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The early origin of feathers

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[Abstract]
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 finds 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, endothermy), as part of a major resetting of terrestrial ecosystems following the devastating end-Permian mass extinction.

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 **non-avian dinosaurs** (see Glossary) also had feathers, including feather types not found in birds today. These discoveries extended the origin of feathers minimally back to about 175 million years ago (Ma), 25 million years (Myr) before the first generally acknowledged bird, *Archaeopteryx*. But this is just a start.

Discoveries of feathers in ornithischian dinosaurs hinted that feathers might be a character of dinosaurs as a whole [1,2], although that has been disputed [5,6]. A startling new discovery [4] shows that even pterosaurs had four kinds of feathers, apparently homologous in form with those of dinosaurs, their closest relatives. Could it be that feathers actually arose about 250 Ma, in 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 fishes, the epidermal scales of reptiles, and the hair of mammals and feathers of birds. Further,

genomic work shows that lizard scales, bird feathers and mammal hairs are the default, and they 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** forms 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 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, did not vary much through geological time from their origins [7].

Modern bird feathers vary dramatically in morphology, which can be assigned to seven types (Fig. 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 about ten to thirty 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 which have hooklets, forming a closed vane that provides streamlined cover to the body), tail feathers (or **retrices**, like contour feathers, and can fan out for flight control or display), and wing feathers (or **remiges**, like the contour and tail feathers, forming a strong wing structure for powered flight).

Among dinosaurs, all these 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 wide range of forms, mostly showing branching barbs, but not always in the simplest monofilaments.

Each of the ten or more described feather morphologies occurs in different parts of the body of the bird or non-avian dinosaur and has a specific function, whether for insulation, display, protection, food gathering, or flight. Further, 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 functions of feathers in fossils can be problematic. Flight feather properties are tuned for stiffness and air capture, while remaining lightweight [10], and they 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, non-avian 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]. Further, some authors have queried whether the fossil structures are indeed feathers, favouring an interpretation as dermal collagen fibres [27]. This view, however, 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 focused 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 the originally keratinous matrix [33,36] are controversial [37], especially evidence from immunohistochemistry [33,36], whose applicability to fossils has not been verified. Infrared spectroscopy can also yield evidence of a fibrous matrix in ancient feathers [4]. Organic matrices surrounding fossil feather melanosomes have also been interpreted as keratinous matrix residues [32,33,38,39], but this is disputed [37]. One of the latter studies, however, did not test for CBPs or keratin residues; another did not use appropriate analytical techniques for detection of CBPs [35]. 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 sulphur-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 non-avian 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, e.g. 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 are thus 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 dismissed [35,54,55]. Arguments that bacteria readily fossilise [35,55], however, do not apply to the carbonaceous compression fossils from Jehol (China) and other **Lagerstätten**, as 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 collapse and compaction of feather tissues [46].

An alternative approach to understanding feather evolution focuses 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 in the late Early Jurassic [56]. How do all these new fossil discoveries relate to 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 fishes). 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 the fibrous proteins

associated with keratins that are present only in 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 (Fig. 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, as 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 in 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 in the ornithischian dinosaur *Kulindadromeus* [1]. In 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 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 sonic hedgehog 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 which 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 a number of units, the barb ridges. The number of barb ridges and rachis formation is 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 multi-modulatory network, including GDF10, and GREM1, and the amount of 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 in embryogenesis but is readily reversed by adjusting the Wnt-BMP-Shh pathways [72,76]. Both imply 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 fishes (cornea).

Aside from the burst of duplication of CBPs, protein evolution appears to play a limited role in feather origins. All the different tools and pathways were already present at least in the amniote ancestors [61] perhaps in all tetrapods or even the first vertebrates. Likewise, the tool kit 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 not only lost most of its hair, but instead shows an intricate network of microchannels adorning the epidermal stratum corneum [77].

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 in the Early Triassic, some 250 Ma (Fig. 3). Close outgroups of Dinosauria were already 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, that drove more than 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 252–244 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 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 enables 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, 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 presumably evolved initially to provide insulation in the warm-blooded small precursors of dinosaurs and pterosaurs.

The diversification of feather types is not fully understood (Fig. 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 presumably 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, nor in the sauropodomorphs. It will be interesting to determine whether early non-armoured thyreophorans and smaller sauropodomorphs might have had feathers before they were either crowded out by their bony armour plates or giant size. Theropods show a greater diversity of feather types, and the clade Coelurosauria, originating in the Late Triassic, shows the same simple feather types as ornithischian dinosaurs and pterosaurs, but members of Maniraptora (Fig. 3) also show pennaceous feathers, as seen in modern birds.

Concluding Remarks

Recent work in developmental biology and palaeontology of feathers 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 and that their set of thirty or more adaptations [78] accumulated stepwise over some 100 Myr. Further, it is too simplistic to say feathers evolved from reptilian scales, as there is evidence some bird and mammal scales evolved from precursor feathers or hairs.

Evidently feathers, endothermy and erect gait all arose together in the Early Triassic ancestors of dinosaurs and pterosaurs, so the small dinosaurian ancestors of birds were preadapted 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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Boxes and figures

Highlights

Feathers are epidermal appendages composed mostly of corneous β-proteins (formerly β-keratins), and 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 fishes, 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 gait and endothermy.

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, that develop adaptations and counter-adaptations against each other.

Autolithification: processes by which bacteria seal and preserve organisms so their soft tissues can be mineralised rapidly

Avemetatarsalians: members of the wider clade that includes dinosaurs (incl. 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: the primary side branch of a feather.

Barbule: the second-order side branch of a barb.

Calamus: the 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: the pit in the skin in which each feather is embedded and provided with nervous and blood supply; 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

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

Odontode: a hard structure in the skin of chondrichthyans (cartilaginous fishes), 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: an embryonic patch in the epidermis or oral epithelium that gives rise to structures such as hair follicles, feathers scales or teeth.

Pycnofibres: the epidermal whiskers and branching structures of pterosaurs.

Rachis: the 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.

Reticulum (pl. reticula): bumps or tuberculate scales on the sole of the foot or palm of the hand in reptiles and birds.

Retrices: tail feathers.

Synapsid: a 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.

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 (Fig. 1). But increasingly palaeontologists 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, consisting of an elongate ribbon-like rachis with a pennaceous tip, comprising neatly organised, radiating barbs (Figure IA–D, L). Similar ribbon feathers are known in some basal birds, especially in the tail, and they may have mainly operated as display structures that could be erected and rattled.

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

More widely among dinosaurs, other kinds of bristles and multiply branching feathers have been noted. For example, the ornithischian *Psittacosaurus* sports a 'fence' of about 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 (Fig. II). The most complex feather type present comprises a scale-like 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 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 seems to have been confirmed by the report of four kinds of feathers 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, L) not seen in modern birds. Images courtesy of Xu Xing.

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: 1 mm scale bars in (A, B). Images courtesy of Pascal Godefroit.

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*, *Dorygnathus* and *Pterodactylus*, most coming from the Upper Jurassic Solnhofen Limestone of southern Germany, 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. In 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 the 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 NE 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 proto-feathers [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, we [4] identified four types of pycnofibers in two anurognathid pterosaur specimens (Figure I(A)). 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 structures. These findings confirm that pterosaurs possessed a dense filamentous covering that likely functioned in thermoregulation, tactile sensing, signalling, and aerodynamics, and such structures are found in all main clades (Figure I (B)). 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]. Art by Yuan Zhang. (C) The four feather types: monofilaments (a, e), tufted monofilaments (b, f), bunched fibres (c, g), and down feathers (d, h).

Box 3. The genomic instructions for making feathers started 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 the corneous β-proteins (CBPs; formerly β-keratins) that make up 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 about 520 Mya. 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 Mya. Plantar bumps or reticula are present in a basal ornithischian [1].

As for the structural proteins that make up the feather, keratins (formerly alpha 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 Mya, and then notably with the ancestor of Mammalia. The feather CBP subfamily was assumed to have evolved from the scale CBP subfamily through a deletion event followed by gene duplication [64]. However, feather genes might be basal to avian scale genes, as the diversification between feather and non-feather CBPs originated deep in archosaur evolution, before the split between crocodilian and avian lineages [65]. The expansion of the feather CBP genes, a burst of duplication giving rise to more than 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 about 86% of feather regulatory CNEEs, both at the origin of Archosauria some 250+ Mya. 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 CBPs in patterned dermal structures emerged. Keratin regulation had already emerged with jawed vertebrates, the gnathostomes, 421 Mya and control of the distinction between plantar and regular dermis with the tetrapods or amniotes, 340 to 320 Mya. Key components for the generation of CBPs emerged with the origin of reptiles, and especially at the origin of archosaurs, over 250 Mya.

Outstanding Questions [box]

Were feathers present in non-avemetatarsalian archosaurs (i.e. crocodilian ancestors)?
Was insulation the initial function of feathers?
How can 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, so 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?

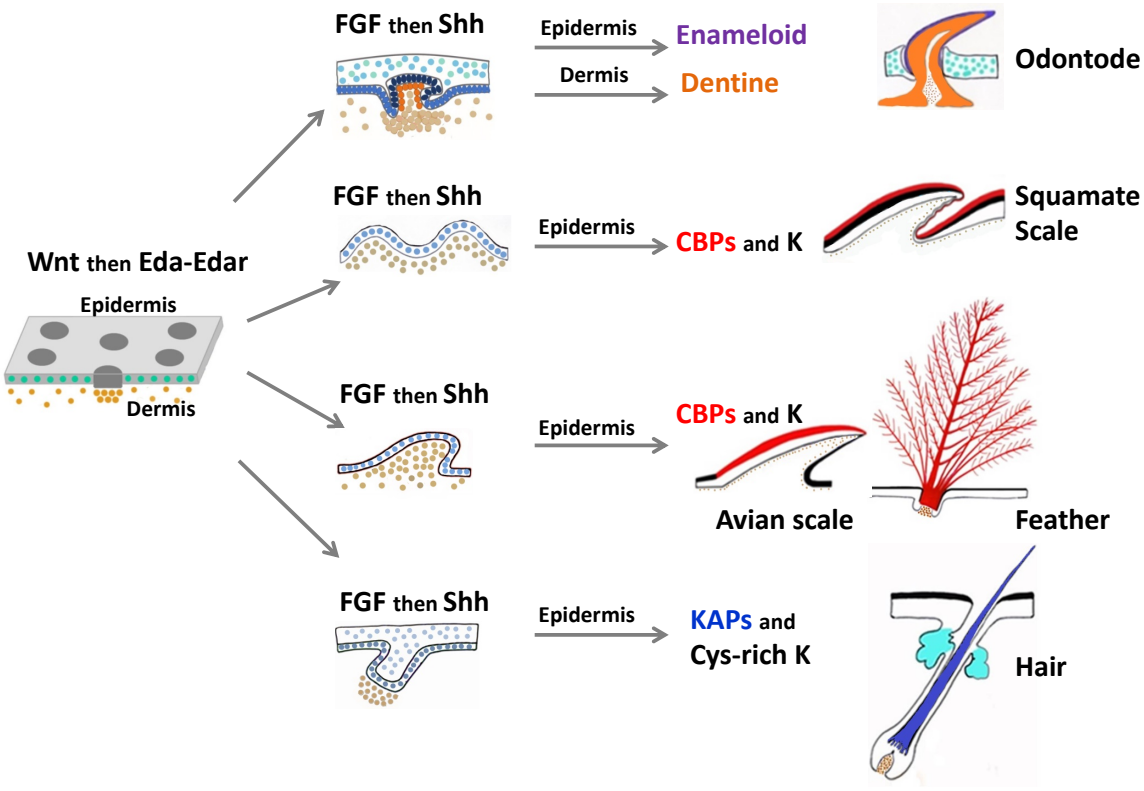
Figures

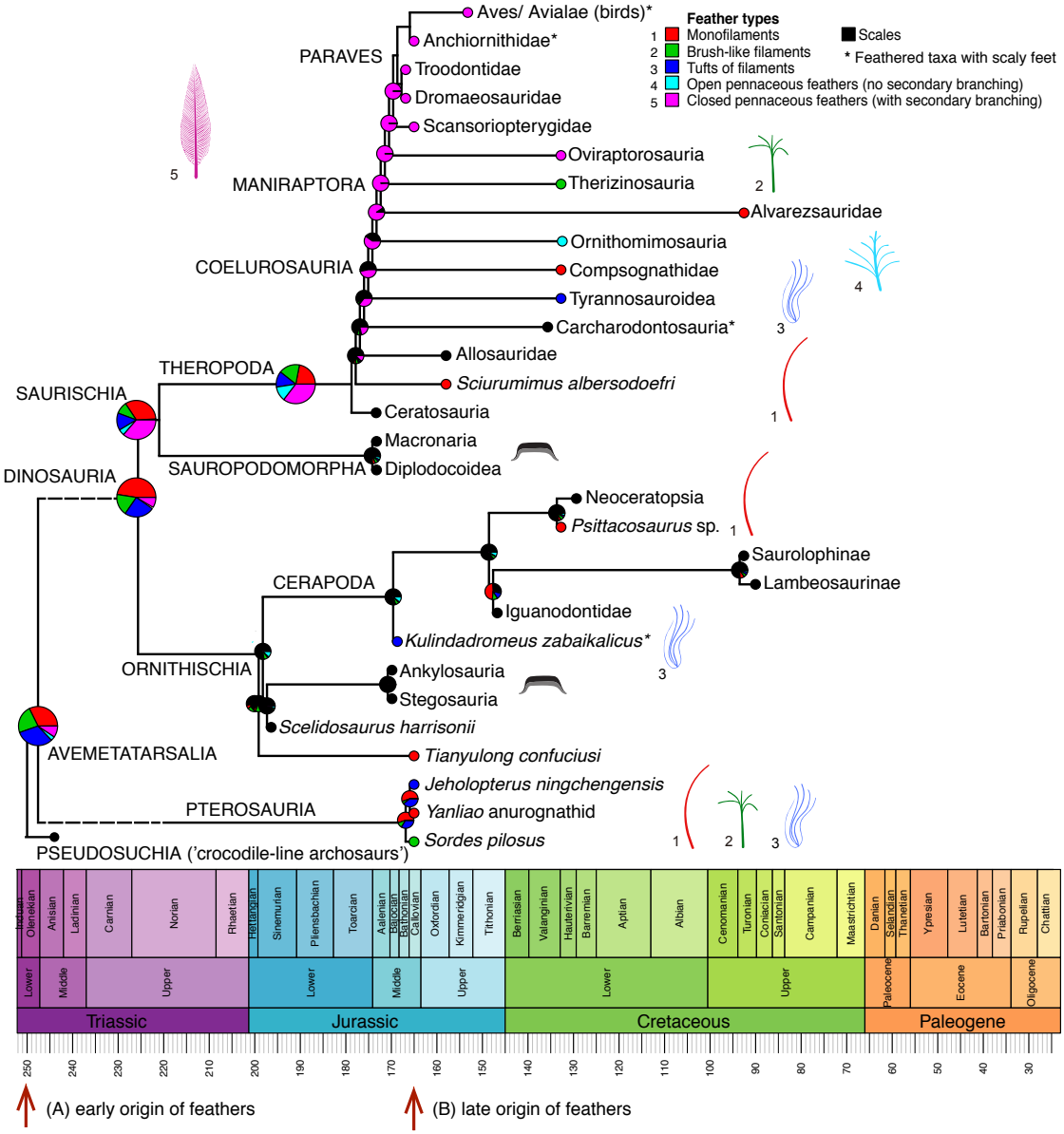
Figure 1. The seven types of feathers seen in modern birds. Image courtesy of the Cornell Bird Academy.

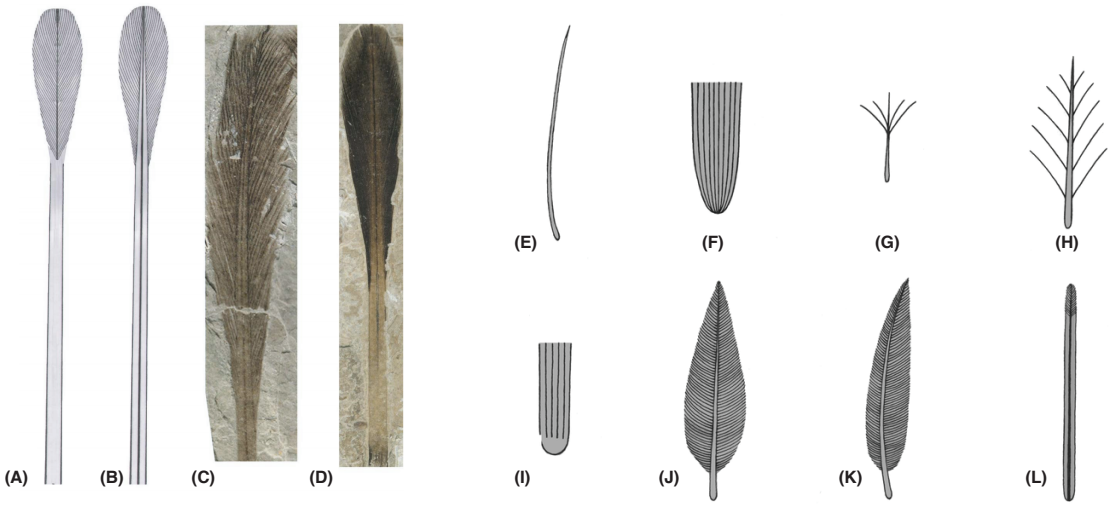
Figure 2. Developmental pathways of denticles, scales, hair and feathers and genomic regulation. Absence of Wnt activation prevents placode initiation of all types of appendages, in all species. The ectodysplasin (Eda-Edar) pathway is activated downstream of Wnt signalling. The placodes express the receptor Edar, while the interplacodal epidermis expresses Eda. Edar triggers among others Fgf and Shh signals, which are required respectively for the formation of the dermal condensation and the growth of the placode. The anatomical starting points of all these structures are thus shared, as are the genome regulatory pathways, and basic biochemistry, across various major groups of vertebrates. According to clade, those interactions produce odontodes (skin denticles), scales, feathers or hairs in sharks, lizards, birds and mammals respectively. Abbreviations of genes: Eda-Edar, Ectodysoplasin A and its receptor R; FGF, Fibroblast growth factor; Shh, Sonic hedgehog; Wnt, Wingless-Integrated.

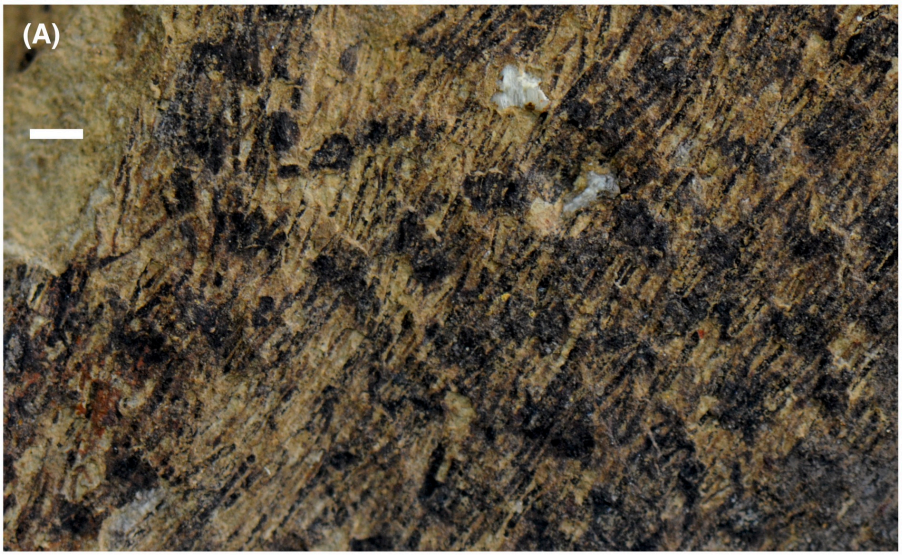
Figure 3. Macroevolution of feathers. The phylogenetic tree shows the major groups of dinosaurs (above) and pterosaurs (below), scaled against geological time. The tree represents a best estimation of ancestral states (shown as probabilities of different states in the pie charts) of scales and feathers 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, probably 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 in the Early Triassic (A) or late origin, at the base of Maniraptora in the Early–Middle Jurassic (B).

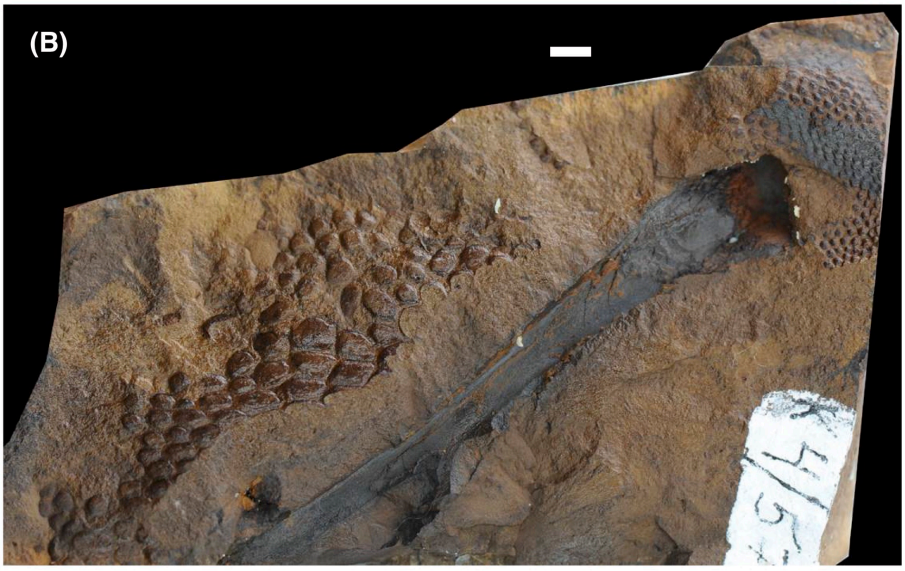

Bristle
Filoplume
Semiplume
Contour
Tail
Down
Wing

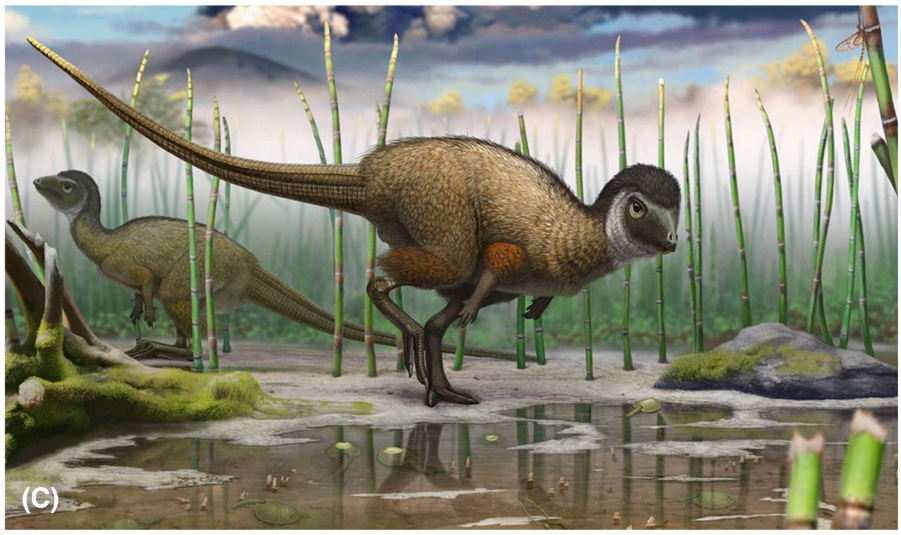

Wnt then Eda-Edar
Epidermis
Dermis
FGF then Shh
Epidermis
Enameloid
Dermis
Dentine
Odontode
FGF then Shh
Epidermis
CBPs and K
Squamate Scale
FGF then Shh
Epidermis
CBPs and K
Avian scale
Feather
FGF then Shh
Epidermis
KAPs and Cys-rich K
Hair

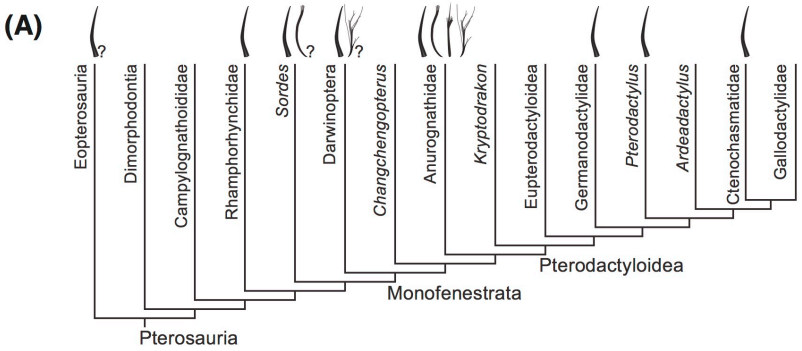

Feather types
1 Monofilaments
2 Brush-like filaments
3 Tufts of filaments
4 Open pennaceous feathers (no secondary branching)
5 Closed pennaceous feathers (with secondary branching)
Scales
* Feathered taxa with scaly feet
Aves/ Avialae (birds)*
Anchiornithidae*
PARAVES
Troodontidae
Dromaeosauridae
Scansoriopterygidae
Oviraptorosauria
Therizinosauria
MANIRAPTORA
Alvarezsauridae
Ornithomimosauria
COELUROSAURIA
Compsognathidae
Tyrannosauroidea
Carcharodontosauria*
Allosauridae
THEROPODA
Sciurumimus albersodoefri
SAURISCHIA
Ceratosauria
Macronaria
SAUROPODOMORPHA
Diplodocoidea
DINOSAURIA
Neoceratopsia
Psittacosaurus sp.
Saurolophinae
Lambeosaurinae
CERAPODA
Iguanodontidae
Kulindadromeus zabaikalicus*
ORNITHISCHIA
Ankylosauria
Stegosauria
Scelidosaurus harrisonii
AVEMETATARSALIA
Tianyulong confuciusi
Jeholopterus ningchengensis
PTEROSAURIA
Yanliao anurognathid
Sordes pilosus
PSEUDOSUCHIA ('crocodile-line archosaurs')
Triassic
Jurassic
Cretaceous
Paleogene
(A) early origin of feathers
(B) late origin of feathers


(A)
(B)
(C)
(D)
(E)
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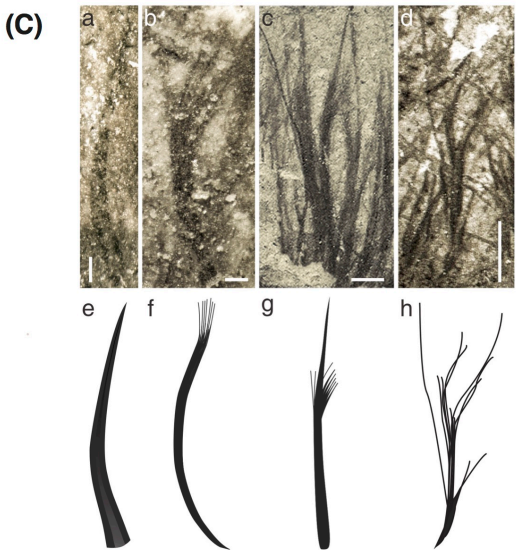

(A)

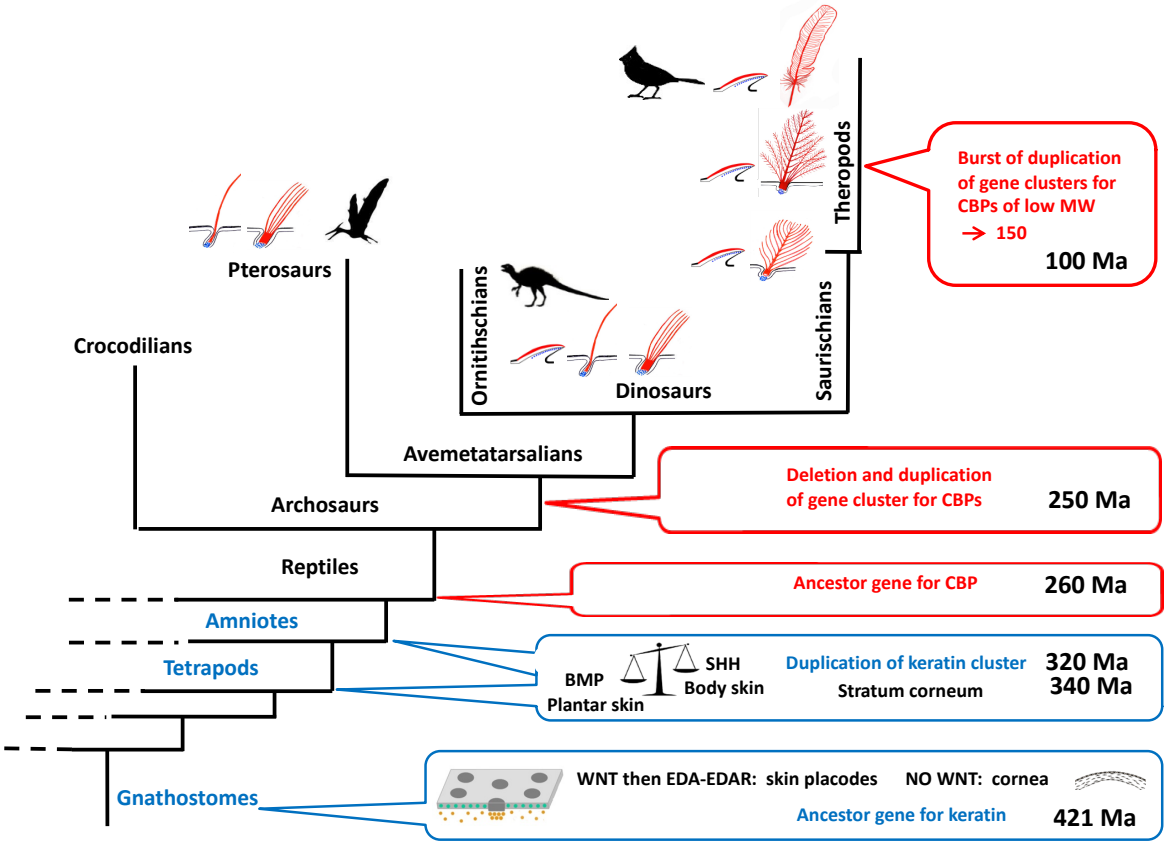

(B)


(C)


(A)
Eopterosauria
Dimorphodontia
Campylognathoididae
Rhamphorhynchidae
Sordes
Darwinoptera
Changchengopterus
Anurognathidae
Kryptodrakon
Eupterodactyloidea
Germanodactylidae
Pterodactylus
Ardeadactylus
Ctenochasmatidae
Gallodactylidae
Pterodactyloidea
Monofenestrata
Pterosauria


(B)


(C)
a
b
c
d
e
f
g
h


Theropods
Burst of duplication
of gene clusters for
CBPs of low MW
→ 150
100 Ma
Pterosaurs
Ornitihschians
Saurischians
Dinosaurs
Crocodilians
Avemetatarsalians
Archosaurs
Deletion and duplication
of gene cluster for CBPs
250 Ma
Reptiles
Ancestor gene for CBP
260 Ma
Amniotes
Tetrapods
BMP
Plantar skin
SHH
Body skin
Duplication of keratin cluster
Stratum corneum
320 Ma
340 Ma
Gnathostomes
WNT then EDA-EDAR: skin placodes
NO WNT: cornea
Ancestor gene for keratin
421 Ma