Skin Appendages

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Contributor: Danielle Dhouailly

The vertebrate integument forms the external body envelope, which creates the boundary between the organism and its environment. It includes both the epithelium, derived from the ectoderm, and the underlying mesenchyme, derived from diverse sources, depending on the anatomic region. The most extensive anatomic constituent is the skin, including both the epidermis, the dermis, and its appendages: glands, scales, feathers, or hair follicle/gland complexes. These structures facilitate a broad range of functions, such as protection, thermoregulation, communication, and locomotion. Integumental surfaces also include a transparent part (the cornea) as well as the anterior three-quarters of the oral cavity, comprising the gingiva and its appendages (the teeth).

evolution feather hair vertebrate integument

1. Introduction

All skin appendages formation results from a set of successive dermal/epidermal interactions, based on the same pathways and initiated at a placodal stage. The main difference between actinopterygians and amniotes is the last responding tissue of these interactions: the dermis for the mineralized fish scales and the epidermis for the amniote cornified appendages, epidermal scales, feathers, and hair. Among the different types of vertebrate skin appendages, one is special, both for its composition and its paleontological significance—the odontodes.

2. Fish Skin Appendages: Odontodes and Elasmoid Scales

Like amniote skin appendages, elasmoid scales of actinopterygians [1] and odontodes of chondrichthyans [2] develop relatively late in ontogeny and are distributed across the skin in a hexagonal pattern. The odontodes are dentine and enamel-rich tooth-like structures which evolved over 420 mya. Sharks and rays have retained these ancient skin appendages which are not only tooth-like in structure but share an ancient developmental gene set that is likely common to all cutaneous appendages [2]. One of the earliest bony fishes that lived more than 400 mya, *Lophosteus*, possesses both teeth and odontodes. Its analysis showed that teeth and odontodes initially take shape together but differentiate as they grow [3]. The results confirm that contrary to the ‘scale-to-teeth’ hypothesis, teeth did not evolve from fully formed odontodes. The two structures form out of one founder: teeth and odontodes are modifications of a single system.

Sire and Huysseune [4] have proposed a scenario for the evolution of elasmoid scales, from the superficial odontodal tissue covering the rhombic scales in ancestral osteichthyans. They suggest that teleosteans elasmoid scale tissues are derived from dental but not from bony tissues. In most species, the elasmoid scale is composed of three tissues, the basal plate, composed of elasmodin, the external layer, calcified extracellular matrix like the dentin, and the limiting layer, a hyper-mineralized tissue devoid of collagen fibrils, structurally close to enamel, and deposited on the scale surface by the epidermis. The elasmoid scale is in the upper region of the dermis, close to the epidermis, which still covers most part of its surface in the adult. In the embryo, the epidermis cooperates with the dermis for its morphogenesis. The genes that control the first stages of the fish scales and the appendages of amniotes are the same, as beautifully shown first by Harris and colleagues for ectodysplasin [5], and they interact in similar ways, which have been elegantly demonstrated recently [6].

3. Amniotes Scales, Feathers, and Hair

A long-held view is that feathers and hairs have been suggested to evolve from epidermal overlapping scales of a common tetrapod ancestor of sauropsids and synapsids [7]. No intermediate form has ever been found between scales and hairs, and the proposal was only based on the development of sensory bristles in the hinge scale region of reptiles. In contrast, the elongated scales of *Longisquama* from Triassic 240 mya, compared to the normal growth of buds during feather ontogeny, suggested that the elongation of a preexisting scale could have led to feathers [8]. A correlated view is that avian scales are directly related to squamate scales (among others: [9][10][11]). For several years I defended two views that oppose the classical ones: that hairs and feathers do not derive from squamates scales, and that feathers are the point of origin for avian scales [12].

Very rapidly after the first sauropsids appeared, c. a. 320 mya, they split into squamates and archosaurs. The oldest known lizard, *Cryptovaranoides,* was living in Triassic, 202 mya [13], but unfortunately this fossil, which comprises a partial head skeleton with unique squamate traits, does not concern skin. Until now, the oldest fossilized scaled integument has been only found in Late Cretaceous mosasaur *Ectenosaurus* [14]. Like those of modern squamates, mosasaur scales varied across the body in type and size. The keeled scales covering the upper regions of the body and smooth scales overlay the lower. An unusual preservation of a squamate skin which dates only about 50 mya (Eocene) shows scales, which are typical of the modern Shinisaurians group [15]. Thus, researchers can only presume that the appearance of scales in squamates was occurring as soon as Triassic and had not varied greatly during several mya. In Triassic a burst of life recovery occurred from end-Permian mass extinction, involving vertebrates such as squamates and the pterosaurs, as well as the first dinosaurs, and the survivor cynodonts which will give rise to mammals in the Jurassic. Pterosaurs have long been recognized as fluffy animals, covered with filaments previously named pycnofibers [16][17], which were recently recognized as feathers comprising isolated filaments or a bunch of simple filaments [18]. Among dinosaurs, the few giant sauropods for which integument is preserved have polygonal imbricated scales [19][20][21]. However, thousands of recently discovered astonishing fossils have shown that theropods (avian lineage), sauropods, and even a basal ornithischian like *Kulindadromeus* [22] had feathers. Did all dinosaurs have feathers? Just because researchers do not find feathers fossilized does not mean they were not there. They are so hard to preserve that exceptional circumstances are required for them to be found. Moreover, the presence of epidermal scales in a large adult individual does not rule out the possibility that younger individuals possessed feathers. Another possibility is that *Tyrannosaurus rex* and its closest cousins were so big that they could have lost their feathers to prevent overheating—the way that elephants have reduced their coat of hair. A 130 mya small primitive tyrannosaur, *Dilong*, was covered from head to tail with downy fluff and primitive feathers [23]. Filamentous feathers on some large tyrannosauroids from China have raised the possibility that similar integumentary structures were widespread throughout the group, even among the largest Late Cretaceous tyrannosaurids. A feather origin has thus been sought for ornithodires, the common ancestor of pterosaurs and dinosaurs, during the Early Triassic, about 250 mya [24].

Protofeathers are simple filamentous structures filled with corneous beta proteins and melanosomes which can be assimilated to single barbs, about 100 µ width/15 mm long, in *Kulindadromeus* [22]. The protofeathers can thus be qualified as hair-like feathers as they appear to have no tubular structure. Several authors wrongly suggested this as being part of the scale to feather origin theory (among others: [10][25][26][27]). These single barbs eventually evolved into branched structures, until the pennaceous feather. This typical feather consists of a central shaft (rachis), with serial paired branches (barbs) forming a flattened, usually curved surface—the vane. The barbs possess further branches—the barbules—and the barbules of adjacent barbs are attached to one another by hooks, stiffening the vane and forming the most complex cutaneous appendage yet to be produced during evolution. It should be noted that the evolution of the feather architecture appears to not always follow the same path, and the rachis formation can precede the formation of the barbules. Moreover, some dinosaurs had feathers that are not seen in modern birds, with the best example being the ribbon-like tail feathers of a maniraptora, *Epidexipteryx* from Middle to Late Jurassic [28]. Theropods show a great diversity of feather types [29], and while the clade *Coelurosauria* shows the same simple feather types as ornithischian dinosaurs and pterosaurs, some show pennaceous feathers, as seen in modern birds. Their functions are varied and correspond to different types of feathers. The first to have appeared during evolution, in ornithodires, was insulation with plenty of single barbs, then with down feathers, which display barbules but lack hooks. Flight was the last to appear in theropods, with the formation of hooks which stiffen the vane in remiges (wing feathers), forming a strong surface for air and rectrices (tail feathers) for control of flight direction. In addition, several other functions involve sensation (bristles), sexual attraction, and camouflage (colored feathers). Moreover, erectable feathers form fans that are linked to sexual courtship or fight.

Both paleontological [30] and genetic evidence [31], as well as developmental biology experiments [32], show that avian overlapping scales, made of corneous beta proteins, are secondarily derived from feathers [12] rather than vice versa. Thus, during the evolution of Avialae, leg feathers were reduced in a proximal to distal direction, with appearance of overlapping scales [30]. Several different types of laboratory experiments easily led to the formation of feathered scales. Retinoic acid treatment in chick embryos at the time of appearance of leg overlapping scales increases the expression of *Shh* [32] and leads to the formation of one to three feathers, or sometimes more fused feathers, growing on the scale tip [32][33]. Ectopic expression of *Wnt/beta-catenin* [34], *Notch/Delta* pathway activation [35], or *BMP* pathway suppression [36] can convert avian scales to feathers. It should be noted that the conversion of a whole scale into one feather was never observed. Moreover, the reverse conversion of feathers into scales was never obtained. At the extreme, in culture toxic conditions of embryonic skin, several feather buds can fuse, forming oblong structures like scales, but forming feather-type corneous beta proteins [37]. Ectopic *Spry2* and *β-catenin* infection can induce new outgrowth not only from chicken scales but also from alligator scales [38]. However, in this context, while chicken scales form barb ridges, the alligator skin just forms elongated scales.

As was the case of feathers preceding birds, hair preceded mammals. However, until now, only a few specimens of the mammal lineage have been discovered with fossilized fur. After the proposal of the origin of hair based on the formation of sensory bristles in the scale hinge region [7], hair was suggested to arise from reptilian claws [39]. This was based on the finding of alpha hair-like proteins in these mostly beta-keratinized structures. However, these data do not prove that an evolutionary link between hair and reptilian claw exists. Cysteine-rich alpha-keratins are not restricted to mammals, meaning that the evolution of hair involved the co-option of pre-existing proteins, which might have been present in a basal amniote, i.e., a common ancestor of synapsids and sauropsids. Less classically, hairs have been proposed to originate from the innervated conical keratinized structures of basal amphibians [40], or from a component of a sebaceous gland apparatus [41]. These two last propositions appear better founded. Indeed, hair follicles cannot be dissociated from sebaceous gland because they display an integrated working mechanism. In living mice, a single placode gives rise to hair follicle and its associated sebaceous glands [42], and all mouse lines with sebaceous deficiency present progressive scarring alopecia [43][44][45]. This integrated development indicates an ancient association, but not a gland-to-hair evolution as previously postulated [41]. Primitive hairs might have developed in conjunction with skin glands in basal synapsids. A Mammaliaform, *Castorocauda* of Middle Jurassic 160 mya [46], was discovered surrounded by a dense fur *halo*, and the first function for hair was insulation. The Early Cretaceous *Spinolestes* belonging to Mammalia 125 mya showed not only dense fur, but remarkably intact guard (primary) hairs and secondary hairs with their bulbs. Their shafts presented different cuticle patterns [47]. This fossil also presents oval horny “scales”, protospines and hair associated to skin folds, i.e., a polymorphism proper to some extant mammals and associated to protection against predators. Hair appears to be at the origin of “scales”, spines, or horn in various modern mammal species. Thus, in contrast to the evolution of feather, from a simple filament to progressive degrees of branched structures, and even to different shapes which do not exist in modern birds, the hair shaft, a simple filament, covered with cuticle cells appears to have not varied, at least from Early Cretaceous. Only the discovery of well-preserved fossils belonging to the sequential radiations of synapsids—pelycosaurs, therapsids, and cynodonts—will confirm if primary hair might have consisted of a corneous wick at ductal openings of glands, functioning to allow the sebum flow. The only known evolutionary modification of hair follicle/gland complex gave rise to the mammary gland [48]. The independence of mammary glands versus hair follicles was acquired only during Cretaceous with the appearance of eutherians. In modern monotremes the mammary gland corresponds to a simple ventral patch of hairy skin producing milk. In marsupials the mammary glands are individualized, but still coexist in young specimens with hair follicles [49].

References

1. Sire, J.Y.; Akimenko, M.A. Scale development in fish: A review, with description of sonic hedgehog (shh) expression in the zebrafish (Danio rerio). Int. J. Dev. Biol. 2004, 48, 233–247.

2. Cooper, R.L.; Nicklin, E.F.; Rasch, L.J.; Fraser, G.J. Teeth outside the mouth: The evolution and development of shark denticles. Evol. Dev. 2023, 25, 54–72.
3. Chen, D.; Blom, H.; Sanchez, S.; Tafforeau, P.; Märss, T.; Ahlberg, P.E. The developmental relationship between teeth and dermal odontodes in the most primitive bony fish Lophosteus. eLife 2020, 9, e60985.
4. Sire, J.Y.; Huysseune, A. Formation of dermal skeletal and dental tissues in fish: A comparative and evolutionary approach. Biol. Rev. Camb. Philos. Soc. 2003, 78, 219–249.
5. Harris, M.P.; Rohner, N.; Schwarz, H.; Perathoner, S.; Konstantinidis, P.; Nüsslein-Volhard, C. Zebrafish eda and edar mutants reveal conserved and ancestral roles of ectodysplasin signaling in vertebrates. PLoS Genet. 2008, 4, e1000206.
6. Aman, A.J.; Fulbright, A.N.; Parichy, D.M. Wnt/β-catenin regulates an ancient signaling network during zebrafish scale development. eLife 2018, 7, e37001.
7. Maderson, P.F.A. When? Why? and How? Some speculations on the evolution of the vertebrate integument. Am. Zool. 1972, 12, 159–171. Available online: http://www.jstor.org/stable/3881739 (accessed on 5 May 2022).
8. Jones, T.D.; Ruben, J.A.; Martin, L.D.; Kurochkin, E.N.; Feduccia, A.; Maderson, P.F.; Hillenius, W.J.; Geist, N.R.; Alifanov, V. Nonavian feathers in a late Triassic archosaur. Science 2000, 288, 2202–2205.
9. Harris, M.P.; Fallon, J.F.; Prum, R.O. Shh-Bmp2 signaling module and the evolutionary origin and diversification of feathers. J. Exp. Zool. 2002, 294, 160–176.
10. Wu, P.; Hou, L.; Plikus, M.; Hughes, M.; Scehnet, J.; Suksaweang, S.; Widelitz, R.; Jiang, T.X.; Chuong, C.M. Evo-Devo of amniote integuments and appendages. Int. J. Dev. Biol. 2004, 48, 249–270.
11. Chang, C.; Wu, P.; Baker, R.E.; Maini, P.K.; Alibardi, L.; Chuong, C.M. Reptile scale paradigm: Evo-Devo, pattern formation and regeneration. Int. J. Dev. Biol. 2009, 53, 813–826.
12. Dhouailly, D. A new scenario for the evolutionary origin of hair, feather, and avian scales. J. Anat. 2009, 214, 587–606.
13. Whiteside, D.I.; Chambi-Trowell, S.A.V.; Benton, M.J. A Triassic crown squamate. Sci. Adv. 2022, 8, eabq8274.
14. Lindgren, J.; Everhart, M.J.; Caldwell, M.W. Three-dimensionally preserved integument reveals hydrodynamic adaptations in the extinct marine lizard Ectenosaurus (Reptilia, Mosasauridae). PLoS ONE 2011, 6, e27343.
15. Conrad, J.L.; Head, J.J.; Carrano, M.T. Unusual soft-tissue preservation of a crocodile lizard (Squamata, Shinisauria) from the green river formation (Eocene) and shinisaur relationships.

Anat. Rec. 2014, 297, 545–559.

16. Kellner, A.W.; Wang, X.; Tischlinger, H.; de Almeida Campos, D.; Hone, D.W.; Meng, X. The soft tissue of Jeholopterus (Pterosauria, Anurognathidae, Batrachognathinae) and the structure of the pterosaur wing membrane. Proc. Biol. Sci. 2010, 277, 321–329.
17. Bakhurina, N.N.; Unwin, D.M. Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota; Sun, A., Wang, Y., Eds.; China Ocean Press: Beijing, China, 1995; pp. 79–82.
18. Yang, Z.; Jiang, B.; McNamara, M.E.; Kearns, S.L.; Pittman, M.; Kaye, T.G.; Orr, P.J.; Xu, X.; Benton, M.J. Pterosaur integumentary structures with complex feather-like branching. Nat. Ecol. Evol. 2019, 3, 24–30.
19. Czerkas, S. The History and Interpretation of Sauropod Skin Impressions. GAIA 1994, 10, 173–182. Available online: http://www.arca.museus.ul.pt/ArcaSite/obj/gaia/MNHNL-0000273-MG-DOC-web.PDF (accessed on 5 May 2022).
20. Ayer, J. The Howe Ranch Dinosaurs: 10 Years of Dinosaur Digging in Wyoming; Sauriermuseum Aathal: Aathal, Switzerland, 1999.
21. Barrett, P.M.; Evans, D.C.; Campione, N.E. Evolution of dinosaur epidermal structures. Biol. Lett. 2015, 11, 20150229.
22. Godefroit, P.; Sinitsa, S.M.; Dhouailly, D.; Bolotsky, Y.L.; Sizov, A.V.; McNamara, M.E.; Benton, M.J.; Spagna, P. Dinosaur evolution. A Jurassic ornithischian dinosaur from Siberia with both feathers and scales. Science 2014, 345, 451–455.
23. Xu, X.; Norell, M.A.; Kuang, X.; Wang, X.; Zhao, Q.; Jia, C. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. Nature 2004, 431, 680–684.
24. Benton, M.J.; Dhouailly, D.; Jiang, B.; McNamara, M. The Early Origin of Feathers. Trends Ecol. Evol. 2019, 34, 856–869.
25. Prum, R.O.; Brush, A.H. The evolutionary origin and diversification of feathers. Q. Rev. Biol. 2002, 77, 261–295.
26. Prum, R.O. Evolution of the morphological innovations of feathers. J. Exp. Zool. B Mol. Dev. Evol. 2005, 304, 570–579.
27. Chuong, C.M.; Homberger, D.G. Development and evolution of the amniote integument: Current landscape and future horizon. J. Exp. Zool. B Mol. Dev. Evol. 2003, 298, 1–11.
28. Zhang, F.; Zhou, Z.; Xu, X.; Wang, X.; Sullivan, C. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. Nature 2008, 455, 1105–1108.
29. Xu, X.; Zheng, X.; You, H. Exceptional dinosaur fossils show ontogenetic development of early feathers. Nature 2010, 464, 1338–1341.

30. Zheng, X.; Zhou, Z.; Wang, X.; Zhang, F.; Zhang, X.; Wang, Y.; Wei, G.; Wang, S.; Xu, X. Hind wings in Basal birds and the evolution of leg feathers. Science 2013, 339, 1309–1312.
31. Wu, P.; Lai, Y.C.; Widelitz, R.; Chuong, C.M. Comprehensive molecular and cellular studies suggest avian scutate scales are secondarily derived from feathers, and more distant from reptilian scales. Sci. Rep. 2018, 8, 16766.
32. Prin, F.; Dhouailly, D. How and when the regional competence of chick epidermis is established: Feathers vs. scutate and reticulate scales, a problem en route to a solution. Int. J. Dev. Biol. 2004, 48, 137–148.
33. Dhouailly, D.; Hardy, M.H.; Sengel, P. Formation of feathers on chick foot scales: A stage-dependent morphogenetic response to retinoic acid. J. Embryol. Exp. Morphol. 1980, 58, 63–78.
34. Widelitz, R.B.; Jiang, T.X.; Lu, J.; Chuong, C.M. Beta-catenin in epithelial morphogenesis: Conversion of part of avian foot scales into feather buds with a mutated beta-catenin. Dev. Biol. 2000, 219, 98–114.
35. Crowe, R.; Henrique, D.; Ish-Horowicz, D.; Niswander, L. A new role for Notch and Delta in cell fate decisions: Patterning the feather array. Development 1998, 125, 767–775.
36. Zou, H.; Niswander, L. Requirement for BMP signaling in interdigital apoptosis and scale formation. Science 1996, 272, 738–741.
37. Kanzler, B.; Prin, F.; Thelu, J.; Dhouailly, D. CHOXC-8 and CHOXD-13 expression in embryonic chick skin and cutaneous appendage specification. Dev. Dyn. 1997, 210, 274–287.
38. Wu, P.; Yan, J.; Lai, Y.C.; Ng, C.S.; Li, A.; Jiang, X.; Elsey, R.M.; Widelitz, R.; Bajpai, R.; Li, W.H.; et al. Multiple Regulatory Modules Are Required for Scale-to-Feather Conversion. Mol. Biol. Evol. 2018, 35, 417–430.
39. Eckhart, L.; Dalla Valle, L.; Jaeger, K.; Ballaun, C.; Szabo, S.; Nardi, A.; Buchberger, M.; Hermann, M.; Alibardi, L.; Tschachler, E. Identification of reptilian genes encoding hair keratin-like proteins suggests a new scenario for the evolutionary origin of hair. Proc. Natl. Acad. Sci. USA 2008, 105, 18419–18423.
40. Elias, H.; Bortner, S. On the phylogeny of hair. Am. Mus. Nat. Hist. Novitates. 1957, 1820, 1–15. Available online: http://hdl.handle.net/2246/4703 (accessed on 10 May 2022).
41. Stenn, K.S.; Zheng, Y.; Parimoo, S. Phylogeny of the hair follicle: The sebogenic hypothesis. J. Investig. Dermatol. 2008, 128, 1576–1578.
42. Nowak, J.A.; Polak, L.; Pasolli, H.A.; Fuchs, E. Hair follicle stem cells are specified and function in early skin morphogenesis. Cell Stem. Cell 2008, 3, 33–43.
43. Miyazaki, M.; Man, W.C.; Ntambi, J.M. Targeted disruption of stearoyl-CoA desaturase1 gene in mice causes atrophy of sebaceous and meibomian glands and depletion of wax esters in the

eyelid. J. Nutr. 2001, 131, 2260–2268.

44. Chen, H.C.; Smith, S.J.; Tow, B.; Elias, P.M.; Farese, R.V., Jr. Leptin modulates the effects of acyl CoA:diacylglycerol acyltransferase deficiency on murine fur and sebaceous glands. J. Clin. Investig. 2002, 109, 175–181.
45. Schneider, M.R. Fifty years of the asebia mouse: Origins, insights and contemporary developments. Exp. Dermatol. 2015, 24, 340–341.
46. Ji, Q.; Luo, Z.X.; Yuan, C.X.; Tabrum, A.R. A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. Science 2006, 311, 1123–1127.
47. Martin, T.; Marugán-Lobón, J.; Vullo, R.; Martín-Abad, H.; Luo, Z.X.; Buscalioni, A.D. A Cretaceous eutriconodont and integument evolution in early mammals. Nature 2015, 526, 380–384.
48. Oftedal, O.T.; Dhouailly, D. Evo-devo of the mammary gland. J. Mammary Gland Biol. Neoplasia 2013, 18, 105–120.
49. Oftedal, O.T. The mammary gland and its origin during synapsid evolution. J. Mammary Gland Biol. Neoplasia 2002, 7, 225–252.

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