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Ultrastructure of the Golgi Apparatus, Mitochondria and Endoplasmic Reticulum[1]

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Golgi apparatus

The Golgi apparatus was first observed by Golgi in 1898 and referred to by him as the "apperato reticulare interno". Notwithstanding the fact that this material has since been described in practically every type of cell, not all investigators are agreed that it is a bonafide cellular structure. In fact, it has been characterized as an artifact by Walker and Allen (1927), Parat (1928), Worley (1946), Palade and Claude (1949), Baker (1950) and Thomas (1951).

Much credit is due Dalton and Felix (1954) for clearly demonstrating the Golgi apparatus by means of the phase-contrast and electron microscopes. In fact, strong evidence is now available which seems to varify unquestionably the presence of the Golgi apparatus in cells (cf. Gatenby, 1955 for references). In addition, it has been recently isolated and chemically analyzed (Schneider and Kuff, 1954). However, a convincing demonstration of its functional significance in somatic cells is still wanting.

It appears under the electron microscope to be of a duplex structure i. e., composed of a series of double membrane lamellae (figures 1 and 2, L) and vacuoles of varying size (figures 1 and 2, V). In the secondary spermatocyte of the cricket the ends of the lamellae seem to separate and surround the larger vacuoles. The relationship of the smaller vacuoles to the lamellae is not altogether clear. Bits of endoplasmic reticulum (see below) are shown at E and in some preparations they seem to extend into the region of the Golgi lamellae. However, further work is necessary to determine whether or not a direct relationship exists between the endoplasmic reticulum and the lamellae of the Golgi apparatus.

It should be pointed out that the ultramicroscopic structure of the Golgi material in the cricket and that in vertebrate cells are fundamentally the same. Furthermore, the Golgi apparatus seems to be unquestionably a genuine cellular structure that must be reckoned with in any over-all study of the cell.

Mitochondria

Although mitochondria were accurately described in the latter

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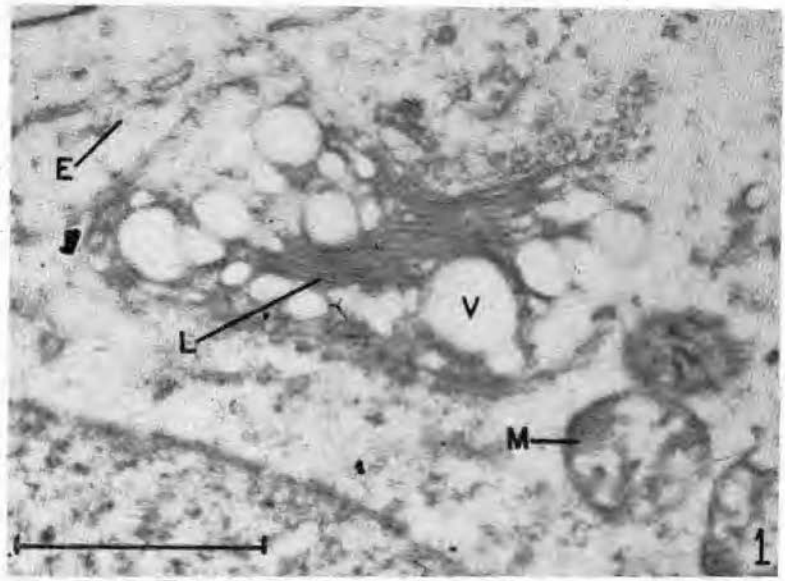

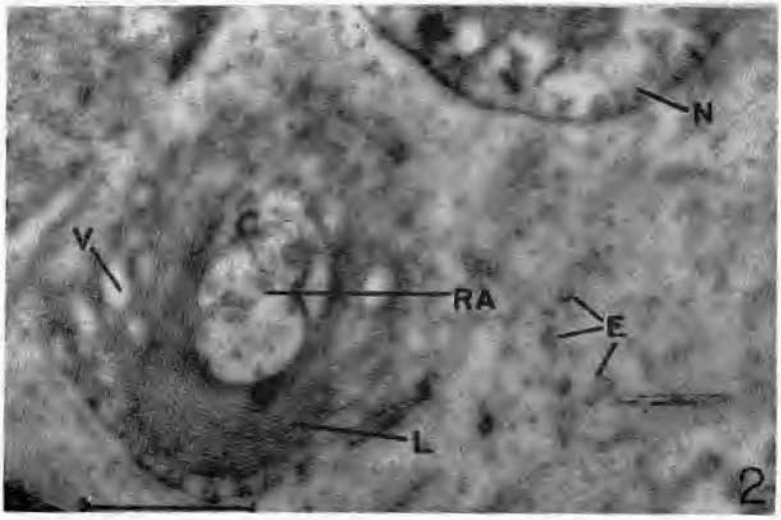

Description of Plates

The scale on each figure equals one micron.

Figure 1. Section through dictysome of second spermatocyte showing lamellae (L) and vacuoles (V). Present also in this figure are bits of endoplasmic reticulum (E) and mitochondria (M).

Figure 2. Golgi body (acroblast) of spermatid showing lamellae (L) and vacuoles (V). The region at RA is where the acrosome forms. Portions of the endoplasmic reticulum (E) and mitochondrial nebenkern (N) are shown in this figure.

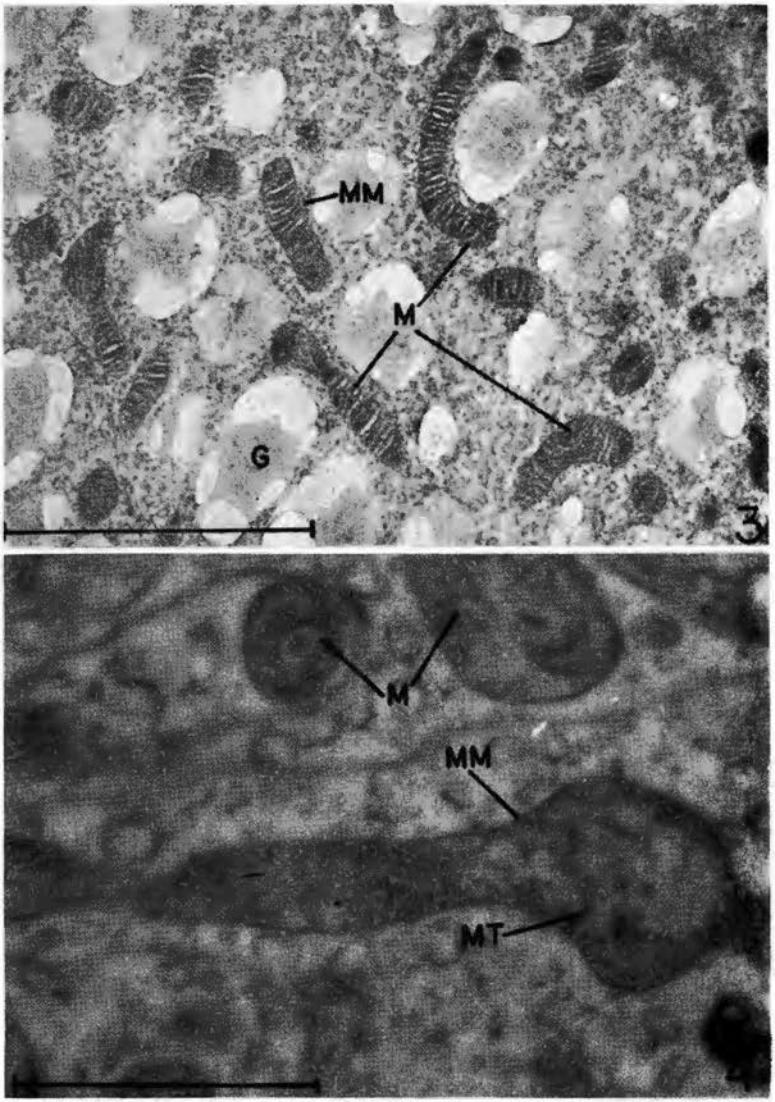

Figure 3. Section through urate layer of the light organ of a firefly showing mitochondria with cristae and double membranes. A limiting mitochondrial membrane is shown at MM and a urate granule at G.

Figure 4. Mitochondrion from Malpighian tubule of grasshopper displaying internal tubules (MT) and a membrane at its surface (MM).

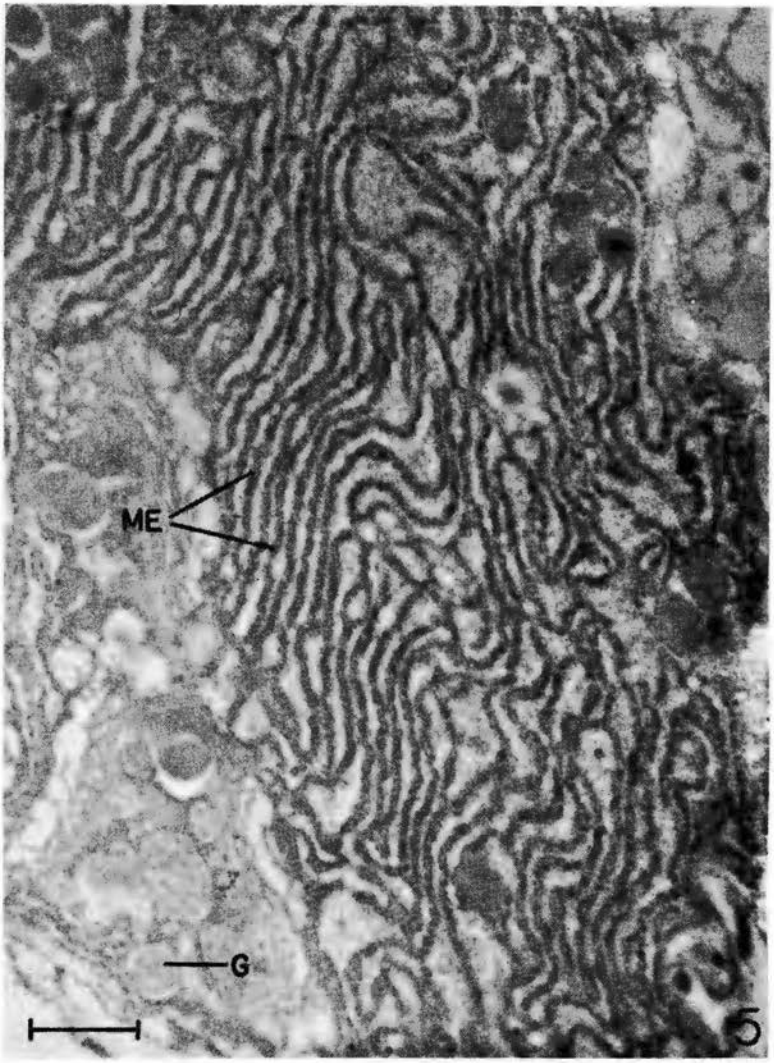

Figure 5. Section showing a portion of a cell of the pharyngeal gland of the earthworm. Note the large amount of endoplasmic reticulum composed of double membranes (ME) with small granules associated with their surfaces. A secretion granule may be seen at G.

part of the nineteenth century clear evidence of their functional significance was not revealed until Bensley and Hoerr (1934) devised methods for their chemical analysis. Such analysis shows them to have a lipoprotein composition and to be the carriers of the respiratory enzyme systems (Greene, 1949; Schneider and Hogeboom, 1951). With the advent of the electron microscope and methods for thin sectioning, efforts were made to analyze the ultramicroscopic structure of the mitochondria and to correlate their structure, insofar as possible, with their function. These studies have resulted in the demonstration that mitochondria contain a characteristic ultramicroscopic structure. Perhaps the commonest type of internal structure is seen in figure 3, M. Here the mitochondria are surrounded by a single or double membrane (MM). Projecting transversally from the inner membrane are folds which partially (cristae of Palade, 1953), or completely (double membranes of Sjöstrand, 1953) traverse the mitochondrial axes. Still a third type of internal membrane has been noted by Beams and Tahmisian (1954) in the male germ cells of *Helix*. Here the internal membranes (lamellae) extend in the longitudinal axes of the mitochondria rather than in their transverse axes.

Other mitochondria, particularly of Paramecium, seem to show a tubular internal structure (Powers, Ehret and Roth, 1955). We have also observed a similar condition in the cells of the Malpighian tubules of grasshopper (figure 4, MT). In this preparation also may be seen a double limiting membrane surrounding the mitochondrion (MM).

Just what the relationship is between the cristae, double membranes and tubules in mitochondria is not known. However, the ultramicroscopic structure of mitochondria, whether cristae, double membranes, longitudinal membranes or tubules, is of a type that conceivably functions in greatly augmenting the intramitochondrial surface area. Such a framework within the mitochondria is undoubtedly favorable for the localization and functioning of the associated enzymes.

Endoplasmic Reticulum

It has long been known that the cytoplasm of certain cells possesses bodies which have selective affinity for basic dyes (cf. J. W. Wilson, 1955 for literature). Such are the Nissl bodies, chromidia, ergastoplasm etc. Mathews (1899), Garnier (1900), Hertwig (1904) and Goldschmidt (1904) have postulated that this material is derived somehow from the chromatin of the nucleus (cytochromatin). In the older literature also a clear distinction was not always drawn between the fibrous staining ergastoplasm and mitochondria. Some have considered the ergastoplasm of the pancreas for example, to be an artifact. However, by use of histochemical and ultracentrifugation methods the cytoplasmic basophilia has

been found to contain a large amount of ribonuclic acid (RNA) which is thought to be involved in cytoplasmic protein synthesis (Caspersson, 1950: Brachet, 1950).

By use of the electron microscope it has been found that the so-called ergastoplasm or basophilic substance is composed of a highly complex and variable reticulum (Porter, 1954; Palade, 1955). An example of endoplasmic reticulum of stupendous proportions is seen in the cells of the pharyngeal glands of the earthworm (figure 5). These cells display marked basophilia and are completely filled by the granular appearing double membrane lamellae that are arranged in a more or less parallel fashion (ME). Scattered among the lamellae are granules of larger size (figure 5, G.) In some cells small granules of about 100 to 200 A in diameter are associated with the membranes of the reticulum. Apparently the small granules on the membranes of the endoplasmic reticulum in figure 5 are similar to those described by Palade (1955). Preliminary evidence seems to indicate that the small granular component (microsomes) of the reticulum is perhaps responsible for the basophilic staining of the cytoplasm.

It is difficult to even speculate on how the endoplasmic reticulum is formed, divides, maintains itself and functions. However, it is clear that it greatly increases the intracellular membrane surface area, a condition which is conceivably involved in the physiology of the cell.

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