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Suggestions for a new look at the lamellar-vacuolar field or "Golgi complex" and their pattern of lower parts

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Abstract

Every cytologist in biology or medicine knows the so-called "Golgi-Complex", but no cytologist can state exactly the structure and the function of this complex. Nevertheless, in the last six years this" Golgi complex" in about 100 different cells has been seen in the electron microscope. That is the reason I have tried to make a comparative study of these fields. I would like to give a short review of this investigation here, having been kindly invited by Prof. S. SENO.

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SUGGESTIONS FOR A NEW LOOK AT THE LAMELLAR-VACUOLAR FIELD OR "GOLGI COMPLEX" AND THEIR PATTERN OF LOWER PARTS

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Every cytologist in biology or medicine knows the so-called "Golgi-Complex", but no cytologist can state exactly the structure and the function of this complex. Nevertheless, in the last six years this "Golgi complex" in about 100 different cells has been seen in the electron microscope. That is the reason I have tried to make a comparative study of these fields. I would like to give a short review of this investigation here, having been kindly invited by Prof. S. SENO.

First I should emphasize that the "Apparato reticulare interno" discovered by C. GOLGI in 1898 has nothing to do with the single bodies impregnated by OsO₄ or silver, described in my theory of 1939. This important fact was discovered by the school of J. R. BAKER at Oxford. I therefore believe that it is not right to use the name of C. GOLGI further in connection with these bodies. I admit it was a misunderstanding on my part to call these structures "Golgi bodies" in 1939.

The theory of 1939 showed on the hand of 735 figures that these bodies consist of a system of an osmiophile substance called "externum" and some osmiophobe vacuoles called "internum". Both structures form a physiological unit: a "functional system". The description and interpretation of these systems in 1939 was correct in general but partially wrong as the investigations with the electron microscope since 1954 have shown.

The history of these electronmicroscopic investigations runs as follows: In 1953 A.J.DALTON and M.D. FELIX found rough "filaments" on those spots where the light microscope had demonstrated the osmiophile substance or externum. The fine structure of these "filaments" was discovered in the spring 1954 by J. RHODIN on the cells of the tubuli of the mouse kidney and by F.S. SJÖSTRAND and V. HANSON on the mouse pancreas, both in the laboratory of F.S. SJÖSTRAND at Stockholm. These two investigations are the "birthday" of a new look, first at the structure of the osmiophile substance: it consists of some double lamellae and second at the osmiophobe substance: it consists of various kinds of vacuoles.

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Both the double lamellae and the vacuoles form a system.

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The identification of these systems in the electronmicroscope with the systems in the light microscope was accomplished by A. J. DALTON and M. D. FE-LIX in 1957 by postosmification. This conformity has been demonstrated since by the topographical identification in the same kind of cell in many other investigations.

Since the early times of the "birthday" in 1954 about 200 electron microscope investigations have been made showing us a system of double lamellae plus vacuoles in about 100 different cells. Many terms have been used most of them with the wrong prefix "Golgi". I propose to avoid this prefix for the reason I mentioned above. After a study of nearly all the investigations since 1954 I came to a comparative picture of the structural pattern of the field in question and propose here the following definitions:

THE LAMELLAR VACUOLAR FIELD

The system of double lamellae with their vacuoles is imbedded in a special complicated field. This field has a basic substance of very small precipitated particles and is usually less dense than the surrounding hyaloplasm. The main point is this; the field is in no case surrounded by a special membrane; it is, therefore, an open system, not sharply limited to the other basic substance of the cell. This is in contradistinction to the mitochondria, plastids and the cell nucleus, which are limited by a double membrane and may be called for this reason cell organelles. In regard to the main structure inside the field I would like to propose to call this total field the lamellar vacuolar field. The logical reason for this new term is the fact that inside this field, among other lower parts, the double lamellae play an important role. The provisional definition (all our definitions in science are provisional!) may be: The lamellar vacuolar field is a special open spot in a cell in which are imbedded one or more special systems of double lamellae together with other typical structures. It is not surrounded with a membrane.

I would like, to emphasize therefore that the structure of the lamellar field is characterized by a special pattern which I will try to define now.

THE SIX TYPICAL LOWER PARTS INSIDE THE FIELD

A survey of the 100 lamellar fields of different cells I saw myself or found in the literature has shown me that not all typical six lower parts are to be seen in every lamellar field; only $2\sim3$ are essential. During the following years some types of lamellar fields will be discriminated, I am sure. There is e. g. a typical difference between the contents in lamellar fields of cells in plants and in aniA New Look at "Golgi Complex" 291

mals and between the same lamellar field during different stages of function in the life cycle of the same cell. Therefore, the construction of every lamellar field changes. But I believe that it may be possible to distinguish generally speaking the following six typical lower parts (Fig. 1).

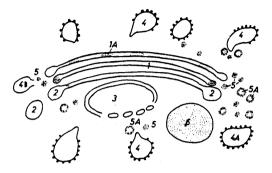


Fig. 1. Scheme of the Pattern of a Lamellar Vacuolar Field ("Golgi complex"). Explanation of the Numerals:

- 1: Lamellar system, containing $2 \sim 20$ double lamellae,
- 1 A: Intralamellar vesicles
 - 2: Vacuoles 1 on the periphery of a double lamella, surrounded by only one lamella,
 - 3: Vacuoles 2, partially surrounded by a double lamella, partially by unknown bodies.
 - 4: Endoplasmic reticulum ER, ending on the frontier of the field,
- 4 A: ER on the outside covered with ribosomes (rough ER),
- 4 B: Extension of the ER-canal in direction to the X-bodies 5.
- 5: X-bodies (~350 Å diameter),
- 5 A: Advanced X-bodies, \sim 700 Å with less dense nuclei.
 - 6: Products of the lamellar system+ER.

1. Lamellar systems. One or several systems are to be found in one lamellar field. Every system consists of two to 30 long double lamellae parallel to each other. Every double lamella is $180 \sim 200$ Å in diameter, every single lamella of the pair of those about 60 Å. The lumen of a double lamella is varyingly $60 \sim 200$ Å. Inside of the lumen the material is less dense than between a pair of lamellae. In some cases very small *elongated vesicles* (Fig. 1, 1A), are to be seen inside a pair of lamellae.

2. All lamellar systems contain vacuoles. They may sometimes be distinguished in two forms: First, the vacuoles I (Fig. 1, 2) are situated on the periphery of nearly all lamellar systems. They are actually a part of the single double lamella on the peripheral end and therefore surrounded by a single lamella. Their content is sometimes more, sometimes less dense than the surrounding matter. It is possible (but not proven) that these vacuoles 1 are formed by the small vesicles (Fig. IA).

3. The vacuoles 2(Fig. 1, 3), however, are unusual. They are surrounded

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partly by a double lamella, not by a single one as the vacuoles I. They are not localized on the periphery of the lamellar system (as the vacuoles I) but just outside the middle of the system. They are never totally surrounded by a double membrane but only partially. The remaining part consists of some bodies, which I cannot identify.

4. The endoplasmic reticulum ER (Fig. 1, 4) very often extends up to the frontier of the lamellar field. I never saw it, however, in communication with the lamellar systems (Fig. 1, 1). The ER (Fig. 1, 4) and the lamellar system (Fig. 1, 1) are always separated from each other and easily distinguished. Outside the lamellar field the ER is covered with ribosomes (Fig. 1, 4A); inside the lamellar field, however, seldom. It happens that some of the ER canals show an extension in the direction towards the X-bodies (Fig. 1, 4B).

5. I call special attention to one of the lower parts of the lamellar field to be found in nearly all fields: i e. single round bodies (Fig. 1, 5) of $350 \sim 700$ Å diameter, always situated between the lamellar system (Fig. 1, 1) on the inside and the ER (Fig. 1, 4) on the outside of the lamellar field. They have up to this moment no name; their function is not certain. For this reason I propose to call them X-bodies. They play some important role, I am sure. Their diameter and shape vary: the smallest of ~350 Å diameter (Fig. 1, 5) are optically dense, seem to be homogenous and are situated in the main part close to the system of double lamellae (IFig. 1, 1). The larger ones (Fig. 1, 5A) with a diameter of $500 \sim 700$ Å are inhomogenous with a less dense "nucleus" inside surrounded by more dense material. This difference in localisation, volume and shape may be a hint at their function.

6. Inside the lamellar field of secreting cells may be found *products* of this field (Fig. 1, 6). They are found either in close neigbbourhood to the lamellar systems or in a certain distance from them. Different gradients have been found in density and in the forming of a membrane surrounding especially the zymogen granules. In defiance of some hypotheses trying to integrate the different gradients no general scheme of the evolution of these bodies has been found up to present. Only a special scheme of the evolution of the products of the exocrine pancreas has been attempted by the author in 1958 and 1960, but not a general one.

This, then is the description of the pattern of a typical and statical lamellar field. It is only by the way of comparative anatomy that I could give it. I may repeat: not all the micrographs of the about 200 known fields contain all these six lower parts. Most essential are the lamellar systems (Fig. 1, I), the vacuoles (Fig. 1, 2) and the X-bodies (Fig. 1, 5).

But the question now arises: what is the physiological dynamical integration of these six lower parts? About this more important question I may write

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another time.

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