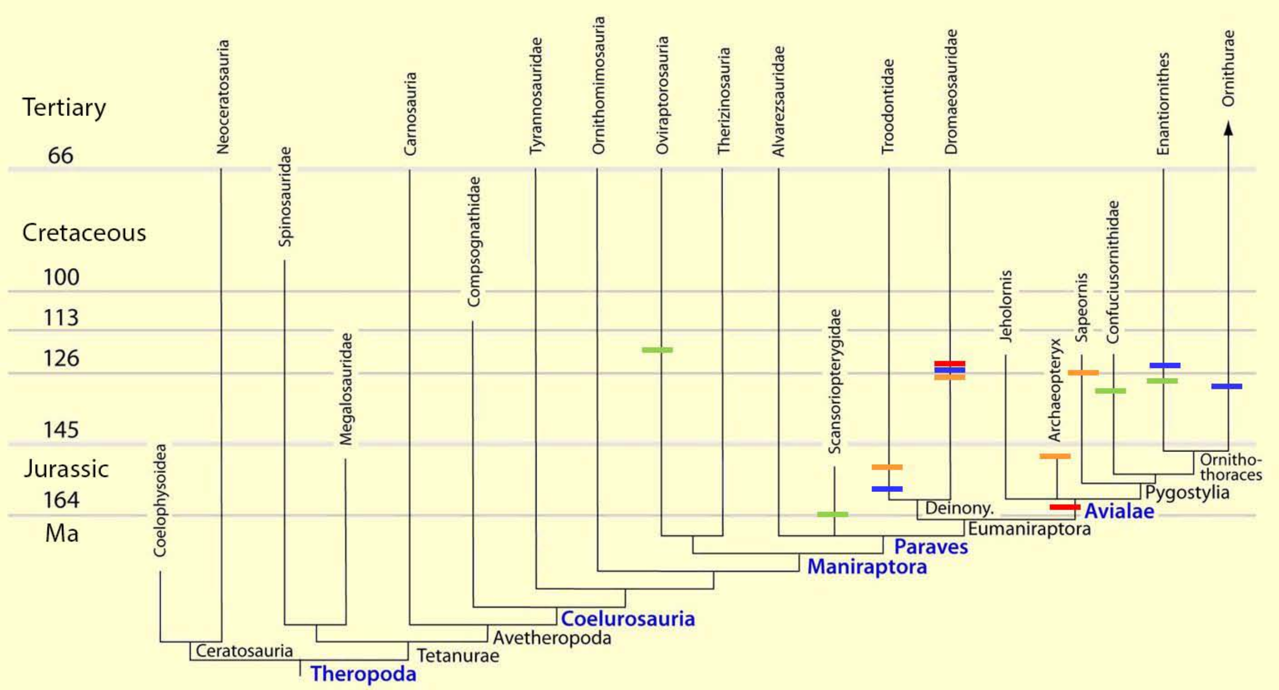

Fig. 4. Time-scaled phylogeny of theropod dinosaur groups and birds. The red bars represent the upper and lower limits of the geological strata in which the groups in question were found. (Assembled from numerous sources; see also the note at fig. 1)

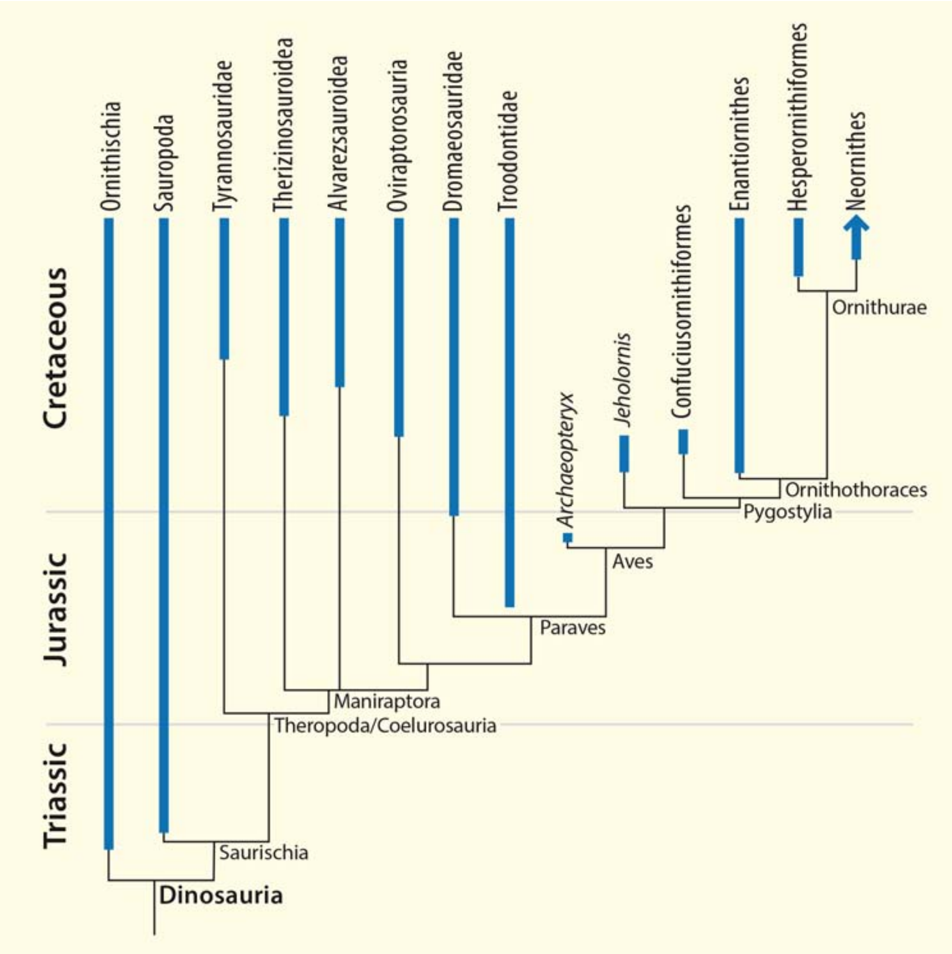

Fig. 5. Time-scaled phylogeny of some dinosaur groups and birds after Varricchio and Jackson (2016).

Quotes on Gradual Acquisition of Bird Characteristics

In the following, some quotations from evolutionary theorists are gathered together, according to which bird-typical characteristics had gradually developed in dinosaurs already before the origination of birds. One of the main goals of this paper is to challenge these claims based on the fossil record.

- "In summary, a great many skeletal features that were once thought of as uniquely avian innovations—such as light, hollow bones, long arms, three-fingered hands with a long second finger, a wishbone, a backward-pointing pelvis, and long hind limbs with a three-toed foot—were already present in theropods before the evolution of birds. Those features generally served different uses than they did in birds and were only later co-opted for flight and other characteristically avian functions, eventually including life in the trees." (Padian and Chiappe 1998a, 44)
- "Preliminary analysis of character evolution suggests that the major avian osteological characters were acquired during the early evolution of maniraptoran dinosaurs." (Xu 2006, 4)
- "However, nearly every single character that at one time was thought to make something a 'bird' is now known to occur progressively earlier in theropod evolution. Therefore, 'bird' is a colloquial term that lacks a meaningful taxonomic or scientific basis as it has no precise phylogenetic meaning." (Turner, Makovicky, and Norell 2012, 14)
- "When placed together on a family tree, these fossils show that many anatomical components of the modern-bird flight apparatus evolved piecemeal over tens of millions of years of dinosaur evolution, for reasons unrelated to flight." (Brusatte 2017a, 793)
- "Indeed, if we look at theropod history across the whole of the Triassic, Jurassic and Cretaceous, we see a gradual, cumulative acquisition of bird-like features, ranging from wishbones and a pneumatised skeleton to complex feathers, a reduced, three-fingered hand, an enlarged sternum (breastbone) and tiny size.…a robust and well-supported model showing a prolonged, directional trend in size reduction in the theropod lineage leading to birds: a trend that is continuous across 50 million years of theropod history, and which shows the animals at successive nodes becoming ever-smaller as we get closer to birds in the phylogeny.…Then there's the fact that, as we get closer to birds in the phylogenetic tree, we see an increasingly elaborate plumage, a more bird-like system of body and hindlimb orientation linked to a shift in the center of gravity, a stiffer, slimmer tail, and a number of behaviors that involve a degree of climbing (Birn-Jeffrey et al. 2012) and gliding (Dyke et al. 2013)." (Naish 2014)
- "most of the 30 or more characteristics that distinguished the small, flying *Archaeopteryx* from ground-dwelling, carnivorous dinosaurs (theropods) emerged much earlier." (Benton 2014, 508)
- "Birds evolved significantly faster than other theropods, but they are indistinguishable from their closest relatives in morphospace. Our results demonstrate that the rise of birds was a complex process: birds are a continuum of millions of years of theropod evolution, and there was no great jump between nonbirds and birds in morphospace, but once the avian body plan was gradually assembled, birds experienced an early burst of rapid anatomical evolution." (Brusatte et al. 2014, 2386)
- "In general anatomical terms, birds are a continuum of millions of years of theropod evolution. There is no great jump between nonbirds and birds in morphospace. Instead, those features that today combine to set birds apart from other vertebrates-feathers, wishbones, air sacs, and hundreds more-evolved piecemeal in Mesozoic theropods," (Brusatte et al. 2014, 2389)
- "What was once seen as a rapid adaptive radiation, in which *Archaeopteryx* rapidly acquired 30 or more avian apomorphies, is now seen as a stepwise process of more than 50 million years." (Puttick, Thomas, and Benton 2014, 1497)
- "Recent discoveries of spectacular dinosaur fossils…demonstrate that distinctive bird characteristics such as feathers, flight, endothermic physiology, unique strategies for reproduction and growth, and a novel pulmonary system originated among Mesozoic terrestrial dinosaurs.…The iconic features of extant birds for the most part evolved in a gradual and stepwise fashion throughout archosaur evolution." (Xu et al. 2014)
- "Thus, there is no sharp line demarcating bird and nonbird – the distinction has become entirely arbitrary." (Witmer 2002, 6)
- "Currently, Aves is without a character-based definition; the last notable attempt—more than half a century ago—employed three skeletal features (the presence of a furcula, retroverted pubes, and a reversed hallux) and the presence of feathers (de Beer 1954). However, these features no longer define Aves, being either present in non-avian dinosaurs (furcula, feathers) or absent in basal-most birds (retroverted pubes, reversed hallux)" (O'Connor and Zhou 2015, 334). However, the authors see possibilities for a biological definition of the birds: possession of a crop and loss of the right ovary.
- "many features that are commonly associated with birds, flight, and arboreal life, such as the thin-walled bones, the furcula, the long forelimbs, the

sideways-flexing wrist, and feathers, evolved in animals other than birds and for purposes other than flight; they were later exapted for other functions." (De Ricqlès et al. 2003, 373)

- "many of the traits that are considered uniquely avian among extant amniotes actually arose before the origin of birds themselves." (Makovicky and Zanno 2011, 10)
- "The fact that scientists are having a difficult time distinguishing the earliest birds from their closest dinosaur relatives illustrates just how bird-like some non-bird dinosaurs were (…), and how the transition between non-bird dinosaurs and birds was gradual." (Brusatte, O'Connor, and Jarvis 2015, 889)

Methodological Preliminary Remarks

The argumentation of the following analyses takes place within the framework of the evolutionary paradigm, which, however, is certainly not regarded as fixed by the author. This approach is taken to demonstrate that even with the evolutionary paradigm the fossil evidence is inconclusive and does not reveal a graduated series of transitions. However, the evolutionary paradigm is so firmly established in research that often no (longer) clear distinction is made between data and interpretations, and presumably a sensitivity to this is largely lacking. Phrases such as "gradual emergence," "Cretaceous birds," "early birds," "basal species," "original" (plesiomorphic), "derived" (apomorphic); "*already* formed," "experimental phase," and others are evolutionary theory-laden. It would be impractical to constantly challenge these terminologies, so they are used in part but are intended to be understood in a descriptive sense. For example, "early birds" are those found in geologic sediments that are assigned a relatively old age in the system of historical geology. "Early" here, however, is *not* meant to imply that an early phase of hypothetical evolution is involved (see table 1 for other evolutionary theory-laden terms).

On the point of the theory-loadedness, it is driven by today's usual designation "non-avian dinosaurs."[9] That term is not used here, but they are instead referred to as "theropod dinosaurs." In this paper, birds are not referred to as dinosaurs.

Again, the aim now is to closely examine the claimed fossil evidence from the evolutionists' perspective and establish that from their own assessments of the fossils that their picture of an evolutionary transition of dinosaurs to birds is totally incomplete and more or less misleading, so that birds simply cannot be designated as "living dinosaurs." The paradigmatic framework of general evolution is abandoned when later the findings discussed are interpreted within the framework of a creation paradigm.

Bird-like Features in Theropods: Antecedents or Convergences?

For a number of important bird-like features in genera placed among dinosaurs, what is known about their distribution in different genera will be examined. The background is the claim, documented in the introductory section, that most bird traits evolved *step by step in* dinosaur lineages. Can this be verified on the basis of trait distribution? And do the stratigraphic positions of those genera interpreted as precursors fit the phylogenetic reconstructions?

For some traits, we simultaneously investigate the extent to which dinosaur-typical or bird-untypical traits gradually decline in birds. Thus, this comprehensive section is concerned with the first three of the abovementioned topics. Not all traits are treated, but a larger representative selection of traits that are typical for today's birds or which sufficiently informative data material could be compiled.

Feather Types and Flight Capability

In a large number of theropod genera which are systematically placed in proximity to birds hair-like or feather-like appendages or even true pennaceous feathers have been fossilized. In the evolutionary literature, a wide variety of body appendages are referred to as "feathers." In many cases, this designation is motivated by evolutionary theory and not by morphological findings, namely in all cases where they are hairy, downy, or bristle-like appendages. For the sake of simplicity, we will nevertheless refer to "feathers" in this broad sense in the following. The fossil forms known in the meantime are even supposed to prove a rather gapless succession of different stages from simple body appendages to flat bird feathers. However, the transitions are by no means smooth. There are clear differences between hair-like, downy (possibly branched), or bristle-like appendages on the one hand, and flat, flight feathers on the other (overview and source evidence in Junker 2017, see fig. 6). There is circumstantial evidence that some pennaceous feathers are to be interpreted as regressions. The forms in question would thus be flightless descendants of birds (more in Junker 2017).

According to Brusatte (2017a, 792), the evolution of flight ability was "chaotic." Different dinosaurs would have "experimented" with different airborne behaviors and different feather arrangements until finally only modern birds survived.[10] Apart from

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[9] See Dodson (2000, 507): "In any case, the point is clear that the conclusion that a bird is a dinosaur is not a fact of nature but literally an artifact of the cladistic system."

[10] Full quote: "According to this story, the development of flight was chaotic, with different dinosaurs experimenting with different airborne behaviors using different airfoil and feather arrangements (see the figure), until ultimately only modern birds survived" (Brusatte 2017a, 792).

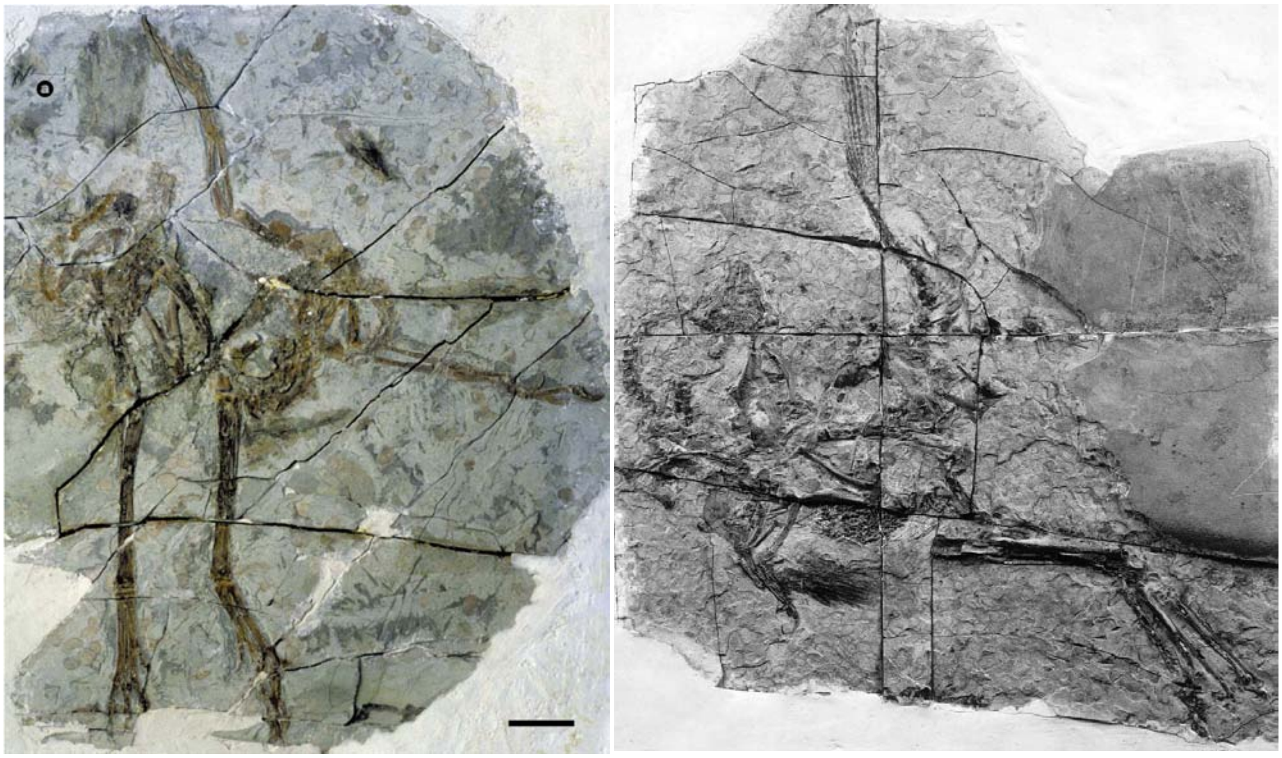

Fig. 6. Oviraptorid genera with symmetrical planar feathers: Left: *Protarchaeopteryx robusta*, holotype Jonathan Chen, "Holotype of Protarchaeopteryx robusta on display at the Geological Museum of China," https://commons.wikimedia.org/wiki/File:Protarchaeopteryx-Geological_Museum_of_China.jpg, CC BY-SA 4.0. Right: *Caudipteryx zoui*, holotype, Gareth J. Dyke and Mark A. Norell, "Photograph of the holotype specimen of *Caudipteryx zoui* (NGMC 97–4–A) described by Ji et al. (1998)," CC BY 2.0). In evolutionary theory interpretation, there is some evidence that feather symmetry is secondary (see Junker 2017).

the fact that the term "experimenting" is highly problematic in evolutionary theory (see later), it is clear from this quotation that there is no question of a linear, step-by-step development. Rather, in evolutionary theoretical reading, different expressions of flight ability are found in different lineages, which at least in part cannot be brought into an evolutionary sequence. For example, four-winged forms such as the dromaeosaurid *Microraptor are* thought to represent a distinct extinct lineage that cannot be interpreted as precursors to two-winged forms. This is also true for the species *Yi qi* (Xu et al. 2015) and *Ambopteryx longibrachium* (Wang et al. 2019) from the family Scansoriopterygidae, which possessed a distinct flying skin and cannot be conclusively placed in a lineage relationship with other Paraves.

In addition, Dececchi, Larsson, and Habib (2016) demonstrated through a biomechanical study that for behaviors supported by fluttering or wing-beating (wing-assisted incline-running, flap running, wing-assisted leaping), there is no discernible continuous trend of refinement in biomechanical performance with respect to these behaviors using the phylogenetic successions of theropod dinosaurs.[11] Some species of Paraves probably could fly or glide, but others very likely could do neither. Based on the many morphological differences among winged Paraves and birds that have survived in the Upper Jurassic and Lower Cretaceous, it follows evolutionarily that active flight arose independently not just once, but in many different groups (Brusatte 2017a, 793; Wang et al. 2019).[12] Not long ago, the possibility of multiple independent origins of active bird flight would have

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[11] "no thrust-based locomotory method succeeded in providing an adequate evolutionary pathway with an obvious evolutionary trend that surpassed biophysical thresholds,…" (Dececchi, Larsson, and Habib. 2016, 28). "Thus, the hypothesis that incremental gains in WAIR would have adaptive benefits and drove forelimb and pectoral evolution in non-avian theropods is not supported as no non-paravian maniraptorans show any capability to perform this behavior" (Dececchi, Larsson, and Habib 2016, 29). Brusatte (2017a, 793) comments, "Furthermore, looking at trends across the family tree, Dececchi et al. found no pattern of progressive refinement in aerial ability beginning with the origin of wings."

[12] "Although some paravians like Microraptor may have been able to power themselves through the air, the authors found that not all paravians had this ability. Nor was the common ancestor of paravians and birds clearly a lift-producing flapper. Coupled with the many morphological differences among winged paravians and early birds, this suggests that powered flight may not have been a singular innovation of the lineage that led to modern birds, but a behavior that many different groups of small, feathered, winged paravians achieved independently" (Brusatte 2017a, 793).

been ruled out evolutionarily. Foth, Rauhut and Tischlinger state (2015, 28): "New phylogenetic analyses of predatory dinosaurs (theropods) show: Wings with *asymmetric* flight feathers arose several times during evolution." And further (page 33): "However, we suspect that such hand wings evolved separately several times, because other dromaeosaurs *(Sinornithosaurus)* and early representatives of the avian lineage *(Anchiornis)* still possessed the original symmetrical pennaceous feathers on the arms. Based on the better aerodynamic properties of the asymmetric feather type, it can further be assumed that consequently also the flight ability within Pennaraptora evolved independently several times, at least twice—an important new finding" (see also Foth and Rauhut 2017; see below). The discovery of *Ambopteryx* (Wang et al. 2019) has added another independent lineage of flight-capable forms from an evolutionary theoretical perspective (or its existence has been confirmed[13]).

In addition, just at the beginning of the presumed evolution of birds, a great variety of feather types have been fossilized, including those that are not known otherwise and among birds today. This is true, for example, of the troodontid *Anchiornis,* which possessed, among other things, a feather type that was neither typically down-like nor exhibited in its shape typical characteristics of a pennaceous feather, nor was it intermediate between these two feather types (Saitta, Gelernter, and Vinther 2017, fig. 7). Moreover, the entire plumage of *Anchiornis* was as unique as that of the recently discovered genus *Serikornis* (Lefèvre et al. 2017; fig. 8) from the same family with, again, a different mosaic of characters regarding feathering that is difficult to classify in evolutionary theory.[14]

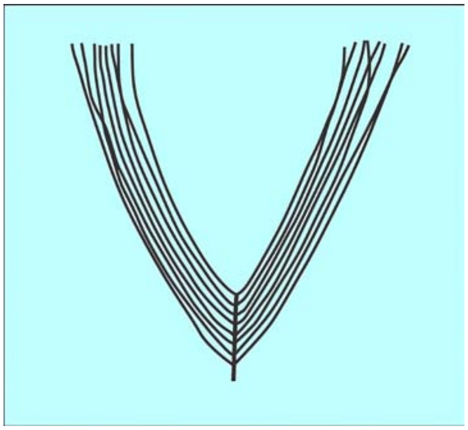

Fig. 7. Newly discovered feather type in *Anchiornis* known only from fossils (after Saitta, Gelernter, and Vinther 2017).

Furthermore, ribbon-like pennaceous feathers were discovered in the Upper Jurassic genus *Epidexipteryx* (fig. 9). Evolutionary theory suggests that this feather type evolved independently at least four times (Xu, Zheng, and You 2010): not only in *Epidexipteryx*, but also in the Confuciusornithids, in some opposite birds (such as one of their oldest genera, *Protopteryx*), and in the oviraptorosaurid *Similicaudipteryx* (Prum 2010). In *Protopteryx,* the tail feathers were unusual and uniquely developed. They were unbranched in the region near the body (Zhang and Zhou 2000, 1957[15]). Other feather types include elongate broad filamentous feathers in the therizinosaur *Beipiaosaurus* (Xu, Zheng, and You 2009, fig. 10) and a previously unknown expression in the Lower Cretaceous genus *Cruralispennia* from the enantiornithine group. Their feathers were wire-like in the proximal region and had distally

Fig. 8. Reconstruction of *Serikornis*. This genus possessed both downy tufted and simple pinnate body appendages. Nevertheless, the interpretation as an intermediate form transitioning to birds is problematic. For more details, see Junker (2017). Emily Willoughby. "Life restoration of *Serikornis sungei*, feathered Paraves | paravian dinosaur from the Upper Jurassic Tiaojishan Formation of Liaoning, China, described in 2017." https://en.m.wikipedia.org/wiki/File:Serikornis.jpg, (CC BY-SA 4.0).

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[13] The interpretation of the related scansoriopterygid species *Yi qi* as a flyer with flying skin was previously not entirely uncontroversial.

[14] The trait combination of simple feathers, feathered legs, short forelimbs, and features indicative of ground life is unexpected in evolutionary theory. See Pickrell (2017): "The distribution and type of feathers on its body are not consistent with the currently preferred scenario about the evolution of bird feathers and flight. That scenario assumes that long pennaceous feathers on arms and legs originated with arboreal four-winged gliders such as Microraptor." For a ground takeoff of a fast runner, feathered legs are disadvantageous; for tree takeoff, the short forelimbs and life on the forest floor do not fit. Further discussion: on Anchiornis: Junker (2018a); on *Serikornis*: Junker (2018b).

[15] "*Protopteryx* retains a feather type that has never before been described: It lacks barbs or rami at the proximal end" (Zhang and Zhou 2000, 1957). Similarly, long tail feathers of *Confuciusornis* were developed. "Such a feather structure, including those of some long tail feathers of *Confuciusornis* (Fig. 1C) and at least four other enantiornithines, is different from those of all other known fossil and modern feathers" (Zhang and Zhou 2000, 1957).

Fig. 9. Reconstruction of *Epidexipteryx*. (Photo: LWL Museum of Natural History, Münster, Germany).

filamentous tips ("proximally wire-like part with a short filamentous distal tip;" Wang et al. 2017d; fig. 11). A greater diversity of feather types than today was established early[16] and occurred quite abruptly. And it does not fit easily into an evolutionary theoretical scheme (see below).

Fig. 10. Reconstruction of *Beipiaosaurus inexpectus*. Matt Martyniuk, "Life restoration of the therizinosaur *Beipiaosaurus inexpectus*, based on skeletal reconstruction by Jaime Headden and feathers as preserved in the holotype and referred specimens," https://commons.wikimedia.org/wiki/File:Beipiao1mmartyniuk.png, CC BY-SA 3.0.

Long feathers on the leg are also said to have been acquired independently several times. The anchiornithid genera *Xiaotingia*, *Pedopenna*, and *Anchiornis* possess long feathers on the midfoot. "However, this particular feature was apparently developed at least twice more in parallel by *Microraptor* and *Sapeornis*" (Moser 2014, 416f.). Leg feathers have also recently been demonstrated in *Archaeopteryx* (Foth, Tischlinger, and Rauhut 2014). Sullivan, Xu, and O'Connor (2017, 13) calculate that leg feathers evolved independently four times (*Anchiornis*, *Archaeopteryx*, some dromaeosaurids, possibly *Sapeornis*).

Fig. 11. Unusual shape of some feathers on the legs of *Cruralispennia*. More details in the text. Scale bar: 10 mm. (From Wang, Li, and Zhou 2017. CC SA 4.0)

The Lower Cretaceous enantiornithine *Schizooura* possessed unusual forked tail feathers, which is uncommon among Lower Cretaceous enantiornithine birds where only fan-shaped tails are otherwise known. Zhou, Zhou, and O'Connor (2012) note in this regard that this tail feather morphology would reduce aerodynamic efficiency in modern birds compared to the fan-shaped tail, but may have played a role in courtship.

Sullivan, Xu, and O'Connor (2017) conclude from the available evidence on the feathering of Paraves and early birds that rapid diversification of aerodynamic structures is conceivable. Either flight ability must have been a primitive trait in Paraves and lost multiple times, or it must have been acquired independently multiple times (fig. 12). And if flight ability was an original trait among Paraves and Aves, it must have been extensively transformed in different lineages (Sullivan, Xu, and O'Connor 2017, 12). Further, they conclude that the reduction of tail feathering to a small number of tail feathers occurred independently in Confuciusornithidae and Enantiornithes (Sullivan, Xu, and O'Connor 2017, 9).

The occurrence of a bastard wing (alula[17]) is also so unsystematically distributed that multiple independent origins are assumed (fig. 13). The bastard wing is important in contemporary birds for steering during slow flight (Lee et al. 2015).[18] Thus, although an alula was developed in the four-winged

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[16] "In combination with the wide distribution of proximally ribbon-like pennaceous feathers and elongate broad filamentous feathers among extinct theropods, this find suggests that early feathers were developmentally more diverse than modern ones and that some developmental features, and the resultant morphotypes, have been lost in feather evolution" (Xu, Zheng, and You 2010, 1338).

[17] In today's birds, the alula serves as a landing flap and prevents the airflow around the wing from breaking off at slow speeds.

[18] "This is the first experimental evidence that the alula functions as a vortex generator that increases the lift force and enhances maneuverability in flights at high angles of attack" (Lee et al. 2015, 1).

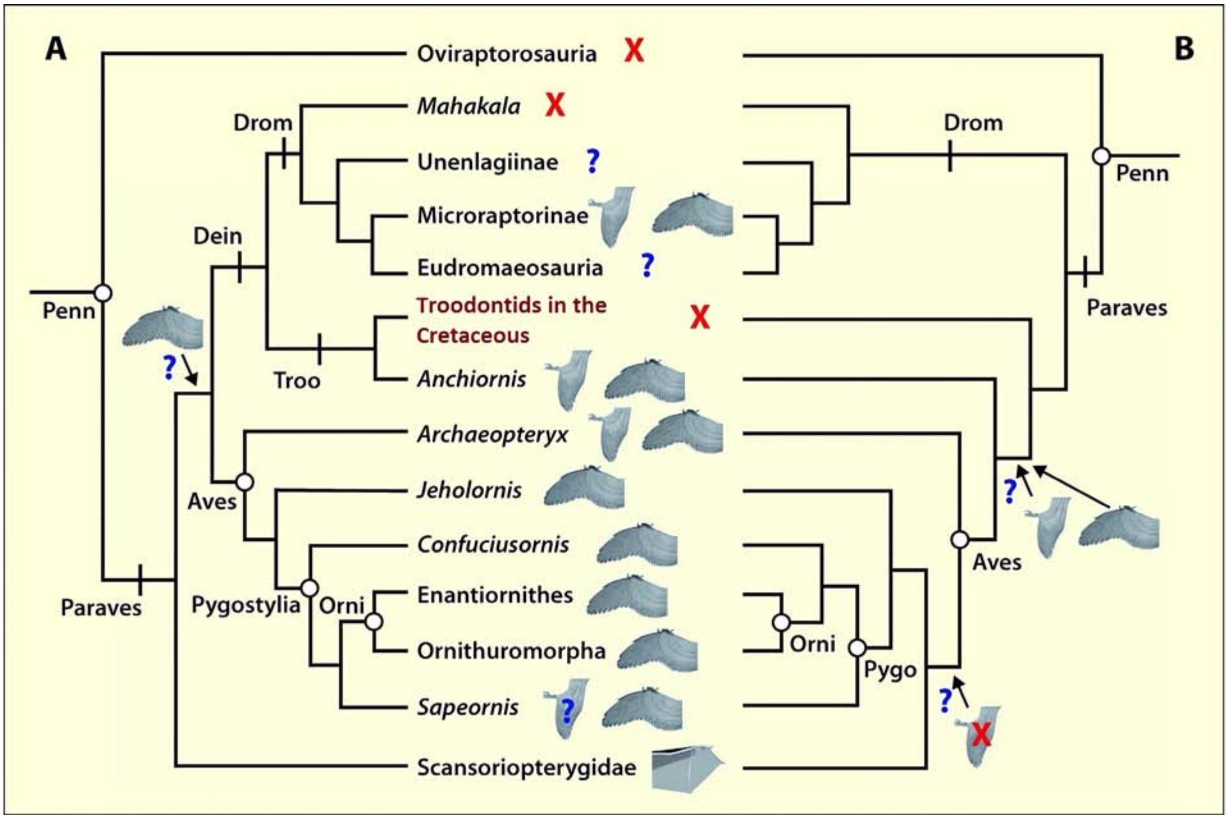

Fig. 12. Distribution of wing shapes among theropods and early birds and their placement in two possible phylogenetic topologies. The wing symbols next to the taxon names represent the putative shape of forewings (Microraptorinae, *Anchiornis*, Aves), hindwings (Microraptorinae, *Anchiornis*, *Archaeopteryx*), and flight skin (Scansoriopterygidae). "X" indicates absence of wing surfaces, "?" indicates an uncertain finding. A. This topology implies multiple independent acquisition of hind wings and early single acquisition of forewings followed by multiple loss. B. This topology implies acquisition of forewings and possibly hindwings in a common ancestor of Anchiornis and the birds, and independent acquisition of both forewings and hindwings in the dromaeosaurs. The acquisition of hindwings at the Anchiornis+Aves node would imply a subsequent loss within the birds. Abbreviations: Dein, Deinonychosauria; Drom, Dromaeosauridae; Penn, Pennaraptora; Orni, Ornithothoraces; Pygo, Pygostylia; Troo, Troodontidae. Adapted from Sullivan, Xu, and O'Connor 2016.

dromaeosaurid *Microraptor gui* (Xu et al. 2003b), it was absent in most basal birds such as *Archaeopteryx*, which Zhou and Zhang (2006a, 93) find "puzzling." The oldest evidence of an alula among Cretaceous birds is in the enantiornithines *Eoalulavis* (Sanz et al. 1996) and *Protopteryx* (Zhang and Zhou 2000). It is also possible that a convergent origin of an alula must be assumed in the other major Cretaceous bird group, the ornithurans; the oldest record was in the genus *Archaeornithura* (Wang, Zheng, and O'Connor 2015). However, Zheng et al. (2017, 448) suggest that an alula and associated flight capabilities were already realized at the base of Ornithothoraces (Enantiornithes and Ornithurae) and thus very early (see below). It is possible that the recently discovered Upper Jurassic genus *Caihong*, which is placed in the Anchiornithidae and thus in the Paraves, also possessed a type of alula (Hu, O'Connor, and Zhou 2015), but again, a convergent origin would have to be assumed in an evolutionary model.

Current cladograms (figs. 14, 15) illustrate the unsystematic distribution of different feather types and feather positions, and fig. 16 shows the enormous diversity of tail types that occurred relatively simultaneously in theropod genera and birds of the Lower Cretaceous and cannot be consistently classified in evolutionary sequences.

Teeth and Beak

A prominent feature of birds is the bill. "Aside from feathers the bill is surely the most quintessentially bird-like feature of the avian body" (Proctor and Lynch 1993, 66). Birds use their bills not only for feeding, but also for grooming their plumage, nest building, defense, and courtship. A thin keratinous layer called the rhamphotheca covers the bony core of the upper and lower beak. The upper beak is supported by the maxilla (upper jaw) and other bones of the skull and is more or less movable by a kind of hinge joint. In most birds, the upper beak also contains two nostrils.

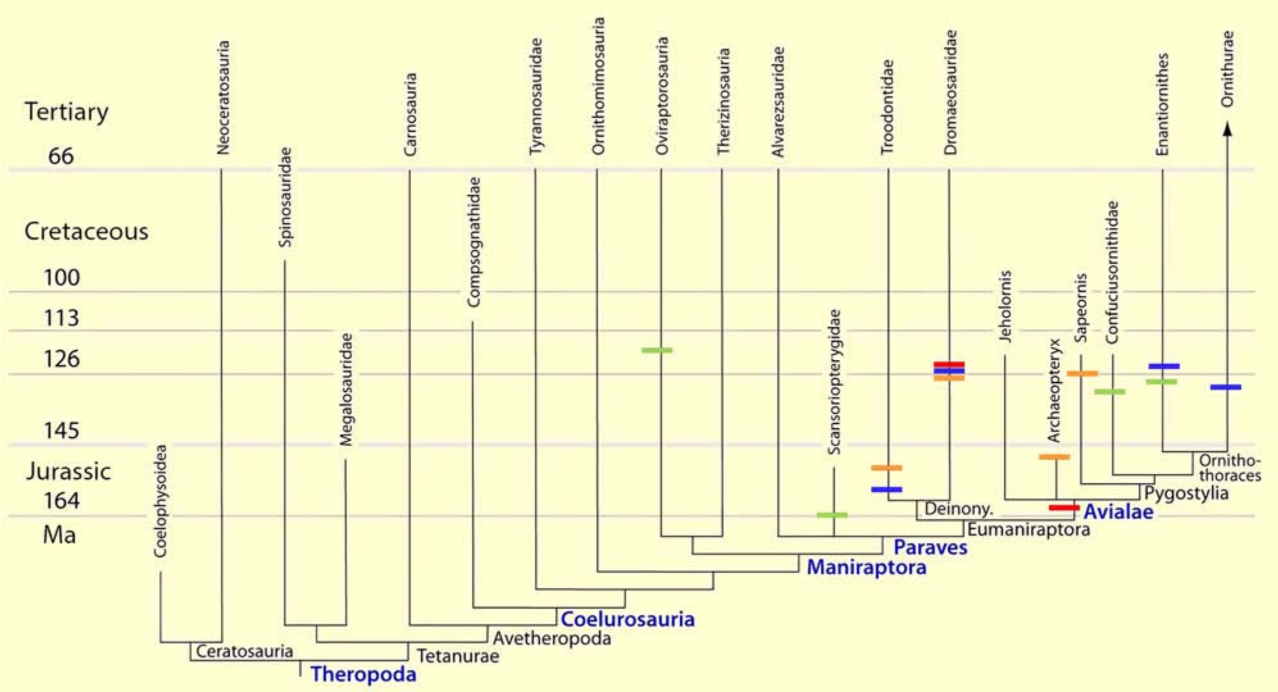

Fig. 13. Cladogram with indication of the time of occurrence with feather types that appear convergently (partly multiple). Red: wing feathers (asymmetrical): Microraptor; Anchiornis; Avialae; blue: thumb feathers: *Caihong*, *Microraptor*, Ornithothoraces (convergent twice in this group in Eoalulavis and Archaeornithura); orange: feathers on barrel: *Microraptor*, *Sapeornis*, Anchiornithidae; light green: band-like feathers: Oviraptorosauria, Scansoriopterygidae, Confuciusornithidae, Enantiornithes. (Assembled according to the sources mentioned in the text.)

The bird's beak must be seen in the larger context of bird anatomy and nutrition. Since chewing food with the beak is hardly possible, a gizzard is needed as a "substitute." Thus, the center of gravity of food processing is shifted to a more aerodynamically favorable position at the same time (Proctor and Lynch 1993, 62).

While all modern adult birds are completely toothless,[19] most fossil birds that have been recorded in Mesozoic strata possessed a toothed jaw or a combination of beak and toothed jaw (for example, *Hesperornis*, Martyniuk 2012, 43). The Rhamphotheca does not have dental alveoli (cavities for teeth) in any known case, even in fossil forms. In toothed birds that have a beak in addition to teeth, the beak and teeth are clearly distributed over different parts of the jaw and serve different tasks in feeding. The expression "teeth in the beak" sometimes used is incorrect (Martyniuk 2012, 43).[20]

The expression of teeth in dentate birds is variable, apparently depending on the type of diet (Louchart and Viriot 2011, 663). The diversity of the expressions of the teeth in dentate birds shows that they are not mere regression stages on a path to the toothless bill.

The formation of a beak is evolutionarily theorized to be related to weight savings. However, given the existence of many toothed birds on the one hand and terrestrial forms with horned beaks on the other, this relationship is not very convincing (see Wang et al. 2017a, 10930; Mayr 2017b, 72; Zhou, Sullivan, and Zhang 2019).[21] There are large runners among toothless theropods for which weight saving is not an option. In many flight-capable species the possession of teeth does not seem to detract from flight ability (O'Connor 2019, 192).[22] The reason for tooth reduction is therefore unclear to evolutionary workers. Natural evolutionary processes are also unable to anticipate the need to save weight.

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[19] Only Hoatzin chicks have small teeth, which they use to hatch from the egg and then shed. https://theconversation.com/how-did-dinosaurs-evolve-beaks-and-become-birds-scientists-think-they-have-the-answer-84633.

[20] Martyniuk (2012, 43) further writes: "A tooth protruding from the beak, relegating the keratin itself to essentially the gums, would have rendered the beak useless anyway. Teeth protruding from a beak would have been a redundancy, an expense that would not have been evolutionarily advantageous."

[21] "Weightsaving hypotheses have been rejected by recent studies and fail to explain the tradeoff between tooth loss and beak development in nonvolant theropod lineages, . . ." (Wang, Li, and Zhou 2017, 10930).

[22] "The larger, cursorial oviraptorosaurs and ornithomimids would be expected to have no such limitations yet teeth disappear rapidly in these lineages. The presence of numerous teeth in the advanced Late Cretaceous ornithurine *Ichthyornis* suggests teeth (and the robust mandible required to bear them) presented no impediment to flight" (O'Connor 2019, 192).

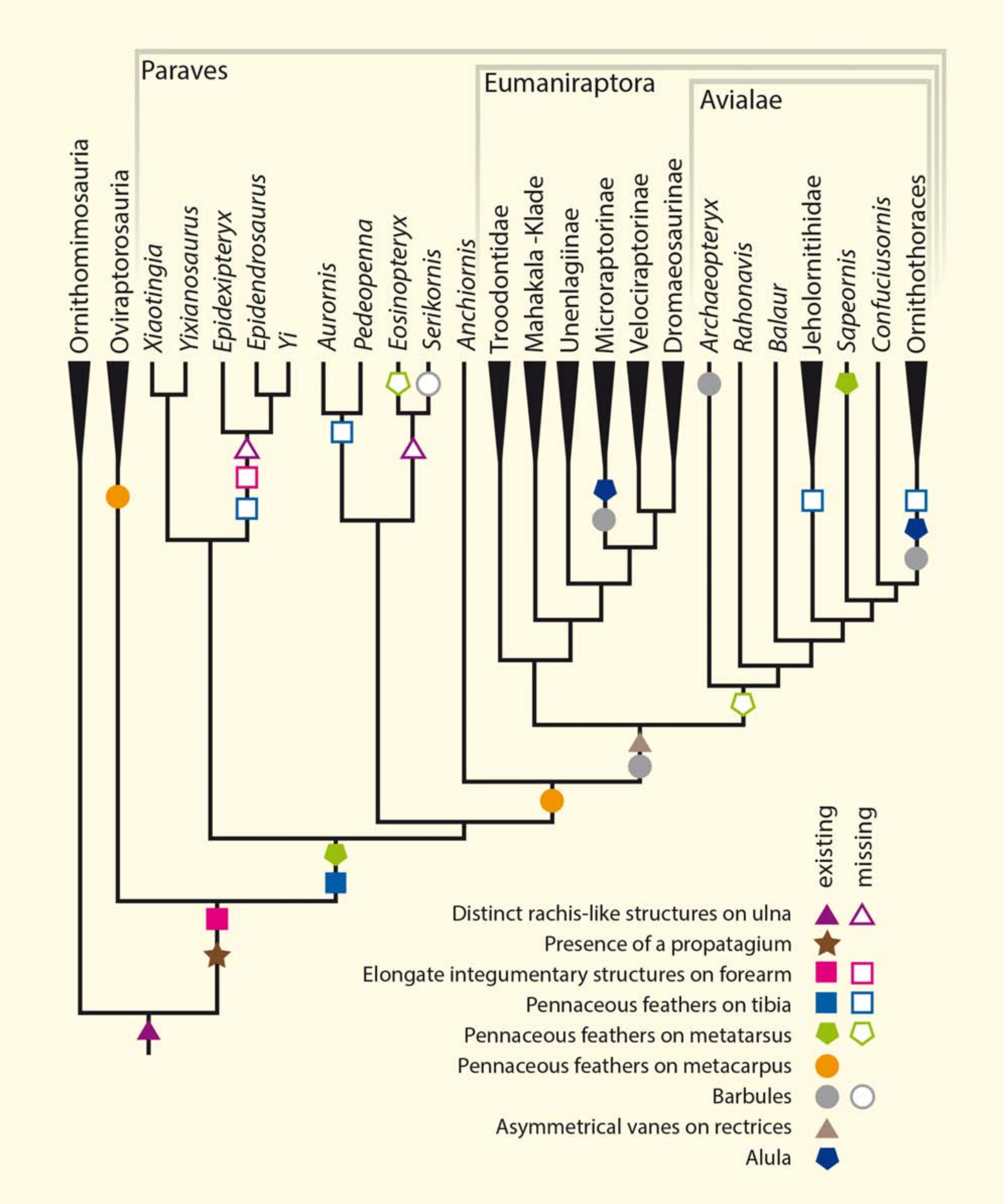

Fig. 14. Consensus tree indicating feather types based on the phylogenetic analysis of Lefèvre et al. (2017). The tree reveals numerous homoplasies.

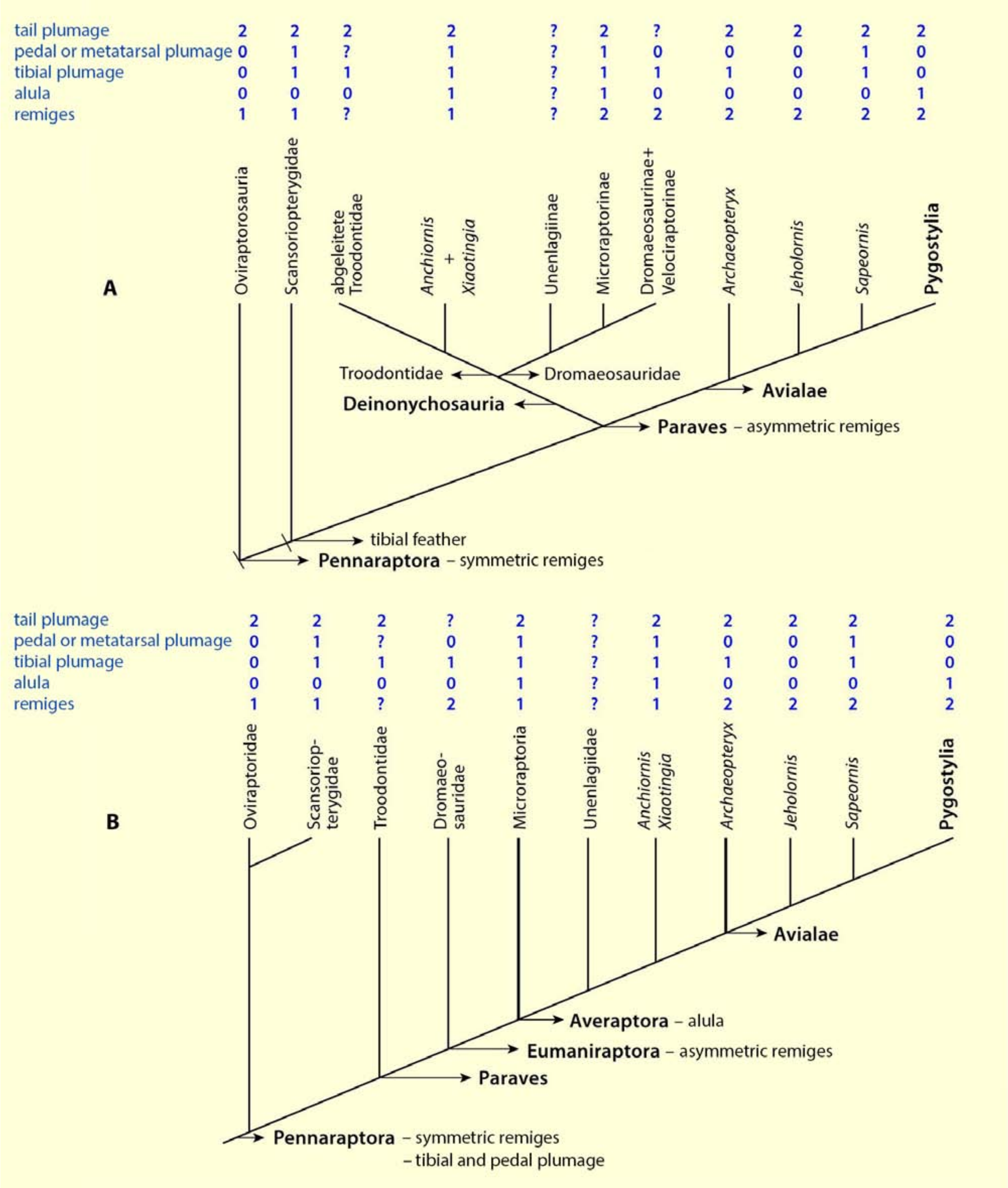

Fig. 15. Simplified cladograms of derived coelurosaurs showing which feather types are present in each group. A cladogram after Gianechini et al. (2017), B after Agnolin and Novas (2013). 0 feature absent, 1 hairy or downy appendages, 2 pennaceous feathers, ? uncertain. Particularly in variant B, there is largely no clear systematics of distributions. Agnolin et al. (2019, 21) comment as follows: "In sum, some of the diverse phylogenetic analyses put forward by different authors indicate that each feather type may have evolved convergently two or three different times, whereas other analyses indicate a single origin for flight feathers. For this reason, the origin and early evolution of the different feather types is far from being well-known and largely depends on the phylogenetic scheme adopted." (Adapted from Agnolin et al. 2019).

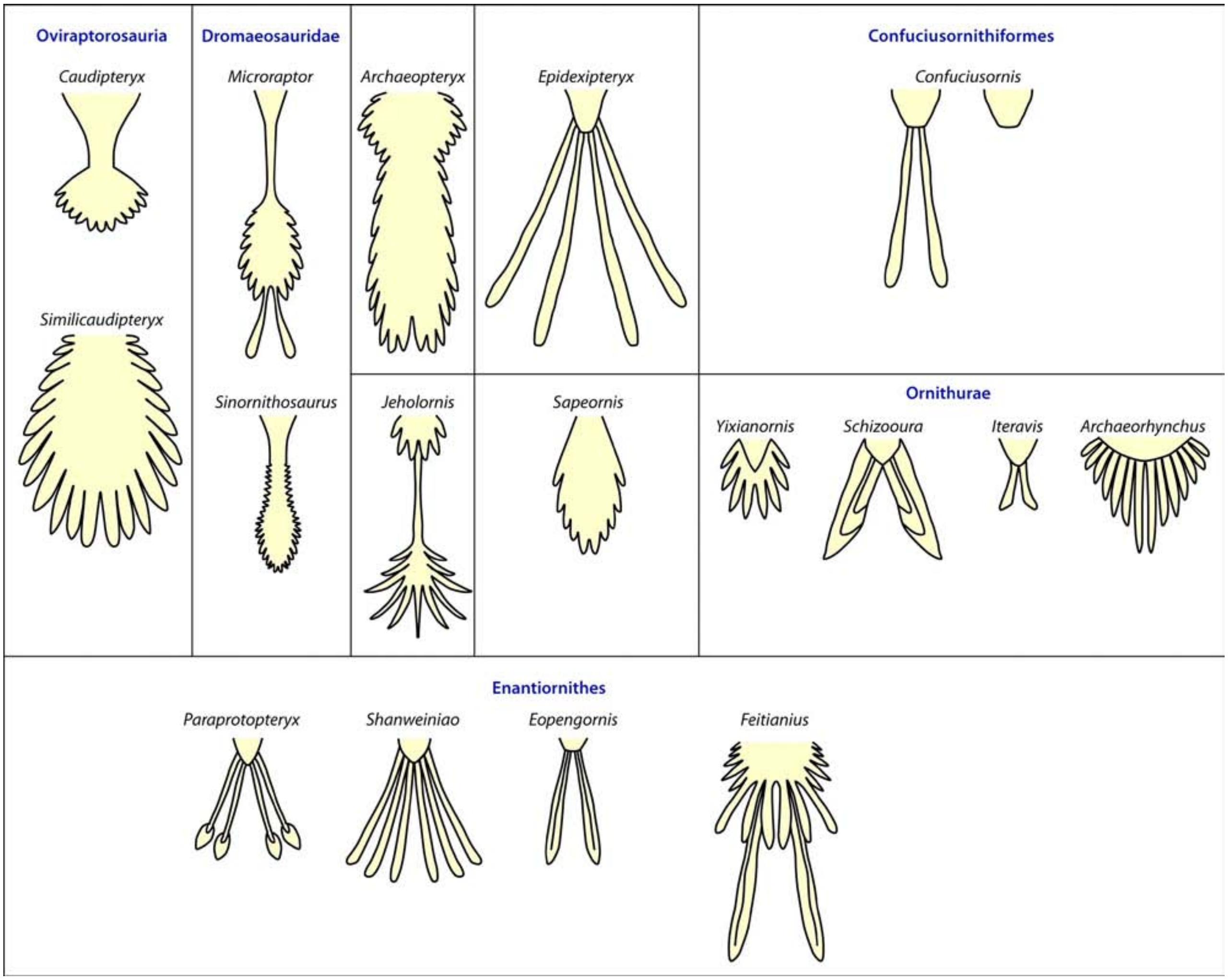

Fig. 16. Variety of different expressions of tails of birds and feathered (presumed) dinosaurs from Lower Cretaceous and Upper Jurassic (*Archaeopteryx*). (According to www. deviantart.com/albertonykus/art/PennaraptorTails-465558142)

Teeth and Beaks in Cretaceous Birds

The opposite birds common in the Cretaceous were mostly fully dentate without the beginnings of a beak, the only exception being the completely toothless genus Gobipteryx from the Upper Cretaceous of southern Mongolia, which possessed a beak (Martin and Zhou 1997). In contrast, ornithurans possessed small beaks at the anterior end of the jaw and teeth in the posterior portion (Martyniuk 2012, 43f.). Archaeorhynchus, of all species, which is at the base of the ornithurans (Wang and Zhou 2016; Zhou and Zhang 2006b, 367), has a completely toothless jaw and a flat, spoon-shaped beak.[23] In evolutionary theory, toothlessness thus occurs surprisingly early. This is also true of Confuciusornis, which is considered even more "primitive" (fig. 17). The completely toothless ornithuran genus Hongshanornis also stands relatively basally and is among the oldest representatives of this group (Zhou and Zhang 2005). Finally, we should mention Jeholornis, which stands at the base of the birds and possessed only three small teeth on the lower jaw (Zhou and Zhang 2003b; fig. 17).

Conversely, Lower Cretaceous *Yanornis* has more teeth than any other Mesozoic bird, suggesting that both increases and decreases in the number of teeth have occurred within Ornithuromorpha (O'Connor 2019, 192).

Tooth Reduction and Beaks in Theropods and Birds

Tooth reduction up to complete edentulism is not only found in Cretaceous bird groups, but also in a number of theropod groups. Here the Oviraptorosauria are to be mentioned first with numerous toothless genera from the Upper Cretaceous, while basal (and stratigraphically older) representatives possessed a small number of teeth (*Avimimus*, *Caudipteryx, Protarchaeopteryx, Incisivosaurus*). *Incisivosaurus* was distinctly heterodont (Xu et al. 2003b).

A similar situation is found in the Ornithomimosauria. Here, too, the more primitive

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[23] The beak is rhynchokinetic.

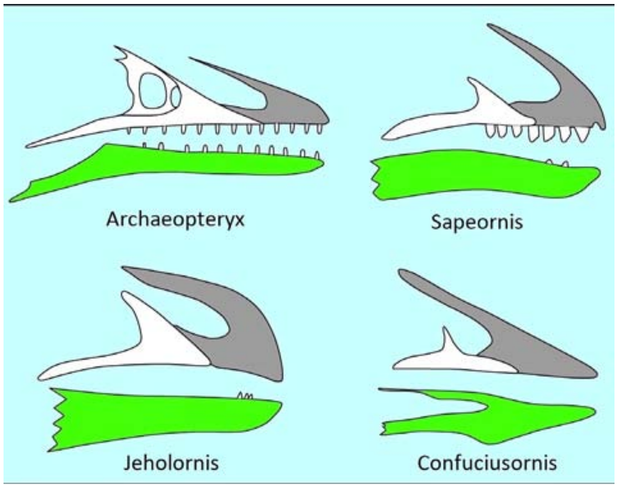

Fig. 17. Comparison of dentition in (from top left) *Archaeopteryx lithographica*, *Sapeornis chaoyangensis*, *Jeholornis prima*, and *Confuciusornis sanctus*. Premaxilla gray, maxilla white, dentals green (after Wang et al. 2017c).

(and older) genera possessed teeth (*Pelecanimimus* bore about 220 small teeth in the maxilla [at the premaxillary and maxillary] and mandible). In all other genera the upper jaw was toothless. *Shenzhousaurus* and *Harpymimus* possessed teeth in the lower jaw, while all other Ornithomimosauria were completely toothless.

Also among therizinosauria, a beak with presumed rhamphotheca was formed on the anterior part of the jaw (premaxilla) in derived genera (*Erlikosaurus*), with the posterior part occupied by many small teeth (Lautenschlager et al. 2013, 20657; Zanno 2010).[24]

Zhongornis haoae, a juvenile species of unclear systematic affiliation that is placed in the base of birds, was also toothless in lower Cretaceous rocks (O'Connor and Sullivan 2014).

Finally, *Limusaurus* must be mentioned. This genus of Ceratosauria possessed a fully developed beak and was completely toothless, but is placed among the basal theropods, and—unlike the other toothless forms—among the coelurosaurs (Xu et al. 2013). As with the other groups, an independent origin of the beak must be assumed (figs. 18–20).

That tooth reduction must have proceeded convergently is also emphasized in part by the fact that the pattern of tooth reduction differs among different groups. Tooth loss began in the posterior part of the jaw in basal birds and in taxa of Oviraptorosauria, whereas in Ornithuromorpha tooth loss began in the praemaxillary (Louchart and Viriot 2011; Mayr 2017a, 71).

Conclusions

Toothless forms or genera with a reduced number of teeth are so unsystematically distributed in the system of theropods and Cretaceous birds that a multiple independent origin of beaks with rhamphotheca or tooth reduction is assumed (figs. 18–20, see "quotes" below). While within individual groups (Ornithomimosauria, Oviraptorosauria, Therizinosauria, Enantiornithes) rough trends towards edentulism are recognizable, Confuciusornis, Archaeorhynchus and Zhongornis disturb this picture considerably. This is because these genera belong to the stratigraphically oldest forms with a beak and appear abruptly. Archaeorhynchus is according to phylogenetic analyses (cladogram) at the base of the Ornithuromorpha instead of at a derived position as expected by evolutionary theorists because of the formation of a beak.

The distribution of toothless forms in the system contradicts with respect to the feature "beak" the thesis that bird features had already evolved in the dinosaur precursors. This is because the beaks in dinosaurs can only be interpreted evolutionarily as convergent formations that arose independently and, moreover, are usually fossilized stratigraphically much later than the oldest completely toothless bird genera (*Archaeorhynchus*, *Confuciusornis*, *Hangshanornis*). With *Confuciusornis* bird beaks suddenly appear in fully developed form and they existed contemporaneously with other forms that possessed a toothed jaw.

Quotes on Convergences in Tooth Loss and Formation of a Beak

The following citations are intended to illustrate that the fossil record requires multiple convergence of tooth loss or origination of a horned beak, but this is implausible from an evolutionary point of view.

- "The loss of teeth must have appeared several times in the evolutionary history of birds because it has occurred independently in extant birds as well as more basal birds such as *Confuciusornis* and *Gobipteryx*." (Zhou and Zhang 2006b, 368)
- "Minimally, there are six lineages of Avialae that show evidence of tooth reduction, with four lineages exhibiting complete tooth loss.…Among avialaen [*sic*] lineages exhibiting tooth reduction or loss, a rhamphotheca has also independently evolved…" (Meredith et al. 2015, 1)
- "The known fossil record shows that the tooth reduction happened independently on multiple lineages of Cretaceous ornithuromorphs" (Wang and Zhou 2017, 13). Note that multiple convergence is assumed within Ornithuromorpha alone.

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[24] "Derived members of this clade are characterized by…an edentulous premaxilla and dentary tip, suggesting the presence of a rostral rhamphotheca;…" (Lautenschlager et al. 2013, 20657).

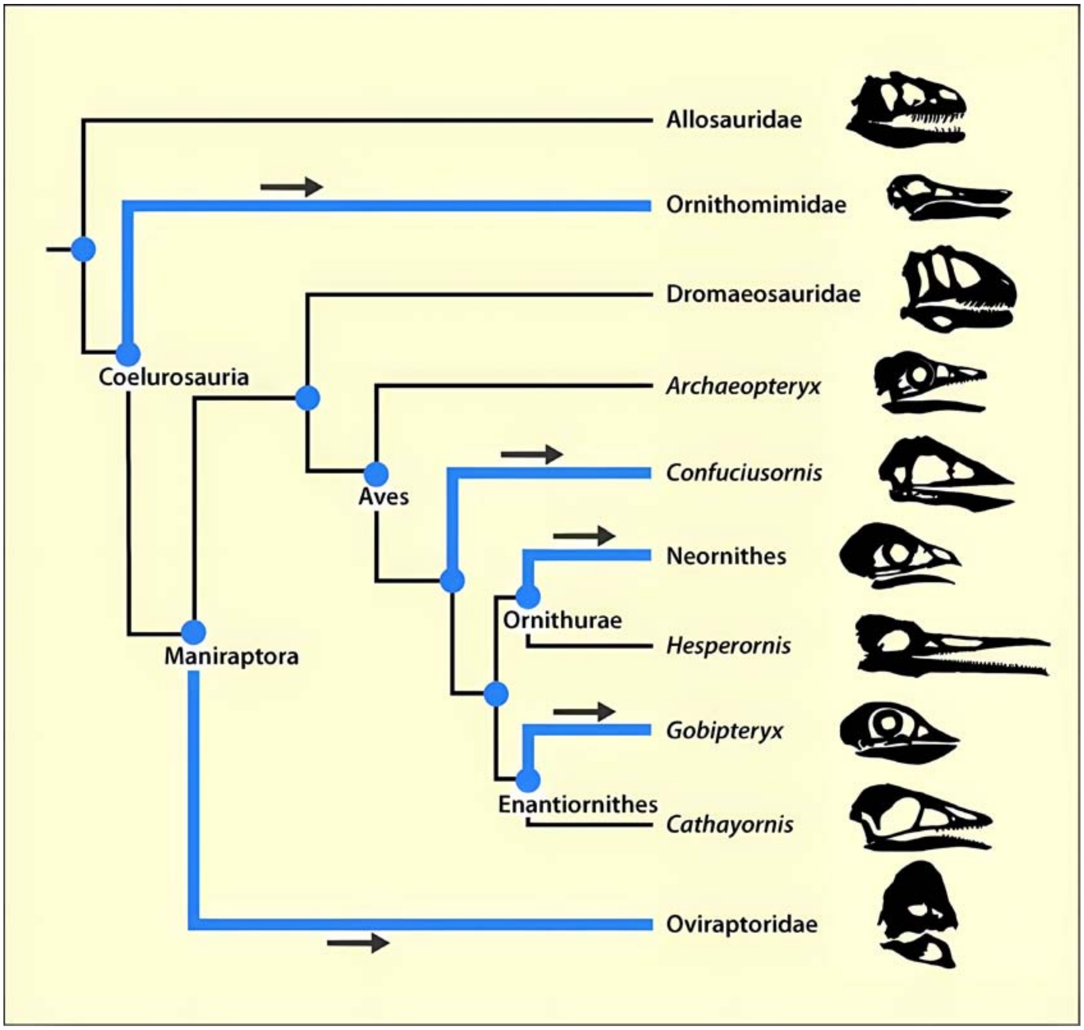

Fig. 18. Cladogram of major lineages of coelurosaur theropods showing five independent cases of tooth loss. If birds evolved, then teeth were lost independently in at least three lineages: the Confuciusornithids, the enantiornithine *Gobipteryx minuta*, and the Neornithes (according to Chiappe et al. 1999, 70).

- "At least seven transitions to edentulism occurred independently in theropod dinosaurs, all presumably accompanied by the appearance of a horny beak." (Wang et al. 2017a, 10930).
- "Teeth have been reduced or lost independently several times in various lineages of early avian evolution [e.g., *Sapeornis*, *Zhongjianornis,* Confuciusornithidae, Enantiornithes and Ornithurae]." (Zheng et al. 2011, 15905)
- "Tooth reduction occurred in many avian lineages and led to complete edentulism in Confuciusornithidae, the enantiornithine *Gobipteryx*, the basal ornithuromorphs *Archaeorhynchus, Zhongjianornis,* and *Schizooura*, as well as in Neornithes" (Mayr 2017a, 71, citing Louchart and Viriot 2011).

Brain and EQ

Birds have a greatly enlarged brain in relation to body weight compared to modern reptiles. This is especially true for the forebrain. The measure of cerebralization, which does not depend on body weight but on other factors, is also called the *encephalization index.*[25] The ratio of the relative brain size expected based on body size to the actual relative brain size is given by the *encephalization quotient (EQ).*

In birds, the encephalization index is six to eleven times higher than in other animal groups; comparably high indices are otherwise known only in mammals (Balanoff et al. 2013, 93f.).[26]

Brain structure and a gradual increase in EQ are included amongst those avian traits that were gradually acquired already in theropod dinosaurs

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[25] See https://www.spektrum.de/lexikon/neurowissenschaft/cerebralisation/1991.

[26] "Birds are distinct among living reptiles in the degree to which their brains, particularly their forebrains, are expanded relative to body size. This index of encephalization ranges from six to eleven times higher in birds than other groups, and comparably large indices are known only among mammals" (Balanoff, Bever and Norell 2014, 93f).

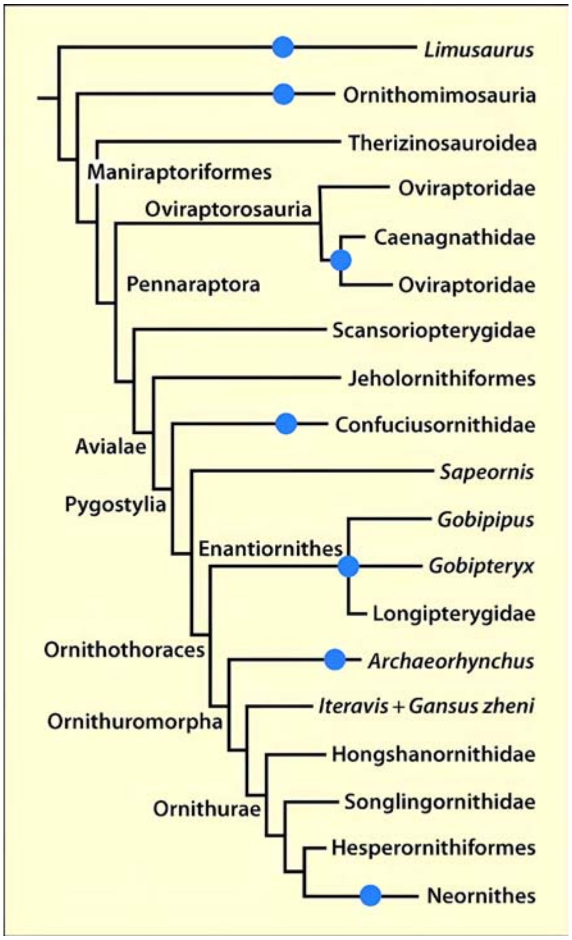

Fig. 19. At least seven independent origins of edentulism (blue dots) in theropods according to Wang et al. (2017a).

(Makovicky and Zanno 2011, 21).[27] However, some avian brain traits and high EQ also occur independently in oviraptorosaurs (Kundrát 2007[28]; Makovicky and Zanno 2011, 21, Balanoff, Bever, and Norell 2014, 13[29]). Moreover, since according to a study by Balanoff et al. (2013, 93) the relative size of the cranial cavity of *Archaeopteryx* was rather below average compared to some theropod dinosaurs. These authors conclude that avian EQ evolved convergently in many cases.[30]

Troodontids also have a higher EQ than *Archaeopteryx*. Their EQ is among the highest among theropod dinosaurs (Hendrickx, Hartman, and Mateus 2015; Makovicky and Norell 2004) and the high value must be considered convergent, as in oviraptorosaurs.

The brain features in basal birds and theropod dinosaurs in detail do not offer a consistent picture from an evolutionary perspective in other respects either. For example, the oviraptorid *Conchoraptor* has on the one hand bird-typical brain features, but on the other hand also those that are classified as more primitive compared to *Archaeopteryx*: "Most of the endoneurocranial attributes, however, have a less bird-like appearance in *Conchoraptor* than do corresponding structures in *Archaeopteryx* and modern birds" (Kundrát 2007, 499[31]; list of features on page 503). Thus, there is a feature contradiction here that forces the assumption of convergence or a secondarily flightlessness of *Conchoraptor*: "The data presented in this study do not allow an unambiguous assessment whether the avian-like endoneurocranial characteristics of the flightless *Conchoraptor* evolved convergently to those of avian theropods, or indicate a derivation of oviraptorosaurs from volant ancestors" (Kundrát 2007, 499).

Archaeopteryx is also close to present-day birds in terms of shape and features of the brain and skullcap, but less so in terms of brain size (Fabbri et al. 2017, 1546[32]; Alonso et al. 2004[33]; Sereno 2004, 996).

In the basal birds *Jeholornis*, *Sapeornis*, and *Confuciusornis, there* is no detailed knowledge about the size of the brain. Remarkable is the finding that in the Triassic archosaur *Megalancosaurus* the extremely enlarged skull is exceptionally bird-like (Feduccia and Wild 1993), which is most likely a convergence.

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[27] Thus, with regard to the evolution of the unique avian brain, phylogeny again demonstrates how highly derived avian traits were acquired in stepwise fashion throughout theropod evolutionary history" (Makovicky and Zanno 2011, 21).

[28] "Contrary to *Archaeopteryx*, the shortened olfactory tract and cerebellum overtopping cerebral hemispheres of *Conchoraptor* resemble conditions in modern birds. Calculating brain mass relative to body mass indicates that *Conchoraptor* falls within the range of extant birds, whereas *Archaeopteryx* occupies a marginal position" (Kundrát 2007, 499).

[29] "structures once considered unique to the avian brain evolved independently, or at least semi-independently" (Balanoff, Bever, and Norell 2014, 13).

[30] From the fact that *Archaeopteryx* was able to fly despite a low EQ, they further conclude that this must also apply in some form to some species not included in the Avialae. This is also confirmed by the feathering of the dromaeosaurid *Microraptor* and the troodontid *Anchiornis* (Balanoff et al. 2013, 93, 96).

[31] A list of features is on page 503 of Kundrát (2007).

[32] "*Archaeopteryx* is closer to crown birds than to non-avian maniraptorans in brain and skull-roof shape despite having a plesiomorphic endocranial volume" (Fabbri et al. 2017, 1546).

[33] "Here we show the reconstruction of the braincase from which we derived endocasts of the brain and inner ear. These suggest that *Archaeopteryx* closely resembled modern birds in the dominance of the sense of vision and in the possession of expanded auditory and spatial sensory perception in the ear. We conclude that *Archaeopteryx* had acquired the derived neurological and structural adaptations necessary for flight" (Alonso et al. 2004, 666). In terms of brain size, *Archaeopteryx* falls below the lower limit of the range for modern birds; however, its brain is three times larger than the brain of reptiles with comparable body size: "Birds with the same body mass as *Archaeopteryx* have from one-third (for example, galliforms and columbiforms) to five times (for example, psittaciforms and passeriforms) larger brains. However, the brain of *Archaeopteryx* is about three times the volume of those of non-avian reptiles of equivalent size" (Alonso et al. 2004, 668).

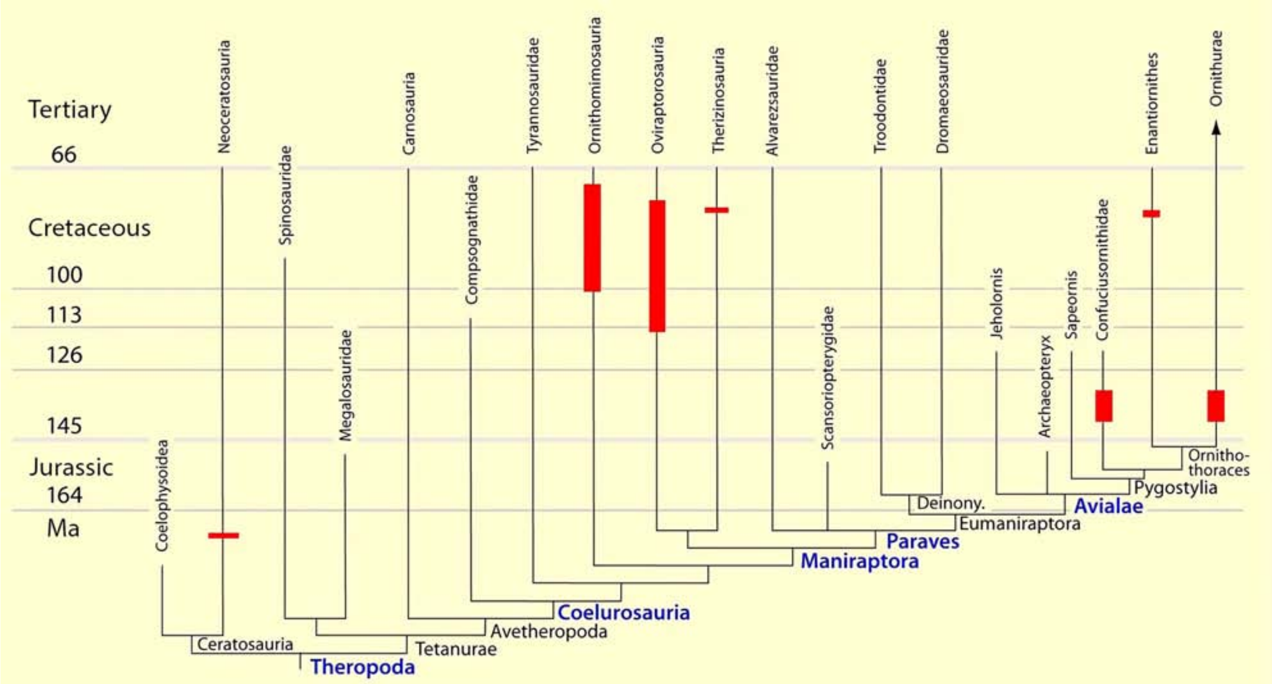

Fig. 20. Cladogram with indication of the time of occurrence showing distribution of theropod and bird groups with beaks (red markings). (Assembled according to the sources mentioned in the text.)

Wishbone

An important bird-typical feature is the wishbone or furcula. It is homologized with the two clavicles, which are fused together to form a V- or U-shaped or bilaterally sigmoid structure (fig. 21). In modern birds, the furcula varies considerably in size, shape, stiffness, and orientation relative to the rest of the shoulder girdle (Bock 2013, 1236; Close and Rayfield 2012, 1[34]). Its function may also vary accordingly. The differences tend to be related to, but not exclusive of, the type of flight. U-shaped wishbones are more common in gliders, and a more curved V-shaped expression in divers (Close and Rayfield 2012, 1).

Surprisingly, there are relatively few studies on the function of the wishbone (Nesbitt et al. 2009, 859). Frequently cited is the function as a taut spring or elastic brace between the shoulder joints that stores energy during wing flapping. The furcula also serves as a reinforcement of the thoracic skeleton to support it during the stresses of flight and as an attachment for the flight muscles, especially when flapping the wings. It also stabilizes the shoulder joint and is connected to the two shoulder blades. In addition, the furcula is thought to function in respiratory movements (Bock 2013, 1236; Jenkins, Dial, and Goslow 1988; Nesbitt et al. 2009, 859[35]).

Together with the coracoid bone and the scapula, it forms a special structure, the foramen triosseum (tri-bone canal, triosseal canal), a gap between these three bones through which runs a strong tendon that connects the supracoracoideus muscle (small pectoral muscle) to the humerus. This system is responsible for lifting the wing.

In fossil birds, the functionality of the furcula was probably partly different from that of modern birds. Olson and Feduccia (1979) assume that in *Archaeopteryx* the furcula partially replaced the weakly developed sternum as an attachment point for the flight muscles, which Bock (2013, 1238) questions. According to Makovicky and Currie (1998, 147), the function as an energy-storing feather only evolved in the Ornithothoraces.

Homology

The homology of furcula and clavicles is justified by their similar location, further by the fact that furcula and clavicles never co-occur and that both undergo similar skeletal development (Hall and Vickaryous 2015, 440).[36] However, this homology is

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[34] "Formed by midline fusion of the clavicles, the furcula is marked by considerable structural diversity (…), varying widely in terms of interclavicular angle, profile curvature (U- to V-shapes), anteroposterior curvature, and development of the hypocleideum and articular facets or epicleideum;…" (Close and Rayfield 2012, 1).

[35] According to Bock (2013, 1236), the functions of the furcula may vary depending on the species: "(a) serving as the site of origin for the cranialmost muscle fibers of the m. pectoralis; (b) maintaining a space for the passage of the esophagus and trachea; (c) acting as a spring maintaining the distance between the right and left shoulders of the pectoral girdle; (d) storing energy of the major flight muscles; (e) serving as protection for the cranial end of the bird's trunk in some diving birds; and (f) assisting in respiration during flight."

[36] "1. occupy a similar, mid-ventral position in the pectoral apparatus; 2. fail to co-exist within the same individual (no vertebrate, fossil or living, has both clavicles and a furcula); and 3. develop via intramembranous ossification, a mode of skeletogenesis that is otherwise atypical for the postcranial skeleton" (Hall and Vickaryous 2015, 440).

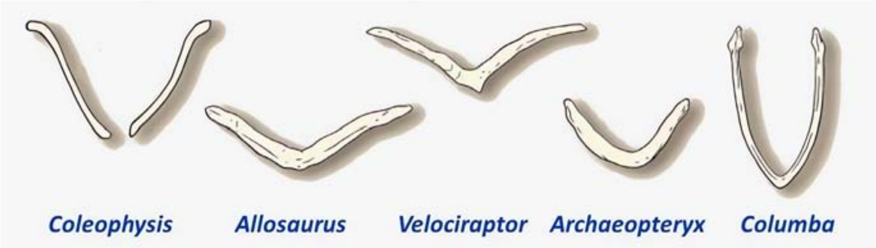

Fig. 21. Wishbones or clavicles of some theropods, in *Archaeopteryx* and in *Columba* (dove). In *Coleophysis* the clavicles are separated (after Padian and Chiappe 1998a).

not without controversy (Bryant and Russell 1993; Feduccia 1999a, 77; Feduccia and Martin 1998; Hall and Vickaryous 2015). Feduccia considers the architecture of the shoulder of dinosaurs to be so dramatically different from that of *Archaeopteryx* and of modern birds that it is unlikely that any of the shoulder bones were similarly connected to the furcula and performed a similar function as in birds.[37] When birds lose their ability to fly, the furcula degenerates, which is further evidence that the furcula in theropods is not homologous with that of birds (Feduccia 1999a, 77; Feduccia and Martin 1998). The occurrence of a furcula in *Longisquama*, a Triassic archosaur not closely related to theropods, shows that such a structure arose independently several times, so it cannot be considered a strong indication of relatedness. Moreover, the genus *Velociraptor*, which is discussed in connection with the question of homologisation, is 75–80 million years younger than *Archaeopteryx* (Feduccia and Martin 1998; see fig. 22). Norell, Makovicky and Clark (1998) express in a rebuttal the opinion that the connection of furcula and scapula in *Velociraptor* was as developed as in today's birds. In addition, there are also maniraptorans with furcula already in the Upper Jurassic, a statement, which is not exactly substantiated by the authors, however.

Based on a review of theropods with verified furcula, Nesbitt et al. (2009, 875) conclude ten years later that there can now be no doubt that the furcula of birds is homologous with the clavicles of other tetrapods (quadrupeds). This follows from both phylogenetic and developmental data.[38] However, Hall and Vickaryous (2015) later denied that homology was assured based on their studies. The furcula could also be homologous with the interclavicle. They argue that the traditional hypothesis implies a threefold loss of the clavicles in Crocodylia, Ornithischia (bird-hipped dinosaurs), and ratites, whereas if the furcula is homologous with the interclavicle, only a twofold loss should be assumed (Hall and Vickaryous 2015, 449). These two authors conclude (page 150), "We still don't know whether the furcula represents the interclavicle, a neomorph or fused clavicles."

Distribution

For a long time, the possession of a furcula seemed to be an avian-specific feature. In his influential standard work, Heilmann (1926) argued that birds could not be directly descended from theropods because this group had lost the clavicle and reevolution was impossible according to Dollo's law of irreversibility of evolution[39] (Hall and Vickaryous 2015, 443; Makovicky and Currie 1998, 143). However, it has since been found that the formation of a furcula was common in theropod dinosaurs (see fig. 23). Therefore, it is now thought that the furcula was coopted for flight in birds (for example, Brusatte 2017b, 54; Lipkin, Sereno and Horner 2007; Norell, Makovicky and Clark 1997).

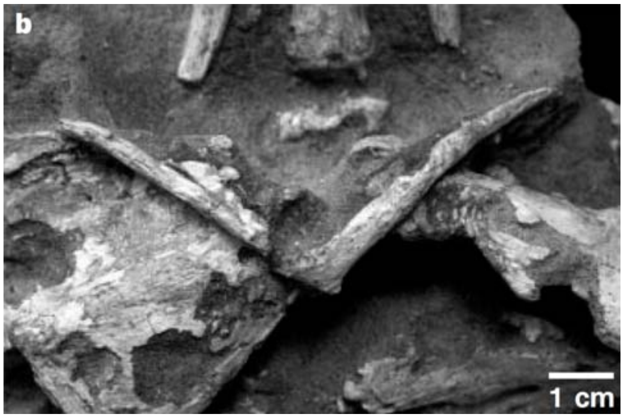

Fig. 22. Wishbone of *Velociraptor* (from Norell, Makovicky, and Clark 1997; with kind permission).

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[37] "Because the architecture of the dinosaur shoulder is so dramatically different form that of *Archaeopteryx* as well as modern birds, it seems unlikely that any of these structures could have articulated or functioned in a manner similar to the bird furcula or the hypertrophied furcula of the first bird, *Archaeopteryx* (Martin 1991), which is a large, flat, U-shaped structure lacking the hypocleidium…" (Feduccia 1999a, 77).

[38] "There no longer remains doubt that the furcula of birds is homologous to the clavicles of tetrapods. Both phylogenetic and developmental data strongly support this conclusion" (Nesbitt et al. 2009, 874).

[39] Dollo's law states that if a structure is said to have been lost in the course of evolution, it can no longer re-evolve in the same form.

The phylogenetically oldest genus in which a furcula has been demonstrated is *Syntarsus* in the Lower Jurassic, which belongs to the Coelophysidae, a basal group of theropods (Nesbitt et al. 2009, 872; Tykoski et al. 2002, 728).[40] Nesbitt et al. (2009) provide an overview of theropod groups in which a furcula has been demonstrated and conclude that all major lineages of theropods possessed a furcula from the beginning (plesiomorphic feature). Thus, the possession of a furcula is characteristic of theropods.[41] The absence of a furcula in Ornithomimosauria and Alvarezsauridae could be attributed to poor fossil preservation[42] and would otherwise be most likely interpretable as a secondary loss.[43] Alternatively, a multiple convergent origin of a furcula would have to be assumed, which Tykoski et al. (2002, 730f.) do not exclude. However, they point to large gaps in knowledge regarding the occurrence of a furcula in many theropod genera, which prevents a clear conclusion.[44] It is still noteworthy that a furcula has not been discovered even in the scansoriopterygids, which are placed close to birds. Rather, two separate clavicles have been found in *Scansoriopteryx* (Czerkas n.d.; Czerkas and Yuan 2002, 6). Based on the phylogenetic position (see fig. 23), the furcula should have re-evolved into clavicles in this group—an implausible scenario.

Nesbitt et al. (2009, 873) interpret the findings of their analysis to mean that most of the features of the furcula of present-day birds evolved early, and there were only minor differences between the furcula of early theropods and more derived forms such as *Archaeopteryx*.[45] Only the early ornithurans possessed a furcula that was typically shaped as in present-day avian lineages.[46] In contrast to the relative uniformity of the shape of the furcula in fossil forms, there is great variation among present-day birds (see above).

Discussion

The furcula can be inserted only conditionally into the series of the bird-typical characteristics, which should be evolved *step by step* already with the theropods. If one follows the phylogenetic analyses, the furcula was already formed at the base of the theropods. Thus it is a plesiomorphic feature and as such not meaningful regarding more exact relationships between theropods and birds. Theoretically, however, within an evolutionary paradigm, the formation of a furcula can be interpreted as a pre-adaptation.

Another question is, how starting from a theropod furcula the conditions in birds evolved? The function as an elastic, energy-storing clasp requires many adjustments in the bird body. This is even more true if one considers that the furcula is polyfunctional. Changing function or integrating new functions is likely to be a formidable challenge for undirected evolutionary mechanisms. What hurdles would have had to be overcome would have to be shown by a closer comparison of forms brought into an evolutionary lineage. However, given the patchiness of the fossil record, one encounters methodological limitations here.

The homology of the furcula of different groups is obvious, but is not regarded as certain by all researchers. The fact that no furcula was found in the scansoriopterygids, ornithomimosaurs, and

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[40] “These specimens mark the earliest confirmed record of furculae to date, both temporally and phylogenetically” (Tykoski et al. 2002, 728).

[41] Similarly, Tykoski et al. (2002, 728, 732). “Given the abundant missing data with respect to basal theropods, the furcula may yet prove apomorphic for Theropoda” (Tykoski et al. 2002, 732).

[42] Nesbitt et al. consider this interpretation possible in alvarezsaurids because of their poor preservation: “alvarezsaurids are known from a few largely incomplete specimens making the absence of a furcula possibly a result of taphonomic processes” (Nesbitt et al. 2009, 872). However, Chiappe, Norell, and Clark (2002, 102) point out, “The scapula, coracoid, and sternum are well known in both *Mononykus* and *Shuvuuia*. Portions of the scapulocoracoid and coracoid are preserved for *Alvarezsaurus* and *Patagonykus*, respectively. None of the available specimens of these taxa preserves a furcula. The fact that some of these (e.g., MGI 100/977) are exquisitely preserved and articulated suggests that this element was probably absent in Alvarezsauridae,…”

[43] Thus, with the Ornithomimosauria. “No unambiguously recognizable clavicle or furcula has been found in any ornithomimid even though well-preserved completely articulated specimens are known from many taxa.…It is unclear if the furcula was never preserved, if it was not ossified, or if it did not form at all. The absence of a furcula would be interpreted as a secondary loss following the phylogeny presented here” (Nesbitt et al. 2009, 872).

[44] It is difficult to say unequivocally whether the furcula arose many times independently or was lost more than once, and for which taxon or taxa its presence is diagnostic. This is because our current knowledge of the distribution of clavicular elements among non-avian theropods is incomplete, no clear consensus with regards to hypotheses of theropod phylogeny” (Tykoski et al. 2002, 730f.). See also Makovicky and Currie (1998, 147): “Rather, the known patchy distribution of the furcula within theropods is most parsimoniously interpreted either as a number of independent evolutions of clavicular fusion (…), or as a large number of independent losses of a plesiomorphic feature. Because clavicles are of dermal origin, the absence of a furcula may reflect an unossified, and perhaps juvenile stage, or simply be due to non-recovery or misidentification.”

[45] “The early evolution of the furcula shows that most features found in the furcula of extant birds are found in all theropods. Only small changes separate the furculae of early theropods such as *Coelophysis bauri* from those of more derived forms such as *Archaeopteryx lithographica*. It is now clear that all major theropod clades have furculae plesiomorphically. Clades and taxa in which furculae are not found can now be interpreted as a result of preservational bias or a secondary loss” (Nesbitt et al. 2009, 873).

[46] “The furculae of early avialans are nearly identical to closely related clades such as Dromeosauridae [*sic*] and Troodontidae. Only the early ornithurines possess a furcula typical of extant avian clades” (Nesbitt et al. 2009, 874).

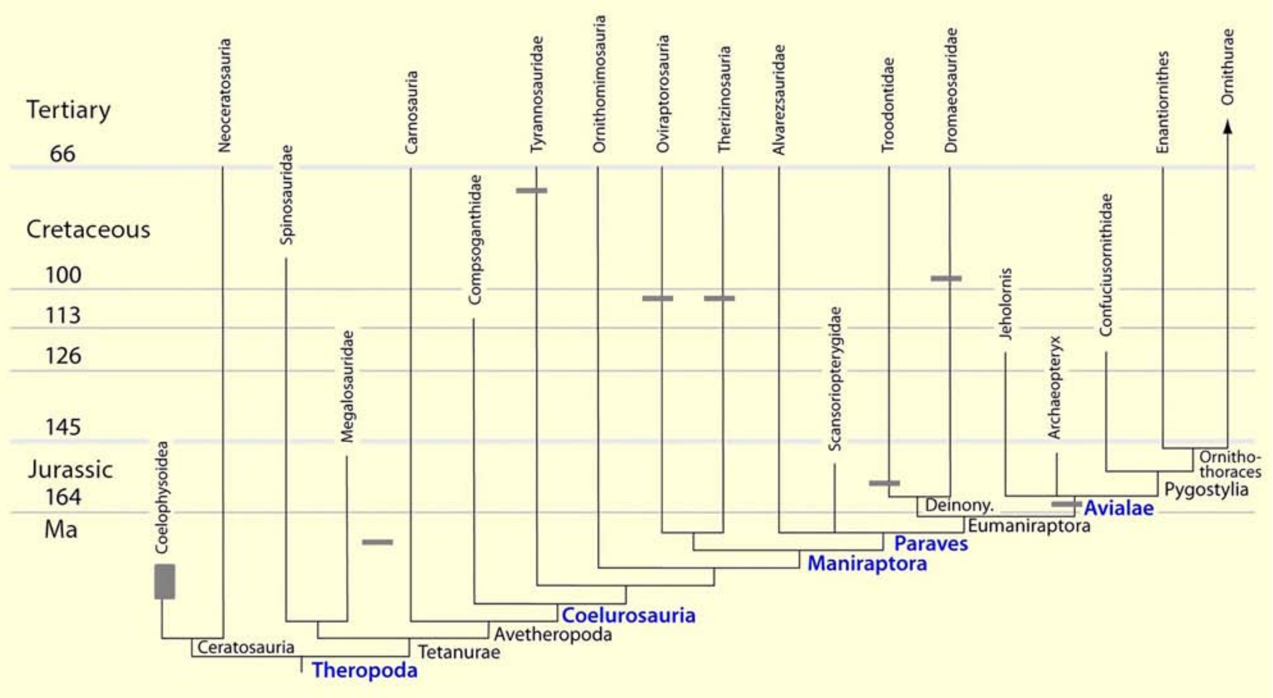

Fig. 23. Distributions of theropod and bird groups with furcula (see markings). Whether there is convergence in all cases or lack of preservation (Ornithomimosauria, Alvarezsauridae) cannot be determined with certainty at this time. The scansoriopterygids were shown to possess separate clavicles. More details in the text. (Assembled from sources cited in the text.)

alvarezsaurids, despite partially good preservation, is problematic from the point of view of evolutionary theory, because it is incomprehensible that a furcula is abandoned again. This case is known for secondarily flightless birds, but one will hardly want to assume such a scenario for these three groups. Alternatively, one could assume a multiple independent emergence of a furcula. However, convergences are always problematic from an evolutionary theoretical point of view (lineages designed by means of cladism are based on the parsimony principle). Therefore, Nesbitt et al. (2009) consider it most likely that a furcula was not detected in the groups in question because of poor fossilization, that is, that its absence is a conservation artifact. In view of partly good preservation and even more in view of the formation of separate clavicles in *Scansoriopteryx*, this explanation is not very reasonable. However, further finds could provide clarity here.

Feduccia takes the regression of the furcula in present-day flightless birds as evidence that the furcula is a new formation in birds. He argues, "If this [loss] is a pervasive characteristic of flightless birds, why would one expect to find a fully developed furcula in flightless bipedal dinosaurs?" (Feduccia 1999a, 265). However, since a furcula occurs in these forms, it must have had a different function than in birds, which argues against its homology with the avian furcula.

Overall, despite Feduccia's objection, there is much to be said for a homology of the furcula of birds and theropod dinosaurs, but this cannot be considered certain. On the homologizability it depends in turn whether the furcula of birds can be interpreted as a feature that was already developed in the non-flying presumed ancestors.

Gastralia, Rib Cage, Sternum

Gastralia

Features that link some theropod dinosaurs to early birds include gastralia (fig. 24). They support the thorax and serve as attachment sites for muscles in the thoracic region (O'Connor et al. 2015c, 133, 143). They may also play a role in respiration. The gastralia interlock to form a type of basket (gastral basket). They are dermal bones that are not connected to the rest of the skeleton.

Gastralia are known from all lineages of early Mesozoic bird groups, including the basal genera *Archaeopteryx*, *Confuciusornis*, *Jeholornis*, and *Sapeornis* (for systematic position, see fig. 4). With 15–16 pairs of gastralia, the early pygostylian *Sapeornis* had the largest known ventral rib cage (O'Connor et al. 2015c, 135; fig. 24). Present-day birds do not possess gastralia. In them, the strongly developed sternum is thought to serve the function of the gastralia. However, there are many fossil bird species that possess both sternum and gastralia (see below). Gastralia have also been described in theropod dinosaurs and sauropods *(Apatosaurus)* and are found among modern lizards in tuataras and crocodilians.

O'Connor et al. (2015c) describe gastralia and their numbers in Troodontidae, Dromaeosauridae, *Archaeopteryx*, *Jeholornis*, *Sapeornis, Confuciusornis*, Enantiornithes, and Ornithuromorpha. Gastralia are also described in the carnosaur *Aerosteon* (Allosauroidea) (Sereno et al. 2008) and the oviraptorid *Citipati* (Tickle, Norell, and Codd 2012, 741) (both from the Upper Cretaceous; see fig. 4 for systematic position). Unfortunately, the complete gastral rib cage is known in only a few derived theropod genera, so evolutionary trends with respect to this feature can largely only be speculated (O'Connor et al. 2015c, 142).[47] The size of the gastral rib cage is not particularly reduced in basal birds. The relationship between body size and the number of gastralia appears to have been markedly different in theropod dinosaurs on the one hand and Mesozoic birds on the other, leading O'Connor et al. (2015c, 144) to conclude that different evolutionary trajectories are present in the two groups.[48] Their studies have also shown that, contrary to intuitive expectations, there is no correlation between the formation of a sternum and the number of gastralia in paravians and basal birds. Thus, *Anchiornis* (without a bony sternum) possessed about 13–14 pairs of gastralia, about as many as *Microraptor gui,* which possessed a sternum that was even rostrocaudally elongated.[49] *Jeholornis* possessed only 8–9 pairs of gastralia despite being about the same size as *Sapeornis* with 15–16 gastralia and despite possessing a sternum quite similar to that of *Confuciusornis*. This situation is incongruent with the situation in other basal birds (O'Connor et al. 2015c, 145; see also Agnolin et al. 2019, 19; see figs. 25, 26).[50] Only among the Ornithothoraces (Enantiornithes+Ornithuromorpha) does there appear to be a trend toward a smaller gastral rib cage with increasingly complex sternum construction.[51]

The conjecture that the relatively large gastral rib cage in basal birds was related to flight and compensated for the lack of a bony sternum, while obvious, is not conclusive because, as noted, among these forms there is no clear relationship between the formation of the gastralia and the possession of a bony sternum. It is not properly understood how the musculature attached to the gastralia could have supported flight. It is possible that it had a function in respiration (O'Connor et al. 2015c, 145).

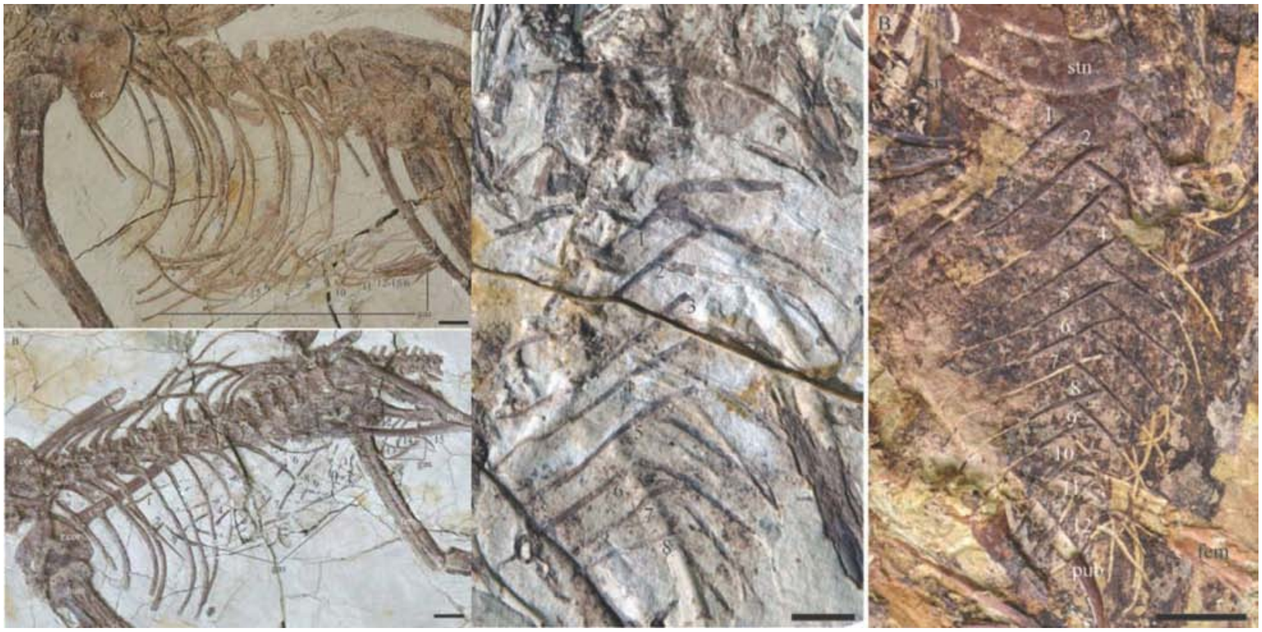

Fig 24. Left, the nearly complete gastral basket of *Sapeornis chaoyangensis*; middle, gastralia of *Jeholornis*; right, of *Confuciusornis*. Abbreviations: 1–16 pairs of gastralia, cor coracoid, fem femur, gas gastralia, hum humerus, pub pubis, sca scapula, stn sternum. Scale bars 10 mm each (from O'Connor et al. 2015c).

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[47] "Unfortunately the complete gastral basket is only known in a handful of derived theropod taxa (n=15) leaving any resultant trends highly subject to distortion due to preservational bias" (O'Connor et al. 2015c, 142).

[48] "Differences in the size range encompassed by Theropoda (ranging a whole order of magnitude) versus Mesozoic Aves indicate that two groups did not share the same relationship (if any) between size and number of gastralia, indicating different evolutionary trajectories (Fig. 4)" (O'Connor et al. 2015c, 144).

[49] "Although intuitively we may infer the presence of a sternum might limit the number of gastralia, restricting them caudally, observations between non-avian paravians and basal birds with and without sterna of similar size are comparable (table 1). The complete gastral basket of *Anchiornis* appears to be composed of approximately 13–14 pairs of gastralia. Despite its rostrocaudally elongate sternum, we estimate the gastral basket in the similarly sized taxon *Microraptor gui* was formed by 14–15 pairs of gastralia" (O'Connor et al. 2015c, 144).

[50] "Incongruous with other Early Cretaceous birds, *Jeholornis* only preserves eight to nine pairs of gastralia (Fig. 3A), despite the fact it is roughly the same size as Sapeornis and has a sternum fairly similar to that of *Confuciusornis*" (O'Connor et al. 2015c, 145).

[51] "Within the derived clade Ornithothoraces (Enantiornithes+Ornithuromorpha) there is an apparent trend towards smaller gastral baskets in more derived taxa with increasingly complex sternal morphologies, with an inverse correlation to body size" (O'Connor et al. 2015c, 145).

It is still remarkable that the gastralia in theropod dinosaurs are strongly derived. They cross the midline of the body and are articulated with two gastralia of the opposite side (Codd et al. 2008, 160).[52] In contrast, while limited by a lack of data, there is a trend toward simplification in Cretaceous birds (see above). *Thus, the conditions in theropod dinosaurs cannot be readily interpreted as precursor stages with respect to the conditions in birds.* An interpretation as precursor stages is also opposed by the stratigraphic position of the theropod genera, which possess Gastralia (fig. 25).

Sternum

The sternum is where the powerful flight muscles attach for the upstroke and downstroke of the wings, and it has many functions related to flight. It is the largest bone, one of the most important and characteristic skeletal features of modern birds, and has a wide range of expression (Zheng et al. 2012, 1, 2).[53]

The distribution of species with an ossified sternum is puzzling from an evolutionary theoretical point of view. This is because the basal avian genera *Archaeopteryx*, *Sapeornis,* and the closely related troodontids *(Anchiornis)* placed in the Paraves lacked an ossified sternum, whereas one has been demonstrated in the theropod groups of Dromaeosauridae, Oviraptorosauria, and others (O'Connor and Zhou 2015; O'Connor et al. 2015c, 135, figs. 27, 28; Zheng et al. 2012). Given approximately 100 and 200 individuals studied, respectively, it can hardly be assumed that the absence is a conservation artifact (Zheng et al. 2014b).[54] In evolutionary terms, this implies a zigzag course, or in other words, the distribution of this trait does not suggest a relationship with the putative phylogeny. O'Connor et al. (2015c, 135) describe this situation as confusing.[55] Zheng et al. (2012, 5) consider it quite possible that the common ancestor of the

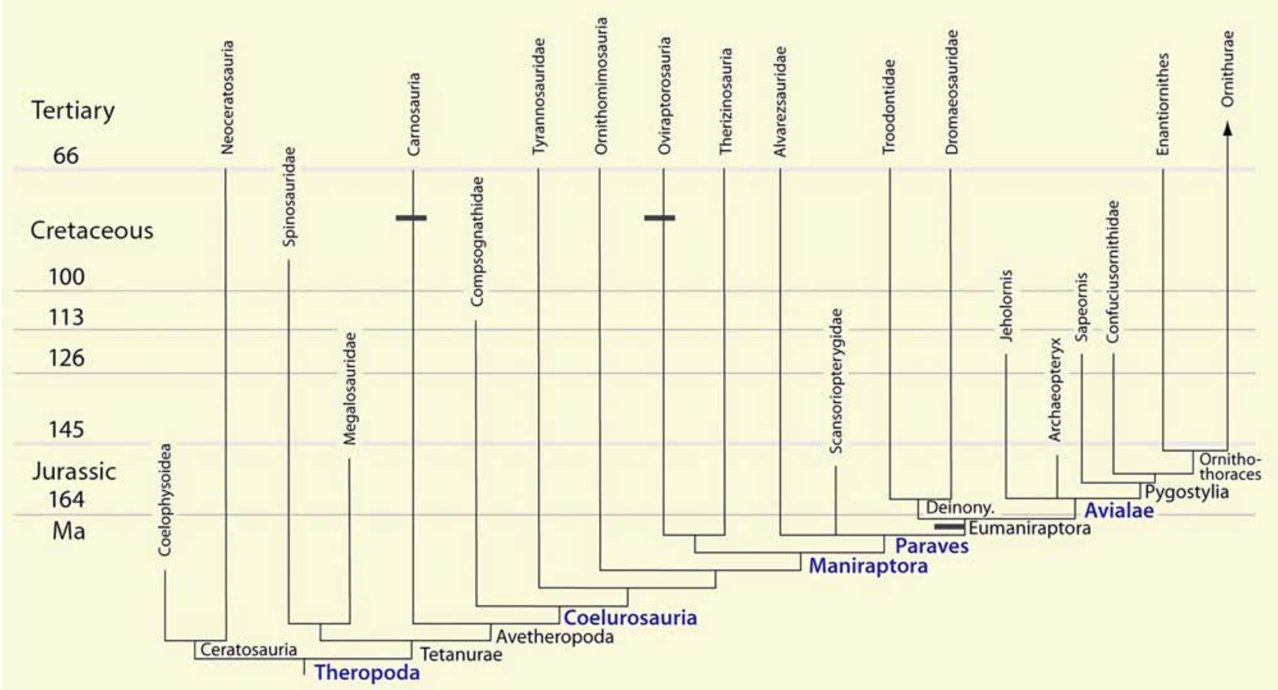

Fig. 25. Distributions of theropod and bird groups with gastral ribs (see markings). (Assembled according to the sources mentioned in the text.)

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[52] "The gastralia of non-avian maniraptoran theropods are highly derived, cross the midline and articulate with two gastralia from the opposite side of the body" (Codd et al. 2008, 160).

[53] "The sternum is the largest bone in the modern avian skeleton; it has many functions, almost of all of which are thought to be related to flight, . . . This large bone provides attachment surface for the powerful flight muscles, the *m. supracoracoideus* and *m. pectoralis*; the former contributes to lifting the wing during flight and is especially important during takeoff, whereas the latter is primarily responsible for the downstroke. These large muscles typically account for 25–35% of the average neornithine body mass" (Zheng et al. 2012, 2).

[54] "We have observed more than 200 specimens of *Anchiornis*, the earliest known feathered dinosaur, and nearly 100 specimens of *Sapeornis,* one of the basalmost birds, and recognize no sternal ossifications. We propose that the sternum may have been completely lost in these two taxa (and *Archaeopteryx* as well) based on histological analysis and the excellent preservation of soft-tissue structures, thus suggesting the absence of a sternum could represent the plesiomorphic avian condition" (Zheng et al. 2014b, 13900).

[55] "*Sapeornis* notably lacks an ossified sternum (Zhou and Zhang 2002a), which is also absent in the basal most avian *Archaeopteryx* (Wellnhofer and Tischlinger 2004) and the Troodontidae, . . . and ossified sternal plates are present in the Dromaeosauridae (Paraves), Oviraptorosauria (Maniraptora), and a number of other groups of dinosaurs (Chiappe et al. 2002; Galton and Upchurch 2004; Norell and Makovicky 2004; Osmólska et al. 2004) making their apparent absence at the base of the avian clade perplexing" (O'Connor et al. 2015c, 135).

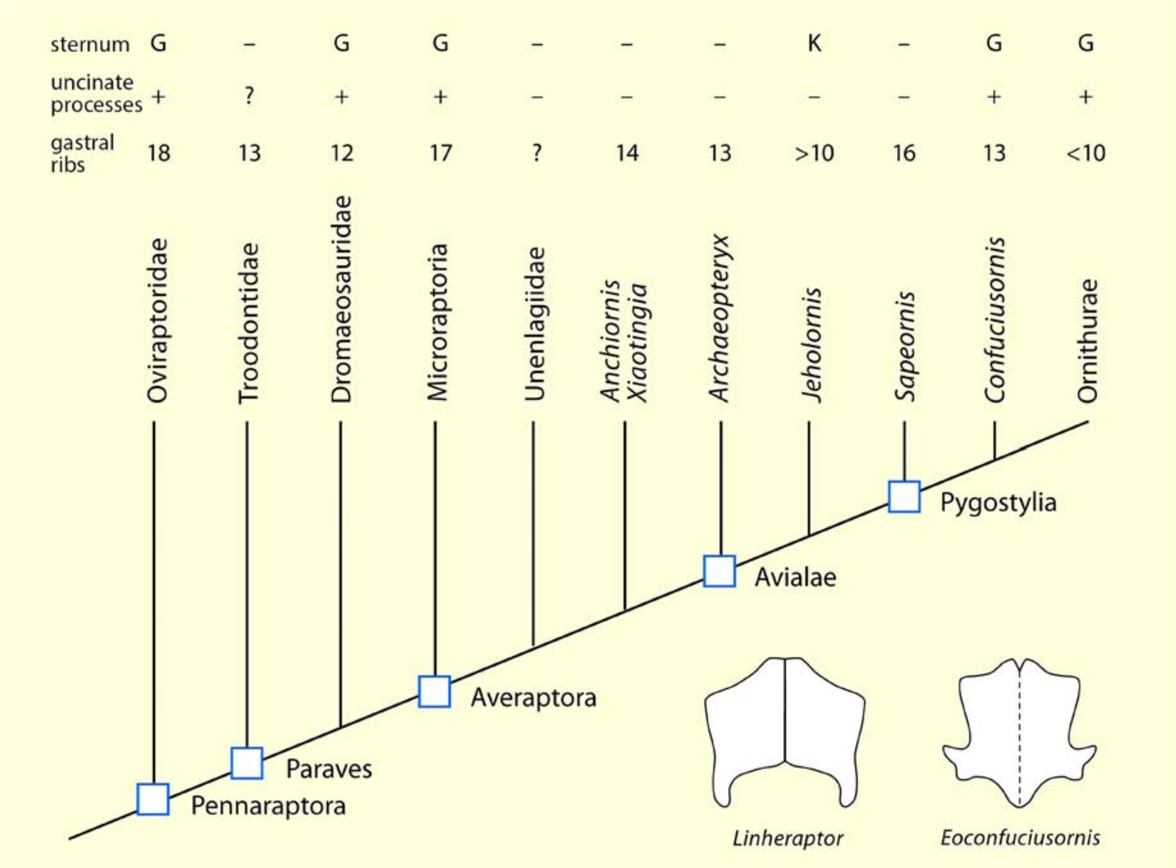

Fig. 26. Simplified cladogram of derived coelurosaurs after Agnolin and Novas (2013) showing the number of gastral rib pairs, occurrence of uncinate processes on the ribs and the relative expression of the sternum. Lower right, pectorals of the dromaeosaurid *Linheraptor exquisitus* and the pygostylian *Eoconfuciusornis zhengi*. G large, K small, + present, - absent, ? uncertain (after Agnolin et al. 2019).

Ornithothoraces (opposite birds and ornithurans, which include present-day birds) did not possess a sternum.[56] In this case, however, this means that *the sternum in some theropod dinosaurs cannot be included amongst the features that link the putative dinosaur ancestors of birds to birds.*

More complex forms of the sternum with posteriorly (caudally) directed processes and a sternum keel are known only in the Ornithothoraces. One of the stratigraphically oldest genera of the opposite birds, *Protopteryx*, already possessed a sternum keel (Zhou and Zhang 2006a). Even among the stratigraphically oldest genera placed among the ornithurans, *Ambiortus* was a genus with a keeled sternum (Kurochkin 1985).[57] In the basal species (which are placed outside the Ornithothoraces) the sternum is simpler and comparable to that of theropod dinosaurs. Intermediate stages are poorly known, and the development and evolution of the complex sternum are largely unknown to date, note Zheng et al. (2012, 2).[58] The sternum of Mesozoic ornithurans (the lineage to which modern birds are included) is essentially modern in appearance, with various appendages, sulci (furrows), and windows, and its evolution from the simple elements of most theropod dinosaurs is unclear (Zheng et al. 2012, 3).[59]

In basal birds, as in dromaeosaurids and oviraptorids, the sternum (when it occurs) is formed from two medially connected plates that fuse late in

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[56] "The distribution of dinosaur sterna suggests that their presence is plesiomorphic in Aves; the ornithothoracine common ancestor probably possessed paired sternal plates, medially fused in the adult. However, given the absence of a sternum in some Mesozoic birds *(Archaeopteryx, Sapeornis)*, it is possible that the ornithothoracine common ancestor did not have an ossified sternum" (Zheng et al. 2012, 5).

[57] Its position in the system is unclear and controversial because of an unusual mix of derived and primitive features (see Kurochkin 1985).

[58] "With all major clades of Mesozoic birds appearing simultaneously in the Early Cretaceous, intervening stages are poorly known, and the development and evolution of the complex sternum has until now been largely unknown" (Zheng et al. 2012, 2).

[59] "The sternum of Cretaceous ornithurines, the clade that includes living birds, is essentially modern in appearance, preserving all major structural features that are present in neornithines (for example, rostrally projecting, ventrally deep keel, deep coracoidal sulci, rostral spine, craniolateral processes, caudal fenestrae). How this complex element evolved from the two simple plates observed in most non-avian dinosaurs is unclear" (Zheng et al. 2012, 3).

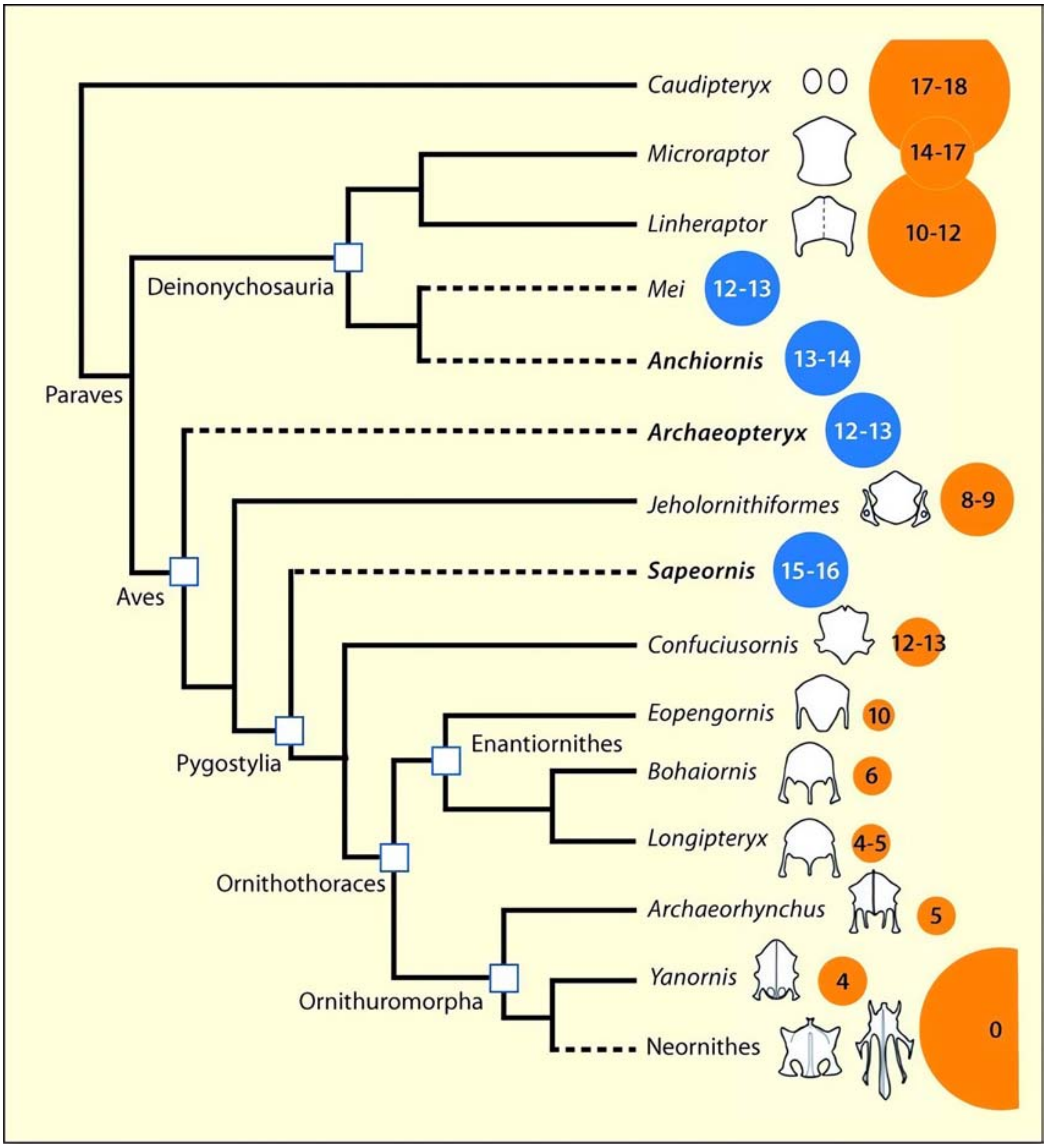

Fig. 27. Simplified cladogram of theropods showing the construction of the sternum. Size of circle reflects body size; blue and dotted lines indicate absence of sternal ossification, yellow indicates presence. The number within the circle indicates the number of gastralia; these are absent from both Neornithes (dashed line). The small light circle within the circle for the Neornithes is to indicate the extreme size difference in fossil and present-day members of this group (adapted from Zheng et al. 2014b; © 2014 National Academy of Sciences).

ontogeny. Such a pattern is also known from present-day flightless birds (O'Connor and Zhou 2015). In contrast, in enantiornithine birds of the Jehol Group of China, the sternum is formed by proximodistally arranged median ossification centers. Therefore, this feature cannot be considered a common derived trait (synapomorphy) of the birds (O'Connor and Zhou 2015, 337f.).[60] Zheng et al. (2012, 1, 2) also note such large differences in the expression and ontogenetic development of the sternum in Enantiornithes and Ornithurae that they hypothesize convergent origins despite comparable sternum complexity.

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[60] "Instead of being formed by medially articulating plates, the sternum is formed primarily by proximodistally arranged median ossification centers (Zheng et al. 2012). Therefore, despite the importance of the boney sternum in living birds, this skeletal feature fails to provide any synapomorphies or autapomorphies for Aves as a whole (Fig. 1)" (O'Connor and Zhou 2015, 337f.).

"Ossification proceeds from the caudal half proximally, which is opposite to the direction of sternal development in living birds...The main body of the sternum in enantiornithines is formed by two ossifications, as in birds and non-avian dinosaurs, but instead of a bilaterally symmetrical pair, they are two proximo-distally arranged vertically symmetrical ossifications of very different morphology" (Zheng et al. 2012, 4).

"The enantiornithine condition, in which the majority of the sternum is formed by two unilateral ossifications, is very different from both the dinosaurian and neornithine pattern of development: formed primarily from bilateral pairs of ossifications" (Zheng et al. 2012, 5).

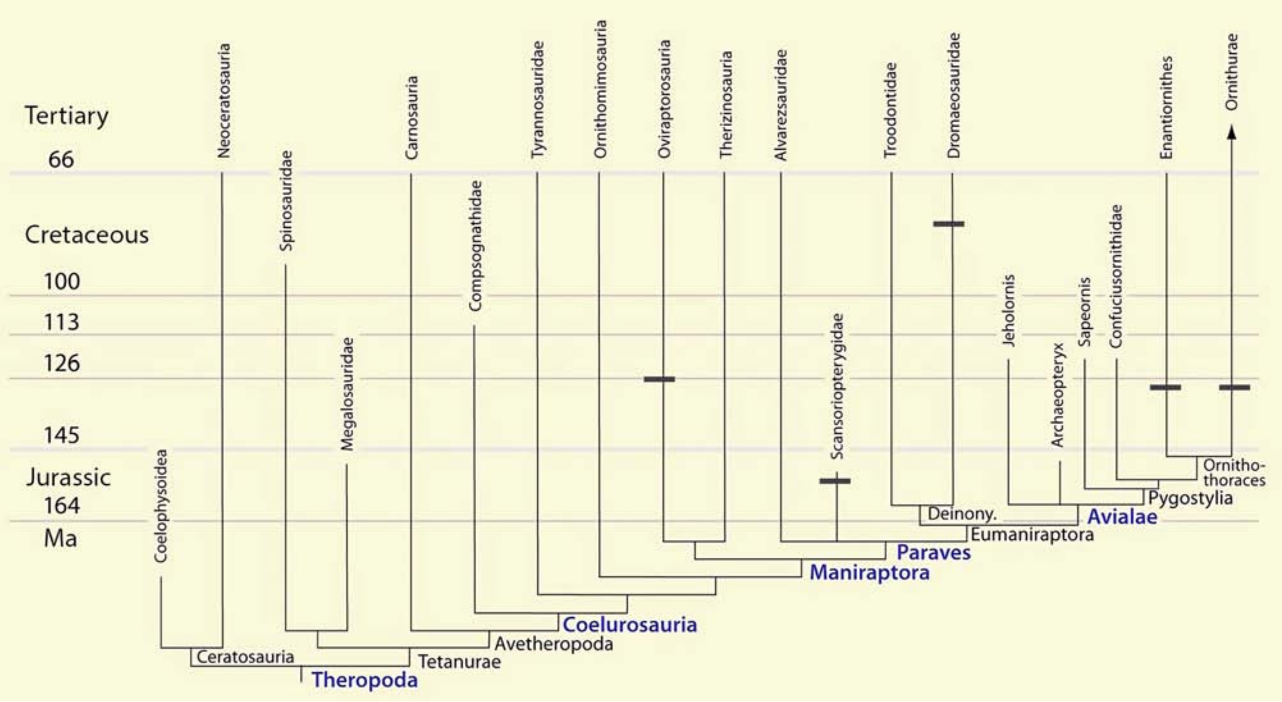

Fig. 28. Distributions of theropod and bird groups with ossified sternum (sternal plates) (see markings) (assembled from sources cited in the text).

Common sternum expressions should be considered parallelisms, not developmental homologies.[61]

Uncinate Processes on the Ribs

A bird-typical feature in the trunk skeletal region is posteriorly directed uncinate processes of the ribs. It has been demonstrated in the oldest known beaked bird, Confuciusornis, as well as in the oldest known ornithuran genus Chaoyangia (Zhou et al. 2000, 253) and one of the oldest enantiornithine genera, Longipteryx (Zhang et al. 2001, 948). Uncinate processes of the ribs also occur in dromaeosaurids and oviraptorosaurs (Zhou et al. 2000; Zhou 2004, 461; Codd et al. 2008, 157f.; Chatterjee and Templin 2012).[62] Therefore, they are also included amongst the avian features that were already developed in the presumed dinosaur ancestors (Codd et al. 2008, 157). Among present-day animals, such uncinate processes are also known in the tuatara (tuatara) and developed in a cartilaginous form in crocodiles.

The uncinate processes on the ribs help strengthen the rib cage by overlapping with the following rib. They also serve as muscle attachment sites for muscles of the scapula and play a role in respiration because they are involved in its mechanics (Zhang et al. 2001, 948f.; Codd et al. 2008).[63] This, in turn, is evaluated by Codd et al. (2008) as indirect evidence for bird-like respiration also in theropod dinosaurs and consequently for a very high activity of these animals.[64] However, a function of the appendages in crocodilians and the tuatara as supporters of ventilation has not been demonstrated; but the

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[61] “Here we show that although basal living birds apparently have retained the dinosaurian condition in which the sternum develops from a bilateral pair of ossifications (present in paravian dinosaurs and basal birds), the enantiornithine sternal body primarily develops from two unilateral proximo-distally arranged ossifications. This indicates that although superficially similar, the sternum formed very differently in enantiornithines and ornithuromorphs, suggesting that several ornithothoracine sternal features may represent parallelism” (Zheng et al. 2012, 1).—“Comparison with the morphology of the sternum in non-avian dinosaurs and the development of the sternum in living birds reveals major differences in the development of this element. This may suggest that shared features of the sternum are parallelisms (not developmentally homologous, . . .), highlighting the large amount of homoplasy that characterizes avian evolution as a result of the constraints of powered flight” (Zheng et al. 2012, 2).
“Although ornithothoracine sterna are superficially similar and far more derived than other groups of Mesozoic birds (for example, Confuciusornithiformes, Jeholornithiformes), enantiornithines retain some basal morphologies (for example, poorly developed keel)” (Zheng et al. 2012, 3).

[62] According to Zhou (2004, 461): Dromaeosauridae: *Microraptor*; Oviraptorosauridae: *Citipati*, *Caudipteryx,* and Oviraptoridae, *Heyuannia*. Zhou (2004, 461) also mentions an occurrence in therizinosaurs, but he does not give a source for this.

[63] “Our geometric model indicates that uncinate processes act as levers which improve the mechanical advantage for the forward rotation of the dorsal ribs and therefore lowering of the sternum during respiration in birds” (Codd et al. 2008, 157).

[64] Their presence in these dinosaurs represents another morphological character linking them to Aves, and further supports the presence of an avian-like air-sac respiratory system in theropod dinosaurs, prior to the evolution of flight” (Codd et al. 2008, 157). “The implications of a putative air-sac system in theropods are that these were highly active animals” (Codd et al. 2008, 160).

muscle attachment sites in the tuatara are at least similar to those in birds (Codd 2008, 159).[65] Because of these uncertainties, the function of uncinate processes in theropod dinosaurs must be assessed with caution. However, based on their research, Codd et al. (2008, 160) conclude that in these genera the uncinate processes, in concert with the specialized gastralia, sternum, and shoulder girdle, facilitated an avian-like respiratory mechanism.[66]

Puzzling Distribution

As mentioned earlier, uncinate processes on the ribs are known in dromaeosaurids and oviraptorosaurs in addition to birds. Codd et al. (2008) consider the uncinateprocesses of birds to be homologous with those of theropod dinosaurs and justify this on the basis of their distribution in the system (fig. 29) and the parsimony principle.[67] According to Zhou et al. (2000, 253), uncinate processes in oviraptorids and in *Caudipteryx* (Oviraptorosauria) are barely distinguishable from those in birds. Tickle, Norell, and Codd (2012, 740) confirm that the geometry of the construction of the thorax in the theropod dinosaur *Citipati* (Oviraptoridae), in the basal avian species *Zhongjianornis yangi* and *Confuciusornis sanctus*, and in the ornithuran *Yixianornis grabaui* allowed rib movement of the same magnitude as in modern birds. These authors take this as evidence that this enabled a flow-through respiratory system in theropod dinosaurs and basal birds, and that uncinate processes of the ribs were a key adaptation for this, established before birds evolved.[68]

Nevertheless, this feature is not well suited to be placed in the series of bird features in dinosaurs. This interpretation is contradicted by the fact that it is missing in the basal birds *Archaeopteryx*, *Sapeornis, Jeholornis,* and *Zhongornis,* as well as in the alvarezsaurids (which are close to birds) (Norell and Makovicky 1999, 27; Tickle, Norell, and Codd 2012, 744; see fig. 29). Thus, according to evolutionary theory interpretation, the uncinate processes should have been lost to reappear later (similar to the sternum, but not consistently in the same species). Alternatively, the formation is convergent despite great similarities (Norell and Makovicky 1999, 27[69]; Zhou et al. 2000, 253[70]). The possibility that the appendages were present in the above genera but are not preserved fossil (Tickle, Norell, and Codd 2012, 744) can hardly be definitively ruled out, but seems unlikely given the good preservation of the genera in question.

Paul (2001, 479) is of the opinion that features of the respiratory apparatus, such as the uncinate processes of the ribs, were more derived in dromaeosaurids and oviraptorosaurids (which are placed in the ancestry of birds) than in *Archaeopteryx* and were developed similarly to those of secondarily flightless birds. He evaluates this as one of the indications that these forms could have been secondarily flightless.[71] But then the genera in question would not be witnesses for a connection between dinosaurs and birds with respect to the feature of uncinate processes.

Pneumatic Bones, Air Sac System and Respiration

For birds, lightweight construction of the whole body is enormously important. An air sac system (fig. 30) and pneumaticity contribute to this. Both are closely coupled with the respiratory system. The bones are air-filled by penetrating diverticula (protrusions) of the air sac system and thus connected to it. The air sac system consists of attachments to the lungs and allows for highly effective respiration (see below). Birds possess varying numbers of air sacs. Usually there are nine air sacs distributed throughout large parts of the body. They fill approximately 15% of the volume of the thorax and abdomen (Britt 1997; Proctor and Lynch 1993, 210). Air is forced into the

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[65] "Cartilaginous or ossified uncinate processes are reported in crocodiles (Hofstetter and Gasc 1969) and the tuatara (Romer 1956); however, their possible role as ventilator structures has yet to be determined.... Indeed, in tuatara (Sphenodon punctatus), the external oblique muscle originates at the margin of the gastral basket and inserts onto the base of the uncinate processes similar to that described in Aves" (Codd et al. 2008, 159).

[66] "Our study indicates that the presence of uncinated processes, coupled with specialized gastralia, sterna and pelvic girdles, provides a mechanism for facilitating avianlike breathing mechanics in non-avian maniraptoran dinosaurs" (Codd et al. 2008, 160).

[67] "Using parsimony, the presence of uncinates in early avian species, their presence in several non-avian maniraptoran groups and their phylogenetic distribution indicate that they are homologous structures" (Codd et al. 2008, 159).

[68] These skeletal characteristics provide further evidence of a flow-through respiratory system in nonavian theropod dinosaurs and basal avialans, and indicate that uncinate processes are a key adaptation facilitating the ventilation of a lung air sac system that diverged earlier than extant birds" (Tickle, Norell, and Codd 2012, 740).

[69] Because of their sporadic distribution, uncinate processes may be a synapomorphy for a clade of theropods including birds, or, owing to their putative absence in alvarezsaurs and *Archaeopteryx lithographica*, may represent convergence" (Norell and Makovicky 1999, 27).

[70] "may indicate that this structure is not a synapomorphy for birds but rather that it had appeared in birds and theropods a lot more times than we expected" (Zhou et al. 2000, 253).

[71] "The presence of respiratory adaptations (ossified uncinate processes and sternal ribs, up to five sternocostal articulations, and long sternal plates) more derived than those of the urvogel in dromaeosaurs, caudipterygians and oviraptorosaurs is interesting, because these adaptations are similar to those of secondarily flightless birds. This adds to the evidence that these exceptionally bird-like dinosaurs may also have been secondarily flightless, and closer to modern birds than archaeopterygiforms" (Paul 2001, 479).

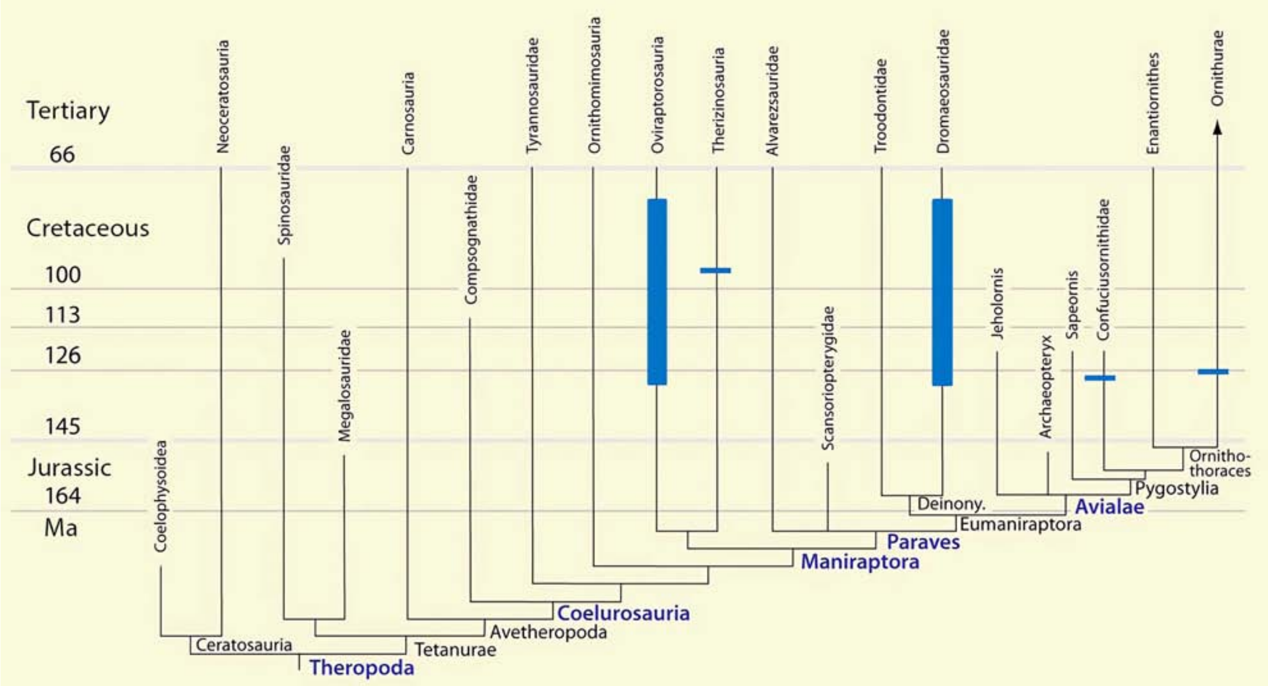

Fig. 29. Distributions of theropod and bird groups with uncinate processes on their ribs (pink markings). (Assembled according to the sources mentioned in the text)

lungs via the air sacs, as by bellows. During the breathing process, the air flows in a kind of one-way street into the posterior air sacs and from there into the lungs, further into the anterior air sacs and then into the trachea (Schmidt-Nielsen 1971; figs. 31, 32). Thus, unlike other vertebrates, there is an air circuit, which allows for a much larger respiratory volume compared to mammals, even though the lungs are very small, accounting for only 2% of the body volume.

Schmidt-Nielsen (1971) describes the details of airflow through the air sacs and lungs. He shows that there is a distinctly sophisticated system. By leaving stale, CO_2-rich air in the trachea during the breathing process, this air first flows into the posterior air sac during inhalation before fresh air is added. This is not a mistake, but is important for the consistency of the blood and the regulation of breathing: "Here we encounter one of the most elegant features of the system. If completely fresh outside air, which contains only .03% carbon dioxide, were passed through the lung, the blood would lose too much carbon dioxide, with serious consequences for the acid-base regulation of the bird's body. Another consequence of excessive loss of carbon dioxide arises from the fact that breathing is regulated primarily by the concentration of carbon dioxide in the blood" (Schmidt-Nielsen 1971, 76).[72]

It is also unusual that the lungs are constant in volume. A network of blood vessels surrounds the finest branches of the bronchial system (parabronchi) of the lung, making it a dense organ and very different from the lightly constructed lungs of other vertebrates. The diameter of the parabronchi is so small that if their inner walls were to touch, refilling would not be possible due to surface tension and the bird would suffocate. This is the reason why the lung tissue must be fixed with the help of the rib cage and by connective tissue so that the lung volume can be kept constant (Britt 1997, 591; Schachner et al. 2011, 1532).[73]

Breathing occurs when the ribs move apart laterally, causing the air sacs to move. This paradoxically causes air to leave the lungs when inhaling and fill them when exhaling. Unlike mammals, birds do not have a muscular diaphragm to drive respiration. The intercostal muscles are used for this purpose (Proctor and Lynch 1993, 205). A diaphragm would be obstructive because of the air sac system. Thus, air exchange is fundamentally different from respiration in other vertebrates. "Almost every part of the avian

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[72] Schmidt-Nielsen (1971, 76) also write, "Hence we see that the avian lung is continuously supplied with a mixture of air that is high in oxygen without being too low in carbon dioxide.... but enough of it remains in the trachea to ensure the right concentration of carbon dioxide in the posterior sacs after the next inhalation."

[73] "The diameters of the parabronchi are so small that if the inner walls of parabronchi touch, surface tension will not allow reinflation and the bird suffocates. For this reason, pulmonary cavity volume is tightly constrained by the rib cage and connective tissues" (Britt 1997, 591).

"The air sac system and lungs of birds are associated with bicapitate ribs with a ventrally positioned capitular articulation, generating a rigid and furrowed rib cage that minimizes dorsoventral changes in volume in the dorsal thorax. The thin walled bronchi are kept from collapsing by fusion of the lung to the thorax on all sides." (Schachner et al. 2011, 1532)

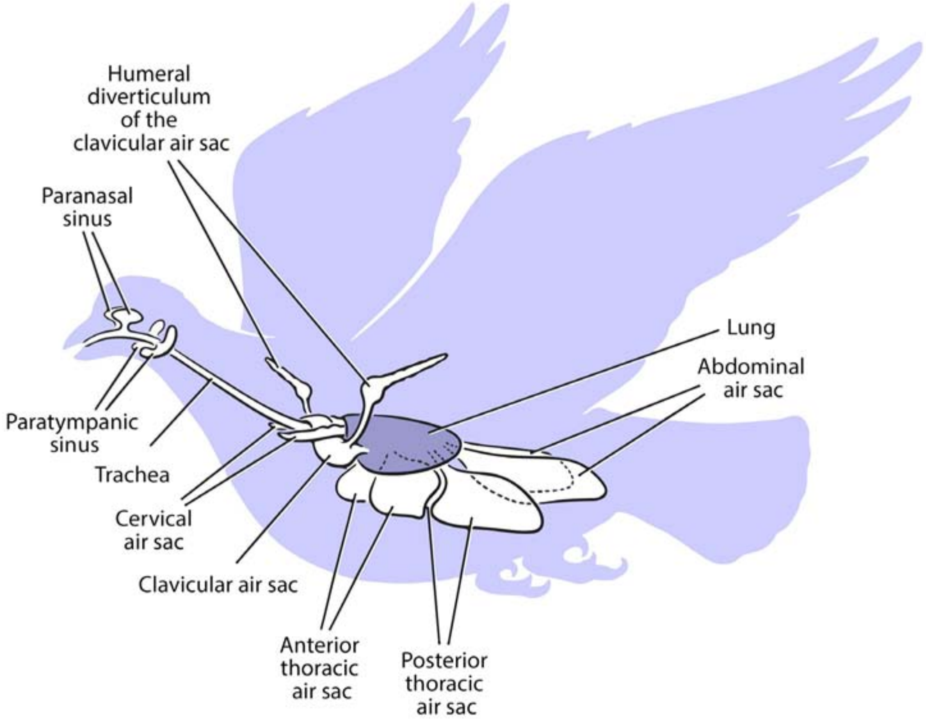

Fig. 30. Lung air sac system in birds. C. Abraczinskas, "Original caption: 'Figure 1. Cranial sinus and postcranial air sac systems in birds. All pneumatic spaces are paired except the clavicular air sac, and the lungs are shaded. Abbreviations: aas, abdominal air sac; atas, anterior thoracic air sac; cas, cervical air sac; clas, clavicular air sac; hd, humeral diverticulum of the clavicular air sac; lu, lung; pns, paranasal sinus; ptas, posterior thoracic air sac; pts, paratympanic sinus; t, trachea,'" https://commons.wikimedia.org/wiki/File:Cranial_sinus_and_postcranial_air_sac_systems_in_birds.jpg. CC BY-SA 2.5.

body is directly related to the respiratory system of the air sacs" (Proctor and Lynch 1993, 205).

The air sacs are also involved in vocalization. Exhalations are modulated into song in the vocal head. Finally, the air sacs and the numerous outgoing diverticula also play an important role in thermoregulation by releasing heat through evaporation. This explains why not only bones but a large part of the bird's body is interspersed with diverticula. Thermoregulation is thus quite different from that in mammals. Sweat glands are not developed, nor would they be effective under the dense plumage. Several very different aspects of avian anatomy and physiology are thus closely coupled, on the one hand, and fundamentally different from conditions in mammals, on the other. In this regard, Proctor and Lynch (1993, 205) state that the respiratory system of birds is "surprisingly dissimilar" to that of most other terrestrial vertebrates.[74]

Fossil Findings

Pneumaticity of the skeleton is known among modern vertebrates only in birds, but was common in extinct archosaurs (Benson et al. 2012, 170), including all theropod lineages (O'Connor and Claessens 2005), pterosaurs, and sauropods, and mainly in the vertebrae but also in the ribs. Pneumaticity has also been detected in cervical and thoracic vertebrae of *Archaeopteryx* (Britt et al. 1998) and in the pelvis of the London specimen (Christiansen and Bonde 2000), which is considered to indicate the existence of air sacs (Wang and Zhou 2017, 20). Therefore, pneumatized bones are among those bird characteristics that are also present in presumed dinosaur ancestors; in the case of this feature, even common. It could be a feature that even the Ornithodira (birds, dinosaurs, and pterosaurs) have in common (Quick and Ruben 2009, 1242). Therefore, this trait is not suitable to determine more precise relationships within this group and between dinosaurs and birds.

Statements about whether air sacs were also formed in fossil preserved forms outside the birds are not possible without doubt. Their existence can only be inferred indirectly or corresponding assumptions, also about the construction of the lungs, can be substantiated by indirect evidence.[75] Pneumatized bones are also important for weight saving. Schachner et al. (2011, 1533) point out that pneumatization of bones has no function in respiration and many findings indicate that it is primarily for weight saving, so pneumaticity does not necessarily indicate

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[74] There are also avian-specific features at the cellular level ("internal respiration") (Proctor and Lynch 1993, 205).

[75] "As in the case of the alveolar lung, we lack a fossil record of the avian lung" (Farmer 2010, 567).

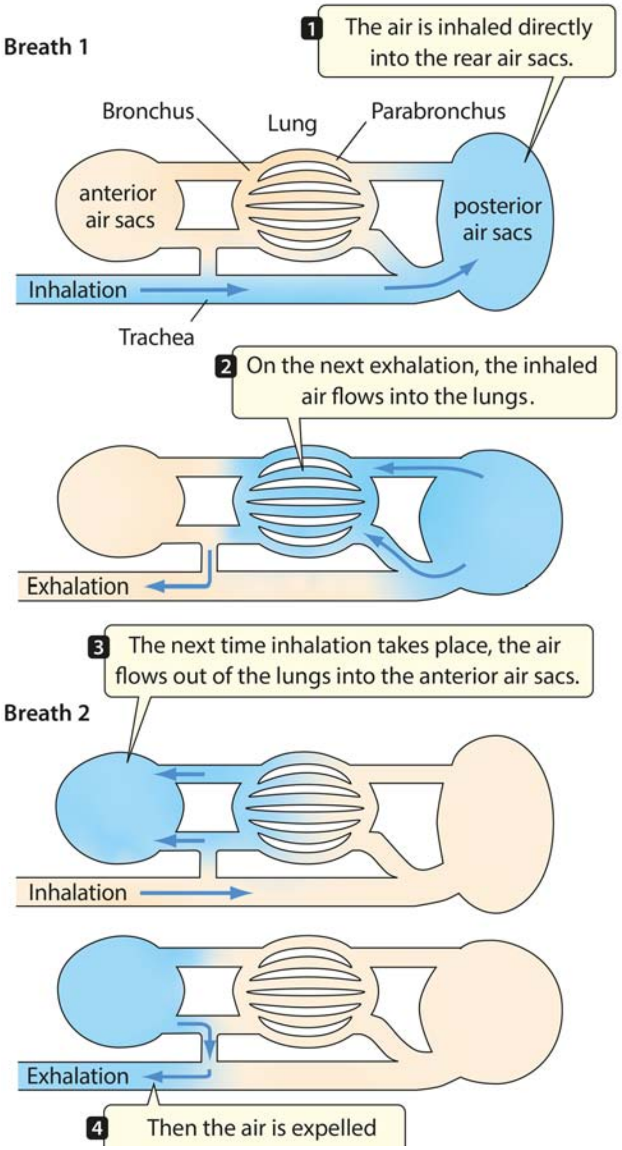

Fig. 31. Respiratory cycle in birds (after Purves et al. 2003).

the existence of air sacs.[76] However, the evidence of pneumatized bones *with air pores* is strong evidence for the existence of air sacs, according to Britt (1997, 591).[77]

O'Connor and Claessens (2005) found pneumatic openings in cervical, thoracic, and pelvic vertebrae in a fossil specimen of the primitive Upper Cretaceous theropod genus *Majungatholus* (later renamed *Majungasaurus*). They conclude on the existence of corresponding air sacs, whose diverticula are to be assigned to different vertebral bodies. The lung construction plan of the birds with flow of the air had been developed with it already with a basal neotheropodan, which is not more near related with the birds.[78] Thus, it could be assumed that flow-through breathing was probably a general characteristic of theropods (O'Connor and Claessens 2005, 253) and not a new acquisition specifically related to the ability to fly.[79]

This conclusion is supported by a study by Sereno et al. (2008) on the also "original" allosauroid genus *Aerosteon* (like *Majungasaurus* from the Upper Cretaceous). The fossil in question exhibits extreme pneumatization of bones, including the furcula, ilium, and gastralia. The researchers conclude that diverticula of the air sac system were formed in the thorax tissues.

Wang and Zhou (2017, 20) also argue that the pneumatization of bones in several theropod lineages indicates that the "modern" avian respiratory system evolved prior to the origin of birds.[80]

Bird-like respiration could also be indicated by the presence of uncinate processes on the ribs, which are also found in some theropod dinosaurs (for example, oviraptorids and dromaeosaurids such as *Velociraptor*, Deinonychosaur, *Microraptor* [Codd et al. 2008]). This is because these are involved in the mechanics of respiration, but this relationship is not

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[76] "Pneumaticity, or the invasion of bone by air cavities, is a good example of a tempting but equivocal correlate of pulmonary form and function. . . . This would be especially interesting if the presence of air sacs was linked to other pulmonary features, such as unidirectional airflow through tubular gas-exchange structures (parabronchi). On the other hand, the use of fossil evidence of pneumaticity to reconstruct respiratory anatomy has been criticized because pneumaticity plays no known role in respiration or gas exchange, and the preponderance of the data indicates its function is lightening the skeleton to aid flight or reduce rotational inertia (Farmer 2006). . . . Thus, while pneumaticity is consistent with the presence of air sacs, it is not necessarily evidence for air sacs, . . ." (Schachner et al. 2011, 1533).

[77] "Pneumatic diverticulae, being soft tissue, are not fossilized. Tracks and traces of these diverticulae, however, are often preserved on the exterior of bones. Also, it is these traces that permit the recognition of bones that were pneumatic in life. . . . The key to recognizing internally pneumatized bones is the presence of a large, pneumatic foramen leading to interior chambers. These large foramina represent the point of invasion by a pneumatic diverticulum" (Britt 1997, 591).

[78] "Postcranial skeletal pneumaticity" [pneumatic vertebrae in cervical, thoracic (dorsal) and sacral regions of the vertebral column; Erg.]. in *Majungatholus atopus*, "documenting these features in a taxon only distantly related to birds. Taken together, these specializations imply the existence of the basic avian pulmonary blueprint in basal neotheropods, indicating that flow-through ventilation of the lung is not restricted to birds but is probably a general theropod characteristic" (O'Connor and Claessens 2005, 253).

[79] Evolutionary theorists speak of "exaptation:" An existing trait is (additionally) used for a new, previously unnecessary purpose. "The fact that homologous features are present in the ancestral theropods, however, negates the flight adaptation hypothesis and suggests that postcranial pneumatization is an exaptation to flight" (Britt 1997, 592).

[80] "Recent fossil evidences have documented occurrences of the postcranial skeletal pneumaticity in several lineages of theropods, . . . suggesting that the modern bird-like respiratory system evolved before the origin of birds" (Wang and Zhou 2017, 20).

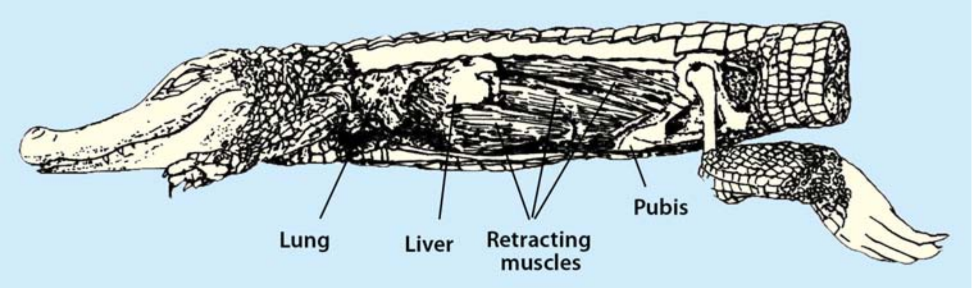

Fig. 32. Respiratory movements in crocodiles: "Recent crocodiles possess . . . a diaphragm-like membrane consisting of a thick layer of connective tissue that separates the thoracic cavity from the abdominal cavity. Although this membrane acts like a diaphragm and provides ventilation to the lungs, it does not contain muscle fibers (as is the case in mammals, for example). The respiratory movement of crocodiles comes about through a retracting muscle on the liver. The liver, with its position between the diaphragm and the retractor muscle, acts like a pumping piston. An anatomical peculiarity of crocodiles is that the liver protrudes dome-shaped into the thoracic cavity" (Zimbelmann 1999).

compelling (Zhang et al. 2001, 948f.; Codd et al. 2008, 157, 159; Tickle, Norell, and Codd 2012; see above for more details).

Controversy About the Respiratory System of Theropods

Quick and Ruben (2009) consider that some anatomical features of many theropod dinosaurs, such as the small sternum and lack of a bird-like thorax, the three-pronged pelvis, and the construction of the legs, contradict the possibility of bird-like respiratory movements because all of these are associated with breathing. The femur of birds is relatively firmly seated, and bone and musculature of the femoral region, along with the synsacrum and posteriorly oriented pubis, are needed to support the body wall, which must be understood in the context of the air sac system and helps keep the avian lungs from collapsing. In contrast, the femurs of the dinosaurs were mobile and therefore could not have fulfilled this task (Quick and Ruben 2009).[81]

In addition, there are (however controversial) indications that the theropods *Sinosauropteryx* and *Scipionyx* from the group of coelurosaurs had a respiratory system similar to that of crocodiles. Indeed, Ruben et al. (1997, 1999) found darkly colored protruding areas in the abdominal region of these two fossil genera that could be traces of the former liver, which in reptiles plays a special role in respiration as a kind of piston by allowing the lungs to expand and contract again by means of muscles and a diaphragm-like septum. In addition, the posterior section of the abdominal cavity appears to have been distinctly separated from an anterior heart-lung section. In *Scipionyx,* scientists also believe they can discern muscle fibers running from the pelvis to the presumed liver, a situation similar to that in present-day crocodilians (see fig. 32). Overall, these findings suggest reptilian respiration that is distinctly different from the flow-through respiration of birds. Meanwhile, simple flow-through respiration has been demonstrated in crocodilians and alligators, but it functions without an air sac system and much differently than in birds (see below).

Some paleontologists, however, dispute that the fossil evidence allows the interpretation of Ruben et al. 1997; 1999). For this the fossils are too strongly flattened and the fossil evidence is not clear (Paul 2001). Wellnhofer (1999) also points out that even if Ruben et al. (1997, 1999) interpret the fossil findings correctly, this is not a counterargument against an evolutionary transition from dinosaurs to birds, because a transition from a reptile lung to a bird lung could have occurred at a later stage of evolution.

In addition, Paul (2001, 479) believes that there was a gradual acquisition of bird-like features of the

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[81] "The thin walled and voluminous abdominal air-sacs are supported laterally and caudally to prevent inward (paradoxical) collapse during generation of negative (inhalatory) pressure: the synsacrum, posteriorly directed, laterally open pubes and specialized femoral-thigh complex provide requisite support and largely prevent inhalatory collapse" (Quick and Ruben 2009, 1232). "Thus, in the absence of a bird-like ribcage, a dearth of space to accommodate fully avian sized abdominal air-sacs in the caudal body cavity or a skeletal mechanism to resist their paradoxical collapse, theropods were unlikely to have possessed functional bird-like abdominal air-sacs" (Quick and Ruben 2009, 1242).

Jones and Ruben (2001; 458) write: "Nevertheless, some maniraptoran theropods (e.g., Velociraptor) may have had a retroverted pubis (Norell and Makovicky 1997). However, in each of these cases the pubis lacks a hypopubic cup . . . and does not extend appreciably beyond the posterior margins of the ischium and ilium—a morphology inconsistent with ventilation of avian-style lungs. . . . In fact, no known theropod shows evidence of reduced reliance on the hepatic piston-diaphragm mechanisms or transition toward features indicative of the presence of an avian-style lung and lung ventilation, as one would expect if the commonly accepted hypothesis of the relationship of dinosaurs and birds are correct. . . .The pubes of theropods and early birds are apparently more broadly distinct from each other, both functionally and morphologically, than is generally assumed."

respiratory system in theropods and that the thorax of the most bird-like dinosaurs was essentially bird-like in construction. However, some features of the respiratory system, such as ossified uncinate processes of the ribs, sternal ribs, the presence of up to five sternal rib joints, and long sternal plates, were more derived in dromaeosaurs, *Caudipteryx*, and oviraptorosaurs than in *Archaeopteryx*. Remarkably, these adaptations resembled those of secondarily flightless birds, which could be taken as an indication that bird-like dinosaurs could also be secondarily flightless (see below).

As mentioned above, there are correlations between the special properties of the avian lung (volume constancy, very sensitive parabronchia) and features of the skeleton (especially ribs and vertebrae) that ensure that the lung volume remains almost constant. Schachner et al. (2011) examined the axial skeleton of a number of very different extinct archosaurs for skeletal features related to lung construction. They found no evidence on the vertebrae of a liver-mediated pump-piston mechanism in any of the taxa studied, but found features that argued for the existence of a rigid lung.

When or in which group of forms the bird-like respiratory mechanism first developed under evolutionary theoretical conditions is ultimately difficult to clarify for methodological reasons, since there are too many unknowns and the coupling of skeletal features with features of the respiratory system is fraught with uncertainties. In any case, a reorganization into avian lungs would require considerable reorganizations because of the abovementioned interconnections, regardless of when and in which lineage this occurred. Realistic evolutionary theoretical modeling would have to take this into account. Ruben et al. (1997) consider an evolutionary transition problematic because it would be stopped by selection at an early stage, and because a bipartite body cavity, as crocodiles possess and need for respiration (see above), would prevent the creation of air sacs. For this would require the abdominal cavity to be separated from the thoracic cavity, which would require a rupture of the diaphragm and destroy its function before further "remodeling" could even begin.[82] The reorganization of thermoregulation would face similar problems. These significant evolutionary problems arise regardless of when or in what lineage the respiratory system of birds evolved.

Decision by a New Study?

In a large-scale study, Brocklehurst, Schachner, and Sellers (2018) recently showed that theropod dinosaurs, as well as other dinosaur genera, have features of the vertebrae, ribs, and costovertebral joints[83] that are also typical of birds and, in them, ensure that the lungs are held immobile. The inside of the chest wall was furrowed, which is important for the fixation of the lung. The immobility of the lungs, in turn, is one of the prerequisites for bird-typical through-flow breathing. This extensive study seems to have finally clarified that dinosaurs possessed a highly efficient respiratory system similar to that of birds. In evolutionary theory terms, this means two things:

(1) The effective avian lung is one of the features that was realized before birds evolved, and
(2) The origin of the bird lung is not connected with the origin of the bird flight.

However, the bone structure of the vertebrae and ribs is not proof of a bird-like lung.

How respiration with immobile lungs evolved is not answered by the research of Brocklehurst, Schachner, and Sellers (2018) (nor was that the goal of the study). Rather, indirect osteological evidence showed that no evolutionary stages to this particular lung structure are detectable among the Dinosauriformes (Brocklehurst, Schachner, and Sellers 2018, 9).[84]

Direct evidence of fossil preserved lungs is believed to have been provided by Wang et al. (2018) in the Lower Cretaceous basal ornithuromorph *Archaeorhynchus*. The lungs are reported to be very similar to those of living birds. This is remarkable in two respects:

(1) *Archaeorhynchus* is placed at the base of the ornithuromorphs; thus a "modern" bird lung, from an evolutionary theoretical point of view, was established early.

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[82] Zimbelmann (1999) adds: "Another serious problem arises during embryonic development. Newly hatched crocodiles fill their lungs with the first breath, while young birds breathe days before hatching in the egg. This pre-hatching respiration is necessary for the development of the tubular lung, which cannot be suddenly inflated. But it also requires a completely different nature of the bird egg compared to the reptile egg, because the bird embryo requires a supply of air in the egg as well as a porous eggshell." See Thomas and Garner (1998, 129), "The modern bird system requires a single thoracic cavity, whereas the crocodile and theropod system require the thorax to be divided into two separate airtight chambers. Ruben and colleagues argue that the earliest stages in the evolution of avian respiration from the theropod system would have required selection for a diaphragmatic hernia in the intermediates. This would have prevented the animal from breathing, and is therefore unlikely to have been subject of strong favorable selection."

[83] Joints that connect the ribs to the spine.

[84] "However, we found limited evidence to support a phylogenetic progression toward an increasingly 'furrowed' thoracic ceiling and a more bird-like lung structure, as all dinosaurian taxa showed osteological correlates of dorsally immobile lungs"(Brocklehurst, Schachner, and Sellers 2018, 9). "There was no observable trend toward an increasingly avian vertebral structure moving crown-forwards toward birds" (Brocklehurst, Schachner, and Sellers 2018, 11).

(2) The skeletal features corresponding to the construction of the lung are "primitive"[85]; a correlation skeleton—lung is given only with restriction, which means in the reverse conclusion that from the construction of thorax and vertebral column the construction of lung and respiratory system cannot be concluded with certainty.

Pneumatization of the Bones and Breathing

Inferring an avian respiratory system from the pneumatization of bones seems rash, as pneumaticity may have had other functions, particularly weight saving, for which there are again reasons other than flight capability. This is evident from an extensive comparative study that examined 158 theropod dinosaur taxa, 131 of which had pneumatized bones (Benson et al. 2012). The authors conclude that an increase in pneumatization of bones occurred independently in 12 lineages, a "remarkably high number of independent acquisitions of an avian-like trait." They say it is striking that lineages in which there are also genera with large body sizes are most affected. This correlation, however, is less striking in lineages more closely related to birds, he said. Since pneumaticity is so widespread, adaptation to flight is out of the question as an explanation; more likely is energy conservation in view of increasing metabolic performance, also in connection with endothermy.[86]

However, the Benson et al. data confirm, in the researchers' estimation, that the patterns of occurrence of pneumaticity in theropod dinosaurs are similar to those in birds and were already developed in basal theropods (Benson et al. 2012, 186).[87] An increase in the maximum extent of pneumatization of vertebrae had occurred abruptly in several lineages in the Upper Jurassic, at the same time that this had also occurred in many lineages of pterodactyloid pterosaurs and sauropodomorphs (Benson et al. 2012, 187).[88]

Flow-Through Respiration in Contemporary Reptiles

An air circuit during respiration has now also been demonstrated in reptiles living today, but without an air sac system and without pneumatized bones. Farmer (2010) and Farmer and Sanders (2010) report this in the alligator and Schachner, Hutchinson and Farmer (2013) in the Nile crocodile (*Crocodylus niloticus).*[89] Thus, this feature would have to be considered original for archosaurs (Crocodilia, pterosaurs, dinosaurs, and birds). According to Farmer and Sanders (2010) studies, the data suggest that airflow is "extremely similar" to birds. However, it is unclear how it occurs without air sacs and by means of the diaphragm, and the mechanism remains to be determined (Farmer and Sanders 2010, 339, 340).[90] Farmer (2015b) found bird-like flow-through breathing in the American alligator, two species of caiman, and three species of crocodile. This demonstrates that flow-through respiration is compatible with a pump-piston mechanism mediated by the liver (see Schachner et al. 2011, 1545).

Surprisingly, Schachner et al. (2014) also demonstrated an air circuit in the lungs of the steppe monitor *(Varanus exanthematicus)*, which is even more distantly related to birds. It is therefore possible that this feature even connects all diapsids (snakes, lizards, crocodilia, and birds). However, according to these researchers, flow-through breathing could have evolved twice independently—in monitor lizards and archosaurs. To test this hypothesis, Cieri et al. (2014) studied respiration in the green *iguana (Iguana iguana)* and found flow-through respiration with simply constructed lungs in this species as well. This confirms the possibility that this trait may have already been evolved in Permian diapsids (see Farmer 2015a). However, according to Cieri et al. (2014), a convergent origin cannot be excluded. Further studies on respiration in different reptile groups are needed for clarification.

Evidence of the occurrence of flow-through respiration in various cold-blooded reptiles refutes the evolutionary hypothesis that this type of respiration arose from increased oxygen demand due to high metabolic outputs (Cieri et al. 2014). Hypothetical other selection pressures are discussed by Farmer (2015b).

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[85] "Skeletal features related to respiration remain primitive, supporting inferences that many physiological adaptations preceded skeletal changes during the evolution of the anatomically modern bird" (Wang et al. 2018, 11555).

[86] Benson et al. (2012, 170) comment, "This suggests a complex situation in which different body size thresholds, and thus, different selective or physiological regimes, drove the evolution of postcranial skeletal pneumaticity in birds and non-avian dinosaurs."

[87] "Our data confirm that patterns in the distribution of pneumaticity in non-avian theropods are similar to those in birds. Non-avian theropods show a 'common pattern' in which the postaxial cervical vertebrae, at least some anterior dorsal vertebrae, and occasionally the axial centrum, are pneumatized (Fig. 3). This evolved among primitive theropods…" (Benson et al. 2012, 186).

[88] "An increase in the maximum extent of vertebral pneumatization occurred abruptly during the Late Jurassic when the extended pattern originated in multiple lineages; notably, a similar transition occurred in multiple clades of pterydactyloid pterosaurs and sauropodomorphs at about this same time" (Benson et al. 2012, 187).

[89] "Here we have shown that Nile crocodiles neither have postcranial pneumaticity nor air sacs and yet have lungs with truly flow-through ventilation. Hence unidirectional ventilatory flow (a flow-through lung in physiological terms) is possible in an ectothermic animal without pneumaticity and without air sacs. This emphasizes that bronchial anatomy, air sac anatomy, and ventilatory patterns can be decoupled from each other in archosaurs and should not be presumed to be correlated in simple ways" (Schachner, Hutchinson, and Farmer 2013, 25).

[90] "Our data suggest that airflow in the alligator is extremely bird-like, but it is unknown how it is possible to have unidirectional flow without air sacs and with diaphragmatic breathing" (Farmer and Sanders 2010, 339).

Conclusion

Based on the widespread pneumatization of bones with air pores in theropod dinosaurs, there has long been considered strong evidence for at least partial avian-type respiration. This is also supported by recent findings of flow-through respiration in some present-day reptiles and the extensive study of theropod dinosaurs by Brocklehurst, Schachner, and Sellers (2018). More specific details cannot be inferred directly from the fossil record, as many avian details of the respiratory system are not fossil preservable and inferences from indirect evidence are fraught with uncertainty. However, the recently published study by Brocklehurst, Schachner, and Sellers (2018) seems to provide clarity that at least the osteological requirements for immobile lungs were present in Dinosauriformes, and thus bird-typical respiration was likely realized.

Whenever the origin of the avian respiratory and thus coupled air sac system is to be assumed under evolutionary theoretical conditions, the conversion is enormous due to the described interconnections (peculiarities in the construction of the lung, respiratory movements, coupling with thermoregulation) and it is unclear how it could have occurred in an evolutionary way. The few proposed remodeling steps (Farmer 2010; Sereno et al. 2008[91]; Schachner et al. 2011; see figs. 33, 34) are very large and the models based on them do not take into account the numerous anatomical and physiological details.

Usually, scientists refer to the "fact" that birds are a branch of theropods, so there must have been an evolutionary pathway for the respiratory system as well. Thus Witmer (2002, 21) writes: "Given the considerable evidence that birds are embedded within Theropoda, it would seem that indeed 'you can get there from here,' even if the physiological or anatomical mechanisms is at present obscure." But this is a classic circular argument. The argument that for functional reasons a reconstruction seems to be impossible is covered up with reference to comparative biology or the cladistic classification. But the latter is only a method to create order, which serves as a basis for a phylogenetic interpretation. If a reconstruction were really functionally impossible, no counterargument could be developed from phylogenetic reconstructions.

Pelvis and Retroverted Pubis

The avian pelvis is characterized by strong fusions, which contributes to the lightweight structure of the skeleton. The last three thoracic vertebrae are fused with the lumbar vertebrae and some caudal vertebrae and together form the synsacrum, which in turn is strongly fused with the ilium. The ilium in turn is fused with the ischium and the anterior part of the pubis. The muscles of the legs and tail attach to the central platform thus formed (Proctor and Lynch 1993, 140). The long, thin pubis, which is fused to the ischium and abuts the ilium, is directed posteriorly (fig. 35).

In most opposite birds and some ornithuromorphs, as well as in the basal genera *Archaeopteryx, Jeholornis*, *Sapeornis*, and *Confuciusornis*, the pelvic bones are not fused but are more or less clearly oriented posteriorly (Wang, Li, and Zhou 2017).[92] Retroverted orientation of the pubis also occurs in many theropod dinosaurs, such as many dromaeosaurs (Elzanowski 2002, 150[93]; Norell and Makovicky 2004[94]), some troodontids (*Sinovenator*, Xu et al. 2002b[95]), therizinosaurs (Clark, Maryańska, and Barsbold 2004), and in the derived genera of alvarezsaurids (Choiniere et al. 2014; Sereno 1997), but not in the upper Jurassic alvarezsaurid genus *Haplocheirus* (Choiniere et al. 2010). Since a retroverted orientation of the pubis is also absent in the basal genera of dromaeosaurs (Makovicky, Apesteguía, and Agnolín 2005[96]) and most troodontids, a multiple convergent origin is assumed. Thus this characteristic cannot be evaluated convincingly as a "bird characteristic with dinosaurs"[97], since it cannot have been developed under evolution-theoretical conditions continuously in the lineage leading to the birds. For example, Zhou (2004, 462f.) notes that, among other things, a retroverted pubis was developed in some theropods[98]

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[91] Sereno et al. (2008) present a four-phase model:
"(1) Phase I-Elaboration of paraxial cervical air sacs in basal theropods no later than the earliest Late Triassic. (2) Phase II-Differentiation of avian ventilatory air sacs, including both cranial (clavicular air sac) and caudal (abdominal air sac) divisions, in basal tetanurans during the Jurassic. A heterogeneous respiratory tract with compliant air sacs, in turn, suggests the presence of rigid, dorsally attached lungs with flow-through ventilation. (3) Phase III evolution of a primitive costosternal pump in maniraptoriform theropods before the close of the Jurassic. (4) Phase IV evolution of an advanced costosternal pump in maniraptoran theropods before the close of the Jurassic."

[92] The ilioischiad foramen, formed by adhesion of the ilium and ischium, is absent in all Mesozoic birds (Wang, Li, and Zhou 2017, 11473).

[93] "A strongly retroverted pelvis in dromaeosaurids... provides a case of convergence with ornithurine birds," (Elzanowski 2002, 150)

[94] Namely, *Microraptor*, *Sinornithosaurus* (both ca. 125 Ma), *Adasaurus*, *Bambiraptor*, and *Velociraptor* (all ca. 70–75 My).

[95] "Unlike other troodontids, the pubis is posteriorly oriented" (Xu et al. 2002b, 783).

[96] In the basal Unenlagiinae, the pubis was vertically oriented (Makovicky, Apesteguía, and Agnolín 2005, 1009).

[97] "Discovery of a number of basal troodontids from the Early Cretaceous Yixian and Jiufotang Formation of China reveals that these traits [such as a retroverted pubis] are homoplastic in derived troodontids..." (Makovicky and Zanno 2011, 17)

[98] By "feathered" species are meant species with so-called dino-fuzz.

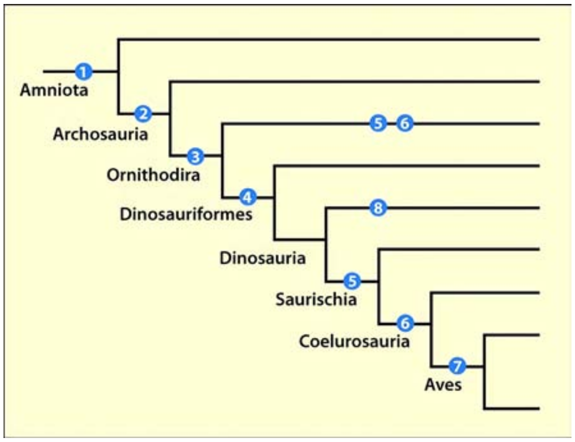

Fig. 33. Phylogeny of the amniotes indicating the major changes associated with the respiratory system of birds. 1 Costal breathing and septate lungs, 2 four-chambered heart, unidirectionally ventilated lungs, 3 possible origin of postcranial pneumaticity and hypothesized associated air sacs, 4 dorsally immobile heterogeneously partitioned multichambered lungs with unidirectional airflow, possible thinning of the blood-gas barrier, 5 confirmed postcranial pulmonary pneumaticity, 6 hypothesized caudally positioned abdominal air sacs, 7 uncinate processes, 8 possible secondary loss of postcranial pulmonary pneumaticity in ornithischians (after Schachner et al. 2011).

but not in the most basal birds.[99] The same is true for *Archaeopteryx* (O'Connor, Chiappe, and Bell 2011, 45). With respect to this and other avian features, O'Connor, Chiappe and Bell (2011, 41) conclude that a highly homoplastic evolutionary history must be assumed based on their occurrence in apparently unrelated theropod groups and their absence in primitive birds (fig. 36).[100]

In the enigmatic scansoriopterygids, which in some respects are close to birds, the pubis is directed forward in a way that is untypical of birds (Czerkas n.d.), and in the fancy genus *Yi* from this group only little of the pelvis is preserved (Xu et al. 2015). Even in oviraptorids, which have a striking number of bird-typical features and are interpreted by some researchers as secondarily flightless birds (see below), the pubic bone was—as far as is known—directed anteriorly (Zhou et al. 2000, 252[101]) and the pelvic bones were not fused (Wang, Li, and Zhou 2017, 11474).

Fusion of the pelvic bones must also have occurred several times based on a current phylogeny, namely in the Upper Cretaceous dromaeosaur *Balaur*, in the enantiornithines *Qiliania, Pterygornis*, and *Enantiornis,* and in the ornithuromorphs, among

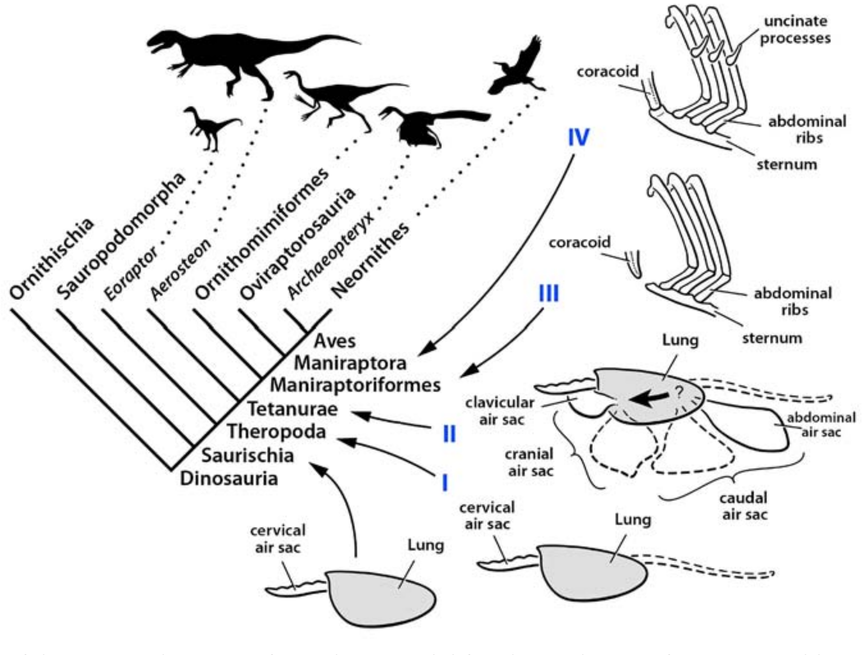

Fig. 34. Cladogram of dinosaurs showing a four-phase model for the evolution of air sacs and lung ventilation within theropods. Phase 1 (theropods): Variable posterior extension of paraxial cervical air sacs. Phase 2 (Tetanurae): air sacs in the clavicle and abdomen become divided and diverticula form under the skin. Stage 3 (Maniraptoriformes): simple respiration with the help of the ribs and sternum. Stage 4 (Maniraptora): advanced respiration using the ribs and sternum. The solid arrow on the lung indicates flow during pulmonary ventilation; the question mark indicates uncertainty about the direction of airflow (uni- or bidirectional) (adapted from Sereno et al. 2008.), CC BY-SA 2.5.

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[99] "uncinate process of the ribs, more caudally retroverted pubes in dromaeosaurids, and a pygostyle, appeared in some feathered theropods but not in the most basal birds" (Zhou 2004, 462f).

[100] "their occurrence within apparently unrelated nonavian theropod groups and their absence in primitive birds suggests a highly homoplastic evolutionary history" (O'Connor, Chiappe, and Bell 2011, 41). Likewise, "Many maniraptorans convergently acquired a retroverted pubis superficially similar to ornithischians" (Hendricks, Hartman, and Mateus 2015, 28).

[101] "the pelvis is similar to oviraptorids in having an anteroventrally oriented pubis rather than a retroverted pubis as in dromaeosaurs and birds . . . ." (Zhou et al. 2000, 252).

which, however, not all genera possess fused pelvic bones (Wang, Li, and Zhou 2017, see fig. 36).[102] According to Wang, Li, and Zhou (2017, 11474), a fused pelvis is also occasionally found in some ornithomimids, coelophysoids, and ceratosaurs. In summary, Wang, Li, and Zhou (2017, 11470) write that fusions in the pelvic region evolved independently in theropod dinosaurs, opposite birds, and ornithuromorphs. They say that fusions of these bones are rare in theropod dinosaurs and Lower Cretaceous birds, but well expressed in Upper Cretaceous and present-day birds. They show a complicated evolutionary pattern of different fusions.[103]

Carrano (2000, 489) notes that theropod dinosaurs have a remarkably uniform general pelvic girdle and hind limb morphology. There is little evidence of divergence to indicate the evolution of more specialized forms of locomotion, he adds. This apparent evolutionary stability makes the locomotor transition from theropod dinosaurs to birds even more remarkable. This transition involved changes in the entire locomotor system, not just the structures directly associated with flight.

Conclusion

Overall, it can be stated: There are enormous differences in the construction of the pelvis between birds known from Cretaceous strata and present-day birds. However, pelvic features typical of birds, such as backward orientation of the pubic bone and fusions in the pelvic region, which occur in theropod dinosaurs, can hardly be evaluated as bird features in dinosaurs, since an independent origin in the respective dinosaur groups is assumed due to the distribution in the system (fig. 37).

Pygostyle

In today's birds, the last tail vertebrae are fused to form a so-called *pygostyle* (fig. 38). It serves as a stable support for the fan-shaped tail feathers. The pygostyle is connected on both sides to a rectrical bulb, a complicated organ of fat, connective tissue and muscle (M. bulbi rectricium), to which the tail feathers attach and through which they can be moved and controlled. Only the two middle tail feathers are directly connected to the pygostyle.[104] The associated ability to change the shape of the tail greatly enhances flight (Gatesy and Dial 1996, 2045ff; O'Connor et al. 2015a, 114). The whole system forms an intricate integrated unit and, together with the wings, enables the formation of a tightly coupled surface during flight (Gatesy and Dial 1996, 2037f).[105] Wang and O'Connor (2017, 291) refer to this as an "elaborate tail complex" and an "integrated whole". The uropygium (rear region) and integument (body covering) are morphologically interrelated, such that the shape of one can predict that of the other. This close interrelationship supports the evolutionary hypothesis that pygostyle and tail feathers co-evolve.[106]

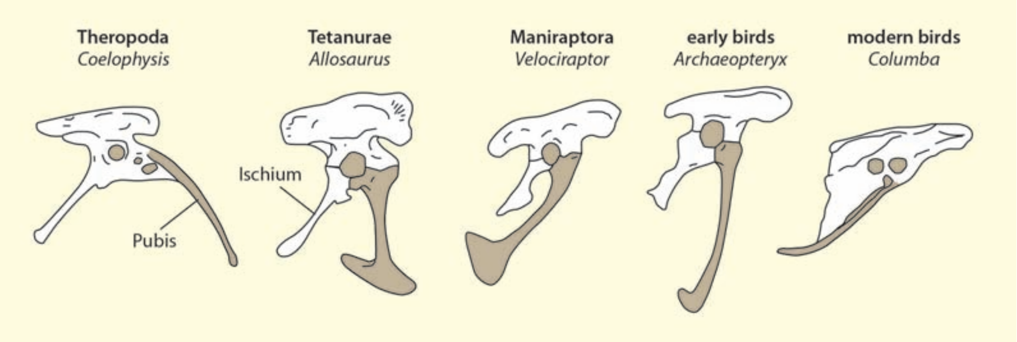

Fig. 35. Pelvic types in some theropods and birds (after Padian and Chiappe 1998a).

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[102] "The ancestor state reconstruction revealed the unfused pelvis as the ancestor condition of Paraves, and the pelvic fusion evolved independently and on multiple occasions in lineages of Dromaeosauridae and Aves" (Wang, Li and Zhou 2017, 11473).

[103] "The fusions of these bones are rare in known nonavian theropods and Early Cretaceous birds but are well established among Late Cretaceous and modern birds, revealing a complicated evolution pattern unrecognized previously. We posit that the developments of bone fusion were polymorphic close to the origin of birds, resulting in the varying degrees of fusion in paraves" (Wang, Li, and Zhou 2017, 11470).

[104] "Paired fibroadipose tissue structures called rectricial bulbs lie on both sides of the pygostyle and predominantly attach to the pygostyle lamina; the calami of the rectrices are imbedded in this tissue, except for the medial pair which attach directly onto the dorsodistal end of the pygostyle (Baumel, 1988). Spiraling around the surface of each bulb is a striated muscle, the rectricial bulb muscle" (Wang and O'Connor 2017, 290f).

[105] "the pygostyle, rectrices, rectricial bulbs, and bulbi rectricium musculature form a specialized fanning mechanism" (Gatesy and Dial 1996, 2037). "The rectrices form a flight surface that is tightly coupled with the wings during aerial locomotion" (2037f).

[106] "This sophisticated tail complex plays a significant role in avian flight. . . . Because the tail complex functions as an integrated whole, the uropygium and integument are morphologically correlated and one can be used to predict the other (Felice and O'Connor, 2014). Furthermore pygostyle morphology can be used to predict flight or foraging style in both extinct and extant birds (Felice, 2014). These results support the hypothesis that pygostyle and rectricial morphology co-evolve (Clark et al., 2006)" (Wang and O'Connor 2017, 291).

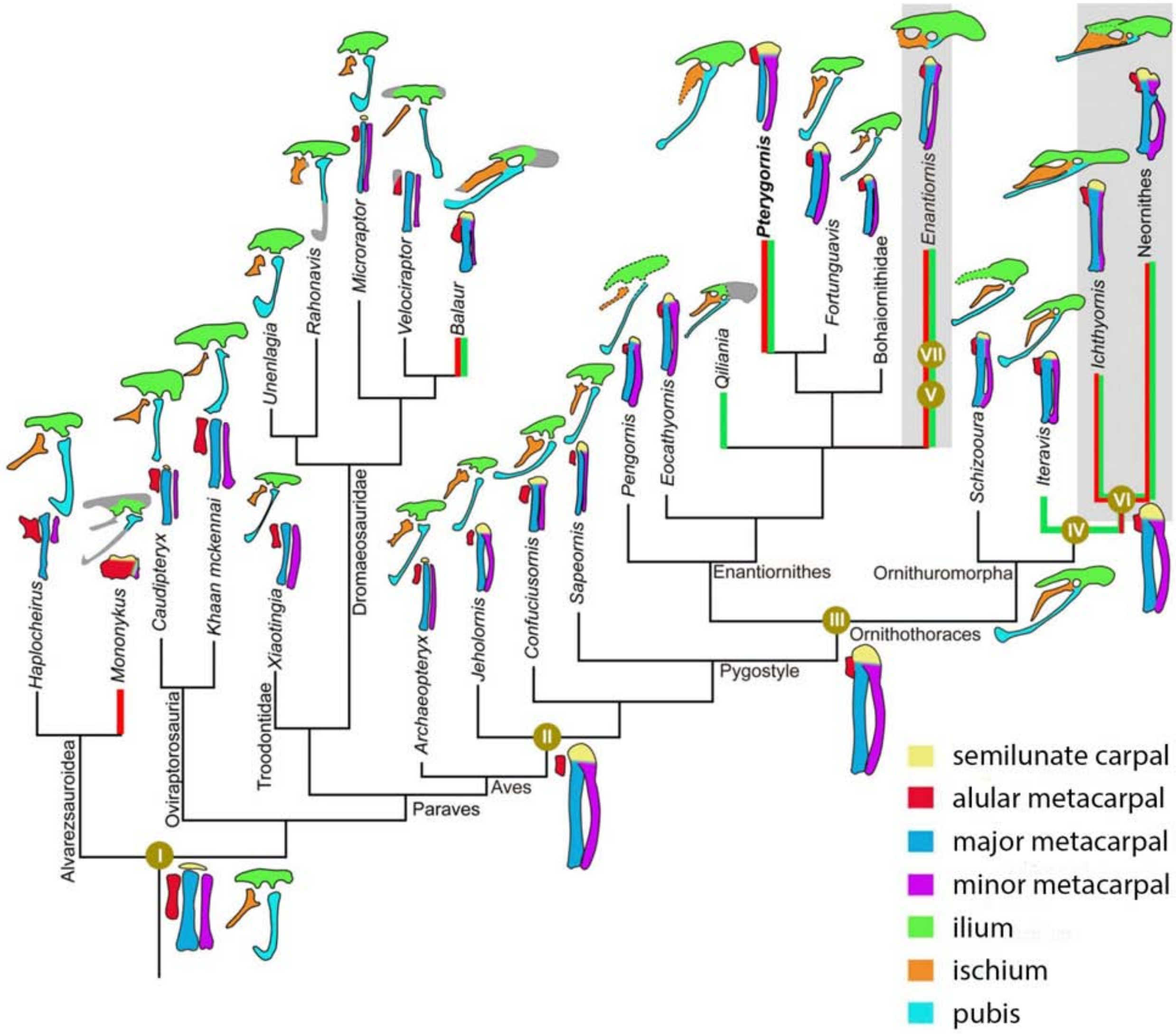

Fig. 36. Paravian phylogeny showing the major changes of manus and pelvis fusions. The ancestral conditions of the pelvis and manus fusions of the major nodes were reconstructed using the parsimonious method in Mesquite. Major changes are summarized below: I, the metacarpals and pelvis unfused in adults; II, the semilunate carpal fused with the proximal ends of the major and minor metacarpals, with the alular metacarpals separated; III, the alular metacarpal fused with the major metacarpal proximally but separated distally; IV and V, the ilium, ischium, and pubis fused around the acetabulum; VI and VII, alular and major metacarpals completely fused along their length. The green thick lines denote the taxa with fused pelvis, and the red thick lines indicate taxa with fused alular and major metacarpals. Late Cretaceous birds are denoted in shaded background. The line drawings are not to scale. It is clear that the fusions occur multiple times convergently and in incongruent distribution (from Wang, Li, and Zhou 2017. © 2017 National Academy of Sciences).

A pygostyle is also developed in most fossil birds. They are grouped together as Pygostylia, although there are more marked differences in expression in basal species compared to present-day species. In contrast, the skeleton of the tail region of *present-day* birds is remarkably uniform despite diversity in tail expression.

Pygostyle Types in Fossil Forms

Three distinct pygostyle types survive among early birds fossilized in the Cretaceous geological system, only one of which occurs among modern birds (Hu, O'Connor, and Zhou 2015, 16f.; Wang and O'Connor 2017, 304[107]; figs. 39–42). The first type is short, plough-shaped, and tapering, occurring in

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[107] "Distinct from that of sapeornithiforms, the pygostyle in confuciusornithiforms is more strongly co-ossified, proportionately longer and more robust" (Wang and O'Connor 2017, 295). "The sapeornithiform pygostyle is relatively smaller and poorly co-ossified compared to most other Early Cretaceous pygostylians. . . . Compared to sapeornithiforms, the pygostyle is proportionately longer in confuciusornithiforms and enantiornithines . . . Differences in pygostyle morphology between these four groups correspond to consistent differences in tail plumage. *Sapeornis* has been interpreted as having a strongly graded fan consisting of approximately eight pennaceous feathers" (Wang and O'Connor 2017, 304).

Sapeornis and the Ornithuromorpha (for example, *Archaeorhynchus, Yixianornis, Hongshanornis*) and is similar to most Neornithes and thus to present-day birds.[108] The second type is stout, forked, and constricted distally and is found in most Cretaceous enantiornithine birds. In *Confuciusornis,* a third type is developed; the pygostyle is stout and rod-like.

It is possible that the pygostyles of the second and third types (in *Confuciusornis* and also in oviraptorosaurids) only allowed for weight savings without playing any particular role in flight performance (Clarke, Zhou, and Zhang 2006).

In contrast, the bipedal theropods generally possessed long tails with dozens of free caudal vertebrae, which presumably served for balance. Robust transverse projections on the anterior caudal vertebrae served as attachment points for the large caudofemoralis muscles, which primarily served as retractors of the hind legs (Rashid et al. 2014, 2).[109] The two tail types—pinnate tail and fan tail—are functionally very different. The hind legs were functionally linked to the long tail (Benson and Choiniere 2013, 1), and to evolve the fan tail, this functional coupling had to be removed, further emphasizing that the transition to a fan tail required significant modification. However, some genera of theropod dinosaurs also possessed a pygostyle (see below).

Distribution

Birds with long "dinosaur tails" (*Jeholornis* and related species, *Microraptor*, and *Archaeopteryx*) and species with pygostyles and fan tails coexisted side by side (Brusatte, O'Connor, and Jarvis 2015, 290; Rashid et al. 2018, 8). Many maniraptorans (with long tails), considered precursor groups of birds, are stratigraphically younger (in some cases significantly so) than numerous Pygostylia. Species with pygostyles or pygostyle-like structures are distributed on different branches in the theropod cladogram in such a way that multiple independent (convergent) origins must be assumed (for Oviraptorosauria and Therizinosauria: Kurochkin 2006[110], Barsbold et al. 2000a[111], b *[Nomingia]*, O'Connor and Sullivan 2014; Persons, Currie, and Norell 2014 *[Nomingia, Citipati, Conchoraptor]*, Xu et al. 2003a *[Beipiaosaurus]*; there is also another convergent tail shortening in the scansoriopterygid *Epidexipteryx*; Rashid et al. 2014, 3; Wang and O'Connor 2017[112]; figs. 41–43).

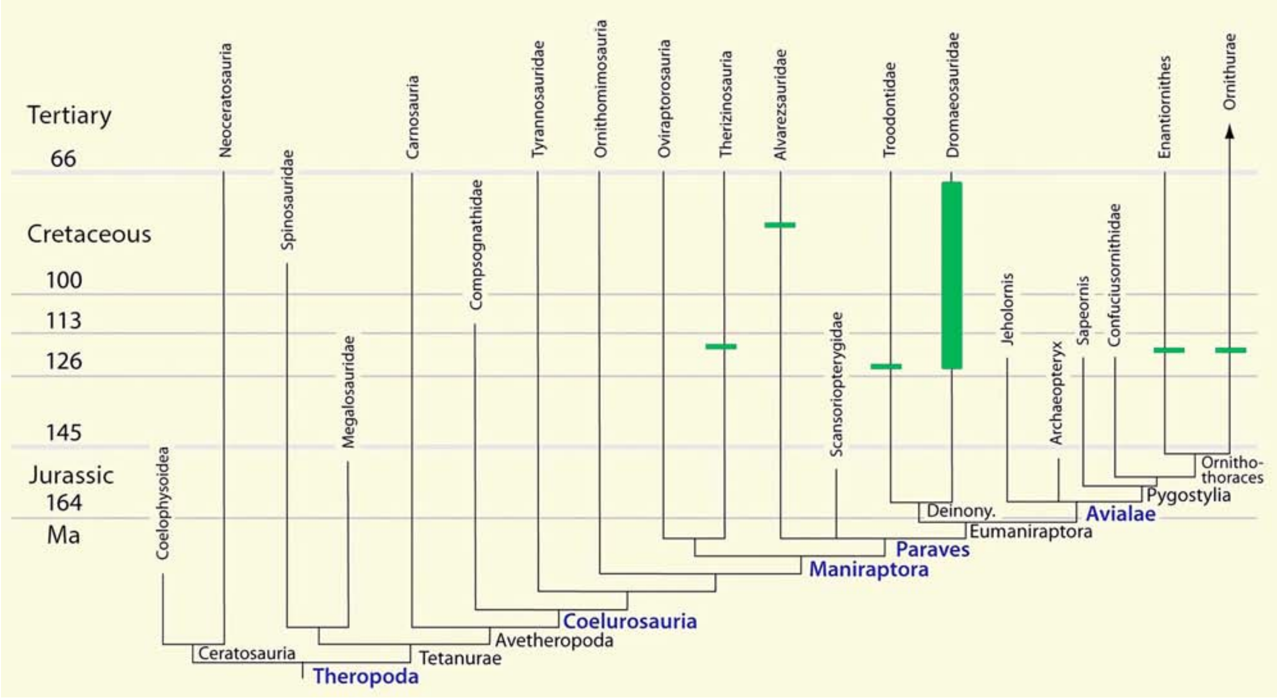

Fig. 37. Distributions of theropod and avian genera with retroverted pubes (green markings) (assembled according to the sources mentioned in the text).

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[108] *Hongshanornis longicresta* (O'Connor, Gao, and Chiappe 2010) is considered the oldest species of ornithurans with "modern" pygostyle.

[109] "It also had robust transverse processes on the proximal caudal vertebrae that would have served as attachment sites for the large caudofemoralis muscles that were the primary hind limb retractors" (Rashid et al. 2014, 2).

[110] "The presence of the pygostyle in oviraptorosaurs and therizinosaurs strongly suggests that such structures of theropods and birds were acquired in parallel" (Kurochkin 2006, 48).

[111] "Although the terminal vertebrae of *Caudipteryx* are not fused, they seem to form a stiffened rod.…Pygostyle-like structures could have evolved independently at least three times in theropods, although the presence of rectrices in two of these taxa suggests a functional association" (Barsbold et al. 2000a, 155).

[112] "One member of the Scansoriopterygidae, *Epidexipteryx*, has a reduced tail consisting of 16 vertebrae ending in a rod-like structure approximately formed by the distal ten caudal vertebrae which are unfused. The distal ten vertebrae are reduced to simple centra without processes. Two pairs of elongate feathers project from the pygostyle in *Epidexipteryx*; described as 'ribbon-like'" (Wang and O'Connor 2017, 294).

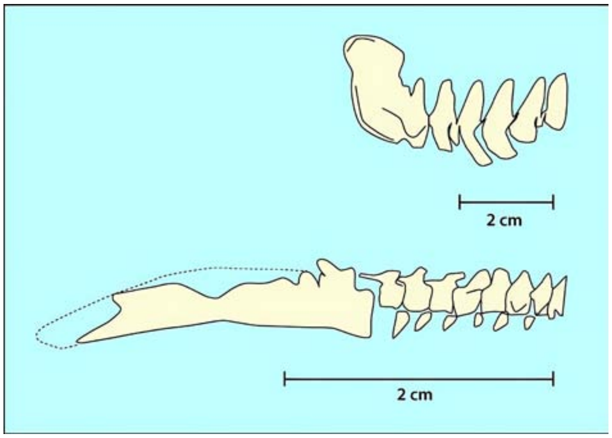

Fig. 38. Pygostyle of the pigeon (top) and the enantiornithine *Iberomesornis* (after Gatesy and Dial 1996).

The different pygostyle types are very likely functionally dissimilar, as mentioned earlier. Wang and O'Connor (2017, 303) consider it unlikely, based on the structure of the pygostyle in oviraptorosaurs, that a rectricial bulb or equivalent structures were developed.[113] Persons, Currie and Norell (2014, 553, 562, 564) believe that the tail region of Oviraptorosauria was unique, did not fit into a transitional position to an avian pygostyle, but was a convergent formation, and most likely had a scooping function.[114] That the different pygostyles must be interpreted as convergent also follows from their distribution in the cladogram (see above), unless one interprets Oviraptorosauria as secondarily flightless birds (see below and Mayr 2017a, 45[115]).

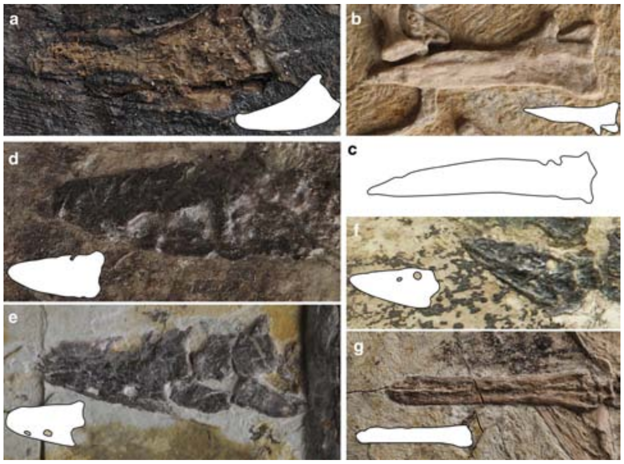

Fig. 39. Pygostyle of the enantiornithines *Cruralispennia* (a), *Pterygornis* (b), *Concornis* (e), the ornithurans *Yixianornis* (d), *Bellulornis* (e), *Piscivoravis* (f), and the basal bird *Confuciusornis* (g) (from Wang et al. 2017d), CC BY 4.0.

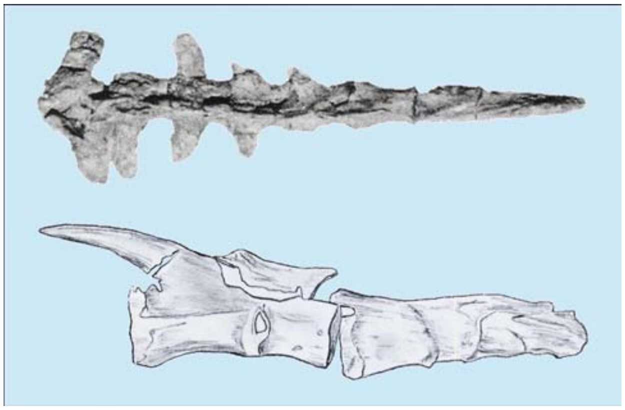

Fig. 40. Pygostyle of the oviraptorid *Nomingia* (from Barsbold et al. 2000b). CC BY 2-0). Pygostyle of the therizinosaur *Beipiaosaurus* (after Xu et al. 2003a).

Fig. 41. *Epidexipteryx* with elongate pygostyle. Jaime A. Headden, http://qilong.deviantart.com/art/Nitpicker-103918005/, CC BY 3.0. License (original).

Transitional Forms?

Wang and O'Connor (2017, 289) refer to the emergence of the pygostyle and the fan-shaped arrangement of feathers as one of the "most remarkable adaptations" of early avian evolution, but a gradual transition between forms without and with a pygostyle is not fossil documented (also O'Connor et al. 2015a, 114[116]; Mayr 2017a, 45[117]). Wang and Zhou (2017, 6) also note that little is known about how the shortening of the tail occurred, as relevant fossils

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[113] "However, morphological differences between these phylogenetically separated taxa indicate these co-ossified structures cannot be considered equivalent to the avian pygostyle.... Although pennaceous tail feathers are present in oviraptorosaurs, the absence of a pygostyle lamina or a similar dorsal ridge makes the development of rectricial bulbs or equivalent structures in this clade unlikely.... fusion in the distalmost caudals of non-avian theropods should be described as pygostyle-like and a true pygostyle should be regarded as a synapomorphy of the Pygostylia (Aves)" (Wang and O'Connor 2017, 303).

[114] "Oviraptorosaur caudal osteology is unique among theropods and is characterized by posteriorly persistent and exceptionally wide transverse processes, anteroposteriorly short centra, and a high degree of flexibility across the pre-pygostyle vertebral series" (Persons, Currie, and Norell 2014, 553). Oviraptorosaurs do not fit neatly into any stage of this sequence,... (page 562; further assumed convergences are described there).

[115] "Surprisingly, monophyly of this latter taxon is now challenged by several analyses, which placed the long-tailed Jeholornithidae within pygostylians... would suggest the convergent origin of a pygostyle in more than one avian clade" (Mayr 2017a, 45).

[116] "However, no fossil directly elucidates this important skeletal transition" (O'Connor et al. 2015a, 114).

[117] "There is a clear-cut distinction between avians that lack a pygostyle and those that have it, and the latter are usually classified in the Pygostylia" (Mayr 2017a, 45).

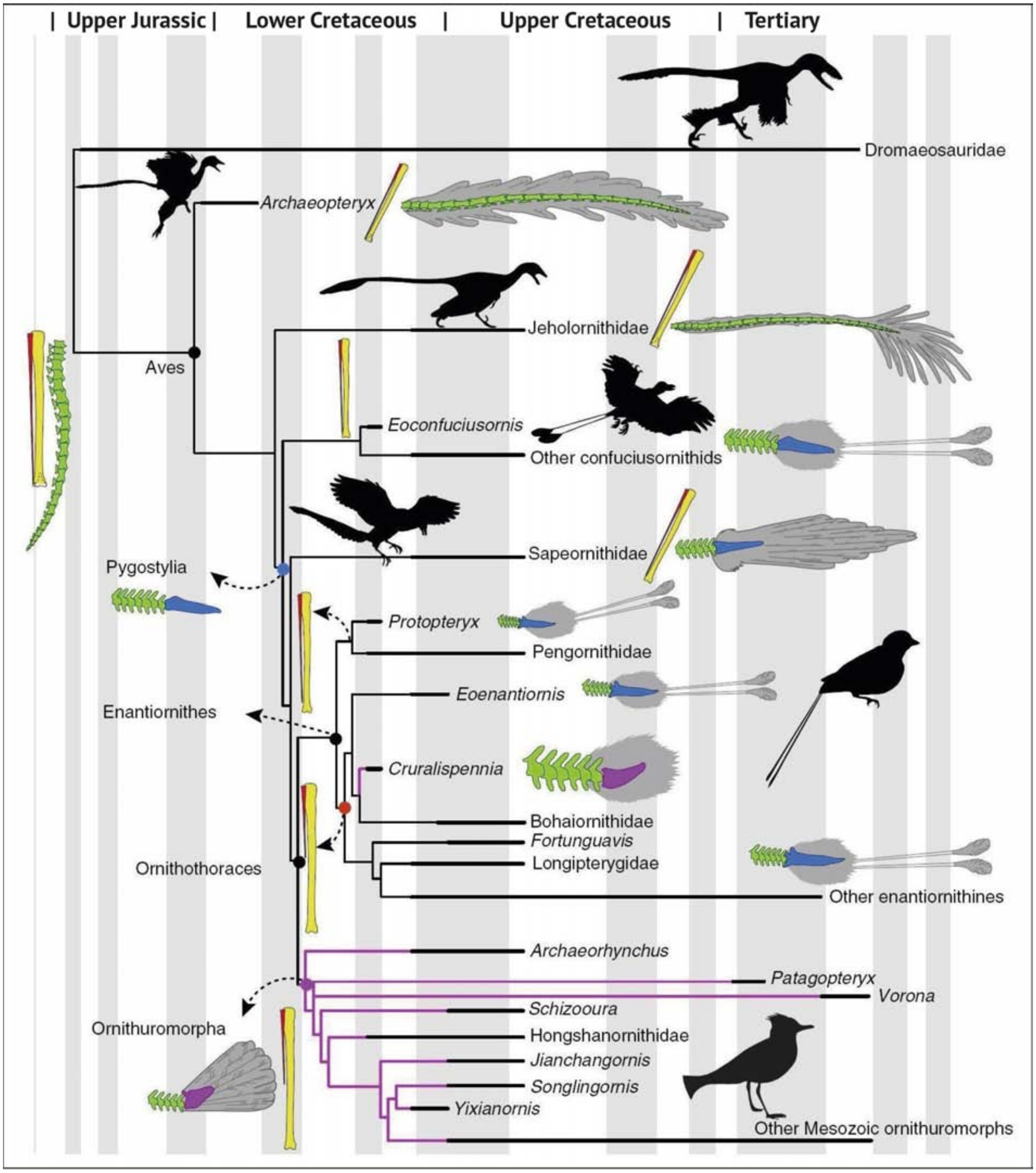

Fig. 42. Fibula and tail morphology (pygostyle) in Mesozoic birds entered into the consensus cladogram after Wang et al. (2017d). The thick lines indicate the temporal range of fossil taxa. An elongate fibula (red) is developed in basal birds (outside the Ornithothoraces) and in the basal enantiornithines *Protopteryx* and the Pengornithidae; a reduced fibula is convergently realized in ornithuromorphs and derived enantiornithines. The enantiornithine *Cruralispennia* has a plough-shaped pygostyle (pink) similar in shape to ornithurans (pink branches) (from Wang et al. 2017d), CC BY 4.0.

documenting this transition are lacking.[118] The oldest pygostyles of all Lower Cretaceous ornithuromorphs are nearly "modern" in form. Together with the occurrence of fan-shaped tail feathers, this argues, according to Wang and O'Connor (2017, 289, 305), that the complete avian tail complex evolved very early in this lineage and that the rectricial bulbs and fan tail evolved together.[119] O'Connor et al. (2015a,

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[118] "Nevertheless, little is known about how the abbreviation of the tail took place without relevant fossils documenting that transition" (Wang and Zhou 2017, 6).

[119] The rectricial bulbs and rectricial fan appear to have coevolved with the plough-shaped pygostyle early in the evolution of the Ornithuromorpha (Wang and O'Connor 2017, 289).

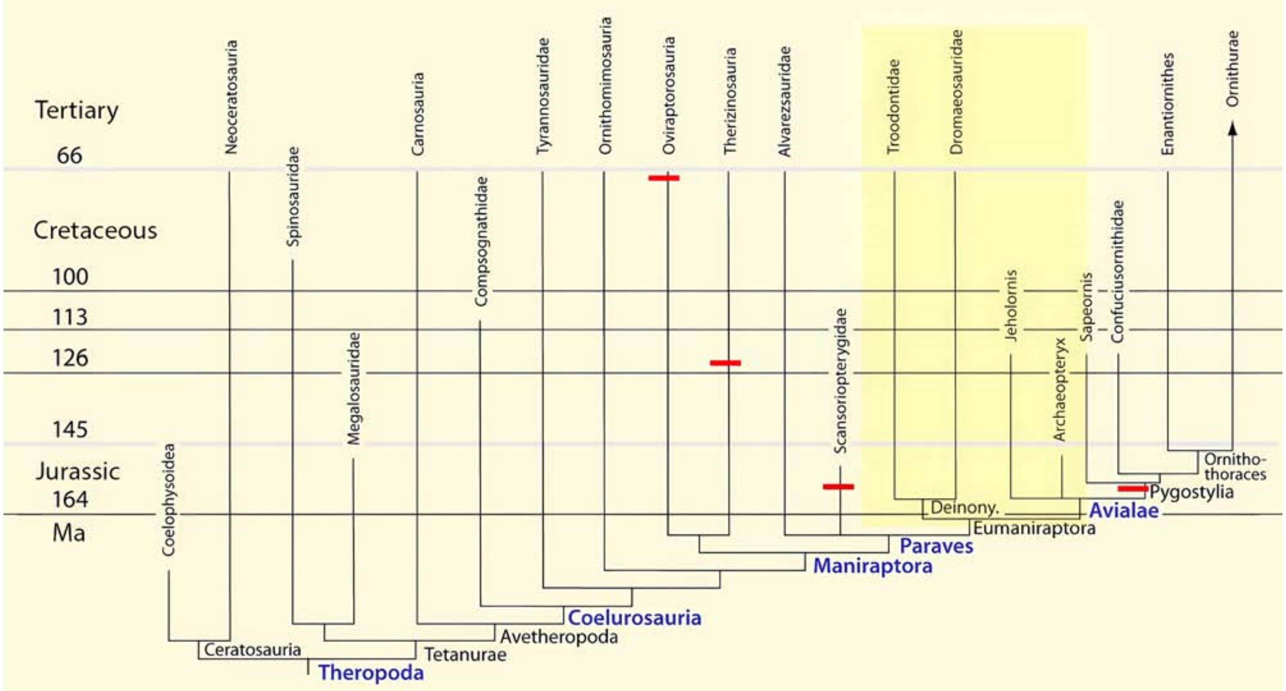

Fig. 43. Distributions of theropod and bird genera with pygostyle (red markings) (assembled according to the sources mentioned in the text).

114) also argue along these lines: The co-occurrence of a pygostyle and aerodynamic tail fans in ornithurans, Sapeornithiformes[120], and pengornithids[121], a basal group of the opposite birds, supports coevolution of the entire tail complex. It is the most parsimonious explanation, he argues, that the rectricial bulb was lost in *Confuciusornis* relatives and some opposite birds.[122] In contrast, O'Connor et al. (2015a, 117) argue that it is incomprehensible that the derived groups of the opposite birds would have abandoned this complex again in favor of a more robust pygostyle and argue for an independent origin of pygostyles with the rectricial bulb. This is also supported by the fact that there are morphological differences in pygostyles.[123]

Zhongornis haoae (a juvenile species of unclear systematic position) was discussed as an intermediate form, but a reexamination of the tail did not confirm this (O'Connor and Sullivan 2014). Rather, about 20 caudal vertebrae are preserved, although the actual number may be even higher (*Archaeopteryx* had 23 caudal vertebrae). The tail is said to be very similar to that of *Epidexipteryx* (Scansoriopterygidae) and *Caudipteryx* (Oviraptorosauria). However, a recent study by Rashid et al. (2018) showed that fusion of the outermost caudal vertebrae into a pygostyle occurs just before skeletal maturation in present-day birds. Therefore, it should be assumed that in the juvenile fossil of *Zhongornis,* the pygostyle was not yet mature.[124]

That the differences between both tail types are significant, Gatesy and Dial (1996, 2046) also note, as well as that the evolutionary bridging is rather weak. Although *Iberomesornis has* already been mentioned here, this genus is clearly in the direction of present-day birds, however (fig. 38 clearly shows this). It is added that the pygostyle in *Iberomesornis* is fused from 10–15 vertebrae; otherwise, it is only 6–8. This situation does not fit to an intermediate form.

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[120] "discovery of a rectricial fan in the basal pygostylian *Sapeornis*. Although proportionately larger, the sapeornithiform pygostyle is morphologically very similar to that of ornithuromorphs" (O'Connor et al. 2015a, 117). Rashid et al. (2014, 2) note a jump to pygostyle and a small number (6–7) of caudal vertebrae in *Sapeornis*.

[121] "A newly discovered pengornithid, *Chiappeavis magnapremaxillo* gen. et sp. nov., preserves strong evidence that enantiornithines possessed aerodynamic rectricial fans" (O'Connor et al. 2015a, 114).

[122] "The consistent co-occurrence of short pygostyle morphology with clear aerodynamic tail fans in the Ornithuromorpha, the Sapeornithiformes, and now the Pengornithidae strongly supports inferences that these features co-evolved with the rectricial bulbs as a 'rectricial complex.' Most parsimoniously, rectricial bulbs are plesiomorphic to Pygostylia and were lost in confuciusornithiforms and some enantiornithines, although morphological differences suggest three independent origins" (O'Connor et al. 2015a, 114).

[123] "If the presence of rectricial bulbs represents the plesiomorphic condition in enantiornithines, as suggested by the basal position of the Pengornithidae [10], it is unclear why more derived enantiornithines would have abandoned this feature in favor of a more robust pygostyle with purely ornamental rectrices. This supports an alternative scenario in which rectricial bulbs and pygostyle reduction evolved independently in sapeornithiforms, pengornithids, and ornithuromorphs (Figure 3). This is supported by morphological differences in the pygostyle:..." (O'Connor et al. 2015a, 117).

[124] "For *Zhongornis haoae* (and for other juvenile Mesozoic avians), this indicates that lack of a pygostyle does not necessarily indicate an intermediate species in the long- to short-tailed evolutionary transition" (Rashid et al. 2018, 8).

The genus *Cruralispennia* is noteworthy. Although it belongs to the opposite birds, the shape of its pygostyle tends rather to the ornithuromorphs and is clearly different from pygostyles of the opposite birds (Wang et al. 2017d; fig. 39). Thus, it is a mosaic form that can only be phylogenetically classified assuming convergence.

Rapid Emergence of the Pygostyle?

Could one or could very few mutations have caused the bird-like situation of the tail region and therefore lack transitional forms? Rashid et al. (2014, 2018) think so. They argue that the reduction in the number of caudal vertebrae and the emergence of the pygostyle occurred in a "very short evolutionary interval." They argue that the features of the tail complex occur in a coupled fashion (plus other features[125]), so that one mutation could lead to multiple changes simultaneously. Experiments with mice, they argue, have shown that mutations can lead to fusions of vertebrae and tail shortening and have pleiotropic effects (that is, have multiple effects simultaneously). Accordingly, a few changes from *Jeholornis* could have led to *Confuciusornis*: "If a vertebral fusion mutation occurred in a primitive bird like *Jeholornis*, which fused additional vertebrae in its synsacrum, truncated its tail, and fused some ribs, the resulting creature would have come a long way toward resembling *Confuciusornis*" (Rashid et al. 2014, 16).

Underlying this argument, however, is the common fallacy of confusing a necessary condition (here, changes in a regulatory gene) with a sufficient explanation. Especially the complexity and integration of the tail region of birds would certainly require numerous changes in downstream areas and tuning of interactions. One or a few regulatory mutations are far from enough. Mutations that lead to fusions are most likely to be severely detrimental on their own and have negative side effects (the abovementioned mice are certainly not selectively advantaged, if they are viable at all). Matching changes in muscle and other tissues would have to occur simultaneously, which is not likely. A scenario of a sudden, large-scale change that would have to involve many matching tunings is an extremely unlikely speculation, even in the age of EvoDevo.

Conclusion

The pygostyle does not belong to the bird-typical structures that supposedly have already evolved in dinosaur-like bird precursors. There is of course (in evolutionary theoretical interpretation) a convergent (independent) origination of pygostyles in younger forms of theropod dinosaurs. However, these are only fossilised well after the appearance of the first birds (fig. 43). Consequently they cannot be interpreted as bird precursors. Various pygostyle types are known, including such not found among present-day birds, but forms with and without pygostyles (and consequently with fan tails and plumage tails, respectively) are clearly separated. There are, however, some bird genera with a pinnate tail, namely *Jeholornis* and *Archaeopteryx*, and the four-winged *Microraptor*.

Reduced Fibula

The fibula in birds is greatly reduced, shorter than the tibia and formed as a kind of bone brace, which helps to save weight. Two tarsal bones are fused with the tibia to form the tibiotarsus.

In contrast, in many Mesozoic birds, the fibula is as long as the tibia.[126] This is also the case in theropod dinosaurs, in which, however, the fibula is narrow and in close contact with the tibia (Botelho et al. 2016, 543). The stratigraphically oldest bird genus with a reduced fibula is *Cruralispennia* from the enantiornithine group. At 131 Ma, this genus is also among the geologically oldest opposite birds (Wang et al. 2017d).

The distribution of genera with reduced tibiae in the system of theropods and birds requires the assumption of multiple independent regressions, namely in the Alvarezsauridae, Oviraptorosauria, and the birds, furthermore, also in the pterosaurs. Moreover, it must be assumed that the reduction in the size ratio of the fibula and tibia occurred independently in different avian lineages (as in *Confuciusornis*, *Quiliania*, and *Gansus*) (Altangerel et al. 1993; Botelho et al. 2016, 543; Makovicky and Zanno 2011; Sereno 1997; Wang et al. 2017d, 8[127]; see figs. 42, 44, 45). There is no consensus in the scientific discussion as to whether the reduction of the fibula should rather be considered an evolutionary by-

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[125] "These short-tailed birds, the confuciusornithids, enantiornithines and early ornithurines, had acquired a number of other more modern bird-like traits that differed from their long-tailed primitive bird predecessors. These traits included more extensive synsacral, sternum, and digit fusion (Figure 1), as well as uncinate processes fused to adjacent ribs. Osteological modifications were coupled to changes in musculature and behavior. With tail truncation and multiple bone fusions came advances in flight mechanics" (Rashid et al. 2014, 2). "Truncation of the bird tail was also concurrent with reduction and shortening of the large caudofemoralis muscle" (Rashid et al. 2014, 3).

[126] For example, *Archaeopteryx*, but with the fibula so closely attached to the tibia that "both bones probably functioned mechanically as a single element" (Peters and Gutmann 1976, 271); in the pengornithids (for example, *Chiappeavis*) and *Longipteryx*, which are classified as basal opposite birds (O'Connor et al. 2017; Wang, Li, and Zhou 2017, fig. 7); in the basal ornithuromorph *Archaeorhynchus* (Zhou and Zhang 2006b, 367).

[127] "*Cruralispennia* documents the oldest record of fibular reduction in the Enantiornithes. The available fossil evidence indicates that postmorphogenetic changes related to fibula development evolved independently in the Ornithuromorpha and derived lineages of the Enantiornithes (Fig. 7)" (Wang et al. 2017b, 8).

product or an adaptive structure (Botelho et al. 2016, 551f.).

Botelho et al. (2016) experimentally manipulated tibia growth in birds and, based on their results, hypothesized that fibula reduction occurred phylogenetically in two steps: first, the loss of the fibula's connection to the ankle, and then its reduction. Thus, both hypothetical processes would have to have occurred independently several times.

Wrist with a Semilunate Carpal

The mobility of the wrist is unique in birds because birds can angle the hand against the ulnar side of the forearm (that is, toward the ulna) and other angles are nearly impossible (Peters 1985, 244). This is made possible by the special construction of the wrist. It has a semilunate carpal bone (carpal, radiale), which faces the distinctly convex trochlea (articular surface) at the anterior end of the carpometacarpus and is important for the strong mobility of the wrist during flight and when folding the wings on the ground (Sullivan et al. 2010, 2027; Vasquez 1992). A semilunate carpal is also found in numerous dinosaurs and characterizes a broad taxon, the Tetanurae (Witmer 2002, 20; Norell and Makovicky 1999, 38[128]; see. fig. 46). In the three-fingered predatory dinosaurs, its function is unclear. Presumably it enabled rotational movements in grasping and manipulating prey (Sullivan et al. 2010, 2031[129]) or, in feathered forms, enabled better protection of the pennibrachium (in coelurosaurs, term for wing-like forelimbs with feathers with which a flight presumably was not possible) (Sullivan et al. 2010, 2032[130]). In *Archaeopteryx* and later birds, it enabled the bird-like rotations in wing flapping.[131] It is commonly assumed in evolutionary theory that the possession of a semilunate carpal was a kind of preadaptation for the requirements of flight and could therefore be coopted for flight.

The wrist bone structure is very similar in all present-day flight-capable birds, despite very different ecologies and lifestyles. This is strong evidence that this bone structure is necessary for flapping flight (Vasquez 1992, 266). In *Archaeopteryx* and theropod dinosaurs, ulnar angulation was probably not as pronounced as in other Mesozoic and present-day birds (Sullivan et al. 2010, 2027[132]), and the wrist of *Archaeopteryx* is not considered capable of sophisticated ground takeoff and active flight abilities comparable to present-day birds (Vazquez 1992[133]; Chatterjee and Templin 2003, 28[134]).

Partially Problematic Homologies

The homology of the semilunate carpal in birds and dinosaurs is not without controversy: "It is possible that the SLC [semilunate carpal] is not homologous throughout Tetanurae, in that different distal carpal elements may contribute to forming the SLC in different taxa or at least contribute to varying degrees" (Sullivan et al. 2010, 2030).

Based on their analyses, Xu et al. (2014, 1) conclude that the semilunate carpal was not formed by the same carpal bones in all theropods. They postulate a homeotic transformation that led to a lateral shift in position during theropod evolution.[135] Curiously, they note that this transformation may have been selected for the purpose of folding wings ("result of selection for foldable wings"), which implies purposefulness, since this process is supposed to have occurred before wings existed. The assumption of a homeotic transformation seems to be an ad hoc explanation for which there is no evidence.[136]

An evolutionary sequence proves to be even more problematic based on a study by Botelho et al. (2014). A synopsis of embryological and paleontological data led these authors to conclude that there had been a remarkable evolutionary regression, namely, a large bony pisiform (one of the carpal bones) had initially

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[128] "This mobility—combined with the presence of a folding mechanism in the wrist distally as a primitive character for maniraptorans—indicates that these features originated phylogenetically before the origin of powered flight in avialans" (Norell and Makovicky 1999, 38 on the dromaeosaur *Velociraptor*).

[129] "The original selective advantage of this enhanced mobility is not clear, but cannot have been related to pennibrachial folding unless relatively basal tetanurans had elongated feathers on the forelimb.... However, it is likely that mobility of the wrist was initially associated with other functions, such as predation" (Sullivan et al. 2010, 2031).

[130] "Whether the pennibrachium was used primarily for display, wing-assisted incline running (Dial 2003) or some other function, it was clearly a biologically significant structure. Damage to the pennibrachium would probably have been costly. Wrist abduction offers a means of protecting a pennibrachium from damage" (Sullivan et al. 2010, 2032).

[131] http://www.spektrum.de/magazin/neue-verwandte-von-archaeopteryx/826725.

[132] "By contrast, Sereno and Rao (1992) argued that *Archaeopteryx* and non-avian theropods were in fact limited in their ability to abduct the wrist joint, at least in comparison with extant birds and some derived Mesozoic ones" (Sullivan et al. 2010, 2027).

[133] "the wrist structure of *Archaeopteryx* strongly suggests that it was incapable of executing the same kinematics displayed by modern birds during flapping flight" (Vasquez 1992, 266).

[134] "The wrist of *Archaeopteryx* is primitively designed in the grade of dromaeosaurs, but lacks the sophistication and complex articulation of modern birds necessary to withstand the powerful compression of flapping flight (Vasquez 1994).... The wrist of *Archaeopteryx* was not appropriately designed for sophisticated ground takeoff (Vasquez 1994)" (Chatterjee and Templin 2003, 28).

[135] "'semilunate' structure underwent a lateral shift in position during theropod evolution, possibly as a result of selection for foldable wings in birds and their close theropod relatives. We propose that homeotic transformation was involved in the evolution of the 'semilunate' carpal" (Xu, Han, and Zhao 2014, 6).

[136] The authors write that such transformations occur more often, but as a justification this would be circular.

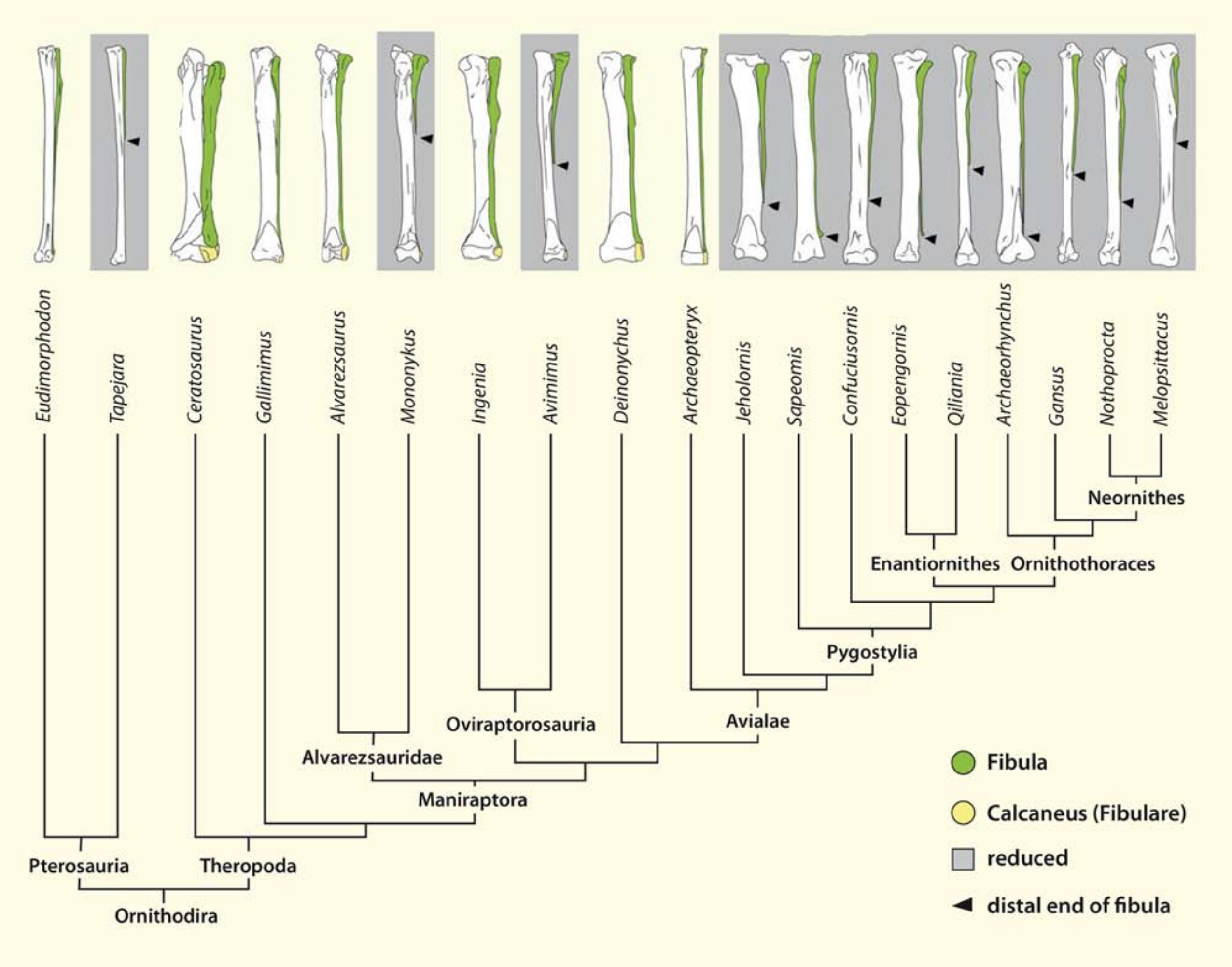

Fig. 44. Convergent reduction of the distal fibula in Ornithodira (pterosaurs and dinosaurs). At its base is a slender fibula with reduced distance between it and the tibia. Based on the distribution in the system, evolutionary theory must assume a reduction of the fibula independently (convergent) in four clades: Pterosauria, Alvarezsauridae, Oviraptorosauria, and birds. In basal Mesozoic birds such as *Jeholornis*, *Sapeornis*, *Eopengornis*, and *Archaeorhynchus*, the fibula was already formed distally in a splinter-like fashion without a distal epiphysis. However, the fibula was only slightly shorter than the tibia. A low size ratio of fibula and tibia is also convergently realized in *Confuciusornis*, *Qiliania*, and *Gansus* (adapted from Botelho et al. 2016, CC BY 4.0).

regressed during evolution, but then reappeared fully formed. In the meantime, it must have either disappeared, or it was not ossified, or it was very small.[137] In contrast, fusions could plausibly be made in other bone elements of the hand (Botelho et al. 2014, 2). These authors also argue a purpose (which should be taboo for evolutionary explanations): “The purpose of the re-evolution of the pisiform was probably to facilitate flight” (Botelho et al. 2014, 2).[138] Such a scenario contradicts Dollo’s law of non-reevolution of more complex structures. Apparently, however, such a process is not “forbidden,” so examples like this only show that there are no laws of (innovative) evolution.

Larry Martin, one of the critics of the dinosaur-bird theory, believes that the maniraptorans are more interpretable as descendants than ancestors of birds, given their hand characteristics, because the wrist is less derived in some respects in *Archaeopteryx* and modern birds (Martin 2004, 981).

No Continuous Change

The angle between the proximal and distal articular surfaces is called the “radial angle” and is thought to have increased in coelurosaurs and especially in maniraptorans. However, this increase is far from continuous, as can be seen from the figures in fig. 46. Accordingly, there is a jump in Therizinosauroidea

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[137] “The combined data provide compelling evidence of a remarkable evolutionary reversal: A large, ossified pisiform reevolved in the lineage leading to birds, after a period in which it was either absent, non-ossified, or very small, consistently escaping fossil preservation” (Botelho et al. 2014, 1). “The researchers discovered that the fourth bone in bird wrists, the pisiform, had a rare evolutionary history. They found that it was lost in dinosaurs, but reevolved in early birds” (Botelho et al. 2014, 2).

[138] “The pisiform enables a forceful downbeat of wings, and restricts the flexibility of the wings on the upbeat” (Botelho et al. 2014, 2).

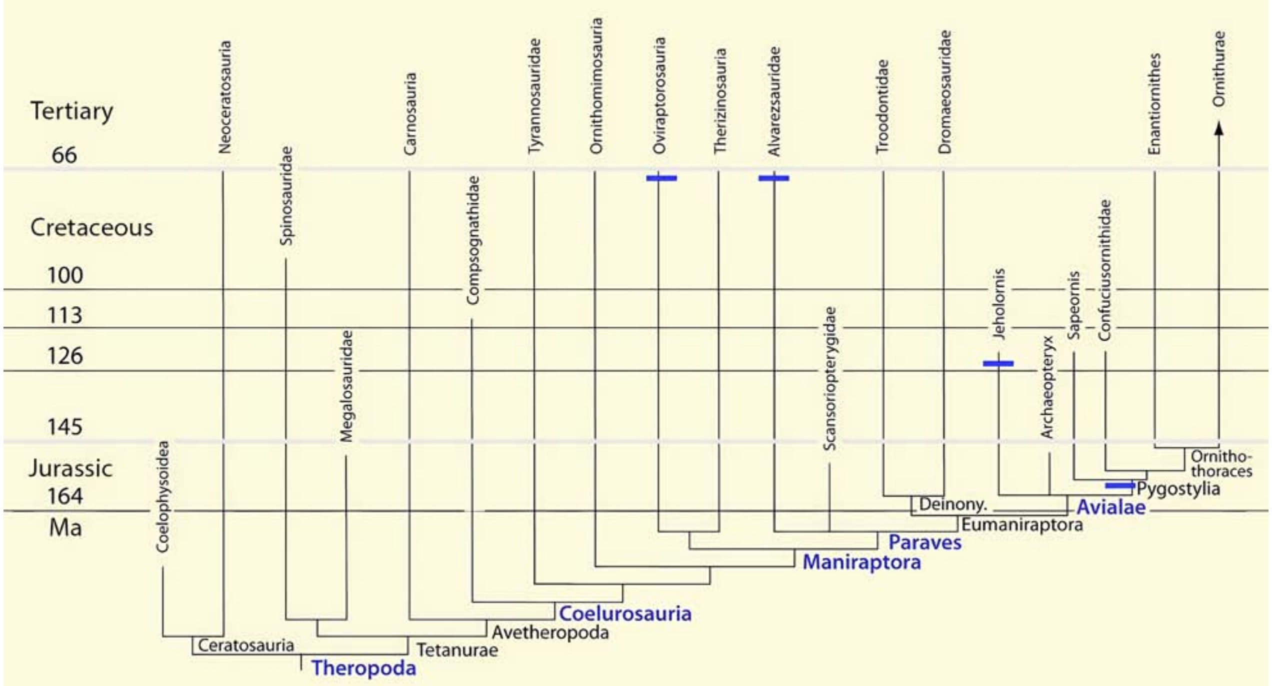

Fig. 45. Distributions of theropod and avian genera with reduced fibulae (blue markings) (assembled according to the sources mentioned in the text).

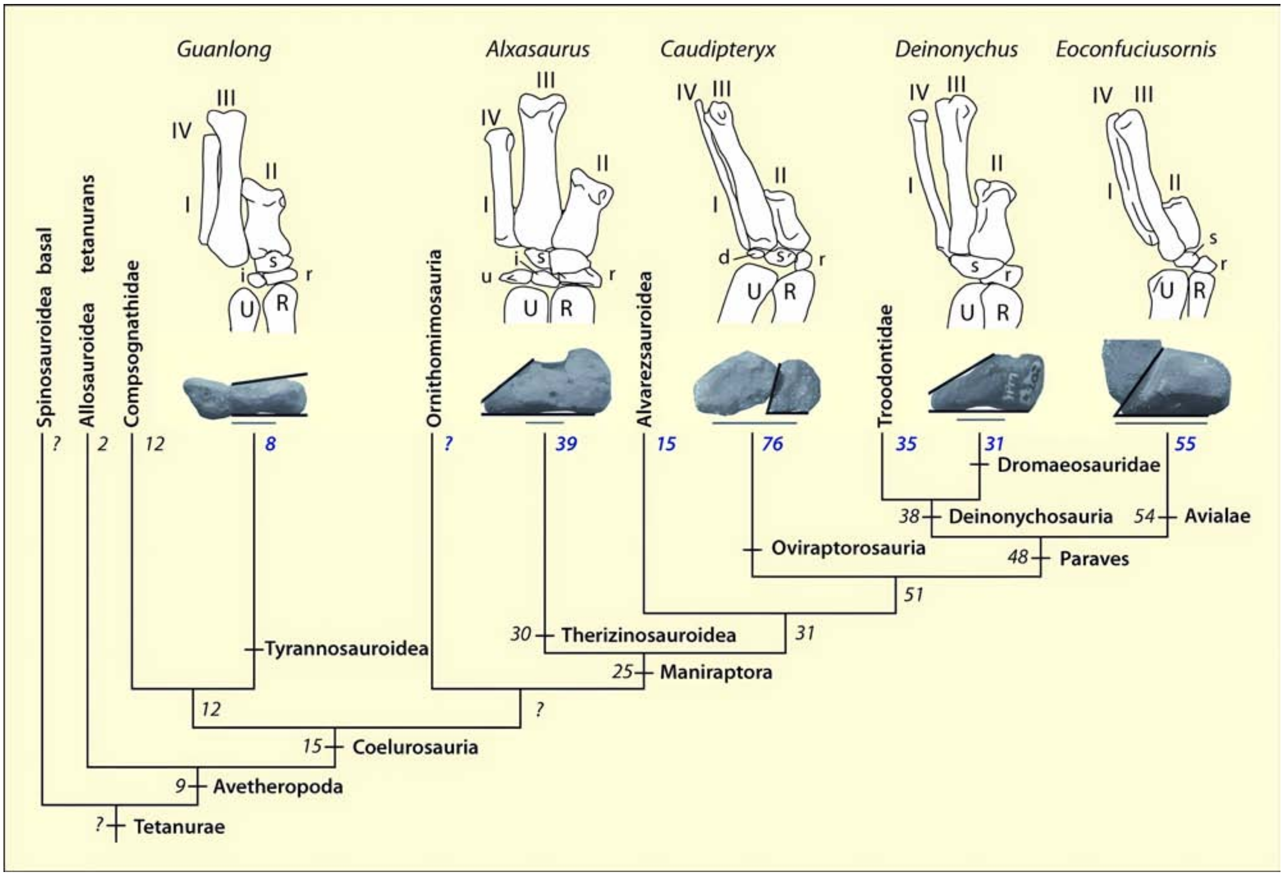

Fig. 46. Wrist structure and radial angle in tetanurans (phylogeny after Smith et al. [2007] and Zanno et al. [2009]). Figures indicate values of radial angle between proximal and distal articular surfaces of the radials in degrees. Values in bold are direct measurements of individual taxa; values in normal italic font are reconstructed ancestral states. II–IV metacarpals II–IV (numbering follows situation in present-day birds), d distal carpals, i intermedium, R radius (radius), r radials. s semilunate carpals, U ulna (ulna); u ulnar. Scale bars: 0.25 cm in *Eoconfuciusornis*, 0.5 cm in *Caudipteryx*, 1 cm in all other taxa (after Sullivan et al. 2010).

from 12° to 39°, then in Alvarezsaurids a decrease to 15°, while in oviraptorosaurids 76° and in Troodontids 35° were determined. Sullivan et al. (2010, 2031) therefore consider that the wrist of oviraptorosaurs evolved independently from that of birds. Fig. 47 shows the situation of the partly unsystematic distribution of trait expressions of further traits related to the wrist.

Another problem for the idea of a more or less continuous change towards bird-like mobility of the wrist is the fact that the restriction to ulnar abduction would be distinctly unfavorable for both a runner and a climber, but favorable for flying (Peters 2002, 350). This implies, however, that corresponding non-flying antecedent forms would have to be distinctly different from birds on functional grounds, arguing against a gradual transition. Climbing ability and flying ability of the anterior extremity contradict each other (Peters 1994, 406; see Peters 1985, 245).

Conclusion

The widespread formation of a semilunate carpal in numerous theropod dinosaurs could be considered a type of preadaptation for the requirements of flight. However, the homology of the semilunate carpal in birds and dinosaurs and within dinosaur groups is controversial. Evolutionary theory must assume that a large pisiform bone initially regressed, but then became fully developed again. In contrast, fusions can be made plausible for other bony elements of the hand.

Eggs, Clutches, and Brood Care

Most modern birds build nests and practice pronounced brood care. Females lay large eggs relative to body size and only *one* ovary is developed (the left one), not two as in reptiles. Accordingly, only one egg is laid in a single laying. In many species both partners breed, in some only the female, rarely exclusively the male. The eggs are turned frequently to ensure even warming. The chalky part of the eggshell has a three-layer structure (Hincke et al. 2012). The cuticle is first followed by a layer of vertically arranged crystals, then comes a palisade layer (with prismatic or scale-like elements) and finally a layer of cone-shaped components (mammillary layer), which is abutted by two membrane layers inside the shell (see figs. 48, 49).[139]

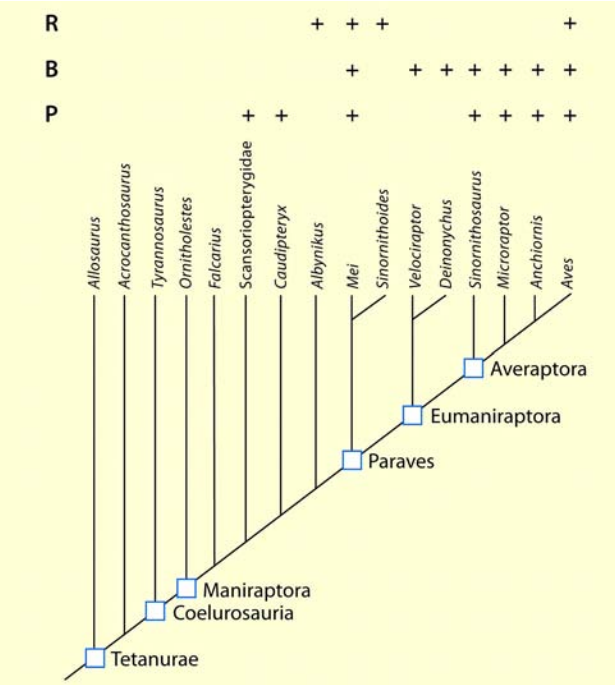

Fig. 47. Simplified cladogram of Tetanurae (see also fig. 4) showing the distribution of the following features: R bird-like resting position of the wings, B good flexion ability of the wrist, P propatagium (anterior flight skin) (according to Agnolin et al. 2019.

A number of bird-like features in egg structure and brood care, as well as bird-like nesting behavior, are also found in theropod dinosaurs, especially oviraptorids (Norell et al. 1995[140]; Zelenitsky and Therrien 2008), but also in troodontids (Varricchio et al. 1997; Varricchio and Jackson 2004a; Varricchio, Kundrát and Hogan 2018; Zelenitsky and Therrien 2008). Eggs with two-layered shells were found in a fossil of the dromaeosaur *Deinonychus* (Grellet-Tinner and Makovicky 2006[141]) and embryos in eggs were fossil preserved in a therizinosaur (Kundrát et al. 2008). In addition, incomplete, three-layered eggshells and two eggs and several other clusters of shell fragments of an alvarezsaurid *(Bonapartenykus)* were discovered in strata of the Upper Cretaceous of Argentina (Agnolin et al. 2012). The shape of the eggs could not be reconstructed here. The pairing of the fossil eggs may indicate that there were two functional oviducts. More detailed information about nests or brood care is not known for *Deinonychus*, *Bonapartenykus*[142] and the mentioned therizinosaur with the fossil embryos in the eggs.

The accumulation of finds of nests with fossils in breeding position in oviraptorids[143] is striking (fig. 50). Norell et al. (2018) conclude that oviraptorids must have been distinctly social animals. Clark,

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[139] See also http://www.ucmp.berkeley.edu/science/eggshell/eggshell2.php; for further details see also https://www.lebensmittellexikon.de/e0002310.php#1.

[140] A large oviraptorid over a clutch of eggs in a typical posture for many birds while brooding.

[141] According to Varricchio and Jackson (2016, 657), the only finding of fossilized eggs in a dromaeosaurid to date.

[142] “No nest structure had been observed in the excavated area; thus this interpretation seems to be implausible” (Agnolin et al. 2012, 43).

[143] “Curiously, the overwhelming preponderance of such specimens are oviraptorids” (Norell et al. 2018, 38).

Norell, and Chiappe (1999) report an oviraptorid fossil preserved in bird-like breeding position over a nest (see Norell et al. 1995, 775).

In rare cases, eggshell microstructure is preserved in theropod fossils, namely *Troodon formosus* and oviraptorids (Grellet-Tinner and Chiappe 2004, 199ff.). Varricchio and Jackson (2004b, 931) describe eggs of *Troodon* that show some avian characteristics.[144] They conclude through their study that no eggshell feature clearly separates birds from theropod dinosaurs (Varricchio and Jackson 2004b, 935[145], also Varricchio et al. 2013; 2018). The eggs of *Troodon* and other troodontids were said to be most similar to those of present-day birds in terms of their asymmetrical shape, low porosity, lack of ornamentation, and three-layered eggshell.[146] Jackson, Horner, and Varricchio (2010) were able to confirm that the eggshells of *Troodon* were trilayered (see also Varricchio et al. 1997, 248).

The species of the oviraptorids and troodontids, in which brood care was proven, all originate from Upper Cretaceous strata (Zelenitsky and Therrien 2008; see fig. 51), the eggs of the dromaeosaurid *Deinonychus* from the Upper Lower Cretaceous (Cloverly Formation, Montana/USA; see Grellet-Tinner and Makovicky 2006). The fossil evidence thus emerges stratigraphically quite late. In contrast, dozens of genera of the Enantiornithes and Ornithurae are already known from the Lower Cretaceous.

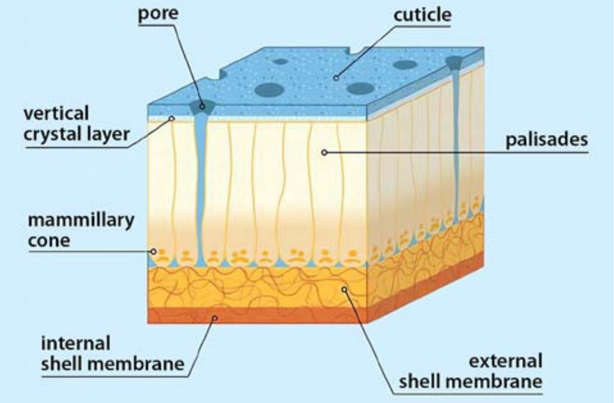

Fig. 48. Structure of an eggshell of modern birds (from Hincke et al. 2012).

Clutches and nests of *Troodon formosus* are interpreted by Varricchio et al. (1997, 248) as indicating that this species produced two eggs simultaneously (one per ovary) at an interval of one or more days (rather than en masse as in reptiles) and incubated the eggs by a combination of ground and body contact. This suggests the existence of two functional ovaries, the absence of egg turning, and partial egg burying, which are "primitive features" untypical of birds. On the other hand, there are features (as mentioned above) common with birds, namely, relative size of eggs and possibly their asymmetry, production of only one egg per oviduct per unit time (one day or more), an open nest, and brooding (see Varricchio and Jackson 2004a, 215; see Sato et al. 2005; Zelenitsky and Therrien 2008). The finding of paired eggs of *Sinosauropteryx* can also be interpreted as evidence for the existence of paired functional ovaries (Chen, Dong, and Zhen 1998).

In summary, according to Grellet-Tinner and Chiappe (2004, 208), the following characteristics of eggs and clutches connect birds with theropod dinosaurs: (at least) two layers of eggshells (bird eggs have three or more layers), aprismatic nature of the layers of eggshells, asymmetry of eggshells, brood care, and monoautochronic ovulation (eggs are laid in the interval of at least one day). While eggshell ornamentation is typical for dinosaurs, eggs in birds are usually smooth, which these authors interpret as reversion. However, even those theropod dinosaurs closest to birds lack some key reproductive features of present-day birds (Varricchio and Jackson (2016, 654, 661, 664), namely, the formation of only a single functional ovary, size of eggs, rotation of eggs in the nest[147], and sediment-free nests.[148] However, among birds, only Neornithes have sediment-free nests (Varricchio and Jackson 2016, 654, 675f.[149]). Finally, the reproductive biology of oviraptorids and

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[144] "Both eggs display several features typical of avian eggs: narrowly spaced nucleation sites, barrel-shaped mammillae with blocky crystal habit, a squamatic-like texture in the prismatic layer, and a third, structural layer.... Several varieties of supposed dinosaur eggs exhibit features such as two structural layers, prismatic shell units and squamatic ultrastructure, which are unique to birds among living taxa..." (Varricchio and Jackson 2004b, 931).

[145] "No single feature unambiguously separates avian from non-avian theropod eggshell" (Varricchio and Jackson 2004b, 935).

[146] "In comparison to oviraptorosaurs, troodontids like *Troodon*, share additional features found in most living birds including a third, external shell layer, an absence of eggshell ornamentation, and a more asymmetrically shaped egg. Further, the common eggshell microstructure and within-clutch egg pairing in these dinosaurs, as well as an oviraptorosaur adult with two internal eggs, indicate that overall ovary and oviduct function in these dinosaurs matched those of modern birds in producing eggs iteratively at daily or greater intervals, but from two active reproductive tracts" (Varricchio, Kundrát, and Hogan 2018, 1).

[147] Which has been inferred indirectly (see above, Varricchio et al. 1997, 248). The turning of the eggs in the nest requires considerable effort in the construction of the egg, namely the formation of the chalaza, which holds the yolk in the center of the calcareous shell and prevents damage in case of shocks.

[148] See Varricchio and Jackson (2016, 664): "Nevertheless, important differences remain between these two maniraptoran clades (oviraptors and troodontids) and modern birds, including two functional reproductive tracts, smaller than expected relative egg size, elongate egg-shape, and eggs still largely buried. These sediment-bound eggs would likely preclude egg rotation and, thus, may have lacked chalazae (Varricchio et al. 1997)." "The highly organized (Zelenitsky 2006) and partially to nearly fully buried clutches found in troodontids and oviraptors differ markedly from those of modern birds" (Varricchio and Jackson 2016, 661).

[149] "The most significant changes between enantiornithines and neornithines are an additional increase in relative egg size and incubation of eggs free of sediment. The latter entailed greater adult-egg contact, potentially improved egg shape, egg rotation, and chalazae" (Varricchio and Jackson 2016, 675f).

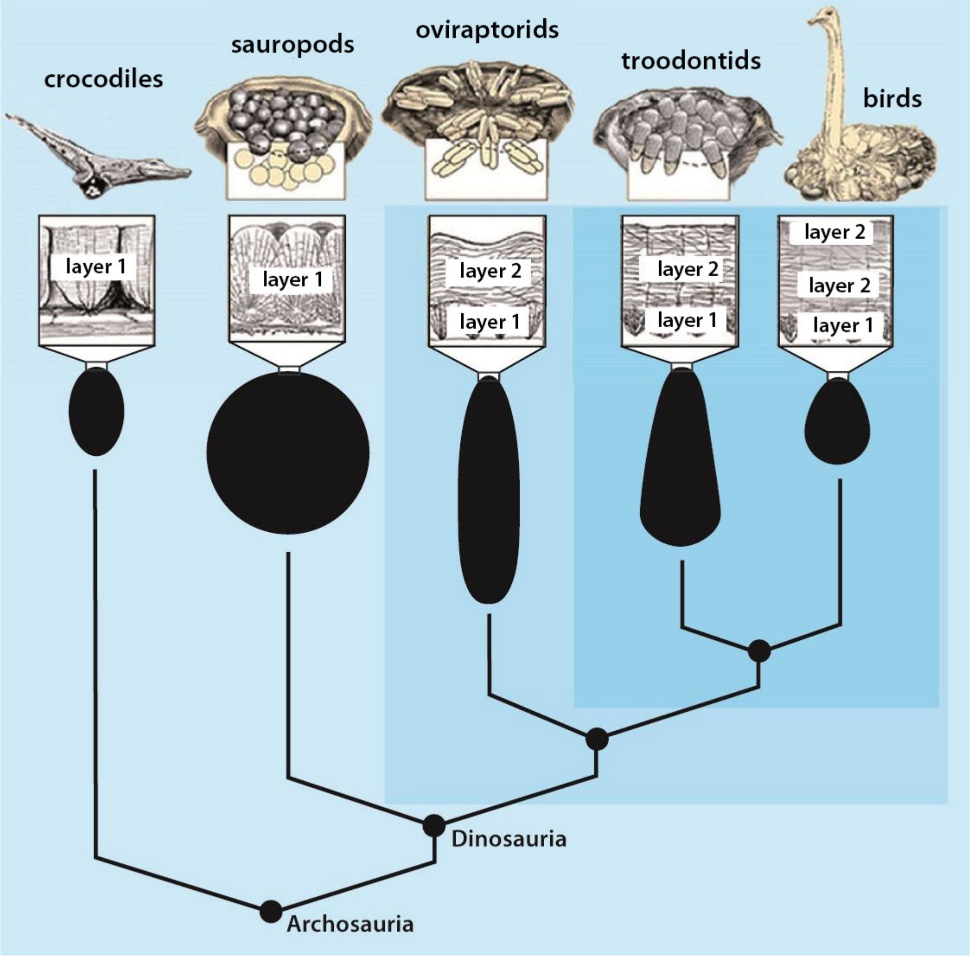

Fig. 49. Characteristics of the eggs and clutches of crocodiles, some dinosaurs, and birds. For example, the presence of at least two crystalline layers in the eggshell and the existence of an asymmetric egg can be traced back to the base of the maniraptorans (Jackson, Horner, and Varricchio (2010) were even able to confirm that the eggshells of *Troodon* were three-layered (see also Varricchio et al. 1997)). The distribution of eggs within a clutch in oviraptorids suggests that these dinosaurs laid their eggs sequentially. There is also evidence that, like birds, they also brooded their clutches (according to Chiappe 2009).

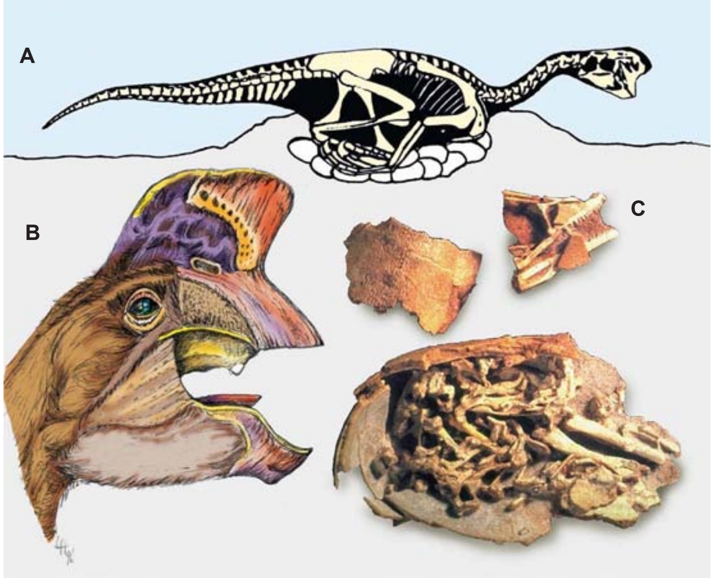

Fig. 50. Oviraptorid sitting on a nest (A; B head of an animal). The ensemble shows evidence of rapid burial. Embryos were fossilized even in the eggs (C) (A. after Norell et al. 1995; B. after Paul in Weishampel 1995; C. from Norell et al. 1996. Reproduced with permission from *Science* 266, © American Association for the Advancement of Science).

troodontids differs markedly from that of most other theropod dinosaurs where something is known about them (Varricchio and Jackson 2016, 660).[150]

Wiemann, Yang, and Norell et al. (2018) published data on color pigments in fossil dinosaur eggs. Using high-resolution Raman spectroscopy, they examined eggshells from representatives of all major dinosaur groups and concluded that colored eggs (presumably for camouflage) represent a common heritage of theropod dinosaurs and did not arise independently multiple times. The type of pigment deposition in the shell structure was also consistent with that of present-day bird eggs.

Early Birds

In all fossil known birds, including the most basal such as *Jeholornis*, only *one* functional ovary was present. As far as is known, they were "modern" in this respect (O'Connor et al. 2014, 16[151], see also Zheng et al. 2013). This, they argue, supports the hypothesis that the loss of an ovary is related to the weight savings required for flight. O'Connor and Zhou (2015) suggest this is a hallmark of birds.[152] In contrast, they argue that there is evidence that follicle maturation was slow and thus similar to that in Crocodilia.

Even in the basal bird *Eoconfuciusornis,* only one cluster of follicles[153] has been detected. This species, of all the species, shows the greatest known extent of hierarchy of follicles among the Cretaceous birds and is the most modern in this respect (Zheng et al. 2017).

Brood Care by Males

Varrichio et al. (2008) were able to demonstrate, based on the size of the nests and on anatomical features of the skeletons fossilized together with the nests, that brood care in *Troodon*, *Oviraptor*, and *Citipati* was performed by males. In birds, males and females perform brood care in over 90% of cases. Only in basal forms such as Palaeognathae[154] do only males care for the nest, which fits the presumed phylogenetic sequence (see also Prum 2008). However, convergence cannot be excluded regarding this behavior, since there are many phylogenetic lineages between the oviraptorids and troodontids on the one hand and the Palaeognathae on the other hand (Prum 2008, 1800), about whose brood care nothing is known.

Brood Care in Ornithischians

Brood care is not only known in maniraptorans,

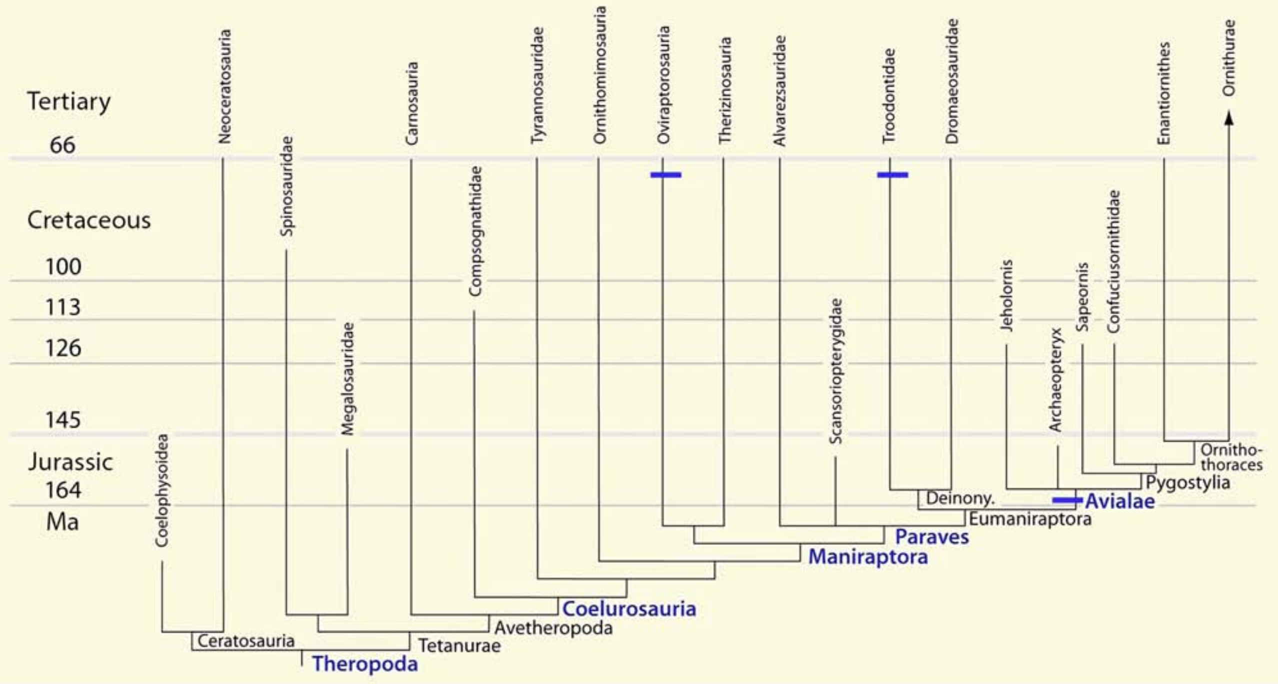

Fig. 51. Distributions of theropod and avian genera with avian-like characteristics in eggs and brood care (blue markings) (assembled from sources cited in the text).

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[150] "The reproductive anatomy and behavior of these 2 clades [oviraptors and troodontids] differs markedly from that of most other non-avian dinosaurs, including various theropods" (Varricchio and Jackson 2016, 660).

[151] "All the avian specimens from the Jehol preserve the cluster of ovarian follicles only on the left side of the body, indicating the presence of a single functional ovary [3]... *Jeholornis*... indicating that even the most basal birds were already modern in this aspect...." (O'Connor et al. 2014, 16).

[152] "With the loss of the right ovary known to have occurred very near the advent of Aves, we propose that the presence of a single ovary may define the avian clade" (O'Connor and Zhou 2015, 340).

[153] A follicle is the unit of egg cell and its surrounding auxiliary cells in the ovary.

[154] Ratites (Struthioniformes) such as ostrich, emu, cassowary or kiwi and breeching fowl (Tinamiformes).

which are close to birds, but has also been demonstrated in ornithischians, the large group of dinosaurs that is not in any close relationship to birds. In *Psittacosaurus,* for example, a larger group of juvenile forms was discovered with an adult form that appeared to have been rapidly embedded while still alive, which Meng et al. (2004, 145) interpret as evidence of brood care.

Already in 1979 Horner and Makela had described a find of 15 equally sized juvenile animals of the hadrosaur *Maiasaura* in nest-like arrangement and together with shell remains (Upper Cretaceous, Campanian). According to Horner and Makela (1979, 297), the fact that 15 juvenile individuals were fed and were together for a longer period of time speaks for distinct brood care. The authors mention three other examples of possible brood care in hadrosaurs and in a horned dinosaur (with fewer individuals in the presumed nest).[155]

Homology or Convergence?

Overall, little is known about egg structure, clutching, and brood care in dinosaur theropods, which are placed in an ancestral position to birds. Data about it are almost only available for some troodontids and oviraptorids from the Upper Cretaceous. Whether brood care was established early from an evolutionary point of view and can be considered original to all dinosaurs is therefore doubtful (Meng et al. 2004, 145[156]; see Zelenitsky and Therrien 2008, 812[157]). But also within the maniraptorans (see cladogram fig. 4) a homology is not assured. While the troodontids together with the dromaeosaurids are mostly classified as a sister group of the Avialae (which supports a homology), the oviraptorids stand further apart. Zelenitsky and Therrien (2008, 812) do present a cladistic analysis that features of eggs and reproduction are consistent with the topology of phylogenies based on skeletal features, but there are few finds to base this on (see also the cladogram of Varricchio and Jackson [2004b], for which the same is true[158]). Zelenitsky (2006, 209, 215) also states that in theropod dinosaurs there are also unique features in reproductive behavior for which there is otherwise no parallel in archosaurs.

Decisive for the decision homology or convergence would be knowledge about clutches and brood care in the intervening lineages (alvarezsaurids, scansoriopterygids) (see Grellet-Tinner and Chiappe 2004). Moreover, the assumption that not only Upper Cretaceous genera, but also Lower Cretaceous troodontids and oviraptorosaurs possess bird-like characteristics in clutching and brood care is obvious, but not self-evident. Stratigraphically, the theropod genera with proven (or very probable) brood care are fossil recorded much later than numerous bird genera.

Varricchio and Jackson (2004b, 935) note that their analysis of trait distributions reveals a striking degree of homoplasy (convergences or reversions) in the evolution of eggshell structure. For example, both the eggshells of *Troodon* and those of an unnamed egg type from their study show a three-layered structure as in many modern birds, but they lack the characteristic scale-like structure.[159] In contrast, the eggshells of oviraptorids have only two layers but possess a scale-like structure. In turn, the eggshells of the theropod genus *Lourinhanosaurus* (unclear systematic position) have three layers but no scale-like structure, and the eggs are relatively small (Varricchio and Jackson 2004b, 935).

Conclusion

In oviraptorids and troodontids, a number of avian characteristics are pronounced in eggs, clutches, and brood care—only one egg per oviduct per day, large eggs relative to body size, complex eggshell structure, egg asymmetry, and brood care. Varricchio and Jackson (2004b, 936) conclude that most of the eggshell features considered typical of avian eggs have already evolved in theropod dinosaurs.[160] However, their distribution in the system requires some degree of convergence. The extent of this

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[155] The authors note that one of the biggest mysteries is that juvenile dinosaurs are found exceedingly rarely. The most popular explanation, they say, is that eggs were laid at higher elevations and the young grew up where they were less preserved by sediment and more easily eroded.

[156] "given the disparity in ecology and physiology between crocodilians and birds, homology of their parental care is debatable. Discovery of similar aggregations for other dinosaurs would strengthen the idea that post-hatching parental care is the ancestral condition in Dinosauria and therefore a homologous character among crocodilians and birds" (Meng et al. 2004, 145).

[157] "However, the question of whether or not some of these characters first appeared among non-maniraptoran theropods will remain unanswered until eggs positively ascribed to more basal theropod clades are discovered" (Zelenitsky and Therrien 2008, 812).

[158] "Two factors contribute to the lack of more definitive results from this analysis: a limited set of characters and homoplasy" (Varricchio and Jackson 2004b, 935). "Currently, cladistic analysis of fossil eggs is somewhat limited by both the number of taxonomically identifiable fossil eggs and distinct eggshell characters" (Varricchio and Jackson 2004b, 936).

[159] "Character distributions in our analysis indicate a significant amount of homoplasy in the evolution of eggshell structure. Both the *Troodon* egg type and the unnamed Two Medicine egg type exhibit the three structural layers present in many modern birds (Nys et al., 1999) but may lack the characteristic squamatic texture" (Varricchio and Jackson 2004b, 935).

[160] "Further, phylogenetic analysis suggests that most features one would consider typical of modern avian eggs (e.g., asymmetric shape, rigid calcite shell comprised of two or more structural layers, squamatic ultrastructure, closely spaced shell units, and straight narrow pores) first evolved within non-avian theropods. The theropod avian-ancestor produced an egg nearly identical to that of a modern bird; this implies a high level of similarity in oviduct function (Mikhailov, 1992) and reproductive physiology (Varricchio and Jackson, 2004)" (Varricchio and Jackson 2004b, 936).

cannot be estimated at this time due to the paucity of data with the associated uncertainty about trait expression in intermediate lineages of theropods.

Quotes on the Widespread Occurrence of Convergences

The following are some quotes from researchers expressing the very common occurrence of convergences (emphasis added in each case).

- "Homoplasy is *common* among theropod dinosaurs" (Xu and Pol 2013, 327). Case study: "Lee and Worthy (2012) found that the deinonychosaurian status of *Archaeopteryx* is supported by more synapomorphies but that these characters are more homoplastic than those supporting the avialan affinities of *Archaeopteryx* (which are fewer but less homoplastic)." (Xu and Pol 2013, 327)
- "An accurate phylogeny is the basis for understanding avian origins, but coelurosaurian systematics is plagued by large amounts of missing data and *prevalent homoplasies*,…" (Xu et al. 2009, 434)
- "Convergent evolution and mosaicism in character evolution among paravians is *commonplace*." (Turner, Makovicky, and Norell 2012, 137)
- "This uncertainty is due to real observed homoplasies; suites of derived characters shared with other different clades of coelurosaurs whose distributions cannot be resolved without some reversals or convergences." (Holtz 2001, 116)
- "Considering the distribution and combination of morphological characters in the fossil record it goes clear that *many or even most characters* considered typical of birds, like reduction of teeth, reduction of manual claws, the horny bill, the pygostyle, reduction of the fibula etc., *evolved more than once*." (Peters 2002, 353)
- "the fact that avian features have arisen repeatedly and independently in theropod evolution now seems to be an inescapable conclusion." (Witmer 2002, 5)
- "The distribution of 'avian' characters strongly suggests evolution in the maniraptoran clade was *highly homoplastic*." (O'Connor and Sullivan 2014, 4, emphasis added)

General Conclusions from the Individual Studies

The individual studies have shown that the bird-typical features are distributed in the system of theropods and Cretaceous birds in such a way that convergences or reversions are assumed almost throughout, often several times. Evolutionarily, this means that these traits must have evolved independently two or more times. O'Connor, Chiappe, and Bell (2011, 40f) conclude that the distribution of avian-like features such as beak, furcula, sternal plates, uncinate processes of the ribs, retroverted pubis, distally nonfused pubic bones, parallel orientation of pubis and ischium, and the formation of a pygostyle are common within maniraptorans in a way "that makes it difficult to determine a clear pattern of origin of the features for most of them. This suggests an earlier origin of many of these traits, while their occurrence in apparently unrelated groups of theropods, and their absence in primitive birds, suggests a highly homoplastic evolutionary history."[161] Numerous authors note that there are confusing relationships and convergences are common (see the citations on convergences and on confusing relationships; see also tables 2 and 3).

In some cases one would have to assume under evolution-theoretical guidelines that "avian features in dinosaurs" are lost again after their emergence, before birds have evolved. In such cases, they can consequently not be precursor traits.

Survey Representative?

The above study may not be representative. The selected characteristics are incomplete. However, the selection was not deliberately selective, but was based on the available material. The result shown in fig. 1 and table 3 was not anticipated by this author. In this respect, it is quite surprising. The starting point of the investigations was the observation that many authors point out that the presumed transition area dinosaur–bird is characterized by very many convergences. The author has followed up this observation more exactly by the present investigation.

Quotes on Unclear Evolutionary Relationships

Below are some quotes from researchers expressing that relationships within theropod dinosaurs close to birds are unclear.

- "the increase in specimen data has complicated rather than clarified the problem of identifying the avian sister-group, revealing a mosaic of

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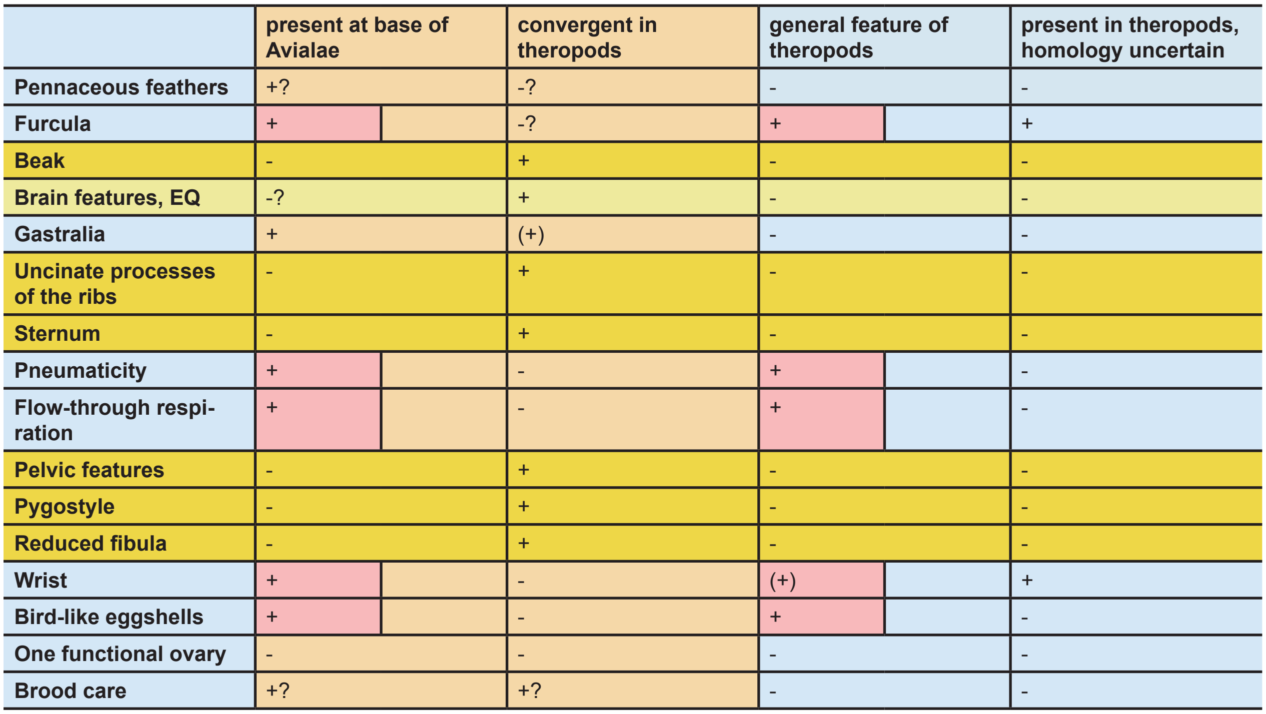
[161] "The distribution of 'avian' characters such as a beak (Clark et al., 2001), furcula (Nesbitt et al., 2009), sternal plates (Norell and Makovicky, 1997; Burnham et al., 2000), uncinate processes (Codd et al., 2007), retroverted pubis (Chiappe et al., 1998; Norell and Makovicky, 1999), distally noncontacting pubes (Chiappe et al., 2002a), parallel pubis and ischium (Chiappe et al., 1998), and a pygostyle (Barsbold et al., 2000) are so spread out through Maniraptora that for most of them it is difficult to determine a clear pattern of character origination. This suggests a deeper origin for many of these characters, while their occurrence within apparently unrelated nonavian theropod groups and their absence in primitive birds suggests a highly homoplastic evolutionary history" (O'Connor, Chiappe, and Bell 2011, 40f).

Table 2. Brief overview of the results of the individual investigations with short summaries on the question to what extent the characteristics in question can be interpreted as characteristics in hypothetical bird ancestors.

Feathers	Flat and today's feathers comparably developed in some troodontids (Anchiornis) and dromaeosaurids (Microraptor), but different type of flight (four-winged) than in Avialae. Whether hair-like or simply feathered body appendages should be called feathers is debatable or theory-dependent (see Junker 2017).
Furcula	At the base of theropods, however, the homology with the furcula of birds is questioned by some researchers.
Beak	Not a precursor feature, but convergent in theropod dinosaurs.
Brain characteristics, EQ	Probably convergent in troodontids and oviraptorids, thus probably not an avian precursor trait.
Gastralia	Although present in some theropod dinosaurs, some trait expressions may have evolved convergently.
Uncinate processes of the ribs	Feature absent in basal birds, therefore likely convergent in theropod dinosaurs and thus probably not an avian precursor feature.
Sternum	Distribution of species with and without sternum does not indicate correlation with presumed phylogeny; probably convergent, thus probably not an avian ancestral trait.
Pneumatization of bones	Commonly present in theropod dinosaurs.
Flow-through respiration	Probably universally present in theropod dinosaurs.
Pelvic features	Convergent in theropod dinosaurs, probably not an avian precursor feature.
Pygostyle	Partly convergent in theropod dinosaurs; not an avian precursor feature.
Reduced fibula	Fibula not reduced in many Mesozoic birds. Reduction convergent in theropod dinosaurs.
Wrist	Bird-like mobility widespread in theropod dinosaurs, but homologies partly uncertain.
Eggshells	Bird-like expression common in theropod dinosaurs.
Only one functional ovary	Only in birds.
Brood care	Recorded in some theropod dinosaurs, but in forms much younger than a large proportion of Mesozoic birds, thus uncertain as a bird precursor trait.

Table 3. Tabulation of the results assembled in table 2. It is striking that many of the avian features examined that are present (+) in theropod dinosaurs are not formed in those forms that are considered immediate avian precursors, but must have evolved convergently (yellow underlay). A large proportion of the other features examined are considered to be general theropod features (light red underlay) and are therefore also not well suited to support a gradual origin of avian features in theropod dinosaurs. +, present; –, absent, ? unclear.



	present at base of Avialae	**convergent in theropods**	**general feature of theropods**	**present in theropods, homology uncertain**
Pennaceous feathers	+?	-?	-	-
Furcula	+	-?	+	+
Beak	-	+	-	-
Brain features, EQ	-?	+	-	-
Gastralia	+	(+)	-	-
Uncinate processes of the ribs	-	+	-	-
Sternum	-	+	-	-
Pneumaticity	+	-	+	-
Flow-through respiration	+	-	+	-
Pelvic features	-	+	-	-
Pygostyle	-	+	-	-
Reduced fibula	-	+	-	-
Wrist	+	-	(+)	+
Bird-like eggshells	+	-	+	-
One functional ovary	-	-	-	-
Brood care	+?	+?	-	-

'avian' morphologies inconsistently distributed among purportedly closely related clades of non-avian dinosaurs.... Basal birds themselves possess disparate morphologies and do not provide a clear picture of the plesiomorphic avian taxon: *Archaeopteryx* strongly resembles troodontids such as *Anchiornis* and *Xiaotingia* (Turner, Makovicky, and Norell 2012; Xu et al. 2011), while the robust skull of sapeornithiforms most strongly resembles those of recently discovered basal oviraptorosaurs such as *Caudipteryx* (Ji et al., 1998) and of the scansoriopterygid *Epidexipteryx*." (O'Connor and Sullivan 2014, 4)

- "As a result of the high amount of homoplasy that characterizes derived maniraptoran evolution, the identity of the avian sister taxon remains debated despite the rapid accumulation of morphological data." (O'Connor and Sullivan 2014, 23)
- "Each of these clades [Dromaeosauridae, Troodontidae, Deinonychosauria] possesses a different combination of avian characters distributed among the included taxa,..." (O'Connor, Chiappe, and Bell 2011, 45)
- "Inferred relationships between theropod clades are complex and have changed dramatically over the past thirty years with the emergence of cladistic techniques" (Hendrickx, Hartman, and Mateus 2015, 1). "Though one might expect few major changes in theropod relationships in the future, large portions of theropod phyletic history remain obscure;..." (Hendrickx, Hartman, and Mateus 2015, 34)
- "The discovery of numerous small-sized paravian theropods in the Late Jurassic and Early Cretaceous of China in the past decades have greatly enhanced our understanding of basal paravian anatomy and evolution. However, they also provided sometimes confusing evidence of widespread convergence and parallel evolution in this clade,..." (Rauhut, Foth, and Tischlinger 2018, 83).

Theropod Characteristics or Lack of Avian Characteristics in Basal Birds

On the one hand, many bird-typical features are present in theropod dinosaurs. Conversely, a number of features typical of modern birds are absent in many early birds, whether in individual genera or in entire groups. "The earliest birds lacked many key features related to powered flight in modern birds, and probably had primitive flight capabilities that varied substantially between groups" (Brusatte, O'Connor, and Jarvis 2015).[162] Much has been discussed in the previous sections, which need only be recalled here. Due to the fame of the "Urvogel", the absence of a pygostyle in favor of a long caudal spine, the absence of a beak, and absence of a bony sternum are familiar features of *Archaeopteryx* (Brusatte, O'Connor and Jarvis 2015; a gastral basket is also not developed). Many enantiornithine birds did not possess a sternal keel (Brusatte, O'Connor, and Jarvis 2015, 892). *Jeholornis* also possessed a long caudal spine instead of a pygostyle (see above). A toothed jaw without a beak was present in a number of Cretaceous bird genera.

More Examples

Benson and Choiniere (2013, 2) point out that the proportions of the hind limbs of most Mesozoic birds are similar to the proportions in theropod dinosaurs. The short-tailed genus *Sapeornis* possessed a shoulder girdle similar to that of deinonychosaurs (Xu et al. 2014, 2). The furcula of basal birds such as *Archaeopteryx* was not formed as an energy-storing elastic brace, but may have served as an attachment point for flight muscles (see above). Gastralia were only developed in Mesozoic birds. There are enormous differences in the construction of the pelvis between birds known from Cretaceous strata and present-day birds. In many Mesozoic birds, the fibula is not greatly reduced as in present-day birds. In the discussion of individual features, the unsystematic distribution of bird features in dinosaurs was pointed out. This situation applies accordingly to the distribution of bird-untypical features in Mesozoic birds.

Avian Precursors or Secondarily Flightlessness?

In the case of some genera or entire groups that are interpreted as bird precursors, a minority of researchers working in this field discuss whether they are secondarily flightless birds. In this case, their features would be eliminated as evidence for a gradual transition from dinosaurs to birds, and this would significantly change the overall picture. Some researchers make a strong case for this interpretation, especially in the case of oviraptorids (Maryañska, Osmólska, and Wolsan 2002). However, this interpretive possibility is also discussed in the dromaeosaurids (Czerkas and Feduccia 2014, 850), the scansoriopterygids (Chatterjee and Templin 2012; Czerkas and Feduccia 2014; Zhang et al. 2008), and the alvarezsaurids (Altangerel et al. 1993; Chiappe 2002b; Peters 2002, 349). For the alvarezsaurids, however, the interpretation as secondarily flightless birds has now become less likely due to new finds (Xu et al. 2018; see below). It has also been brought into play for *Archaeopteryx* by Michael Habib that its flight ability may have been partially forfeited

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[162] Apparently, there was a diversity of ways of flying (see Brusatte, O'Connor and Jarvis 2015, see above), some of which are not realized under present-day forms and which cannot easily be put into an evolutionary scheme (see the later discussion).

(Kaplan 2013). He concludes this by comparing leg lengths and feather symmetries in *Archaeopteryx* and present-day birds. These are similar in *Archaeopteryx* as in present-day secondarily flightless birds.[163]

In the section on rib construction, Paul (2001, 479) was already quoted as saying that features of the respiratory apparatus, such as the uncinate processes on the ribs, were more derived in dromaeosaurids and oviraptorosaurids than in *Archaeopteryx* and were developed similarly to secondarily flightless birds, which could indicate a secondarily flightless status (see also Codd et al. 2008). Maryañska, Osmólska, and Wolsan (2002) argue for an "avian status" of Oviraptorosauria based on a cladistic analysis (compare fig. 52 with Fig. 4).[164]

The basal oviraptorosaur genus *Caudipteryx* also exhibits a number of bird-typical features, most notably flat, symmetrical feathers with a shaft (Martin and Czerkas 2000, 691[165]; Feduccia 1999b, 4742[166]; Wellnhofer 2002, 470, 474[167]). The construction of the hand is to be understood hardly differently than as inheritance of a flight-capable ancestor (Martin and Czerkas 2000, 691).[168] According to Peters (2002, 350), *Caudipteryx* has anatomical features very similar to flightless ratites, which gives a clear indication that *Caudipteryx is* a bird and had flightless ancestors. Because of the smallness of the feathers and the forelimbs, *Caudipteryx* and also the in some respects similar *Protarchaeopteryx* may not have been capable of flight. However, it is implausible to consider these two genera as avian ancestors (Peters 2002, 349). The relative proportions of the posterior extremities of *Caudipteryx* are in sharp contrast to other bipedal dinosaurs. They are indistinguishable from ratites[169] and the center of gravity is significantly more forward in the body than in all bipedal dinosaurs, according to Jones et al. (2000, 727). Therefore, the interpretation of *Caudipteryx* as a secondarily flightless bird is most plausible, even though cladistic analyses place the genus among the coelurosaurs.[170] Ruben and Jones (2000, 594) consider that features that would clearly support an avian precursor status are either absent or questionable in *Caudipteryx*.[171]

Feduccia and Czerkas (2015, 1067) enumerate a whole series of bird-typical features in *Caudipteryx*[172] and still particularly refer to the possession of an aerodynamic propatagium (flight skin in the area of the wings) in some specimens of *Caudipteryx,* which also argues that this genus and thus the oviraptorosaurs as a whole were derived flightless ground dwellers.[173] Propatagia were also discovered in the dromaeosaurid *Microraptor* (Agnolín and Novas 2013), the troodontid *Anchiornis* (Wang et al. 2017b), and *Scansoriopteryx* (Czerkas and Feduccia 2014), which, among other indications, supports flight capability or possibly secondary flight loss in flightless genera of these families (see Feduccia and Czerkas 2015, 1070).

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[163] Of course, this hypothesis is controversial, and biologist Ahsley Heers notes that a better understanding of the relationship between anatomy and lifestyle must be achieved to better interpret the fossil record; it must also be taken into account that many present-day birds may fly better when young than when adult (Kaplan 2013).

[164] They enumerate the following traits of Oviraptorosauria that are otherwise present in "more advanced" birds: "extensive pneumatization; enlargement of the parietal portion of the skull roof; double-headed otic process of the quadrate...; lateral cotyla on the quadrate for articulation with the quadratojugal...; functional loss of contact between the palate and jugal; shallow or rod-like jugal.... This set of traits is absent in non-avian theropods but is present in advanced birds.... In addition, there is a massive furcula, well stabilized on the acromion, similar in shape to those in *Archaeopteryx* and *Confuciusornis*. Moreover, in all known oviraptorosaurs, the tail is shorter than in any of non-avialan theropods" (Maryañska, Osmólska, and Wolsan 2002, 105). Accordingly, some postcranial features are interpreted as reversions (Maryañska, Osmólska, and Wolsan 2002, 106).

[165] "Several of these features indicate that *Caudipteryx* is specialized beyond *Archaeopteryx* and may be closer to *Confuciusornis* (Fig. 2) including loss of teeth in the maxillary and dentary; a mandibular foramen in the mandible; enlargement of the premaxillary; reduction of the maxillary; reduction of the hyperpubic spoon; ball-shaped head on the femur; reduction of the fibula;..." (Martin and Czerkas 2000, 691).

[166] "Indeed, *Caudipteryx* shows a suite of features that show it to be a secondarily flightless bird, a Mesozoic kiwi, including a protopygostyle (fused tail vertebrae), an avian occiput, reduced fibula, wing feathers attached as in archaic birds, etc." (Feduccia 1999b, 4742).

[167] "*Caudipteryx* may now arguably be classified as a secondarily flightless bird, although according to its skeletal structure it exhibits more primitive theropod-like features than are present in *Archaeopteryx*" (Wellnhofer 2002, 474; translated).

[168] "It is hard to see how this hand makes any sense except as an inherited complex from a flighted ancestor" (Martin and Czerkas 2000, 691).

[169] "Accordingly, *Caudipteryx* probably used a running mechanism more similar to that of modern cursorial birds that to that of all other bipedal dinosaurs" (Jones et al. 2000, 716).

[170] See also (Olson 2002, 1204): "meaning that flightlessness must have evolved very early in avian history and in a completely different lineage from any other known flightless bird."

[171] Similarly Geist and Feduccia (2000, 668): "A number of non-theropodan, derived avian features of *Caudipteryx,* including a shortened, incipiently fused tail ('protopygostyle'), a ventrally oriented foramen magnum, vaned feather structure, along with questionable identifications of crucial characters of the skull (e. g., the nature of the quadrate-quadratojugal complex), make the theropodan classification of these fossils unwarranted."

[172] They comment on these features, "Yet, the large number of highly sophisticated avian characters in the oviraptorosaurs has been difficult to explain if they were derived from earth-bound dinosaurs" (Feduccia and Czerkas 2015, 1068).

[173] "The discovery here of an aerodynamic propatagium in several specimens provides new evidence that *Caudipteryx* (and hence oviraptorosaurs) represent secondarily derived flightless ground dwellers, whether of theropod or avian affinity,..." (Feduccia and Czerkas 2015, 1067).

Kundrát (2007) considers it possible that the oviraptorid *Conchoraptor*, with bird-like brain features, descended from ancestors capable of flight.[174]

Usually, it is argued that the cladograms are less contradictory if the groups concerned are placed in an ancestral position to the birds. But the cladistic argument is not very strong, because it has been shown more and more that convergences can occur frequently. This, however, calls into question the parsimony principle that underlies the creation of cladograms. This would be even more true if some biologists were right, who meanwhile even claim that convergent development is something like the "way of life" of evolution.[175] Zhou et al. (2000, 252), while considering *Caudipteryx* more likely to be an avian ancestor among theropod dinosaurs on the basis of cladistic results, note that the parsimony principle of cladism is "philosophically untestable". So, it must be conceded that there is no compelling evidence that it was not a flightless bird.

Dyke and Norell (2005), on the basis of their analysis, counter that there is no reason, either in terms of phylogeny, morphometrics, or any other facts, to conclude that *Caudipteryx is* anything other than a small theropod dinosaur. Chiappe and Dyke (2002, 109) consider an avian status of *Caudipteryx* implausible because problematic reversion would have to be assumed such as reevolution of a bony tail,[176] development of new phalanges and renewed elongation of fingers, changes of the sternum back to small and separate sternal plates, and reversion of fusion of multiple bones and pelvic features.[177] Throughout, the arguments for avian status were based on faulty methodology in their opinion (Chiappe and Dyke 2002, 107).[178] For Witmer (2002, 11), the primitive features of *Caudipteryx* also argue against an avian status for this genus. Consensus has not been reached on the status of *Caudipteryx* and the Oviraptorosauria as a whole.

Noteworthy in this context is the fact that flightlessness is always considered secondary in present-day species with true feathers and is very common (Chiappe 2002a).[179] Today's flightless birds live on sites (mainly islands) where flight ability could be forfeited without loss of fitness. A path back to flight ability was never taken and it is therefore even less likely for first-time flight acquisition.

Striking Jumps

A gradual appearance of various individual traits (see preliminary remarks) does not automatically mean that the emergence of these traits is also plausible in evolutionary theory. This was explained above with some examples. On the other side, some traits appear relatively abruptly. For example, Xu et al. (2014, 1341) write: "However, new data also highlight occasional bursts of morphological novelty at certain stages particularly close to the origin of birds and an unavoidable complex, mosaic evolutionary distribution of major bird characteristics on the theropod tree." And Brusatte (2017b, 55) notes that the first birds evolved at exaggerated rates, namely, once the building blocks ("lego-kit") were complete, incredible evolutionary potential was unlocked, so to speak.[180]

A relatively sudden appearance has already been noted for some traits above. This is especially true for the pygostyle (for example, Rashid et al. 2014; Wang and Zhou 2017, 6). Further, the avian beak emerges suddenly in fully developed form with *Confuciusornis*. Other genera classified as basal, *Archaeorhynchus* and *Hangshanornis*, also have a beak and are toothless or nearly so. Although there are many genera with diverse expressions of dentate jaws that also have a beak (see above), stratigraphically the first forms with fully developed beaks appear abruptly.

In the section above on clutches and brood care, it was mentioned that all fossil known birds, including the most basal such as *Jeholornis,* had only one functional ovary as far as is known, and even the geologically oldest birds were "modern" in this respect (O'Connor et al. 2014, 16, see also Zheng et al. 2013).

Dececchi and Larsson (2013, 2741) have shown that when body size was taken into account, there

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[174] "The data presented in this study do not allow an unambiguous assessment whether the avianlike endoneurocranial characteristics of the flightless *Conchoraptor* evolved convergently to those of avian theropods, or indicate a derivation of oviraptorosaurs from volant ancestors" (Kundrát 2007, 499).

[175] For example, Hejnol (2014). He comments that the new view of the independent emergence of two distinct nervous systems (Moroz et al. 2014) is a blow to the anthropocentric view that complex traits evolved gradually, culminating in the emergence of humans, and that complex traits do not evolve twice. But evolution does not work in such a one-line fashion, he writes.

[176] However, the basal birds *Archaeopteryx* and *Jeholornis* also had long bony feather tails.

[177] As far as is known, the pubic bone was anterior in oviraptorids (Zhou et al. 2000, 252) and the pelvic bones were not fused (Wang, Li, and Zhou 2017, 11474).

[178] "Morphological arguments in favor of an avian placement of *Caudipteryx* have relied on characters that are either incorrect, circular, or also found among other non-avian coelurosaurians" (Chiappe and Dyke 2002, 107).

[179] "a combined set of functional and phylogenetic analyses indicates that all flightless birds, with the possible exception of the alvarezsaurids, if they were to be considered avian . . . , are descendants of flighted ancestors. . . . At least 12 avian lineages have extant flightless representatives and a large variety of extinct and recently extirpated birds are known to have been, or have been interpreted as, flightless" (Chiappe 2002a).

[180] "Those earliest-emerging birds that lived alongside their dinosaur forebears were evolving at supercharged rates-faster than *Velociraptor, Zhenyuanlong* and other nonbird species. It seems that once a small, flight-capable dinosaur had been assembled, once that Lego kit was complete, incredible evolutionary potential was unlocked" (Brusatte 2017b, 55).

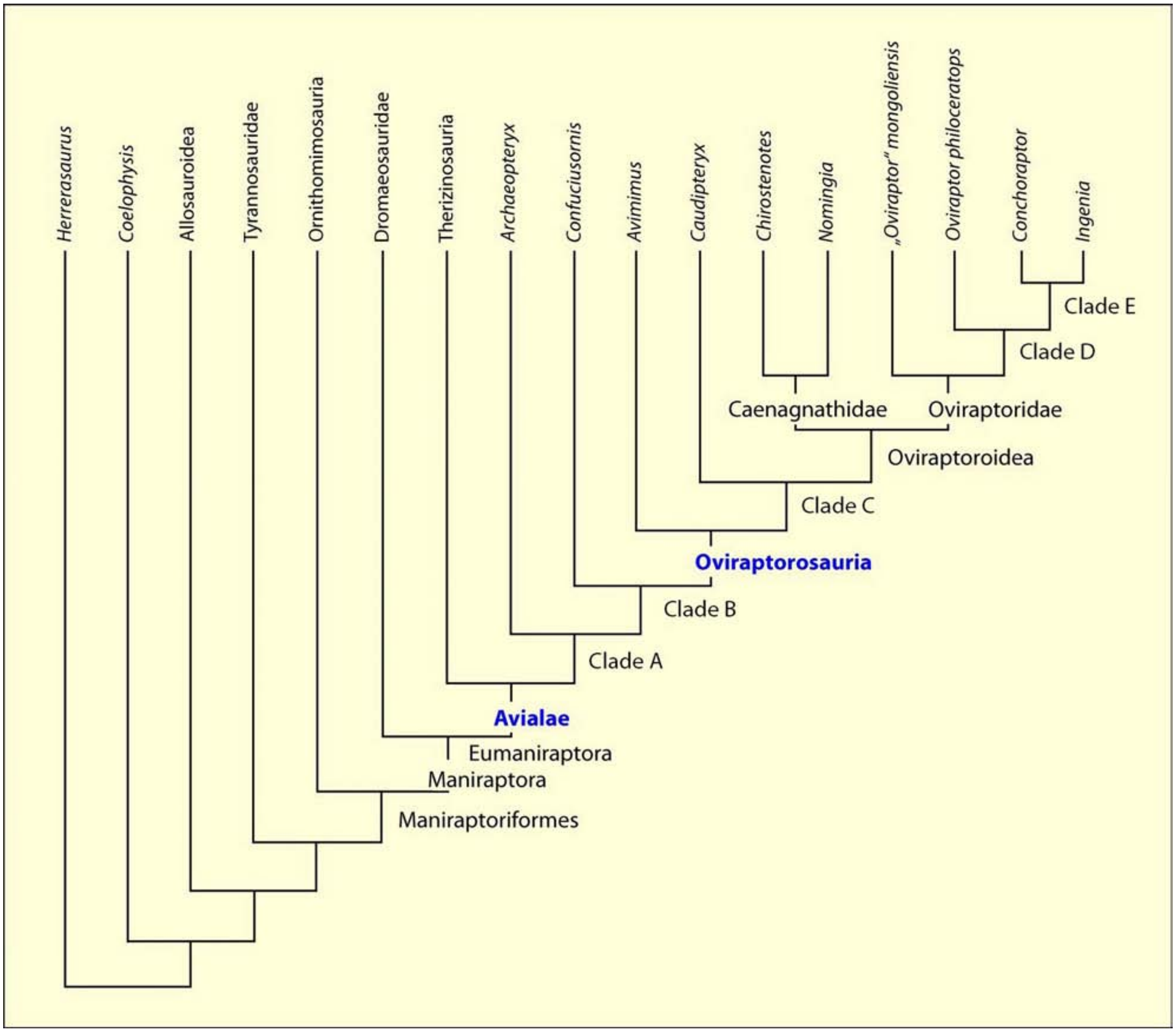

Fig. 52. Cladogram after Maryańska, Osmólska, and Wolsan (2002), according to which the oviraptorosaurids are nested within the birds (Avialae).

was no trend of an increase in forelimb length in theropod dinosaurs and this suddenly changed in birds.[181] Similarly, Carrano (2000, 489) notes with respect to pelvic girdle and hind-limb morphology that this has been remarkably uniform in theropod dinosaurs, showing little variation toward specialized forms. This apparent evolutionary stability makes the transition of the locomotor system to birds even more remarkable.[182]

According to Sanz et al. (2002), the formation of the derived wing proportions and the rod-shaped raven leg correlates with the shortening of the tail and the formation of a pygostyle in early birds. Accordingly, the decoupling of the hind leg and tail and the new connection of the thoracic and tail modules to form the flight apparatus occurred simultaneously.[183]

Zheng et al. (2014a, 7) point out that the alimentary canal was already formed in basal

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[181] "Once body size is factored out, there is no trend of increasing forelimb length until the origin of birds. We report that early birds and nonavian theropods have significantly different scaling relationships within the forelimb and hindlimb skeleton. Ancestral forelimb and hindlimb allometric scaling to body size is rapidly decoupled at the origin of birds,..." (Dececchi and Larsson 2013, 2741).

[182] "showing little evidence for deviations that would imply development of more specialized forms of locomotion.... This apparent evolutionary stability makes the locomotor transition from non-avian theropods to birds even more remarkable. This transition involved modifications of the entire musculoskeletal system, not simply the structures directly associated with flight" (Carrano 2000, 489).

[183] "the known Early Cretaceous avian record (e.g., *Iberomesornis* and the other birds from Las Hoyas, *Sinornis*, *Cathayornis*) appears to indicate a correlation between the evolution of the modern avian pectoral and tail modules. The evolution of derived wing proportions and strutlike coracoids, along with the furcula, correlates with a shortened tail and the presence of a pygostyle. Thus, the evidence of *Iberomesornis* (confirmed later by other taxa) shows a simultaneous, more than a sequential, development of stages (2) and (3) above. Thereby, (2) decoupling of the hindlimb and tail; and (3) novel allegiance of the pectoral and tail modules to form the flight apparatus" (Sanz et al. 2002).

ornithuromorphs very similar to present-day birds.[184]

The architectures of the shoulder girdle of *Archaeopteryx*, *Jeholornis*, and *Sapeornis on* the one hand and the advanced Ornithothoraces on the other hand are clearly different. In the former, the supracoracoideus muscle was probably attached only to the coracoid bone, whereas in the latter a supracoracoideus traction was developed and the muscle also attached to the sternum. The two constellations probably reflect different features of locomotion (Mayr 2017b, 865). Sanz et al. (1996, 442) see a structural gap between *Archaeopteryx* and the basal Ornithothoraces that would have significantly enhanced their flight capabilities.[185]

New examination methods such as laser-assisted fluorescence microscopy have recently made it possible to detect previously unknown details of soft tissue anatomy (ligaments, muscles, tendons). This has shown that *Confuciusornis* (fig. 53) possessed "a suite of relatively modern soft tissue structures that are more advanced than may be expected" (Falk et al. 2016, 6). In addition, well-developed and resistant flight skins (propatagium and postpatagium on the inner and outer sides of the wings) were detected, which, according to Falk et al. must have enabled enormous lift and, together with the robust feather shafts, argued for the ability to fly actively. Using evolutionary theory, the authors conclude that the flight skin system evolved early and may be a common feature (synapomorphy) of all birds (Falk et al. 2016, 8).[186] Based on the new findings, the researchers conclude that *Confuciusornis* could fly short distances well and possessed many relatively "advanced" avian anatomical features. Overall, then, the Confucius bird was by no means primitive, which is why the authors speculate, in terms of evolutionary theory, that its modern features must have arisen much earlier than previously thought. Older rock strata could perhaps provide relevant answers about precursors.[187] Soft-tissue features were also identified in an unnamed mating bird from Lower Cretaceous strata, characterized as surprisingly modern and suggestive of very good flight ability (Navalón et al. 2015; fig. 54), so a revision regarding flight ability was made in this case as well. The enantiornithine birds, to which the find is included, are now considered good flyers. The bastard wing was also already developed among geologically ancient forms of the opposite birds (Zhou 2004, 457).[188]

The Upper Jurassic troodontid *Anchiornis*, which is feathered with pennaceous feathers and is (incorrectly?) not considered a bird, was also found to have a flight skin using the new study methods (Wang et al. 2017b; fig. 55). The forearm, hand, lower leg, and foot each had 10–13 long flight feathers. Therefore, this four-winged form was probably able to fly much better than previously thought. The flight skin at the elbow helps modern birds take off from the ground. Thus, it may have helped *Anchiornis* achieve this ability as well, according to the scientists. However, this cannot be determined with certainty. Furthermore, the symmetry of the feathers clearly argues against the ability for active flight. The characteristics of *Anchiornis* contradict altogether in any case a gradual emergence of the flight ability.[189] The distinct avian features only make sense if *Anchiornis* was capable of flight in some—so far probably unknown—way.

One of the geologically oldest enantiornithine genera, *Protopteryx,* classified as primitive, possessed an alula (Zhang and Zhou 2000). Thus, it must be assumed that the associated flight abilities occur early in the avifauna, presumably in the base of Ornithothoraces (see Zheng et al. 2017, 448[190]). This is because the genus *Archaeorhynchus,* placed at the base of Ornithothoraces, also possessed an alula (Zhou and Zhang 2006b). In contrast, an alula has not been recorded in the genera *Archaeopteryx, Confuciusornis, Jeholornis,* and *Sapeornis, which* are considered basal (Peters and Ji 1999; Zhou and Zhang 2003a, b, 2006a).

All of these findings suggest that flight capability has emerged abruptly, as it were, as a total package.[191]

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[184] "The combination of crop and gizzard morphologies recognized among basal ornithuromorphs indicates that different lineages had evolved diet-specific morphologies of the alimentary canal, very similar to living birds." (Zheng et al. 2014a, 7)

[185] "Structural disparity between *Archaeopteryx* and basal ornithothoracines indicates important differences in their ability to fly.... This suggests that basal ornithothoracines had substantially improved their flight capabilities" (Sanz et al. 1996, 442).

[186] "This suggests that the patagial system in birds developed early in their evolution and, when available for study, may be a uniting synapomorphy.... The extensive and robust propatagium in *Confuciusornis* would have generated a large amount of lift" (Falk et al. 2016, 6).

[187] "If *Confuciusornis*, a primitive bird quite basal on the avian tree (e.g. see [39]), possessed a suite of characters so modern, it suggests that these features arose much earlier than perhaps previously implied. If that is so, then earlier rocks may contain the answers to many questions about the origin and early evolution of birds" (Falk et al. 2016, 13).

[188] "it is most likely that this advanced flight feature appeared at the origin of the Enantiornithes" (Zhou 2004, 457).

[189] Michael Pittman, one of the researchers comments; "The laser images show that this non-bird dinosaur had wings that were remarkably similar to those of living birds, down to the soft tissues." (http://www.bbc.com/news/science-environment-39126987).

[190] "An alula (bastard wing) is a synapomorphy of Ornithothoraces, to which Confuciusornithiformes are commonly resolved as the out group. In *Eoconfuciusornis*, at least one elongated pennaceous feather is attached to the proximal end of the alular digit representing an incipient stage in the evolution of the alula" (Zheng et al. 2017, 448).

[191] Regarding *Iberomesornis,* Sanz et al. (2002, 227) write: "In conclusion, the fossil birds from Las Hoyas have provided evidence indicating that enhanced flight capabilities similar to those of neornithine birds were already present at the outset of the Cretaceous" (Details and explanations there).

Fig. 53. Numerous skeletons of *Confuciusornis sanctus* are fossil preserved. Eduard Solà, "*Confuciusornis sanctus* fossil specimens exhibited in Cosmocaixa, Barcelona," https://en.wikipedia.org/wiki/File:Confuciusornis_sanctus.jpg, CC BY-SA 3.0.

Given the numerous requirements for active flight, this is ultimately not surprising.

Soft tissue is fossil preserved from the basal ornithuromorph *Archaeorhynchus*, and it can be concluded from the fossil remains that the lungs were "very similar to the lungs of present-day birds" (Wang et al. 2018). These authors see this finding in a set of features on soft tissue systems (for example, digestive and respiratory systems) that are typical of birds living today and were established early, before changes in the skeleton occurred.[192]

Conclusion

Many avian traits are classified as early established under evolutionary theory and abruptly emerge in fossils. This situation is a challenge for evolutionary mechanisms, as rapid emergence is not to be expected under evolutionary theory.

Early Diversity and Mosaics

On the basis of the distributions of traits in early birds and the dinosaurs close to them and their stratigraphic positions, on the one hand, it is a picture of different mosaics and consequently of a network of similarity relations; on the other hand, a rather abrupt appearance of multiple forms emerges. Both do not correspond to earlier formulated evolution-theoretical expectations. In addition, the following are some examples of the networked situation and the fast-appearing variety.

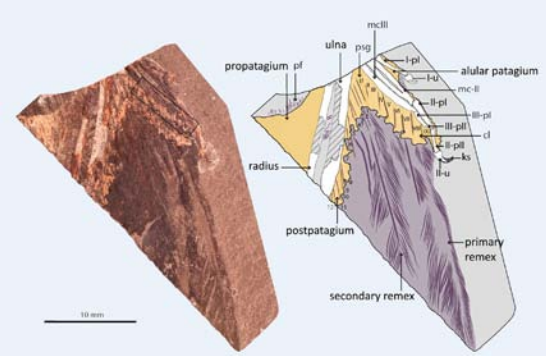

Fig. 54. Fossil and interpretive drawing of enantiornithine MCCMLH31444 from Las Hoyas, Spain. The framed portion includes the region of transition between bone and soft tissue. Abbreviations: I, II, III refers to fingers I, II, and III, cl calamus; ks keratinized sheath, mc metacarpal, p phalanges, pf down feathers, u claw (from Navalón et al. 2015, modified), CC BY 4.0.

Cross-linked Relationships

Some researchers note that trait relationships among taxa tend to be reticulate rather than tree-like.

- Wellnhofer (2000, 37) assesses the situation based on the discovery of *Confuciusornis as* follows: "With this new finding, the phylogeny of birds seems to have proceeded in an increasingly complex manner, in bushy branching and with parallel developments rather than in a straightforward sequence with *Archaeopteryx* as the central ancestral form."
- "[T]he original diversification of birds was probably also a complicated bush with many extinct lines that may at one time have been more advanced in some features than their ultimately more successful contemporaries" (Hou et al. 1999, 681). *Confuciusornis* must be regarded as an early branch of a bush-like radiation that was neither a precursor of modern birds nor of opposite birds.[193]
- The best known witness of this situation is the famous urvogel *Archaeopteryx*, because despite possessing "modern" feathers, it is placed by many researchers on a side branch that does not lead to other birds due to special traits (Hou 2001, 7[194]; Martin 1985, 182[195]; Shipman 1998, 116[196]; Zhou

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[192] "This adds to growing evidence that many physiological modifications of soft tissue systems (e.g., digestive system and respiratory system) that characterize living birds and are key to their current success may have preceded the evolution of obvious skeletal adaptations traditionally tracked through the fossil record" (Wang 2018, 11555).

[193] "The combination of distinctively advanced and primitive features found in the skull provides new evidence for a mosaic pattern in the early evolution of birds. *Confuciusornis* is not the progenitor of either modern birds or later enantiornithines, but must be regarded as an early twig in a bush-like radiation of birds" (Hou et al. 1999, 681f).

[194] "Currently, a majority of workers consider *Archaeopteryx* as representing a side branch and not a stem group in the evolution of the class" (Hou 2001, 7).

[195] "*Archaeopteryx* is not ancestral to any group of modern birds. It has specializations in its tarosmetatarsus and skull which show conclusively that it is on a side branch of avian evolution" (Martin 1985, 182).

[196] "Features of its hindlimb and skull are so specialized that it is usually placed on an evolutionary side branch, albeit the earliest avian side branch known" (Shipman 1998, 116).

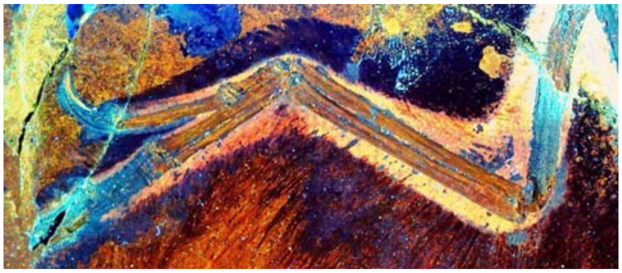

Fig. 55. Wings of *Anchiornis* under laser-induced fluorescence. The skin folds (patagia) in front of the elbow and behind the wrist were covered with feathers as in modern birds. Photo: Wang X. L., Pittman M. et al., *Nature Communications* 2017, CC BY-SA 4.0.

and Hou 2002, 179[197]; Xu and Pol 2013, 331[198]).

- Sumida and Brochu (2000, 492) state that avian features already present in dinosaurs were distributed among different species and that no species possessed all of these characteristics.[199]
- "As has been the case with the enantiornithines, the increase in ornithuromorph taxonomic diversity has not resulted in greater systematic clarity—rather the known diversity shows no clear pattern of character acquisition." (O'Connor and Zelenkov 2013, 1280)
- Xu et al. (2014, 1341) write that the main avian features show a complex mosaic evolutionary distribution on the theropod tree.[200]

Fast Diversity

Some researchers note that, assuming evolutionary origination, rapid changes must be assumed (which would be implausible in evolutionary theory).

- "This discovery, together with many others in recent years, suggests that by the Early Cretaceous, early birds had not only *diverged significantly* in morphology, size and ecology, but had also differentiated with respect to feeding adaptation." (Zhou and Zhang 2002, 409).
- "There is now a picture of *rapid radiation of* birds after the initial establishment of flight with at least three significant lineages—Confuciusornithidae, Enantiornithes and Ornithurae.... Each shows a considerable degree of specialization, with apparently competent flight performance broadly comparable to that of extant species, albeit with less overall morphological diversity." (Rayner 2001, 372)
- Sullivan, Xu, and O'Connor (2017, 3) speak of "*rapid diversification of* aerodynamic structures" in the Paraves, of great diversity of bauplans with respect to skeletal and integumentary structures in Yanliao (Upper Jurassic) and Jehol (Lower Cretaceous), there is a "high level" of "experimentation" (for this term, see below), and homoplasies and exaptations with respect to the aerodynamic apparatus.

For example, the Lower Cretaceous enantiornithine *Longipteryx* (fig. 56) had relatively long and powerful wings and a very well-developed flight apparatus, and probably specialized in fish feeding as a predator lurking on shores (Zhang et al. 2001). Zhou (2004, 457) evaluates this as evidence that ecological diversity increased rapidly in the Lower Cretaceous.[201]

The enantiornithine genus *Huoshanornis,* also from the Lower Cretaceous, possessed a relatively "modern" hand that allowed "extraordinary maneuverability," which, according to Wang et al. (2010, 436), "highlights once again the rapid evolution the avian manus."[202]

Fig. 56. *Longipteryx*, Beijing Museum of Natural History. Jonathan Chen, "Fossil specimen of Longipteryx chaoyangensis on display at the Beijing Museum of Natural History," https://en.m.wikipedia.org/wiki/File:Longipteryx-Beijing_Museum_of_Natural_History.jpg, CC BY-SA 4.0.

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[197] "*Archaeopteryx* is most likely the oldest known side branch of avian evolution" (Zhou and Hou 2002, 179).

[198] "*Archaeopteryx*... in an evolutionary side branch near the origin of the birds,..." (Xu and Pol 2013, 331).

[199] "One aspect shared by all of these putative bird relatives is the presence of one or a few outwardly bird-like characters. *Megalancosaurus* has grasping feet and a straplike scapular blade, *Longisquama* has structures that resemble a furcula and feathers, and *Euparkeria* has cranial features found in birds. But we are faced with a problem—none of them shares all of these features" (Sumida and Brochu 2000, 491).

[200] "new data also highlight... an unavoidable complex, mosaic evolutionary distribution of major bird characteristics on the theropod tree" (Xu et al. 2014, 1341).

[201] "*Longipteryx* also shows that enantiornithines had experienced a rapid increase in ecological diversity by the Early Cretaceous" (Zhou 2004, 457).

[202] "The morphology of the manus may also suggest that at low flight speeds the new bird's maneuverability was exceptional" (Wang et al. 2010, 432). "The discovery of *Huoshanornis* adds to our knowledge of the morphological and taxonomic diversification of the Enantiornithes, and it highlights once again the rapid evolution the avian manus had undergone by the Early Cretaceous" (Wang et al. 2010, 436).

O'Connor et al. (2015b, 1559) note that a remarkable range of complex forms of the sternum has rapidly evolved within birds.

Dececchi and Larsson (2013) showed, on the one hand, that the relative elongation of the forelimb in putative avian progenitors is an allometric effect of the reduction in body size, yet when body size is taken into account, there is no trend of forelimb elongation. On the other hand, there are sudden significant differences in the relation of the forelimb and hindlimb skeleton in birds compared to theropod dinosaurs, namely, there would be a rapid decoupling of forelimb and hindlimb in relation to body size at the origin of birds.[203] Early birds would also have rapidly diversified ecologically.[204]

- Brusatte, O'Connor, and Jarvis (2015, 893) note that there has been a "*huge spike*" in the rate of anatomical evolution in the earliest birds.[205]
- "The refinement of flight capability and manoeuvrability and the evolution of a fully opposable digit for perching *proceeded rapidly* once primitive avians were airborne." (Sereno 1999, 2143)
- "Frond-tailed birds, ribbon-tailed birds and fan-tailed birds all co-existed during the rapid diversification of avialans in the early Cretaceous." (Martyniuk 2012, 28).

Of all species, the oldest known genus of ornithurans, the blackbird-sized *Archaeornithura* from northern China (fig. 57), belongs to the derived forms of this group (Balter 2015, Wang, Zheng, O'Connor et al. 2015). Wang, Zheng, O'Connor et al. (2015, 6) speak of inconsistencies between stratigraphy and phylogeny. This, they argue, necessitates the assumption of so-called ghost lineages, that is, the existence of evolutionary lineages for which fossil evidence is lacking. The whole group of ornithurans does not appear in the fossil succession in the form of a growing diversity, but rather abruptly in differently differentiated forms (see also O'Connor and Zelenkov 2013, 1280).

- Also, the second major group fossilized in the Lower Cretaceous, the opposite birds (Enantiornithes), appears suddenly and in great diversity from the beginning of the fossil record and, moreover, simultaneously with the ornithurans (see Feduccia 2001, 142[206]). There are indeed genera that cannot be clearly assigned to the Enantiornithes or to the Ornithuromorpha (O'Connor and Zhou 2013). However, this is not primarily due to primitive traits, but to mosaic distribution of derived traits as well. For example, the ornithouran *Schizooura lii* has a Y-shaped furcula, a coracoid without lateral process, and a flat scapula, which is typical of enantiornithines, but on the other hand derived features such as an elongate sternum with a pronounced sternal keel, which in turn is lacking in the basal ornithouran *Archaeorhynchus,* whose sternum is more reminiscent of opposite birds (O'Connor and Zhou 2013, 903f; Zhou, Zhou, and O'Connor 2012).

Fig. 57. Reconstruction of *Archaeornithura*, one of the geologically oldest genera of Ornithurae. Credit: Zongda Zhang/Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

The species *Cruralispennia multidonta,* which is placed among the opposite birds, also possesses characteristics typical of the other large Cretaceous bird group, the Ornithurae ("bird-tails"). *Cruralispennia* occupies a derived position among the opposite birds and is not interpretable as a transitional form between the two groups. Moreover, this genus is among the oldest birds after *Archaeopteryx*—a "stratigraphic-phylogenetic discrepancy" (Wang et al. 2017d).

- "Early Cretaceous birds show a wide range of specializations of the wing and shoulder girdle bones." (Mayr 2017b, 860)

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[203] "we have demonstrated that early birds diverged radically from both the forelimb and hindlimb bauplan of nonavian theropods. The first birds have a marked elongation and integration of the forelimb and pectoral unit that is not present in nonavian theropods. These results signal a fundamental shift in the appendicular skeletal development between avian and nonavian theropods and suggest significant behavioral and ecological divergence between these clades" (Dececchi and Larsson 2013, 2750).

[204] "Although nonavian theropods were terrestrial cursors (Gatesy and Middleton 1997; Dececchi and Larsson 2011), birds rapidly diversified ecologically (for example, swimming, perching, wading, etc.) and show evidence for a further decoupling of within limb modules…" (Dececchi and Larsson 2013, 2750).

[205] "However, there apparently were some bursts of evolution in the early history of birds. Once a small flight-capable dinosaur had been assembled, there was a huge spike in rates of anatomical evolution in the earliest birds. Later, the early evolution of short-tailed birds (Pygostylia) in the Cretaceous was associated with high rates of hindlimb evolution and greater than normal speciation" (Brusatte, O'Connor, and Jarvis 2015, 893.

[206] "It therefore appears that, unexpectedly, there was an early avian dichotomy, as we now have both opposite birds and well-developed ornithurine birds from deposits of early Cretaceous age" (Feduccia 2001, 142).

Contradictory Distribution of Characteristics

The situation of a "complicated bush" stems from the fact that combinations of features of different genera are contradictory, so that their graphical representation is more easily reticulate than tree-like. Here are some examples:

- *Zhongornis haoae*, a basal bird was toothless (advanced feature) but possessed similarities to basal oviraptorosaurs (for example, a short, deep skull) and to scansoriopterygids (hand and pelvic features) (O'Connor and Sullivan 2014).
- The arboreal opposite bird, *Liaoningornis,* had a toothed jaw, while the ground runner, *Confuciusornis,* found in the same strata and considered more primitive, had a horned beak. In contrast, adaptations to flight were again more "modern" in *Liaoningornis* than in *Confuciusornis*. The sternum is well developed and has a sternal keel as an attachment point for the flight muscles. Together with a wide and reinforced thorax, this suggests that *Liaoningornis* possessed air sacs and a well-developed respiratory system like modern birds (Hou et al. 1996).
- The "primitive" bird genus *Jeholornis* had altogether a more modern anatomy compared to *Archaeopteryx* and in contrast to the latter's pronounced dentition only three very small teeth in the lower jaw. On the other hand, with 27 vertebrae, it possessed a longer caudal spine than *Archaeopteryx,* which had only 23 caudal vertebrae, and the tail feathers are shaped more like those of dromaeosaurs than those of *Archaeopteryx* (O'Connor et al. 2012, 29[207]; Stokstad 2002; Zhou and Zhang 2002; Zhou and Zhang 2003a, 220). In addition, *Jeholornis* possessed special features, namely a unique fan-shaped strand of tail feathers, presumably for lift and as a stabilizer (O'Connor et al. 2013). According to these authors, this shows that tail development was complex and did not proceed as a simple transition from a pinnate to a fan tail.
- The temporal region of the skull of *Confuciusornis* is diapsid in construction, that is, with two completely separate temporal windows, which is considered a more primitive condition, whereas the otherwise more primitive *Archaeopteryx* possessed a more modern cranial anatomy (Peters 2002, 352). Martin et al. (1998, 288f.) note that *Confuciusornis* is a "curious evolutionary mosaic." The anterior part of the skull is more advanced than that of *Archaeopteryx* and *Cathayornis,* while the posterior part is less advanced, they say. However, based on a recent study of 13 *Confuciusornis* skulls and a comparison with *Eoconfuciusornis,* which is dated 6 million years older, Elzanowksi, Peters, and Mayr (2018) conclude that the diapside construction is secondary and an autapomorphy. The shoulder girdle and hand are more similar to the expressions in *Archaeopteryx* than in other birds, whereas the pleurocoels on the vertebrae and the formation of a pygostyle are modifications indicative of the enantiornithines. Therefore, *Confuciusornis* as an outgroup is further evidence that there are many extinct lineages among early birds that (in evolutionary perspective) independently develop evolutionary innovations that became standard in later birds.
- The genus *Cathayornis* from the opposite bird group possessed a primitive skull similar to *Archaeopteryx* in *Cathayornis* after the inferred postcranial differences between the opposite birds and the ornithurans had already become established. According to Martin and Zhou (1997), this suggests that the modern ornithuran skull with avian-like mobility would have evolved independently in the ornithurans.
- Among the basal ornithurans, on the one hand, there are several toothless taxa (*Archaeorhynchus,* possibly the Hongshanornithids, *Zhongjianornis*), while the derived ornithurine genera *Ichthyornis* and *Hesperornis* possessed teeth (O'Connor and Zhou 2013, 904).
- According to Holtz (2001), the anatomy of the skull and metatarsus of troodontids support an assignment to the Arctometatarsalia (clade that included all Coelurosauria except the closer bird relatives, later combined into Ornithomimosauria), while the extremities and tail region suggest an assignment to the maniraptorans.[208]
- The ornithurian genus *Chaoyangia* possesses plesiomorphic ("primitive") features in the pelvic region (unfused pelvic elements and a pubic symphysis) on the one hand, and large ossified hooked processes on the ribs (Chiappe 1995, 351), a "modern" shoulder girdle, and a well-developed sternum on the other (Zhou and Hou 2002, 176). The dentition, in turn, is a primitive feature (Martin and Czerkas 2000, 693).
- The oviraptorid *Conchoraptor* has a shortened olfactory tract and a cerebellum that covers the hemispheres of the brain, which is similar to the situation in modern birds, and the estimated ratio of brain mass to body mass is also within the range

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[207] "The Early Cretaceous long bony-tailed bird *Jeholornis* prima displays characters both more basal than *Archaeopteryx* and more derived, exemplifying the mosaic distribution of advanced avian features that characterizes early avian evolution and obfuscates attempts to understand early bird relationships" (O'Connor et al. 2012, 29).

[208] See Holtz (1998, 46): "Even for taxa for which the anatomy is relatively well-known, such as Troodontidae, the mosaic of derived features resulting in any phylogenetic position requires some degree of homoplasy."

of modern birds. Most endoneurocranial features are less avian than corresponding structures in *Archaeopteryx* (Kundrát 2007, 499).

- *Eoconfuciusornis* is classified as a basal bird on the one hand, but on the other hand this species shows the greatest known extent of hierarchy of follicles[209] among Cretaceous birds and is the most modern in this respect (Zheng et al. 2017).
- Zhang et al. (2008, 1107) refer to the appearance of scansoriopterygids as "bizarre" because their features are exquisitely combined in a mosaic fashion, some bird-like, some similar to those of oviraptorosaurs and, to a lesser extent, therizinosaurs. While some pelvic features are not otherwise known in theropods. This situation suggests that the morphological diversity among maniraptorans at the base of the origin of birds is greater than previously thought.[210]

Jianianhualong and *Sinusonasus*

Xu et al. (2017, 9f.) describe conflicting trait mosaics in the troodontid genera *Jianianhualong* and *Sinusonasus:*

> Comparison of the morphological features of *Jianianhualong* with those of other troodontids shows that *Jianianhualong* has forelimbs and a pelvis very similar to those of basal troodontids, but a skull and hind legs more similar to those of derived troodontids. For example, *Jianianhualong* has forelimb and pelvis features found in basal troodontids such as *Anchiornis* and *Sinovenator*.…Many features of the skull and hind legs of *Jianianhualong* resemble those of derived troodontids…

In contrast, the situation is partially reversed for *Sinusonasus*: "The only other troodontid from Jehol that exhibits a mosaic of plesiomorphic and apomorphic osteological characters is *Sinusonasus magnodens*, which also has transitional anatomical features. *Sinusonasus* has a skull that closely resembles basal and non-derived troodontids, and a pelvis and hind legs that more closely resemble those of derived troodontids than basal ones." Primitive and derived parts are thus here formed exactly the other way around, thus presenting conflicting traits.

They further state, "Troodontidae is a small theropod family displaying a relatively low morphological disparity, but the distinct spatial organization of the mosaic of plesiomorphic and apomorphic osteological features in Jianianhualong and Sinusonasus raises the possibility of modular evolution in troodontids. The mosaic of plesiomorphic and apomorphic osteological features identified in Jianianhualong and Sinusonasus appears to show some correspondence to the expression domains of Hox genes …"

General Assessments

- According to O'Connor and Zhou (2015, 333f.), the available data do not allow us to elucidate a pattern of acquisition of the derived avian skeletal traits.[211]
- "There is still mixed debate about the closest kin group from which the primordial birds emerged, although the fossil record has increased considerably." (Kämpfe 2003, 40)

The diversity of early birds also includes relatively large forms, which is not unproblematic in evolutionary theory. For energetic reasons, an evolutionary transition should most likely occur with forms that are as small as possible (Zhang et al. 2014, 823). In this regard, the putative four-winged dromaeosaurid *Microraptor* fits the bill, but this genus is placed on a side branch because of its unusual flight apparatus (four-wingedness). In contrast, the feathered Upper Jurassic genus *Anchiornis* was relatively large, with a body length of a good half meter. The pigeon-sized *Archaeopteryx* and the approximately 30-cm *Confuciusornis* and Sapeornis, all considered among the most "primitive" birds, were also significantly larger than many Lower Cretaceous enantiornithines. Among these, however, there were also large forms (Zhang et al. 2014, 823).

Matching Precursors? Mismatched Mosaics

The statement, that bird characters evolved step by step already in dinosaurs, is relativized—besides the already discussed findings—also by the existence of numerous mosaic forms, whose combinations of characteristics do not fit into a transitional position and whose systematic position is for this reason often unclear or disputed. Some examples are discussed below.

Rahonavis

Rahonavis (fig. 58) was found in Upper Cretaceous sediments of Madagascar (Maastrichtian). Preserved

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[209] A follicle is the unit consisting of the egg cell and its surrounding auxiliary cells in the ovary.

[210] "The bizarre appearance of scansoriopterygids indicates that morphological disparity among maniraptorans close to the origin of birds is higher than has previously been assumed, and underscores the importance of Jurassic theropods for understanding avian origins." (Zhang et al. 2008, 1107)

[211] "yet these data have failed to reveal a pattern in the acquisition of derived 'avian' skeletal features. Instead, the early evolution of birds has often been described as mosaic: confuciusornithiforms (including *Confuciusornis* and *Eoconfuciusornis*) represent the oldest beaked avian clade but have a diapsid skull with a fully formed postorbital bar (Chiappe et al. 1999; Zhang et al. 2008a) whereas the postorbital is reduced in *Archaeopteryx*; *Sapeornis*, like *Archaeopteryx*, has no sternum despite being the largest Early Cretaceous bird and the presence of well-developed sterna in all other avian clades (Zheng et al. 2014b); and Jeholornis has a boney-tail longer than that of *Archaeopteryx* in both overall length and number of caudal vertebrae."

Fig. 58. Reconstruction of *Rahonavis*. Nobu Tamura, “Rahonavis ostromi, a dromaeosaur from the Late Cretaceous of Madagascar, pencil drawing,” https://commons.wikimedia.org/wiki/File:Rahonavis_BW.jpg, CC BY 2.5.

are parts of the vertebral column and pelvis, legs, fore-limbs, and shoulder girdle. The genus combines a mosaic of theropod-like features typical of dromaeosaurids and avian-like features (Forster et al. 1998, 1915). Dromaeosaurid features include a long caudal spine of 13 elongated vertebrae, vertebral construction, a foot with unfused metatarsals, and a distinct sickle claw. The pelvic girdle shows similarities to *Archaeopteryx*, but also to *Confuciusornis* and enantiornithines (for example, fused sacral vertebrae). Clearly avian, however, are a reduced fibula, and knobs on the ulna (attachment points for arm wings). The glenoid fossa at the glenohumeral joint shows a bird-like lateral alignment (Chiappe and Dyke 2006; Forster et al. 1998, Wellnhofer 2009, 181). Also bird-like are the backward-facing first toe (for grasping around a branch) and the pneumatized bones. Possibly *Rahonavis* was an active flyer.

The systematic position of *Rahonavis* was discussed controversially. According to a cladistic analysis by Forster (1998), *Rahonavis* stands between *Archaeopteryx* and the Pygostylia and is to be included within the birds, so also more recently according to Agnolin and Novas (2013[212]). However, due to the dromaeosaurid features, the genus is now usually placed in the Unenlagiinae subfamily of dromaeosaurids despite the avian features (Makovicky, Apesteguía, and Agnolín 2005; Norell et al. 2006). Complicating matters further, the genus is dated about 80 million years younger than *Archaeopteryx*. *Rahonavis* is on the one hand more “primitive” than *Archaeopteryx* with respect to some features, but with respect to others it is clearly more avian, thus not suitable as a transitional form. Assignment to the dromaeosaurids would have as a consequence the avian features in *Rahonavis* having evolved convergently independently of the birds (Makovicky, Apesteguía, and Agnolín 2005, 1009).[213] Overall, a place in the avian phylogenetic tree for this mosaic form with very primitive and highly derived features can only be found by putting it on a blind-ending side branch and assuming substantial convergence.

Mononykus

The genus *Mononykus* (fig. 59) is placed in the alvarezsaurids, a family of slender and long-legged animals that grew to half a meter to two meters in length. The systematic classification of the alvarezsaurids is highly controversial (Chiappe, Norell, and Clark 2002). This family can only be placed in the theropod and bird system assuming homoplasies (Novas and Pol 2002, 124).[214] Cladistic studies initially placed this group closer to modern birds than to *Archaeopteryx* (Chiappe and Dyke 2002, 99; Chiappe, Norell, and Clark 1998, 277). According to Choiniere et al. (2014, 1f), the derived forms of Alvarezsauroidea possess remarkably avian-like features including a lightly built, mobile skull, several vertebral modifications, a keeled sternum, a fused carpometacarpus, a retroverted pubis and ischium, and delicate hind legs. Later analyses yielded results that argued against a closer relationship with birds and favored different positions for this group within the coelurosaurs (Chiappe and Dyke 2002, 99), implying that many bird-like features of the Alvarezsauridae should have evolved convergently in this group.

The genus *Mononykus* is taken as an example for the problems with the systematic position of the alvarezsaurids. *Mononykus* is a bipedal runner about 1 m long with a long neck and tail and long

Fig. 59. Reconstruction of the skeleton of *Mononykus*. Thomas Cowart, “Mononykus skeleton, AMNH,” https://en.wikipedia.org/wiki/File:Mononykus_skeleton_fix.jpg, CC BY 2.0.

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[212] “Our current analysis also supports *Rahonavis* as a basal bird more derived than *Archaeopteryx*.” (Agnolín and Novas 2013, 18)

[213] “According to our phylogenetic results, the particularly elongate forelimbs of *Rahonavis* and inferred potential flight capability originated independently of Aves” (Makovicky, Apesteguía, and Agnolín 2005, 1009).

[214] “We are facing a group that presents *homoplasies* wherever it is located within Coelurosauria.” (Novas and Pol 2002, 124)

and delicate hind legs. Upper and lower legs are very similar to those of modern birds. However, metatarsalia 2–4 are not fused and metatarsale 3 is greatly shortened from the proximal end (Peters 1994, 412). *Mononykus* exhibits a distinct mosaic of characters. Very unusual is the short, robust anterior extremity with a single strong claw. Together with the keeled sternum, this could suggest a burrowing function of the forelimbs, especially since the highly modified forelimb resembles that of burrowing animals, while a sternal keel is a good attachment point for the powerful muscles required for burrowing (Zhou 1995). However, Chiappe, Norell, and Clark (2002, 117) believe that the body is too gracile and the forelimbs are too short for a burrowing lifestyle. Senter (2005), after a detailed study of the forelimbs, concludes that the lifestyle of *Mononykus* could not have been digging, but rather that the claw served to break open insect nests as in anteaters.

In addition to the formation of a sternal keel, a reduced fibula, fused carpal bones, and other features place *Mononykus* closer to birds than to *Archaeopteryx,* but other bird-typical features are absent (Altangerel et al. 1993, 623, 625; Padian and Chiappe 1998b, 23). On the other hand, *Mononykus* possessed a number of features, such as the sickle claw on the feet that are typical of dromaeosaurs (Chiappe and Dyke 2002, 102; Zhou 1995, 961).

Controversial Systematic Position

Similar to *Rahonavis*, avian status is also discussed for *Mononykus* due to its many avian-typical features (for example, Chiappe, Norell, and Clark 2002; Padian and Chiappe 1998b, 22; see Makovicky and Zanno 2011, 16), but this is rejected by some researchers. For example, according to Sereno (1997, 461), the absence of many avian characteristics seriously calls into question the avian status. If *Mononykus* is granted avian status, it was a sister genus to all birds except *Archaeopteryx*. Some features of alvarezsaurids are more similar to present-day birds than *Confuciusornis* (Makovicky and Zanno 2011, 16).[215] However, an avian status would mean that we must assume a secondary flight loss in *Mononykus.* Problematic in this case would be the consequence that wings were transformed into burrowing organs (or, according to Senter [2005], for breaking open insect nests). This seems very doubtful.[216]

If, on the other hand, *Mononykus* is interpreted as the *primary* flightless sister group of all birds except *Archaeopteryx,* this would mean that the flight ability of *Archaeopteryx* evolved independently of the other birds, hence bird flight evolved twice independently (Norell, Chiappe, and Clark 1993), also a problematic consequence, since multiple independent origins of bird flight have usually been ruled out due to the enormous requirements for flight ability.

Finally, if *Mononykus* is classified outside of birds (as, for example, Zhou 2004), some bird-typical traits that were previously considered synapomorphies (homologies) must be classified as independently evolved, that is, convergent (Novas and Pol 2002, 122).[217] This would thus be one of uncounted examples showing that there is no objective criterion to distinguish between homologies (descent-related similarity) and convergences (independently originated traits). The discovery of *Haplocheirus*, classified as a basal alvarezsaurid (Choiniere et al. 2010), provided strong support for this classification.

Two new Lower Cretaceous alvarezsaurid finds, *Xiyunykus* and *Bannykus,* are intermediate in the construction of their forelimbs, but also stratigraphically, between the Upper Jurassic genus *Haplocheirus* and the Upper Cretaceous alvarezsaurids with their highly reduced forelimbs. Describers Xu et al. (2018) see these finds as transitional stages in the evolution of alvarezsaurids. However, *Bannykus* shows only a slight proportional reduction of forelimbs compared to *Haplocheirus*, while the same is true for *Xiyunykus*. However, typical features of parvicursorines (Upper Cretaceous subgroup of alvarezsaurids) and special features[218] are also developed on the forelimbs (Xu et al. 2018, 5). If the two new genera are interpreted as transitional forms, they support the interpretation that the avian features of the alvarezsaurids are convergences.

All interpretations for evolutionary classification are therefore quite problematic and this results from the conceptual default of evolution. Without this presupposition *Mononykus* can be interpreted as a special mosaic form without ancestral connection. The evolutionary theoretical problem is underlined by the fact that such a remodeling of the anterior extremity is problematic in all discussed directions. Novas and Pol (2002, 121) discuss the critical objection that the forelimbs of *Mononykus* cannot be wing precursors because the “morphological difference” is too great, and suggest that this argument also speaks against

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[215] “A number of these traits, such as the reduced postorbital, streptostylic quadrate, keeled sternum, and reduced fibula, are also encountered in birds more derived than *Confuciusornis*,…” (Makovicky and Zanno 2011, 16).

[216] If *Mononykus* were interpreted as a descendant of an advanced avian lineage, an additional difficulty would be that a “dramatic tail reelongation” would have to be assumed (Gatesy and Dial 1996, 2047).

[217] “It has been shown that certain characters originally hypothesized to be synapomorphic of Metornithes evolved independently in *Mononykus* and ornithurine birds” (Novas and Pol 2002, 122).

[218] “some unusual manual features in *Bannykus* suggest a specialized function” (Xu et al. 2018, 5).

a relationship of *Mononykus* to ornithomimids, maniraptorans, coelurosaurs, theropods, or even dinosaurs. The cladistic analysis is considered decisive, while functional considerations are secondary (Novas and Pol 2002, 122). Such reasoning is highly questionable, however, because cladistic analyses do not clarify evolutionary mechanisms, as a suitable cladogram may very well be opposed by a functional impossibility. The omission of functional aspects is decidedly unbiological and therefore to be rejected.

The example of *Mononykus* shows that the existence of avian characteristics does not necessarily mean that the animal in question actually has a closer phylogenetic relationship to birds.

Avimimus

The Upper Cretaceous oviraptorosaurid genus *Avimimus* (fig. 60), an approximately 1.5-meter-long, bipedal walking theropod with a relatively small skull and largely toothless beak, is described as "enigmatic" by Vickers-Rich, Chiappe and Kurzanov (2002). *Avimimus* combines some unusual bird-like features with those of more primitive coelurosaurs and some peculiar specializations (Clark, Norell, and Makovicky 2002, 38; see also Molnar 1985, 213f.; Zhou 1995, 962). It is one of the most avian-like oviraptorosaurids, and it is characterized by many unusually avian-like features, including a toothless jaw (although some small teeth are preserved in some individuals), a protruding antitrochanter of the hip joint, and fusion of various skeletal elements, including the cranial roof, carpometacarpus, synsacrum, tibiotarsus, and tarsometatarsus. The shape of the pelvis indicates that the tail was long. With the extremely long and slender legs, *Avimimus* was probably a highly specialized runner. The discoverer S.M. Kurzanov reconstructed *Avimimus* with well-developed feathers, for which he cited elevations on the ulna as indirect evidence (these could be attachment points for arm wings), but this interpretation is controversial (Funston et al. 2016, 1).

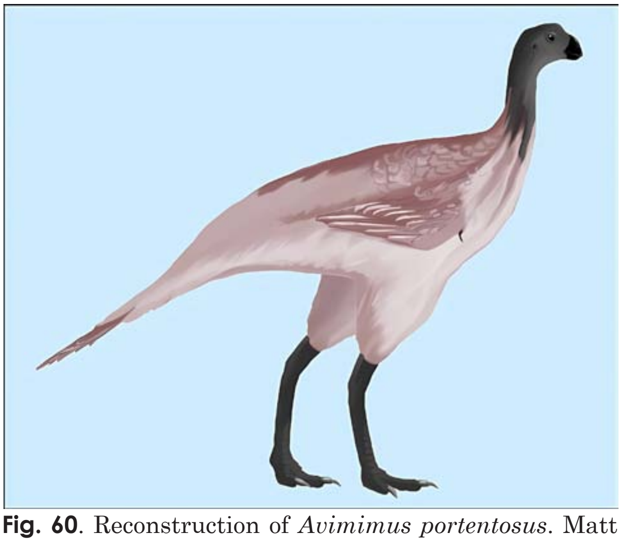

Fig. 60. Reconstruction of *Avimimus portentosus*. Matt Martyniuk, CC BY-SA 3.0.

For Vickers-Rich, Chiappe, and Kurzanov (2002, 65), the phylogenetic position of *Avimimus is* a "puzzle that remains to be solved." This genus has been considered a theropod dinosaur close to the origin of birds (with some convergently evolved avian features) or a secondarily flightless basal bird (Vickers-Rich, Chiappe, and Kurzanov 2002, 65). The stratigraphic position in the Upper Cretaceous does not fit either alternative. Norman (1990) concluded that *Avimimus* was an unusual theropod dinosaur with a highly idiosyncratic combination of features, some of which are found in other groups of theropod dinosaurs or in birds.[219] There were features pointing to theropod dinosaurs, others to sauropods, ornithopods, tetanurans, ornithomimids, or birds. Holtz (1994) placed *Avimimus* in a taxon he established, Arctometatarsalia, which is not closely related to the origin of birds. According to Holtz, Arctometatarsalia includes all Coelurosauria except those more closely related to birds. This taxon is considered obsolete today and is barely used.

Tsuihiji et al. (2017) used additional finds with previously unknown details to show that the head morphology of *Avimimus* is not as avian as previously thought, but intermediate between Early Cretaceous oviraptorosaurs and the diverse oviraptorosaurian subgroup Caenagnathoidea.

Incisivosaurus

Oviraptorosaurs are an unusual group of theropod dinosaurs with highly specialized skulls. As discussed above, numerous features are developed in these forms that associate them more with birds rather than with theropod dinosaurs. The Oviraptorosauria genus *Incisivosaurus* (fig. 61) is interesting in that it is closer in some features to other theropod groups than more derived forms. Thus, it narrows the morphological gap to other groups.[220] The skull is low and the jaws are dentate. Since *Incisivosaurus*

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[219] In detail: Premaxilla resembles the hadrosaurid subfamily Lambeosaurinae; the cranium resembles that of birds and sauropods; the vertebral column is typical of small theropod dinosaurs, the pelvis is also typical of theropod dinosaurs; the hind legs also resemble theropod dinosaurs; the remains of the metatarsal bone are unusual for Late Cretaceous forms of this group; the forelimbs are the most puzzling; the humerus is typical for a bipedal theropod dinosaur; the fragment of the metacarpal bone is bird-like.

[220] "*Incisivosaurus* displays an intermediate cranial morphology between the typical coelurosaurs and the unusual oviraptorids, and shortens the morphological distance between the two groups. Cladistic analysis places *Incisivosaurus* as the most basal oviraptorosaur" (Xu et al. 2002a, 292).

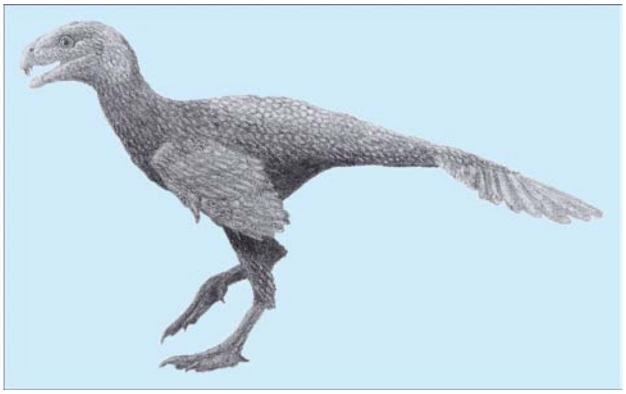

Fig. 61. Reconstruction of *Incisivosaurus*. Tomopteryx, "Incisivosaurus reconstruction by Tom Parker (Tomopteryx/Tomozaurus)," https://en.wikipedia.org/wiki/Incisivosaurus#/media/File:Incisivosaurus_(pencil_2013).png. CC BY-SA 3.0.

is at the same time one of the geologically oldest genera of this group (Lower Cretaceous, Barremian), the phylogenetically reconstructed position also fits stratigraphically (Xu et al. 2002a).

The teeth of *Incisivosaurus,* however, are not intermediate in formation, but are markedly specialized. One pair of premaxillary teeth is reminiscent of rodent teeth known in mammals, while the molars were lanceolate with large wear surfaces, features otherwise unknown in Theropoda and indicative of an herbivorous diet (Xu et al. 2002a). The pencil-shaped premaxillary teeth are comparable to the dentition of some herbivorous sauropod dinosaurs, the lanceolate molars resemble those of therizinosauroids (Xu et al. 2002a, 293), and connections to other groups appear reticulate in dentition features.

The differentiation of the dentition is much more pronounced in *Incisivosaurus* than in other theropod dinosaurs.

From an evolutionary theoretical perspective, this genus supports the interpretation that oviraptorosaurs were *not derived* from birds but acquired their numerous avian traits convergently (Xu et al. 2002a, 292; see Balanoff et al. 2018, 126[221]). The overall view that follows is: On the one hand, in Oviraptorosauria and Alvarezsauridae, the derived and stratigraphically younger members are more bird-like than the basal taxa in a number of characters,[222] while on the other hand, in other lineages such as Dromaeosauridae and Troodontidae, the derived members are less bird-like, which is interpreted by reversion to more primitive characters. "This leads to conflicting results in reconstructing the phylogeny of maniraptorans and highlights the importance of including basal members of each group when attempting to reconstruct the phylogeny" (Xu et al. 2002a, 292f.).[223]

Unenlagia

The dromaeosaurid *Unenlagia* (fig. 62) was about 2 m long, only fragmentarily preserved (the skull is missing completely) and can be placed in the morphological gap between *Archaeopteryx* and dromaeosaurids in some features (Norell and Makoviocky 1999; Novas and Puerta 1997). Several features are more bird-like than in any other theropod dinosaur known to 1997. *Unenlagia* resembles *Archaeopteryx* in morphology of the scapula, pelvis, and legs, while several features of the pubis, ischium, and proportions of the hind leg bones were primitive and therefore suggest that *Unenlagia* may be the sister taxon of Avialae. Remarkably, the construction of the forelimb suggests that folding was possible in a bird-like fashion and that the ability to flap the forelimb upward, necessary for active flight, was already present in bipedal, non-flying theropod dinosaurs (Novas and Puerta 1997, 390).

Novas and Puerta (1997, 391) consider that the size of *Unenlagia* combined with short forelimbs argues for flightlessness, but that the phylogenetic position argues against *Unenlagia* being descended from flightless forms. However, *Unenlagia* is not fossilized until the Upper Cretaceous (Turonian-Coniacian, ~90 Ma). Thus, there is a clear discrepancy between morphology and stratigraphy.

Eoalulavis

The enantiornithine genus *Eoalulavis* (fig. 63) is notable for documenting a surprisingly early formation of the bastard wing (alula) (Sanz et al. 1996; Sanz et al. 2002). It "illustrates the surprisingly early diversity and complexity of flight adaptations" (Shipman 1997, 31). The basic structure of the modern flying machine had been formed, making it possible to fly at low speeds and with high maneuverability (Sanz et al. 1996, 442).[224]

In addition, *Eoalulavis* had a particular mosaic of features—the sternum is unusually narrow, spear-shaped, and possesses a weakly developed keel, the furcula is robust, the shoulder girdle is more

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[221] "Extensive pneumatization, relative enlargement of the parietal, a double-headed otic process of the quadrate, and a host of other equally detailed skeletal features characterize crown birds and deeply nested oviraptorosaurs. These features tend to be absent in *Incisivosaurus*, which conserves a more plesiomorphic theropod morphology" (Balanoff et al. 2018, 126).

[222] This is especially true for the alvarezsaurids due to the discovery of the Upper Jurassic genus *Haplocheirus* (Choiniere et al. 2010).

[223] "This leads to conflicting results in the reconstruction of maniraptoran phylogeny, and reinforces the importance of including basal members of each group when attempting to reconstruct the phylogeny" (Xu et al. 2002a, 292f).

[224] "had evolved a sophisticated structural system that enabled them to fly at low speeds and to attain high maneuverability" (Sanz et al. 1996, 442).

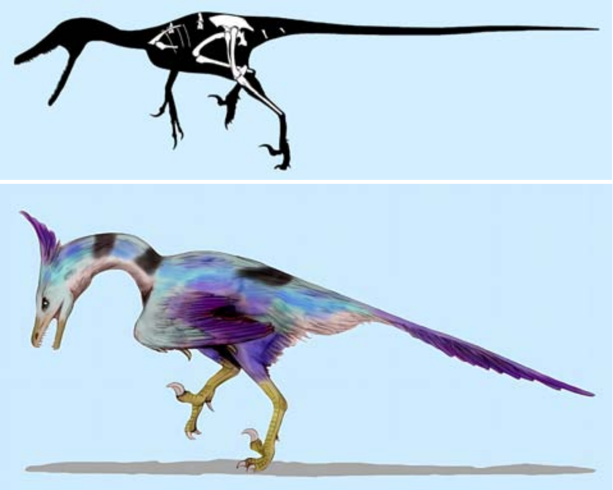

Fig. 62. Reconstructions of Unenlagia. (Top: Jaime A. Headden, "Skeletal reconstruction of Unenlagia comahuensis," https://en.m.wikipedia.org/wiki/File:Unenlagia.jpg. CC BY 3.0. Bottom: Nobu Tamura, " Unenlagia comahuensis, a dromaeosaur from the Late Cretaceous of Argentina, pencil drawing, digital coloring," https://en.wikipedia.org/wiki/File:Unenlagia_BW.jpg, CC BY 3.0.

Fig. 63. Reconstruction of *Eolalulavis*. © Eloy Manzanero, dinodata; http://dinodata.de/animals/birds/pages_e/eoalulavis.php, CC BY 4.0.

"modern" than in the related species *Iberomesornis*, but the fingers possessed primitive claws of unknown function (Sanz et al. 1996; Shipman 1997, 31). The morphology of the foreleg in *Eoalulavis* is remarkably primitive compared to other enantiornithine genera (O'Connor, Chiappe, and Bell 2011, 82ff.). Although many inferred characters readily permit assignment to Enantiornithes, the precise relationships are unclear (Sanz et al. 1996, 443).[225]

Fig. 64. Reconstruction *Ambiortus dementjevi*. Scott Reid, https://a-dinosaur-a-day.com/post/167928034680/ambiortus-dementjevi.

Ambiortus

The approximately crow-sized *Ambiortus* (fig. 64) is one of the geologically oldest ornithuromorphs. This genus exhibits a "mosaic of archaic and specialized features" (Kurochkin 1985, 271). Some features relate it to "more highly evolved" birds from the palaeognath group (Kurochkin 1985) and the Ichthyornithes (Kurochkin 1999). Thus, *Ambiortus* possessed a keeled sternum and a bird-like shoulder girdle (Kurochkin 1985, 272).[226] This author distinguishes three types of features in *Ambiortus*—generalized features typical of true birds, features it shares with certain groups of fossil and some modern birds, and unique features that require a new taxon of high rank.[227]

Most analyses identify this genus as belonging to the ornithurans, but without being able to position it more precisely in this group, or as a primitive genus of the ornithuromorphs. O'Connor and Zelenkov (2013, 1270) state, "In general, the mosaic pattern of character distribution among early ornithuromorph taxa does not reveal obvious relationships between taxa."

Protopteryx

The approximately starling-sized enantiornithine *Protopteryx* (fig. 65) is one of the geologically oldest opposite birds and is also classified as primitive (for example, the fibula is not greatly reduced, there is no fused tibiotarsus, the hand bones are relatively long, the thumb bone is long, and the external carpal bones and metacarpals are not completely

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[225] "The skeletal morphology of *Eoalulavis* exhibits a large number of derived characters used to diagnose the Enantiornithes . . . Despite the fact that *Eoalulavis* is easily identifiable as a member of the Enantiornithes, its precise interrelationships must await a comprehensive phylogenetic study of this speciose group" (Sanz et al. 1996, 443).

[226] O'Connor and Zelenkov (2013, 1280) also mention: rectangular, medially projecting procoraoid; lateral process on coracoid; U-shaped furcula; curved scapula; rounded deltopectoral crest.

[227] "The details of the structure of *Ambiortus* are of three types: (1) generalized features typical of true birds; (2) features held in common with particular groups of fossil and some modern birds; and (3) features that are unique to *Ambiortus* and that require its separation as a new taxon of high rank" (Kurochkin 1985, 272). Details are described there.

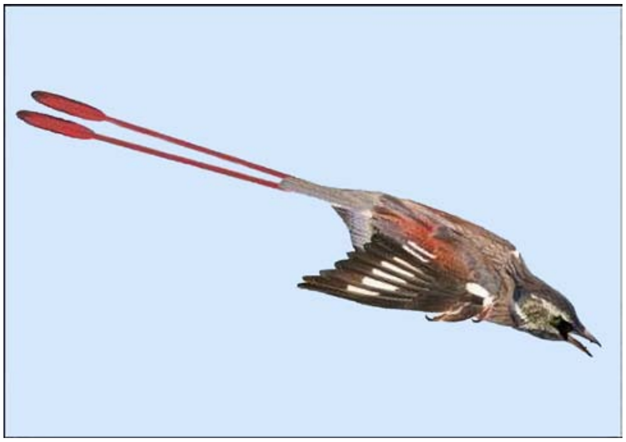

Fig. 65. Reconstruction of *Protopteryx*. es.dino.wikia.com, CC-BY-SA.

fused into the carpometacarpus). The genus has many skeletal transitions between *Archaeopteryx* and *Confuciusornis* and more advanced birds according to Zhang and Zhou (2000, 1955). At the same time, *Protopteryx* also had special and more derived features, most notably two long scale-like tail feathers that were unbranched in the region near the body, an otherwise unrecognized feather type (Wang et al. 2014; as discussed above). The number of teeth appears to be greatly reduced. With modern birds, *Protopteryx* shares a process on the procoracoid process and a lateral process of the coracoid. In addition, a bastard wing (alula) is developed as a "modern" feature (although Zheng et al. [2017, 448] suggest this feature is a common inheritance of Ornithothoraces).

Geologically even slightly older is *Eopengornis*, which along with the other pengornithids is placed on a much more derived position within Enantiornithes (Hu, O'Connor, and Zhou 2015).

Archaeorhynchus

Another remarkable discovery was made in the ornithuromorph *Archaeorhynchus spathula* (fig. 66). The ornithuromorphs ("bird tails") are the group of birds from which today's birds are thought to have evolved, and they include them. Their fossils occur in considerable diversity since the Lower Cretaceous. *Archaeorhynchus spathula* from the Lower Cretaceous of China (Jehol Formation, dated to 120 million radiometric years) was about the size of a starling and is classified as "basal" based on skeletal features, although this species also has a number of "modern" avian features (a toothless beak, sternal quill, furcula shape, and asymmetrical feathers). Of note is the preservation of soft tissue, which Wang et al. (2018a) interpret as fossilized lungs, which they consider a likely interpretation. Wang et al. (2018a) conclude from the fossil remains that the lungs were "very similar to the lungs of present-day birds." The specializations of the lungs, such as the highly subdivided parenchyma, were "modern." The researchers found structures they thought resembled parabronchi (which are very fine capillaries in the lungs of today's birds). These features indicated that the amount of oxygen required for powered flight could be absorbed in this species. The fossil evidence further showed that the lungs were fixed directly to the wall of the cavities, as in modern birds, making the lungs virtually immobile, as is the case in modern birds. This fixation makes it possible for the parenchyma to be divided into extremely fine capillaries without collapsing the tissue, allowing for a large airway area and the development of an extremely thin blood-gas barrier (Wang et al. 2018, 11559).

The authors see this finding in a set of features on soft tissue systems (for example, digestion and respiratory system) that are typical of birds living today and were established early, before changes in the skeleton occurred.[228] In contrast, the skeletal features associated with respiration were primitive.

Features of the tail are also unusual. In addition to the ordinary tail feathers, two particularly long, narrow tail feathers protrude above the rest of the feathers (called a "pintail"). This type of feather was previously unknown in Cretaceous birds, but occurs in present-day birds as in some species of hummingbirds.

Evaluation

All in all, *Archaeorhynchus* shows a distinct mosaic of features, which hardly fits into an evolutionary transitional position. And once more it shows that requirements for flying, here bird-typical efficient lungs, were developed from the beginning.

Orienantius

Another species to be presented here is placed in the genus *Orienantius* from the opposite birds (Enantiornithes).[229] It belongs to the geologically

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[228] "This adds to growing evidence that many physiological modifications of soft tissue systems (e.g., digestive system and respiratory system) that characterize living birds and are key to their current success may have preceded the evolution of obvious skeletal adaptations traditionally tracked through the fossil record" (Wang et al. 2018, 11555).

[229] There is no consistent rationale in the literature for the designation "opposite birds." It is pointed out two anatomical peculiarities that distinguish the opposite birds from other birds: first, the type of fusion of some foot bones, and second, the construction of the joint between the scapula and the coracoid. In the opposite birds, the articular head and socket are, so to speak, interchanged in comparison with all other birds. It is difficult to imagine how one anatomical expression could be evolutionarily transferred to the other.

Fig. 66. Artistic representation of *Archaeorhynchus spathula*, which was slightly larger than a dove. Brian Choo, "An artist's interpretation of the dinosaur-era bird *Archaeorhynchus spathula*, which was a bit larger than a modern pigeon," https://carnivora.net/archaeorhynchus-spathula-t3783.html.

oldest opposite birds and was discovered in the Huajiying Formation of China, which is dated to 131 million radiometric years. Soft tissues are also fossilized and preserved in this find, namely parts of the flight skins (patagia). Liu et al. (2018, 16) write, "The morphology of the preserved soft tissues shows that the main patagia (propatagium, postpatagium, and metapatagium characteristic of the wings of modern birds were already present in the earliest known enantiornithines."[230] (fig. 67) Their expression suggests that these birds could maneuver very well and alternately flap and glide, comparable to present-day small and medium-sized birds (Liu et al. 2018, 17).

Fig. 67. Detail of the anterior extremity of *Orienantius ritteri* under UV light. White arrows point to the base of the calami of the ten primary hand wings in the postpatagium. Abbreviations: met metapatagium, pos postpatagium, pro propatagium (from Liu et al. 2018, with kind permission).

Several years ago, Navalón et al. (2015) had already detected flight skins on an unnamed opposite bird, which they interpreted as evidence of good flight skill (summarized by Junker [2015]).

The researchers further demonstrated that the preserved contour of the musculature of the leg is identical to that of modern birds. The soft tissues around the foot bones indicate that the feet of *Orienantius ritteri* had no major muscles, mirroring the situation in birds living today (Liu et al. 2018, 16).

Evaluation

In the case of *Orienantius, it is* also evident that good flight ability, as well as other avian-typical traits, are expressed within the opposite birds from the beginning, in the geologically oldest forms. Liu et al. (2018, 18) conclude that this new taxon exhibits numerous features that are typical of later taxa, and that the opposite birds already exhibit a significant degree of taxonomic differentiation in their earliest appearance in the fossil record.

Jinguofortis

Another example of "chaotic" evolution (Min Wang[231]) is the approximately crow-sized fossil species *Jinguofortis perplexus,* also described in 2018 (fig. 68). Its systematic position is not clearly determined. It is placed in the newly erected family Jinguofortisidae along with the similarly enigmatic genus *Chongmingia* (Wang et al. 2016; Wang, Stridham, and Zhou 2018). Because it possessed a pygostyle (fused caudal vertebrae) like modern birds, it is included in the pygostylians, which include all birds except the famous *Archaeopteryx* and *Jeholornis* (these two genera possessed a long caudal spine and, correspondingly, a pinnate tail that was constructed differently from the fan-shaped tail usually formed in birds). Another distinctly "modern" feature is the greatly reduced fingers.

However, in addition to bird-typical features, features otherwise known in theropod dinosaurs anduntypical of birds also occur. These include claws on the fingers of the wings, a boomerang-shaped, presumably rigid furcula (clavicle),[232] a jaw with tiny teeth instead of a beak, and a fused shoulder girdle (scapula and coracoid). Since the latter feature

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[230] "The morphology of the preserved soft tissues indicates that the main patagia characteristic of the wings of modern birds (propatagium, postpatagium, and metapatagium) were already present in the earliest known enantiornithines" (Liu et al. 2018, 16).

[231] According to one of the authors of the technical article, Min Wang, in a commentary, "this new bird fossil shows that the evolution of flight was much more messy" (https://www.nationalgeographic.com/science/2018/09/news-new-species-fossil-bird-dinosaurs-flight-evolution-paleontology).

[232] In present-day species, the furcula is usually flexible and performs the function of a taut spring or elastic brace between the shoulder joints, storing energy during wing beating.

Fig. 68. Reconstruction of *Jinguofortis perplexus*. © Chung-Tat Cheung.

appears unfavorable for flying because it limits flexibility for flapping flight, the species received its species name "*perplexus*." Nevertheless, the broad, short wings of *Jinguofortis* were typical of birds that could maneuver well among trees. Perhaps a previously unknown mode of flight was realized. In modern birds, a comparable fusion of the two shoulder joint bones is known only in flightless forms. However, that *Jinguofortis* was also secondarily flightless seems rather unlikely, especially since the wing feathers were distinctly asymmetrical (Wang, Stridham, and Zhou 2018, 10710).

The fused shoulder girdle (scapula and coracoid) is similar to the situation in some theropod dinosaurs, but nevertheless this feature is not suitable as evidence for a phylogenetic link between dinosaurs and birds, because in *Archaeopteryx* these two bones were not fused. Therefore, an independent (convergent) origin is assumed, and moreover, also convergent in *Confuciusornis* (Wang et al. 2016, 2018b). Wang et al. (2018b) suggest that accelerated bone formation is causative.

The possession of teeth is common in Mesozoic birds, and also with respect to this feature the expression in *Jinguofortis* does not fit well from an evolutionary theoretical point of view. Because in *Jinguofortis* premaxilla and maxilla were toothed, while in *Archaeopteryx* and the Ornithothoraces (Enantiornithes [opposite birds] and Ornithurae ["bird-tails"]) the tip of the premaxilla and in *Jeholornis* the whole premaxilla is toothless. Therefore, with respect to this feature, evolutionary theory would have to assume a regression or, as with the shoulder girdle, a kind of evolutionary zigzag course, which is generally considered implausible.

Evaluation

Wang et al. (2018b, 10708) note that *Jinguofortis* increases the known diversity of early pygostylians and suggest that developmental plasticity played an important role and that putative evolution is mosaic.[233] (Plasticity is the ability to express traits differently depending on environmental influences and has nothing to do with evolution per se.) The Jinguofortisidae contribute to the widespread occurrence of mosaic evolution (Wang, Stridham, and Zhou 2018, 10710). Brusatte comments in *National Geographic* on this finding that there has been much "experimentation".[234] However, both mosaic evolution and experimentation are foreign bodies in an evolutionary scenario. As experimentation is a purposeful process, the term obscures a finding that is unexpected in evolutionary theory. Trait distributions do not fit into a hierarchical nested system. Therefore, convergences must be assumed to a large extent, which is called "mosaic evolution." But why and by what means does a natural, future-blind evolutionary process arrive at similar constructs many times independently? Moreover, the mosaic of features is such that it does not fit altogether as an evolutionary transitional form, but must be assumed to be an evolutionary lineage of its own.

Conclusion

Further genera could be cited here. However, the discussed examples already give a good impression of the frequently occurring feature contradictions, which require the assumption of numerous convergences in an evolutionary-theoretical interpretation, that is, in a tree representation of the relationships.

Summary and Evidence for Creation

The findings compiled here in this paper show that the similarity relationships of the diverse forms of Jurassic and Cretaceous theropod dinosaurs and avian genera are more reticulate than tree-like. One author even uses the term "chaotic" (Brusatte 2017a, 792). This can be seen in the following points:

- It is not clear which group is at the base of the birds (Brusatte et al. 2014, 2386; Currie 1997, 230; Xu et al. 2014, 1).[235]

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[233] "The discovery of *Jinguofortis* increases the known ecomorphological diversity of basal pygostylians and highlights the importance of developmental plasticity for understanding mosaic evolution in early birds" (Wang, Stridham, and Zhou 2018, 10708).

[234] "There was a lot of experimentation in flight styles among early birds." (https://www.nationalgeographic.com/science/2018/09/news-new-species-fossil-bird-dinosaurs-flight-evolution-paleontology).

[235] "there is an unresolved debate on what are the most basal birds. Suggested taxa include the probably flighted *Archaeopteryx* and *Rahonavis*, the enigmatic scansoriopterygids, the four-winged *Anchiornis* and its kin, and the Gondwanan unenlagiid theropods" (Xu et al. 2014, 1).

"for the first time, a TWiG [Theropod Working Group] analysis recovers a polytomy between avialans, dromaeosaurids, and troodontids, meaning that the immediate relative of birds cannot be clearly identified." (Brusatte et al. 2014, 2386)

"Within the Theropoda, there has been considerable debate about which families are most closely tied to the origin of birds" (Currie 1997, 230).

- As a rule, a multiple independent (convergent) origin of bird-typical traits must be assumed and, depending on the underlying trait, partly different relationships are suggested (see fig. 1). For example, Kurochkin (2006, 45) notes that bird-like traits occur in various combinations in dromaeosaurs, troodontids, oviraptorids, therizinosaurs, and tyrannosaurs, but that no group of coelurosaurs possesses the complete set of bird-like traits. This suggests that theropods and birds acquired them in parallel.[236] The large extent of homoplasy means that cladograms are not stable and new finds can lead to major changes (Leigh 2014, 2; see also Feduccia 2012, 188).[237]
- There is controversy in some genera or entire groups as to whether they are avian precursors or secondarily flightless birds.
- The oldest bird groups are already strongly differentiated at the base and there are partly also "modern" characteristics in the oldest representatives of a group.
- Especially in plumage characteristics, the greatest degree of diversity is seen near the base of the bird groups.
- Most theropod dinosaur genera possessing bird-like features are geologically younger than the geologically oldest birds. The genera with avian features are in many cases fossilized only from the Upper Cretaceous, when a great diversity of avian forms had long been established (Kurochkin 2006, 46[238]; see also Dodson 2000, 504f.[239]; Currie 1997, 230; see figs. 4, 5).

In a review paper, Agnolin et al. (2019, 22) conclude that a consensus on the phylogenetic relationships of Paraves is far from being reached. Therefore, they argue, knowledge about the steps involved in the acquisition of anatomical and behavioral traits that contribute to the origin of avian flight is still uncertain and in flux. The authors further state that they could not find a clear sequence of evolutionary innovations. Also, they say, the fossil record is sparse in the area of the transition from dinosaurs to birds, and new fossils are needed to fill in the gaps between the various clades of Paraves.[240] The nature of the early radiation of Paraves and birds is "completely uncertain," as are their center of origin and dispersal routes, they said.[241] If evolution had really occurred, one would not expect such a result ("totally uncertain").

"Experiments"

This situation regarding early trait diversity and presumed blind evolutionary ends prompts numerous authors to speak of evolutionary "experimentation." For example, Sullivan, Xu, and O'Connor (2017, 1, 3) speak of "rapid diversification of aerodynamic structures" in Paraves, showing a "surprising amount of homoplasy and evolutionary experimentation." The scansoriopterygids have been called an "evolutionary experiment near the base of the avialan tree" (Sullivan et al. 2014, 269).[242] Also for O'Connor, Chiappe, and Bell (2011, 49), some Cretaceous birds show an "unforeseen quantity of evolutionary experimentation and homoplasy," on the one hand with typical features of maniraptorans that are absent in *Archaeopteryx,* and on the other hand also features that were more primitive than in *Archaeopteryx,* although phylogenetically closer to modern birds. The origin of all major groups was accompanied by a "wide range of evolutionary

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[236] "however, they are presently known in various coelurosaurian groups. At the same time, they occur in various combinations in the Dromaeosauridae, Troodontidae, Oviraptoridae, Therizinosauridae, and Tyrannosauridae. None of the theropod groups possesses the entire set of these characters. This suggests that theropods and birds acquired them in parallel" (Kurochkin 2006, 45).

[237] "Current methods of inferring phylogenies from phenotypic characteristics are, however, far from robust. One new specimen can cause major changes in the inferred phylogeny (compare Figure two of Hu et al. 2009, Figure four of Xu et al. 2011, and Figure three of Godefroit et al. 2013). Hu et al. (2009) proclaim *Anchiornis* a troodontid; Xu et al. (2011) proclaim it an archaeopterygid" (Leigh 2014, 2).

"However, when one ascends to the family, ordinal, and even higher levels, cladistics and other approaches often lose their ability to divide relationships because of multiple complexities, including primarily massive convergences and resulting homoplasy" (Feduccia 2012, 188).

[238] "It is noteworthy that these theropods are predominantly known from the Upper Cretaceous and none of these superfamilies or families has the entire set of avian characters" (Kurochkin 2006, 46).

[239] "The current cladistic analysis of bird origins posits a series of outgroups to birds that postdate the earliest bird by up to 80 million years" (Dodson 2000, 504). "none of the known small theropods, including *Deinonychus, Dromaeosaurus, Velociraptor, Unenlagia,* nor *Sinosauropteryx, Protarchaeopteryx,* nor *Caudipteryx,* is itself relevant to the origin of birds; these are all Cretaceous fossils" (Dodson 2000, 505).

[240] "As indicated throughout the text, a consensus about the phylogenetic relationships of paravians is far from being reached. For this reason, knowledge of the steps toward the acquisition of anatomical and behavioral traits contributing to the origin of avian flight is still uncertain and in a state of flux. We were not able to find a clear sequence of evolutionary novelties. Also, the fossil record of the dinosaur-bird transition is sparse, and new fossils are needed to bridge the gaps among the various paravian clades" (Agnolin et al. 2019, 22).

[241] "Along similar lines, the nature of the early paravian and avialan radiation is totally uncertain, as are its center of origin and dispersal routes" (Agnolin et al. 2019, 22).

[242] "The scansoriopterygids *Epidendrosaurus* and *Epidexipteryx* are also the oldest known avialans, and this apparently endemic clade may represent a short-lived, localized evolutionary experiment near the base of the avialan tree" (Sullivan et al. 2014, 269).

experimentation," as Chiappe (2009, 248) also suggests. Closely related lineages, whether coexisting or not, would thereby converge to a greater or lesser extent on the characteristic features of the new group. Glaubrecht (1998, 36) makes a similar point: "Some primordial birds are but witnesses to abandoned experiments in evolution." The evolution of flight was chaotic, Brusatte (2017a, 792) was quoted at the outset, with different dinosaurs supposedly experimenting with different flight behaviors and with different wing and feather arrangements.[243] Many lineages of the Paraves supposedly experimented with different modes of flight during the Upper Jurassic and Lower Cretaceous, according to Puttick, Thomas, and Benton (2014, 1497).[244]

It has been claimed for a long time that much apparent experimentation takes place and many convergences occur when a new "adaptive zone" is reached, Agnolin et al. (2019, 22) also state. Therefore, they argue, the adaptive breakthrough of the evolution from dinosaurs to birds is accompanied by numerous convergences in closely related lineages in bird-like traits. The degree of evolutionary experimentation and convergences in "avianness" highlighted by recent discoveries, particularly from China, meant that consensus on phylogenetic relationships remained elusive.[245] Further statements of this sort could be cited.[246]

However, this situation is problematic in evolutionary theory for the following reasons:

- Classically, evolutionary theory predicts that the diversity of forms can be represented in a reasonably consistent tree-like fashion. The tree-shaped representation has often been inversely interpreted as evidence for evolution. Strongly reticulate or even chaotic trait relationships go in the direction of the opposite of what is predicted by evolutionary theory. Further findings cannot unravel this network either, but they could strengthen it.[247]
- Strictly speaking, one can only speak of "experiments" if there is also an experimenter. Since this does not exist in evolution, this frequently used term is misleading. It suggests a steering, because an experimenter, who tries out different things, pursues a goal. But evolutionary processes as pure natural processes cannot do that. Ultimately, the "experiment" metaphor conceals a problem in evolutionary theory. For even if this term is of course meant *metaphorically*, it should *represent* a reality. But this is just not the case. If then also failed experiments are mentioned (for example, in the case of the four-winged forms), a goal orientation is also implied, because failure can only be spoken of in relation to a goal.
- Both Enantiornithes and Ornithurae appear relatively abruptly in the fossil sequence in great diversity, temporally in common with forms such as *Confuciusornis*, *Jeholornis*, and *Sapeornis*, which are classified as more primitive. Although there are partial trends within individual groups, this sudden appearance is striking.
- Mismatched mosaic forms lead to dilemmas or trilemmas (Alvarezsauridae) when evolution is assumed.

Ghost Lineages

The cladogram published by Foth and Rauhut (2017) shows that for a large part of the coelurosaurs long ghost lineages have to be assumed (fig. 69). That is, it must be assumed under evolutionary theoretical conditions that many lineages left no fossils during 20–30 million years of their assumed existence and in some cases even more, while fossil remains of other lineages in comparable geological strata have survived. Such a situation is problematic in evolutionary theory and in a long-term framework.

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[243] "According to this story, the development of flight was chaotic, with different dinosaurs experimenting with different airborne behaviors using different airfoil and feather arrangements (see the figure), until ultimately only modern birds survived" (Brusatte 2017a).

[244] "Traits associated with Aves evolved before their origin, at high rates, and support the notion that numerous lineages of paravians were experimenting with different modes of flight through the Late Jurassic and Early Cretaceous" (Puttick, Thomas, and Benton 2014, 1397).

[245] "It has long been known that much experimentation and convergence occurs when a new 'adaptive zone' is being crossed into (Gould, 1989). It is possible that the adaptive breakthrough of evolving from a non-avian dinosaur into a bird was accompanied by much convergence in closely related lineages on bird-like features (Feduccia, 2013). The degree of evolutionary experimentation and convergence on 'bird-ness' demonstrated by recent discoveries, especially those from China, may ensure that a consensus on phylogenetic relationships remains elusive" (Agnolin et al. 2019, 22).

[246] Benton (2014, 508): "The fossils showed that from about 170 to 120 million years ago, all these dinosaurs-the Paraves-were experimenting with flight in various modes, including parachuting, gliding, and leaping from tree to tree." And Brusatte, O'Connor, and Jarvis (2015, 892), "If derived bird-like dinosaurs were experimenting with using different body structures to evolve flight in parallel, it follows that different dinosaurs may have evolved different flightworthy feathered wings in parallel as well."

[247] Agnolin et al. (2019, 2) write: "The origin and early evolution of paravian theropods is one of the most hotly debated topics in vertebrate paleontology.... evolutionary transition to birds was considerably more complex than previously thought... largely obscured by the mosaic distribution of anatomical traits across the theropod phylogenetic tree.... Unfortunately, the paleontological community is far from reaching such a phylogenetic consensus, as evidenced by the diverse hypotheses on paravian phylogeny that have been published to date." (See the comparison of different cladograms in their fig. 2.)

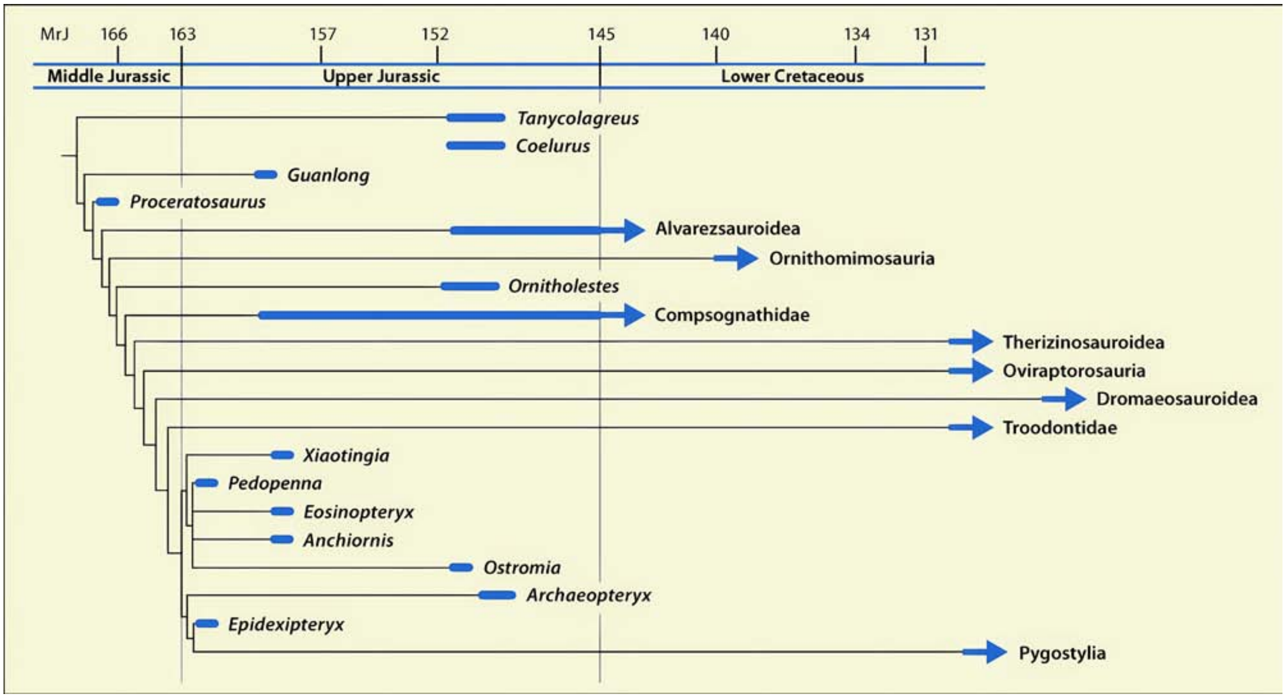

Fig. 69. Simplified phylogeny of maniraptorans. According to Foth and Rauhut (2017), the stratigraphic and geographic distribution indicates rapid radiation in the late Middle to earliest Late Jurassic in East Asia (according to Foth and Rauhut 2017; simplified).

Anomalies for Evolution and Evidence for Creation

In the questions on origins in biology usually only explanations are discussed which are committed to the naturalistic paradigm. That means only (purely) natural, blind, non-spiritual processes are allowed, which can be described lawfully (if necessary by statistical regularities), as well as random boundary conditions are admitted. This determination leads logically to an evolutionary approach. Accordingly, an attempt is made to represent the diversity of life-forms in a tree-like manner and to prove an essentially gradual variation. For the basic mechanisms of evolution are descent and speciation with usually dichotomous branching of parent species into two daughter species. Horizontal inheritance (from one species into another), which does not proceed via sexual reproduction, is almost unknown in multicellular organisms and therefore cannot be taken into account.[248]

Since, according to all that is known about evolutionary mechanisms, the evolutionary process is not goal-directed[249] (which also corresponds to the naturalistic paradigm), according to evolutionary theory it was expected that convergences would be rare and all the more unlikely the more complex the structures in question are. Accordingly, it was expected that the diversity of forms could be easily represented in tree diagrams. Cladism is based on these expectations. Indeed, if convergences were expected to occur easily and therefore to occur frequently, cladism would be methodologically at an end. However, the overwhelming majority of biologists do not see it that way.

In addition, it is clearly to be expected from evolutionary theory that forms, which are classified as "primitive" (see table 1) appear in the fossil sequence stratigraphically (in evolutionary theory interpretation also temporally) before the more derived forms, at least as a tendency, as soon as the "sample" is sufficiently large (that is, a larger variety of forms is fossilized). Furthermore, it follows from the effect of the evolutionary mechanisms that a sequence of increasing diversity can be found in the sedimentary sequences.

The comments made here have shown that all these expectations have been met only to a limited extent or almost not at all (see table 4):

- Convergences are extremely frequent. Accordingly, the cladograms usually have low consistency indices.
- A representation by tree diagrams is always possible, but the concrete form is sometimes controversially discussed and often had to be changed by new fossil findings.

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[248] In contrast, horizontal gene transfer is common in protozoa.

[249] Mutations are copying errors and only in rare cases lucky errors, which in any case did not occur towards a previously existing goal. In selection it is often claimed that there is a direction here (better adaptation, better competitiveness, more offspring), but selection is also future-blind. Only the current benefit can be "evaluated."

Table 4. Evolutionary theoretical expectations and observations on the putative evolution of birds from dinosaurs.

Evolutionary expectations	Observations
Convergences are rare and less likely with increasing complexity.	Convergences are extremely frequent.
Shape diversity is easily represented in tree diagrams (cladism).	Cladograms are unstable, often changed, controversial, reticular relationships.
"Primitive" forms are (tend to be) recorded fossil before derived forms.	Relatively derived forms at base, presumed ancestors partly "younger" than descendants.
Fossil sequence shows increasing diversity in time.	Fossil sequence shows explosive occurrence.
Known mechanisms explain the way of occurrence of the diversity of forms.	Known mechanisms do not explain sudden occurrence.

- Accordingly, the groups of shapes could be arranged in the form of networks on the basis of the feature distributions, but this is not practiced because it does not correspond to the underlying approach.
- The diversity of forms of Mesozoic birds occurs explosively in the Lower Cretaceous in considerable diversity.[250] The Jurassic birds or genera that are morphologically close to the birds are hardly suitable as possible precursors or only with reservations.
- The majority of dinosaurian genera with apparent avian characteristics are geologically dated younger than a large number of opposite birds and ornithuran birds and the basal avian genera *Archaeopteryx*, *Confuciusornis*, *Jeholornis*, and *Sapeornis*.
- Some genera classified as relatively derived are among the oldest of their respective groups (this is the case with both Enantiornithes and Ornithurae).
- A number of bird-like features appear abruptly. Although many of them seem to be found in some genera of theropod dinosaurs, in these they are partly distributed unsystematically (different groups show different bird characteristics) and convergent evolution must be assumed, which occurred only after the establishment of the birds (with which in these cases the features in question cannot be precursor features).
- The known evolutionary mechanisms seem to be clearly overwhelmed by the need to produce a large variety of forms relatively abruptly in geologically short periods of time.[251]

Alternatively, if we assume a creation of basic types (Scherer 1993), that is, created kinds, the above findings can be explained as follows:

- The explosive occurrence of the variety of forms reflects the existence of basic types, which were created in finished distinct and diverse form.
- The numerous, most different mosaic forms are expression of manifold combinations of characteristics, whose expression is explained by the respective way of life and not by a preceding evolution. A creator is free in his actions, while by evolution can be rebuilt only gradually (from which the expectations mentioned above follow, but did not come true).
- The difficulties (if not aporias) that arise for evolutionary theoretical modeling of how the various mosaic forms arose are unnecessary if the traits can be freely combined according to the requirements for particular lifestyles and habitats.
- The discussed problem of an "experimentation" is omitted. There is no "experimentation," but an initial variety of forms, which was originally in some respects the greatest (especially for feather types and flight forms).
- The question of evolutionary mechanisms for rapid and diverse occurrence of a wide variety of forms is not applicable.

However, some findings appear to be interpreted well from an evolutionary theoretical point of view. Some mosaic forms could appear to be close to evolutionary transitional forms. However, most mosaic forms are not suitable for this, because their feature combinations do not fit into basal positions of groups. In some groups, trends can be traced throughout the Cretaceous (for example, different expressions of beaks and different degrees of tooth reduction, as well as different pygostyle types).[252] The fact that many apparent avian features occur in different theropod dinosaur groups could also be taken as a point for evolutionary interpretation, but with the limitations already discussed above.

Creation

Let us finish with some brief remarks about creation. By "creation" is generally meant a supreme spiritual causation. Spirit endowed beings (persons

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[250] In evolutionary theory, particularly rapid evolution is thought to have occurred at the base of birds (Brusatte et al. 2014, 2387); however, the mechanisms for this are unclear and speculative. "Robust evidence that birds (and their stem lineage) evolved faster than other theropods and that their origin was associated with an early burst of rapid morphological evolution" (Brusatte et al. 2014, 2387).

[251] Here, the so-called waiting time problem of evolution plays an important role (see Lemaster 2018).

[252] This was discussed in detail above in "Avian features in theropods."

like us who can design and make machinery, or especially the Creator God of the Bible) have self-consciousness, value categories, thinking ability, set goals and pursue them deliberately, etc. They can visualize things, that is, imagine them mentally (intentionality), plan accordingly, select means to reach the goal, take obstacles and possibly detours into account, set intermediate steps and can in principle consider any number of requirements in *advance* and organize their actions accordingly. Intentionality also enables a subject to act creatively and technically. In doing so, it can *anticipate* technical means, which it has derived from the consideration and analysis of its objective as well as from its background knowledge, again as sub-objectives and systematically bring them to bear (Widenmeyer and Junker 2016).

Non-spiritual, purely natural processes cannot do all this. They are, so to speak, "blind" with respect to goals or the achievement of a goal by suitable means; thus, they have no abilities in goal setting, the analysis of goals with respect to the choice of means, and, accordingly, the systematic pursuit of goals. Whatever boundary conditions are given, things simply proceed according to the laws of nature. Explanations that are not based on intentionality, that is, purpose setting and deliberate choice of means, can only refer to three factors—laws of nature, (statistically qualified!) chance, and plausible boundary conditions.

Therefore, the characteristics of products of mental versus non-mental causation are usually very different and easy to distinguish (Romans 1:19–20).

Glossary

Derived: → Apomorphic.

Apomorphic: Designation for a trait or a trait state that is evaluated in evolutionary theory as being more highly developed or derived.

Carpale: One of the wrist bones.

Cladism: Method for the determination of relationships. Common → apomorphic features (→ synapomorphies) are taken as a basis, on the basis of which the relationships (ancestry relationships) of the taxa studied are brought into a tree diagram (→ cladogram).

Cladogram: → Cladism.

Convergence: Similar expression of structures of organisms unrelated in ancestry, which are interpreted in evolutionary theory as having arisen independently.

Enantiornithes: Opposite birds. Only in Cretaceous sediments is this fossil bird group found, whose special characteristic is the articulation between the scapula and the coracoid. On the shoulder blade there is a socket and on the coracoid bone a joint pin, the other way round to that in other bird groups. In Carpometacarpus, the third metacarpal bone extended outward beyond the length of the second metacarpal bone. Most species were dentate and were forest dwellers.

Exaptation: An existing feature is (additionally) used for a new, previously unnecessary purpose.

Furcula: wishbone; in birds and some dinosaurs, a forked bone element fused from the two clavicles.

Homoplasy: Collective term for → convergences, parallelisms, and reverse developments (reversions).

Ornithomimosauria: "Bird mimicking lizards;" dinosaurs from the theropod group that resemble ratites.

Ornithothoraces: Bird group that includes both the → Enantiornithes and the → Ornithurae.

Ornithurae: "Bird tails," birds with a fan tail, to which today's birds also belong, fossilized from the Lower Cretaceous upwards.

Opposite birds: → Enantiornithes.

Ornithuromorpha: Group consisting of the → Ornithurae and the two genera *Patagopteryx* and *Vorona*.

Oviraptorosauria: Group of dinosaurs within the → theropods. Avimimidae, Oviraptoridae and Caenagnathoidea with a very bird-like appearance are counted among them.

Paraves: Birds and their evolutionarily most closely related groups, usually the deinonychosaurs (Troodontidae and Dromaeosauridae) are included (see fig. 4).

Parsimony principle: Principle in the creation of → cladograms according to which as few → convergences as possible occur.

Patagium: Flying skin.

Phylogeny: Evolutionary reconstructed lineage based on cladistic analysis.

Plesiomorph: Designation for a trait or a trait state that is evaluated as primitive or original in evolutionary theory.

Pneumaticity: Presence of air spaces in bones.

Pygostyle: Bone formed by the fusion of several vertebrae at the end of the spine of birds.

Pygostylia: Birds that have a → pygostyle.

Synapomorphy: → Apomorphic feature common to two or more groups.

Stratigraphy: Stratigraphic description, sequence of geological sedimentary layers.

Taxon (pl. **taxa**): Generally, a unit of classification, whether species, genera, families, orders, or other groups of living things, usually regarded as units of descent.

Therizinosauria: Group of mostly large → theropod dinosaurs with very long claws on their forelimbs.

Theropods: Only fossil preserved bipedal mostly predatory dinosaurs; they are placed in the dinosaur subgroup Saurischia (see fig. 1). In evolutionary theory, they are considered almost unchallenged as the forerunners of birds, which is critically considered in this work. The theropods include from a cladistical perspective also the birds; however, this assignment is not followed in this paper, but rather "theropod dinosaurs" are spoken of in distinction to them. Which groups among the theropods are to be counted to birds is partly disputed (see the section "Avian Precursors or Secondarily Flightlessness?").

Triosseal canal: Between the furcula, coracoid, and scapula in birds is a gap, the foramen triosseum (tri-bone canal, triosseal canal), through which runs a strong tendon connecting the small pectoral muscle (supracoracoideus muscle) to the humerus. This system is responsible for lifting the wing.

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