The Integumentary Morphology of Modern Birds—An Overview[1]

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SYNOPSIS.   Avian integument is thin, elastic, and loosely attached to the body, giving birds the freedom of movement needed for flight. Its epidermis is both keratinized and lipogenic, and the skin as a whole acts as a sebaceous secretory organ. The skin is covered by feathers over most of the body, but many birds show colored bare skin or integumentary outgrowths on the head and neck. Heavily cornified epidermis covers the beak, claws, spurs, and the scales on the legs and feet. These structures (except the back of the leg and underside of the foot) contain beta-keratin like that in reptilian scales. Most birds have sebaceous secretory glands at the base of the tail and in the ear canals. Feathers are the most numerous, elaborate, and diverse of avian integumentary derivatives. Their diversity is due to the possibilities inherent in their basic plan of a shaft with two orders of branches and the use of modified beta-keratin as a strong, light, and plastic building material. The evolution of feathers in birds has been accompanied by the development of complex systems for producing colors and patterns, the innovations of feather arrangement and follicles with their musculature and innervation, and the process and control of molting.

INTRODUCTION

To begin thinking about the evolutionary origin of feathers, it is useful to put them into a morphological context. This survey of the integumentary derivatives of modern birds may provide a little insight into the nature of the ancient reptilian skin that gave rise to feathers. It will show that avian integument has gained the capacity to undergo various modifications and produce diverse outgrowths. In addition, it will demonstrate that the evolution of avian feathers has been accompanied by major adjunct innovations in their implantation, coloration, arrangement, operation, growth, and molting.

BASICS OF AVIAN INTEGUMENT

Macroscopic features

The skin of birds is fundamentally adapted to their life as active homoiothermic animals. It is largely concealed by the feathers, and its properties have been shaped by them. The ordinary skin is usually pale pink or bluish pink, elastic, often translucent, and thinner in birds than in mammals of equal size. Over most of the body, a bird fits loosely inside its skin, like a baby in a sleeper, having the freedom of movement required for flight. The skin is firmly attached with little or no modification on the skull, the wing tips, and other regions. The integument is unfeathered, solidly attached to the skeleton, and highly modified on the beak, the feet, and certain other parts.

General histology

Avian epidermis is generally thin in areas covered by feathers and thick in bare areas. Its germinative layer is like that in reptiles, but the corneous layer is much thinner in birds than in reptiles. As the feathers provide mechanical protection, the epidermis is simpler than reptilian epidermal generation. Also, a pliable integument and the reduction of body weight are advantages for flight. Epidermal cells proliferate, differentiate, and slough from the surface either continuously as individual cells, or periodically as fragments or larger pieces of the corneous layer. In avian skin, as in mammalian and the soft parts of reptilian skin, the cells become filled with alpha-keratin as they differentiate. The proteins differ in

amino acid composition, molecular size, and organization among the various integumentary derivatives (Brush, 1980*a, b*; Brush and Wyld, 1982; Homberger and Brush, 1986).

Avian skin lacks sweat glands and sebaceous glands, yet the epidermis itself, in a variety of species produces neutral fats and phospholipids (Lucas, 1968, 1980; Lavker, 1975). It is strongly lipogenic, in general contrast to reptilian epidermis. Since avian epidermal cells include both lipogenesis and keratinization in their differentiation, they have been called "sebokeratinocytes" (Wrench *et al.*, 1980). The entire skin acts as a sebaceous secretory organ, with the preen gland and the ear glands as specialized parts (Menon *et al.,* 1981). The sebum serves as a moisture barrier and also probably helps to maintain the pliability of the keratinized epidermis.

The dermis is thicker than the epidermis in most areas and is divisible into several layers. It contains blood vessels, fat deposits, nerves and free nerve endings, several types of neuroreceptor organs (Stammer, 1961; Dorward, 1970; Gottschaldt, 1985), and a complex set of smooth muscles that move the feathers and exert tension on the skin (Lucas and Stettenheim, 1972). In places, the underlying subcutis carries striated muscles that attach to the underside of the skin and probably also control its tension (see Homberger and de Silva, 2000).

Functions

The skin serves many of the same functions in birds as in reptiles and mammals, though to a different degree. It shields the underlying musculature but does not help to hold the internal organs in place. A protective envelope for the body, the skin keeps out injurious substances and gasses while retaining vital ones. The corneous layer impedes, but does not block the flow of water vapor in and out of the body (Spearman and Hardy, 1985; Menon *et al.,* 1996). The continual renewal of this layer acts to repel parasitic microorganisms. Sensory receptors for various modalities in the skin detect ambient conditions. Importantly, the skin produces and supports feathers, which themselves have many functions. Together with the feathers, the skin is more active in thermoregulation in birds than in reptiles. Its surface radiates excess body heat, absorbs solar radiation, and cools the body by cutaneous water loss (Bernstein, 1971; Bartholomew, 1972). The feathering (=feather covering) is a much lighter and more efficient thermal insulation than reptilian scales, owing to the air trapped within it. This system has presumably evolved along with the evolution of homeothermy (Stevens, 1973).

BARE SKIN AND EPIDERMAL OUTGROWTHS

General characteristics

Avian integument is regionally modified or transformed in a great variety of ways. Bare, non-scaly skin appears in a continuum of conditions ranging from sparsely feathered thin skin without distinctive coloring to bare, colorful, extravagant outgrowths. In between, thickened integument may be sparsely bristly or bare, plain or brightly colored. Such modified skin occurs extensively on the head, where the surface may be smooth, as in rockfowl (*Picathartes*), but more often is thick and covered with tubercles, as in guineafowl, vultures, colies (*Colius*), and many storks, ibises, spoonbills, and cranes. It may extend just around or beyond the eyes, *e.g.,* cariamas, falcons, sheathbills (*Chionis*), parrots, cuckoos, broadbills, bare-eyes (*Phlegopsis*), lyrebirds (*Menura*), and helmet-shrikes (*Prionops*) or around the corner of the mouth, as in gulls. The thickenings and projections are often called "fleshy" structures, but this term is inaccurate because "flesh" properly refers to muscle or fat, which they generally lack.

These modifications or outgrowths are almost always on the head or neck, where they are most visible. Outgrowths are commonly larger, brighter, or present only in adult males of a species. Their coloring, which often contrasts with the adjacent plumage, is due either to intrinsic pigments or structural mechanisms in the epidermis, or to blood in the superficial capillary network (Lucas, 1970; Prum *et al.,* 1994).

The bare areas and outgrowths of adults develop with age, being absent or rudimen-

tary in young birds. In species such as certain ibises and storks, areas that are feathered in young birds subsequently become bare, losing feather follicles as well as feathers. The epidermis of these areas shows a high degree of lipoid secretion (personal communication, G. K. Menon). Once developed by adults, the integumentary structures are usually permanent, but may vary in size or color in relation to the birds' breeding activity.

Throat and neck pouches

The skin of the throat or the neck on many nonpasserine birds is bare, loose, and distensible. In most cases, the floor of the mouth and the upper throat are well-vascularized and formed into a pouch that is fluttered by the hyoid apparatus so as to move air and lower body temperature. Pelicans use the pouch not only for cooling, but also to catch and hold fish for the young birds. The distensible oral sac of male Great Bustards (*Otis tarda*) does not serve for cooling, but is inflated in display (Garrod, 1874).

Similar pouches occur on the throat or sides of the neck in male frigatebirds, certain storks (*Leptotilos*), male grouse of several species, and others. These, however, are inflated by swelling of the upper end of the esophagus as mouth action directs air into the glottis (Johnsgard, 1983). The bare skin is normally constricted or even concealed, and then inflated and displayed in courtship or social displays. Bright coloring in some species enhances its role as a visual signal. Additionally, in grouse and Painted-Snipe (*Rostratula benghalensis*), the pouches augment the vocalizations by enlarging the sound resonating chamber.

Caruncles, wattles, combs

Birds exhibit various integumentary outgrowths on the head and upper neck. These cannot be neatly categorized because they vary widely in size, shape, color, and location, and many of them intergrade. Caruncles are simple, rounded protuberances found on turkeys, Magpie Geese (*Anseranas semipalmata*), Spur-winged Geese (*Plectropterus gambensis*), Southern Ground-hornbills (*Bucorvus cafer*), sheathbills, In-

dian Black Ibises (*Pseudibis papillosa*), and certain curassows, megapodes, and cathartid vultures.

Wattles, the commonest of soft integumentary outgrowths, are larger protuberances or flaps. They are located on the sides of the head or neck, especially at the base of the bill and around the eyes. In some birds they hang beside the mouth or under the throat. Wattles occur in cassowaries, many cracids, megapodes, ptarmigan, pheasants, guineafowl, turkeys, rails, jacanas, lapwings, alcids, cotingas, starlings, honeyeaters, and wattlebirds.

Wattles are always flexible to some degree, and in a few cases are also distensible. Such wattles arise on the base of the upper bill in male turkeys (Lucas and Stettenheim, 1972) and certain male bellbirds (*Procnias alba, P. tricarunculatus*; Snow, 1982). The protuberance in turkeys, known as a "frontal process" or "snood," can stretch into a long, narrow, flexible cylinder that droops over the side of the bill. It is extended by action of smooth muscles and filling of large blood vessels.

A comb is essentially a thick, upright wattle on the top of the head. Single, mid-dorsal combs occur in junglefowl (including domestic fowl), certain brush-turkeys (*Aepypodius arfakianus, A. bruijnii*), Comb-crested Jacanas (*Irediparra gallinacea*), and male Andean Condors (*Vultur gryphus*). Adult grouse have paired combs above the eyes, larger in males than in females, which enlarge during the breeding season (Johnsgard, 1983). Combs are colored red, orange, or yellow, owing to blood in the richly vascularized superficial dermis and presumed carotenoid pigments in the epidermis.

The rictus is the soft border of the mouth from its angle grading forward into the upper and lower cutting edges of the bill. The rictal integument is bare, with a rugose or smooth surface, a thin epidermis and a well-vascularized thick dermis. It is sometimes brightly colored and thickened, grading into wattles. Such rictal outgrowths develop before the breeding season in Crested Auklets (*Aethia cristatella*) and puffins and are molted afterward.

Earlobes are soft, bare, pendent integu-

mentary thickenings located almost directly below the external ear opening. Histologically, they resemble wattles except that the dermis contains far more collagenic tissue (Lucas and Stettenheim, 1972).

Integumentary outgrowths and conspicuous areas of bare skin serve in many cases as visual signals for social or sexual behavior. They often indicate physical fitness because they change or shrivel when a bird is unhealthy. Thus, they may disclose the condition of a potential mate or competitor, indicating dominance, age, or vigor, as in certain curassows and Wild Turkeys (Buchholz, 1991, 1997). Both inter- and intrasexual selection seem to favor such traits, regardless of mating system (personal communication, J. Hagelin). Areas of bare or sparsely feathered skin on the head and neck in some cases serve for thermoregulation, radiating body heat or absorbing solar radiation (Buchholz, 1996). Bare skin also avoids matting or soiling the plumage in birds which feed on carrion (*e.g.*, vultures) or soft fruit (*e.g.*, certain parrots).

<center>RHAMPHOTHECA</center>

Morphology

The bones of the beak are covered with thick, modified integument, entirely on the outside and partly in the lining of the mouth. This covering, the rhamphotheca, is hard and heavily cornified in most birds, yet still flexible in the flexion zone of the upper bill. In flamingos and anseriforms, the covering is mostly thin and leathery with hard tips (nails) on the upper and lower bills. It is soft, especially at the tip, in sandpipers.

The rhamphotheca is basically shaped by the underlying bones and modified by local thickenings. It is formed into a variety of external plates, knobs, ridges, and other projections in many kinds of birds (*e.g.*, penguins, procellariiforms, puffins, guans, barbets, pelicans, several anseriforms, rails, coots, jacanas, and sheathbills). The edges of the bill (tomia) are modified according to a bird's food habits. They are usually rounded to sharp, but are finely serrated for straining food particles (*e.g.*, flamingos, anseriforms, and certain prions [*Pachyptila*]), or furnished with one or more pointed projections for holding prey (*e.g.*, mergansers, falcons, barbets, toucans). Internally, the roof of the mouth also has local thickenings, *e.g.*, papillae or spines for holding prey in fish-eating birds, and longitudinal or transverse ridges for holding and cracking seeds in cockatoos, parrots, finches and buntings (Ziswiler, 1965; Homberger, 1980). Nares are located within the basal one-third of the upper bill in most birds and at the tip of the upper bill in kiwis. They are usually a simple hole or partly shielded, but are tubular in procellariiforms. The rhamphotheca at the base of the upper beak is sometimes soft and thickened, enclosing the nostrils or lying posterior to them. This structure, the cere, is partly feathered in many parrots, but bare and often brightly colored in other parrots plus pigeons, falconiforms, owls, and some cracids.

A relatively stiff, yet pliable, keratinized cuticle, the lingual nail, covers the ventral and lateral surfaces of the tip of the tongue in parrots (Homberger and Brush, 1986) and certain other birds. In parrots, the histology of the nail resembles that of the rhamphotheca, but the beta-keratin filaments are arranged much as in scutellate scales.

Histology

The epidermis of the rhamphotheca is thick, especially on the tomial edges, with many closely packed cornified cells firmly bonded by long-lasting cell junctions (Lucas and Stettenheim, 1972). Its cells produce beta-keratin like that of avian scutes and claws, which in turn resembles reptilian keratins (Frenkel and Gillespie, 1976; Brush 1980*a, b*; Homberger and Brush, 1986). Calcium salts deposited in the cytoplasm between the keratin proteins add to the strength and hardness of the rhamphotheca (Pautard, 1963; Bonser, 1996*a*). The strength of the beak as a whole depends on the particular arrangement conferred by a layer of keratin, bound by a thin dermal layer to a firm bed of bone.

The dermis contains at least two types of somatosensory receptors. Herbst (lamellar) corpuscles are highly sensitive to vibration and Grandry corpuscles respond to rapidly-acting movement (Gottschaldt, 1985). Their

location and number in the beak appear to be related to the way this part is used as a tactile exploratory organ in feeding. They are especially numerous in the beak bones of anseriforms and sandpipers, plus the nail and edges of the palate in anseriforms and parrots (Berkhoudt, 1980; Gottschaldt, 1985).

Transitory nestling structures

Embryos or nestlings develop various accessories on the rhamphotheca that are lost before fledging. In nearly all birds, an egg "tooth" (egg callosity) forms on the tip of the upper beak, like that of crocodilians and turtles. It punctures the shell membrane, helps to break the egg shell, and is usually shed within a few days after hatching. Altricial nestlings of many species develop enlarged flanges on the rictus that are often brightly colored. These open instantly when touched or the birds are even slightly shaken, as when a parent returns with food (Welty and Baptista, 1988). The flanges visually arouse the parents to give a feeding response and serve as a target for delivering the food. Nestlings of certain brood parasitic species (honeyguides and Striped Cuckoos, *Tapera naevia*) have bill hooks with which they kill their nestmates (Friedmann, 1955; Morton and Farabaugh, 1979). In many estrildine and viduine finches, nestlings have tiny reflective knobs on the roof of the mouth that, together with the gape flanges, provide a strong visual signal for parent birds bringing food, an adaptation to their dark, covered nests (Steiner, 1960; Welty and Baptista, 1988; R. B. Payne, personal communication).

Functions

The rhamphotheca is more than a cover for the bones. It adapts the beak as a bird's chief tool for interacting with its environment. The same beak that seizes live prey also manipulates nest material and preens the feathers. It chiefly takes food and prepares it to be swallowed and digested. The rhamphotheca may also serve as a sensory organ, with tactile receptors for detecting live prey (*e.g.,* kiwis, anseriforms, sandpipers) or thermal receptors for measuring the temperature of the nest mound as in megapodes. Conspicuous by its location and movement, the beak commonly presents visual signals employed in identification and displays.

CASQUES

Numerous birds have a hard, bare, heavily cornified projection known as a casque on top of their head or their bill. In most cases, the integument overlies a bony extension of the skull, but in cassowaries it covers a core of tough, elastic, foam-like, collagen above the bone. Where the casque is on the crown or forehead, it is massive in cassowaries, and spike- or knob-shaped in the Maleo (*Macrocephalon maleo*), Horned Guan (*Oreophasis derbianus*), several curassows (*Crax*), and the Helmeted Guineafowl (*Numida meleagris*). The casque in hornbills covers a light, bony core above the bill and is distinctively shaped among the species, sometimes with ridges or notches on the sides. In the Helmeted Hornbill (*Rhinoplax vigil*), the keratin is uniquely formed into a thick, ivory-like knob.

PODOTHECA

The integumentary covering of the feet, the podotheca, is a layer of scales from the tibiotarsus or beyond to the ends of the toes. Feathers tend to diminish distally on the legs as scales arise and become prominent, the transition usually occurring about the intertarsal joint. Feathers and scales are variously situated in relation to each other in parts of the foot and among birds, but they never intergrade structurally (Blaszyk, 1935). The podotheca is generally heavily cornified in land birds, softer and more flexible in water birds.

Scales are flat, rounded, or conical raised thickenings of highly keratinized epidermis, separated by inward folds of thinner, less keratinized epidermis. They vary in size, shape, amount of overlap, and degree of fusion on different parts of the foot, not to mention among species. Those on the anterior and caudal surfaces of the tarsometatarsus and the dorsal surface of the toes (scutellate scales) tend to be larger, more rectangular, and more regularly arranged than those on the remaining surfaces (retic-

ulate scales). Tarsal scales, not needing flexibility, are often fused, especially on the anterior surface.

The two types of scales differ embryologically and histochemically as well as morphologically (Brush and Wyld, 1980). Scutellate scales contain beta-keratin, the same as the rhamphotheca and the claws (Stewart, 1977), whereas reticulate scales are composed of alpha-keratin. These differences indicate that they have different evolutionary histories. Scutellate scales, being very similar to crocodilian scales, appear to have come directly from reptilian scutes, whereas reticulate scales are apparently a later, derived form with different properties (Brush and Wyld, 1980) .

The reticulate scales (papillae) on the underside of the toes and the distal end of the tarsus are formed into thick pads to withstand compression, especially in terrestrial species. The pads underlie the joints and are separated by transverse furrows or gaps, which open and close as the toes are bent. The pads and papillae vary morphologically and histologically among the toes and among species according to the length of the toes, their need for support, and the nature of the substrate that the birds use (Lennerstedt, 1975a, b).

Young woodpeckers, barbets, toucans, kingfishers, jacamars, and trogons develop an extra-thick pad below the distal end of the tarsus. This accessory, on which they rest during their long growth period in a nest cavity, is shed when they fledge.

The feet of most waterbirds are formed into paddles by sheets of thin, flexible, leathery integument between the toes, the webs. Pelecaniforms have full webs connecting all four toes; loons, procellariiforms, anseriforms, lari, and alcids have full webs between the three forward toes; grouse, plovers, and some sandpipers have basal webs between the forward toes. Grebes, rails, and finfoots (Heliornithidae) accomplish the same end with flat lobes on independent toes.

Grouse and ptarmigan develop fringes of scales along the toes (Johnsgard, 1983) that, together with toe feathering in ptarmigan, enlarge the surface of the foot, enabling the birds to walk on the snow (Höhn, 1977).

These accessories are grown in the fall and molted in spring.

CLAWS

Avian claws, like those of reptiles, are coverings of heavily cornified integument over the bone of a terminal phalanx. All birds have toe claws and many birds have wing claws as well. A toe claw is composed of a dorsal plate that curves downward on the tip and sides and a ventral plate that fills the space between the sides underneath (Lucas and Stettenheim, 1972). The dorsal plate is the harder, containing heavy deposits of beta-keratin plus calcium salts.

Toe claws vary in length, curvature, and pointedness in relation to their usage and the substrate where a bird lives. They are flattened in grebes, contributing to the foot paddle. The claws have pectinate (comb) edges, used for grooming the feathers in nightjars, herons, frigatebirds, and pratincoles.

Wing claws are simple sheaths, not composed of plates. They were present on all three wing digits in the Jurassic bird *Archaeopteryx lithographica* and several Cretaceous dinosaurs. Since Hoatzin (*Opisthocomus hoazin*) chicks possess functional wing claws on two digits, this species was formerly regarded as primitive. Young Hoatzins use these small hooks for climbing around branches and shed them at 70–100 days of age (Thomas, 1996). Adult loons, storks, screamers, galliforms, Secretary Birds (*Sagittarius serpentarius*), owls, finfoots, and charadrii forms have small, nonfunctional claws on the tip of the alular digit. Adult cassowaries, however, have a large, pointed claw on the tip of the main digit, which they use as a formidable weapon.

SPURS

A spur is a solid, usually pointed projection from a limb bone, consisting of a heavily cornified sheath over a bony core. Spurs occur both on the legs and the wings. They arise on the back of the tarsometatarsus in cassowaries, pheasants, guineafowl, and turkeys. In the gallinaceous birds, they are well-developed in males and small or absent in females. Each leg has a single

spur, except in peacock-pheasants (*Polyplectron* sp.), which have two or more. All these birds have polygamous mating systems and the spurs are used in combat between males.

Spurs arise on the radial side of the carpus or metacarpus in cassowaries, screamers, Spur-winged Geese (*Plectropterus gambensis*), certain jacanas and lapwings, and sheathbills. They vary in length, sharpness, and number. They are larger in the dominant sex (usually males, but females in jacanas) and used in intrasexual combat. Other jacanas (*Irediparra gallinacea, Metopidius indicus*) lack spurs but have hard, heavily cornified leading edges to the radii (Jenni, 1996).

Curiously, many birds that have spurs also have bare skin or integumentary outgrowths on the head. This co-occurrence does not seem to be a response to a particular form of sexual competition because the species differ in their mating systems.

UNIQUE STRUCTURES

Several birds have unique epidermal outgrowths that expand the range of the integument's structural capability. A few are mentioned here.

The Horned Screamer (*Anhima cornuta*) is named for a stiff, slender, whitish, cornified spine that curves forward from the middle of the forehead. The spine is not an unbranched, modified feather shaft. It grows continuously, up to about 15 cm. but tends to break off at the tip. Not being firmly attached to the skull, it sways back and forth as the bird shakes its head (Todd, 1979).

Wild Turkeys have a tight bundle of coarse, stiff, black, cornified fibers, the "beard," which hangs down from the base of the neck. It is present in nearly all males (both wild and domestic) and in a few females. The fibers number from 150 to over 650. Unlike feathers, they grow continuously, reaching a maximum length of about 677 mm. Although mostly epidermal and solid, with a thick corneous layer, they contain dermal pulp at the base. The fibers do not arise from follicles but from an elevated area of thickened, bare skin (Lucas and Stettenheim, 1972).

Hoatzins have an elliptical, heavily cornified patch of midventral skin, the sternal callus, outside the rear tip of the sternum. The birds spend much time perched, resting on this callosity, while fermenting plant matter in their very large muscular crop and lower esophagus (Thomas, 1996). This thickening differs histologically in several respects from the sternal bursa (keel cyst), an abnormal formation in some domestic chickens and turkeys (Lucas and Stettenheim, 1972).

INTEGUMENTARY GLANDS

Uropygial gland

Avian skin as a whole acts as a sebaceous secretory organ, but it is specialized for this purpose in the uropygial gland and the ear glands. The uropygial gland (preen gland) is a bilobed structure on the base of the tail, situated between the dorsal skin and the body muscles. Inside a connective tissue capsule, each lobe is composed of numerous holocrine secretory alveoli that open into a central cavity (Lucas and Stettenheim, 1972; Menon *et al.*, 1981; Jacob and Ziswiler, 1982). The secretion passes through ducts to openings at the tip of a papilla on the posterior end of the gland. When a bird preens, the sebum is smeared on the bill and the head plumage, either directly or by a tiny feather tuft on the papilla. From there, it is rubbed onto the rest of the plumage and the podotheca.

The uropygial gland may be homologous with small, oily, sebaceous-like glands in crocodilian skin. Present in most birds, it is relatively large in many aquatic species, weakly developed in pigeons, herons, and the Kagu (*Rhynochetos jubatus*), and absent in ratites, bustards, and some parrots.

The uropygial secretion consists chiefly of monoester waxes, and also contains other waxes, triglycerides, and hydrocarbons (Jacob, 1978). It can be distinguished chemically from the skin secretion. The composition of the uropygial sebum further varies among avian species (Jacob and Ziswiler, 1982), but the functional significance of these differences has not been studied. Both uropygial and skin secretions are deposited

on the feathers (Wrench *et al.*, 1980), their relative amounts varying among species.

The functions of the uropygial secretion, although much studied, ought to be re-examined with regard to the skin secretion, which was long unknown. Together, the two substances keep the keratin of the integument and its derivatives flexible and in good condition. This is particularly important for the feathers, whose waterproofing depends chiefly on tiny air bubbles held within the meshwork of their barbs (Rijke, 1970, 1989; Kostina *et al.,* 1996). In order for that to work, the barbs and their branches must be pliable and properly spaced apart. Uropygial waxes have the optimal properties both for impermeability and the flexibility of feather parts.

The uropygial secretion also has antibacterial and anti-mycotic properties (Pugh and Evans, 1970*b*) and hence is thought to regulate the microflora of the plumage (Jacob and Ziswiler, 1982). It also has an odorant and/or pheromonal function in petrels, Musk Ducks (*Biziura lobata*), Kakapos (*Strigops habroptilus*) and other species. Since the sense of smell is better developed in birds than was formerly realized, these roles deserve more study.

Ear glands

Shallow acinar holocrine sebaceous glands are located in a fold of skin on the floor of the ear canal (Menon and Salinukul, 1989). Their structure at all levels and their secretion differ greatly from those of the uropygial gland and the epidermis. Their metabolic pattern is oriented toward lipogenesis and their cells do not disintegrate completely. The ear wax, a mass of partially lysed cells, appears to trap extraneous particles and to keep the ear canal clear.

Vent glands

Many birds possess small, simple, tubular glands on the lips of the vent, either outside or deeper within (Quay, 1967; King, 1981). The glands open directly onto the surface of the stratified, squamous epithelium. Unlike the uropygial and ear glands, the vent glands secrete only mucoproteins. During the breeding season, they hypertro-

phy and undergo histochemical changes which suggest that the secretion serves in reproduction, possibly in the mechanics of internal fertilization (Menon *et al.,* 1987).

FEATHERS

Structure

Feathers are the most conspicuous, complex, and varied integumentary derivatives of birds. They are one of the defining characters of the Class Aves, even though they were also present in the early Cretaceous dinosaurs, *Protarchaeopteryx robusta* and *Caudipteryx zoui* (Ji *et al.*, 1998). Like hair, feathers are produced and supported by follicles in the skin. The basic plan of a feather consists of a shaft with regularly spaced branches on either side. The shaft has a short, tubular basal portion (calamus) implanted in the follicle and a much longer, pith-filled portion (rachis) above the skin. The branches (barbs) along the rachis collectively form sheets or vanes, the most visible part of a feather. Many feathers also have an accessory known as an afterfeather on the underside, consisting of an auxiliary shaft and lateral barbs, attached to the upper end of the calamus.

A barb repeats most of this plan, having a central axis (ramus) with many, closely spaced branches (barbules) on either side. The barbs and their barbules determine the nature of the vanes. Each barbule is basically a stalk of single cells, serially differentiated along its length. Several cells at the base are compressed and fused, while those beyond are more cylindrical and jointed. Many of the cells are enlarged into various projections at their distal ends.

The simplest barbules are short and tapered to the tip with only slight distinction between the cells and few, if any, projections. Vanes with such barbules are flat, as in ordinary body feathers, but with an open texture.

Downy (plumulaceous) barbs are slender, flexible, and fuzzy, creating vanes with a thick, fluffy texture. Their barbules have a long distal portion that resembles a bamboo stalk, with small outgrowths at the nodes of some of the cells. These tiny prongs somehow keep the barbules from becoming en-

tangled and matted. In this way, the barbs remain fluffy, trapping air in the plumage for thermal insulation. Additional structural factors influence the fuzziness of the barbs and hence their insulative value (Lucas and Stettenheim, 1972). Plumulaceous barbules are not primitive or deficient as they are sometimes thought to be, but specialized for maintaining downy texture.

Pennaceous barbs, though homologous, are thicker and stiffer, close together and parallel, creating vanes that are firm, flat, and closely-knit. Their barbules, likewise closely spaced and parallel, differ on opposite sides of a ramus. Those along the distal side of each barb reach across and interlock with those on the proximal side of the next higher barb in a vane, using an assortment of cellular projections (barbicels). This creates a strong, flexible, self-adjusting mechanism that keeps the vane intact. Other barbicels affect air flow, water repellency, appearance, and other properties. These features vary within and among feathers according to functional requirements. They are best developed in the outer remiges and rectrices (wing and tail quills), which are subjected to the aerodynamic stresses of flight (Lucas and Stettenheim, 1972). In body contour feathers, the hooklets and other barbicels are commonly reduced or absent; although the barbs here do not interlock, they are kept properly aligned by stiffening flanges at their bases.

Studies on the origin of feathers have focused on the structure of the earliest feathers and their initial role. Downy structure is taken to indicate that they arose for thermal insulation and pennaceous structure is taken to indicate flight. Both types of barbules have been said to be primary, yet it is difficult to imagine how either could have evolved from the other. They are both specialized, but for different ends, the one for holding the barbs together and the other for keeping them apart. It seems more reasonable to assume that both types evolved from simple barbules with little or no differentiation (Becker, 1959).

Properties and composition

In order for birds to fly, their feathers must be light and strong. They must also resist wear and damage because they are replaced only infrequently, at regular molts, and lost or broken feathers impair flight or other functions (Bonser, 1996*b*). In addition, feather parts must have the right degree of stiffness or flexibility according to their roles. These properties depend on a part's cross-sectional shape and internal construction (Rutschke, 1966*a*) and on the keratin that constitutes it.

Feathers are about 90% protein, mostly beta-keratin. This is stronger, yet more flexible than other avian keratins, owing to differences in amino acid composition and molecular structure (Brush, 1980*a, b*). The molecular weight of feather keratin is almost 30% less than that in scales, beak, and claws (Brush, 1978*a*). The keratin even varies in amino acid composition among feather parts, related to physical properties required at each site. The remainder of a feather consists of various nitrogenous non-keratin compounds and small amounts of lipids and heavy metals, especially mercury (Brush, 1978*a*).

Structural types

Feathers occur in great diversity, thanks to the possibilities afforded by their basic plan and the properties of keratin as a building material. Every part of a feather, from the shaft to the barbicels, varies in form and size. Several structural types of feathers can be distinguished but they are not absolute because most of them intergrade with each other (Lucas and Stettenheim, 1972). They differ in: implantation (in the skin or on the skeleton), thickness and stiffness of the rachis, relative sizes of rachis and barbs, type, spacing and placement of barbs, symmetry and curvature of vanes, presence and structure of an afterfeather, and melanin pigmentation.

Two types of feathers have unique properties that deserve mention. Powder feathers are modified downy or pennaceous feathers that shed a fine powder of microscopic keratin granules. The powder is derived from cells that surround the barbules in a growing feather, and in some birds also from disintegration of feather parts (Schüz, 1927). It is used in preening and, being non-wettable, is thought to confer water-

proofing on the ordinary feathers. Powder feathers occur in the Kagu, mesites (Mesitornithidae), herons and bitterns, pigeons, most cockatoos, and some parrots and sandpipers.

Filoplumes are hairlike feathers that do not grade into the other types. They have a slender, glistening, unpigmented rachis with a few short barbs or barbules at the tip. Filoplumes are always situated close beside other feathers, more numerously with the flight feathers than elsewhere. They are the only feathers that lack muscles.

Coloration

The evolution of feathers has involved several developments besides the structures, themselves. The most conspicuous has been the elaboration of systems for producing colors and patterns. Most birds are diurnal and they rely heavily on vision for orientation and communication. Much of their social and sexual behavior depends on visual signals from their plumage and other epidermal structures. The color mechanisms are best known in feathers, where they are most pronounced and easiest to study, but they are similar elsewhere.

Birds exhibit both pigmentary and structural colors, the first by far the more common. Melanin pigments are produced in birds in the same way as in other organisms and are deposited as black or dark brown granules within the epidermal cells. They create color effects by themselves, in combination with other pigments, and as the physical basis for structural colors. In addition to their visual roles, melanins add strength and abrasion-resistance to keratins (Burtt, 1979; Bonser, 1996b). They also serve in thermoregulation by absorbing infrared and solar radiation, and possibly radiating heat away from the body.

Carotenoid pigments are derived from carotenes in plant foods in the diet, chemically altered, and deposited diffusely in fat globules in feather cells (Brush, 1978b). Birds do not have distinct xanthophores as in fish, amphibians, and reptiles (Spearman and Hardy, 1985). Several types of these bright yellow or red pigments are known in epidermal structures of at least half the orders of birds. Within the feathering, they occur almost exclusively in contour feathers. In addition to their prominent visual roles, they are involved with vitamin A in vision and possibly with reproduction in the yolk. Carotenoids and melanins combine to produce colors such as dull green.

Porphyrins are iron- or copper-containing pigments derived by catabolism in the liver and by synthesis from glycine (Brush, 1978b). As some of them are labile when exposed to light, they tend to occur in feathers protected from sunlight. This may also explain why they have not been reported in other epidermal structures.

Structural colors in feathers are created by the scattering of light by ordered layers of melanin granules or air vacuoles within the keratin of the barbs (Dyck, 1976, 1987). Such colors in bare skin and epidermal outgrowths are produced by ordered arrays of collagen macrofibrils (Prum et al., 1994). In feathers, these colors are either constant or iridescent (i.e., changing with the viewing angle). Constant structural colors of feathers result from constructive interference between light waves scattered coherently by the minutely spongy core (medulla) of the barb rami (Prum et al., 1998, 1999). Iridescent colors result from interference on the same scale within the distal pennaceous barbules (Durrer and Villiger, 1962; Rutschke, 1966b; Durrer, 1977). The systems that produce them must be extremely precise to achieve their effects, with dimensions in some cases varying less than 0.01 μ.

Pigmentary colors plus both kinds of structural colors can occur in patterns in the same feather, showing the elaborateness of avian color systems. Moreover, they are capable of either repeating exactly from one set of feathers to the next or varying to produce apparent differences between sexes, age groups, and populations.

Feathering

Feathers cover the entire body of most adult birds, except for the beak, lower legs, and feet. Their quantity and size vary with body mass among species, ranging from fewer than 1000 feathers in small hummingbirds to more than 25,000 in swans.

Feather mass averages 6% ($r = 4$–8%) of body mass for most birds.

Despite appearance, feathers do not arise uniformly over the body. Contour feathers are arranged in discrete areas (tracts) separated by bare or sparsely feathered zones (apteria). This layout is as basic and characteristic a feature of all birds as feathers themselves. Tracts cover only about one-half the skin area of land birds, more in waterbirds. Even in species where the tracts seem to cover the body completely (adult ratites, penguins, screamers), their boundaries are clearly defined in late embryos.

Eight major feather tracts can be distinguished but their configuration varies widely among groups of birds (Nitzsch, 1867; Clench, 1970). The various arrangements have been hypothesized as adaptations for reducing the total weight of the feathering, accommodating the movements of the body and the feathers, thermoregulation via radiation of body heat from the apteria, and accommodating apterial dermal muscles that counteract the feather muscles (see below) in shrinking the tracts (Homberger and de Silva, 2000).

Within each tract, the feathers are set in rows and spaced regularly in each row. The arrangement at the borders of the tracts tends to be less regular than in the interior. Down feathers may either replace contour feathers at the ends of the rows (*e.g.*, galliforms) or reside among contour feathers (*e.g.*, ducks).

Feathers vary in a regular manner within and among tracts in size, shape, and color pattern. They are generally fanciest on the head, neck, or tail, the most conspicuous parts of the body when a bird is standing, perched, or swimming. The largest feathers are usually the quills on the wings and the tail, where modifications for flight are paramount.

A unique community of organisms occupies the protected microhabitat formed by the feathering and the skin. Bacilli (Burtt and Ichida, 1999) and fungi (Pugh and Evans, 1970*a*) live on the feathers and degrade them. Mites, bird ticks, feather lice, and other insects feed on flakes of skin, fragments of feathers, scales, tissue fluids, and blood. They damage the feathers, cause

diseases and skin infections, and transmit diseases.

Follicle and muscles

Follicles are cylindrical sockets in the skin that produce feathers and hold them tightly around the calamus. Their keratinized lining is surrounded by germinative epidermis and dense collagen with elastic fibers (Ostmann *et al.,* 1963; Lucas and Stettenheim, 1972). The outer dermal tissues are vascularized and well supplied with general somatic sensory fibers (Stammer, 1961). Since follicles and their accessories are not known in reptilian skin, they are an important innovation associated with feathers.

Feathers of all types except filoplumes are actuated by tiny bundles of smooth muscle that link adjacent follicles. The muscles attach to the follicular wall by way of elastic tendons that ramify into the collagen. Every follicle in a tract is generally connected to several others nearby. Antagonistic pairs of feather muscles cross each other, and the repetition of these units forms a network across the tract (Lucas and Stettenheim, 1972). Isometric contraction on the elastic fibers appears to squeeze the follicle around the calamus, holding it in the socket. Isotonic contraction raises, lowers, or rotates the feathers or pulls them together, depending on the arrangement of the muscles. Fat deposits in the dermis and subcutis act as hydrostatic cushions on which the feathers move as levers (Homberger and de Silva, 2000). The musculature varies in size and complexity according to feather size and function. The remiges and rectrices have extra muscles for adjusting their position; feathers used in displays have more musculature than non-displayed feathers, especially in males (Osborne, 1968). Thanks to the muscular network, feathers are positioned in a regular manner across a tract.

The system for operating the feathers must have sensory input to know what they are doing. Herbst corpuscles situated close beside the outer wall of a follicle detect a feather's position and the forces pressing on it (Borodulina, 1966; Dorward, 1970; Gottschaldt, 1985). Contour feathers each

have 1–2 of these receptors and filoplumes have more.

Follicle morphology is nearly the same for all kinds of feathers in many kinds of birds. Highly conservative, it varies only in size and in feather musculature. A follicle's histology gives no hint of the kind of feather that will grow from it, let alone the details of that feather.

Feather growth and replacement

Embryology. Feather rudiments begin to form in an embryo through a series of inductive interactions between local thickenings of ectoderm and dermis. Protein growth factors induced in the ectoderm regulate the spacing of the rudiments in rows (Noramly and Morgan, 1998). Each rudiment then elongates, becoming a thimble of epidermis over a finger of dermis. The epidermis begins differentiating, first into three concentric layers and then within the intermediate layer. The epidermal ring at the base of the rudiment invaginates, separating the feather germ from that of the follicle. As the follicle deepens, cell division becomes localized in a germinal ring at its base, the source of subsequent growth.

A feather forms as an elongating cone of epidermis around a core of vascularized mesenchyme. The innermost epidermal layer encloses the core and is lost with it when the feather is fully grown. The outermost layer forms the sheath, which is likewise lost when a feather opens. It is the intermediate layer that differentiates into all the feather parts, from barbs to calamus (Lucas and Stettenheim, 1972). Owing to this developmental plan, a feather has been considered homologous with the intermediate layer of a reptilian scale and its sheath homologous with the corneous layer of a scale (Spearman and Hardy, 1985), but these equivalencies are open to question.

As cells are pushed upward from the germinal ring, they cease dividing, undergo intense protein synthesis, enlarge, and alter their shape. Feather parts form by changes in, and fusion of, cells. The distal and peripheral parts arise first, followed by progressively more proximal and central parts (Lillie, 1942). Barbs at the tip of a feather are thus the first parts to be formed and the

calamus is the last. Hormones and other factors that affect feather growth exert their influence in this sequence.

Feather parts begin to keratinize after their morphological development is complete, again starting at the tips. The process is similar to that in reptilian epidermis although it happens much later. The rachis arises on the dorsal side of the feather tube and the barbs, lengthening basally, grow around to join it. The shaft and barbs of an afterfeather, if any, arise on the ventral side of the tube. Barbules likewise form in place and join the rami. Barb formation eventually ceases and the final production from the germinal ring yields a simple tube, the calamus.

After a chick hatches, the feather sheath dries, cracks, and flakes off, allowing the barbs and barbules to unfurl. Cell division ceases in the germinal ring, leaving a papilla of epidermis and dermis as the germ (blastema) for the next feather.

Growth of subsequent feathers. A follicle usually produces a series of feathers during the life of a bird. As the key event in molting, changes in photoperiod and hormone levels activate the blastema to resume mitosis and form a new collar of germinal epidermis. A replacement feather often starts growing before the old one is shed, and pushes it out of the follicle (Watson, 1963). Development of the new feather resembles that in the embryo except that the follicle is already formed, the feather grows from the blastema, and its structure is more complicated. Since the juvenile feather is larger than the natal down, its tip is completely grown and above the skin before the lower parts have finished or even started to form. As soon as the upper barbs are finished, they start to emerge from the sheath.

A developing feather is supported by a reticulum of mesenchyme containing blood vessels and a network of motor fibers. This is entirely resorbed during the last phase of growth (Lillie, 1942), leaving no blood vessels or nerves in a fully-grown feather. The remaining dermal papilla and its epidermal covering constitute the blastema for the next feather.

Molts and plumages. Chicks of most species produce at least one set of natal downs,

even those that are naked at hatching. Thereafter, birds produce several more sets of feathers at regular intervals throughout their lives. This practice of periodically losing and replacing a complete, mature epidermal generation appears homologous with the skin-shedding of lizards and snakes. Each generation of feathers is a plumage and the process of feather loss and replacement is a molt. In most birds, molting takes place in a regular sequence within and among tracts and replacement of all the feathers takes about two months.

Birds typically molt into their first set of contour feathers when they are 1–3 wk old. This set is replaced within a few months by another, which is held until one year of age. Many species, particularly songbirds, replace some of the body feathers once more before the breeding season, gaining a more colorful appearance. The entire feathering is replaced after the breeding season every cycle (usually one year). Each new plumage changes a little in appearance until the adult, constant condition is attained. In songbirds, this usually happens within 1–2 yr but in other species it may take up to seven years.

The production of new feathers requires much nutrition and energy, and may impair flight or swimming. Accordingly, molting is usually timed so as to interfere the least with breeding and migration, if any, the other demanding events in the annual cycle. The fourth innovation with feathers, therefore, is the molt process and the photoperiodic and hormonal mechanisms that control it (Voitkevich, 1966; Payne, 1972).

Incubation (brood) patches. Birds of nearly all species temporarily shed their feathers on single or paired areas of the breast or abdomen early in the breeding season. The bare skin increases in vascularity, which aids it in transferring body heat for incubating the eggs and brooding the chicks. Development of these incubation (brood) patches is prompted by rising levels of estrogen. They form in whichever sex cares for the eggs and young, usually females but often males as well. The lost feathers are replaced in the complete molt following the breeding season.

Functions

The anatomical and physiological support systems for feathers have evolved presumably because feathers are very useful to birds. Feathers serve more than twenty different functions in birds as a whole (Stettenheim, 1976). Even within an individual feather, the parts are commonly modified for different roles. An ordinary body contour feather, for example, shields the body, repels water, and contributes to the appearance on the exposed, pennaceous part of the vanes, and provides thermal insulation in the downy part underneath. This versatility is further evidence of the potential afforded by the basic structural plan with keratin as the building material.

Feather functions that are universal in birds include thermal insulation, control of body temperature, physical protection against the environment, tactile sensation, and appearance and visual signaling. Downy feathers, wholly or in part, provide thermal insulation by trapping air against the skin. Contour feathers help control body temperature by adjusting position so as to retain heat or let it escape. Bristles, semibristles, and contour feathers screen the eyes and ear openings and give other physical protection on the head and trunk. Filoplumes detect air currents acting on flight or contour feathers; bristles and semibristles on the head appear to detect obstacles or prey. Color patterns on single feathers or groups of feathers determine appearance and send a myriad of visual signals for identification or display. Modifications for display are more numerous and extreme than those for any other purpose.

In most birds, feathers are essential for flight and water repellency. Modifications for flight range from the overall shape of the wing and tail to the shape of individual feathers and tiny details of the barbules. Water repellency depends on chiefly on the meshwork of pennaceous barbs and the uropygial secretion. Other common feather functions are: propulsion and buoyancy in swimming, support via a strengthened tail, brushing the preen gland secretion on the bill, cleanliness of the head, aiding hearing, and making sounds in flight.

CONCLUSIONS

The integument of modern birds has been modified in a wide variety of ways, differing in morphology, histochemistry, and function. Its derivatives are far more diverse in birds than in reptiles. In addition, early embryos have the potential to produce different structures from the same piece of integument, as shown by transplantation experiments (*e.g.,* Cairns and Saunders, 1954; Sengel *et al.,* 1980).

The integument's capability to produce many kinds of outgrowths has probably increased during the history of birds. Integumentary experimentation in ancient reptiles began at least by the late Triassic, as shown by the long, mid-dorsal scale-like structures on *Longisquama insignis,* a presumed thecodont (Feduccia, 1996). The capacity for such tryouts must have been a prerequisite for the invention of feathers. After *Archaeopteryx,* various Cretaceous dinosaurs developed feathers or other outgrowths in the form of densely packed filaments or fibers (*Pelecanimimus polyodon,* Pérez-Moreno *et al.*, 1994; *Sinosauropteryx prima,* Chen *et al.,* 1998; *Beipiaosaurus inexpectus,* Xu *et al.,* 1999*a*; *Shuvuuia deserti,* Schweitzer *et al.*, 1999, *Sinornithosaurus millenii,* Xu *et al.,* 1999*b*).

The evolution of feathers and their accessories as we see them today has involved several major innovations. First are feathers themselves, which are diverse and structurally complex at levels from molecular to gross. Second are the follicles, with their intricate musculature and innervation. Third are the systems for creating colors and patterns, far advanced over those in fish, amphibians, and reptiles, and fourth is the layout of feather tracts. Last are the process and control of molting, which transcend the integument. Feathers are produced not just once, but repeatedly during the life of a bird, and successive feathers from the same follicle may vary with age or plumage. Considering all these morphological and physiological aspects, feathers are the most complex integumentary structures of all vertebrates.

ACKNOWLEDGMENTS

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