THE STRUCTURE AND FUNCTION OF THE GOLGI SYSTEM IN THE LIVING CELLS OF DEVELOPING MOLLUSCS

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Practically all of our knowledge of the Golgi apparatus has been built up through the study of fixed, osmic or silver, preparations, it not being generally realized that this important cytoplasmic inclusion can be revealed in many living cells by means of vital methylene blue staining. Reliance on the fixed preparations has created a great deal of confusion with regard to the structure of the Golgi bodies, because their nature is such that they only rarely lend themselves to faithful preservation by fixing fluids. In molluscs, these inclusions are of such large size that it has been possible to follow their behavior in intact embryos over periods of several days and considerable new information has been gathered regarding their structure and function.

Such observations reveal that the generalized Golgi body in molluscs is typically a more or less spherical, simple vesicle, possessing a chromophilic, gel-like, relatively lipoidal pellicle covering a relatively more protein, fluid, chromophobic core. The pellicle is thickened over one surface of the sphere forming a bowl-shaped structure which, through the microscope, looks like a crescent (Fig. 1 (A)). The relation between the thickened, bowl-shaped portion of the chromophile and the chromophobe is somewhat like the relation that exists between the "crescent" moon and the moon as a whole, except that in the Golgi body a thin layer of chromophilic material completely encloses the chromophobe. These generalized bodies are clearly endowed with the ability to keep the lipoidal and protein components segregated, hence the visible differentiation into chromophile and chromophobe. But they are the immediate descendants of homogeneous droplet-like forms where no such ability is manifest (Fig. 1 (B)). These droplets, in turn, are derived from smaller and presumably more solid granules which may be considered "reserve" forms (Fig. 1 (C)).
The enlargement of the granules to form droplets and the development of the droplets into larger, simple vesicles are due, with very little doubt, to the absorption of substances from the cytoplasm. This absorbing quality, together with the segregating tendency already referred to, constitute the two most fundamental physiological characteristics of the Golgi substance in these species.

In developing mollusks, the generalized Golgi bodies give rise, following gastrulation, to exceedingly active and highly specialized forms. By this period, quantities of the original yolk have been dissolved in the cytoplasm and although much has, no doubt, been oxidized, the Golgi elements absorb large amounts of the material and increase considerably in size, forming elaborate, compound vesicular bodies (Fig. 1 (D)). Within the chromophilic material, new vesicles continually make their appearance and, in the trochophere larva, small (1 μ) fat droplets are continually discharged into the cytoplasm. In the pelecypod Mytilus, the absorption by the Golgi bodies of all of the ultramicroscopic, pigmented fat particles of the single-celled egg results in the freeing of the ground cytoplasm of pigment and the deposition of this pigment in the Golgi inclusions.

The discharge from each enlarged Golgi body of large (4–6 μ) protein spheres (the original chromophobes) is characteristic, in nudibranchs and tectibranchs, of the early veliger larva. In this process, the chromophilic portion of the structure withdraws from around the chromophobe and

FIGURE 1
Living Golgi bodies seen in trochophere of the tectibranch Navanax (X 1000). A, generalized form, showing "crescent"-like chromophile, and chromophobe; B, droplet; C, granule; D, compound vesicular forms, each showing several chromophobes.
condenses into a chromophilic, pycnotic mass, which can be shown to be rather solid. The pycnotic phase, however, is soon followed by a stage in which the mass becomes resolved into a number of spherical, relatively fluid, droplets. Each of these soon differentiates into a generalized vesicle as the segregating tendency is resumed and the cycle of the system begins anew.

The breaking up of the pycnotic Golgi body into droplets is the reproductive phase of the cycle and is the only method by means of which the Golgi elements increase in number during early development. In other words, there is no "dictyokinesis" accompanying every division of the cells, all multiplication being a mass division of the sort just described and always occurring after the assumption of a pycnotic condition following a period of marked synthetic activity. This also appears to be the situation during oögenesis where the synthetic period results in the deposition of large quantities of fat and protein yolk in the oöcyte. The multiplication period clearly increases the number of Golgi elements, thereby in tectibranchs providing a sufficient number for the new cells of the growing embryo. In the event that the embryo is not increasing in size during this period, as in Mytilus, this increase in number may be offset by a fusion phase preceding the active synthetic period. The fusion phase reduces the total number of Golgi bodies, but the original number is approximately restored during the multiplication period.

In the account just given, the internal chromophobe of each Golgi body is a potential protein or fat product which gradually becomes much more viscous as development proceeds. The elaboration of such products, in molluscs, occurs chiefly within the Golgi vesicle, but elaboration outside the vesicle is employed in Mytilus in the development of certain large oily yolk droplets. In this case, the product first makes its appearance within a group of small Golgi bodies, all of which appear to contribute to the single common yolk sphere. The mechanism involved in this process is not clear, but it is significant that elaboration of a product can take place merely through contact of the Golgi body with the ground cytoplasm.

In developing molluscs, the function of the Golgi system appears to be the continual mobilization of the fat and protein reserves within the cell. Why the embryo should continually dissolve its formed yolk inclusions, only to elaborate new ones is not immediately evident, but that the phenomenon is of fairly general occurrence in animals is indicated by the work of Schoenheimer\(^1\) who finds that almost all of the proteins of the body are continually undergoing synthesis and breakdown. Should the Golgi system be found to be concerned in this protein turnover in higher animals, as it seems to be in the molluscs, it would prove to be a cytoplasmic constituent of greater metabolic significance than we have realized.
Summary.—For the first time, the Golgi system has been continuously followed in living, developing animal eggs. The multiplication of the Golgi elements has been observed and the rôle of the Golgi substance as an absorbing mechanism and protein and fat elaborating system is described. The active Golgi bodies are found to originate from minute, chromophilic “reserve” granules.

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THE RELATION BETWEEN THE GOLGI APPARATUS AND "DROPLETS" IN THE CELL STAINABLE VITALY WITH METHYLENE BLUE

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There has been considerable difference of opinion concerning the nature of certain “droplets” that become visible in cells when the tissue is stained with various basic vital dyes. One group of workers, notably Beams,1 Ludford,2 Chang3 and others, holds that these are “neoformations” resulting from the vital dye treatment and that they have no counterpart in the unaltered, living cell. Another group of investigators, notably Covell and Scott,4 Cowdry and Scott,5 Ma,6 Owens and Bensley7 and Parat,8 are of the opinion that these “dye droplets” represent the living Golgi material and that the classical Golgi apparatus of the fixed and osmicated cell results either from a precipitation of the osmic salt in and around these droplets, or from their running together and fusion as the result of fixation. In recent years, the tendency has swung in favor of the first contention, but crucial proof of neither of these views is at hand.

In my work, “droplets” of this kind have been revealed by means of supra- or intravital methylene blue staining of the tissues of many invertebrates, including the salivary gland cells of the larva of the midge Chironomus, and the smooth muscle, pancreas, liver and gall bladder of the frog and the smooth muscle, adipose tissue, pancreas, liver, kidney, thymus, bladder and pars distalis of the kitten. Usually, these “droplets” are opaque and show, in life, no internal structure and the reasons for their being considered “dye droplets” by so many workers are evident.

However, in all cases thus far examined, when living tissues containing