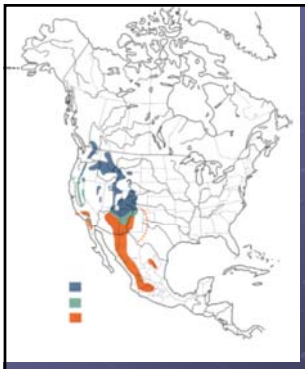
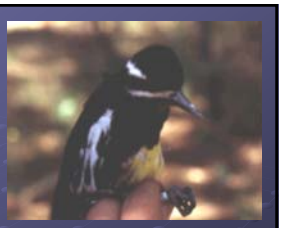
Anatomy of the Avian Integument

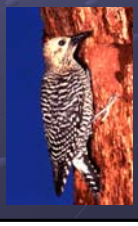
I. Skin

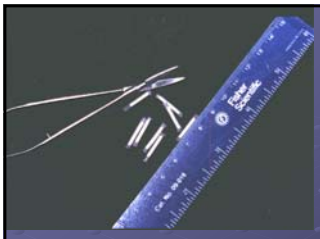
highly specialized,
semi-transparent,
elastic organ.

In birds the skin is very thin, particularly in Caprimulgiformes, and Strigiformes.



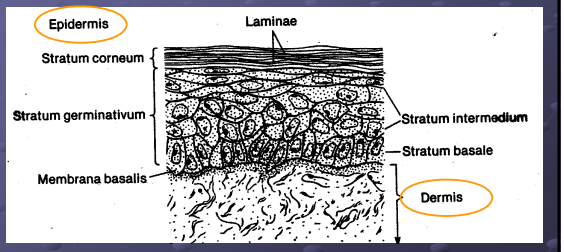






A. Layers

Skin composed of two tissue layers



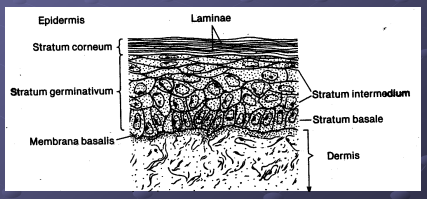
1. Epidermis
Derived from embryonic ectoderm
4 layers

Deep layer of dividing cells, *stratum germinativum*, and superficial layer of keratinized cells, *stratum corneum*

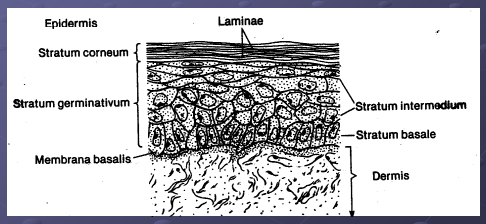
a. Stratum germinativum

separated from dermis by *stratum basale* layer whose cells continuously divide

these cells enlarge and form intermediate layer



Stratum intermedium – middle epidermal layer, signs of keratinization (*stratum granulosum* name applied in mammals)



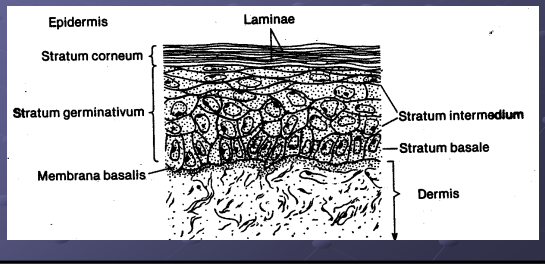
As cells mature, carried toward surface of skin and flatten

Once flattened cells become keratinized and die forming horny *stratum corneum*

b. *stratum corneum*

horizontally flattened keratinized cells

Living cells synthesize keratin



Feathered areas – layer 2-3 cells thick

other areas (feet) – much thicker and greatly modified

Keratin –

- highly resistant to chemical or physical breakdown
- functions as a water barrier
- amino acid sequence similar for all birds

2 types of keratin found in birds

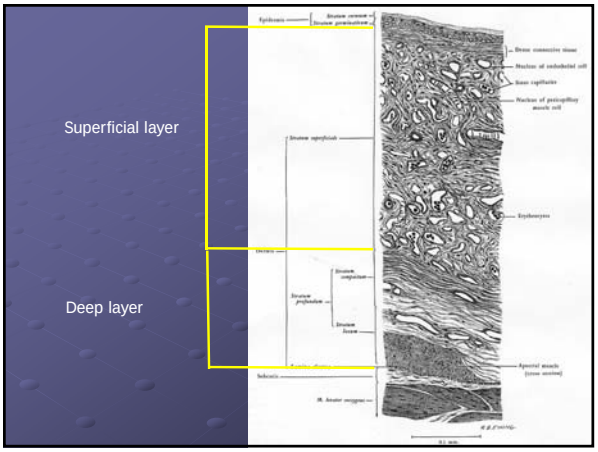
Theta keratin – feathers, scales of legs

Alpha keratin – epidermis between feather follicles

2. Dermis

lies between epidermis and subcutaneous tissue

divided into superficial and deep layers



Derived from embryonic mesoderm

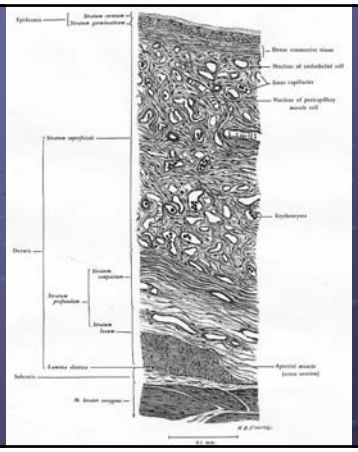
consists of

- connective tissue
- adipose
- blood vessels
- smooth muscles
- sensory structures

Dermis very pliable but scattered elastin and collagen throughout.

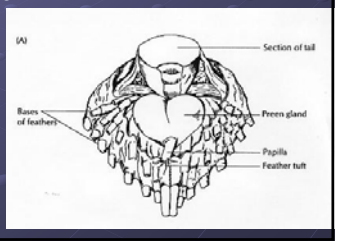
Also thick type of elastin joined together to form tendons which run to smooth muscle

Muscles run throughout dermis and move feathers

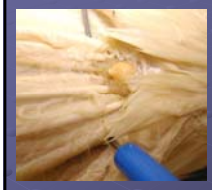


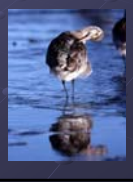
B. Cutaneous Glands

- small wax secreting glands in external wall of auditory meatus
- small mucous secreting vent glands
- large uropygial gland



bi-lobed gland located dorsally along the midline of trunk above base of pygostyle





Each gland is lined with secretory cells that open into central cavity

Shape varies between species and familes

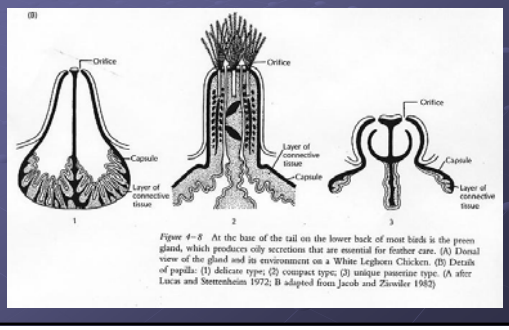


Figure 4–8 At the base of the tail on the lower back of most birds is the preen gland, which produces oily secretions that are essential for feather care. (A) Dorsal view of the gland and its environment on a White Leghorn Chicken. (B) Details of papilla: (1) delicate type; (2) compact type; (3) unique passerine type. (A after Lucas and Stettenheim 1972; B adapted from Jacob and Ziswiler 1982)

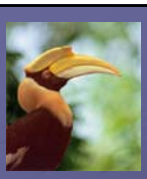
Absent in Ostrich, Amazon Parrots and close relatives.

When massaged, gland produces droplet of oil. Bird wipes bill on papilla and spread over body

Secretion – lipid based, some proteins and ions

Function –

- lubricate scales on bill, tarsus
- keep feathers pliable
- provides waterproofing
- vitamin D precursors
- antibacterial/antifungal properties



Secretion can be colored

Yellowish in Hornbill's

Some birds substance can be odorous

Green Woodhoopoes use secretion as predator deterrent

C. Sweat glands

Birds **do not** possess sweat glands

Feathers extremely good insulators!

Evaporative cooling occurs through respiratory system

II. Feather Structure and Function

Feather phylogeny, ontogeny and molt

A. Phylogeny

Origins of feathers puzzling

Hampered by false leads!!

Longisquama

New evidence for idea that developmental processes can provide window into origin of structures

Long held –

1. feathers evolved from scales through elongation,
2. then scales split
3. finally developed hooked barbules

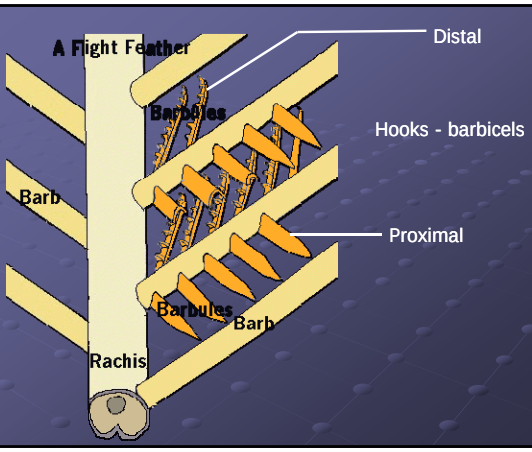
(see previous version of Gill pg 28; now revised pg 91)

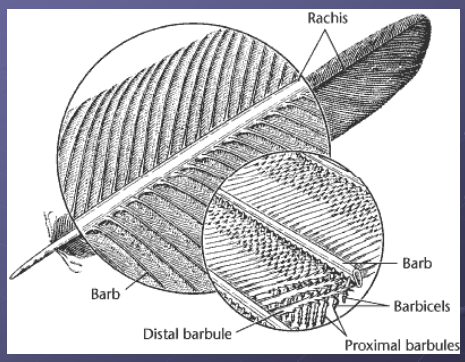
Recent research in developmental biology refutes this hypothesis

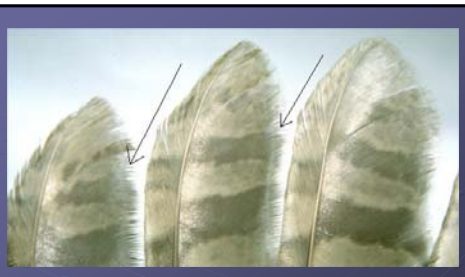
Prum and Brush 2002. The evolutionary origin and diversification of feathers. Quarterly Review of Biology 77:261-295

To understand this hypothesis first need to understand feather structure and development!

B. Feather Structure







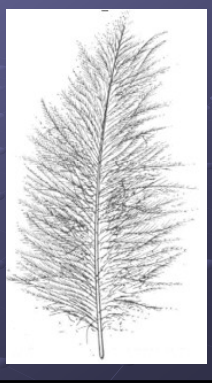
Owls - ends of flight feathers lack barbules, the edges are softer and reduces the noise they make

C. Feather Types

1. Contour – Flight feathers, body feathers, some have aftershaft

2. Semiplumes

- Soft plumaceous barbs, no barbicels



3. Down feather

No central rachis

4. Bristles

Tactile structures

5. Filoplume

Provide sensory information

- Positioning of feathers
- Airspeed

6. Powder feathers

Barbs disintegrate into fine powder as feather matures.

Thought to aid bird in grooming/waterproofing.

Specific function unknown

D. Feather Ontogeny

Feathers grow from base not tip (unlike plant growth)

Region of actively growing cells base of feather next to body.

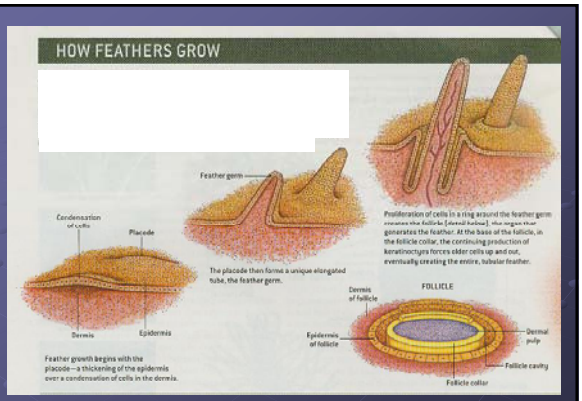
1. 5th day of incubation

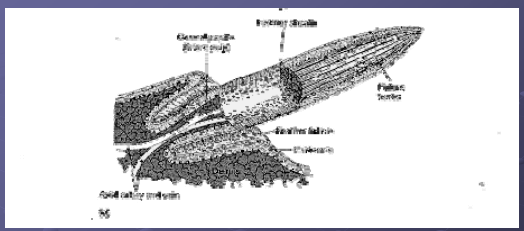
Thickening in epidermis – mitotic activity

Placode

2. 8th day placode forms unique elongated tube, papilla (feather germ) begins to form and continues to grow into cone.

Base begins to sink creating a circular moat. "Moat" becomes feather follicle.





Stratum corneum – feather sheath

Stratum germinativum – rachis, barbs, and barbules

3. Day 13 – 19 keratinization begins, rachis begins developing on dorsal surface of papilla.

Dermal pulp begins to withdraw

Barbs begin forming

Aftershaft (if present) begins forming

Down Feather Development

Pennaceous Feather Development

Dermal papilla remains as regeneration zone.

Thyroid and its hormones very important in regulating process.

Feather constructed of epidermal cells but,

dermal cells determine type of feather produced!

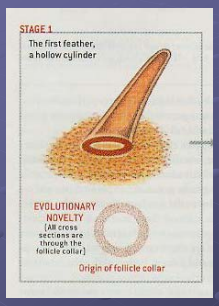
E. Evolution of Feathers – Revisited

Prum et al.

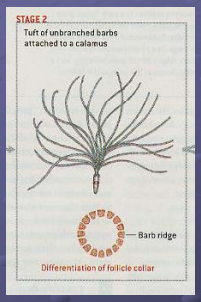
Mechanisms of development can help understand evolutionary sequence.

Model proposes – unique characteristics evolved through series of evolutionary novelties (each stage essential for subsequent stages).

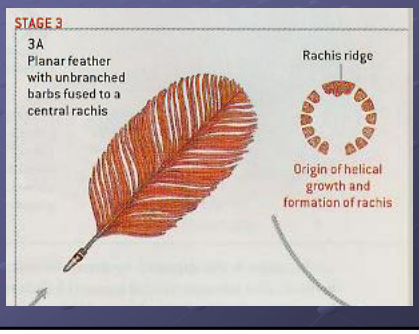
Stage 1 – 1st feather, hollow cylinder



Stage 2 – Tuft of unbranched barbs attached to a calamus



Stage 3a – Feather with unbranched barbs fused to central rachis



Stage 3b – Feather with barbs and barbules attached at the base to a calamus

Stage 4 – Closed pennaceous vane

Stage 5 – Closed asymmetrical vane

Support for Model

1. Diversity of feathers in modern birds

All hypothesized stages are within developmental capacity of feather follicles

(no theoretical structures needed!)

2. Molecular findings

Pattern formation genes – *Shh*, *Bmp2*

genes important for growth of vertebrate limbs, digits, integumentary appendages (hair, teeth and nails)

Shh and *Bmp2* – function as signaling molecules

- *Shh* induces cell proliferation
- *Bmp2* regulates extent of proliferation and fosters cell differentiation

i. *Shh* and *Bmp2* expression begins in feather placode (anterior-posterior pattern) – mediates elongation of placode

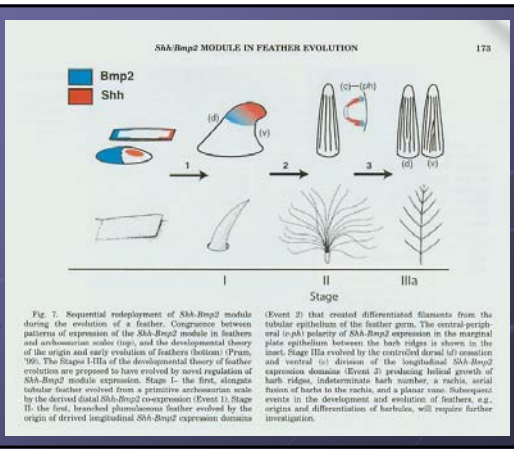
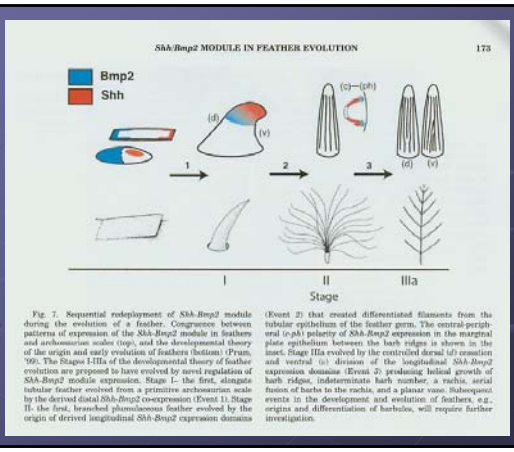


Fig. 7. Sequential redeployment of *Shh-Bmp2* module during the evolution of a feather. Congruence between patterns of expression of the *Shh-Bmp2* module in feathers and archosaurian scales (top), and the developmental theory of the origin and early evolution of feathers (bottom) (Prum, '99). The Stages I-IIIa of the developmental theory of feather evolution are proposed to have evolved by novel regulation of *Shh-Bmp2* module expression. Stage I– the first, elongate tubular feather evolved from a primitive archosaurian scale by the derived distal *Shh-Bmp2* co-expression (Event 1). Stage II- the first, branched plumulaceous feather evolved by the origin of derived longitudinal *Shh-Bmp2* expression domains (Event 2) that created differentiated filaments from the tubular epithelium of the feather germ. The central-peripheral (c-ph) polarity of *Shh-Bmp2* expression in the marginal plate epithelium between the barb ridges is shown in the inset. Stage IIIa evolved by the controlled dorsal (d) cessation and ventral (v) division of the longitudinal *Shh-Bmp2* expression domains (Event 3) producing helical growth of barb ridges, indeterminate barb number, a rachis, aerial fusion of barbs to the rachis, and a planar vane. Subsequent events in the development and evolution of feathers, e.g., origins and differentiation of barbules, will require further investigation.

ii. evolution of a novel pattern of longitudinal stripes of *Shh* and *Bmp2* results in differentiation of epithelium into barb ridges = branched structure

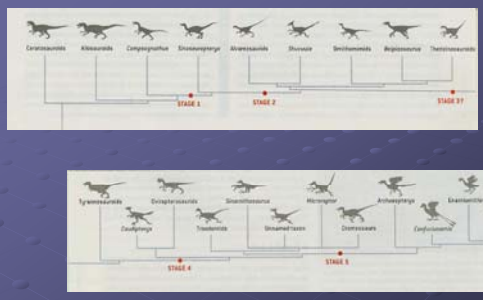


Each stage in development has distinct pattern of *Shh* and *Bmp2* signaling

subsequent events dependent on earlier stages!

3. Paleontological findings

Findings of feathered theropods consistent with model



- New evidence damaging to classic hypothesis (– feathers evolved from elongated scales)
- rejects hypothesis that feathers evolved for flight
- feathers evolved as series of developmental innovations (each may have evolved for different original function)

- insulation
- water repellency
- courtship
- camouflage
- defense

F. Molt

1. Function

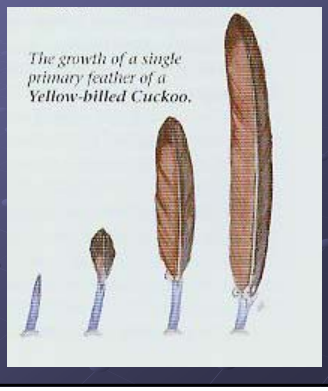
Prime function – replacement of worn feathers.

As feathers become worn, they loosen in follicle and are dropped

Secondary function –

Partial molt just before breeding season provides brightly colored courtship plumage.

Feather forms inside sheath which grows from follicle.



Typical pattern in adults – replace all feathers 1x per year (following breeding season)

However, many variations on typical pattern.

Some species have partial molts before breeding season

HY birds may grow feathers continuously during 1st year.

2. Energy

Energy demands are heavy during molt

Birds partition molting so it doesn't overlap with other energy demanding activities.

190 African species - < 4% showed overlap

Adelie Penguin – molt all feathers at once.

Premolt fattening followed by inactive period.

Wght loss during molt -

45 – 53% of premolt mass

Migratory species often molt at faster rate than nonmigratory birds.

Long distance migration never performed as long as primary or secondary is growing.

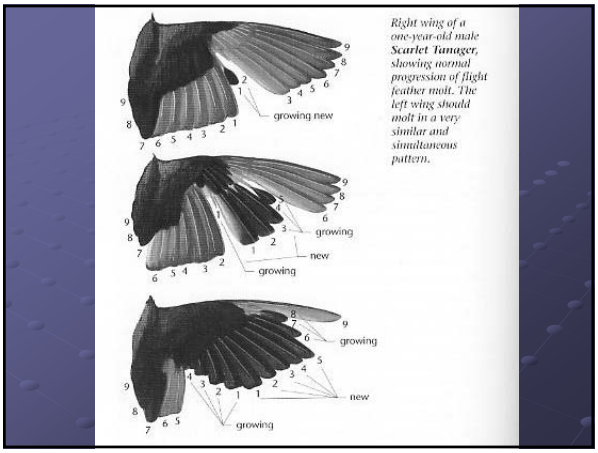
3. Patterns of molt

Feathers don't fall out randomly but in a symmetrical pattern

Pattern constant within species

Primary and secondary feathers numbered.

Typical pattern – descending or centrifugal molt (from center out).



Right wing of a one-year-old male ***Scarlet Tanager****, showing normal progression of flight feather molt. The left wing should molt in a very similar and simultaneous pattern.*

Many exceptions to pattern –

Ascending molt (rails)

Synchronous molt (Anseriformes)

Chaotic molt (turaco's)

4. Terminology

Humphrey-Parkes system

Complete molt – molt in which all feathers are replaced

Prebasic molt (late summer early fall) → basic plumage (renewed each year)

Some species undergo additional molt where some feathers replaced (head, body) often in late winter

Prealternate molt → alternate plumage

New feathers found with old feathers

Definitive stage – adult plumage

F. Feather Care

Feather Care