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The Development of the Sauropsid Integument: A Contribution to the Problem of the Origin and Evolution of Feathers¹

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SYNOPSIS. Developmental anatomical data are insufficient to discuss plausible intermediates between an ancestral, scaled, reptilian skin and appendage-bearing, avian skin. We also review adult tissue replacement and ubiquitous mechanisms underlying skin morphogenesis. Combining developmental data *sensu lato* with consideration of necessary biological roles permits evaluation of major form/function trends in skin evolution. New data on feathers reveal retention of the sauropsid synapomorphy of vertical alteration of α - and β -keratogenesis. By identifying roles that were obligatorily maintained throughout evolution, we demonstrate constraints on hypothetical skin morphologies in preavian taxa. We analyze feather origins as a problem of emergence of complex form via modulations of morphogenesis. While existing data do not permit presentation of sequential, hypothetical, intermediates culminating in a plumage, the analysis: (1) implies that a protofeather and its follicle are most easily derived from isolated, flattened, elongate, reptilian scales; (2) explains diversification of feather morphs from a contour-like “basic” feather and the similarity between feather and hair follicles; and thus (3) reveals several developmental constraints on structures proposed as antecedent to avian feathers, whether hypothetical constructs or palaeontological interpretations. Although these conclusions do not depend on any previous scenario, they are consistent with Regal’s (1975) model and the limited, fossil evidence, especially that of the “basal archosaur” *Longisquama*.

INTRODUCTION

All *pre-1970* theories of feather origins and evolution (Lucas and Stettenheim, 1972, pp. 255, 344–346) discuss skin form and embryogenesis in living sauropsids (*sensu* Laurin and Reisz, 1995, p. 180). They are difficult to evaluate because: (1) detailed study of amniote scale development began only recently (Sawyer *et al.*, 1986); (2) classical accounts of reptilian skin morphology (reviewed in Lange, 1931) are nomenclatorially and conceptually confused (Maderon, 2000; Maderon *et al.*, 1998, pp. 19–22); (3) data on molecular aspects of all keratogenic tissues were, until recently, limited (Bereiter-Hahn *et al.*, 1986); (4) sauropsid skin form/function re-

mains poorly known compared to mammalian skin (Maderon and Homberger, 2000); (5) classical scenarios did not consider form in an appropriately precise sense (Bock and von Wahlert, 1965).

Because development underlies emerging form/function of any organ system, evolutionary discussion minimally demands knowledge thereof. The weak database for sauropsid skin *pre-1970* makes problematic any consideration of earlier scenarios invoking selective pressures favoring transformation of scaled reptilian skin into an avian plumage. Maderon’s (1972a) model for feather origins used available data on archosaurian scale form and development and keratin biology. In an ecophysiological approach, Regal (1975) argued that selective forces facilitating behavioral thermoregulation in an ancestral reptile produced changes in scale form, protoadapted (Gans, 1979) for later selection. He proposed an ingenious, but then unsubstantiated, hypothetical intermediate between scales and

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feathers. Data from the past 25 years permit reconsideration of the problem of the evolutionary origin of complex form, aided by trends in developmental biology.

Use of embryonic data in evolutionary discussions was extended beyond form when, in the 1960s, research revealed the limited repertoire of cellular mechanisms underlying morphogenesis (Maderson, 1975, 1983; Wessels, 1981). Comparable recent advances in molecular biology extend appreciation of ubiquity of process, reinforcing its relevance to evolutionary change. Thus, recent texts not only summarize rapidly accumulating data on growth factors, cell adhesion molecules, regulatory genes, etc., they explicitly relate such to evolution (Gilbert, 1997). Evolutionary Developmental Biology (Hall, 1998) aids consideration of soft tissue evolution where fossil evidence will never be available and makes it possible to assert the value of specific investigations when existing data are inadequate.

The above is particularly relevant to the problem of feather origins. In some ancestral clade, changes occurred in the morphogenetic mechanisms underlying the formation of a scaled integument that led eventually to the avian pelage. New fossils will eventually resolve questions of that clade's systematic status and perhaps inform us on its integumentary form. Other fossils may reveal such in later avian antecedents, but they will never document morphogenesis *sensu stricto*. Paleomorphogenetic speculations are justified for two, inter-related reasons. First, postulates of possible antecedent morphogenetic pathways in hypothetical "protofeathers" address the palaeontologists' question: "What should we be looking for?" Second, they can provide testable insights into a unique aspect of the problem. Reconstructing the evolutionary path from scales to feathers is a problem of a morphological transformation series. The unresolved question: "Which of various morphs in living birds is the basic feather?"—leaves open the issue of the form of the end-result. Is it a down feather, a contour feather, a flight feather or what?

While significant gaps remain in the database, gaps identified *en passant*, we pre-

sent arguments to support several assertions. (1) The avian plumage evolved via modulations of the processes responsible for development of the scaled, reptilian integument. (2) The requirement that all intermediate steps in adult form along the transformation series continuously support identifiable biological roles constrains models of feather origins. These constraints are largely independent of any specific functional scenario and/or its systematic context. (3) The constituent units of the avian plumage, *i.e.*, feathers, share many features with reptilian scales. (4) A contour-like feather can be derived from an elongated reptilian scale by modulations of keratinocyte behaviors produced by heterochrony. (5) Contour feathers are probably "basic" because other morphs can be derived therefrom by similar developmental changes.

To support the above assertions we explore successively three areas. First, we review amniote skin development to validate the distinction between "scales" and "integumentary appendages" (Maderson, 1972*b*). Second, we show how current knowledge of the functional significance of keratin distribution in amniotes illuminates understanding of adult feather form and replacement. Third, we integrate data from the first two sections to identify obligatory roles essential to any evolutionary scenario and make brief comment on available fossil material.

EMBRYOGENESIS OF THE AMNIOTE INTEGUMENT

The usefulness of the database in evolutionary discussion

For birds, data concern primarily one species, *Gallus domesticus*, for which there is a large body on the dorsal pterylya (feather tract), a more comprehensive database for leg scales and a few studies dealing with other specializations. For reptiles, descriptive accounts are available for species representing all major extant taxa. Using avian data in evolutionary contexts requires caution. The several adult feather morphs make it difficult to judge whether the first-formed embryonic units might be specialized because we know little of the succession

emerging from single follicles. Past allusions to “avian” as distinct than “reptilian” scales are confusing because of diversity *inter alia*.

Development of any organ system involves cytodifferentiation and pattern formation. For amniote skin, the former alludes most importantly to the appearance, always prior to hatching or birth, of specific epidermal proteins and lipids. Pattern formation in developing vertebrate skin is expressed at two levels. Major or minor differences in different body regions represent qualitative patterning. A quantitative aspect is the geometric organization of constituent units. Amniote integuments show both levels whether these are “scales” (in reptiles) or “integumentary appendages” (in a plumage or pelage) (Maderson, 1972*b*).

Scales arise as folds in a previously flat embryonic integument and all tissues in the mature adult system are part of a scale. By contrast, appendages are: “localized centers of specialized epidermal and/or dermal cell proliferation and differentiation *within an otherwise unspecialized integument*.” (Maderson, 1972*b*, p. 160, emphasis added). This distinction (1) avoids semantic problems caused by use of the word “scale” in different contexts and (2) accommodates experimental data. In the 1950s–1970s research showed that in adult hairs, feathers, nails etc., the dermis exerts inductive influences on overlying epidermis, but this is not true in reptiles. The distinction has proved useful in many contexts. We show later that recent data suggest that an antecedent reptilian scale could have been evolutionarily transformed into an appendage—a feather.

Early development of amniote skin

Epidermis is first an epithelium of attenuated cells (assumedly of ectodermal origin) overlying an unorganized mass of stellate mesenchymal cells (demonstrated to be of somatic mesodermal and/or neural crest origin depending on location [LeDouarin, 1982]) that represents presumptive dermal components. In the ubiquitous “2-cell condition” of primary epidermal differentiation (Maderson, 1985, p. 531), beneath a single layer of epithelial cells, the periderm (the

mammalian epitrichium) is a stratum germinativum. Its cuboidal cells lie on a basement membrane produced by epithelial-mesenchymal interaction (Hay, 1991), but no other changes characterize dermis at this stage. Depending on species and body location continuing proliferation forms a multilayered periderm (Alibardi, 1998*b*, 1999*a*) before further differentiation occurs. Subsequent events differ between scaled reptilian and appendage bearing avian or mammalian integuments.

Later development of integumentary appendages in endotherms: feathers with comments on hairs

Earliest feather primordia have long been depicted as hexagonally spaced units, symmetrical and slightly rounded in profile (Rawles, 1955; Dhouailly *et al.*, 1998). In vertical sections, a discrete placode (*de facto* a slightly convex bowl of epidermal cells) rising above the general body surface lies atop a condensation discrete from adjacent, more loosely packed, mesenchyme. Hair primordia are similar (Table 1) but whether placode precedes condensation, or vice-versa, varies between body hair and vibrissae (Hardy, 1992): geometric spacing is less obvious than in feathers (Maderson, 1972*b*). The validity of this “typical” morphology for feather primordia is questionable. Study of the entire integument of chick embryos (Mayerson and Fallon, 1985) permits three conclusions. (1) Primordial form differs between pterygiae because shapes and/or sizes of placodes and/or condensations vary. (2) Between pterygiae, pattern and rate of spread of primordial differentiation from primary rows are different (Linsenmayer, 1972). (3) Early primordia may be found somewhere on the body from 8.0–14 days of incubation.

Later development of avian leg scales

Three adult morphs are distinguishable by their form and keratins: anterior scutae/posterior scutellae, mesial and lateral interstitiae and plantar reticulatae (Table 1). All start as upthrusts making an erstwhile flat skin wavy. Specific features distinguish them *inter alia* and, *in toto*, from feather primordia (Sawyer *et al.*, 1986, 2000) (Ta-

TABLE 1. *Developmental anatomical comparisons among ten amniote integumentary structures (1–10, 1st column). Keratin types and distribution in mature unit (2nd column). Presence or absence of placodes and condensations indicated respectively in 3rd and 4th columns. Temporal duration of condensations (5th column). Empirical assessment of mesenchymal cell density from light microscopy, range very dense (XXXXXXX) to very sparse (X) (6th column). Data unavailable (“?”) and (“??”). Precursors of adult dermal papilla (*). Non-applicable (N.A.). Data from text citations.*

MATURE	MATURE	EMBRYONIC FEATURE			
		Epidermal Placode	Mesenchymal Condensation is Present?	Duration of Mesenchymal Condensation	Density of Mesenchyme
(1) <i>Feather</i>	<i>Vertical Alternation</i>	Yes	Yes	<i>Permanent*</i>	XXXXXXX
(2) Scuta exposed surface	β-	Yes	Yes	Transient	XXXXXX
(3) Scutella exposed surface	β-	Yes	Yes	Transient	XXXXXX
(4) Interstitia exposed surface	β-	?	?	?	?
(5) Hinge regions	α-	No	No	N.A.	XXX
(6) Interfollicular epidermis	α-	No	No	N.A.	XXX
(7) Apterium	α-	No	No	N.A.	XX
(8) Reticula	α	No	No	N.A.	X
(9) <i>Reptilian scale</i>	<i>Vertical Alternation</i>	No	Yes/No	??	X or XXXX
(10) Mammalian hair	Homogeneous α-	Yes	Yes	Permanent*	XXXXXXX

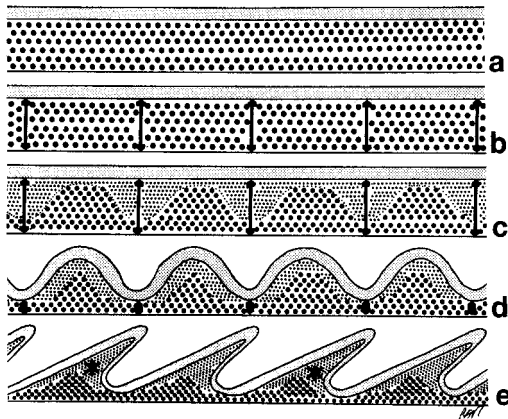


FIG. 1. Flat, early integument of reptile embryos (a–c) forms rounded symmetrical scale anlagen (d) which then become asymmetric (e). Epidermis (fine stipple) has no placodes and maintains uniform thickness until inner scale surface and hinge regions appear at asymmetrization (e). Primordial dermis (very heavy stipple, a and b) forms anchoring complexes (lines with heavy arrowheads, b and c). A model proposes that anlagen elevation involves contraction of elements within anchoring complexes as the dermis differentiates into superficial, loose (medium stipple, c–e) and deeper, compact (heavy stipple, c–e) components. Mesenchymal condensations (* in e) may occur in some species. Modified from Dhouailly and Maderson (1984).

ble 1). Placodes in scutae/scutellae lie above transient condensations at the apices of the so-called scale ridges, but both placodes and condensations differ from those of feather germs. Neither interstitiae nor reticulae have condensations, and placodes are absent from reticulae. All morphs differentiate in temporo-spatial patterns within proscribed domains reminiscent of the spread of feather primordia within pterygiae supporting suggestions that avian scales (or groups thereof in the case of reticulae) are appendages (Maderson, 1985, p. 586–587).

Later development of reptilian scales

Although variability in adult form within and between taxa (Otto, 1909) far exceeds that of avian scales (Lucas and Stettenheim, 1972, Fig. 42), all studies show uniformity of development (Alibardi, 1998a, b, 1999a, b; Alibardi and Thompson, 1999a, b, c, 2000a, b). Flat, early embryonic integument develops rounded, symmetrical elevations that then become asymmetric depending on their degree of overlap (Fig. 1). Placodes never occur, and condensations are absent from earliest anlagen. Dhouailly and Maderson (1984) addressed the question of the mode of anlage formation and asymmetrization in the absence of placodes

and condensations. They suggested a unique role for extra-cellular matricial elements (Fig. 1). Studies of other species confirm their morphological observations, but their model needs experimental testing.

Reptilian scale development involves emergence of a complex architecture of dermal collagen fibers, unique among living amniotes. Knowledge of this feature, even in adult scales, has advanced little since Lange's (1931) review. Precocity of collagen differentiation makes reptilian dermis more like that of anamniotes than birds or mammals (Dhouailly and Maderson, 1984; Alibardi and Thompson, 2000b).

Debate concerning mesenchymal condensations in reptile scales (Maderson, 1985, pp. 531–532) continues. They occur in elongate dorsal spines in some lizards (Katdare and Mulherkar, 1978), and in some imbricate scales (a snake, Kadirova *et al.*, 1997) but not in others (a skink, Alibardi and Thompson, 1999c). Further study might illuminate the evolutionary origin of dermal papillae.

Later development of integumentary appendages in reptiles

The asserted distinction between scales and appendages has an important corollary. While an appendage cannot, by definition, “bear or house” a scale, logically the converse does not apply. Thus, scales in many teleosts (Whitear, 1986) and reptiles (Zylberberg and Castanet, 1985) house dermal sclerifications. Reptilian scales bear epidermal appendages—glands, sense organs, climbing footpads (Maderson, 2000). The last-named are expressions of the oberhautchen's ability to form microornamentations (Alibardi, 1999a; Maderson *et al.*, 1998). Revealed at shedding, the resultant surface patterns are, by definition, appendages that first appear in late embryos.

FUNCTIONAL IMPLICATIONS OF AMNIOTE KERATIN DISTRIBUTION PATTERNS: VERTICAL ALTERNATION AND FEATHER REPLACEMENT

Evolutionary trends in skin form/function 1970–2000

In adult amniote epidermis, distribution of α - and β -keratins, exemplified respec-

tively by hair and feather, varies. Baden and Maderson (1970) concluded mammalian α -keratins were homogeneously distributed, but in sauropsids, where both occur, patterns were described as horizontally (crocodilians, birds and most turtles) or vertically (lepidosaurs) alternated. Those conclusions had several implications. Because mammals possess only α -keratins, it seemed that β -keratins, present in “cotylosaur” ancestors, were later lost (Maderson, 1972b). In 1970, presence of both keratins in sauropsids raised questions. Lepidosaurian vertical alternation was clearly associated with skin shedding, but did not explain its function. Maderson (1972a) emphasized similarities between crocodilian and avian scales (those later designated as scutae/scutellae [Sawyer *et al.*, 1986]) and suggested why feathers, then thought to contain only β -keratin (see below), are surrounded by α -keratogenic tissues.

The 1970 ignorance of either evolution or function of the two keratins has been ameliorated by diverse data that provide an historical picture of form/function of vertebrate skin. A summary permits discussion of new data on feather structure.

We identify 14 integumentary characters (Chars. 1–14, Fig. 2). Osteichthyans/tetrapods descended from a scaled (Char. 1) osteostracan agnathan (Forey and Janvier, 1993) whose epidermis possessed α -keratin (Char. 10) precursors. It was presumably mucogenic as in “cyclostomes,” most osteichthyans (Whitear, 1986) and lissamphibians (Fox, 1986). Total or near absence of scales (Char. 2) in many anamniotes, mammals and birds, is derived. Knowledge of skin form in the first terrestrial tetrapod, an anthracosaur or “basal amniote,” is limited to inferring it was scaled (Maderson, 1972b, p. 161). Knowing nothing of its epidermis, we cannot assess which taxon first had a stratum corneum showing α -keratinization (Char. 6), with lamellar bodies (Char. 12) forming a barrier to water loss (Menon and Menon, 2000).

Scales were lost (Char. 2) soon after synapsids appeared. Keratohyalin granules (Char. 11) perhaps helped produce a tough, flexible epidermis, uniform across the body (Char. 7). Within this, hairs (Char. 4), con-

Phylogenetic Distribution of Fourteen Integumentary Characters in Osteichthyan/Tetrapod Vertebrates

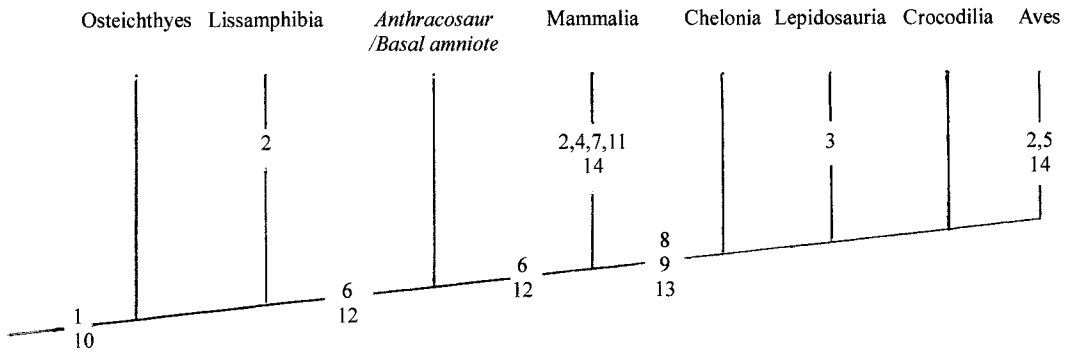


FIG. 2. Skin characters in osteichthyans and tetrapods. Gross anatomical:—(1) SCALED—body covered with overlapping and/or tuberculate scales; (2) UNSCALED—body lacks scaled covering; (3) EPIDERMAL GENERATIONS—units shed from entire body surface of lepidosaurs; (4) HAIR—epidermal appendages characterizing mammals; (5) FEATHERS—epidermal appendages characterizing birds. Histologic:—(6) α -KERATINIZATION—stratified squamous stratum corneum with α -keratogenic cells; (7) HORIZONTAL HOMOGENEITY—stratified squamous epidermis and appendages comprising only α -keratogenic cells across entire body; (8) β -KERATINIZATION— β -keratogenic, stratified squamous epithelium covers body; (9) VERTICAL ALTERNATION—all over body, stratified squamous α - and β -keratinogenic epithelia lie in vertical sequence. Fine structural/biochemical:—(10) α -KERATINS—epidermal cells contain 70A tonofilaments; (11) KERATOHYALIN GRANULES—intracellular, basophilic granules characterizing mammalian α -keratinization; (12) LAMELLAR BODIES—lipogenic organelles forming barrier to cutaneous water loss; (13) KERATOHYALIN-LIKE GRANULES—intracellular, acidophilic granules characterizing sauropsid α -keratinization. Experimental results define character (14) DERMAL PAPILLAE. Some characters, *i.e.*, 2 and 14, have evolved independently in different clades. Character 1 has reappeared in pholidote and edentate mammals. Data from text citations. Derived conditions in certain taxa (Baden and Maderson, 1970) omitted.

trolled by dermal papillae (Char. 14), evolved. No new data support further, or refute, the scenario where these interpretations were presented (Maderson, 1972b), but the rigor of cladistic analysis now implies that therapsid epidermis was never β -keratogenic, a conclusion supported by analysis of mammalian genes (Sawyer, 1987). New methods for characterizing fossil keratins (Davis and Briggs, 1998) suggest the need to reexamine synapsid material (Chudinov, 1968). In therapsids, the roles of physical protection of both organism and barrier tissues must have resided in a thickened stratum corneum before these roles were assumed by a pelage (Maderson *et al.*, 1998). Similar events accompanied emergence of avian plumage.

β -keratinization (Char. 8), a sauropsid synapomorphy, toughens a scaled integument. It is a unique example of the evolutionary appearance of new genes coding for new proteins (Sawyer *et al.*, 2000). However, because β -synthesizing keratinocytes

lack lamellar bodies, forming barrier tissues necessitates periodically “turning off” β -keratogenesis (Maderson *et al.*, 1998). Thus, epidermal generations (Char. 3), long-associated with lepidosaurian skin shedding, are an extreme expression of vertical alternation of keratogenesis (Char. 9)—another sauropsid synapomorphy.

The classical literature often states that epidermal generations characterize sauropsid scales (Lange, 1931; Maderson *et al.*, 1998, p. 19). TEM/immunocytochemical studies of avian scutae/scutellae show that all suprabasal cells have α -keratin precursors before β -keratins appear (Sawyer *et al.*, 2000). Whatever the adult phenotype of a particular tissue, TEM studies of sauropsid skin development reveal 30A filaments in the first sub-peridermal cells (Alibardi, 1998a, b, 1999a, b, 2000; Alibardi and Thompson, 1999a, b, c, 2000a). The relationship between the switch from α - and β -keratogenesis and keratohyalin-like granules (Char. 13) is not yet understood (Ali-

bardi, 1999c). Thus, horizontal alternation of keratins as described by Baden and Maderon (1970) is a temporal artifact. The entire sauropsidan epidermis possesses the capacity for vertical alternation: regional post-embryonic suppression of β -keratogenesis may be related to somatic growth (Maderon *et al.*, 1998). These new insights have implications for understanding feather form/function.

The functional morphology of pulp cap epithelia

Does molting affect avian water loss? If β -synthesizing keratinocytes lack lamellar bodies, whence comes a lipid/protein complex (Menon *et al.*, 1996) to “seal the hole” when a feather is lost? We read accounts of relevant tissues (Lucas and Stettenheim, 1972, Figs. 159, 160, 238, and 240, and related text). Figures 159 and 160 show an axial artery traversing successive pulp cavities along the calamus. After alluding to distal to proximal pulp resorption accompanying feather outgrowth, the text describes contents of a mature cavity: “A cornified strand, the remains of the axial artery in the pulp, runs through the centers of the caps.” (p. 236) Such remains are absent from Figures 238 and 240 that detail epithelial histogenesis. Puzzled by this we questioned how an artery could penetrate an epithelium.

Ultrastructural analysis provided unequivocal, and unexpectedly enlightening, results. Pulp epithelia are not penetrated (Fig. 3). Lucas and Stettenheim’s (1972) Figures 159 and 160 do not show “. . . remains of [an] axial artery,” they show the position it occupied prior to pulp resorption (*loc. cit.*, Fig. 240). TEM shows mature cells with 70A filaments and intracellular lipid droplets derived from lamellar bodies (G. K. Menon, personal communication) as in interfollicular epidermis (Menon *et al.*, 1996). Thus, we identify two events in feather evolution (Char. 5, Fig. 2): α -keratogenic and lipogenic capacities of follicular cells (Chars. 6 and 12, Fig. 2) are retained but temporally modified by a dermal papilla (Char. 14, Fig. 2). Other data (Alibardi, 2000) give new insights into feather form and evolution.

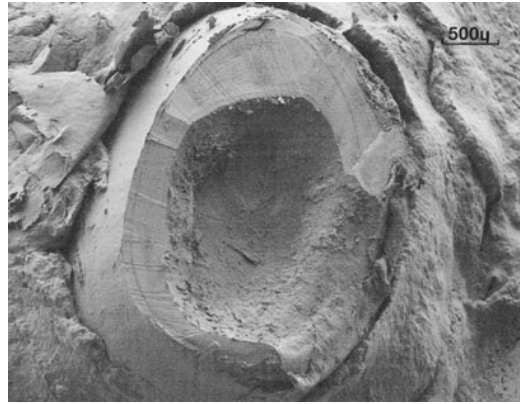


FIG. 3. SEM of proximal calamus of molted wing covert of swan *Cygnus* spp. Cutting off tip (flat surface) exposed uniform, dome-shaped, inner aspect of distal epithelium of last formed pulp cavity. Dorsal portion of inferior umbilicus (smooth lip, bottom right). Bar = 500 μ m. Photograph courtesy Gopi Menon.

Cell and tissue topographies in a growing feather

Understanding feather development is challenging because the need to consider simultaneously all parts, from single cells to the entire follicle, necessitates continuously changing one’s perception of size and scale. We offer schemae comparing a late stage in feather growth (Fig. 4A) with the pre-molt completion of the “old” appendage and the beginning of its successor (Fig. 4B).

The vane is born on a rachis, truncated to accommodate scale (Fig. 4A). The flattened whole is branched thus: rachis \rightarrow ramus \rightarrow barbs \rightarrow barbules \rightarrow hooklets. Barbules with derived hooklets are single cells, but all other parts are multicellular with a cortex surrounding pith. The entire structure, including the contiguous calamus, has an outer layer (OFCL, Fig. 4A). We ignore the hyporachis of an after-feather, often seen pressed against the ventral proximal rachis (Lucas and Stettenheim, 1972, Figs. 158–161): these tissues comprise the calamus’ median ventral wall. Mature tissues described thus far contain only β -keratins: α -keratogenesis and lipogenesis characterize pulp epithelia.

A schema distinguishing between tissues of the pulp, calamus and follicle must exaggerate empty spaces: air passes through

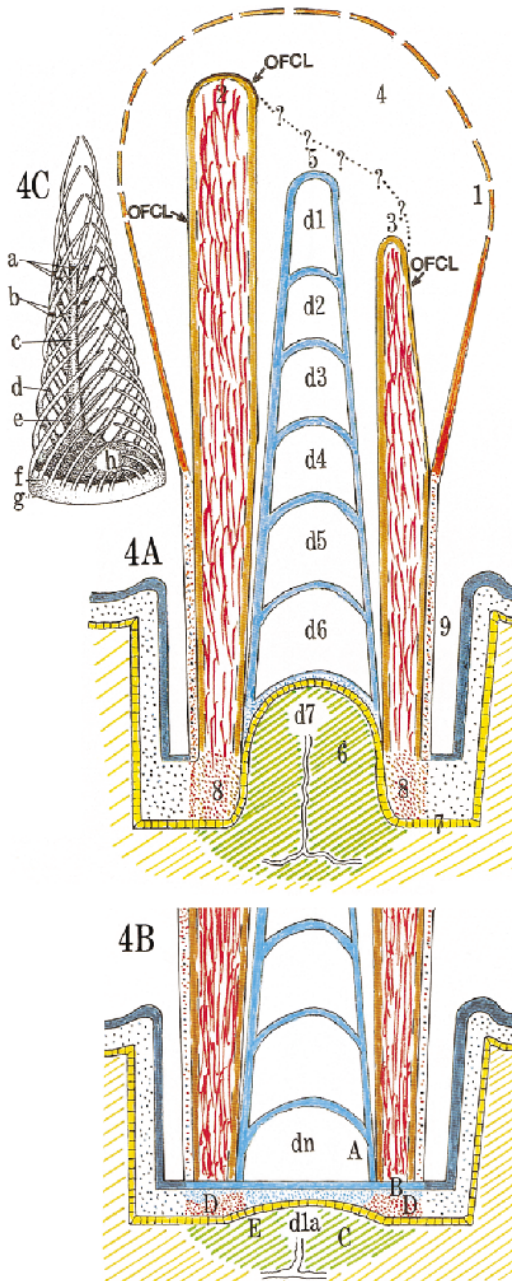


FIG. 4. Schematic mid-sagittal sections along A-P axis of a growing feather (4A) and its completion (4B) and model of barb ridge formation (4C). Oldest tissues uppermost. In 4A, 4B, follicular microanatomy simplified by omission of vase-shaped dermal papilla and encircling epidermal collar, follicular connective tissues and muscles inserted thereon. Relative scale of parts ignored to accommodate absolute size differences. Based on histology (Lucas and Stettenheim, 1972), TEM studies (Alibardi, 2000) and unpublished SEM/TEM data. The β -keratogenic sheath (4A, 1) bursts

open (broken orange line) during feather elongation: its most proximal tissues (orange and blue spots) were initially only α -keratogenic. The vane (not shown) is born on dorsal calamus (2). Outer feather cell layer (OFCL) bounding multicelled unit includes barbules with hooklets (thickened line). β -keratogenic barb, rachis and calamus, have outer cortex (including OFCLs) (brown) and pith (red streaks). Tissues of ventral calamus (3) similarly color-coded. Precise relationship between OFCLs of dorsal and ventral calamus across superior umbilicus (5) uncertain ("...?..."). Spaces (4) formed when barb ridges separated. Dermal papilla (6, close-packed, dark green diagonals), nourished by an axial artery, is surrounded laterally and proximally by other dermal cells (widely separated, light green diagonals). Cells forming a feather, its sheath and follicular and interfollicular epithelia derive from contiguous stratum germinativum (7, yellow). Immature, potentially β -keratogenic cells that will comprise epidermal collar form feather (red dots) and sheath (orange dots) (8), but adjacent immature cells are potentially α -keratogenic and lipogenic. Within circular collar some (light blue dots) form pulp epithelia (solid light blue), and lateral to it, others (dark blue dots) form interfollicular and follicular epithelia (solid dark blue). Follicular lumen (9) exaggerated. Six mature pulp cavities ($d^1 - d^6$) lie within cylindrical calamus. Location where next cavity will mature when the papilla regresses is shown as d^7 . In 4B, several sequential events in completing the old feather and beginning another are compressed in time. Note: (1) newest pulp cavity (A) in old feather, the last-formed (d^6) in the series $d^1 - d^6$ (Fig. 4A); (2) cornified plate (B) occluding the inferior umbilicus; (3) papilla (C), whose regression caused formation of pulp cavity A; (4) collar (D) and its daughter cells; (5) location d^{1a} where first pulp cavity in new feather will eventually form. Around time represented by 4B, only α -keratogenesis occurs, thus all light and dark blue tissues, especially occluding plate (B) have a barrier cytology. Immature cells (light blue dots) lying between plate and stratum germinativum will form apex of new sheath are initially α -keratogenic. Once sheath has been laid down, collar cells *sensu stricto* (D) resume production of presumptive β -keratogenic cells to begin apex of new vane. When, much later, the latter is completed, keratinocytes within the collar (light blue dots) form pulp cavities. In model of ridge formation (Fig. 4C), distal portion of a growing feather is viewed from 45° left of its posterior surface: sheath and other follicular tissues not shown. Older (a) and newer (b) transverse portions of ridges, born on distal rachis (c), formed simultaneously within ramogenic zone. More proximally, some ridges have just joined rachis (d): others are still growing (e). Circular collar has distal ramogenic zone (f) and proximal proliferative zone (g). Pulp epithelia form later in collar's center (h). Modified after Sengel (1976).

those of a mature vane. All morphogenesis and cytogenesis occurs within a sheath. Originally, every constituent cell was part of an immature mass derived from the epidermal collar. That mass was confined within the elongated, thimble-shaped sheath, itself derived from the collar. At some point, the sheath burst open as the distal vane began to assume its mature form. Later, more proximal elements emerged. Empty spaces alluded to above were originally extracellular domains. Detailed TEM studies are lacking for many of these events, but loss of cell-cell contact during maturation involves changes in adhesion molecules (Chuong, 1998).

Changing cell-cell contacts: the bases for epigenetic interactions underlying feather form

A model of barb ridge formation (Fig. 4C) shows that throughout growth, at all point(s) in space and time, every, potentially β -keratogenic OFCL contacts cells of either or both of two other populations. Initial contact is with the innermost sheath at a time when its cells are undergoing α -keratogenesis: their β -keratogenic capacity is expressed later as they assume a more distal position (Haake *et al.*, 1984; Meyer and Baumgartner, 1998). Eventually, OFCLs contact the outermost, α -keratogenic pulp epithelia. These transient associations involve sequential, changing contacts between cells from populations showing dissimilar patterns of gene expression: they underlie the epigenetic interactions patterning a feather (Brush, 2000). Further consideration may explain barbule and hooklet evolution.

Hooklet formation resembles events in squamate epidermis prior to skin shedding. The shedding complex forms at the location, and during the time, that α -keratogenesis switches to β -keratogenesis. Cytoskeletal changes that occur during the interdigitation of the cells of the two juxtaposed epithelia comprising the complex deform the membranes and produce the patterned microornamentations that characterize the mature squamate β -layer (Maderson *et al.*, 1998). Experimental data suggest the

need for detailed TEM study of hooklet formation.

Dhouailly (1977, p. 106) reviews heterospecific recombinations of chick and duck embryonic tissues. She describes barbules of resultant chimaeric feathers as: "... [conforming to] the specific origin of the epidermis..." but emphasizes that all other aspects of their form, size, general shape, number of barbs, presence or absence of a rachis are: "... in conformity with [the specific origin] of the [foreign] dermis." These observations, heretofore an evolutionary mystery (Maderson, 1983, p. 234), are now explicable. While epidermis possesses the information necessary to form barb ridges, all other aspects of feather form are dermally controlled (Dhouailly, 1977). The dermal papilla controls rates and patterns of proliferation in follicular epidermis (Sengel, 1986; Goldsmith, 1991; Chuong, 1998). Cells leaving the collar interact during subsequent distal growth affecting expression of genes controlling cell shape and adhesivity. Thus most chimaeric form results from proliferative kinetics controlled by foreign mesenchyme. However, after presumptive barbule cells move away from the collar, their subsequent fate depends on interactions with presumptive sheath cells. Both populations have the same genotype, so the chimaera bears "epidermis-specific" barbules. These data suggest a testable explanation for another problem in feather evolution. "Morphologically identical" follicles produce different feather morphs in different locations and/or at different times throughout life. Within and among such follicles, comparative studies of proliferative kinetics, and/or subsequent patterns of distal cell migration, would predictably reveal quantifiable differences having their origins in discernible metabolic differences in the dermal papillae.

Completing an old feather and beginning a new one

We have emphasized interactions between cells with differing keratogenic capacities during feather growth that involves proximal addition of pulp cavities. We arbitrarily show six cavities, labeled d¹ through d⁶ (Fig. 4A). The proximal epithe-

lium of d^6 matures as mesenchymal resorption proceeds in the location d^7 . Vertical alternation of keratogenesis permits two, almost simultaneous events—completing the old feather and beginning its replacement (Fig. 4B).

After complete regression of mesenchymal tissues (compare d^7 in Fig. 4A with d^{1a} in Fig. 4B), the old feather has formed its newest pulp cavity (Fig. 4B, A). Maturation of its proximal epithelium has produced a flat plate occluding the inferior umbilicus contiguous with corneous tissues of the follicle wall and interfollicular epidermis. All these epithelia have identical cytologies—all cells have 70A filaments and lipid droplets. Thus, briefly, as a feather is “completed,” all cell maturation in a follicle produces barrier tissues (Menon *et al.*, 1996) including even those collar-derived cells that, in a still-growing feather, contribute to β -keratogenic calamus tissues (Fig. 4A).

What of the undifferentiated cells lying beneath the occluded inferior umbilicus (Fig. 4B)? The germinal layer is a convex cap due to the lentoid shape of the regressed mesenchymal tissues (Fig. 4B, d^{1a}). Eventually, as the new feather elongates distally, the youngest immature cells immediately beneath the occluding plate will form the apex of a new sheath. Initially, sheath cells express only α -keratogenesis. By the time they later switch on β -keratogenesis, a circular collar “reappears.” Later still, the first new barbs of the distal vane appear.

An oft-quoted feature is corrected. Feathers contain both α - and β -keratins. Unlike interfollicular tissues, follicles show vertical alternation of α - and β -keratogenesis throughout life.

DEVELOPMENT, FORM AND ADAPTATION IN SAUROPSID INTEGUMENT

Developmental data facilitate identification of biological roles of archosaurian skin

Although many anatomical data on embryonic skin now exist, their use alone does not support discussion of feather origins. We add information on all aspects of morphogenesis through adult tissue turnover,

including ubiquitous, underlying controls (Chuong, 1998). Correlated with identifiable roles, developmental data *sensu lato* constrain possible models of morphologies intermediate between reptilian skin and avian plumage.

Continuous physical protection and provision of a physiological barrier were obligatory throughout all intermediate steps towards feathers. These interrelated roles constrain integumentary form (Maderson *et al.*, 1998, pp. 9–11). Thus, feathers (plumage) and hairs (pelage) protect both organism and barrier tissues. By contrast, reptilian epidermis combines the two levels of protection because of the tough, β -keratogenic tissues, continuous across the body, while the scaled organization accommodates locomotion. Whatever the systematic status of the ancestors, or selective pressures involved, the evolutionary origin of birds and/or flight and/or feathers occurred in a terrestrial environment. Thus, evaporative water loss and possible abrasive, environmental contact influenced viability. The dual roles of avian skin in retaining water and losing heat (Menon *et al.*, 1996) also constrain evolutionary models. Insulation, the one aspect of thermal balance usually mentioned in discussions of feather origins, demands a minimal morphology (Porter *et al.*, 2000). Single feathers lack insulatory properties: the faculty resides in a plumage that must cover all or most of the body. Thus, selection could not have seen insulatory faculties during initial evolutionary stages (Maderson, 1972*b*). This does not preclude the possibility that initial morphologies, whatever their asserted selective value, were “excessively constructed” and therefore protoadapted (Gans, 1979) for a later insulatory role.

Controlled maneuverability of feathers depends on a microanatomy quite different from scales in reptiles (Maderson and Homberger, 2000), animals showing no comparable faculty. While gastrosteges play an active role in snake locomotion, reptilian skin mobility is usually passive *e.g.*, nuchal or gular skin extension in iguanian throat displays. Studying scales used in such displays might show how movement influences dermal form, but their restriction to specific lo-

cations limits their relevance to feather origins. Any model converting a scaled integument to a plumage must account for the initial emergence of controlled maneuverability simultaneously over the entire body for three reasons. (1) The faculty depends on geometrically arranged cutaneous muscles interacting with cutaneous fat (Maderon and Homberger, 2000) for which spatially patterned scales, with their fatty tissues (Lange, 1931; Alibardi and Thompson, 2000b) are likely precursors. (2) Even in the absence of developmental information, logic suggests constraints on models of muscle origins. Their insertion onto “protopillicles” must have evolved in consort with modulated development of dermal architecture of antecedent, reptilian scales. Could a protopillicle have evolved first and acquired muscles later? Such a sequence is improbable for another reason. (3) A muscle needs innervation: its actions must be integrated with those of other muscles. Evolving protopillicles one by one, each with muscles and associated motor neurons and integrating them later seems unlikely. Only the *initial* form associated with controlled maneuverability was constrained. Once a “protoplumage” existed, diversification of feather morphs reflecting refinement of function (? primarily associated with improving flight) probably occurred asynchronously in different body regions. Such form/function changes probably produced apteria that have no reptilian homologue.

The above conclusions derive from basic principles of skin form/function and development. Excepting the necessary allusion to insulation and thus, implicitly, to endothermy, they are divorced from previous postulates. These conclusions constrain possible models of hypothetical intermediates. Form/function analysis supports the assertion that evolutionarily, a plumage is most easily derived from a reptilian integument wherein flattened, elongated scales became placed further apart on the body surface as they assumed characteristics of appendages—protofeathers.

Skin form/function in extant reptiles: a search for models

In aquatic turtles, contiguous scalation is often reduced or absent along with a reduc-

tion or loss of superficial β -keratogenic tissues (Baden and Maderon, 1970; Alibardi and Thompson, 1999a, b; Maderon, unpublished data). These trends diminish physical protection, but are possible within the chelonian *Bauplan* because increased skin flexibility enhances limb mobility during swimming and facilitates their withdrawal into the shell. Reduced scalation is not primarily an aquatic adaptation because crocodylians, that also have a reduced barrier function, have a relatively inflexible skin comprising mechanically protective scales. The specialized ecomorphology of these taxa suggests lepidosaurs as models for understanding how the skin of terrestrial reptiles accommodates the faculties of mechanical and physiological protection.

Lepidosaurian scale form varies: a correlation with relative mobility of different body regions seems possible, but no systematic evaluation exists. Various morphs accommodate passive flexibility (*vide supra*). Two generalizations are valid for lepidosaurian skin. (1) Vertical alternation of α - and β -keratogenesis always occurs. (2) Scales always have distensible hinge region and/or inner surfaces with reduced β -keratogenic tissues. This organization combines mobility and protection.

Until recently, relevance of lizard skin *per se* to feather origins was confined to its being a non-avian system showing certain behaviors of β -keratogenic cells. When Maderon (1972a) used such data, then-known patterns of keratin distribution had neither evolutionary nor functional explanations. From all points-of-view, the uniqueness of vertical alternation demanded its interpretation as a derived, lepidosaurian feature, of uncertain functional significance. Regional reductions of β -keratogenesis across scales made it tempting to suggest these were incipient, avian interfollicular tissues. Defining an archosaurian scale was complicated when embryonic crocodylian scales were shown to resemble those of other reptiles (Maderon, 1985), but new data (Alibardi, 1998a, b, 1999a, b, 2000; Alibardi and Thompson, 1999a, b, c, 2000a, b) resolve such problems.

Horizontal alternation of keratogenesis (Baden and Maderon, 1970) is misleading

because living sauropsids retain the capacity for vertical alternation. However, in several non-lepidosaurs, β -keratogenesis is regionally suppressed in adults, *e.g.*, avian apertures, interfollicular tissues and reticulae. Thus, feathers resemble reptilian epidermal tissues in both constituent keratins and roles of α -keratogenic components. This conclusion demands explanations of the differences between an overlapping scale and an avian feather in its follicle, and the presence of a dermal papilla in the latter. Such arise from other developmental data.

Morphogenetic mechanisms in postulates of feather origins

If a feather plus its follicle is a modified reptilian scale, development should provide clues of affinity. Both similarities and dissimilarities exist (Table 1). However, absence of placodes from reptilian scales, and their presence in feather, hair and tooth germs imply they characterize integumentary appendages. One explanation for the morphogenetic role of feather placodes, equally applicable to other example, is the need to position ectodermal cells relative to interacting mesenchyme. From a placode's basement membrane emerge anchor filaments that surround the subjacent condensation, precursor of the dermal papilla. Hair and feather papillae exert inductive effects on superjacent epidermis (Fleischmajer and Billingham, 1968; Sawyer and Fallon, 1983; Sengel, 1986), mediated by the metabolism of the contained extracellular matrix proteins (Hay, 1991). Genes involved in the processing of these proteins have been studied in birds and mammals (Goldsmith, 1991; Widelitz *et al.*, 1997; Chuong, 1998; Viallet *et al.*, 1998). The many similarities reflect molecular aspects of the ubiquitous mechanisms involved in generating complex forms with axial organization. Molecular studies of spatial patterning suggest that similar genes and gene products occur in both skin and limb buds (Chuong, 1998; Crowe *et al.*, 1998; Wolpert, 1998). The ubiquity of mechanisms underlying such dissimilar organs has evolutionary significance.

Few molecular data concern reptile skin and such could never be obtained for non-

fossilizable embryos. Results from pioneering studies of avian tissue interactions (Fleischmajer and Billingham, 1968) were later confirmed for other tetrapods (Sawyer and Fallon, 1983; Hinchliffe *et al.*, 1991). Cellular bases of morphogenetic mechanisms, originally demonstrated in standard research models, were later confirmed in other species. Ubiquity of process at the molecular level across eukaryote taxa brings new strengths to comparative biology permitting the extrapolation of mechanistic data to contexts where direct information is lacking, or even where direct study will never be possible.

The keratinized feather: the evolutionary emergence of new form

Without reference to functional scenarios, we may consider the problem of feather origins as one of the emergence of new form. Developmentally, a scaled integument resembles a plumage. Results from xenoplastic recombination among embryonic, amniote, skin tissues show that the same mechanisms pattern constituent units (Dhouailly, 1977; Sengel, 1986; Dhouailly *et al.*, 1998). In contrast to papillar control of feather or hair morphogenesis, differentiation of squamate epidermis is controlled intrinsically, independent of dermis (Flaxman *et al.*, 1968).

Let us assume that (1) forms of appendages are more complex than that of an epidermal generation and (2) producing greater complexity requires more information, *i.e.*, more sources of signals. Justifying the assertion that an appendage has a more complex form than that of a stratified, squamous, epithelium [a basic definition of an epidermal generation (Maderison *et al.*, 1998)] could explain similarities of form and morphogenetic function between avian and mammalian systems. This approach permits dividing the problem of "feather form" into two: the origin of (1) that of the keratinized feather itself and (2) that of its follicle. These issues are inter-related in mature tissues: without a "protofollicle," a "protofeather" would not have possessed the faculty of controlled maneuverability for later selection. We consider first the feather.

The material shed from a single, imbricate scale of a lizard, e.g., the iguanid *Sceloporus*, is a hollow, somewhat flattened, but essentially conical object with definable surfaces and axes. The median keel along the outer scale surface (1) comprises more cells than more lateral tissues and (2) projects beyond the scale apex. The projection is a solid mass of β -keratogenic cells. Elongated in other iguanids, it is termed the “free margin” (Lillywhite and Maderson, 1968). Ultrastructural study of shed lizard skin reveals two other aspects of form (Maderson *et al.*, 1998). TEM shows the inner, α -keratogenic, barrier tissues as everywhere more uniform in thickness than the outer, β -keratogenic tissues. SEM shows microornamentation on the latter’s surface.

Fundamentally, a contour feather resembles material shed from a lizard scale except in relative proportions. The calamus, with outer β -keratogenic components surrounding α -keratogenic pulp tissues (Fig. 4) is much shorter than the branched, solid vane. Two features distinguish a β -keratogenic vane from a free margin. (1) Tissues lying lateral to its median axis (the rachis) are sub-divided into barbs. (2) Of all β -keratogenic cells on its surface (OFCLs, Fig. 4A) only those on the distal surfaces of barbs show microornamentation—hooklets on barbules.

We do not suggest that a lizard scale evolved into a feather. We merely unify facts concerning amniote, keratinocyte behaviors with those concerning the mechanistic basis of form. Without trivializing the differences between forms as distinct as those of a free margin and a vane, we can identify four processes required to effect the necessary changes from one to the other. (1) New signals could have emanated from a new inductive system, the dermal papilla (Maderson, 1972a). (2) The resultant change in complexity of proliferation patterns could have produced cells forming lateral branches (protobarbs) from the primary axis (protorachis). (3) The specific angles of protobarbs emerging from a protorachis could have derived from changes in adhesion molecules (Chuong, 1998). Barb ridge formation might have been predicted to in-

volve apoptosis but TEM study reveals none (Alibardi, 2000): a study using appropriate techniques (Widelitz *et al.*, 1997, p. 456) is needed. (4) A preexisting capacity for membrane complexity at interfaces between α - and β -keratogenic cells required only cytoskeletal changes to produce hooklets. Although details of many events in feather replacement are unavailable, their absence does not prevent this conclusion. If the same genes control patterning and axial organization in all three-dimensional structures, other genes, acting downstream, produce specific evolutionary changes. This implies that, relative to an antecedent scale, protofeathers would likely have conserved those aspects of form, and the mechanisms controlling such, shared with “descendant” feathers.

Similar concepts explain feather diversity. If modulated cell behaviors in a scale-like protofeather produced a contour-like appendage two further morphogenetic changes could have produced a flight feather. Prolonging cell production (heterochrony) would produce a longer rachis with more barbs, while downstream modulation of genes responsible for bilaterality (Wood, 1997) would produce asymmetric form. Other heterochronies in patterning the distal pennaceous region of a typical contour feather could have produced a relative increase in the proximal plumulaceous portion. Down-regulation of patterning genes could produce various contour morphs and, eventually, down feathers, bristles and filoplumes. Such an hypothesis could be tested by studying gene expression during differentiation of secondarily apterous tissues (Menon and Menon, 2000). Meanwhile, the known reduction or absence of bilaterality in down-feathers, bristles and filoplumes, supports the conclusion that developmental data constrain models of morphologic transitions and associated functional postulates.

Whatever selective factors favored initial changes in a scaled integument, if such involved losing axial organization in scales, it would raise a major developmental problem. If the “ancestral feather” (a term used without prejudice to distinguish it from our “protofeather”) lacked axial organization, its restoration would be difficult. Subse-

quent evolution of morphs possessing such organization would have necessitated a major change *upstream* in the genetic cascade. One possibility, invoking an hypothesis of gene repression rather than loss, would require mutations restoring the ancestral pattern of gene expression. While implausible, it is superior to the alternative: mutations produced new patterning genes. This would contradict the demonstrated ubiquity of molecular process.

Developmental constraints and the origin of follicular form

We have argued that a protofeather could have evolved via modulated cell behaviors in developing reptilian scales.

Applying a similar approach to follicle origins reveals developmental constraints on the germinal region and subjacent mesenchyme. These are informative because they explain the similarity, surprising given the differences between their derivatives, between feather and hair follicles.

Tissues producing epidermal appendages must have a follicular form for several reasons. Keratinocyte differentiation involves transforming a rounded to a flat shape. Mature tissues derive strength from the resultant areas of contact between dead cells. The flat, free margin of a lizard scale can be generated by distal migration of β -keratogenic cells (Maderson, 1972a, Fig. 1b) from a planar stratum germinativum. The latter could not produce and maintain the mass of undifferentiated cells needed to produce a unit with more complex form. There are constraints on the shape of such a mass and its organization relative to the dermis. It must be rounded to accommodate flattening during cell differentiation, but convex distally. Transcription and translation of proteins associated with the cytoskeleton, cell adhesion, structural keratins, etc. and lipogenesis means that cells throughout the mass are metabolically active and need oxygen, nutrients, protein precursors, etc. The thimble-form of the germinal layer maximizes its surface area facilitating diffusion from the subjacent mesenchyme and accommodates a papilla. Follicular topography provides a mechanical *milieu*.

Because a hair is fundamentally a rod of cells growing from a hole (Maderson, 1972b), mechanical stresses have relatively little effect on its mature form. However, distal extension of the mesenchymal component into a feather follicle accommodates molding of the barbs prior to later vane flattening. Pulp regression (Fig. 4) resembles events accompanying epidermal renewal on elongated lizard scales (Lillywhite and Maderson, 1968). No available data permit speculation on the sequence of topographic changes involved in follicle evolution. Study of developing elongate reptilian scales with late-forming condensations (Table 1) might reveal foci of growth factor production (Chuong, 1998).

No existing data suggest models for studying two aspects of form/function origins in feather follicles—the evolution of muscles inserting on follicular connective tissues and the vase-shaped papilla. These could not have evolved before the sinking of a protofollicle below the general skin surface. For the mechanical reasons noted above, repositioning the germinal layer and ramogenic zone would have facilitated *later* elaboration of the protofeather. The question is: “What factors favored scale repositioning *early* in the evolutionary transformation?” Seemingly they were associated with the origin of controlled maneuverability but no data elucidate the issue directly. Insight comes from considering existing data from a different perspective.

Developmental models, existing scenarios and fossils

We pose two, apparently quite different, questions: (1) are our developmental arguments consistent with scenarios for feather origins? (2) do any data offer direct support for such?

Maderson's (1972a) postulated transformation of spatially separated, elongated, reptilian scales into protofeathers explicitly ignored function, but, as amended and corrected here it accommodates obligatory maintenance of biological roles. The model fitted Regal's (1975) thesis that movable, elongated scales, initially facilitating behavioral thermoregulation—not insulation per se, had a form protoadapted for later selec-

tion in both aerodynamic and insulatory contexts. This form resulted from fraying of tissues lateral to the scales' median axes producing a pennaceous morphology. In 1975, this ingenious speculation had two flaws. No such fraying of reptile scales had been documented: had it been, its morphogenetic basis would have been inexplicable! Now, many data concerning adhesion molecules and, perhaps, cell death, tell us that such form could have existed, the question is, do we have any evidence that it did?

Fossil evidence for feather origins is limited and debatable (Martin and Czerkas, 2000). The most interesting data concern the Lower Triassic *Longisquama* (Sharov, 1970). A new translation of the original text by a Russian speaker familiar with skin (T. Dujsebayaeva, personal communication) clarifies details of the version originally available to Anglophones, now confirmed and extended (Jones *et al.*, 2000).

Longisquama's body was covered by delicate, overlapping scales, somewhat elongated on the neck, but especially so in the row along the post-axial margin of the forelimb. This latter feature alone supports Sharov's (1970) view of *Longisquama* as a sophisticated glider because it resembles and analogous integumentary modification in the lemur *Propithecus* (Feduccia, 1993). However, the form of the 6–8 pairs of very elongate units lying paraxially on the dorsum is relevant here.

Reinterpreted as “non-avian feathers” (Jones *et al.*, 2000), impressions show a short, pliable, distal vane with barbs running transverse from a median axis with distal rachis and proximal calamus. Within the latter, most proximally, are pulp cavities that decreased mass while maintaining strength. The major difference from typical avian feathers is the persistent sheath surrounding the proximal 2/3 of the quill/barb complex. The complex form of these non-avian feathers, probably homologous with true avian appendages, suggests they must have developed within a follicle, possibly with associated muscles. This implication, which in turn implies controlled maneuverability, is supportable on logical grounds: whatever their biological role, it is unlikely that structures 2–3 times longer than the

snout-vent length, would have “flopped about” passively.

Longisquama's feathers show that morphogenetic programs similar to those described here (Fig. 4) existed in a Triassic archosaur. Thus, the form predicted by the presently discussed developmental and functional constraints is confirmed in a species whose non-integumentary morphology implies volant behaviour. New material showing more impressions of body and limb scales could clarify the sequence of forms between scales and feathers and their patterning. *Longisquama* lacks a “plumage,” but such could have evolved easily by subsequent spreading of the primordial units over the dorsal body, and eventually the forelimbs. Considerations of integumentary development and form/function suggest that even the available *Longisquama* material is more informative in the context of feather origins than any others fossils.

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