Z. Säugetierkunde 54 (1989) 9–21

ISSN 0044-3468

Histochemistry of complex carbohydrates in the scrotal skin of the monkey *Macaca cyclopis* (Swinhoe)

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Receipt of Ms. 21. 9. 1987

Abstract

Studied the scrotal skin of the monkey, *Macaca cyclopis* (Swinhoe), by means of a series of selected histochemical methods for the detection of carbohydrates, including peroxidase-labelled lectin-diaminobenzidine procedures. The results obtained were most distinct in the two tubular gland types (apocrine glands, eccrine glands), and, to some extent, in the sebaceous glands, and the upper layers of the vital epidermis. Weak staining reactions were limited to the dermis.

The cytoplasm and free surface of the secretory cells, and the luminal secretions of the apocrine glands, and, in particular, the eccrine glands contained only very few acidic glycoproteins, including small amounts of sialic acid, but mostly neutral glycoproteins with various saccharide residues: α-D-mannose, α-D-glucose, β-D-galactose, α-D-galactose, N-acetyl-D-galactosamine in the apocrine glands; and β-D-galactose, α-D-galactose, N-acetyl-D-galactosamine, α-fucose, N-acetyl-β-D-glucosamine in the eccrine glands (superficial cells). These glands additionally exhibited small amounts of glycogen. The sebaceous glands contained glycoproteins with the following sugar residues: α-D-mannose, α-D-glucose, N-acetyl-α-D-galactosamine and sialic acid.

The secretions of the three gland types in the scrotal skin of the monkey are mixed on the surface of the scrotum, forming a mucous coat of mainly neutral glycoproteins. Their most important function may be connected with the release of volatile odorous substances after microbial degradation. The odours produced could be significant for intraspecific communication by the signalling of sexual activity. Thus, the scrotal skin of cercopithecoid species may act as a glandular organ, as hitherto assumed only for prosimians or ceboid species.

Introduction

Recent histochemical studies on the scrotal skin of different mammalian species demonstrated that the tubular apocrine glands of this specific body region have a relatively broad functional significance, and are not only concerned with thermoregulation. This is especially due to the type of secretion elaborated by these glands, particularly in relation to the mucus released on the skin surface (Tsukise and Yamada 1981; Tsukise and Meyer 1982, 1987; Tsukise et al. 1985; Meyer et al. 1986). The substances in question could be essential for the production of different odours, i.e. they would be important for intraspecific communication. In mammals, chemical signals are often involved in priming reproductive functions, and mediating sexual and social communicatory behaviour (see e.g. Mykytowicz and Goodrich 1974; Cheal 1975; Albone 1984). This is also true of primates, but only with special reference to many prosimians (Tupaiidae, Lemuridae, Lorisidae) or families of the Ceboidea (Callithricidae, Cebidae) (see e.g. Epple 1976; Schilling 1979; Zeller 1986), and is probably reflected by the high development of their rhinencephalon (Starck 1965).

The Cercopithecoidea (old world monkeys), however, are relatively devoid of specialized skin scent glands and ritualized scent-marking behaviour patterns, although olfactory investigation, including mutual investigation is very common in most species. The genitals provide a major focus of attention, in females (vaginal odour, urine) as well as

in males (Marler 1965; Gautier and Gautier 1977; Albone 1984). Information about the scrotal skin of primates other than man is generally scarce, and largely confined to prosimian groups (Wislocki 1930; Schaffer 1940; Ellis and Montagna 1959; Fiedler 1959; Starck 1969). For macaques, this is in contrast to the broad evidence available on the structure of the hairy skin and most specific body regions, including several aspects of eccrine gland function (see e.g. Lee 1960; Machida et al. 1964; Montagna et al. 1964; Im and Montagna 1965; Johnson and Elizondo 1974; Sato 1983). In this connection, and in view of the problems discussed above, it seemed appropriate to analyse the scrotal skin of a macaque species, using carbohydrate histochemical methods. Thus, this study primarily supplies a differentiation of the secretions of the three gland types present, with special reference to the tubular eccrine glands which are not found in the scrotal skin of other mammalian groups.

Materials and methods

Four adult males of the Formosa macaque, *Macaca cyclopis* (Swinhoe, 1862) (Catarrhina, Cercopithecidae), were examined in the present study. After the animals were sacrificed, skin specimens from ventrolateral parts of the scrotum were dissected out, and fixed for 48 h at room temperature in the following solutions: Bouin's solution, 10 % formalin containing 2 % calcium acetate (Leppi 1968), and 10 % formalin in 95 % ethanol (McManus and Mowry 1958). After dehydration in a series of graded ethanol concentrations, the tissue pieces were embedded in paraffin wax, and cut 6 μm. Sections were deparaffinized in xylene, rehydrated through graded ethanol concentrations and stained with the following procedures:

Haematoxylin and eosin (H-E); periodic acid-Schiff (PAS) (Spicer et al. 1967); alcian blue (AB), pH 1.0 (Lev and Spicer 1964), and AB, pH 2.5 (Pearse 1968); dialysed ironferrocyanide (DI-FCY) (Yamada 1973); AB, pH 2.5-PAS (Mowry 1963); coupled tetrazonium procedure (TZ), (Pearse 1968); and lectins labelled with horseradish peroxidase (PO) (purchased from E. Y. Laboratories, U.S.A.) – concanavalin A (Con A), peanut agglutinin (PNA), *Dolichos biflorus* agglutinin (DBA), *Ricinus communis* agglutinin-I (RCA-I), *Maclura pomifera* agglutinin (MPA), *Ulex europaeus* agglutinin-I (UEA-I), soy bean agglutinin (SBA), wheat germ agglutinin (WGA), *Griffonia simplicifolia* agglutinin-I and -II (GSA-I and -II), and *Limulus polyphemus* agglutinin (LPA) (Collard and Temmink 1974; Kiernan 1975; Yamada and Shimizu 1977, 1979; Stoward et al. 1980; Tsukise and Yamada 1981; Alroy et al. 1984). The activity of peroxidase employed for labelling was revealed by a diaminobenzidine-hydrogen peroxide system (DAB; purchased from Sigma Chemicals) (Yamada and Shimizu 1977).

The following confirmatory and control experiments were performed:

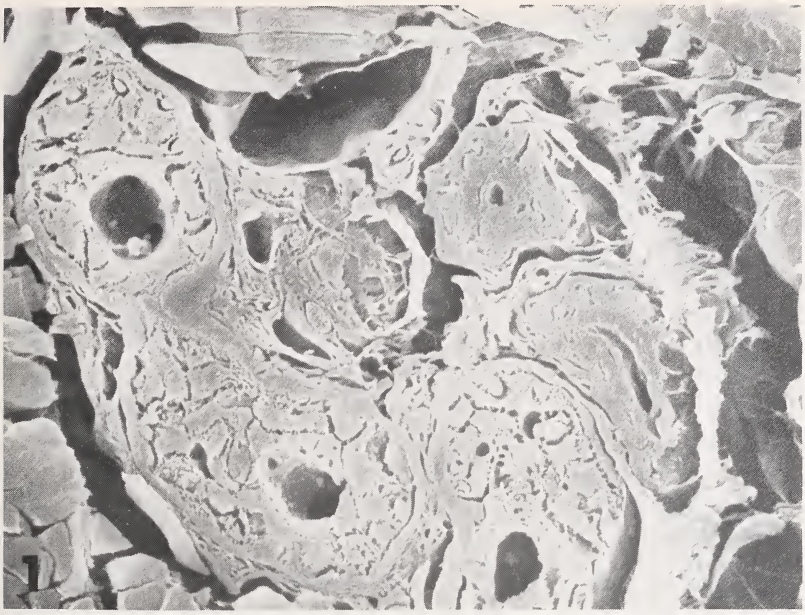
1. Enzyme digestion: α-amylase (Sigma Chemicals) 1 mg/ml in 0.1 M phosphate buffer (pH 7.0) at 37 °C for 3 h (Casselman 1969), prior to staining with PAS or PO-Con A-DAB. For the enzyme digestion experiments, two types of controls were performed: (a) some tissue sections were incubated in the buffer solution without enzyme, under identical conditions of temperature and duration; (b) other sections were kept intact without any incubation procedures.
2. Chemical modification: sulfation (Yamada and Hoshino 1972), prior to staining with AB (pH 1.0).
3. Lectin controls: the following saccharides were added at a final concentration of 0.01 M to the respective lectin solutions: α-methyl-D-mannoside for Con A, lactose for PNA, N-acetyl-D-galactosamine for DBA, galactose for RCA-I, SBA, MPA and GSA-I, L-fucose for UEA-I, N-acetyl-D-glucosamine for WGA and GSA-II, and N-acetyl-neuraminic acid for LPA.

   To detect endogenous peroxidase activity in tissues, certain control sections were reacted with DAB only.

Additionally some skin specimens were prepared for scanning electron microscopy according to Meyer and Neurand (1985). After coating with gold-palladium, the samples were viewed in a JEOL JSM-35C scanning electron microscope at 25 kV.

Results

The scrotal skin of the monkey, *Macaca cyclopis,* is only sparsely studded with hair follicles, including the relatively large sebaceous glands of the latter, and shows in close proximity apocrine and eccrine tubular glands (Figs. 1–3, 18–21). The apocrine glands



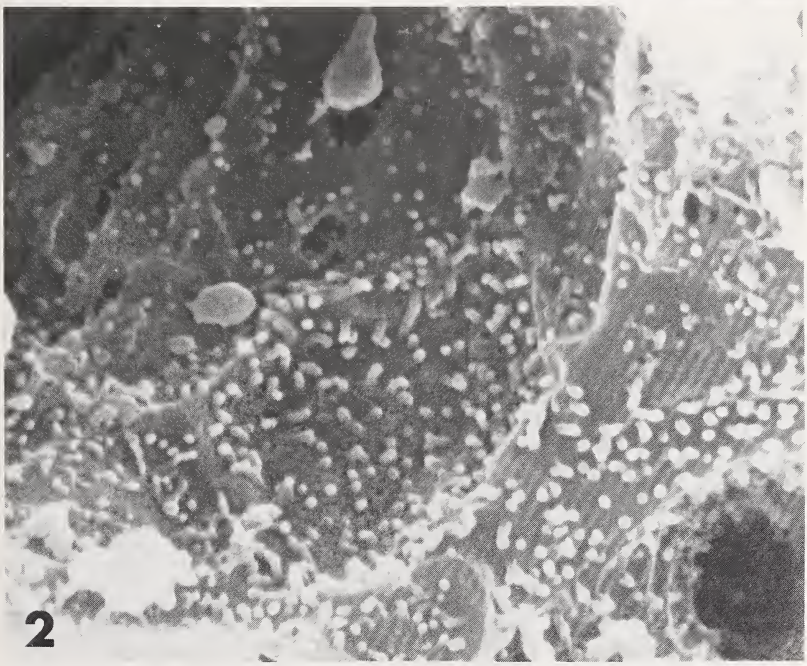


Fig. 1. SEM of tubules of eccrine glands; ×810. – *Fig. 2.* SEM of the luminal surface of superficial cells of eccrine gland; ×1440

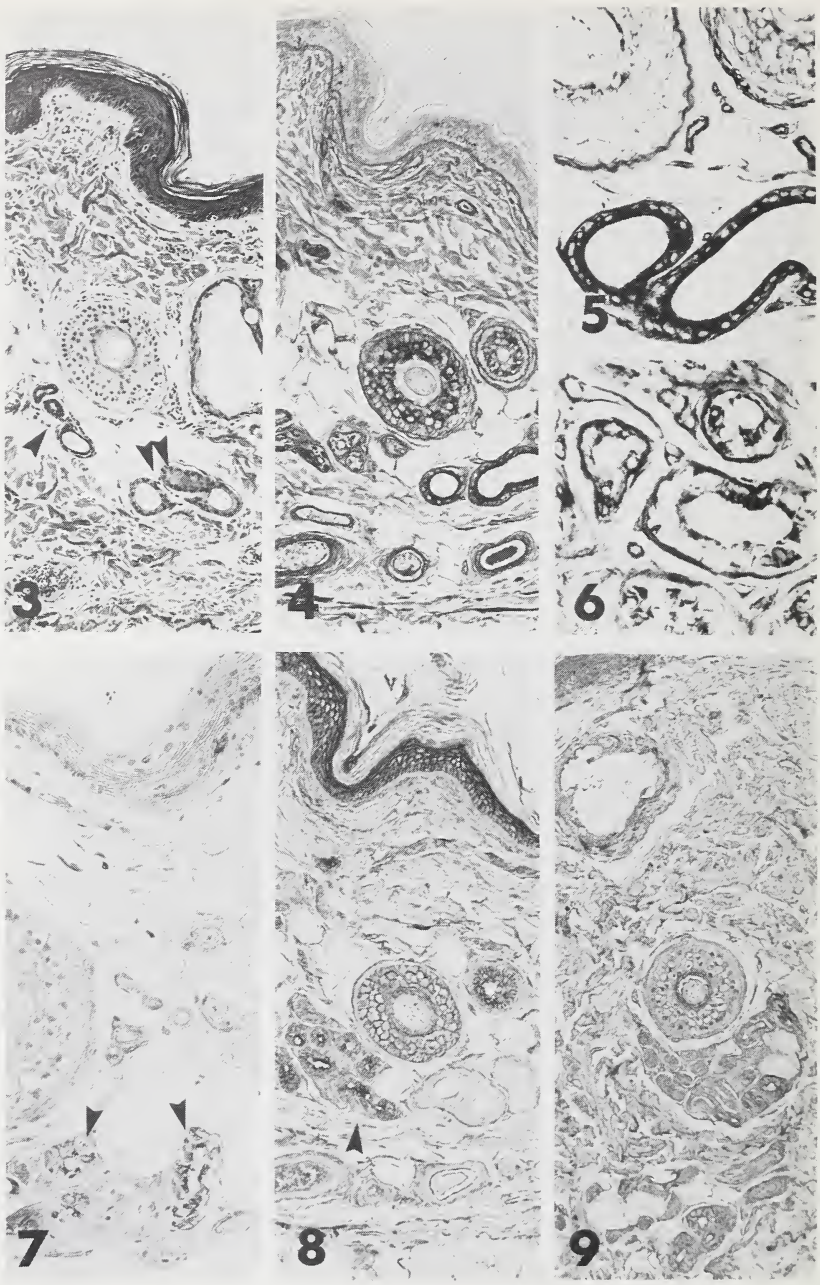


Fig. 3. General view of monkey scrotal skin with eccrine (arrow) and apocrine tubular glands (double arrow); H.E., ×90. – *Fig. 4.* as Fig. 3: PAS stained, ×90. – *Fig. 5.* apocrine gland tubules; AB (pH 2.5)-PAS, ×180. – *Fig. 6.* eccrine gland tubules; AB (pH 2.5)-PAS, ×180. – *Fig. 7.* AB (pH 2.5), with clearly positive reactions in superficial cells of eccrine glands (arrow), ×360. – *Fig. 8.* PO-WGA-DAB, clearly positive reactions only in eccrine glands (arrow), ×90. – *Fig. 9.* PO-LPA-DAB, ×90

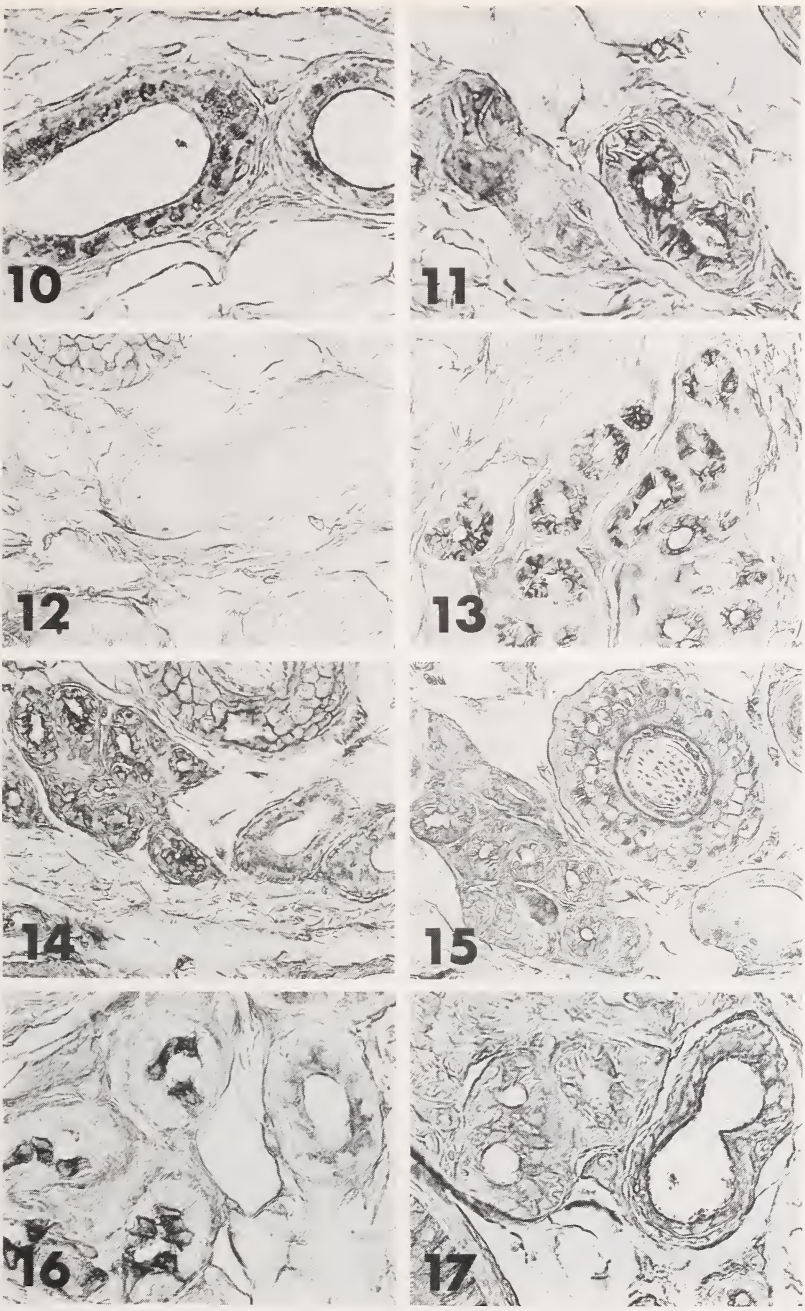


Fig. 10. PO-SBA-DAB; apocrine gland tubules, ×360. – *Fig. 11.* PO-SBA-DAB; eccrine gland tubules, ×360. – *Fig. 12.* PO-UEA-I-DAB; apocrine gland tubules, ×180. – *Fig. 13.* PO-UEA-I-DAB; eccrine gland tubules, ×180. – *Fig. 14.* PO-RCA-I-DAB; eccrine and apocrine gland tubules (right), ×180. – *Fig. 15.* PO-DBA-DAB; eccrine and apocrine gland tubules (right), ×180. – *Fig. 16.* PO-GSA-I-DAB; strong reactions only in superficial cells of eccrine glands, ×360. – *Fig. 17.* PO-MPA-DAB; stronger staining of the luminal surface of apocrine glands, ×360

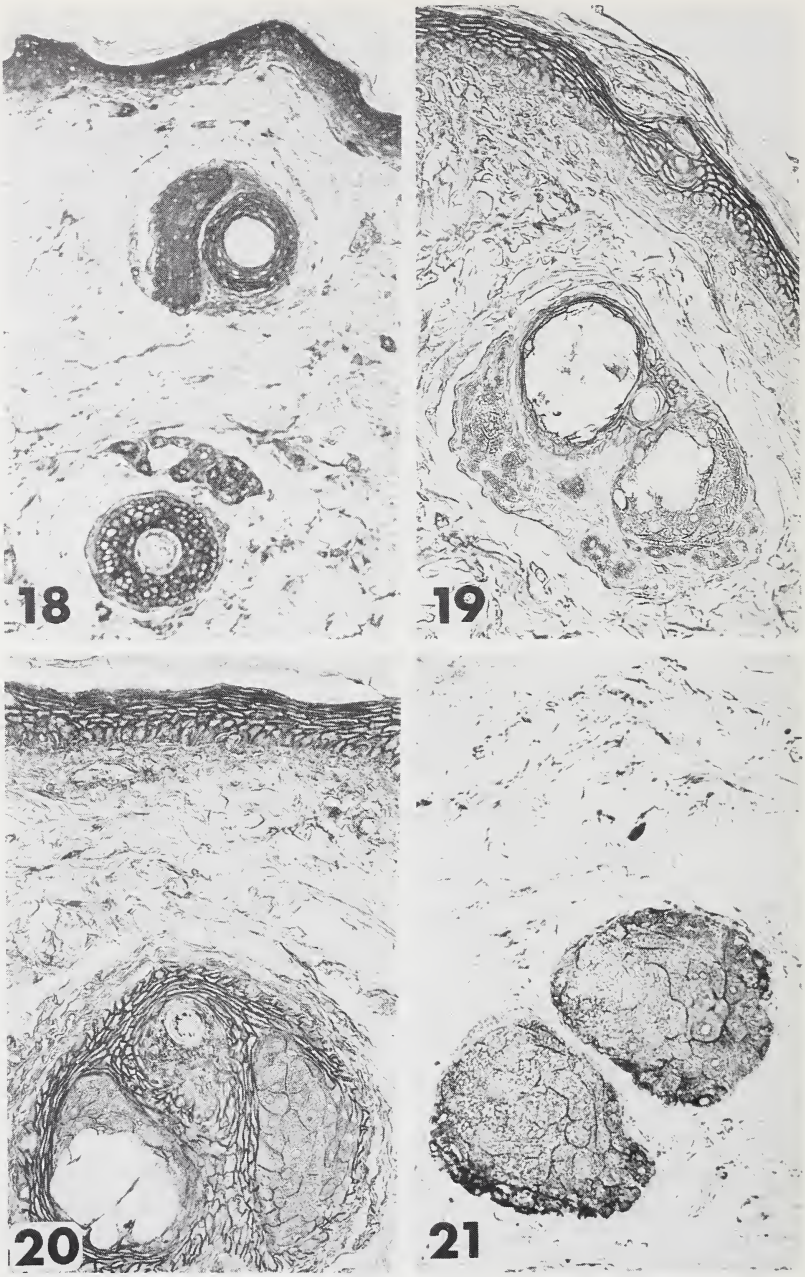


Fig. 18. PO-Con A-DAB; ×90. – *Fig. 19.* PO-PNA-DAB; strong staining of epidermal intercellular substances, positive reactions also in sebaceous gland cells (below), ×180. – *Fig. 20.* PO-RCA-I-DAB; distinct reaction of intercellular substances, ×180. – *Fig. 21.* PO-DBA-DAB; clearly positive reactions especially in peripheral cells of sebaceous glands, ×180

exhibit a comparatively flat secretory epithelium with only slight apocrine protrusions at the cell apices. The eccrine glands are composed of the typical pattern of superficial and basal secretory cells (dark and clear cells), and the luminal surface of the cells is provided with a sparse coat of short microvilli (Fig. 2). The epidermis is normally structured, with several layers of the stratum spinosum, one continuous layer of the stratum granulosum, and a few lamellae of the stratum corneum. The dermis is relatively thin and includes a densely interwoven meshwork of fine and medium-sized collagen fibre bundles.

The selected histochemical methods used in the present study demonstrated a variety of distribution patterns of complex carbohydrates. The results obtained in the different skin structures are summarized in Tables 1 (skin layers), 2 (apocrine glands and eccrine glands) and 3 (sebaceous glands). The strongest reactions were observed in the apocrine glands, the eccrine glands, and, to some extent, in the sebaceous glands, less intense stainings were generally limited to the skin layers, especially the dermis.

PAS, AB (pH 2.5), DI-FCY and AB (pH 2.5)-PAS staining resulted in positive colourations of moderate to strong intensities of the secretory cells and luminal secretions of both tubular gland types, but particularly in the apocrine glands (Figs. 4, 5). In the secretory epithelium of the eccrine glands strong reactions were confined to the superficial cells (dark cells) (Figs. 6, 7). Clearly positive reactions for these staining procedures were also visible in the sebum of the sebaceous glands, the inner surface of the blood vessels, and the connective tissue elements of the dermis and subcutis. Digestion with α-amylase failed to notably alter the PAS staining of all skin structures investigated, except for the superficial cells of the eccrine glands. The AB (pH 1.0) reaction intensity was significantly increased by prior sulfation. The tetrazonium staining procedure coloured moderately or strongly nearly every skin structure, particularly the secretory cells of the apocrine glands and the superficial cells of the eccrine glands.

The reactions of PO-labelled lectins with the structures of the monkey scrotal skin exhibited somewhat different staining patterns, depending on the lectins employed. Markedly and strongly positive reactions were confined to the secretory epithelium

Table 1. **Carbohydrate histochemical reactions in the skin layers of the monkey scrotum**

Reactions	Epidermis				Dermis		Subcutis
	Stratum corneum	Stratum granulosum	Stratum spinosum	Stratum basale	Connective tissue	Blood vessels	Connective tissue
PAS	–	+	+	(+)/+	+/++	++/+++	+
AB (pH 1.0)	–	(+)	(+)	(+)	(+)/+	(+)	(+)/+
AB (pH 2.5)	(+)/+	++	++	+/++	+/++	+/++	+
AB (pH 2.5)-PAS	–	+	+	(+)/+	+/++	++/+++	+
AMYL-PAS	–	+	+	(+)/+	+/++	++/+++	+
SUL-AB (pH 1.0)	+	+/++	+	+	++/+++	+/++	+/+++
TZ	++/+++	++/+++	++	+	++	+/++	++
PO-Con A-DAB	(+)	++/+++	++/+++	+	+/++	++	+/++
PO-PNA-DAB	(+)/+	++/+++	++	+	+/++	+	+/++
PO-DBA-DAB	(+)/+	++	+/++	+	+	+/++	+
PO-RCA-I-DAB	(+)/+	++/+++	++	+	++	+	++
PO- MPA-DAB	(+)/+	++	+	+	+	+	++
PO-UEA-I-DAB	(+)	++	+/++	+	+	(+)	+
PO-SBA-DAB	+	++	++	+	+	+	+
PO-WGA-DAB	+	++/+++	+/++	+	+	+	+
PO-GSA-I-DAB	+	+/++	+	(+)/+	+/++	+	+/++
PO-GSA-II-DAB	+/++	(+)/+	(+)/+	(+)	+	+	+/++
PO-LPA-DAB	+	++	++	++	+/++	+/++	+/++

Reaction intensities (for all Tables): – = no reaction visible, (+) = very weak, + = weak, ++ = moderate, +++ = strong

Table 2. **Carbohydrate histochemical reactions in the apocrine and eccrine glands of the monkey scrotum**

Reactions	Apocrine glands				Eccrine glands			
	Secretory cells	Luminal secretion	Excretory durct cells	Myoepithelial cells	Secretory cells		Luminal secretion	Excretory duct
					Superficial	Basal		
PAS	++/+++	++	++	(+)	++	(+)/+	(+)	+
AB (pH 1.0)	++	+	+	(+)	(+)/+	–	(+)	(+)
AB (pH 2.5)	++/+++	++	+/++	+	++/+++	(+)	+	+
AB (pH 2.5)-PAS	+++	++	++	+	++	(+)/+	+	+
AMYL-PAS	++/+++	++	++	(+)	+/++	(+)/+	(+)	(+)
SUL-AB (pH 1.0)	++/+++	+	+	+	+	(+)	+	+
TZ	+++	++	++/+++	++	++/+++	+	++	+/++
PO-Con A-DAB	+/++	(+)	(+)	(+)/+	++	+	+	+
PO-PNA-DAB	+	(+)	(+)	(+)	+/++	(+)	(+)	(+)
PO-DBA-DAB	(+)	(+)	(+)	(+)	+/++	(+)	(+)	(+)
PO-RCA-I-DAB	++	(+)	(+)	(+)	++/+++	(+)	+	+
PO-MPA-DAB	+/++	(+)	(+)	(+)	++	(+)	(+)	(+)
PO-UEA-I-DAB	–	–	–	–	++/+++	–	(+)	–
PO-SBA-DAB	++	+	(+)	(+)	++/+++	(+)	(+)	+
PO-WGA-DAB	(+)	(+)	(+)	–	++/+++	(+)	(+)	(+)
PO-GSA-I-DAB	+	(+)	(+)	–	+++	(+)	+	(+)
PO-GSA-II-DAB	–	–	–	–	(+)	–	–	–
PO-LPA-DAB	(+)	(+)	(+)	–	+	(+)	(+)	(+)

Table 3. **Carbohydrate histochemical reactions in the sebaceous glands of the monkey scrotum**

Reactions	Sebaceous glands			
	Peripheral cells	Central cells	Excretory duct cells	Secretion
PAS	+/++	+	+	+/++
AB (pH 1.0)	(+)/+	–	–	(+)/+
AB (pH 2.5)	+	(+)/+	(+)/+	(+)/+
AB (pH 2.5)-PAS	+/++	+	+	+++
AMYL-PAS	+/++	+	+	+/++
SUL-AB (pH 1.0)	+/++	+	+	++
TZ	+/++	+	+	+
PO-Con A-DAB	++/+++	++	++	++
PO-PNA-DAB	++	+/++	+	++
PO-DBA-DAB	++/+++	+/++	+	++
PO-RCA-I-DAB	++	+/++	+	++
PO-MPA-DAB	++	++	+	++
PO-UEA-I-DAB	+/++	+	+	++
PO-SBA-DAB	+	(+)/+	(+)/+	+/++
PO-WGA-DAB	+/++	++	+	++/+++
PO-GSA-I-DAB	+	(+)/+	+	++
PO-GSA-II-DAB	(+)/+	+	(+)	++
PO-LPA-DAB	+/++	++	+	++

(superficial cells) of the eccrine glands (RCA-I, UEA-I, SBA, WGA, GSA-I) (Figs. 8, 11, 13, 14, 16), the sebaceous glands (Con A, DBA) (Figs. 18, 21) and their secretion (WGA, LPA) as well as the stratum granulosum and stratum spinosum of the epidermis. In the latter, the strong reaction stainings could only be observed in the intercellular substances (Con A, PNA, RCA-I, WGA) (Figs. 8, 18–20). Of all the lectins used, the PO-LPA staining was generally weak in most skin structures, including, for example, the two tubular gland types and their secretions. In the sebaceous glands, however, a weak to

moderate intensity for PO-LPA was found in the cells, the sebum and the interlobular and peripheral connective tissue. In the control procedures for the PO-labelled lectin staining, the addition of particular saccharides to the PO-lectin solutions diminished greatly, or abolished the intensity of the lectin reaction in all the skin structures tested.

Discussion

The results obtained in the course of this histochemical study have demonstrated that glycoconjugates, such as neutral and acidic glycoproteins, are clearly present in the scrotal skin of the monkey, *Macaca cyclopis* (Swinhoe). The well established properties of the PAS, AB (pH 1.0), AB (pH 2.5), AB (pH 2.5)-PAS, and several PO-lectin stainings indicate that the distribution patterns of the complex carbohydrates observed, to some extent, are similar to those shown in the scrotal skin of other mammals (Tsukise and Yamada 1981; Tsukise and Meyer 1982, 1987; Tsukise et al. 1985; Meyer et al. 1986). Differences, however, are evident when the tubular glands and their secretions are compared.

The reaction stainings as visible from the skin layers were most remarkable in the epidermis, where the glycoconjugates in the cell walls and, particularly, in the intercellular substances exhibited the presence of the following sugar residues: α-D-glucose, α-D-mannose, β-D-galactose, N-acetyl-α-glucosamine. These findings are in general accordance with observations from the human skin (Holt et al. 1979; Nemanic and Elias 1979; Reano et al. 1982; Ookusa et al. 1983; Schaumburg-Lever et al. 1984), or mammals with a sparse hair coat like the domestic pig (Tsukise and Meyer 1983; Meyer 1986). The intercellular substances include glycoproteins for cell adhesion (Hashimoto et al. 1974; Rauvala et al. 1981) or glycolipids to prevent epidermal water loss (Wertz and Downing 1982; Odland 1983; Meyer 1986). Thus, the large amounts of glycoconjugates among the upper layers of the vital epidermis of scrotal skin seem to compensate for the reduced protective properties of the normally sparse hair coat of the scrotum (see also Meyer 1986). The observations on residue distribution and staining intensity in fibre bundles of the dermis correspond to that demonstrated in the scrotal skin of other mammals (Tsukise and Yamada 1981; Tsukise et al. 1985; Tsukise and Meyer 1987).

As already emphasized in the introduction, the most interesting aspects of the macaque scrotal skin may be connected with the secretions elaborated by the three different gland types found. Carbohydrate histochemical differentiation showed that the cytoplasm, the free surface of the secretory cells, and the luminal secretion of the apocrine glands and, in particular, the eccrine glands contained mostly neutral but only very few acidic glycoproteins, including small amounts of sialic acid. The results of the PO-lectin-DAB procedures indicate that the following saccharide residues are predominant in the neutral glycoproteins present: α-D-mannose, α-D-glucose, β-D-galactose, α-D-galactose, N-acetyl-D-galactosamine in the apocrine glands; and, somewhat different, β-D-galactose, α-D-galactose, N-acetyl-D-galactosamine, α-fucose, N-acetyl-β-D-glucosamine in the eccrine glands (superficial cells); and α-D-mannose, α-D-glucose, N-acetyl-α-D-galactosamine, sialic acid in the sebaceous glands (for residue demonstration see e.g. Kiernan 1975; Yamada and Shimizu 1977; Stoward et al. 1980; Tsukise and Yamada 1981; Alroy et al. 1984).

The histochemical characteristics as obtained for the apocrine glands are in keeping with findings described for this gland type in the scrotal skin of other species (Tsukise and Yamada 1981; Tsukise and Meyer 1982, 1987; Tsukise et al. 1985; Meyer et al. 1986), although it was quite obvious that in the monkey the amounts released were distinctly smaller. The eccrine glands, on the contrary, seemed to be more active, and their spectrum of saccharide residues mainly agrees with that observable in human eccrine glands of the common integument (see e.g. Ookusa et al. 1983; Schaumburg-Lever et al. 1984), or

that found in the eccrine glands of the pig snout (Tsukise et al. 1983). Our results also confirm the view of Constantine and Mowry (1966) assuming that this gland type in humans contains acidic carbohydrates only with carboxyl groups and only a few sialic acid residues. In addition, the eccrine glands in the monkey scrotal skin exhibited small amounts of glycogen, a feature common also to these glands in the human skin or the pig snout, and probably related to high energy demands during sweating or secretion production, respectively (Smith and Dobson 1966; Ellis 1968; Tsukise et al. 1983).

The secretions of the two tubular gland types are finally released onto the skin surface. Here, their functions are manifold, and can only be evaluated in view of the fact that they soon become parts of a mixture of different substances when those glycoconjugates are included which are elaborated by the sebaceous glands (see also Tsukise and Meyer 1987). As could be expected from the generally neutral pH of the eccrine gland secretions in monkeys and man (Sato 1983), the acidity of this mixture is rather low, so that the suppression of pathogenic microorganisms may be of minor importance, as should be evaporative cooling because of the relatively small scrotal evaporative area.

The most important function of the mucous coat of neutral glycoproteins on the scrotum of monkeys may be related to volatile odorous substances as released by microbial degradation (for literature see e.g. Albone 1984). The odours produced could be significant for intraspecific communication by the signalling of sexual activity. Monkeys and apes may generally make more use of olfaction than is at present appreciated, and, as visible from their sensitive discrimination between edible and non-edible food or objects, macaques have highly developed olfactory senses (Cole 1963; Marley 1965). The relation to sexual life may be closely connected with changes in scrotal gland structure and secretory rates in times of sexual activity or inactivity due to androgenic influences, as demonstrated in humans (Wilson and Walker 1969; Ebling 1980; Kutenn et al. 1980). In macaques, for example, the blood level of testosterone increases two-fold in males upon interaction with sexually active females (Rose et al. 1972). Thus, the scrotal skin is probably a glandular organ, not only in prosimians (Fiedler 1959) or Ceboidea (Starck 1969), but, to a certain degree, also in the Cercopithecoidea.

Zusammenfassung

Die Histochemie komplexer Kohlenhydrate in der Skrotalhaut des Formosa-Makaken, Macaca cyclopis (Swinhoe)

Die Skrotalhaut des Formosa-Makaken, *Macaca cyclopis* (Swinhoe), wurde mit einer Reihe von histochemischen Methoden zur Darstellung von Kohlenhydraten untersucht, wobei auch Peroxidase-gekoppelte Lektine zur Anwendung kamen. Die kräftigsten Reaktionen waren in den zwei tubulären Drüsentypen (apokrine Drüsen, ekkrine Drüsen) sowie z.T. in den Talgdrüsen und den oberen Lagen der vitalen Epidermis zu entdecken. Schwächere Anfärbungen beschränkten sich auf die Dermis.

Das Cytoplasma und die freie Oberfläche der sekretorischen Zellen sowie das Sekret im Lumen der apokrinen Drüsen und, im besonderen, der ekkrinen Drüsen enthielt zwar nur wenig saure Glykoproteine, einschließlich geringer Mengen an Sialinsäuren, dafür aber deutlich mehr neutrale Glykoproteine mit verschiedenen Zuckerresten: α-D-Mannose, α-D-Glukose, β-D-Galaktose, α-D-Galaktose, N-Azetyl-D-Galaktosamin in den apokrinen Drüsen; und β-D-Galaktose, α-D-Galaktose, N-Azetyl-β-D-Glukosamin in den ekkrinen Drüsen (dunkle Zellen). Diese Drüsen wiesen auch geringe Mengen an Glykogen auf. Die Talgdrüsen besaßen Glykoproteine mit folgenden Zuckerresten: α-D-Mannose, α-D-Glukose,N-Azetyl-α-D-Galaktosamin und Sialinsäuren.

Die Sekrete der drei Drüsentypen in der Skrotalhaut des Formosa-Makaken bilden als Sekretmischung auf der Oberfläche des Skrotums eine dünne muköse Schicht aus zumeist neutralen Glykoproteinen. Ihre wichtigste Funktion könnte die durch mikrobielle Zersetzung hervorgerufene Freisetzung von flüchtigen Geruchssubstanzen sein. Die so produzierten Düfte haben im Rahmen der innerartlichen Kommunikation vielleicht die Aufgabe, sexuelle Aktivität zu signalisieren. Die Skrotalhaut der Cercopithecoidea kann daher, ebenso wie bei Prosimiern und Ceboidea, eventuell als Drüsenorgan verstanden werden.

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