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LIPIDS OF MUCOUS SECRETIONS

1. INTRODUCTION

The surface epithelium of the alimentary, respiratory, and reproductive tracts of mammals is covered by an extracellular and renewable layer of a viscous mucus [1, 4, 5, 7]. This mucus layer consists of proteins, glycoproteins and lipids in the form of a gel imbibed with water and electrolytes [1, 22]. The viscoelastic and protective qualities of mucus are thought to be due to its major component called mucins. These high molecular weight glycoproteins have been implicated in a number of functions attributed to mucous secretions such as lubrication, water-proofing, interaction with bacterial and viral agents, binding of cations, and the protection of mucosal surfaces from potentially injurious acids and proteolytic enzymes [1, 3-5, 22].

While the glycoproteins of mucous secretions received considerable recognition [1, 4, 5, 7, 23, 29, 39, 41, 47], until recently, only scant attention has been paid to identifying other components of the secretions which can affect the physico-chemical and functional properties of mucus, namely lipids. Newer data, however, are beginning to illustrate the complexity of mucous secretions with respect to lipids. This article is intended to provide update on lipids of mucous secretions and their role in the protection of underlying epithelial surfaces.

2. COMPOSITION AND CONTENT

The data on composition of mucous secretions of the alimentary and respiratory tracts indicate that lipids constitute 12.5% dry weight of the tracheobronchial mucus, 17.6% of the intestinal mucus and 19-29% of the gastric mucus [26, 27, 37]. Considerable quantities of lipids are also present in gastric secretion and saliva (Table 1) [2, 35, 36]. The lipids present in these secretions are comprised of neutral lipids, glycolipids and phospho-

Table 1

Lipid content of mucous secretions

Source	Total lipids content
	% dry weight
Dog gastric mucus	26.5
Hog gastric mucus	28.0
Rat gastric mucus	29.1
Rat intestinal mucus	17.6
Human tracheobronchial mucus	12.5
Human gastric mucus	24.3
	mg/100 ml
Human submandibular saliva	7.9
Human labial saliva	42.4
Human basal gastric secretion	19.7
Human stimulated gastric secretion	10.9

lipids. The neutral lipids are represented by free fatty acids, cholesterol and its ester, and glycerides, while the phospholipids exhibit high content of phosphatidylcholine, phosphatidylethanolamine and sphingomyelin [2, 22, 26, 27, 34-37]. The glycolipids of mucous secretions consist of glyceroglucolipids and simple glycosphingolipids. The latter compounds, although present in basal gastric secretion and tracheobronchial mucus, are only minor constituents of pentagastrin stimulated gastric secretion, saliva, and gastric and intestinal mucus [27, 34, 35]. Since under resting conditions mucous secretions are heavily contaminated by the exfoliated epithelial cells, these glycosphingolipids probably originate from the cell membranes [34].

The glycolipids which appear to be native constituents of mucous secretions of the alimentary and respiratory tracts are glyceroglucolipids. These compounds, originally found in human gastric secretion and saliva [30, 31, 33], differ from those of the cell membranes with respect to sugar composition and the nature of their lipid core. The glycosphingolipids of the cell membranes are composed of the ceramide and one or more sugar residues [32], whereas the glyceroglucolipids found in secretions consist of a series of neutral and sulfated compounds composed of monoalkylmonoacylglycerol lipid core and variable number of glucose residues.

3. SALIVARY SECRETIONS

Saliva is a complex mixture of the secretions of serous, mucous and mixed salivary glands located in the oral cavity. The secretions of parotid glands are purely serous, the products of acinar cells of submandibular glands are 75% serous and 25% mucous, whereas the sublingual and minor salivary glands are exclusively mucous [12]. The secretions of serous glands contribute most of the salivary amylase and proline-rich cationic glycoproteins in whole saliva, while the mixed and mucous glands are the major source of mucins which are responsible for the viscoelastic properties of saliva [12, 16].

3.1. SUBMANDIBULAR SALIVA

The lipids of submandibular glands secretion consist primarily of neutral lipids and glyceroglucolipids, and of lesser quantities of phospholipids. Occasionally, traces of the glycosphingolipids are also present. The content and composition of lipids in saliva depends upon the health status of the individual (Table 2). Submandibular saliva of heavy calculus formers contains about 50% more lipids than that of light calculus formers, and exhibits an elevated level of glyceroglucolipids, cholesteryl esters and free fatty acids. The level of cholesterol and triglycerides is, however, higher in the light calculus formers [36]. Significant differences in lipids of submandibular saliva also exist between the caries-resistant and caries-susceptible subjects [15, 48]. The cariesresistant individuals contain about 33% less lipids/100 ml of saliva, and exhibit considerably lower content of neutral lipids and phospholipids, but do not differ from caries-susceptible group with respect to the content of glyceroglucolipids (Table 2).

The data on lipids in submandibular saliva of patients with cystic fibrosis indicate that cystic fibrotic saliva contains 66% more lipids/100 ml of saliva than that of normal, and is enriched in neutral lipids, phospholipids and glycolipids [2, 46]. The cystic fibrotic, samples contain 58% more of neutral lipids, 65% more of glycolipids and 95% more of phospholipids (Table 2). The neutral lipids derived from saliva of cystic fibrotic patients are considerably richer in free fatty acids (54%), triglycerides (35%) and cholesterol (42%). The glycolipids or normal submandibular saliva consist entirely of glyceroglucolipids, whereas those

Table 2

Content and composition of lipids in submandibular and labial saliva

Constituent	mg/100 ml of saliva				
	LS	NS	CFS	CRS	CSS
Free fatty acids	5.71	1.97	3.04	1.39	2.34
Mono- and diglycerides	0.29	0.18	0.27	0.12	0.19
Triglycerides	2.03	1.69	2.28	0.59	1.34
Cholesterol	1.52	0.71	1.01	0.50	0.51
Cholesteryl esters	3.51	0.63	1.58	0.62	1.26
Glycolipids	17.93	2.25	3.73	1.46	1.56
Phospholipids	9.21	0.22	0.43	0.10	0.15
Total lipids	42.38	7.87	13.07	5.20	8.01

LS - labial saliva, NS - normal submandibular saliva, CFS - cystic fibrosis submandibular saliva, CRS - caries-resistant submandibular saliva, CSS - caries-susceptible submandibular saliva.

of cystic fobritic saliva in addition to glycerоglucolipids also contain simple glycosphingolipids. These compounds constitute 0.2--0.5% of the glycolipid fraction and consist mainly of lactosylceramide and glucosylceramide [46]. The neutral glycerоglucolipids of normal saliva exhibit higher content of di- and octaglucosyl glycerоglucolipids, while those of cystic fibrotic saliva contain more of mono- and hexaglucosyl glycerоglucolipids. The predominant sulfated glycolipid of normal and cystic fibrotic submandibular saliva is a tetraglucosyl glycerоglucolipid [46]. The major phospholipids identified in both types of samples are phosphatidylethanolamine, phosphatidylcholine, lysophosphatidylcholine, sphingomyelin and phosphatidylserine. These five compounds account for 83% of the total phospholipids in normal saliva and 86.6% in the saliva of cystic fibrosis patients (Table 3).

3.2. LABIAL SALIVA

Since the secretion of submandibular glands is only partially mucous, more representative data on lipids of mucous secretions of the salivary glands are derived from the analysis of labial saliva [50]. These data indicate that secretion of labial salivary glands ocntains 42.4 mg of lipids/100 ml of saliva. The lipids of labial saliva, like those of submandibular saliva, are represented by the neutral lipids, phospholipids and glycolipids (Table 2). The neutral lipids constitute 32.4% of the labial saliva lipids and are composed of free fatty acids (mainly hexadecanoate,

Table 3

Phospholipid composition of submandibular and labial saliva

Phospholipid	% total lipid phosphorus				
	LS	NS	CFS	CRS	CSS
Phosphatidylethanolamine	16.3	27.4	28.9	26.0	21.6
Phosphatidylcholine	13.8	18.3	19.6	21.3	22.8
Phosphatidylserine	11.4	10.1	10.5	6.2	7.1
Phosphatidylinositol	8.8	2.9	3.2	1.4	2.5
Sphingomyelin	13.2	12.5	11.8	12.3	14.2
Lysophosphatidylcholine	6.9	15.3	15.8	13.2	18.1
Lysophosphatidylethanolamine	1.3	1.3	0.9	3.0	3.4
Phosphatidic acid	8.1	0.4	0.3	0.8	2.3
Phosphatidylglycerol	5.2	-	-	-	-
Diphosphatidylglycerol	7.8	2.7	2.8	4.8	4.1
Unidentified	7.2	9.1	6.2	11.0	3.9

Abbreviations: see Table 2.

octadecanoate, and octadecenoate), cholesteryl esters, cholesterol and triglycerides. Glycolipids constitute 44.6% of labial saliva lipids and in addition to glyceroglucolipids also contain about 2% of simple glycosphinogolipids. Phospholipids represent 23% of labial saliva lipids and are characterized by a high content of phosphatidylethanolamine, phosphatidylcholine, sphingomyelin and phosphatidylserine (Table 3).

Comparison of the data on labial salivary lipids with those found in submandibular saliva, indicate that labial saliva contains 4-5 times more lipids/100 ml of saliva, and exhibits a higher percentage of phospholipids and glycolipids. These differences may be a consequence of different processes by which serous and mucous cells liberate their products, or they may reflect the differences in the interaction between the lipids of glandular membrane and the proteins and glycoproteins of secretions. A high content of phospholipids and the presence of glycosphingolipids in labial saliva suggest that the secretion of labial glands contains the elements of the mucous cells membrane. This is in keeping with the eletronmicroscopic observations [52], which indicate that mucous cells liberate their products by a partly apocrine process during which part of the cell membrane is shed and excreted. In the light of our recent studies which showed that lipids in saliva exhibit a high affinity for mucins [49], it is also possible that the glycoproteins elaborated by mucous cells of labial glands interact with the membrane lipids and that these lipid-enriched mucosubstances are secreted into the saliva.

4. GASTROINTESTINAL TRACT

4.1. GASTRIC SECRETION

Considerable differences exist in lipid content and composition between the basal and pentagastrin stimulated gastric secretions(Table 1). The basal secretion,which contains material from sloughed epithelial cells and blood plasma, in comparison to the stimulated secretion, exhibits an elevated level of total lipids, and contains substantial quantities of glycosphingolipids and phospholipids [34, 35].The lipids of the stimulated secretion consist primarily of neutral lipids and glycerogluco1ipids,and are essentially deviod of phospholipids and glycosphingolipids. Analyses of the lipid extracts from human gastric secretion indicate that glycerogluco1ipids constitute up to 30% of the lipid fraction [38], whereas in gastric secretion from dog Heidenhain pouch and from ligated rat stomach the glycerogluco-lipid fraction comprises up to 50% of the total lipids [38]. Result of structural studies performed on the major glycerogluco-lipids of gastric secretion from man, dog and rat, indicate that all three species contain a similar glycolipids which are composed of one or more glucose (up to eight in human) residues linked to a monoalkylmonoacylglycerol lipid core.

Studies on gastric secretion of patients with gastrointestinal disorders indicate that pathological samples. as compared to normal, exhibit an elevated levels of glycerogluco1ipids and phospholipids [25, 34].While the secretion of healthy individuals contains about $0.73 \pm 0.20 \mu M$ of glycerogluco1ipids/100 ml of secretion, the content of glycerogluco1ipids in gastric secretion of patients with gastritis and duodenal ulcer reaches the values of $2.45 \pm 0.46 \mu M$ and $3.08 \pm 0.65 \mu M$, respectively. The lysopho-sphatidylcholine constitutes over 75% of phospholipid fraction in the secretion of patients with chronic gastritis and 83% in patients with gastric hypersecretion [25].

The data on lipids in gastric secretion of patients with cystic fibrosis [28], indicate that the secretion of these individuals contains 80 to 140% more lipids than that of healthy subjects, exhibits an elevated level of neutral lipids, and contains alkyl- and alkylacylglycerols. The level of glycolipids is, however, higher in normal gastric secretion (Table 4). The overall phospholipid composition of both types of samples is

Table 4

Content and composition of lipids in gastric and tracheobronchial secretions

Constituent (mg/g protein)	Gastric		Tracheobronchial	
	N	CF	N	CF
Protein (% dry weight)	50.0	54.7	65.8	71.5
Total lipids	189.7	410.8	190.0	233.6
Neutral lipids	69.6	304.8	75.1	75.3
Phospholipids	64.5	87.1	42.2	54.5
Glycosphingolipids	25.8	7.4	48.4	90.2
Glyceroglucolipids	18.8	5.5	24.3	13.6

N - normal, CF - cystic fibrosis.

Table 5

Phospholipid composition of gastric and tracheobronchial secretions

Phospholipid	Gastric		Tracheobronchial	
	N	CF	N	CF
	% total lipid P			
Phosphatidylcholine	50.4	60.7	32.2	33.0
Phosphatidylethanolamine	8.1	7.7	12.4	11.9
Phosphatidylserine	4.0	5.3	3.2	5.8
Phosphatidylinositol	2.7	3.1	1.1	1.5
Sphingomyelin	15.1	9.7	15.8	20.7
Phosphatidic acid	1.1	2.7	0.5	0.5
Lysophosphatidylcholine	11.4	5.2	29.5	21.4
Lysophosphatidylethanolamine	2.8	2.0	1.9	2.1
Lysophosphatidylserine	2.5	1.0	-	-
Unidentified	1.9	2.6	3.4	3.1

Abbreviations: see Table 4.

similar, but somewhat higher content of phosphatidylcholine and lower amount of sphingomyelin prevails in the cystic fibrosis samples. More pronounced differences are observed in the content of lysophospholipids. In cystic fibrotic secretion the content of these lipids is about 50% lower than in controls and represents on the average 8.2% of the total phospholipids, compared to 16.7% in normal secretion (Table 5). The glycolipids in gastric secretion of patients with cystic fibrosis consist of glycosphingolipids, and the neutral and sulfated glyceroglucolipids. The glycosphingolipids are represented by mono-, di- and trihexosylceramides, and their content is about three times lower than that

in normal secretion. The major neutral glycero glucolipid of normal secretion is a tetraglucosyl glycero glucolipid, whereas cystic fibrosis samples are rich in hexa- and octaglucosyl glycero glucolipids [28].

4.2. GASTROINTESTINAL MUCUS

Investigations on the origin of lipids in gastric secretion established their presence not only in the soluble portion of gastric secretion, but also in the mucus layer lining the surface of the mucosa and in the preformed intracellular mucus contained within the secretory granules of the epithelial cells [22, 24]. Furthermore, it has been shown that instillation in vivo of various noxious agents such as ethanol, aspirin, lysophosphatidylcholine and hyperosmotic NaCl causes various degree of solubilization of gastric mucus constituents [22, 24, 40, 44]. The most effective agent for the removal of gastric and intestinal mucus in relatively pure from is 2M NaCl [9]. The lipids derived from 2M NaCl instillates of rat stomach constitute 20-30% of the dry mucus weight and comprise of neutral lipids (50%), glycolipids (45%) and phospholipids (5%) [22]. The gastric mucus of dog stomach contains 18-21% of lipids, while their content in rat intestinal mucus ranges from 17 to 22% (Table 1).

Studies on the distribution of lipids in the different regions of dog and rat stomach revealed that highest levels of lipids are present in the antral mucus and the lowest in the mucus derived from the body area of the stomach [26, 37]. The antral mucus also contains the highest level of sulfated glycero glucolipids. The level of these compounds in dog antral mucus is three times greater as compared to the fundus and four times greater as compared to the body [26]. In rat gastric mucus, the level of sulfated glycero glucolipids in antrum is eight times higher as compared to the body and four times higher as compared to the forestomach [37].

5. TRACHEOBRONCHIAL SECRETIONS

Tracheobronchial secretions consist of a heterogeneous population of macromolecules which together with salts and water form a viscous layer of mucus, the function of which is to protect the underlying epithelial cells against airborne microorganisms and irritants. This mucus layer, scanty in amounts in healthy indivi-

duals, accumulates in the airways of the patients with cystic fibrosis, causing obstruction and leading to coughs and sputum production [4, 17, 27]. Major components of the tracheobronchial mucus include mucin-type glycoproteins, serum proteins and lipids [4, 18]. The lipids constitute 12.5% of the dry weight of tracheobronchial secretions from normal subjects and 16.7% of the mucus weight in patients with cystic fibrosis (Table 4). Of the total lipids from normal secretions, about 40% are represented by neutral lipids, 22% by phospholipids, 25% by glycosphingolipids and 13% by glyceroglucolipids [27]. In cystic fibrosis secretions the neutral lipids constitute 32% of the total lipids, phospholipids 23%, glycosphingolipids 39%, and glyceroglucolipids 6% (Table 4).

Although the secretions from normal and cystic fibrosis individuals exhibits a similar spectrum of lipids, those derived from normal subjects are considerably richer in free fatty acids, while those of cystic fibrosis individuals contain more cholesterol and cholesteryl esters. The phospholipids of cystic fibrosis patients exhibit higher content of sphingomyelin and phosphatidylserine, whereas those of normal subjects contain more lysophosphatidylcholine (Table 5). The glycosphingolipids of tracheobronchial secretions consist mainly of lactosylceramide (46-48%) and glucosylceramide (33-37%), and their content is quite similar in both normal and cystic fibrosis samples. The glyceroglucolipids of each type of sample consist of neutral and acidic compounds. The predominant neutral species of the normal secretions is tetraglucosyl glyceroglucolipid, whereas hexa- and octaglucosyl glyceroglucolipids constitute 70% of the neutral glyceroglucolipids of the cystic fibrosis secretions.

6. FUNCTION OF LIPIDS IN MUCOUS SECRETIONS

Although the presence of lipids in mucous secretions of the respiratory and alimentary tracts has been recognized for some time [6, 10, 11, 13, 55], their effect on the physico-chemical and physiological properties of mucus remained obscure. In more recent years, however, a number of fuctions for lipids in mucous secretions have been demonstrated. In the respiratory tract, the lipids associated with mucus glycoproteins participate in the protection of epithelial surfaces against airborne irritants and microorganisms, and affect the rheological properties of mucus by

decreasing its viscosity and elasticity [4, 14, 18]. In the oral cavity, the level of lipids in salivary secretions is directly linked to the development of plaque, calculus, caries and periodontal diseases [12, 15, 36, 48]. The salivary lipids affect the penetration of the oral mucosa by lipophilic substances, and are capable of alteration of the interaction of mucins with calcium [8, 21, 53]. Some of the salivary lipids also affect the glucosyltransferase activity associated with the cariogenic potential of the bacteria [20]. The relatively high content of lipids in the secretions of labial salivary glands may be of importance in the protection of labial mucous membranes in the oral cavity against the loss of water [50].

The lipids in gastric mucus assist in cytoprotection of gastric mucosa by slowing down the rapid rate of hydrogen ion diffusion [19]. The higher content of lipids in mucus derived from antrum as compared to other stomach regions, may be directly linked to the ability of antral mucus to protect the underlying mucosa against cytolytic effect of the duodenal refluxes to which the antral area of the stomach is most frequently exposed [9,15]. Some of the lipids of mucous secretions, i.e., glycoroglucolipids, remain in tight association with mucins [43, 54], and hence may augment the functions of gastrointestinal mucins such as lubrication, interaction with bacteria, and protection of mucosal surfaces from potentially injurious proteolytic enzymes [1, 5, 51]. The involvement of glycoroglucolipids in the regulation of peptic activity in the stomach has been recently demonstrated [43, 45]. Also, the elevated levels of lipids in mucous secretions in patients with cystic fibrosis points toward their involvement in the alteration of physicochemical and physiological properties of mucus associated with this pathological state.

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LIPIDY WYDZIELIN ŚLUZÓWKOWYCH

S t r e s z c z e n i e

Badano lipidy jako składnik śluzu wydzielanego przez nabłonek powierzchniowy układu trawiennego i oddechowego. Dotychczas glikoproteiny stanowiły główny obiekt zainteresowań w badaniach składu i funkcji śluzu, co wynikało z przypisywania tym cząsteczkom najważniejszej roli w procesie formowania i funkcjonowania śluzu. Lipidy stanowią 12,5% śluzu wydzielanego w układzie oddechowym, 17,6% śluzu jelitowego i 19-29% śluzu żołądkowego, w przeliczeniu na suchą masę śluzu. Obecność znacznych ilości śluzu stwierdzono także w ślinie i soku żołądkowym. Stwierdzono lipidy obojętne, glikolipidy jak również fosfolipidy. Wśród lipidów obojętnych wykazano obecność kwasów tłuszczowych, cholesterolu i jego estrów oraz glicerydów. Główne fosfolipidy to fosfatydylocholina, fosfatydyloetanoloamina i sfingomielina. Gliceroglukolipidy stanowią główny składnik glikolipidów porównując z niewielką ilością prostych glikosfingolipidów.

Podano szczegółowy skład lipidów śliny z uwzględnieniem ślinianek podszczękowych i wargowych, następnie skład lipidów soku żołądkowego, śluzu żołądkowo-jelitowego oraz wydzieliny płucnej.

Przedstawiono również obecne poglądy na rolę lipidów zasocjowanych z glikoproteinami w aspekcie fizjologicznych właściwości śluzu.

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