Trends in Ecology & Evolution

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Review

The Early Origin of Feathers

Michael J. Benton,[1,*] Danielle Dhouailly,[2] Baoyu Jiang,[3] and Maria McNamara[4]

Feathers have long been regarded as the innovation that drove the success of birds. However, feathers have been reported from close dinosaurian relatives of birds, and now from ornithischian dinosaurs and pterosaurs, the cousins of dinosaurs. Incomplete preservation makes these reports controversial. If true, these findings shift the origin of feathers back 80 million years before the origin of birds. Gene regulatory networks show the deep homology of scales, feathers, and hairs. Hair and feathers likely evolved in the Early Triassic ancestors of mammals and birds, at a time when synapsids and archosaurs show independent evidence of higher metabolic rates (erect gait and endothermy), as part of a major resetting of terrestrial ecosystems following the devastating end-Permian mass extinction.

Highlights

Feathers are epidermal appendages comprising mostly corneous β-proteins (formerly β-keratins), and are characteristic of birds today.

There are close connections in terms of genomic regulation between numerous regularly arrayed structures in the epidermis, including denticles in sharks, dermal scales in teleost fish, epidermal scales in reptiles, feathers in birds, and hairs in mammals.

The discovery that genes specific to the production of feathers evolved at the base of Archosauria rather than the base of Aves or Avialae (birds) is matched by fossil evidence that feathers were widespread among dinosaurs and pterosaurs, the flying reptiles.

This suggests that feathers arose first, as simple monofilaments, probably for insulation in the archosaurian ancestors of birds and dinosaurs during the Early Triassic, a time when land vertebrates were speeding up in terms of physiology, with erect gaits and endothermy.

Early Origin of Feathers

It is shocking to realise that feathers originated long before birds because feathers have generally been regarded as the key avian innovation [1–4]. However, thousands of astonishing fossils from China have shown that many **nonavian dinosaurs** (see Glossary) also had feathers, including feather types not found in birds today. These discoveries extended the origin of feathers minimally back to ~175 million years ago (Ma), 25 million years (Myr) before the first generally acknowledged bird, *Archaeopteryx*. However, this is just a start.

Discoveries of feathers in ornithischian dinosaurs hinted that feathers are a character of dinosaurs as a whole [1,2], although this has been disputed [5,6]. A startling new discovery [4] showed that even pterosaurs had four kinds of feather, apparently homologous in form with those of dinosaurs, their closest relatives. Could it be that feathers in fact arose ~250 Ma, during the Early Triassic, when life was recovering from the devastating end-Permian mass extinction? This would place the origin of feathers at a time of **arms races** between **archosaurs** and **synapsids**, when their postures became erect, metabolic rates were speeding up, and they became capable of sustained activity. These new fossils provide a novel perspective on the drivers of early feather evolution, and they open macroevolutionary questions about their function: insulation first, then display and flight?

These fossil discoveries tie with a developing consensus on the genomic regulation of feather development [7]. The Wnt, Eda-Edar, BMP, and Shh developmental pathways in vertebrates are shared by the denticles of sharks, the mineralised scales of bony fish, the epidermal scales of reptiles, the hair of mammals, and feathers of birds. Furthermore, genomic work shows that lizard scales, bird feathers, and mammal hairs are the default, and can be suppressed by additional genomic regulators to stop them developing on the eyes or the soles of the feet, for example. The absence of feathers in large sauropod dinosaurs and armoured dinosaurs could be explained by suppression. But what is a feather?

Feathers, Ancient and Modern

A feather comprises a single filament or involves numerous filaments or **barbs**, which, if connected by a **rachis**, form a branched structure. The barbs or rachis derive from a hollow **calamus**, which grows from a circular epidermal wall around a dermal papilla, both being inserted in a **follicle**. Feathers are made mostly from fibrous corneous β-proteins (abbreviated

[1]School of Earth Sciences, University of Bristol, Bristol, UK
[2]UFR Biologie, Université-Grenoble-Alpes, Grenoble, France
[3]School of Earth Sciences and Engineering,
Nanjing University, Nanjing, China
[4]School of Biological, Earth and Environmental Sciences, University of Cork, Cork, Ireland

*Correspondence:
mike.benton@bristol.ac.uk
(M.J. Benton).

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CBPs; formerly termed β-keratins), the reptile and bird-specific keratin-associated proteins, which not only surround, but substantially replace the keratins (formerly termed α-keratins) [8]. Feathers have evolved considerably through geological time, some structures having appeared and disappeared, and modern vaned feathers are the most complex outgrowths of vertebrate skin. By contrast, mammalian hairs are single filaments that grow from an epidermal cone on top of a dermal papilla, both inserted in a follicle. The hair shaft structure, mainly made from cysteine-rich keratins with amorphous keratin-associated proteins, has not varied much through geological time from its origins [7].

Modern bird feathers vary dramatically in morphology, which can be assigned to seven types (Figure 1) that are either filaments or pennaceous. The filaments include three types: bristles (stiff rachis, to protect eyes and face); filoplumes (stiff rachis, bearing a few apical barbs, with a sensory function); and down feathers (very short rachis bearing ~10–30 laterally branching barbs, each bearing a double row of **barbules** lacking hooklets, mainly for insulation). The four types of **pennaceous** feathers all have a central axis, the quill-like rachis, and laterally branching barbs. The rachis is inserted on the dorsal side of the calamus, sometimes associated with an additional and ventral hyporachis. Pennaceous feathers include semiplumes (barbs branch from central rachis, but barbules lack hooklets, so the open vane is fluffy and insulating), contour feathers (central rachis, barbs, and barbules that have hooklets, forming a closed vane that provides streamlined cover to the body), tail feathers (or **retrices**, similar to contour feathers; can fan out for flight control or display), and wing feathers (or **remiges**, similar to contour and tail feathers, forming a strong wing structure for powered flight).

Among dinosaurs, all seven feather types have been identified [2,9], and more. Palaeontologists were surprised when they found feathers in some fossil specimens (Box 1) that did not match the modern forms [2,9]. The conclusion is evident: feathers can adopt a range of forms, mostly showing branching barbs, but not always in the simplest monofilaments.

Each of the ten or more described feather morphologies occurs on different parts of the body of the bird or nonavian dinosaur and has a specific function, whether for insulation, display, protection, food gathering, or flight. Furthermore, they do not occur randomly across the phylogenetic tree; some, such as the simplest monofilaments, may be widespread, whereas others, such as the pennaceous contour, tail, and flight feathers, are restricted to clade Coelurosauria, including birds and all theropod dinosaurs closest to them phylogenetically.

Interpreting the functions of feathers in fossils can be problematic. Flight feather properties are tuned for stiffness and air capture, while remaining lightweight [10], and are arranged in overlapping arrays in wings. Display functions can be determined for feathers that do not form wings and that may show striking colour patterns, elongation, or arrangement as erectable fans in the tail [11]. Some aspects of camouflage, such as countershading, can also be determined from colour patterns in dinosaurs [12].

Even in exceptionally well-preserved fossils of early birds, nonavian dinosaurs, or pterosaurs (Box 2), it may be possible to identify only two or three feather and scale types, even though others might have been present. In addition, determining that simple filaments or scales are homologous across the tree is harder than for more complex feather morphologies. These issues raise important questions concerning the **taphonomy** of soft tissues, including feathers.

Preservation of Ancient Feathers

The morphology of fossil feathers can be hard to determine because of alteration during the fossilisation process (taphonomy) and the limitations of traditional light microscopy [26].

Glossary

Archosaur: a member of clade Archosauria, including birds, crocodilians, dinosaurs, and all their ancestors back to the Late Permian.

Arms race: a form of competition where two clades interact directly over a span of time, sometimes as predators and prey, which then evolve adaptations and counter-adaptations against each other.

Autolithification: processes by which bacteria seal and preserve organisms such that their soft tissues are mineralised rapidly

Avemetatarsalians: members of the wider clade that includes dinosaurs (including birds) and pterosaurs, and their ancestors, commonly called the 'bird line' of archosaur evolution, as opposed to the 'crocodilian line', which diverged in the Early Triassic.

Barb: primary side branch of a feather.

Barbule: second-order side branch of a barb.

Calamus: lower part of the rachis and/or barbs, providing attachment to the feather follicle.

Diagenesis: geological processes, such as heat and pressure, that alter rocks and fossils during and after burial.

Follicle: pit in the skin in which each feather is embedded and provided with nervous and blood supplies; site of feather stem cells.

Lagerstätte (pl. Lagerstätten): a fossil site where soft tissues are preserved.

Melanosome: a cellular organelle rich in the pigment melanin and responsible for contributing to the colour of feathers, hair, and skin

Nonavian dinosaurs: the 'traditional' dinosaurs, meaning the dinosaurs that are not birds, because birds are part of the clade Dinosauria.

Odontode: hard structure in the skin of chondrichthyans (cartilaginous fish), with a soft internal pulp surrounded by dentine and covered with mineralised enamel or similar substance.

Pennaceous feather: a feather with a rachis from which barbs branch on each side, either symmetrically or asymmetrically.

Placode: embryonic patch in the epidermis or oral epithelium that gives rise to structures such as hair follicles, feathers, scales, or teeth.

Pycnofibres: epidermal whiskers and branching structures of pterosaurs.

Furthermore, some authors have queried whether the fossil structures are indeed feathers, favouring an interpretation as dermal collagen fibres [27]. However, this view is not consistent with morphological and taphonomic evidence [1,28] and is not widely accepted.

New visualisation techniques, such as laser-stimulated fluorescence [29], can reveal otherwise invisible macro- to microscopic details of fossil feathers. Other microscopic and chemical approaches have focussed on the preservation of key feather components: CBPs, keratin, and melanin [30–33]. In feathers of extant birds, a fibrous matrix of CBPs and keratins envelopes melanin-rich organelles called **melanosomes**; in certain taxa, this fibrous matrix is infused with non-melanin pigments. CBPs are extensively cross-linked via disulfide bonds, conferring chemical stability [34]. Claims of preserved chemical evidence for CBPs and keratins, forming the fibrous matrix [36] are controversial [35,37], especially evidence from immunohistochemistry [36], the applicability of which to fossils has not been verified. Infrared spectroscopy can also yield evidence of keratinous residues in ancient feathers [4]. Organic matrices surrounding fossil feather melanosomes have also been interpreted as fibrous matrix residues [32,38,39], but this is disputed [37]. One of the latter studies, however, did not test for CBPs or keratin residues [37]. However, **taphonomic experiments** reveal that feather parts, which are mostly made of CBPs, can survive under certain conditions where melanosomes are destroyed [40]. A potentially important technique is synchrotron-aided sulfur spectroscopy (XANES), which yields useful information on fossil feather chemistry, especially the degradation of sulfur-bearing feather proteins [31].

Early studies suggested that preservation of fossil feathers as carbonaceous compressions resulted from bacterial **autolithification** based on association of microbe-like microstructures with fossil feathers. Following a landmark reinterpretation of these features as fossil melanosomes [30], fossil colour has emerged as a new field in palaeobiology. The feathers of diverse fossil birds and nonavian dinosaurs preserve melanosomes [28,38,39,41–43], the size and shape of which can be used to infer original melanin-based coloration, ecology, and behaviour [38,39,41]. Such colour reconstructions are, however, partial [38,41]; non-melanin pigments, for example, carotenoids, commonly co-occur with melanosomes in feathers of extant birds. Attempts to recover evidence for non-melanin pigments in fossil feathers have thus far been unsuccessful [44].

Intriguingly, maturation experiments have shown that melanosomes shrink during fossilisation [32], but perhaps not enough to impact dramatically on inferred colours [45]. Future studies of original feather colour will require careful analysis of melanosome origins; melanosomes are widespread in vertebrate internal organs [46].

Physical data on fossil melanosome preservation are increasingly supported by chemical evidence for preservation of the melanin molecule [47–49]. Fossil feathers vary widely in chemistry [50]; this may relate to taxonomic factors [50], but the impact of **diagenesis** has not been explored fully. Fossilisation of melanin (and melanosomes) has been attributed to the high resistance of melanin to microbial degradation and hydrolysis [49], but diagenetic incorporation of sulfur (sulfurisation) is also important in preservation [51]. Key elements, including copper and zinc, are enriched in melanosome-rich regions of fossil feathers [31,52]; associated chemical spectra indicate that these metals are chemically bound to, and, thus, are biomarkers for, melanin. Even standard light and electron microscopy can inform on melanin distributions in fossils: the visible hue of fossil feathers correlates with melanosome concentration [53].

Despite the exhaustive literature supporting the preservation of fossil melanin and melanosomes, not all researchers are convinced, claiming that a microbial origin cannot be

Rachis: feather structure that bears the barbs, which may be very short in down, but well developed in contour, tail, and wing feathers.
Remiges: wing feathers.
Reticula: bumps or tuberculate scales on the sole of the foot or palm of the hand in reptiles and birds.
Retrices: tail feathers.
Synapsid: member of clade Synapsida, including mammals and all their ancestors, sometimes called 'mammal-like reptiles', back to the Carboniferous.
Taphonomic experiments: controlled, often laboratory-based, experiments investigating the processes of fossilisation: decay, mineralisation, and/ or maturation of organic matter
Taphonomy: the study of how organisms decay and become fossilised.

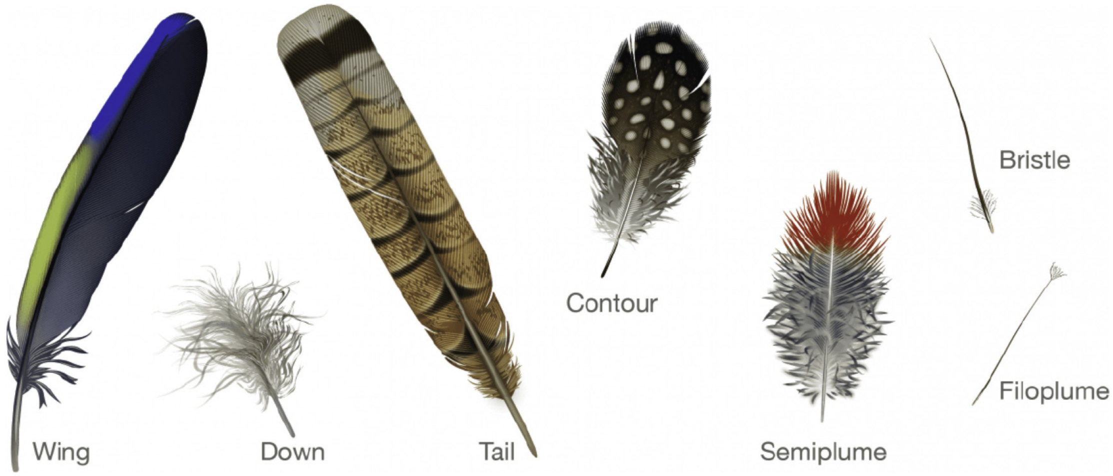

Figure 1. The Seven Types of Feather Seen in Modern Birds. Image courtesy the Cornell Bird Academy.

dismissed [35,54,55]. However, arguments that bacteria readily fossilise [35,55] do not apply to the carbonaceous compression fossils from Jehol (China) and other **Lagerstätten**, because bacteria are not known to fossilise as organic remains in compression fossils. Similarly, claims that the sparse distribution of melanosomes in some modern feathers are inconsistent with densely packed melanosomes in fossils do not consider that melanosomes might be concentrated during fossilisation as a result of the collapse and compaction of feather tissues [46].

An alternative approach to understanding feather evolution focusses on feather-associated anatomical structures in the skin; recent fossil evidence reveals acquisition of anatomically modern features of the epidermis even in taxa with primitive feathers and a burst of innovation in feathered skin during the late Early Jurassic [56]. How do all these new fossil discoveries relate to our current understanding of genomic regulation?

Genomic Regulation of Feather Development

A dense pattern of cutaneous appendages covers the body of vertebrates. These include tooth-like scales (denticles or **odontodes**) in chondrichthyans (sharks and rays) and mineralised dermal scales in actinopterygians (bony fish). Odontodes comprise a base of bone-like tissue and a dentine cone covered by a hypermineralised layer secreted by the epidermis [57]. Alpha-polypeptides of keratins are an evolutionary novelty of vertebrates [58], while CBPs, the toughest natural polymers known [8], are fibrous proteins associated with keratins that are present only in the cutaneous appendages of reptiles and birds. A burst of duplication in the CBP genes of Archosauria is the only signal of innovation at the protein level in feather origins [59].

All vertebrate integumentary appendages develop from an epithelial **placode**, associated with dermal cells (Figure 2). Placodes develop by a patterning process, established through the distribution of activating and inhibiting molecules [60]. Such molecular control must date back to the origin of vertebrates over 500 Ma, because all living and fossils vertebrates show scalation, plumage, or fur (Box 3). Indeed, genomic comparisons show that protein-coding regions involved in placode patterning are part of an ancient developmental toolkit [59]. Developmental studies show that conserved ectodermal–mesenchymal signalling pathways, mostly Wnt and Eda-Edar, lead to placode formation. In zebrafish and the bearded lizard, mutations in the Eda-Edar pathway lead to the absence of scales and teeth [66,67], as well as deficient hair and teeth in humans. The targets of Eda include diverse signalling pathways, such as FGF20 and Shh, regulating the growth of the placode, making Eda-Edar a key initiator. Moreover, 32 genes in the feather gene set were identified as present in the amniote ancestor [59]. The homology of messages leading to cutaneous appendage formation was established from early recombination experiments between embryonic epidermis and dermis from lizard, chick, and mouse [68]

In addition to feathers, some birds carry scales on their legs [69], as in some theropod dinosaurs [70], and on the legs and tail of the ornithischian dinosaur *Kulindadromeus* [1]. During theropod evolution, leg feathers became reduced from the foot to thigh, and scales replaced them [70]. Likewise, such scales are present together with hair in a Cretaceous mammal [71], as well as over the whole body in the pangolin or along the tail in rodents, such as rats and mice. These scales are commonly interpreted as primitive holdovers from reptilian ancestors, but palaeontological and genetic evidence suggests that they are secondarily derived from feathers or hairs.

Evo-devo experiments [7,72,73] show that feathers are the default outcome in modern birds, and feather development has to be inhibited for leg scales to appear. This inhibition of feather growth depends on inhibition of the Shh pathway, which is partially lost in breeds with feathered feet [73]. Moreover, experiments show that the molecular profiles of chick scales are similar to chick feathers, but different from alligator scales [74]. The final architecture of scales, feathers, and hairs may be generated by patterns of similar signalling pathways, but differentially expressed in time and space. Experiments [68] showed that, when the time of culture was expanded, scales were formed in the lizard epidermis, arrested feathers with disorganised barb ridges (despite the absence of a cylindrical follicle) in the chick epidermis, and elongated hair buds that never organised into hair follicles in the mouse epidermis.

During bird morphogenesis, when the feather bud elongates as a hollow tube, its base invaginates in the skin and forms a cylindrical wall, which cornifies to form the calamus. On top of it, the epidermal wall is divided into several units, the barb ridges. The number of barb ridges and rachis formation are regulated by the dermal pulp, as shown by heterospecific recombinations between chick and duck [75]. The molecular pathways involved have been intensively studied (e.g., [61,62]). Barb ridge formation appears to be regulated by BMP and Noggin, and barb growth by Shh, while a high BMP:Noggin ratio leads to rachis formation by fusion of barb ridges. The mesenchyme key regulators of pennaceous feathers involve a multimodulatory network, including GDF10, and GREM1, and the retinoic acid gradient modulates barb–rachis angles.

The pennaceous feathers of coelurosaurian theropods, including birds, are the most complex cutaneous appendages ever found. By contrast, scales are simple. In the chick, the large scales or scuta that cover the dorsal foot express a limited set of CBPs associated with keratins, while the bumps or **reticula** of the plantar surface contain only keratins. Reticula were shown to be feathers that had been blocked at their initiation step [73]. In areas such as the amnion, cornea, or plantar pads, the formation of feathers in birds or hair in mammals is prevented early during embryogenesis, but is readily reversed by adjusting the Wnt-BMP-Shh pathways [72,76]. Both imply not only epidermal plasticity and default competence, but also conserved mechanisms, which might have been present in the first amniotes (amnion), tetrapods (plantar skin), and chondrichthyan and actinopterygian fish (cornea).

Aside from the burst of duplication of CBPs, protein evolution appears to have a limited role in feather origins. All the different tools and pathways were already present at least in the amniote ancestors [59] perhaps in all tetrapods or even the first vertebrates. Likewise, the toolkit to build epidermal scales was likely present in the ancestors of land vertebrates, and scales might have formed several times along different evolutionary branches. The absence of feathers in giant dinosaurs might be a disappearance linked to their size. It should be noted that the African elephant has lost most of its hair, but instead shows an intricate network of microchannels adorning the epidermal stratum corneum [77].

Box 1. Fossil Feathers: Unexpected Morphologies

When feathers were first identified in dinosaur specimens from China [2,13–15], their morphologies matched the feather types known from modern birds (Figure 1). However, palaeontologists increasingly realised that some of the fossil feather morphologies could not be matched in living birds. For example, the ribbon-like feathers of the oviraptorosaur theropod dinosaur *Similicaudipteryx* from the Early Cretaceous of China [9] were entirely unexpected, comprising an elongate ribbon-like rachis with a pennaceous tip, with neatly organised, radiating barbs (Figure IA–D,L). Similar ribbon feathers are known in some basal birds, especially in the tail, and may have mainly operated as display structures that could be erected and rattled.

The simple bristle type of feather (Figure IE), while widespread among theropod dinosaurs, was lost in most birds, as were the brush feather (Figure II) and ribbon-like feather (Figure IL). The reasons for these losses are uncertain.

More widely among dinosaurs, other kinds of bristle and multiply branching feather have been noted. For example, the ornithischian *Psittacosaurus* sports a ‘fence’ of ~100 cylindrical bristles along the midline of its tail, each up to 160 mm long [16]. The heterodontosaurid ornithischian *Tianyulong* [17] also had bristles along its back. Most dramatically, the Middle Jurassic ornithopod *Kulindadromeus* from Siberia [1] shows a great range of feathers and scales of all sizes, including monofilaments around the head and thorax (Figure II). The most complex feather type present comprises a basal plate from which five to seven slender filaments emerge. The basal plates are arranged in regular patterns over the surface of the skin, and the filaments run backwards (Figure IIA). The scales were unexpectedly large and widely distributed: rhomboid scales in neat arrays up and down the legs, and broad scales above and below the tail. The describers [1] suggested that these were not ‘primary’ scales, meaning inherited unchanged from ancestors, but some at least were likely secondarily derived from feathers, just as chicken scales and pangolin scales are said to be secondary.

Diverse feathers throughout theropods and birds, and then in ornithischian dinosaurs, led the describers to speculate that feathers might have originated at the base of Dinosauria rather than within Theropoda [1,2]. This appears to have been confirmed by the report of four kinds of feather in pterosaurs [4], the sister group of dinosaurs (see Box 2).

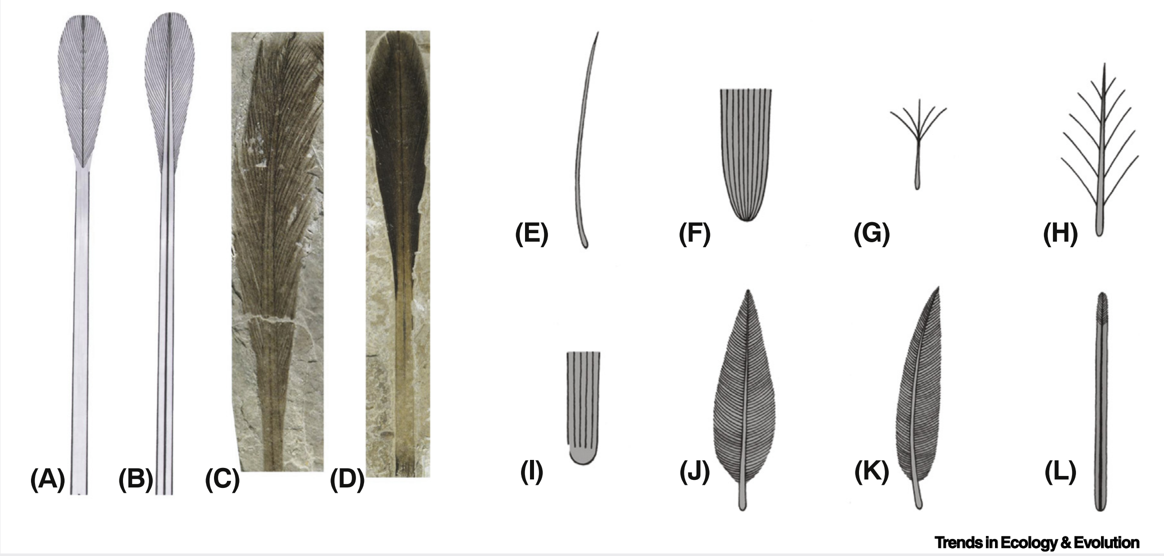

Figure I. Diversity of Fossil Feathers. Some dinosaurs had feathers not seen in modern birds. For example, some theropods and extinct birds had ribbon-like feathers with expanded tips, seen in the oviraptorosaurian theropod *Similicaudipteryx* (A), an unnamed maniraptoran (B), an enantiornithine bird (C), and a confuciusornithid bird (D). The diversity of feather types seen in theropod dinosaurs (E–L) includes some morphologies (E, I, and L) not seen in modern birds. Images courtesy Xu Xing.

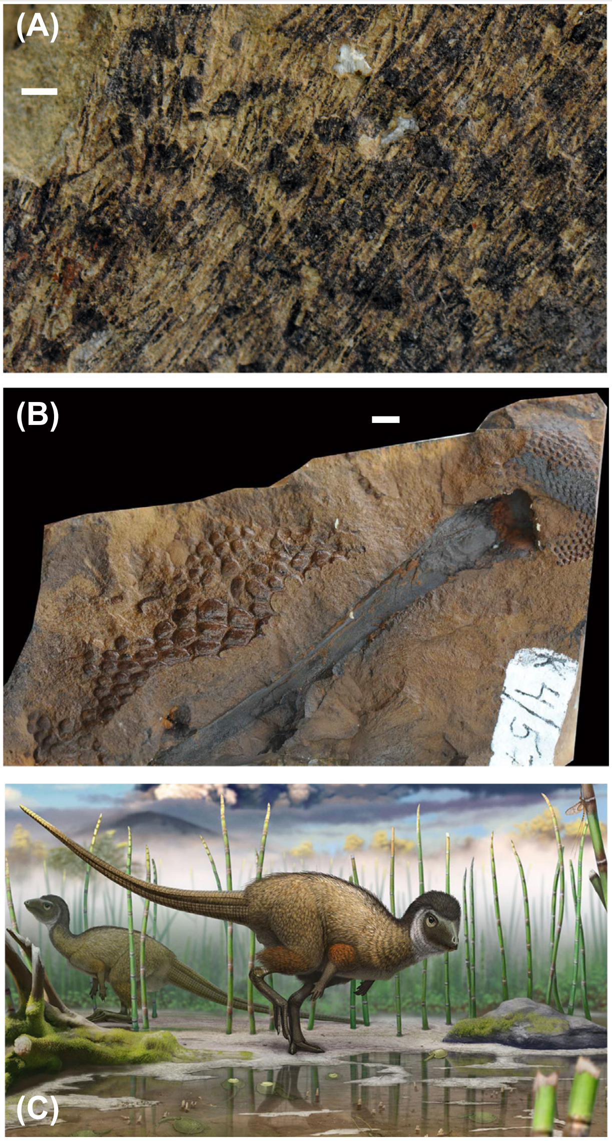

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Figure II. Feathers and Scales from the Ornithischian *Kulindadromeus*. (A) Feathers, comprising a basal plate and six or seven feather barbs trailing backwards from the region of the femur. (B) Two types of large scales from the leg, some beside the tibia in the shin, and smaller scales (right) over the knee. The feathers are of a type not seen in modern birds, and the substantial scales over the legs and tail are likely secondarily derived from feathers in these areas of the body. (C) Life reconstruction by Andrey Atuchin. Scale bars: 1 mm in (A, B). Images courtesy Pascal Godefroit.

Feather Evolution

With a rich fossil record, and a robustly supported phylogenetic tree, it is possible to reconstruct the key stages in feather evolution. Most cladistic analyses concur that Pterosauria is nearest major sister group of Dinosauria [78,79]. The recent [80] rearrangement of the relationships of the three key dinosaurian clades does not affect the analysis of timing of feather origins.

If feathers occur across dinosaurs and pterosaurs, then their origin has to be sought minimally during the Early Triassic, some 250 Ma (Figure 3). Close outgroups of Dinosauria were already

Box 2. Pterosaur Feathers

The first fossil epidermal structures were identified in some exceptionally preserved pterosaur specimens as long ago as 1831 [18]. This first record was in a specimen of *Scaphognathus*, and then stitch-like pits were described in a specimen of *Rhamphorhynchus*, which were later interpreted as remnants of a covering of hair. Hair- or fur-like structures were subsequently reported in specimens of *Anurognathus*, *Pterodactylus*, and *Dorygnathus*, most from the Upper Jurassic Solnhofen Limestone of southern Germany, the source of the 'first bird' *Archaeopteryx* with its feathers. The pterosaur fluff was preserved as external moulds, and these fossils were often challenged as taphonomic or even artificial products [19].

It took a long time before pterosaur fluff was noted from another locality. During the 1970s, the pterosaur *Sordes* was reported from the Upper Jurassic Karatau Formation of Kazakhstan, bearing extensive fibres preserved as carbonaceous impressions, which were interpreted as hair-like structures [20]. The fibres in the wing membranes were subsequently reinterpreted as decomposed actinofibrils, while those in the other areas were accepted as pelage [21]. With discoveries of exceptionally preserved hair-like structures in several specimens of *Jeholopterus*, *Pterorhynchus*, *Gegepterus*, and an undetermined genus from the Middle–Upper Jurassic Haifanggou and Lower Cretaceous Yixian formations in northeast China since the early 2000s [22–24], pterosaurs with hair-like integumentary coverings have been widely accepted. Some densely aligned pinnate fibres that formed distinct tufts in a diamond- and V-shaped pattern covering the wing were interpreted as protofeathers [23].

However, their interpretation was questioned by Kellner [25], who named the hair-like structures **pycnofibres** to differentiate them from mammalian hair and avian feathers. Most recently, four types of pycnofibre were identified in two anurognathid pterosaur specimens [4] (Figure IA). They demonstrated that pycnofibres share key characteristics with feathers: a tube-like structure of the calamus, melanin-containing melanosomes throughout the barbs, and morphologies that include three kinds of branching structure. These findings confirm that pterosaurs had a dense filamentous covering that likely functioned in thermoregulation, tactile sensing, signalling, and aerodynamics, and such structures are found in all main clades (Figure IB). This interpretation, that pterosaurs carried feathers, an innovation shared with their sister group, the dinosaurs (including birds), is likely to be controversial.

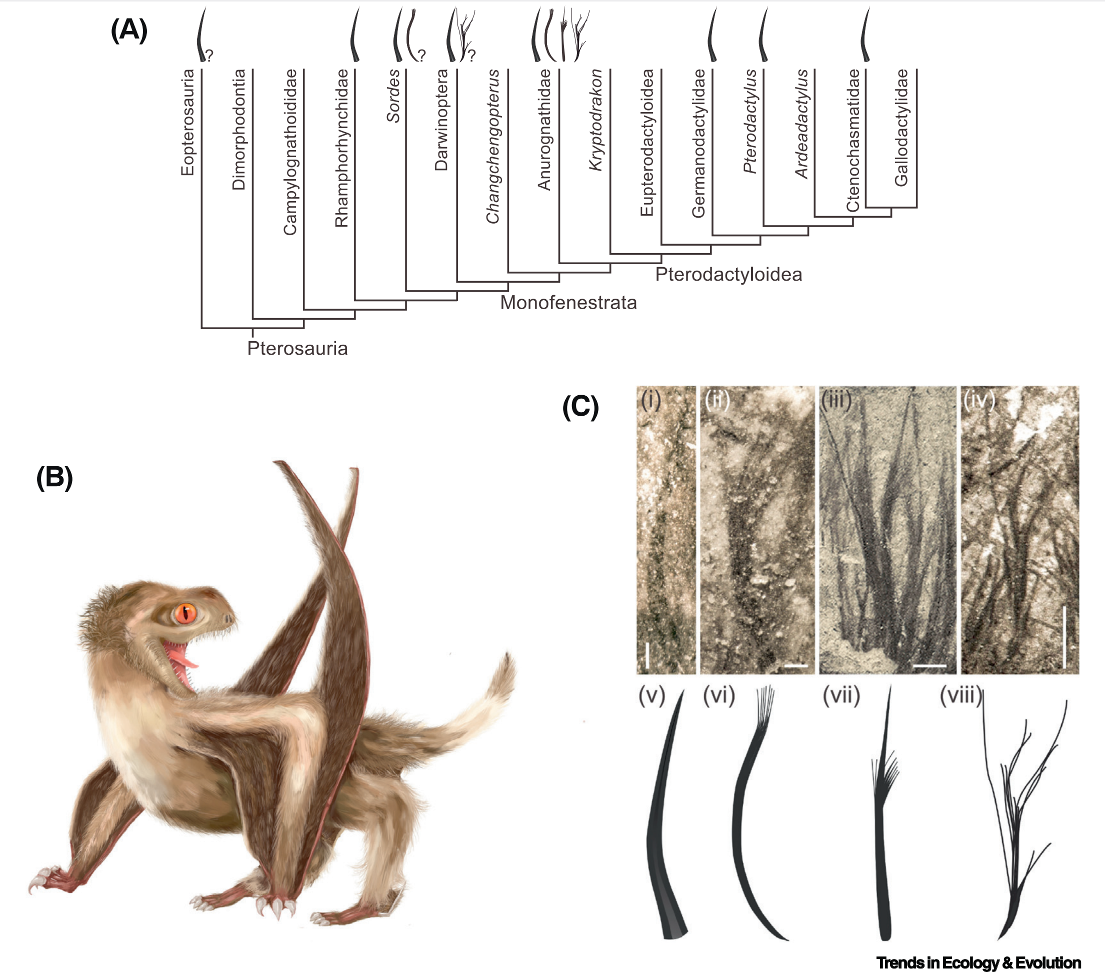

Figure I. Pterosaur Feathers. (A) Simplified phylogeny of pterosaurs, showing the occurrence of fossilised fluff (= pycnofibres, = feathers) throughout the group; silhouettes are explained in (C). (B) An anurognathid pterosaur from the Middle Jurassic of China, from which the four feather types were identified [4]. (C) The four feather types: monofilaments (i and v), tufted monofilaments (ii and vi), bunched fibres (iii and vii), and down feathers (iv and viii). Art by Yuan Zhang (C).

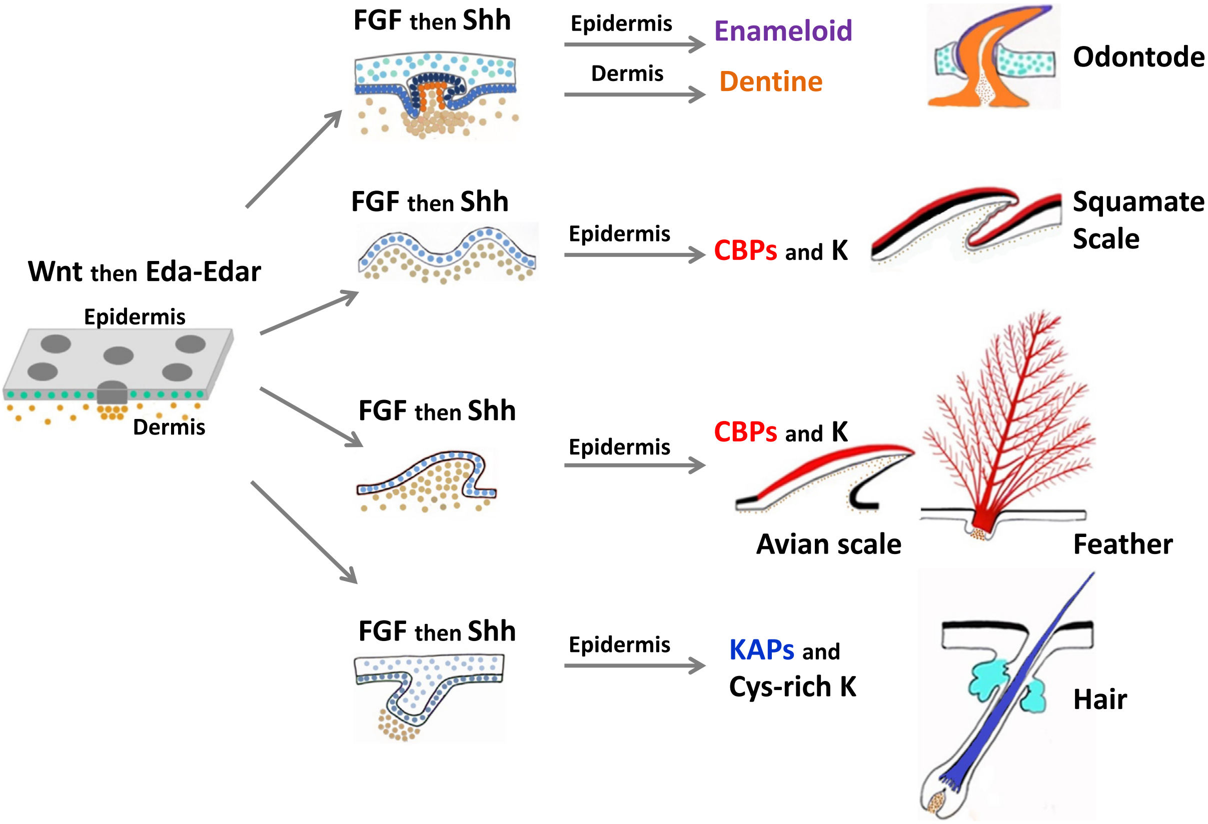

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Figure 2. Developmental Pathways of Denticles, Scales, Hair, and Feathers, and Their Genomic Regulation. Absence of Wingless-integrated (Wnt) activation prevents placode initiation of all types of appendage, in all species. The ectodysplasin A [Eda-Eda receptor (r)] pathway is activated downstream of Wnt signalling. The placodes express the receptor Edar, while the interplacodal epidermis expresses Eda. Edar triggers, among others, fibroblast growth factor (FGF) and Sonic hedgehog (Shh) signals, which are required for the formation of the dermal condensation and the growth of the placode, respectively. Thus, the anatomical starting points of all these structures are shared, as are the genome regulatory pathways and basic biochemistry, across various major groups of vertebrate. According to clade, those interactions produce odontodes (skin denticles), scales, feathers, or hairs in sharks, lizards, birds, and mammals, respectively. Abbreviation: K, keratin.

established at the end of the Early Triassic [81,82], even though convincing fossils of dinosaurs and pterosaurs are not known before the Late Triassic

This then shifts the origin of dinosaurs and pterosaurs back into a time of considerable disruption of Earth and life, the 8-Myr span of recovery from the end-Permian mass extinction [83,84]. Massive volcanism across the Permian–Triassic boundary, 252 Ma, led to a series of environmental catastrophes, including rapid global warming, acid rain, mass wasting, and ocean stagnation and acidification, which drove >90% of species on land and in the sea to extinction. These sharp environmental perturbations were repeated several times through the Early and early Middle Triassic, from 252 Ma to 244 Ma [85], and the recovery of life was initiated and quashed several times. Modern-style ecosystems emerged at the end of the maelstrom, comprising ancestors of many modern groups (e.g., lissamphibians, turtles, lizards, crocodilians, dinosaurs, and mammals)

Several studies show how medium-sized vertebrates on land enhanced their physiological and ecological pace with higher metabolic rates and greater ability to acquire food. For example, abundant fossil trackways from around the world show a shift from sprawling to erect postures across the Permian–Triassic boundary [86,87]. Bone microstructure shows that Triassic

Box 3. The Genomic Instructions for Making Feathers Originated a Long Time before Feathers

Comparative study of vertebrates shows that genes associated with feather development existed long before the origin of Dinosauria [59]. Out of 193 feather-related genes, examples of conserved nonexonic elements (CNEEs), 67 are involved in making CBPs (formerly β-keratins) that comprise the feather, and 126 in governing feather skin patterning, as well as feather architecture (e.g., formation of calamus, rachis, barbs, and barbules). When did they originate?

The molecular pathways responsible for feather initiation and morphogenesis [61,62] are present in all vertebrates because the formation of patterned dermal structures, such as teeth, mineralised or epidermal scales, hairs, and feathers, are all governed by the same regulatory pathways [7]. The set of genes that establish the pattern of placodes that underlie denticles, scales, hairs, and feathers existed in the common ancestor of all vertebrates ~520 Ma. Likewise, the balance of expression of the genes *Shh* and BMP, which regulates the choice between plantar tissues and the rest of the body skin in birds and mammals, must have been present in the first tetrapods 340 Ma, given that plantar bumps (reticula) are present in a basal ornithischian [1].

As for the structural proteins that comprise the feather, keratins (formerly α-keratins) appear with the first vertebrates and CBPs appear with reptiles (Figure I). The duplication of keratin genes might have occurred first with the origin of Amniota 320 Ma, and then notably with the ancestor of Mammalia. The feather CBP subfamily was classically assumed to have evolved from the scale CBP subfamily through a deletion event followed by gene duplication [63]. However, feather genes might be basal to avian scale genes, because the diversification between feather and nonfeather CBPs originated deep in archosaur evolution, before the split of the crocodilian and avian lineages [64]. The expansion of the feather CBP genes, a burst of duplication giving rise to >150 genes, accompanied the evolution of feathers in Theropoda [65].

The sequence of acquisition of key genes (Figure I) suggests that a full complement of feather-patterning genes had been acquired by the origin of Amniota, followed by a burst of CBP gene duplication, corresponding to the stabilisation of ~86% of feather-regulatory CNEEs, both at the origin of Archosauria some 250+ Ma. The postulated timing of early feather origins from fossils [4] corresponds to this age.

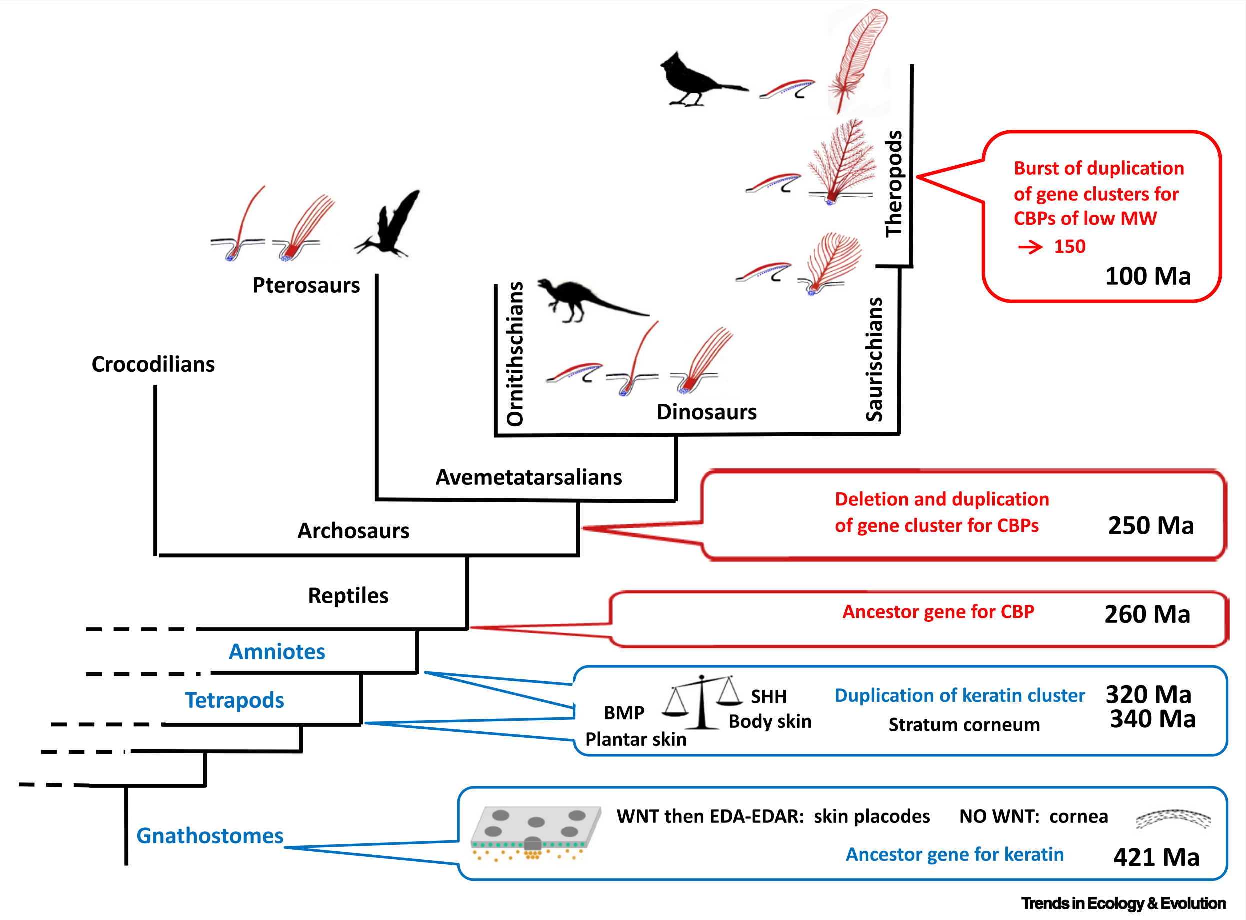

Figure I. Major Genomic Events Underlying the Origin of Feathers. The simplified phylogeny of vertebrates shows key points at which regulatory genes concerned with the formation of keratins and corneous β-proteins (CBPs) in patterned dermal structures emerged. Keratin regulation had already emerged with jawed vertebrates, the gnathostomes, 421 million years ago (Ma) and control of the distinction between plantar and regular dermis with the tetrapods or amniotes, 340–320 Ma. Key components for the generation of CBPs emerged with the origin of reptiles, especially at the origin of archosaurs, over 250 Ma. Abbreviation: MW, molecular weight.

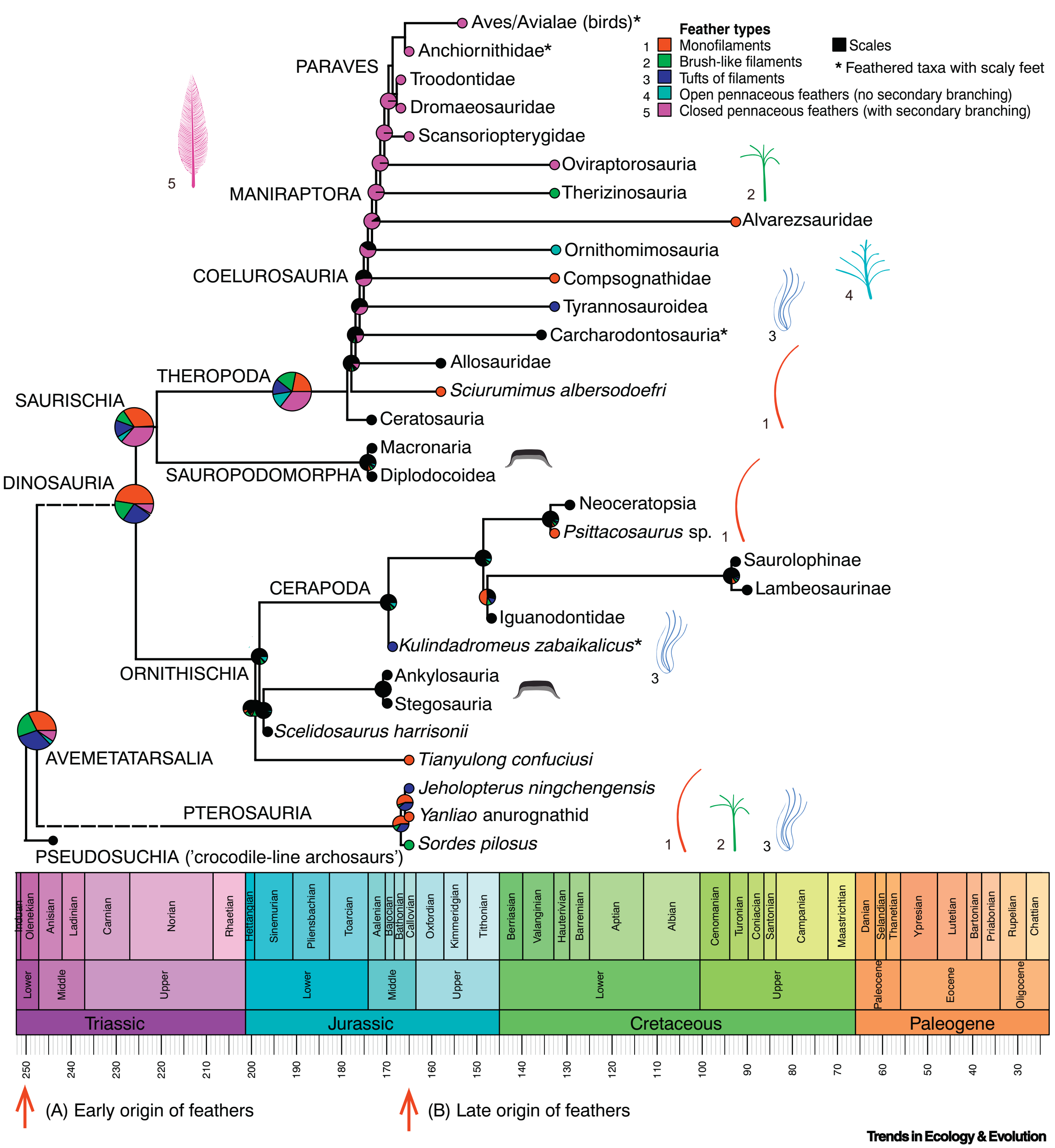

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Figure 3. Macroevolution of Feathers. The phylogenetic tree shows the major groups of dinosaur (above) and pterosaurs (below), scaled against geological time. The tree represents a best estimation of ancestral states (shown as probabilities of different states in the pie charts) of scales and feathers throughout the phylogenetic tree, from a computational analysis [4]. Each of five feather morphologies, numbered 1–5, and scales, are shown based on fossil evidence for each major group. The ancestral state reconstruction shows a combination of monofilaments, tuft-like filaments, and brush-type filaments as the ancestral state for Avemetatarsalia and Dinosauria. Some dinosaurs and birds have scaly feet, which probably reflect a secondary modification of feather primordia to scales. The estimated ancestral state for Theropoda comprises all five feather states. Two hypotheses for the timing of avian feather origins are indicated: early origin, at the base of Avemetatarsalia during the Early Triassic (A) or late origin, at the base of Maniraptora during the Early–Middle Jurassic (B).

archosaurs and synapsids had small cortical canals and cell lacunae, indicating they had small red blood cells and high aerobic capacity [88]. Bone microstructure also indicates fast growth rates in Early and Middle Triassic archosaurs, just as in dinosaurs and pterosaurs, and more like those of birds than crocodilians [89–92]. Oxygen isotopic measurements from fossil bones suggest that endothermy evolved in synapsids, possibly multiple times, during the Middle or Late Permian [93]. Dinosaurs, pterosaurs, and their ancestors all show postcranial skeletal pneumaticity, evidence for supplementary air sacs and unidirectional air flow, as in birds [94], suggesting they all had increased activity levels and endurance. These fundamental postural and physiological changes are linked in that upright posture enabling an animal to breathe while running (sprawling lizards must either breathe or run). They evolved in parallel in the two great Triassic terrestrial tetrapod lineages (archosaurs and synapsids), which confirms that ecosystems operated at a different pace from Permian ecosystems, and high activity levels and speed were essential in the predator–prey arms races.

It is no surprise then that synapsids from the Late Permian onwards [93,95], and archosaurs from the Early Triassic onwards bore insulating pelage, whether hair or feathers. The endothermy of pterosaurs and dinosaurs, and indeed their **avemetatarsalian** ancestors [94], indicate the likelihood of an insulating epidermal covering of some kind, especially in the smaller (<2-m body length) species that could not rely on mass homeothermy. Therefore, ancestral state reconstructions [95], fossil finds [88–91,94], and isotope studies [93] confirm endothermic physiology probably from the beginning of the Triassic in both avemetatarsalian archosaurs and synapsids. Feathers in pterosaurs [4] extends their origin to the Early Triassic, coincident with all the other physiological and locomotory changes; feathers likely evolved initially to provide insulation in the warm-blooded small precursors of dinosaurs and pterosaurs.

The diversification of feather types is not fully understood (Figure 3). At present, we can suggest that pterosaurs and ornithischians had a variety of simple feather types, none of them with a contour or aerodynamic function, but simple monofilaments, bristles, quills, and tufted and bunched filaments, all probably for insulation. In the ceratopsian *Psittacosaurus*, the cornified bristles stand up straight on the tail, and so were likely used for display [16]. Feathers have not been identified in the armoured ankylosaurs or stegosaurs among ornithischians, or in the sauropodomorphs. It will be interesting to determine whether early nonarmoured thyreophorans and smaller sauropodomorphs might have had feathers before they were either crowded out by either their bony armour plates or giant size. Theropods show a greater diversity of feather types, and the clade Coelurosauria, originating during the Late Triassic, shows the same simple feather types as ornithischian dinosaurs and pterosaurs, but members of Maniraptora (Figure 3) also show pennaceous feathers, as seen in modern birds.

Concluding Remarks

Recent work in the developmental biology and palaeontology of feathers has changed our views and opened many new questions (see Outstanding Questions). The new work concurs that these remarkable innovations originated long before the origin of birds, even before the origin of dinosaurs. This does not diminish the importance of feathers as key to the success of birds, but shows that birds did not emerge rapidly from reptiles, but that their set of 30 or more adaptations [78] accumulated stepwise over some 100 Myr. Furthermore, it is inadequate to say that feathers evolved from reptilian scales, as both morphogenesis [72] and CBPs [64] of feathers are basal to those of avian scales, and that the molecular profiles of avian scales are similar to feathers, but different from reptilian scales [74]. Future studies incorporating taphonomic data will shed light on key evo-devo questions relating to the origins of the feather follicle, alpha keratins, CBPs, and of coloration mechanisms, especially those relating to eu- and phaeomelanin [96].

Outstanding Questions

Were feathers present in nonavemetatarsalian archosaurs (i.e., crocodilian ancestors)?

Was insulation the initial function of feathers?

How can the camouflage and display functions of feathers be tested in fossils?

What were the functions of the feather types known only in fossils, and not in modern birds?

How did feathers evolve in different groups of pterosaurs, dinosaurs, and birds?

Melanin occurs in protofeathers, but when did the diversity of other pigments appear in feathers?

When did feathers acquire nanostructural adaptations to give iridescence?

What are the genomic regulatory networks behind all these changes?

Evidently feathers, endothermy, and erect gait all arose together in the Early Triassic ancestors of dinosaurs and pterosaurs; thus, the small dinosaurian ancestors of birds were pre-adapted for a life as active flyers. The Early Triassic, some 250 Ma, was a time of evolutionary turmoil, as life recovered from the greatest mass extinction of all time at the end of the Permian, 252 Ma, and was repeatedly perturbed by further crises over a span of 8 Myr. The new terrestrial ecosystems of the Early and Middle Triassic, dominated by archosaurs and synapsids, including ancestors of birds and mammals, respectively, were higher energy than Palaeozoic ecosystems. In studying feather development and function, we jump back 80 Myr and consider their role at a very different time, long before the first birds, such as *Archaeopteryx*, came on the scene.

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