A STUDY OF THE GOLGI APPARATUS

By

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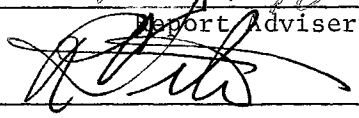

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PREFACE

In the various fields of scientific study relating to cells, there exists a controversy about the so-called "Golgi apparatus." A great amount of research has been conducted in attempts to elucidate the nature of the Golgi apparatus, but researchers have been unable to make a firm correlation between different types of cells in regards to the morphological, chemical, and ontological aspects of the Golgi apparatus.

The purpose of this report is to assimilate various research reports and conclusions in order to provide a better understanding of the problems encountered in the study of the Golgi apparatus.

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CHAPTER I

INTRODUCTION

The cytoplasmic component we call the Golgi apparatus was first observed by an Italian neurologist, Camillo Golgi, in 1898. He treated brain tissue with a silver salt and noticed that each of the nerve cells contained a dark reticular network in the cytoplasm. His original preparation is described in Appendix A of this report. Golgi named it the "internal reticula apparatus." Later it was renamed the Golgi apparatus in honor of its discoverer.

Golgi originally described the apparatus as a system of canals, and during the period 1899 to 1908, many investigators reported similar systems of canals in the cytoplasm of a variety of cells. In 1902, the German scientist, Kopsch, demonstrated the same structures by treating tissue in 2 per cent osmium tetroxide (Brachet and Mirsky, 1961. Vol. V). Kopsch's technique of staining is described in Appendix A of this report. The Golgi method and the osmium tetroxide method of staining are acceptable methods of demonstrating the Golgi apparatus.

The Golgi apparatus was generally described by Cowdry (1924) as an area of the cytoplasm frequently of reticular shape, displaying a dense or compact network depending on the immediate activity of the cell, sometimes situated with a definite cellular

polarity, and ranging in size from as large as the nucleus to small disc shaped bodies the size of the nucleolus. In association there may be rimmed vacuoles called Golgi vacuoles (Baker, 1957).

Obviously, the above description is not specific; however, the varying descriptions and attempts at morphological correlation leave little else than reserved generalizations. It should also be noted that due to the generalized description, many writers hesitate to give a specific name to the apparatus and terms such as Golgi region, Golgi substance, and Golgi complex have been used. The author will use the term Golgi apparatus to avoid confusion.

CHAPTER II

OCCURRENCE

While the author of this report is primarily concerned with the Golgi apparatus in metazoan cells, the occurrence in other forms of life must not be over looked.

To date, there are no references on the existence of a Golgi apparatus in bacteria, and it is assumed that the Golgi apparatus does not exist in bacteria. Eric C. Noller, Department of Microbiology, Oklahoma State University, verified the above assumption in a personal interview on April 13, 1965.

After the first description of the Golgi apparatus in mammalian tissue, Bensley (1910) observed a fine vacuolar, canal-like network in the meristematic cells of lilly, iris, and onion root tip. Bensley postulated that the networks differentiated into the vacuoles of mature plant cells and that the vacuolar system of plants is the physiological and morphological equivalent of the Golgi apparatus in animal cells.

Following Bensley's observations, many other plant cytologists reported observations of the Golgi apparatus; however, they did not share Bensley's views. Brachet and Mirsky (1961, Vol. VI) generalized these observations by stating that the so-called Golgi apparatus in plants was a network of fine filaform

vacuoles which characterize the meristematic cells of plants. Bensley's postulation has not received further evidence to support it.

Bowen (1927) was able to demonstrate osmophilic platelets called dictyosomes in plants which were similar to plate-like Golgi bodies of animal cells. On ultracentifugation the platelets separated into distinct layers. Also the platelets did not take up stains regarded as specific for vacuoles or mitochondria.

The osmophilic platelets in plants are randomly distributed in the cytoplasm while in animal cells, the Golgi apparatus frequently shows proximity and orientation with respect to the nucleus or other structures. In a few large plant cells of varying groups, the osmophilic bodies show localization and orientation i. e. Antirrhinum and Chalamydomonas (Brachet and Mirsky, 1961, Vol. VI).

At present it is highly possible from the indications of size, form, and staining properties, the platelets are similar to the lamellar plates of the Golgi apparatus in animal cells. These bodies have been reported by other observers in many dicotyledons, monocotyledons, a fern, all chief groups of mosses, liverworts. and many algae.

Grimstone (1961) in correlating protozoan fine structures with metazoan cells, observed that the parabasal bodies of protozoa in other kinds of cells consists of piles of smooth membranes joined in pairs to form sacs. He noted that the parabasal bodies resemble those of other invertebrates and are usually more or less disc shaped. Also, they are found in representatives of all main groups of protozoa although most ciliates have no Golgi material present. He suggested a relational aspect among the parabasal bodies found in some flagellates

which are generally cylindrical and are attached to the centriole by a filament. This attachment is of interest due to the frequent association of the Golgi apparatus with the centriole in other types of cells. In addition he describes the parabasal bodies as always lying near the nucleus.

Although the plant dictyosomes and the parabasal bodies of protozoa are often simpler in appearance than the Golgi apparatus of animals, the resemblance is quite striking (Brachet and Mirsky, 1961, Vol. VI).

In work done by Causey (1925) on the amoeba Endamoeba ginivals, the food vacuoles that gradually faded away left crescent-shaped bodies free in the cytoplasm. These strained intensely and showed irregular thickenings on the rim. The thickened rim of the vacuole itself may elongate irregularly and closed systems form which resemble the Golgi apparatus of metazoan cells. These were demonstrated by osmification.

Causey suggested that the origin of the Golgi apparatus is from a region of intense metabolic activity, the food vacuole wall, and favors the view that the Golgi apparatus of the amoeba takes part in cellular metabolism. He also suggested that the Golgi apparatus may further the ultimate utilization of the products of vacuolar digestion.

Gatenby (1919) stated that the Golgi apparatus or its representative is present in every cell of vertebrates and invertebrates. Obviously this statement is too encompassing since today with improved techniques, the Golgi appartus has not been found in non-nucleated erythrocytes. There is, however, a possibility that the Golgi apparatus found in living cells are homologous, but additional evidence is necessary to establish this as a fact.

CHAPTER III

OBSERVATIONS

It was suggested by Baker (1957) that the term Golgi apparatus be discarded and the structures studied be termed as cytoplasmic inclusions. This view is supported by the objects in cells causing the reduction of osmium tetroxide (Golgi technique) or silver nitrates (Kopsch technique) are not a natural catagory of cytoplasmic inclusions but are different bodies in different cells and, therefore, are not justified in sharing a single name. It is further noted that Golgi and Kopsch techniques often give a false impression of the form of cytoplasmic inclusions. This was demonstrated by Schlottke (1931) when he described the action of osmium tetroxide (Baker, 1957). Osmium tetroxide is easily deposited on a free surface and the amount of deposition on a surface is proportional to the length of time the surface is exposed to the tetroxide (Garr, 1960). In this case a fine filamentous network was described as becoming very dense and the structure was obliterated completely.

Baker concluded that a single name could be given if all the objects (a) possessed essentially the same structure, in which case they could be defined morphologically, or (b) if they reacted specifically to particular techniques and had essentially the same chemical composition, or (c) if they were derived from similar antecedents in the egg or embryo.

In contention to the views of Baker and Nath, it is considered that in nearly all cells of animals there exists homologous structures which stain black with the Golgi technique (Cowdry, 1950). In this line of reasoning, the Golgi and Kopsch techniques are believed to give a lifelike representation of the object and the Golgi apparatus would be considered a cell organelle and classified with the nucleus, nucleolus, and mitochondria.

The question proposed by the preceding views is whether or not to consider the Golgi apparatus as a characteristic cytoplasmic inclusion or a cell organelle.

The Golgi apparatus has been linked by various observers with secretory activity, since during the process of cytological differentiation an enlargement of the apparatus occurred until it resembled a large, tortuous, sometimes discontinuous network (Brachet and Mirsky, 1961, Vol. V).

Kirchesky and Mandel (1953) attempted to correlate the Golgi apparatus in the uterine glands of a pregnant rabbit with the specific functions of nutrition of the blastocysts and lubrication. Their experimental observations have been tabulated in Appendix B of this report. From their experiment the two conclusions related to the Golgi apparatus are (a) the Golgi apparatus in the uterine gland cells in a rabbit undergo characteristic changes during the course of pregnancy and (b) if it is assumed that a dispersed Golgi apparatus is indicative of increased secretory activity, then the description of the secretory cycle of uterine gland cells during pregnancy does not offer support to the proposed view of the functions of their secretion namely, nutrition of the free blastocyst and lubrication.

On examining the findings of Kirchesky and Mandel, it was noted that the Golgi apparatus they described was in a juxta-nuclear position between the nucleus and the luminal edge which is also the edge where the cell secretion is extruded. Ham and Leeson (1961) made the general observation that in cells that secrete through one of their surfaces, the Golgi apparatus commonly lies between that surface and the nucleus. The first conclusion by Kirchesky and Mandel does indicate a relational change in size and shape of the Golgi apparatus during secretional activity. The second conclusion is based on specific secretory activity. Brachet and Mirsky (1961, Vol. VI) observed that there is no strong evidence relating the Golgi apparatus to the synthesis of any specialized product. They also stated that the primary function of the Golgi apparatus may not be secretory since the apparatus is well defined in certain nonsecretory cells.

It was suggested by Godman and Porter (1960) that certain constituents of the cytoplasmic substance were amassed within the Golgi apparatus and were subsequently extruded from the cell. Carneiro and Leblond (1959) demonstrated this by the use of radioactive isotopes. The isotopes become localized in the area of the Golgi apparatus during an active secretional stage and were then moved into intercellular areas. While these findings are significant in relating the Golgi apparatus to secretion, Carneiro and Leblond did not define the method of secretional movement into the intercellular spaces.

Information of the chemical composition of the Golgi apparatus

would provide an indication of the possible functions of the Golgi apparatus.

As previously mentioned, osmium tetroxide and silver nitrates are easily reduced on a free surface; however, osmium tetroxide stains lipids black (Gurr, 1957). In noting the results of using osmium tetroxide, the Golgi apparatus will stain first and then other organelles may stain with osmium. This is not to be construed as a fast reaction, in fact the opposite is true. The reduction of osmium is a very slow process. Another indication of the lipid content of the Golgi apparatus is the action of fat solvents found in certain fixatives. Lee (1928) noted that fixatives containing alcohols, ether, chloroform, benzene, or acetone dissolved the Golgi apparatus. True fats are soluble in acetone, benzene, chloroform, or ether.

Baker (1957) conducted histochemical experiments and found phospholipids and cerebrosides present in the Golgi apparatus. These observations indicate in general that the Golgi apparatus has a lipid nature or contains an appreciable amount of lipid material. While only two lipid derivatives have been identified, others may be present.

In attempting chemical analysis, Schneider and Kuff (1954) obtained elements of the Golgi apparatus as a fractionation of epididymal tissue homogenates. By using a sucrose-sodium chloride density gradient during ultracentrifugation they obtained a good separation. Their findings were similar to that of Baker.

One particularly useful chemical reaction is the use of neutral red chloride in vital staining techniques. It is not only a stain but also a pH indicator with a pH range from 6.8 to 8.0 and a color range from brilliant red to yellow respectively (Gurr, 1960). Gatenby (1931) supravitally stained human spermatic cells with neutral red. The neutral red was absorbed and gave a red color of approximately 7.0 to 7.2 pH which shows a slightly low pH as compared to the rest of the cytoplasm. He also reported that the Golgi was easily distinguishable.

Gatenby (1953) observed the Golgi apparatus in sympathetic ganglion cells of the mouse by use of a phase-contrast microscope. Here again the Golgi apparatus was present and gave rather interesting data. In the young animals, the Golgi apparatus was fairly compact and continuous while in older animals where there was active secretion the Golgi apparatus was more diffuse. The intimate relation to the nucleus was further noted in the young animals. Gatenby concluded that the position and structure of the Golgi apparatus was due to the age and activity of the cell. The main significance of Gatenby's work is the observation of the Golgi apparatus in living tissue which indicates the Golgi apparatus is not an artifact of staining but a true system in the living cell.

The existence of a membrane around a cell structure is a factor in establishing the structure as a true organelle. Cell researchers have questioned the existence of a limiting membrane around the Golgi apparatus; however, with the advent of electron microscopy the question has been resolve.

Brachet and Mirsky (1960, Vol. IV) feel the Golgi apparatus should be a system of broad, flat channels or vesicles bounded by a 100 Å thick granular membrane and the vesicles should be 200 Å to 1000 Å wide. Lacy (1957) after studying the neurons of the limpit and pancreas cells of the mouse, described it as a chromophilic substance composed of paired membranes lying close together and enclosing a chromophobic material inside the vesicles. The membrane was 50 Å to 100 Å thick and the space between the folds of the vesicles varied from 50 Å to 200 Å. He also observed related structures which were round or oval inclusions 300 Å to 800 Å in diameter which he interpreted as liposomes.

Godman and Porter (1960) described the Golgi apparatus in connective tissue cells in which the Golgi apparatus was composed of a mass of small rounded vesicles with varying internal density and a complex of elongated sacs, each sac being 1 micron in length and bounded by a smooth membrane. They further noted that droplets of various sizes and low optical density arise in the Golgi zone and are not derived by pinocytotic activity.

Finean (1961) described general observations in secreting cells fixed in osmium. The membrane was 60 Å thick and could enclose vacuoles or patches of parallel layering lying in a region adjacent to the nucleus. He further described small vacuoles or "microvesicles" in the same region. Finean also noted that the proposed membrane exhibited properties of lipid and lipoprotein materials.

Mollenhauer et al (1961) described the Golgi apparatus as having a 70 Å thick membrane and with a phase microscope observed small vesicles forming at the distal ends of the apparatus. The freed

vesicles appeared to be moving away from the Golgi apparatus to the plasma membrane. They appeared to fuse with the plasma membrane and release their contents outside of it.

There are many other reports in which the observers using the electron microscope have reported the existence of a membrane surrounding the Golgi apparatus. Based on their observations, it is concluded that the Golgi apparatus does have a limiting membrane.

The author of this report has hesitated to discuss certain structures related to the Golgi apparatus until the results of electron microsopy had been examined. In the cytoplasm surrounding the Golgi apparatus there are many vesicles or vacuoles which vary in size and whose significance is not clearly understood. Some of these vesicles are termed Golgi vacuoles and the others are called microvesicles. The existence of these bodies has been described by many observers using the light microscope, phase microscope, and electron microscope. Most of the persons cited in this report acknowledge the existence of these bodies.

Mollenhauer (1961) described the movement of the microvesicles from the Golgi apparatus while Brachet and Mirsky (1960, Vol. IV) described the movement of the Golgi vacuoles towards the Golgi apparatus.

Dalton and Felix (1956) have described the Golgi apparatus as being made of three components based on studies with the electron microscope. They are vacuoles, microvesicles, and aggregations of smooth surfaced double layered membranes. The membranes have been previously described. The vacuoles or Golgi vacuoles may be as large

as mitochondria and are arranged in groups. These vacuoles upon treatment with osmic acid appear to contain a dense granular material.

The microvesicles or granules are about 400 Å in diameter and are lighter in contrast to the RNA granules in the cytoplasm. The microvesicles appear to trail from the membranes of the Golgi apparatus towards the cell membrane.

Dalton and Felix feel the Golgi apparatus is not a separate isolated part of the cell but may be continuous with the endoplasmic reticulum.

A possible conclusion which may be drawn from these observations is that both the movements of the Golgi vacuoles toward the Golgi apparatus and the microvesicles away from it are connected to the function of secretion.

CHAPTER IV

CONCLUSIONS

From the literature cited in this report the author concludes that the Golgi apparatus does exist in most metazoan cells and is a true organelle because (a) the descriptions of the fine structure and stain specificity of the Golgi apparatus show a homologous relation; (b) the fine structure of the Golgi apparatus changes during cell activity; (c) the polarity exhibited by the Golgi apparatus in metazoan cells and particularly in secretional cells; (d) a limiting membrane is present; (e) the Golgi apparatus can be observed in living cells.

If there is to be a function for every structure in living organisms, the author concludes that the Golgi apparatus is related to the function of secretion because of (a) the position or polarity exhibited in secretional cells; (b) the changes in fine structure exhibited during secretional activity; (c) the presence of Golgi vacuoles and microvesicles which may represent the secretion and/or products related to secretion. The Golgi apparatus may form a protective coating around certain types of secretion and facilitate the transport of the secretion out of the cytoplasm. This conclusion is drawn from the origin, structure, and movement of the microvesicles.

While previous studies of the Golgi apparatus have been scattered and inconclusive, it still provides an excellent field for reserach.

A possibility for further research might be to determine whether the Golgi apparatus has an active or passive function.

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APPENDIX A

STAINING TECHNIQUES OF THE GOLGI APPARATUS

THE GOLGI METHOD OF SILVER IMPREGNATION (DAVENPORT, 1960)

Procedure:

1. Fix pieces of mammalian neural tissue not over 10 millimeters thick in a 3% aqueous solution of potassium dichormate at 15-20 degrees centigrade. Remove pieces of tissue from solution after ten days, fifteen days, and thirty days of fixation.
2. Transfer to a 0.75% aqueous solution of silver nitrate, the volume of which is estimated to be fifteen to twenty times that of the tissue. Shake the container occasionally and after 0.5 to 1.0 hours discard the fluid and replace it with fresh solution. Allow the specimens to remain in the silver solution for 24 hours to several days.
3. Wash, dehydrate, embed and section as usual. Either paraffin or nitrocellulose may be used. Cutting may be done from 25-50 microns.
4. Mount the sections on a slide, remove the paraffin with xylene and cover with thick synthetic resin.

Results:

A fine black reticular network should be visable in the cytoplasm.

A MODIFICATION OF THE KOPSCH METHOD FOR THE GOLGI APPARATUS (DAVENPORT, 1960)

Procedure:

1. Fix small blocks of tissue for 18 hours at room temperature in the following mixture (Mann's fixing fluid):

Mercuric chloride, saturated in physiological salt solution	50 ml
Osmic acid, 1% aqueous solution	50 ml

2. Wash 30 minutes in distilled water.
3. Place in 2% osmic acid solution kept at 30 degrees centigrade for 3 days.
4. Transfer to water, also at 30 degrees centigrade for 1 day.
5. Dehydrate, clear, embed in paraffin and section.

Results:

A discrete black network within the cytoplasm of cells is revealed when the method is successful. The network may be either at one side of the nucleus or surrounding it.

APPENDIX B

CHANGES IN THE GOLGI APPARATUS IN UTERINE GLAND CELL DURING PREGNANCY IN THE RABBIT (KRICHESKY AND MANDEL, 1953)

The description of the Golgi apparatus by Krichesky and Mandel has been arranged in tabular form to provide a comparison of size and change during the secretory phases of the uterine glands of the pregnant rabbit.

TIME PERIOD	CELL SIZE	GOLGI SIZE	DESCRIPTION
Non Pregnant (Control)	10.9 X 6.0 Micra	2.2 X 3.1 Micra	Small condensed networks atipical position midway between lateral borders of cell, appears as a thick ring.
4 Days Pregnant	16.1 X 6.0 Micra	2.6 X 3.0 Micra	Less compact, slightly thinner but more numerous anostomosing strands.
6 Days Pregnant	14.1 X 6.2 Micra	2.5 X 3.2 Micra	No change in Golgi.
10 Days Pregnant	13.1 X 5.6 Micra	5.6 X 5.3 Micra	Golgi very large, highly dispersed loose network occupying most of the cellular space above the nucleus.
23 Days Pregnant	15.4 X 6.9 Micra	6.9 X 4.3 Micra	Extremely loose network in some cells to dispersed fragments in others.
30 Days Pregnant	----	----	No change from 23 day measurement.
1 Day Postpartum	13.8 X 5.6 Micra	7.6 X 5.5	Golgi becomes hypertrophied and disperses into rodlets or blebs.
3 Days Postpartum	13.8 X 5.6 Micra	3.6 X 3.2 Micra	Golgi approaches non pregnant condition, no trace of fragments.
8 Days Postpartum	10.9 X 6.0	2.2 X 3.1	Golgi is undistinguishable from non-pregnant conditions.

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