Evolucija pera

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Undergraduate thesis / Završni rad

2023

Sveučilište u Zagrebu
Prirodoslovno-matematički fakultet
Biološki odsjek

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Završni rad

Zagreb, 2023.

University of Zagreb
Faculty of Science
Department of Biology

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Evolution of the feather

Bachelor thesis

Zagreb, 2023.

Ovaj završni rad izrađen je u sklopu studijskog programa molekularna biologija na zavodu za molekularnu biologiju biološkog odsjeka Prirodoslovno-matematičkog fakulteta u Zagrebu pod mentorstvom prof. dr. sc. Damjana Franjevića.

TEMELJNA DOKUMENTACIJSKA KARTICA

Sveučilište u Zagrebu
Prirodoslovno-matematički fakultet
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Sažetak

Pero je najbolje definirana karakteristika ptica. Dugo vremena se mislilo da je pero koevoluiralo s evolucijom ptica, ali nedavna otkrića su dovela ovo mišljenje pod povećalo. Čini se da je pero zapravo bila karakteristika koju je dijelila većina, ako ne i sve grupe dinosaura. Nova otkrića perja u pterosaura koja su, čini se, homologna onima u ptica, pomiče evoluciju pera još dalje u prošlost do zajedničkog pretka grupe Avemetatarsalia. To omogućuje rekonstrukciju upotpunjenijeg filogenetskog stabla evolucije pera temeljenog na tipovima pera koja nisu prisutna u modernim ptičjim vrstama. Istraživanja su upotpunjena novim saznanjima u razvojnoj biologiji perja i drugih pokrovnih struktura kralježnjaka kao što su ljuske, dlake i riblje krljušti. Sve ovo stvara temelje za hipotezu o ranom podrijetlu perja prema kojoj je pero evoluiralo u vrijeme oporavka od masovnog izumiranja na kraju perma. Pero je u početku vjerojatno imalo ulogu u izolaciji životinje od okolišnih čimbenika kao i ulogu u komunikaciji između jedinki. Pernate životinje bi tako imale prednost nad ostalim kompetitivnim skupinama tog perioda kao što su sinapsidi i drugi arkosauri.

Ključne riječi: Avemetatarsalia, biologija razvoja, evo-devo eksperimenti, morfologija pera, filogenetičke analize perja, perja u pterosaura

(Stranica: 24, slika: 6, literaturnih navoda: 56, jezik izvornika: engleski)
Rad je pohranjen u Središnjoj biološkoj knjižnici.

Mentor: prof. dr. sc. Damjan Franjević

BASIC DOCUMENTATION CARD

University of Zagreb
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Evolution of the feather

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Abstract

Feather is the best-defined trait of birds. For a long time, it was thought that feather coevolved with the evolution of birds, but recent discoveries have challenged this view. It now seems likely that feathers were in fact shared across many, if not all dinosaurs. Recent discoveries of feathers in pterosaurs, probably homological to those of birds, extends this view even further to the ancestor of Avemetatarsalia. This makes it possible to reconstruct a more exhaustive phylogenetic tree of the evolution of the feather according to different feather types that haven't been found in modern bird species. The research is complemented by studies in developmental biology of feathers and other integumentary structures present in vertebrates such as scales, hairs and odontodes. This makes a foundation for an early origin of feathers hypothesis that puts their emergence at the time of recovery from the End-Permian mass extinction event. It seems likely that, initially, feathers served a function of insulation and signaling and thus provided their carriers with an evolutionary edge against other competitive groups of that period such as synapsids and other Archosarus.

Keywords: Avemetatarsalia, developmental biology, evo-devo experiments, feather morphology, phylogenetic analyses of feathers, pterosaur feathers

(Pages: 24, figures: 6, references: 56, original in: English language)
Thesis is deposited in Central Biological Library.

Mentor: prof. dr. sc. Damjan Franjević

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1. Introduction

Feather is the most recognizable trait of modern birds. Not all birds can fly but all of them have feathers. For a long time, it was perceived that this trait coevolved with the evolution of birds, but years of discoveries of many beautifully preserved feathered dinosaur fossils changed this. The most influential are those in recent years from China which show exquisite feather patterns and morphologies. These fossils have been profoundly studied to find out everything about specimens morphology, traits, behavior and even color. Color can be inferred by studying sizes and shapes of feather melanosomes and comparing them with those of modern birds. Relatively recent discovery of melanosomes in pterosaurs has put this to the test once again (Benton et al., 2019).

Birds have emerged from a dinosaur group Coelurosauria which in itself was a part of a therophod group. In the eyes of the many this makes them last surviving members of a dinosaurs which are now often called non avian dinosaurs. The closest relatives of dinosaurs is the group which includes famous pterosaurs with whom dinosaurs form a clade Avemetatarsalia (Benton et al., 2019). Pterosaurs were flying reptiles from Mesozoic whose members reached massive wing spans of up to 12 meters. According to some recent studies they also might have had simple feathers (Yang et al., 2019). These two groups share their Permian origins with crocodilians or Pseudosuchians forming a larger group of Archosauria or *ruling reptiles* (Padian & Chiappe, 1998).

These relationships were obtained by a study of phylogenetics, a field of science that tries to find relationships between different individuals, species, or larger groups by comparing their key characteristics such as shapes of bones or presence and absence of traits like the feathers (Semple C & Steel M., 2003). There seem to be more fossilized feather types than there are today, so it is possible to make a phylogenetic tree of species based on presence and type of fossilized feathers.

Knowledge made by studying developmental processes of feather formation can also be used to find out additional information about relationships between relevant groups. This can be done by performing evo-devo experiments on embryos. This means shutting down certain key regulatory mechanisms and analyzing the result. If we then compile these results with chemical analysis of different compounds like proteins, they become useful for complementing our phylogenetic analyses (Benton et al., 2019; Chen et al., 2015).

2. Feather Morphology and Types

2.1. Feather Morphology and Chemical Composition

In order to analyze the evolution of feathers it is necessary to determine their characteristics and morphology, both for the modern and the fossilized ones. A feather is a protrusion on a skin of birds and, according to a fossil record, their extinct ancestors the dinosaurs. It compromises a single or numerous filaments called barbs which are connected to a rachis from which they form a branched structure. Both barbs and the rachis derive from a hollow calamus, a structure that grows from a circular epidermal wall around a dermal papilla inserted in a follicle (Benton et al., 2019). β-proteins (CBPs; often known as β-keratins) are fibrous corneous proteins which comprise most of the chemical composition of feathers and are found in many reptiles. They surround and often even substantially replace the keratins (often known as α-keratins) (Benton et al., 2019). The difference between feathers and mammalian hairs is that hairs are single filaments that grow from an epidermal cone on top of the dermal papilla inserted in a follicle. Instead of β-proteins, mammalian hairs are made of cysteine-rich keratins along with amorphous keratin-associated proteins. Hairs have not evolved much throughout the evolutionary time (Dhouailly et al., 2019).

2.2. Types of Modern Feathers

There are seven feather types in modern birds which, in contrast to mammalian hairs, attest to their morphological diversity (Fig 1.). Feathers can be filaments or pennaceous. Filaments include three types of feathers: bristles that have a stiff rachis which serve a function of protecting eyes and face, filoplumes that also have a stiff rachis but bearing a few apical barbs as they serve a sensory function and a down feathers that have a very short rachis with laterally branching barbs, each carrying a double row of smaller barbules without hooklets. They are mostly used for thermal, or in some cases, water insulation. The primary characteristics that define the pennaceous feathers are that they all have a central axis with the quill-like rachis and laterally branching barbs. Their rachis is inserted on the dorsal side of the calamus and it sometimes has an additional ventral hyporachis. This feather group includes semiplumes with barbs branching out from a central rachis whose barbules lack hooklets what makes their vane open, fluffy and insulating. Also contour feathers with hooklets on central rachis, barbs and barbules what makes a vane closed and provides streamlined cover of the body. Tail feathers sometimes called retrices are similar to contour feathers and are mostly used for flight control and display. Last are wing feathers often called remiges with similar contours to tail feathers but used to form a strong wing structure used mostly for powered flight (Benton et al., 2019). All these forms (Fig.1.) have been found in dinosaur fossil evidence along with several other types that can no longer be found in modern birds (Xu et al., 2010a).

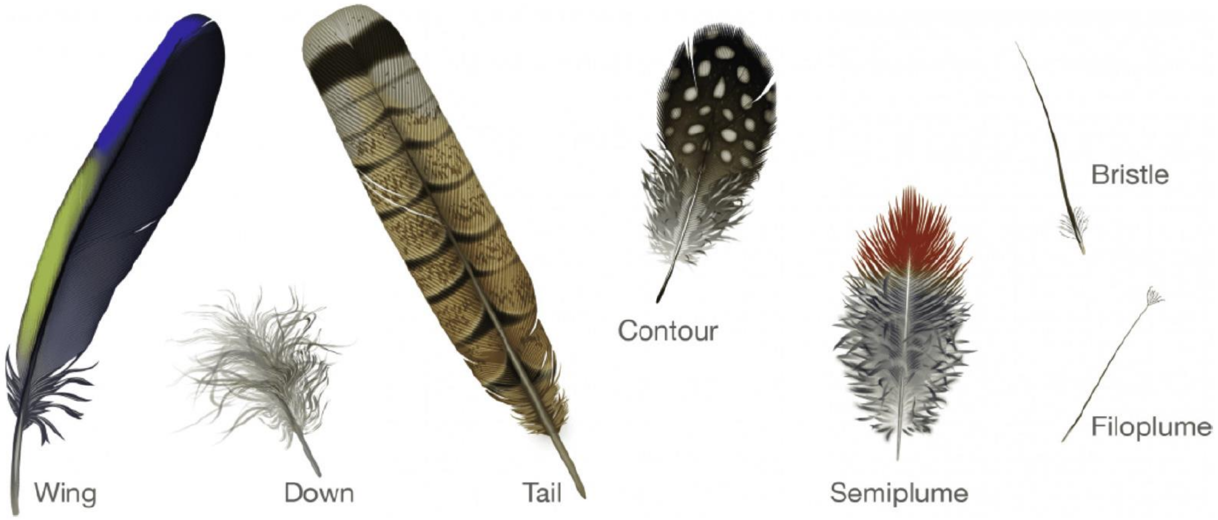

Figure 1. The seven feather morphologies found in modern bird species. From Benton et al. (2019), credited to the Cornell Bird Academy

3. Genomic Regulation of Feather Development

3.1. Appendages of Vertebrates

Basic understanding of the feather development is necessary to create an evolutionary relationship of different genes and genetic mechanisms that are essential for growing cutaneous appendages that cover bodies of vertebrates. These appendages along with scales, feathers and hairs include tooth-like scales denticles or odontodes found in chondrichthyans together with mineralized dermal scales in actinopterygians (Balic & Thesleff, 2015). An evolutionary novelty of vertebrates that made these appendages possible are alpha-polypeptides of keratins. In reptiles and birds. They are further complemented with CBPs which are the toughest naturals polymers known to science (Alibardi, 2016). A burst of *CBP* genes of Archosauria are the only genetic signal of innovation at the protein level in feather origins (Lowe et al., 2015).

3.2. Development Process

The first step in feather development is the formation of feather tracts. For example, in chicken this begins at embryonic day 6,5 when a single epithelial layer overlays a single dermal layer. Tract formation is regulated by *Noggin* which is a *BMP* antagonist and *Shh* (Sonic hedgehog) which has been shown to induce feather-producing skin. The process itself is not researched enough but other important developmental factors that are known to be involved in tract formation are firstly *cDermo-1* whose expression induces dense dermis formation along with subsequent ectopic feathers and scales but also early *Wnt* and β-*catenin* (Chen et al., 2015).

The next step is bud induction. During this process periodic patterning takes place. This happens as the originally homogeneous field divides into feather bud and interbud regions (Lin et al., 2006). As the skin matures, epithelial-mesenchymal interactions within the dorsal track lead to the formation of feather bud precursors. They first appear along the midline and progress bilaterally over time. After a while these dermal condensations form below epithelial placodes (Chen et al., 2015). Placode is an embryonic patch situated inside the epidermis or an oral epithelium that gives rise to integumentary appendages of all vertebrates. These include hair follicles, scales, teeth, and feathers (Benton et al., 2019). Placode formation (Fig. 2.) is initiated by the activation of the ectodysplasin A pathway via its Eda-Edar receptor downstream of the Wnt signaling. Edar importantly triggers *FGF* (fibroblast growth factor) and *Shh* signals which are required for the formation of the dermal condensation on which the placode grows. With the absence of Wnt signaling placodes will not form (Benton et al., 2019).

On the avian body surface feathers are usually arranged in repeated hexagonal patterns (T. X. Jiang et al., 2004). The patterning process is controlled via a set of activating and inhibiting molecules (Chuong et al., 2013) including Wnt-7a, β-catenin, L-Fringe and NCAM (neural cell adhesion molecule) (Chen et al., 2015). The process remains insufficiently researched but two main theories have been proposed. Some suggest a pre-patterning mechanism (Oster et al., 1983) while others argue for an afore mentioned model of combinations of different activators and inhibitors according to the rules of the Turing model (Chen et al., 2015; T. X. Jiang et al., 1999; Maini et al., 2006). A second set of genes is not expressed early but is induced after the feather bud primordium is initiated in a de novo expression. These include *Msx2* (Msh homeobox 2) and *Shh* that is expressed in the distal feather bud (Chen et al., 2015). This molecular control is thought to be a trait shared by all vertebrates that evolved 500 Ma. This is because all of them, living or fossilized, show scalation, plumage or fur. Furthermore, genomic comparisons of protein-coding regions in placode development show this to be a part of an ancient developmental toolkit (Lowe et al., 2015).

Feather patterning and bud induction is followed by the formation of the bud anterior-posterior axis from the originally dome-shaped feather primordia (Chen et al., 2015). The feather elongates on a rostral-caudal direction and the initial polarity may derive from interactions between *Wnt-7a* and β-*catenin* (Widelitz et al., 1999). Bud elongation is further enhanced via cell proliferation controlled by *WNT6* (Chodankar et al., 2003). The feather bud epithelium then invaginates to form the follicle structure (Chen et al., 2015). Next, the feather follicles are formed during folliculogenesis by wrapping of the epithelium around the dermal papilla and its subsequent invagination into the underlying mesenchyme (Chen et al., 2015). When the bud elongates as a hollow tube its base invaginates to form a cylindrical wall which cornifies forming the calamus. On the top, the epidermal wall divides into barb ridges. The number of ridges and rachis formation are regulated by the dermal pulp. *BMP* and *Noggin* are responsible for the barb ridge formation.

Barb growth is influenced by Shh and rachis formation by the fusion of barb ridges depending on the BMP:Noggin ratio (Benton et al., 2019; Danielle et al., 1970). Feather is fully formed after branch formation and differentiation of anterior-posterior and proximal-distal axes (Chen et al., 2015).

3.3. Shared Ancestry of Vertebrate Appendages Developmental Mechanisms

Feathers seem to be the default outcome for skin appendages in modern birds. This was shown by evo-devo experiments where feather development had to be inhibited by the inhibition of the *Shh* pathway for scales to appear (Benton et al., 2019).

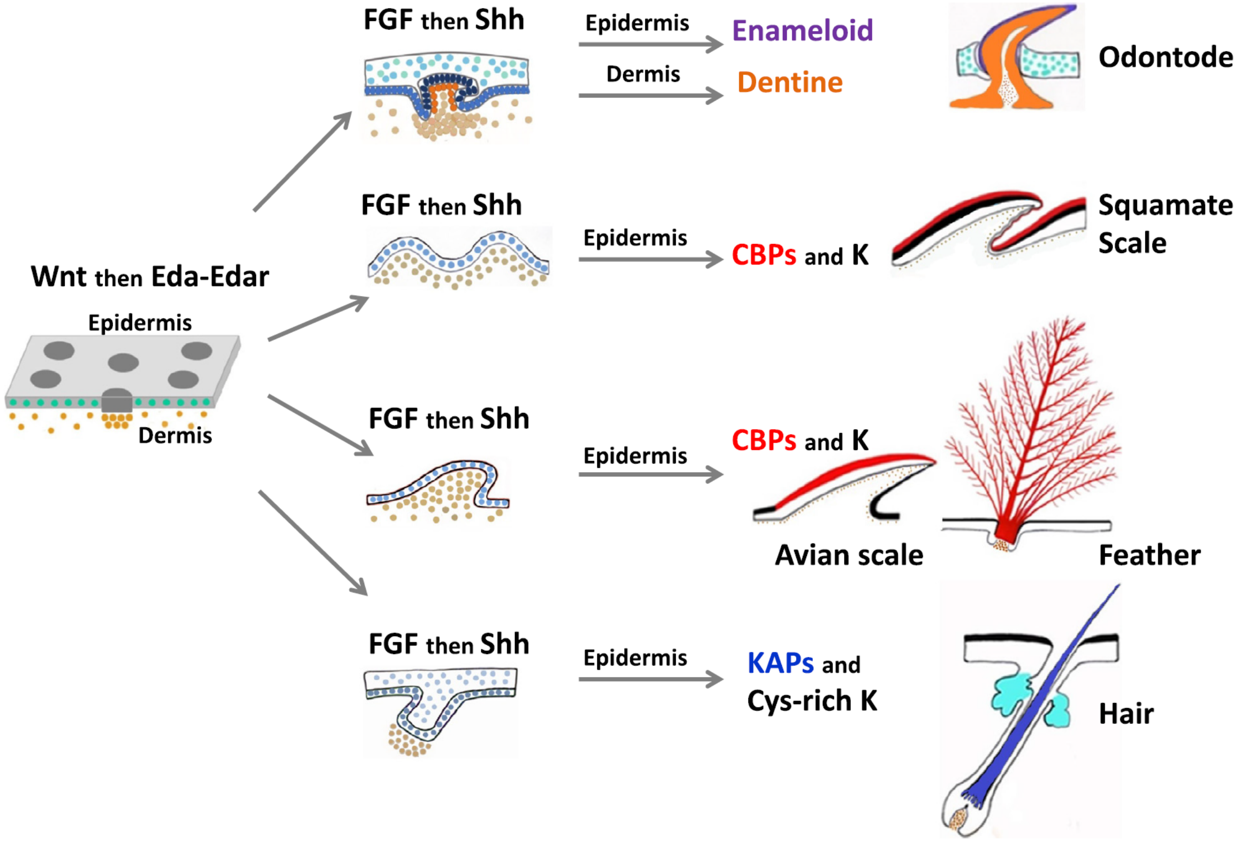

Figure 2. Comparison of Developmental Pathways of Different Vertebrate Appendages. The ectodysplasin A pathway with its Eda-Edar receptor is activated downstream of Wnt signaling. Because of this, absence of *Wnt* (Wingless-integrated) activation blocks placode initiation in all species. The Edar receptor, expressed in the placodes, triggers *FGF* (fibroblast growth factor) and *Shh* (Sonic hedgehog) signals that are required for the formation of the dermal condensation from which the placode grows. This is the same for all vertebrate appendages. From Benton et al., (2019).

To gather further evolutionary insight, chicken (order Galliformes) CPBs (of which there are 111) were compared with those of the zebra finch (order Passeriformes) and alligators (Chen et al., 2015). Results showed that reptile (alligator) *CBP*s form a monophyletic group with avian scale and feather *CBP* genes (Greenwold & Sawyer, 2013). When compared with the Nile crocodile, *CBP*s showed 75-90% identity with chicken CBS (Dalla Valle et al., 2009). When comparing molecular composition of chick scales, they seem to be similar to chick feathers but show difference when compared with alligator scales (Wu et al., 2018). Furthermore, molecular phylogeny methods imply that avian *CBP*s started to diverge some 216 Ma from their archosaurian ancestor while in extant birds they haven't began to diverge until 143 Ma (Greenwold & Sawyer, 2011).

Scales are much simpler structures than feathers. In chicks large scales called scutas, which cover the dorsal foot, express only a limited set of CBPs associated with keratins. Similarly, bumps often called reticula, that cover planar foot, contain only keratins (Benton et al., 2019). Furthermore, reticula formation was initiated by blocking the initiation step of the feather development (Prin & Dhouailly, 2004). During embryonic development, feather development is blocked in the amnion, cornea and plantar pads. However, this is readily reversed by adjusting the *Wnt-BMP-Shh* pathways. All this suggests epidermal plasticity and the default competence for placode formation (Fig. 2.) along with conserved mechanisms that could have been present in the amniote ancestor (Benton et al., 2019).

It seems that, aside from the burst of duplication of *CBP*s, protein evolution has a limited role in feather evolution. All necessary tools and pathways were already present at least in all amniotes (Lowe et al., 2015). Scales might have formed several times following different evolutionary branches. It should be noted that feathers in giant dinosaurs might be absent for a variety of reasons as, for the example, similar to the African elephant which lost most of its hair (Benton et al., 2019).

4. Fossil Evidence of Feathers

4.1. Difficulties of Interpreting the Fossil Record of Feathers

Interpretation of fossilized feathers is often challenging. This is a result of a fossilization process (taphonomy) itself, but also due to the limitations a traditional light microscopy (Benton et al., 2019; Xu & Norell, 2006). Problems like these even caused debate whether the fossils are even feathers themselves as some interpreted them as fossilized dermal collagen fibers (Lingham-Soliar et al., 2007). However, this view is not widely accepted due to inconsistencies with morphological and taphonomic evidence (Benton et al., 2019; Smithwick et al., 2017).

4.2. Information from Fossilized Melanosomes

Advances in visualization methods, such as laser-stimulated fluorescence have allowed researchers to show previously unknown macro- and microscopic details of fossilized feathers. Furthermore, other microscopic and chemical approaches were extensively used to analyze some of the key feather components including CBPs, keratins and melanins (Benton et al., 2019; Pan et al., 2019). In feathers of extant birds there are structures called melanosomes, responsible for the color of feathers (Benton et al., 2019). They are melanin-rich fibrous matrices composed of envelopes of CBPs and keratins respectively. CBPs are very chemically stable due to their extensive cross-linking via disulfide bonds (Benton et al., 2019). This has caused interest in research concerning the ancient CBPs that assume their presence in contemporary fossils. Aim of such research is to use CBP data to find answers to the questions such as the ability of a powered flight in a fossilized organism (Benton et al., 2019; Pan et al., 2019). Although fascinating, these studies and claims are controversial, especially in studies that used immunohistochemistry since the method has not been verified on fossils. On the other hand, there is a study made by Slater et al., (2020) whose results made by taphonomic experiments go in favor of preservation of ancient melanosomes and their properties needed for immunohistochemical analyses.

In the early days of studies of fossilized feathers, it was thought that fossilized melanosomes were, in fact, just remnants of autolithification of bacteria which played a vital role in preservation of feathers as carbonaceous compressions (Benton et al., 2019). This paradigm has shifted in favor of interpreting these features as previously described melanosomes (Vinther et al., 2008). As a result, fossil colors have emerged as a new field in paleobiology. Melanosomes come in various shapes and sizes and can be used to gather information about color (Fig. 3.), but also information about behavior and ecological role of a species. It should be noted that these reconstructions, however fascinating, are still incomplete due to a fact that it's not possible to gather information about other co-occurring pigments such as carotenoids (Benton et al., 2019; Li et al., 2010; Thomas et al., 2014).

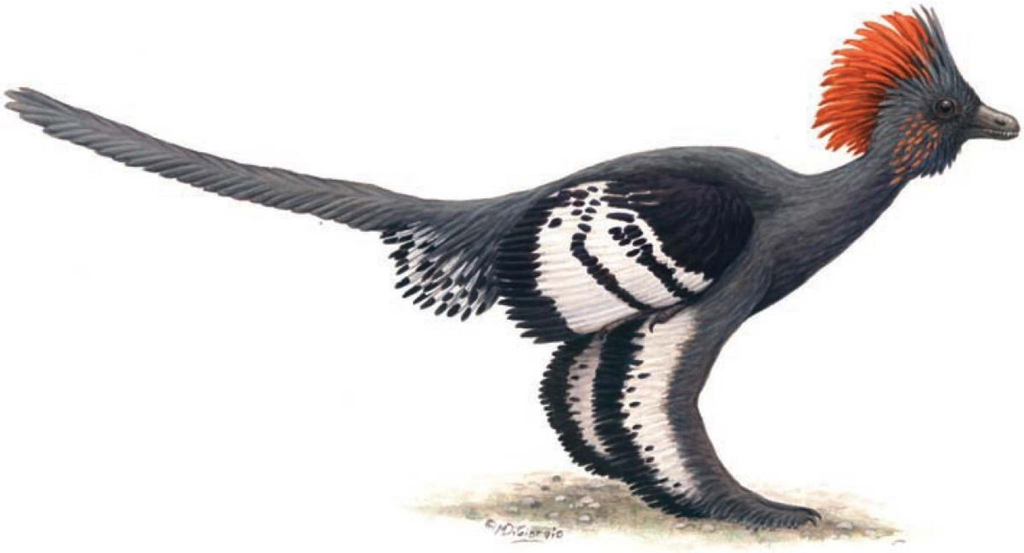

Figure 3. Reconstruction of the color pattern of the Jurassic troodontid *A. huxleyi* made by composing body, limb and head melanosome information from specimen BMNHC PH828 and tail information from specimen LPM-B00169. Image from (Li et al., 2010); specimen LPM-B00169 described in (Hu et al., 2009); color plate by M. A. DiGiorgio.

There are points of criticism that should be further analyzed. For instance, the fact that melanosomes shrink during fossilization (McNamara et al., 2013). This could have an impact on perceived color but perhaps not enough to dramatically impact finds. Furthermore, melanosomes should be inspected for their origin since they are widespread in vertebrate internal organs (McNamara et al., 2018). Also, the impact of diagenesis has not been fully explored (Benton et al., 2019). An argument that pushes the idea that bacteria are readily fossilized does not apply to carbonaceous compression fossils. Additionally, claims that the sparse distribution of melanosomes in some modern bird feathers is inconsistent with densely packed melanosomes in fossilized feathers fails to consider that melanosomes could be concentrated during fossilization process because of the collapse and compaction of feather tissues (McNamara et al., 2018).

4.3. Additional Feather Morphologies Found in the Fossil Record

Continuing the discussion made in chapter *2. Feather Morphology and Types* there have been several more feather types that were discovered in dinosaurs, but also, surprisingly, in pterosaur remains. Interpretation of their functions can, however, be problematic. Feathers used for flight should be tuned for stiffness and air capture and still be lightweight. They should also be arranged in overlapping arrays in wings. If they are used for display functions that can be determined if the feathers can't form wings and show distinctive color patterns, elongation or are arranged in erectable display formation, for instance in the tail (Foth et al., 2014). The function of a camouflage can also be determined based on color patterns, for example if used for countershading (Vinther et al., 2016).

Important notice is that, even though the fossils themselves might be stunningly well preserved, it may only be possible to identify two or three feather types even if others were present during the animal's life. In addition, determination of homology is harder for simple filaments than it is for more complex feather morphologies. This is especially relevant in the case of supposed pterosaur feather remains and raises important questions regarding the taphonomy of such soft tissues (Benton et al., 2019).

Additional feather morphologies found in dinosaur specimens and not seen in modern birds prove that feathers can adopt a wide range of forms. They usually show branching barbs, but not always such is the case in simplest monofilaments (Benton et al., 2019; Xu et al., 2014; Xu et al., 2010b). Each of these (Fig 1. and Fig 4.) ten, or even more, described morphologies occur in different parts of the body of a bird or a nonavian dinosaur. They each have a specific function such as insulation, display, protection, food gathering and, of course, flighting. They also do not occur randomly throughout the phylogenetic tree. Simplest monofilaments indeed are widespread but others, such as the pennaceous contour, tail feathers, but also feathers used for flight are restricted to the clade Coelurosauria which includes birds and all their closest theropod relatives (Benton et al., 2019).

These additional feather morphologies have been identified, along with modern ones, in specimens found in China. Examples are the ribbon-like feathers found in the oviraptorosaur theropod dinosaur *Similicaudipteryx* that lived during the Early Cretaceous period (Xu et al., 2010b). They comprise an elongate ribbon-like rachis with a pennaceous tip which has neatly organized and radiating barbs (Fig 4. A-D, L). Another type is the simple bristle feather (Fig. 4. E) that was widespread among theropod dinosaurs but was lost in most birds along with a ribbon-like feather (Fig. 4. L). The reasons for these losses have not been ascertained (Benton et al., 2019). Feather morphologies that were spread more widely among dinosaurs are other kinds of bristle and multiply branching feathers. Cylindrical bristles were present in a row-like fashion along the midline of the tail of the ornithischian *Psittacosaurus*. Each of those feathers was 16 cm long (Mayr et al., 2016). Bristles were also present in the heterodontosaurid ornithischian *Tianyulong* (Zheng et al., 2009). The Middle Jurassic ornithopod *Kulindadromeus* that lived in what is now modern-day Siberia shows a great range of feathers and scales of all sizes but most notably monofilaments that grew around its head and thorax. This find is important because this dinosaur seems to have had both feathers and secondarily derived rhomboid scales in neat arrays up and down the legs with broad scales above and below the tail (Godefroit et al., 2014).

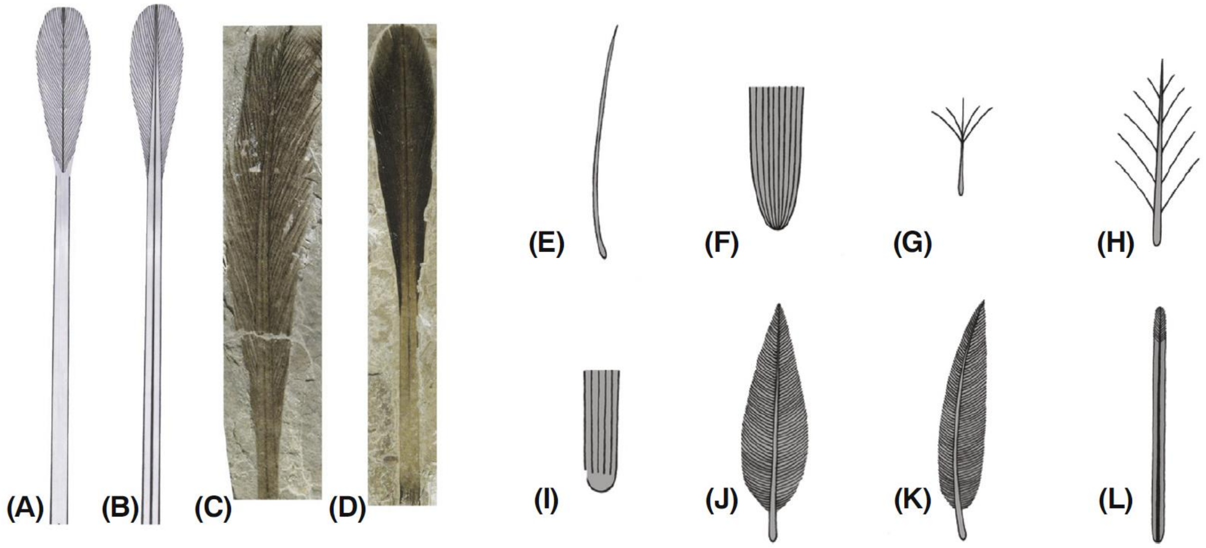

Figure 4. Diversity of Fossil Feathers. Dinosaurs had unique feather morphologies that are not present in modern birds. Oviraptosaurian theropod *Similicaudipteryx* had ribbon-like feathers with expanded tips (A), an unnamed maniraptoran (B), an Enantiornithine bird (C) and a Confuciusornithid bird (D). Feather morphologies (E-L) show their diversity in theropod dinosaurs and include some morphologies not seen in modern birds (E, I and L). From Benton et al., (2019) who credited Xu Xing.

Since bird scales are also thought to be secondarily derived from feathers, as shown with evo-devo experiments, this is a major find (Benton et al., 2019). All this diversity found throughout theropods, birds and ornithischians led researchers to speculate that feathers could have originated at the base of Dinosauria rather than within Theropoda (Godefroit et al., 2014; Xu et al., 2014). Recent report of feathers in pterosaurs (Yang et al., 2019), a sister group of dinosaurs, pushes this claim even further.

4.4. Pterosaur Feathers

Since the discovery of some exceptionally well-preserved pterosaur specimens from as long ago as 1831, it was known that pterosaurs possessed epidermal structures (Benton et al., 2019). For most of the time since their discovery they have been interpreted as hair- or fur-like structures. They were also often challenged as being taphonomic or even artificial products (Frey & Martill, 1998). Additionally, fibers from the wing membranes of the specimen found in Kazakhstan in 1970 were reinterpreted as decomposed actinofibrils. Nevertheless, this interpretation of epidermal structures being hair-like integumentary coverings has been cemented by repeated discoveries in China (Benton et al., 2019). Interestingly, some densely aligned pinnate fibers that formed distinct tufts in a diamond- and V-shaped patten on the wings of a Rhamphorynchoid were interpreted as protofeathers by Czerkas & Ji, (2002).

However, this seemingly cemented interpretation in now being questioned. Kellner et al., (2010) named pterosaur hair-like structure pycnofibres to differentiate them from mammalian hair and avian feathers. Discoveries of two anurognathid pterosaur specimens (Fig 5. B) showed four types of pycnofibres. It was also demonstrated that these pycnofibres share many key characteristics with feathers. For example, they have a tube-like structure of the calamus and melanin-containing melanosomes throughout the barbs. There are also three distinct morphologies (Fig 5.) of branching structures (Yang et al., 2019). They are thought to have served a role of dense filamentous covering that had functions in thermoregulation, tactile sensing, signaling and aerodynamics (Benton et al., 2019).

It should be stated that this is an area of an open debate and not everyone is convinced that these integuments are indeed pterosaur feathers (Unwin & Martill, 2020). However, a response to these counterarguments seems to shift the conclusion in favor of the feathers interpretation

(Yang et al., 2020). Additionally, a recent study from Cincotta et al., (2022) has found that pterosaur melanosomes supported color signaling functions which would at least show that regulation of melanosome chemistry and shape was active early in feather evolution and, as such, would indicate a deep evolutionary root of feathers.

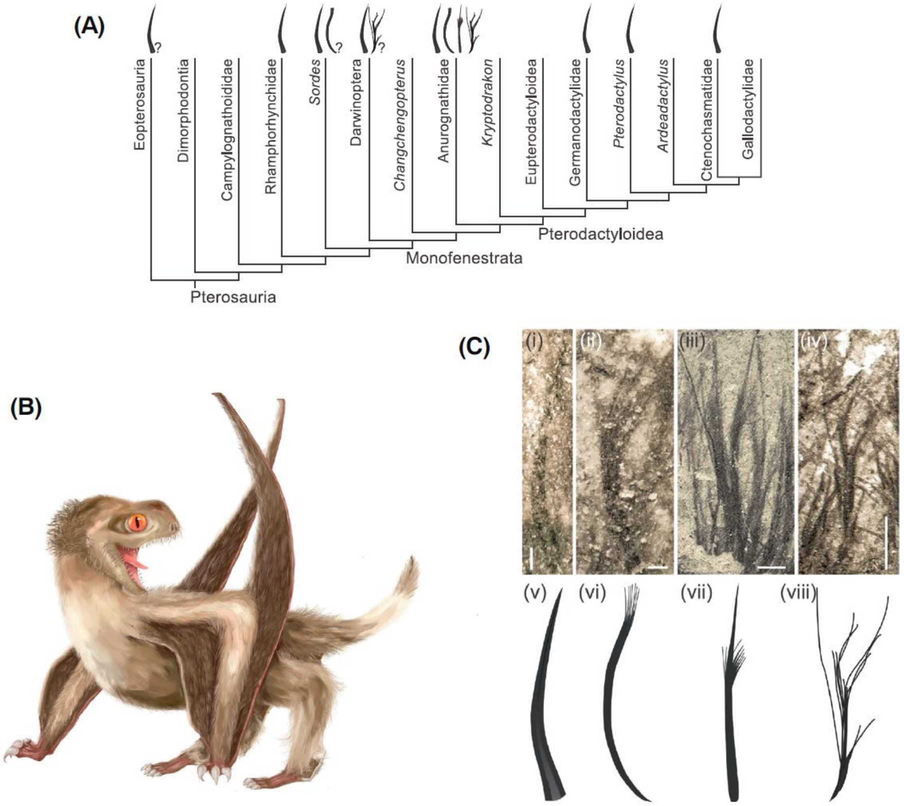

Figure 5. Controversial Pterosaur Feathers. (A) Simplified phylogeny of pterosaurs, showing the occurrence and types of fossilized fluff (pycnofibres or feathers); (B) A reconstruction of a anurognathid pterosaur from the Middle Jurrasic discovered in China in which four feather types were identified (Yang et al., 2019); (C) Four feather types including monofilaments (i and v), tufted monofilaments (ii and vi), bunched fibers (iii and vii) and down feathers (iv and viii). From Benton et al., (2019); art by Yuan Zhang (C).

5. Current Theory of Feather Evolution

5.1. Early Origin of Feathers Hypothesis

After years of research and with an abundant fossil record, it is now possible to reconstruct major events in feather evolution. If Pterosauria, the closest group to Dinosauria (Brusatte et al., 2010), did have feathers as discussed in chapter 4.4. *Pterosaur Feathers* then this would at least put their emergence during the Early Triassic, around 250 Ma (Benton et al., 2019). Close outgroups of Dinosauria were already fully established by the end of the Early Triassic period (Benton et al., 2014) so this makes the groundwork for early origin of feathers hypothesis (Fig 6. A).

5.2. End-Permian Mass Extinction and its Impact on the Evolution of Life

The Early Triassic period was a time of considerable challenges for life. It was an 8-Myr timespan of recovery from the end-Permian mass extinction (Benton et al., 2019), the biggest mass extinction in Earth's history. This extinction around 252 Ma was a result of a massive volcanic activity in what is now modern-day Siberia (Zhang et al., 2021). There was massive acid rainfall, rapid global warming, mass wasting and ocean acidification. The result was an extinction of about 90% of all species both on land and in water (Benton et al., 2019). The climate has rapidly shifted in many times between 252 Ma and 244 Ma, with times of life recovery and its repeated destruction (Payne et al., 2004). Nevertheless, at the end emerged modern-style ecosystems with ancestors of many modern groups like lizards, lissamphibians, turtles, mammals, crocodilians and, most importantly for this discussion, dinosaurs (Benton et al., 2019).

5.3. Evolutionary Connections Between Relevant Groups

Evolution of higher metabolic rates was the main selection factor behind evolution of enhanced physiological characteristics of medium-sized land-based vertebrates resulting in a greater ability to acquire food (Benton et al., 2019). One of the best examples, well documented in the fossil record, is a shift from a sprawling to erect postures during the Permian-Triassic boundary (Kubo & Benton, 2007).

Triassic archosaurs and synapsids probably had small red blood cells resulting in a high aerobic capacity. This is indicated by small cortical canals and cell lacunae (Huttenlocker & Farmer, 2017). Bones of archosaurs from the Early and Middle Triassic had fast growth rates as indicated by bone microstructure. This is also the case in dinosaurs and pterosaurs, more so than in crocodilians (Benton et al., 2019). All this indicates greater metabolic activity.

Dinosaurs, pterosaurs and their ancestors show postcranial skeletal pneumaticity. This can be interpreted as evidence that these groups had supplementary air sacs and an unidirectional air flow, similar to today's birds (Butler et al., 2012). This would allow them an increased activity and endurance by allowing them to breathe by running. This is in contrast with animals such as sprawling lizards which must either run or breathe (Benton et al., 2019). Evolution of these traits, that allowed for a higher activity, seem to have been necessary to compete in predator-prey arms race with other major groups of the Triassic period, archosaurs and synapsids. Similarly, synapsids evolved endothermy during the Middle and late Permian (Benton et al., 2019; Vin Rey et al., 2017). In this context it seems logical that both synapsids from the Late Permian and archosaurs from the Early Triassic evolved some form of insulating pelage, whether being hair or feathers. Since the endothermy in pterosaurs and dinosaurs (group Avemetatarsalia) is currently accepted theory, it shouldn't be surprising that insulating epidermal coverings, like feathers, were present it those groups, especially in smaller species that probably couldn't rely on mass homeothermy alone. If feathers were indeed present in Pterosauria, then they probably evolved coincident with other physiological and locomotory adaptations, probably with an initial function as an insulation of the endothermic small ancestors of dinosaurs and pterosaurs (Benton et al., 2019).

5.4. The Diversification of Feather Types

First and foremost, this topic is not fully understood. The oldest types of feathers, like those supposed to have been shared between pterosaurs and ornithischians, were simple monofilaments, bristles, tufted and bunched filaments (Fig 6. 1-3). They most definitely weren't used for flying but for insulation (Benton et al., 2019). They were also used for display as seen in the ceratopsian

Pstittacosaurus discussed in chapter 4.3. *Additional Feather Morphologies Found in Fossil Record* (Mayr et al., 2016). There are also groups of dinosaurs without evidence of possessing

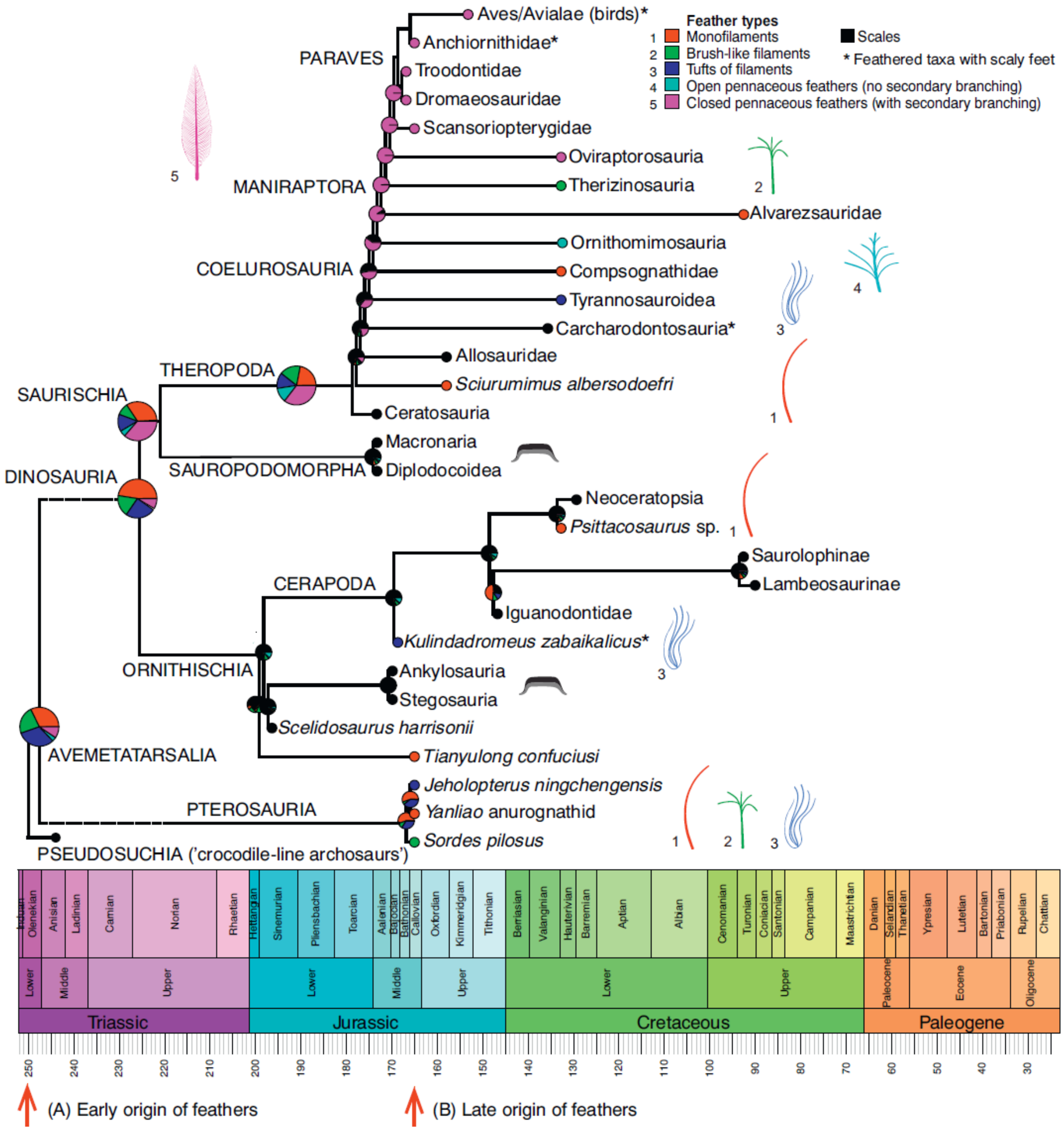

Figure 6. Chronogram that Shows a Macroevolution of Feather Types. Major groups of dinosaurs (upper part) and pterosaurs (lower part) are present on the chronogram scaled against geological time based on a computer analysis by (Yang et al., 2019). The presence of five feather morphologies, numbered 1-5, and scales is indicated in pie charts next to each phylogenetic group. They represent the best estimation of ancestral states. Two hypotheses for the timing of evolution of feathers are indicated below the time scale. An early origin of feather (A) at the base of Avemetatarsalia which includes pterosaurs and dinosaurs and a late origin of feathers (B) timed at the base of Maniraptora during the Early through Middle Jurassic. Chronogram from Benton et al., (2019) based on research by (Yang et al., 2019).

feathers. These include armored ankylosaurs and stegosaurs that belonged to ornithischians and sauropodomorphs. Nevertheless, there is still a possibility that these groups did possess feathers but got crowded out by their bony armor plates or giant size similar to how modern elephants have greatly reduced hair covering (Benton et al., 2019). The greatest diversity of feather types is, however, found in theropods in the clade Coelurosauria which originated during the Late Triassic. They show simple feathers like the other groups together with more complicated, pennaceous feathers present in Maniraptora (Fig 6. 5,6) (Benton et al., 2019). This is the basis for the late origin of feathers hypothesis (Fig 6. B) which states that true feathers were at least present in the base of Maniraptora.

6. Conclusion

Discovery of potential feathers in pterosaurs puts the evolution of the feathers further 80 Ma years into the past than previously though. If so, they've evolved during the Early Triassic. This was a time of great challenges for life since it was recovering from the aftermath of the greatest mass extinction in the history of our planet. Evolution of the feather would have allowed ancestors of Avemetatarsalia better insulation since it has been proven that they were endothermic and subsequently given them ecological advantage over other groups of that time, archosaurians and synapsids by enabling them greater levels of activity.

It now seems likely that birds haven't evolved rapidly from reptiles but that they've accumulated a set of adaptations over the time of approximately 100 Myr. It has also become inadequate to state that feathers evolved from reptilian scales since morphogenesis and feather *CBP*s are basal to avian scales as shown by experiments in feather development. Simply put, avian scales are chemically more similar to feathers than to reptilian scales. More research is, however, needed to study feather follicles, alpha keratins, CBPs and coloration mechanisms. If the early origin of feathers hypothesis turns out to be correct than all dinosaurs had the precondition of growing feathers, but they could've been lost in some groups due to armor or great size. It is however almost certain that feathers at the latest evolved at the base of the group Maniraptora from which eventually, in the Latte Jurassic, evolved birds with complex pennaceous feathers.

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8. Biography

I was born in Zagreb on 11th of November 2001. In the seventh grade of primary school, I participated in a national competition in chemistry and biology. I graduated from XV. Gymnasium Zagreb in 2020. where I participated in multiple national competitions in geography and biology winning the second place in biology in both third and fourth grades. This has granted me the City of Zagreb Scholarship of Excellence in a duration of three years. In 2020. I have enrolled in a bachelor's degree of molecular biology at the University of Zagreb. During the fourth semester I've had a chance to participate in a molecular phylogeny workshop at Johannes Gutenberg University Mainz which was led by Professor Herlyn Holger.

At the beginning of 2023. I have been accepted to Lund University for a Master's programme in Molecular Biology, Molecular genetics and Biotechnology where I plan to graduate by 2025. I'm interested in studies about epigenetics and I would love to study this area in the context of ancient DNA research.