Studies on the Embryology and Histology of the Salivary Glands and Their Endocrine Nature

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The author presents this as a review article on the current state of knowledge on the salivary glands. It was prepared at an NSF In-Service Institute at the University of Detroit.

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Introduction

Three large paired glands, the parotid, the submandibular (submaxillary) and the sublingual, are usually considered as constituting the salivary glands. However, numerous smaller glands scattered throughout the buccal mucosa contribute toward the saliva. They are situated outside the digestive tract and their secretions are carried to the oral cavity through individual ducts.

They are considered exocrine glands and their primary function is to transform and secrete materials brought to them by the circulating body fluids. They produce and discharge such complex enzymes as mucin and ptyalin, not found in the circulating blood or lymph fluid. They have as a secondary function to excrete certain substances.

They play an essential role in regulating the water balance of the body. In 1932 Cannon pointed out that when the body is in need of water, their secretion of about 98% water is reduced. As a result, the mucous membrane of the mouth and pharynx becomes unpleasantly dry and the sensation of thirst results.

The Parotid Glands

Parotid meaning, beside the ear, is the name given to the largest of the three pairs of salivary glands. They are located between the mastoid process and the ramus of the mandible. They overflow into the face below the zygomatic arch and their ducts (Stenson's) running parallel to the arch, penetrate through the buccinator muscle and open into the vestibule of the mouth opposite the second molar tooth.

They are enclosed in a well-defined fibrous connective tissue capsule and in a compound tubulo-alveolar gland of the serous type.

They are especially characterized by many and prominent interlobular ducts.

The Submaxillary Glands

These lie in contact with the inner surface of body of the mandible, and their main ducts (Wharton's) open into the floor of the oral cavity, anterior to the tongue and behind the lower incisor tooth.

They are compound alveolar or tubulo-alveolar glands. Although of the mixed type, the majority of their secretory units are of the serous variety. Mucous units are usually capped by serous demilunes. Like the parotid glands, they are well-defined capsules and fairly prominent duct systems.

The Sublingual Glands

These glands lie well forward, near the mid-line below the mucous membrane of the floor of the mouth, and their secretions empty by several ducts (Rivinus) that open along a line behind the openings of Wharton's ducts. Unlike the other salivary glands, they are not so definitely encapsulated.

They are compound tubulo-alveolar glands of the mixed type, but different from the submandibular glands in that the majority of their alveoli are of the mucous type.

Numerous Smaller Glands

There are numerous smaller glands of minor secretion, the oral and labial glands, the palatine, the anterior lingual of Blandin or Nuhn, the posterior lingual of von Ebner.

The labial glands located on the inner surface of the lips are of the mixed type. They are not encapsulated. Both serous and mucous cells line the lumen of the secretory portions, but more often demilunes are formed. The buccal glands which are a continuation of the labial glands, bear a marked resemblance to those of the lips. Those which drain in the third molar region are designated as retromolar and are the human representatives of the orbital glands of the carnivora.

The glossopalatine are pure mucous glands and are located in the isthmus region and are a continuation of the lesser sublingual glands.

The palatine glands also of the pure mucous variety, occupy the roof of the oral cavity and are divided into (1) glands of the hard palate, (2) glands of the soft palate and uvula. There are approximately 250 in the hard palate, 100 in the soft palate, and 12 in the uvula.

The structure of the palatine glands is that of the long-branched tubulo-alveoli connecting with single ducts.

The lingual glands are serous, tubular, branched, simple glands whose secretions contain a high content of albumin and hence are called "albuminous" glands.

The anterior lingual glands (Blandin or Nuhn) and buccal glands which are a continuation of the labial glands in the cheek are furnished with demilunes.

According to Maximow and Bloom, the glands of the oral cavity in various mammals show great structural variations. Even in closely related species, the same gland may have a totally different composition. In the dog and cat, for instance, the mandibular glands consist for the most part of mucous cells, with a few albuminous cells forming typical demilunes. In rodents, on the contrary, the same gland does not contain any mucin, and is therefore, a pure albuminous gland. In insectivora, (hedgehog), the gland seems to contain only albuminous cells, but of two different varieties. The term "sublingual gland" has been applied to different glands in different animals. It is now termed "retrolingual." In animals such as rodents, it has been described as pure mucous; in others such as the dog, cat, and pig, as a mixed gland with demilunes.

The Embryology of the Salivary Glands
Origin and Development

Origin and Development

The salivary glands are formed during fetal life as solid buds of oral epithelium with club-shaped ends pushing into the adjacent mesenchyme. As the bud grows, it proliferates distally forming a cord of cells, with the most distal portion forming the alveoli or functional elements. From undifferentiated polyhedral or cuboidal cells, they undergo many mitoses until a lumen or glandular cavity develops, around which the cells align themselves, according to the characteristics of the type of alveoli, they are to become. The cord which remains attached to the oral epithelium during the growth of the gland, later develops into the duct system.

Meanwhile in the development of the gland alveoli, the mesenchyme cells become concentrated and assume a concentric arrangement at the periphery to form a capsule. The supporting tissue of the ducts has a similar arrangement. However the sublingual gland and the smaller gland elements do not develop a definite capsule.

During the fourth week of fetal life, the bud of the parotid gland appears as a shelf-like outgrowth of epithelium at the angle of the maxillary process and the mandibular arch. The bud of the submaxillary appears in the sixth week and that of the major sublingual during the eighth to ninth week at the median angle of the hollow between the tongue and the mandibular arch. The anterior lingual glands appear for the first time at ten weeks. The labial glands develop simultaneously with the anterior lingual glands. Mucigen appears in the adult cells in the

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ninth fetal week. Zymogen granules do not make their appearance until somewhat later. Lymphoid tissue is frequently found in the fetal salivary glands, especially the parotid.

The Histology of the Salivary Glands

Orban records that the microscopic plan of the human salivary glands, regardless of their size, is uniformally similar. They are all compound racemose glands. The functional elements in the adult are arranged in tubular alveoli or acini which form the lobules. The secreting surfaces of a cell border a lumen, as a continuous sheath of cells resting upon a basement membrane and are in turn supported by connective tissue so that each lobule may be likened to a simple gland. In the larger glands, the lobules are grouped into lobes, held together by a framework of connective tissue.

The human salivary glands are classified according to location and according to the type of cells. Those which liberate mucin are mucous cells; those which secrete some form of protein, (enzyme) are albuminous or serous cells. It is now evident that all mucous cells as well as all albuminous cells do not produce the same products. In some cases, the granules of albuminous cells give a distinct reaction for mucin with mucicarmine, indicating the possibility that they produce both mucin and protein substances. Accordingly the glands are best classified as albuminous, mixed, and mucous glands. Those in which both serous and mucous cells are present are referred to as predominantly mucous, or predominantly serous, depending upon the ratio of the cell types. Those with a few mixed cells include the submaxillary (and the parotid of the newborn). Those predominantly mucous in character include the labial, small buccal, anterior lingual, and sublingual. In the human, pure mucous glands are at the base and border of the tongue, the glossopalatine, and palatine glands.

Both the albuminous and mucous cells vary in appearance with the functional changes of the gland.

Although the albuminous or serous cells of the parotid gland and other glands of the mouth probably do not perform identical functions, the cells resemble each other closely. Their secretion is a thin watery fluid containing a high percentage of organic or inorganic substances.

Albuminous cells are roughly pyramidal or polyhedral in shape and form globular alveoli, the lumina of which are very narrow. They drain for the most part by intracellular secretory capillaries or canaliculi. In resting cells of a fixed specimen the small highly refractive secretory granules are the antecedents of the enzyme ptyalin. They are found between the nucleus and the free end of the cell. They are easily dissolved by chemical agents, but are more stable than the granules in the mucous cells. Following stimulation they diminish in number.

In addition to the secretory granules, the cytoplasm contains rod-shaped mitochondria, a Golgi net, and a cytocentrum which can be demonstrated only by special staining. The nucleus is large, oval, and filled with abundant chromophil substance. Its size and location are somewhat dependent upon the stage of activity of the cell.

Most albuminous glands show a series of lamellae or striations at the base of the cell which appear as short brush marks in a stained preparation. They are accumulations of chromophil substance and stain heavily with basic dyes; they are not mitochondria and their functions are unknown. On the free cells, the albuminous cells are provided with terminal bars. Occasionally mitoses are encountered.

Fixative agents can produce artifacts. A true insight into the functional activity of the salivary glands, can be gained by cutting the thin edge of the lobule of a gland of a living animal with scissors or knife, mounting in a physiologic medium, such as salt solution, serum or saliva and observing the changes during various stages of rest and activity.

For example, the parotid of a fasting rabbit taken fresh and examined immediately, presents a uniform granular appearance. Cell outlines are indicated by clear lines between the cells. Nuclear outlines are obscure or missing. During activity the appearance of the alveoli changes. The granules become more clear and accumulate in the inner part of the cell. After prolonged stimulation the granules disappear. During glandular activity, the salivary flow diminishes, the cells shrink, and separate slightly at the inner bor-

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der, causing the lumina of alveoli to become larger and the cell boundaries more distinct. Finally secretory granules begin to be rebuilt in the resting cell, a process which is accomplished from several minutes to several hours.

Langley has recorded some interesting experiments in which the submaxillary salivary gland was treated with different chemical agents. Two cells irrigated with water showed the reticular network of the swollen mucigen granules. Cells were irrigated with 5% NaCl followed by 1% NaCl. Fat globules showed up in the network. Cells were irrigated with dilute ammonia followed by 1% HCl. Mucin issued from the upper pole of the cell.

The submaxillary glands, described by Balint as ovoid in form, loosely encapsulated, and about the size of a walnut, are a pair of branched alveolar glands found in the floor of the mouth each being drained by the submaxillary duct, (Wharton's) which opens on the sides of the frenulum linguae near its front margin. Sometimes this duct is joined by the ductus sublingualis major so that the two have a common outlet. Its mouth may be lined by stratified epithelium, but this soon is replaced by the two-layered form. Secretory ducts are well enveloped and their basally striated cells contain a yellow pigment.

The secretory epithelium is arranged in alveoli, which appear either light or dark in sections stained with hematoxylin and eosin. The light ones are mucous alveoli and they are few in number. The serous alveoli are more strongly colored by hematoxylin and eosin and are much more numerous. With special methods, secretion antecedents in the form of zymogen granules are revealed in them. Sometimes the serous cells do not form a complete serous alveolus but are applied as a crescent of Gianuzzi, or demilune to one side of a mucous alveolus.

In the mandibular gland of man, the greater number of secretory portions are purely albuminous, while some are mucous and albuminous in the blind ends. Typical demilunes are rare. In some individuals some albuminous cells show a slight mucoid reaction. The mucous cells are smaller than in the sublingual or pure mucous glands. Some isthmuses are short, others are long and branching. The striated tubules are numerous, very long, and have many branches.

The sublingual glands are two groups of glands, one on each side of the median line under the mucous membrane in the front of the mouth. They are mixed glands with a markedly varying structure in their different parts. The mucous cells are far more numerous than in the mandibular gland, while the albuminous cells are in the minority and have a pronounced muco-albuminous character. Their microscopic appearance is different in different parts of the gland. In some units only mucous, secreting units and mucous units with serous demilunes may be found.

The connective tissue septa are usually more prominent than they are in the parotid or submandibular glands.

The pure mucous glands of the mouth are simple branched alveolotubular glands located on the soft palate and on the hard palate (palatine glands), along the borders of the tongue (lingual glands), and in greater numbers in the root of the tongue. There they may open into the tonsillar pits through ducts lined with columnar epithelium, which are sometimes ciliated. The wall of the tubules consists of a structureless basement membrane and of columnar mucous cells which vary according to their functional condition. The empty cells are narrower than the others, and the nuclei, although at the base of the cell and transversely oval are not as flat as in cells full of secretion. Seldom are cells found completely filled with unaltered protoplasm. A single gland or even a single alveolus may contain cells in different phases of secretion as is clearly seen when special mucin stains are used. Secretory capillaries are not found in purely mucous glands.

Mucous cells at rest form granules in a manner similar to serous cells. While in the serous cell the formation and discharge of granules takes place rapidly, in the mucous cells the completion of the cycle may take several days or weeks. Mucigen first appears during regeneration as small acidogenic granules around the nucleus near the free end of the cell.

The mixed oral glands include the sublingual, the submaxillary, the labial, buccal, and the malar glands. The parotid also is said to contain mucous end-pieces in the newborn which disappear later in childhood. In all the salivary glands, in the terminal por-

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tion as well as in the ducts are found peculiar basal or "basket" cells. Orban describes them as spider-like structures embracing the alveoli, viewing them from the periphery. The body is made up of a dark, angular nucleus with scanty cytoplasm containing fine, straight fibrils, which continue into tentacle-like processes encircling the basal portion of the alveolar cells. The nuclei are visible only in cross-section. Cells become especially prominent after treating fresh gland tissue in a state of active secretion with osmic acid or by teasing fresh gland substance in water.

These cells, presumably of epithelial origin are supposed to act as smooth muscle cells. Through contraction they facilitate movement of the secretion into the excretory ducts, and since they resemble the myo-epithelial of the sweat glands are sometimes called "myo-epithelial" cells.

Ducts

Ducts

The duct system is complex and branching. The smallest excretory channels are the intercalated ducts or the so-called necks or isthmuses. They vary in length depending upon the type of gland which they drain.

The relationship of the mucous cells to the intercalated indicates that mucous cells arise through transformation of these duct cells. Also, the more numerous the mucous cells in the secreting alveolus, the shorter is the intercalated duct. The parotid has long intercalated ducts, while in the sublingual gland they are absent or very short and inconspicuous.

An outstanding characteristic of the intercalated ducts is their thin-walled and relatively small diameter. They are always surrounded by myo-epithelial cells which take ordinary stains poorly.

In the parotid and the submaxillary glands, striated ducts intervene between the intercalated ducts and the larger excretory ducts. These ducts secrete water and inorganic salts which act to dissolve the antecedents secreted by the alveolar cells. There is a finely granular cytoplasm which contains a nucleus which is centrally placed. The perpendicular striations from which the cells derive their name are confined to the outer or basal zone near the basement membrane.

Ducts less than 0.05 mm in diameter have a simple columnar epithelium which in a few becomes low and basally striated to form the secretory ducts. The terminal secretory portions of the gland are somewhat tortuous structures. Only the serous cells are provided with branched intercellular secretory capillaries. Elastic tissue surrounding the alveoli has been thought to aid in expelling the secretion through the ducts.

Characteristic of compound glands in general is the presence of secretory capillaries or canaliculi which rise from the smallest excretory ducts and penetrate between the functional cells at their borders. The purpose of secretory capillaries is to increase the drainage capacity of alvoeli of multiple layers of cells. The capillaries are most effectively demonstrated with silver impregnation.

Endocrine Glands or Exocrine Glands

The question arises as to whether these are endocrine or exocrine glands.

Although all epithelial cells of an exocrine gland belong to the same family, they are not all differentiated to the same degree. The more highly differentiated are those specialized for secretion, and the less highly differentiated are those that line the ducts which carry the secretion to the surface. The secretory cells are found at the end of a duct. They are arranged to form a cluster which we call a secretory unit. Each posses-ses a cavity or a lumen into which the secretion is liberated and is continuous with the duct.

Exocrine glands are classified in several different ways. If the secretory portion is tubular, it is a tubular exocrine gland; if it is flask-like, it is an alveolar or acinus gland; if both, it is tubuloalveolar gland. If the duct doesn't branch, it is a simple gland; if it branches, it is a compound gland. The struture of endocrine glands is considerably simpler than exocrine, because they possess no ducts. As their secretory cells discharge into capillaries, the secretory cells must be arranged in such a way that all abut on capillaries. They may be arranged either in straight or irregular cords separated by capillaries, or in clumps surrounded by capillaries.

All endocrine glands store their secretion. This is accomplished in most by intracellular storage. For example, endocrine glands

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which make insulin, store enough to kill a person if it were all secreted at one time.

Sometimes the cells of a clump secrete inwardly and the cells surrounding the area is termed a follicle.

Secretory granules are the immediate forerunners of a secretion from endocrine glands. These usually require special histologic technique.

Endocrine glands are enclosed by capsules which extend into the glands as trabeculae, and they account for the lobulated appearance of some endocrine glands under the microscope.

The total daily output of saliva is approximately 1500 cc. This is subject to variation depending on age, weight, and diet. It is influenced by physical and psychologic stimulation. Of the total amount secreted the large salivary glands (parotid, submaxillary and sublingual) contribute the greatest amount. The quality depends on the type of glands which participate in its formation.

Mixed saliva is a frothy, slightly opalescent fluid containing water, proteins, mineral salts, ptytalin, mucin, food particles, desquamated epithelial cells, and salivary corpuscles. Its viscosity is influenced by the predominating type of saliva secreted; serous saliva gives it a watery appearance; mucin renders it thick and ropy.

The specific gravity varies from 1.000 to 1.020, and the freezing point is lower than that of any other of the secretions of the digestive glands. Hydrogen-ion determinations vary greatly, owing to individual, time of day, and difference in methods used. The mean of average pH is about 6.8, ranging from 5.6 to 7.6, the highest being just before meals. Other influencing factors may be the oral hygiene and the type of oral flora. From the chemical standpoint, human, mixed saliva is a dilute solution containing about 0.2% inorganic and 0.5% organic matter. Potassium and phosphate ions make up the inorganic portion. Other elements found in appreciable amounts are as follows: CL, P, Na, K, Mg, Ca, and S. About 90 mg/100 cc is NaCl; 13 mg of carbonate is present as CO_2. Oxygen is present in the human parotid in varying amounts from 0.84 to 1.46 cc per 100 cc.

About 0.4% of organic matter in mixed secretions is mucin. The principal organic constituents are albumin, globulin, amylase, cholesterol. Others are urea, uric acid, creatinine, maltase, and ammonia. Sulfocyanate is found to the extent of several milligrams per cubic millimeter. It is greatest in habitual smokers.

The role of the salivary enzymes in the digestion of food is questionable. Amylase breaks down starch to maltose in an alkaline or slightly acid medium.

Although ptyalin is able to split starches to the simple-sugar stage, it leaves the carbohydrates in the form of double sugars. Double sugars taken by the mouth as such, (for example, ordinary cane sugar) are unaffected by ptyalin. This striking example of enzyme specificity is puzzling.

The primary function of the salivary glands is to transform and secrete materials brought to them by the circulating fluids of the body.

A secondary function is to excrete certain substances such as saliva. The saliva is the term applied to the accumulated secretory and excretory products discharged by the salivary glands into the oral cavity. It is the first of many digestive fluids to act upon the food elements in the diet. It assists in the mastication of food, acts as a solvent to bring components into solution, and facilitates the stimulation of the taste organs. It facilitates the expectoration of injurious or distasteful objects from the mouth. In man it makes speech easier. In some animals, including the dog, the functions of the saliva seem to be of an entirely non-digestive nature. Albuminous or serous cells of the gland liberate the enzyme ptyalin or amylase, causing a preliminary breakdown of carbohydrates.

The mucous cells liberate mucin which counteracts tendencies of the oral membrane to dessication and aids in the lubrication of food for deglutination. The proteins and salts act as buffers which counteract the acids and alkalies in the oral cavity. It serves to flush the surfaces of the teeth and mucous membranes; it removes bacteria from ducts and surfaces and is a safeguard against infection.

The stimulus that evokes secretion may be mechanical or chemical. For example, the presence of food (or even pebbles or dry powders in the mouth) stimulates the ordi-

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nary nerve endings and causes salivary secretion. Stimulation of many sensory nerves other than those of the oral cavity may initiate a salivary reflex, provided the reflex has been conditioned.

We are all familiar with the work of Pavlov, the famous Russian physiologist, who showed that the only stimulus that would evoke stimulation in a newborn puppy was the actual presence of food in its mouth. The afferent pathway activated in this instance would be a pathway leading from receptors in the mouth itself. In its brain the puppy had inherited a preferred connection between the afferent pathway and the efferent pathway that controls the salivary glands. Then Pavlov showed that after the puppy had been fed a few times, he would salivate as soon as food was placed before him. This, obviously, would require a different afferent pathway from the first one employed — one from the nose rather than from the mouth. There must be some connection in the brain between the afferent pathways from the nose and the afferent pathways from the mouth, which permit the puppy to associate the taste of food with the smell of food. Once this association is built up the proper stimulus applied to the nose brings about the same reflex response as does food in the mouth. This can be applied in many other responses. For example, a pup can learn to salivate at the sight of food and even at the ringing of a bell, if the bell is rung at the same time the pup is fed.

Yosoji, Jun Kawada Ito did some work in 1935 which would indicate the endocrine nature of salivary glands. No more was heard from him until 1962. Some work he did on the salivary glands of rats is recorded in the *Biological Abstracts* of the January-February issue of that year

He administered $KC10_4$, MMI (1-methyl-2-mercaptiomidazole) TU (thiouracil) and MTU (6-methyl-thiouracil) for two to seven weeks and KI for three weeks in the drinking water to adult rats. The relationship between the change in weight of the salivary glands and iodine metabolism was examined using radio-iodine.

Observations showed that the inhibition of iodine metabolism by the thyroid gland did not always result in decrease in weight in the salivary glands. There seemed to be little evidence for a direct relationship between the function of the thyroid gland and the salivary glands from this experiment. Significant iodine concentration by the salivary glands was not observed in normal animals. The antithyroid drugs used had no influence upon concentration.

Ham and Leeson as well as Edmund Cowdry state in their works that no hormone appears to have any affect on salivary secretion. Ordinarily it is controlled by nervous reflexes. It may not be simply vasoconstriction or vasodilation, because as Stormant has demonstrated in the rabbit's submaxillary, both sympathetic and parasympathetic fibers pass directly to the epithelial components and are distributed differently

Conclusions

Extensive research through many books and current literature as well has yielded many interesting hours, but not a great store of information. I believe that this could be a field for further research. I feel that more will be done in relation to cancer of the lips, mouth, and oral cavity.

The enzyme activity seems to be limited, especially the activity of ptyalin in splitting starches to the simple sugar stage, but having no effect on double sugars, such as cane sugar; for example such as taken by the mouth. This enzyme specificity is puzzling.

The numerous salivary glands are necessary for the large amount of salivary secretion.

There seems to be no basis for the endocrine nature of the gland or any proof of hormone secretion or activity.

The activity is governed by the nervous system alone.

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is to help build some firm value commitments of students in regard to themselves, their conduct and their relationships with their peers and the rest of the world, shouldn't biology teachers concern themselves with this dimension in analyzing the content of the courses they teach? Perhaps teachers should look at their courses systematically, asking of themselves not only what biological content and skills are they communicating, but also (and perhaps more important) what attitudes and values are they reinforcing.

Perhaps teachers have an obligation to have these latter considerations in the forefront of their thinking as they choose content of the course they teach, and as they plan the techniques for working with this content. While the biology content and skills they are dealing with are important, the values they communicate may be even more critical in terms of the survival of the individuals they teach and of society as we know it.

Hulda Grobman
Associate Editor

Solvent Sniffing Still a Problem

Sniffing such products as glues, paint thinner, fingernail polish remover, cleaning and lighter fluid, although not the fad of recent years, has become a permanent and relatively common form of abnormal childhood behavior, which can lead to accidents, violence and antisocial acts.

So conclude Edward Press, M.D., Illinois Department of Public Health, and Alan K. Done, M.D. Department of Pediatrics, University of Utah College of Medicine, in the April 1967 issue of *Pediatrics*.

"Various observations of the problem," the authors point out, "suggest that sniffing provides a chemical escape from reality which is more adaptable, and therefore more readily accepted, by young children than are such other intoxicating practices as alcohol ingestion or the use of narcotic drugs.

The article points to the relative inexpensiveness, ease of concealment, and ease of procurement "for supposedly legitimate purposes," as explainable reasons for the popularity of solvent sniffing among youngsters today.

"The result is the development of dependence or habituation of youngsters at a far younger age than would otherwise be likely."

Dr. Done and Dr. Press indicate in their paper that solvent sniffing may be the counterpart in the young child "of the abuse of narcotics, alcohol, or LSD in older individuals."

Enumerating results of studies conducted to characterize solvent sniffers, and to assess the importance, potential dangers, and ef-

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