Glandular Functions of Avian Integument: An Overview

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Abstract This paper attempts a synthesis of available information on glandular functions of avian integument, a topic which has not received adequate attention. Morphologically distinct glands in the skin of birds are limited to the uropygial gland, ceruminous (wax) glands in external ear canal and integumentary glands of the vent (anal glands). Of these, only the uropygial gland has been studied in a considerable manner., whereas taxonomic and functional status of the latter two remain unclear at the present juncture. The holocrine ceruminous glands, though lipoid producing, differ greatly from the uropygial gland in structure and functions. The glands of the vent are the only mucoid producing glands found in avian skin. Thus the avian integument, on gross examination, appears to be poorly endowed with glands compared to that of other vertebrates. However, cells of avian body epidermis show a unique lipogenic potential, producing both keratin and sebum like lipoid material. Aptly termed as 'sebokeratocytes', the epidermal cells in glabrous portions of skin as well as specialized regions such as the rictus and toe web exhibit a remarkably high degree of sebogenic activity. Possible significance of this epidermal lipoid secretion in enhancing water repellancy of skin; preventing excessive cutaneous water loss; screening off harmful radiations, imparting colouration to the skin etcetera are discussed. In light of the widespread nature of epidermal lipoid secretion and the knowledge that many specialized types of feathers in various species produce and maintain a supply of material such as powder, grease or both, used in cosmetic purposes, the concept of secretory activity is reexamined. It is proposed that on a functional basis, the secretory epidermal regions and specialized feathers be considered as glandular units of skin, though they lack the conventionally accepted glandular profile.

Introduction

Textbook descriptions of avian skin customarily emphasize the paucity of integumentary glands that supposedly characterise the class. However, an assumption that the skin of birds is completely aglandular with the sole exception of the uropygial gland (Hodges 1974) rest on feeble grounds. The wealth of information on secretory functions of avian epidermis scattered in specialized literature seldom catches the eyes of ornithologists. This summarization is aimed at compiling presently available information on the topic to illuminate the widespread nature of secretory activities of avian epidermis, and also to reevaluate the concept of secretion based on function, rather than conventionally accepted glandular morphology and structure.

Organised Glandular Units

The discrete secretory units of avian skin having the benefit of anatomically and

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histologically accepted glandular profile include the uropygial gland, the anal glands (of vent) and the wax glands of the ear canal (Greschik 1914, Quay 1967, 1977, Lucas & Stettenheim 1972, Stettenheim 1972).

Uropygial gland

There is an extensive literature on anatomical and histological (Paris 1913, Hsu 1936, Lucas & Stettenheim 1972) histochemical (Cater & Laurie 1950, Das & Ghosh 1959, Kanwar 1961, Bhattacharyya 1972, Ghosh & Bhattacharyya 1978) and biochemical (Jacob 1978) aspects of the uropygial gland (Preen gland, oil gland) of various species. Aspects of embryonic development (Gomot 1959) and tissue interactions in development (Bride 1978) of the uropygial gland of duck are also reported.

The gland located above the base of tail, has two lobes separated by an interlobular septum and surrounded by a connective tissue capsule. The numerous alveoli opening into the paired central lumen radiate from the centre and end blindly against the capsule. Thin trabaculae extending from the capsule separate adjacent alveoli. On the basis of histological and histochemical characters, the secretory tubules have been divided into three zones, namely, peripheral, intermediate and inner, or zones I, II and III respectively (Stern 1905, Lucas & Stettenheim 1972). While zones II and III are often indistinguishable from one another, zone I differs in having less osmiophilic reaction and paucity of enzymes like esterase and acid phosphatase. The diameter of the tubular lumen increases from zone I to III. Light microscopy showed that the secretory layer consists of two parts, one where the sudanophilic secretion globules are formed and stored, and the other where the cells get hypertrophied; the globules coalesce and cell membranes break and release the contents into the glandular lumen (Fig. 1). Speculations on the role of various cellular organelles in the secretory process (Hsu 1935, 1936; Bowen 1926, Cater & Laurie 1950, Das & Ghosh 1959, Kanwar 1961) have been put to rest with transmission electron microscopic study (Wagner & Boord 1975) which showed that the smooth endoplasmic reticulum is involved in sebogenesis. In the terminal cells, apparently non-pycnotic nuclei and intact mitochondria are ejected out with secretion globules and cell contents (Menon *et al.* 1981). Detailed and excellent biochemical analysis of the composition of secretion from large number of avian species is available. The predominant components of preen gland secretion are monoester waxes, though di- and triester waxes are also found in the oil (Jacob 1978). Uropygial gland is absent in ratites and some pigeons (Jacob 1978), but is relatively well developed in aquatic birds (Kennedy 1971). A progressive simplification of the secretion composition associated with the classification scheme and representing phylogenetic sequence has been brought to light and possible taxonomic significance of glandular products has been suggested (Jacob 1978). Major functions of the secretion are in plumage maintenance and aiding and abating water repellency of feathers, providing a source of Vitamin D (Rijke 1970, Hou 1928, Uva *et al.* 1978) and prevention of bacterial and fungal growth on the skin (Jacob 1978). The secretion is odorous in petrels, musk ducks and incubating hoopoes (Stettenheim 1972) where it may serve as a sex attractant or even repellent for defence. Possible role of the secretion in olfactory communication has also been alluded to (Jacob 1978). Since olfactory sense has been implicated

in navigation, homing and foraging at least in some birds including Petrels (Papi 1976, Grubb 1979), this deduction merits consideration. Speculations on the preen gland as being a site of steroidogenesis (Ghosh & Bhattacharyya 1978) has been disputed recently (Kotak & Padmanabhan 1980). The normal functioning of the uropygial gland is found to be influenced by various hormones (Kar 1947, Maiti & Ghosh 1972, Bhattacharyya *et al.* 1977, Chakraborty *et al.* 1979, Menon & Kotak 1981) but the relative significance of these hormones are yet to be assessed.

Anal glands (Integumentary glands of the vent)

The widespread occurrence of the integumentary glands of the vent region among various taxonomic groups of birds was illuminated by Quay (1967). These simple or branched tubular glands opening directly onto the stratified epidermis of the vent region (Fig. 2) are truly epidermal glands, and not to be confused with the cloacal glands. The secretory products predominantly consist of mucopolysaccharides; lipids are absent within the gland cells or in the secretion (Quay 1967). Ultrastructurally, the cells of anal gland resemble other mucoid producing cells in features such as numerous apical microvilli; prominent golgi complex, endoplasmic reticulum and large number of vesicles containing secretory products of varying electron density (Menon & Salinukul, in preparation). Preliminary histochemical studies (Shah, Jani & Menon, unpublished results) suggest that the anal glands of female House Sparrow, *Passer domesticus* are hyperactive during the breeding season, but not while incubating. The large gland in the cloacal-anal region of the Japanese Quail, *Coturnix coturnix* is known to produce a 'maringue-like froth', mucoid in nature, purportedly associated with the mechanics of internal fertilization (Coil & Wetherbee 1959). Quay (1967) suggested that this gland is a member of the anal gland series and not of the cloacal wall. The gland reportedly respond to androgen treatment and it has been suggested that the 'foam' condensing on the droppings may be of value as a marker of territory and probably facilitate locality finding in the wild birds (Schleidt & Shalter 1972). However, interpretation of the functional and evolutionary significance of anal glands still appears to be difficult (Quay 1977).

Ceruminous glands of external ear canal

A row of shallow, acinus shaped glands extending longitudinally into the ear canal cavity has been designated as the sebaceous (wax) glands of the external ear canal (Lucas & Stettenheim 1972). Though holocrine in nature, these glands differ greatly from the uropygial gland in structure and metabolic aspects. Though vacuolar spaces are found in the cells that stain with lipid specific stains, the fat spheres are smaller in dimensions (Lucas & Stettenheim 1972). The stratification of epithelium within the gland also differs from that of the skin epidermis (Fig. 3). In domestic fowl, a row of 5-7 glands are located on each lobe of a bilobed skin fold on the floor of the ear canal. At the fine structural level, the cells show progressive accumulation of moderately osmiophilic masses of lipids, in which respect they differ from the uropygial gland or general body epidermis wherein the lipids are electron loose in character (Menon & Salinukul 1982). The ear wax glands appear to bear more similarities with the holocrine glands of re-

ptilian skin than with the rest of avian integumentary glands. Functional and taxonomic significance of the wax (ceruminous) glands is far from clear at this juncture.

Secretory Activity of the Body Epidermis

After Vericak (1938), who noticed presence of fat in epidermis of toe web in chicken, elaboration of lipoid matter by avian body epidermis has been reported independently by various investigators. Lucas (1968, 1970) recognized this lipogenic activity as active secretion and emphasised the secretory nature of the epidermal cell. Since then, active lipogenesis has been documented in the epidermal cells of the rictus, comb and interdigital web of the domestic fowl (Lucas & Stettenheim 1972, Ishida *et al.* 1973) epidermis of pigeons (Jacob & Grimmer 1971, Shah & Menon 1973) and certain ciconiform and Gruiform birds (Shah *et al.* 1977, Menon *et al.* 1979, 1980). Jacob & Pomeroy (1979) believe that certain components of plumage grease of the Marabou Stork *Leptoptilos crumeniferus*, such as cholestanol and cholestanon which are not detected in the preen gland secretion are derived from the epidermis. Studies of Lavker (1975) using labelled fatty acids showed that the lipids are actively synthesised in the basal cells and not taken up from the dermis, and that incorporation of fatty acids continue well into the transitional layer. Lipogenesis, though an intrinsic property of avian epidermal cell- aptly named a 'sebokeratocyte' (Freinkel 1972, Wrench *et al.* 1980)-is manifest to a high degree in certain locations of the body such as the rictus (Figs. 4 & 6) and toe web (Fig. 5) of chicken and the cere of pigeons (Lucas 1980, Wrench *et al.* 1980, Menon *et al.* 1981, Menon & Aggarwal 1982). In the histological profile, superficial similarity between the hypertrophied fat laden cells of rictus and the uropygial gland are striking (Compare Figs. 2 and 4). The profile of lipoid spheres in epidermis from the free edge of the web, reticulate scales on ventral surface of the web and those on the foot pad bear similarities (See Lucas & Stettenheim 1972 and Sawyer & Borg 1979) but it is distinctly different in epidermal layers of the hard dorsal reticulate scales on the web. Here the epidermis is characterised by a paucity of lipids except for the basal cells (Lucas 1980, Menon & Aggarwal 1982). Considering the widespread and unique lipogenic property of avian epidermis, Lucas (1980) used a revised terminology wherein the basal, intermediate and transitional layers are included under *Stratum germinativum*. This terminology has the merit of a functional basis, i.e., endogenous generation of lipoid matter by the cells, and highlights the point that avian epidermis is distinctly different from that of the rest of vertebrates.

In general, the epidermis of apteria show higher degree of sebogenic activity than that in feather tracts. This inverse relation between the degree of sebogenesis and insulation of skin has indeed been confirmed for regions of body that lose feathers and secondarily become naked, such as the incubation patch of house sparrow where the hyperplastic epidermis exhibit an enhanced lipogenic activity (Jani 1979). This is probably true of the patch of canary also (See plates in Kern & Loruzzi 1979). In certain species of Storks and Ibises, formation of secondarily apteric regions due to permanent feather loss on head/neck region characterise attainment of maturity. A tremendous increase in lipoid secretion by epidermis accompanies such changes in the

capital region of the Painted Stork *Ibis leucocephalus* (Shah *et al.* 1977) and the White Ibis *Threskiornis melanocephala* (Menon *et al.* 1979). A similar inverse relation between structural complexity of cutaneous appendages and the epidermal lipoid secretion is seen in case of the Sarus Crane *Grus antigone* where epidermis from the bristle bearing areas of skin show relatively more lipogenic activity than the feathered parts (Menon *et al.* 1980). Bristles are structurally simpler than contour feathers which they replace in the head region during post-juvenile moult in the Sarus Crane, thus exposing the skin which acquire bright pigmentation and a papillose nature. The secreted lipids act as a solvent for the carotenoid pigments in the epidermis (Fig. 7) thus aiding in visual signalling (Shah *et al.* 1977) as well as screening off harmful ultraviolet radiation (Spearman 1980). Lucas (1970) proposed that the uropygial gland secretion takes care of the plumage while the epidermal secretion is enough to maintain the rest of the skin.

At least in one instance epidermal secretion is involved in cosmetic colouration of the plumage. Uchida (1970) found that in Japanese Crested Ibis, *Nipponia nippon*, a 'black substance' produced by a specialized region of skin under the face, is smeared over the plumage by a characteristic daubing behaviour during the breeding season. Thus the white birds undergo a colour transformation without a moult, resulting in the grey forms. Knowledge of seasonal changes in epidermal secretory activity in this bird should be highly interesting.

Feather Production as a Secretory Function

Quay (1972) considered feathers as 'secreted products' of avian skin, derived from the proteinaceous glandular stem. Shah *et al.* (1977) opined that in view of the complex array of morphogenetic events and tissue interactions involved, formation of feathers be considered as 'organogenesis' rather than secretion. In light of these views, it is of interest to consider feathers with a distinct function of generating material that is used for waterproofing and plumage maintenance, or cosmetic (and other unknown) functions, the like of which in vertebrates are conventionally discharged by specialized glands of the integument rather than by cutaneous appendages. Notable in this category are the powder feathers that shed fine keratinous powder matter. Though certain semi-plumes and downy portions of contour feathers usually produce some amount of powder, in its most specialized form, the powder feathers are downy. Extreme development of powder feathers is seen in Tinamous, Herons, Mesites and Cuckoo-rollers (Stettenheim 1972). Use of powder down material by birds in dressing the plumage has been confirmed by Pycraft (1908), Wetmore (1920) and Hindwood (1933). The powder granules also affect the plumage colouration by making it dimmer or paler (Stettenheim 1972). In Herons, powder downs occur clumped together in the breast and flank regions, in patches with as many as 120–160 feathers per square centimeter (Fig. 8). The calamus above skin surface is short and creamy in appearance, whereas the unsheathed portions are white in colour (Fig. 9). These feathers, unlike the rest of the plumage, are in a state of constant growth and shed a copious amount of powder. Neutral lipids are abundant in the pulp and epithelial cells of powder downs of Herons (Menon, unpublished observation). The functional similarity between these feathers

and oil gland tempted Wetmore (1920) to suggest possible evolution of the gland through amalgamation of separate feathers, a hypothesis since rejected owing to obvious structural differences between the two. However, it is interesting to visualise these feathers as glands which are everted out, instead of having the usual glandular feature of being invaginated into the dermis. The continuous growth, loss of 'secreted material' and lack of restitution of 'secretion' or synthesis of powder granules by the same cells indicate a holocrine nature. Of further interest are the fat quills in Columbiformes such as the Nuremberg Swallows and the South German Shield Pigeons (Eislen 1939, Levi 1952); the feathers of Pied Imperial Pigeon, *Ducula bicolor* producing a creamy matter (Abdulali 1966, Berthold 1967) and the resinous secretion on the back of the Heart-spotted Woodpecker, *Hemicircus canente* (Bock & Short 1971). The feathers of *Ducula bicolor* appear to be intermediate between powder feathers and fat quills. Investigations of Berthold (1967) revealed that the creamy matter is an adherant that glues the barbs together and holds relatively large particles of powder (Fig. 10), both of which are removed when treated with fat solvents (Fig. 11). It remains to be confirmed whether all the lipid matter is intrinsically produced by the feathers or it originates in part from the uropygial gland. Much remains to be learned about the resinous secretion on the back of *Hemicircus canente* also. An odorous matter clumping the bristly feathers together in a tuft is present on the back of this bird (Ali 1969). The odour disappears in preserved skins (Ali & Ripley 1970). Bock & Short (1971) did not find any discrete glandular structures or ducts opening onto the epidermis here. The possibility of the secretion originating from the feathers themselves appear strong, though an origin from the body epidermis cannot be completely ruled out at this juncture. Detailed studies are warranted to ratify this assumption and to elucidate the chemistry of the secretion.

The use of products such as powder, fat and probably resin elaborated by the feather forming tissue itself, for cosmetic functions or plumage maintenance indicate that there is only a thin line of demarcation between the process of secretion and organogenesis of cutaneous appendages in the avian skin. Examination of diverse glandular units ranging from uropygial gland through fat quills, fat and powder producing feathers of *Ducula*, specialized powder downs of Herons and others, and contour feathers of most birds which produce some amount of powder, illuminate possible transition from lipid secreting to keratinizing units. Thus it becomes imperative that consideration of feathers as 'secreted products' be accepted on a functional basis. In this context, attention may be drawn to the parallel between the hard secreted 'rods' of vertebrate integument such as the mammalian hair and the condensation of secreted matter in reptilian holocrine glands, so elegantly drawn by Maderson (1972). The powder downs or fat/resin producing feathers appear to fit into such an evolutionary scheme as they form the intermediate stage between that seen in reptiles on one hand and in mammals on the other.

Figs. 1-3. Cytological features of Zone 1 of pigeon urophylial gland tubule showing progressively enlarging lipid droplets from basal to transitional cells. 1μ thick section of glutaraldehyde fixed, plastic embedded material. Methylene blue staining. $\times 750$. 2. Histology of the anal glands of breeding female House Sparrow. a. Paraffin section, Masson's trichrome staining. $\times 800$. b. Low power electron micrograph of secretory cells of anal gland. $\times 2100$. 3. Histological profile of wax glands of ear canal from Spotted sandpiper. Paraffin section. Masson's trichrome stain. $\times 90$.

Abbreviations: AC, Anal canal; GE, Germinal epithelium; AG, Anal gland; I, Intermediate cell; B, Basal cells; LD, Lipid droplets; C, Corneum; N, Nucleus; D, Dermis; O, Opening of gland; E, Epidermis; OS, Oral surface; ES, External surface; T, Transitional cell.

Figs. 4-7. 4. Cytological features of secretory epidermis from rictus of domestic fowl, showing progressive cellular hypertrophy and enlargement of lipid droplets. $1\ \mu$ thick section of gluteraldehyde fixed, plastic embedded material. Methylene blue staining. $\times 1200$. 5. Low power electron micrograph of basal epidermal cells from toe web of domestic fowl. Note large lipid globules around nucleus. $\times 6400$. 6. Photomicrograph of section passing through external and oral surfaces of rictus of chicken, stained with Fat Red 7 B to show localization of neutral lipids. Note absence of staining in the oral surface (OS). $\times 400$. 7. Photomicrograph of section of skin from capital region of adult painted stork, showing abundance of carotenoids in basal epidermal cells. Frozen section, unstained. $\times 60$.

Figs. 8-11. 8. Photograph of portion of powder down patch in the breast region of cattle egret. 9. Isolated powder downs from cattle egret. 10. 'Creamy feathers' of pied imperial pigeon. Note the clumping of barbs and powder material on the vane. 11. Similar feather as in Fig. 10, after treatment with a lipid solvent. Note that the adherent and powder material have been removed.

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鳥の皮膚の腺機能 —概説—

本論文は、まだあまり注目されていない鳥の皮膚の腺機能について、得られた情報を総合しようと試みたものである。

鳥の皮膚において形態的にはっきりした腺は尾腺、外耳管の中の耳道腺及び肛門（総排泄口）の皮膚腺である。これらのうち、尾腺のみがいろいろの方法で研究されてきたが、他の2つの分類と機能は、現時点では不明確である。全分泌腺は類脂質を分泌するが、その構造および機能は尾腺と非常に異っている。そして肛門腺は鳥の皮膚に見られる唯一の粘液分泌腺である。このように鳥の皮膚は、大まかな調査では、他の脊椎動物の皮膚と比べて腺機能が貧弱であるかのように見える。しかし、鳥体の表皮細胞は独特の脂肪生成の可能性を持ち、ケラチン及び類脂質に似た皮脂分泌物を出すのである。くちばしや脚指の皮膜のように特殊化した部分だけでなく、皮膚の無毛の部分における表皮細胞は、皮腺硬蛋白細胞の名の如く、非常に高度な脂肪分泌活動を示す。この表皮類脂質分泌は次の諸点一すなわち、皮膚の水反発性を高めること、皮膚面からの著しい水分消失の防止、有害放射線の遮断、皮膚への色の伝達等一に関係していると思われるので、これを論じた。

表皮類脂質分泌の一般的性質と、いろいろな種の鳥の特殊な形態の羽毛の多くが、装飾的な目的に使用される粉末様物質、油性物質を生成しその供給を維持しているという知識を踏まえて、分泌活動の概念について再検討した。一般に認められた腺の概念にそぐわないところもあるが、機能を基準に考えれば、分泌腺を有する表皮と特殊化した羽毛は、皮膚の腺構造単位のものであると見なすことができると提案したのである。