2. Comparison of the bile salts with those of the morphologically similar South American coypu (*Myocastor coypus*) previously examined (Haslewood, 1954) supports the view of Wood (1955) that the two rodent species are not closely related in an evolutionary sense.

The authors thank Dr D. C. Erinne for help in the collection of cutting-grass bile. They express their gratitude to Dr R. K. Callow, F.R.S., and to Dr I. D. P. Wootton for their kindness in the determination and interpretation of infrared spectra. The biological problem here discussed was brought to the notice of the senior author by Professor J. E. Webb of the Department of Zoology, University College, Ibadan; the authors thank him and also Dr J. H. Elgood for their interest in this work. They are indebted to Dr G. G. Simpson, of the American Museum of Natural History, New York, for his valuable advice on rodent classification.

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Studies of Sebum

9. FURTHER STUDIES OF THE COMPOSITION OF THE UNSAPONIFIABLE MATTER OF HUMAN-FOREARM 'SEBUM'*

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The unsaponifiable matter of human-forearm 'sebum' (skin-surface fat) has been shown to contain hydrocarbons (30–46 %), cholesterol (14–19 %) and wax alcohols (about 20 %). The hydrocarbon fraction contains 30–40 % of squalene and a normal chain paraffin. A sterol-like substance was detected in the unidentified fraction as were oxidation products of squalene (MacKenna, Wheatley & Wormall, 1950, 1952).

A further examination of the sterol fraction has now been made, and the composition of the wax alcohols has been studied by gas chromatography.

EXPERIMENTAL

Collection of 'sebum'. A bulk collection of sebum was obtained from normal male medical students by immersion of the forearms in acetone (twice-redistilled) as already described (MacKenna *et al.* 1952).

Isolation and fractionation of the unsaponifiable matter. The sebum was saponified as previously described (MacKenna *et al.* 1952) and the unsaponifiable matter isolated. The latter was then fractionated on grade II alumina (Brockman & Schodder, 1941) as described in previous work. In addition, however, the column was washed finally with acetic acid in an attempt to effect a more complete recovery.

Gas chromatography of the wax alcohols. A similar procedure was used to that described for the fatty acids of sebum (James & Wheatley, 1956). The column used had as stationary phase Apiezon M vacuum grease (Shell Chemicals Ltd.) on Celite 545 (Johns-Manville Co. Ltd.) (2·5 parts of Apiezon M to 10 parts of Celite, 40–90 mesh) and was maintained at a temperature of 197° with boiling ethylene glycol. The sample (4·6 mg.) was applied to the top of the column with a micropipette and a flow rate of 60 ml. of N_2/min. was used. Tentative identification of the peaks followed the procedure used for the identification of the fatty acids of sebum (James & Wheatley, 1956); the relative retention times of peak emergence used in these identifications were calculated with reference to octadecanol (cf. James & Martin, 1956). Unsaturated alcohols were removed by the bromination method (James & Martin, 1956) and a second run was made of the saturated members only. Peak areas were measured by the triangulation method and corrected to octadecanol as described by James & Wheatley (1956). From the corrected areas the proportions of each component were calculated.

* Part 8: Boughton, MacKenna, Wheatley & Wormall (1957).

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Table 1. *Chromatographic fractionation on alumina of the unsaponifiable material from a bulked sample of human-forearm sebum*

Fraction	Eluent	Percentage of total unsaponifiable matter	Appearance	Nature*
1	Light petroleum	37·5	Soft white solid	Hydrocarbons
2*a*	5% $CHCl_3$–light petroleum (first 100 ml.)	0·4	Yellow wax	—
2*b*	5% $CHCl_3$–light petroleum	20·6	Yellow wax	Wax alcohols
3*a*	10% $CHCl_3$–light petroleum (first 200 ml.)	3·9	Yellow wax	—
3*b*	10% $CHCl_3$–light petroleum	13·7	White crystalline solid	Cholesterol
4	$CHCl_3$	3·6	Brown–yellow oil	Other sterols
5	Methanol	6·4	Grey wax	—
6	Acetic acid	3·0	Grey–yellow viscous liquid	—
	Total recovered	89·1		

* According to MacKenna, Wheatley & Wormall (1952).

With the column temperatures available, alcohols with chain length longer than 20 carbon atoms could not be detected.

Examination of the sterol fractions

Digitonin precipitation. For a 100 mg. sample the following procedure was used. To a solution of the sterol in 5 ml. of 90% ethanol at 60° an equal volume of a solution of 300 mg. of digitonin in the same solvent was used. The mixture was allowed to stand overnight at room temperature and the white precipitate which formed was filtered and washed with 90% ethanol. The filtrate and washings were evaporated to small bulk, a small amount of digitonin in 90% ethanol at 60° was added and the process repeated. The second crop of digitonide precipitate was added to the first. Sterols not precipitated by digitonin were recovered from the mother liquors and the washings by ether extraction after addition of water.

The cholesterol digitonide was decomposed by dissolving it in 2 ml. of pyridine at 70° and leaving the solution overnight at room temperature (Schoenheimer & Dam, 1933). On adding excess of ether, the digitonin precipitate could be centrifuged off and the cholesterol recovered from the supernatant.

Zimmermann reaction. The method used was that described by Callow, Callow & Emmens (1938).

Girard T separation of ketonic and non-ketonic sterols. The Girard T complex (Girard & Sandulesco, 1936) was formed by heating an ethanolic solution of the sterol with 0·5 ml. of a 10% solution of the reagent in acetic acid in a boiling-water bath for 30 min. Most of the ethanol and acetic acid was removed under reduced pressure, water was added to the residue and the non-ketonic sterols were extracted with ether. The water-soluble ketonic sterol complex was decomposed by acidifying the aqueous layer with HCl, and the ketonic material was recovered from this by extraction with ether.

Absorption spectra. These were measured with a Unicam SP. 500 spectrophotometer.

RESULTS

Details of the chromatographic fractionation of 1 g. of the unsaponifiable material of human-forearm sebum are given in Table 1. The various fractions were then further examined as described below.

Wax alcohols

The composition of the wax alcohols present in fraction 2*b* (Table 1) was studied by means of gas chromatography. Under the conditions used alcohols of chain length greater than C_{30} could not be detected, but it was calculated that about half the sample consisted of compounds with less than 20 carbon atoms/molecule. The results are given in Table 2 and the gas chromatogram is shown in Fig. 1. The figures for the component fatty acids of forearm sebum (Wheatley, 1957) are given for comparison. The alcohols formed a homologous series similar to the fatty acids of sebum. There were fewer highly branched and unsaturated alcohols in comparison with the acids, and the average chain length of the major alcohol components appeared to be somewhat longer than that of the major acid components. These findings are in general agreement with those of Brown, Young & Nicolaides (1954) who, from mass-spectroscopy evidence, concluded that the average chain length of the alcohols was 20 carbon atoms compared with 16 carbon atoms for the acids.

'*Alkane* 1:2-*diols*'. Fractions 5 and 6 (Table 1) were subjected to periodate oxidation (Karnovsky & Rapson, 1946). Since adequate controls on solvents etc. were run simultaneously it has been concluded that the periodate-oxidizable materials

Table 2. *Quantitative analysis of the wax alcohols and component fatty acids of human-forearm sebum*

Results are expressed as percentage of total material recovered from the gas chromatogram. This is estimated as about 50% of the total sample of alcohols. The analysis of the acids was made by Wheatley (1957). *iso* is used to denote a single methyl branch near the end of the carbon chain.

Type of compound	Alcohol (%)	Acid (%)
n-C_6	0·05	—
n-C_8	0·1	—
iso-C_9	0·1	—
n-C_9	0·1	—
n-C_{10}	0·2	0·3
Highly branched C_{11}	Trace present not estimated	—
n-C_{11}	0·2	0·2
iso-C_{12}	—	0·1
n-C_{12}	0·6	4·4
Highly branched C_{13}	0·2	0·4
iso-C_{13}	—	0·5
n-C_{13}	0·2	0·4
Highly branched C_{14}	—	0·1
iso-C_{14}	0·2	0·3
Mono-unsaturated C_{14}	—	1·9
n-C_{14}	9·8	7·8
Highly branched C_{15}	1·3	1·5
Di-unsaturated C_{15}	—	1·0
iso-C_{15}	—	2·0
Mono-unsaturated C_{15}	—	1·9
n-C_{15}	3·3	4·2
Highly branched C_{16}	—	1·3
iso-C_{16}	0·9	—
Mono-unsaturated C_{16}	—	12·0
n-C_{16}	14·3	22·7
Highly branched C_{17}	0·4	3·4
Di-unsaturated C_{17}	—	1·6
iso-C_{17}	2·8	2·1
Mono-unsaturated C_{17}	3·9	1·4
n-C_{17}	2·4	1·6
Highly branched C_{18}	—	2·9
iso-C_{18}	2·8	—
Mono-unsaturated C_{18}	—	17·2
n-C_{18}	21·4	5·7
iso-C_{19}	1·7	—
Mono-unsaturated C_{19}	1·4	—
n-C_{19}	4·1	—
iso-C_{20}	10·2	—
n-C_{20}	17·5	—

present in these fractions were probably alkane 1:2-diols. It is possible, however, that certain 'oxidation products' of squalene would also react. Calculated as the C_{20} diol the percentages of diols in these fractions were 18·6 and 14·5% respectively.

Sterols

According to MacKenna *et al.* (1952) fraction 3*b* should be composed mainly of cholesterol and fraction 4 of mixed sterols. An attempt was made to fractionate these mixtures further by precipitation of the 3β-ol sterols with digitonin, the residual material being separated into ketonic and non-ketonic portions by means of the Girard T reagent.

Detection of 7-dehydrocholesterol. The digitonide from fraction 3*b* was decomposed with pyridine and the recovered cholesterol recrystallized from methanol. The ultraviolet-absorption spectrum of this purified cholesterol fraction was compared with that of a pure specimen of 7-dehydrocholesterol (Fig. 2). Measurement of the peak at 282 mμ, after correction for end-absorption, gave a value of 0·08% of 7-dehydrocholesterol in this purified fraction.

17-Oxosteroids. The two keto steroid fractions gave a positive Zimmermann reaction. The time of development and the colour produced were not the same in each case, and were qualitatively different from the colour produced with dehydro*iso*androsterone. There was, however, insufficient material available to investigate this further.

*iso*Cholesterol. Fractions 1, 5 and 6 gave a brownish hue with the Liebermann–Burchardt reagent, whereas fraction 2*b* gave a deep-yellow with a green fluorescence similar to that observed by MacKenna *et al.* (1952). The latter workers ascribed this colour to an unidentified oxidation product of squalene. *iso*Cholesterol, however, under the same conditions gives an orange solution with a green fluorescence, and the absorption spectrum of the solution shows a characteristic absorption maximum at 460 mμ. This absorption peak has been used by Lederer & Tchen (1945) to identify and estimate the presence of *iso*cholesterol in sterol mixtures.

The absorption spectra of the Liebermann–Burchardt colours produced by cholesterol, *iso*-cholesterol and fraction 2*b* are shown in Fig. 3. The curve for fraction 2*b* followed the *iso*cholesterol curve and had a maximum at 460 mμ. After allowing for irrelevant absorption at this wavelength the concentration of *iso*cholesterol was calculated as 0·35% of the fraction. On this basis it appears that some of the chromogen in this fraction, believed by MacKenna *et al.* (1952) to be 'oxidized' squalene, is in fact *iso*cholesterol. The above results have been summarized in Table 3.

DISCUSSION

A further study of the unsaponifiable matter of human-forearm sebum has yielded more information of the complex nature of this lipid. The sterol fraction is obviously a complex mixture with *iso*-cholesterol, 7-dehydrocholesterol and keto steroids occurring in trace quantities.

*iso*Cholesterol, which is a mixture of closely related trimethylsterols, principally lanosterol (Windaus & Tschesche, 1930), is known to be a constituent of the sebum of certain ruminants such as the sheep, llama, goat and dromedary (Lederer & Tchen, 1945), but has not previously been

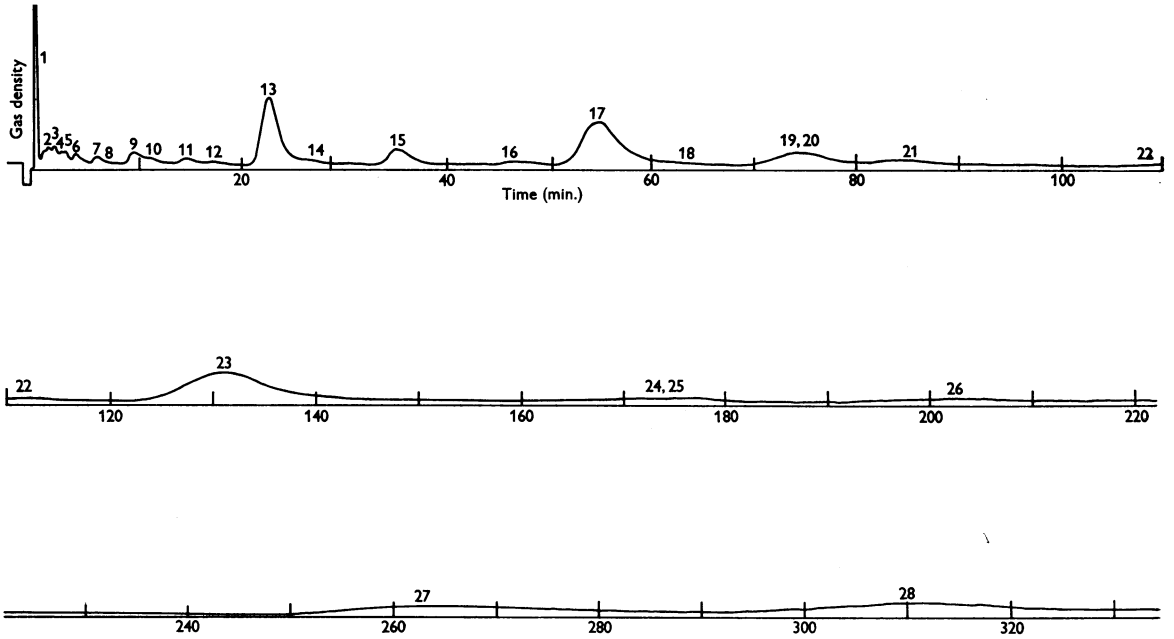

Fig. 1. Analysis of 4·6 mg. of the wax alcohols from human-forearm sebum. Peaks in order of appearance: (1) air introduced in loading column; (2) *n*-hexanol; (3) *n*-octanol; (4) *iso*nonanol; (5) *n*-nonanol; (6) *n*-decanol; (7) highly branched C_{11} alcohol; (8) *n*-undecanol; (9) *n*-dodecanol; (10) highly branched C_{13} alcohol; (11) *n*-tridecanol; (12) *iso*tetradecanol; (13) *n*-tetradecanol; (14) highly branched C_{15} alcohol; (15) *n*-pentadecanol; (16) *iso*hexadecanol; (17) *n*-hexadecanol; (18) highly branched C_{17} alcohol; (19) *iso*heptadecanol overlapping (20) mono-unsaturated C_{17} alcohol; (21) *n*-heptadecanol; (22) *iso*octadecanol; (23) *n*-octadecanol; (24) *iso*nonadecanol overlapping (25) mono-unsaturated C_{19} alcohol; (26) *n*-nonadecanol; (27) *iso*eicosanol; (28) *n*-eicosanol. Column temperature 197°; length 4 ft.; flow rate 60 ml. of N_2/min. Stationary phase: Apiezon M vacuum stopcock grease.

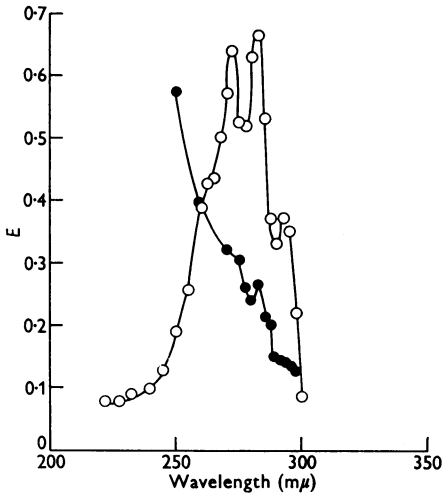

Fig. 2. Ultraviolet-absorption spectra of the ethereal solution of pure 7-dehydrocholesterol (○) and purified cholesterol (●) isolated from human-forearm sebum unsaponifiable matter.

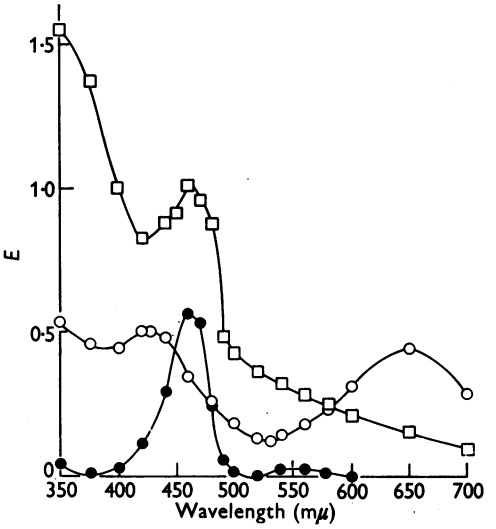

Fig. 3. Absorption spectra of the Liebermann–Burchardt colours produced by cholesterol (○), fraction 2*b* of the unsaponifiable matter of human-forearm sebum (□) and *iso*cholesterol (●).

Table 3. *Some of the constituents of the unsaponifiable matter of human-forearm sebum*

Substance	Detected in fraction no.	Percentage of fraction	Percentage of total unsaponifiable matter	Percentage of whole sebum
7-Dehydrocholesterol	3*b*	0·08	0·003	0·001
*iso*Cholesterol	2*b*	0·35	0·07	0·02
Alkane 1:2-diols	5	18·6	1·62	0·46
	6	14·5		

identified in human sebum. Lanosterol is implicated in the synthesis of cholesterol from squalene (Clayton & Bloch, 1956), and both of these substances occur in human sebum.

7-Dehydrocholesterol is the precursor of vitamin D_3 and is converted into the latter substance by ultraviolet irradiation. It was considered by Helmer & Jensen (1937) that the precursor was secreted in the sebum on to the skin surface and that the vitamin, formed there by irradiation, was reabsorbed through the skin. The precursor has been shown to be present in human (Hentschel & Schindel, 1930) and animal (Koch & Koch, 1941) skin and 7-dehydrocholesterol has been isolated from pig skin (Windaus & Bock, 1937), but previous attempts to detect its presence in the surface-skin lipids (MacKenna *et al.* 1952; Festenstein & Morton, 1952) were unsuccessful. In the present study a trace, only 0·001%, has been detected in the surface lipids. It has now been shown that the 7-dehydrocholesterol of human skin occurs principally in the epidermis (Wheatley & Reinertson, 1958), the bulk of this must be converted into the vitamin, or otherwise decomposed, before it reaches the skin surface. It now appears more likely that the cells of the Malpighian layer, rather than the sebaceous gland, form the 7-dehydrocholesterol of human skin.

The presence of 17-oxo steroids in human sebum was first claimed by Dubovii (1954) on the basis of the Zimmermann reaction. The presence of ketonic material giving a positive Zimmermann test has been demonstrated in the sterol fraction, but there is insufficient evidence to conclude that this material is, in fact, a 17-oxo steroid.

The study of the wax alcohols of human-forearm sebum by gas chromatography has confirmed and extended the analyses of these compounds already made on hair fats. Brown *et al.* (1954) found odd- as well as even-numbered alcohols, and a monoolefinic series extending from C_{18} to C_{27} as well as the normal saturated alcohols. Hougen (1955) found three homologous series of alcohols present, the normal saturated, the *iso* and the monoolefinic. The analyses described in this paper show yet another group of highly branched compounds, with 11, 13, 15 and 17 carbon atoms, as well as small amounts of the lower members of the normal and *iso* series of alcohols.

The highly branched compounds may be intermediates in the synthesis of squalene from acetate; the C_{15} member may possibly be farnesol. This has been shown to be an intermediate in the biosynthesis of cholesterol (Dituri, Cobey, Warms & Gurin, 1956) and evidence for its presence in human-hair fat has been obtained by Dr N. Nicolaides (unpublished results).

The longer carbon chains of the alcohols compared with the fatty acids, and the presence of relatively fewer highly branched compounds make it unlikely that these two series of compounds have the common biosynthetic route proposed by Rothman & Schaaf (1929).

SUMMARY

1. A further study has been made of the sterol and wax alcohol fractions of the unsaponifiable matter of human-forearm sebum.

2. Gas chromatography was used to study the composition of the alcohols with up to 20 carbon atoms in the molecule. The alcohols formed a homologous series similar to that of the fatty acids of sebum. There were fewer unsaturated and highly branched alcohols in comparison with the acids and the average chain length of the major alcohols appeared to be longer than that of the major acids.

3. The sterol fraction contained traces of 7-dehydrocholesterol (0·003% of the unsaponifiable matter), *iso*cholesterol (0·07% of the unsaponifiable matter) and unidentified keto steroids.

4. Alkane 1:2-diols, calculated as C_{20} diols, appear to account for 1·6% of the unsaponifiable matter.

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The Inhibition of Bacteriophage Multiplication by Proflavine and its Reversal by certain Polyamines

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Bacteriophages have been known for some time to consist almost entirely of deoxyribonucleic acid and protein, but recently in some *Escherichia coli* phages minor components have been discovered. Hershey (1957) has described two unidentified components, A1 and A2, and a peptide containing aspartic acid, glutamic acid and lysine in trichloroacetic acid extracts of phage T2. Ames, Dubin & Rosenthal (1958) have found the polyamines putrescine and spermidine in phages T2 and T4 and consider them to be identical with components A1 and A2. These findings prompted an examination of a phage in use in this Laboratory known as phage 3, which is similar in many ways to T4. Putrescine and spermidine were found. Before this experiments had been made on the production of incomplete phage particles by the treatment of phage-infected cells with proflavine, as described by De Mars, Luria, Fisher & Levinthal (1953). It was known from the work of Foster (1948) that proflavine could inhibit phage multiplication while permitting cellular lysis. De Mars *et al.* (1953) found that lysis of these cells liberated particles, devoid of nucleic acid, which they believed to be empty phage heads. These they named 'doughnuts' from their appearance in the electron microscope, and suggested that they might be precursors of complete phage. More recently, Kellenberger & Séchaud (1957) have shown that these 'doughnuts' are present in equal amounts in phage lysates whether proflavine is present or not and have cast doubts on the precursor theory. Nevertheless, it seems clear that proflavine can inhibit phage production without interfering with lysis or synthesis of deoxyribonucleic acid (Manson, 1954), although Astrachan & Volkin (1957) maintain that deoxyribonucleic acid from proflavine-treated phage-infected cultures is different from normal phage deoxyribonucleic acid.

The structural similarity between proflavine (2:8-diaminoacridine) and the phage polyamines suggested that the action of the former might be due to interference with the latter. The present paper examines the effect of various polyamines on the inhibition of phage multiplication by proflavine and discusses a possible mode of action of the inhibitor.

MATERIALS AND METHODS

Bacteriophage and host organism. Phage 3 was isolated from Oxford sewage (Fildes & Kay, 1957) and has been found to resemble the well-known coliphage T4 morphologically (Kay & Sampson, 1957) by its possession of the unusual pyrimidine 5-hydroxymethyl cytosine and by its dependence on tryptophan for adsorption. Two mutant forms have been found, one of which ($tryp^+$) requires tryptophan for adsorption to the host bacteria whereas the other ($tryp^-$) adsorbs rapidly in the absence of tryptophan. Phage 3 differs from T4 in numerous details, but in particular it fails to attack the host of T4, *Escherichia coli* B.