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THE MICROSCOPIC APPEARANCE OF THE CHLOROPLAST

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With 5 Text-figures

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Two excellent reviews concerning the structure of chloroplasts have recently appeared in the pages of Protoplasma. WEBER (1937) dealt with the reduction of silver nitrate by the chloroplast and FREY-WYSSLING (1937) discussed the recent work giving an indication of the submicroscopic structure of the chloroplast. It is the purpose of this paper to bring together those investigations dealing with the microscopic appearance of the chloroplast. As no comprehensive review on the microscopic phase of the subject has been published since that of BREDOW in 1891 it will be necessary to consider the work of the older investigators in some detail.

Investigations on chloroplast structure have, in general, followed a cycle. The earliest workers were unable to discern any structure in the chloroplast and concluded that it was optically homogeneous. MEYER in 1883 described the chloroplast as possessing a colorless, or almost colorless, stroma or ground substance in which chlorophyll-impregnated granules or grana were embedded. While MEYER's work was very carefully executed and, in general, supported by SCHIMPER (1885), it was not generally accepted. A large number of subsequent investigators considered the chloroplast to be composed of fibrils of one type or another with the chlorophyll either coating the fibrils or confined to interstices formed by them. In 1912 LIEBALD called attention to the fact that chloroplasts frequently appeared to be homogeneous and modern textbooks have held to this opinion (KÜSTER, 1935; GUILLIERMOND, 1933). Recently the work of DOUTRELIÈNE (1935), HEITZ (1936), and WEIER (1936) have emphasized the granular structure described by MEYER and SCHIMPER. Within the last year papers have appeared which suggest that, at least submicroscopically the plastid is composed of parallel fibrils or lamellae (SCARTH, 1924; FREY-WYSSLING, 1937; MENKE and KÜSTER, 1938). It has been the tendency for workers holding to one type of structure to consider all others to be either pathological or artifacts. WEIER (1938) has, however, shown that the granular and homogeneous aspects are normal, for cells containing either of these two plastid types will accumulate neutral red and the chloroplasts themselves will reduce silver nitrate and elaborate and hydrolyse starch.

THE GRANULAR TYPE OF CHLOROPLAST

Previous to MEYER's investigations a number of observers (BÖHM, 1856; NÄGELI, 1855; SACHS, 1862) had noted granules of an unknown nature in the chloroplast which did not stain with iodine. The tendency was to consider them
either as starch grains which did not stain because of their small size, or as the precursors of starch.

SACHS (1862, 1863) and others had well established the protein nature of the background substance or stroma. It stained yellow with iodine, violet with copper sulphate and potassium hydroxide, and yellow with nitric acid and potassium hydroxide. SACHS, furthermore, emphasized that the stroma was in many respects similar to the cytoplasm of the cell and that it should be considered as such.

MEYER'S monograph on the chloroplast still remains one of the outstanding works in this field. His studies concerning the microscopic structure were carried out mainly on the chloroplasts present in the green buds of the orchid Acanthophyllum sylhetense. These results were confirmed on the chloroplasts present in Phajus grandifolius, Vallisneria spiralis, Adoxa moschatellina, and Iris germanica. Acanthophyllum is a native of the moist, hot, shaded jungles of Java. The chloroplast is large and the starch grain is confined to one side of the chloroplast. The conditions under which the plants grow are apparently just those which are very favorable for the formation of large and distinct grana (WIEB, 1938).

The normal chloroplast appeared to have a perfectly colorless stroma, although MEYER was not able to reach a definite conclusion as to whether or not it was absolutely colorless. Chlorophyll-impregnated granules, to which MEYER gave the name "grana", were embedded within this stroma. These bodies were regularly arranged in rows parallel to the starch grain and seemed to spiral around the plastid. They appeared to him to be a trifle brighter and perhaps somewhat thicker on the periphery of the chloroplast (Fig. 1).

When thick sections of buds of Acanthophyllum were laid in water one of two changes was noted to occur in the chloroplasts. Less frequently they took on a homogeneous green appearance. More usually a small vacuole or clear space appeared in each granum. The latter swelled slightly (Fig. 2). With the continued action of water the granum enlarged, the vacuole increasing concurrently in size. Most plastids remained in this state. However, in some cases the vacuoles burst so that the grana became granular and faded out (Fig. 3). With chlora hydrate a similar change took place, except that the chlorophyll collected within the vacuole and finally diffused out of the grana.

Of particular interest is his description of the action of alcohol. The chlorophyll was, of course, extracted and the stroma shrank slightly. The grana remained behind distinctly visible as hollow, darker bodies embedded in the lighter stroma (Fig. 4).

MEYER suggested from these experiments that the chloroplast might be composed of only two substances, chlorophyll and the proteinaceous stroma; or of the three substances, the stroma, chlorophyll, and a third water-soluble material. While MEYER was not acquainted with colloids, the suggestion of at least a two phase, aqueous-lipoidal system is thus to be found in his work.

In the case of the two substances MEYER noted that the chlorophyll was extracted by alcohol but was not affected by water, being neither soluble in it nor swelling through its action. The ground substance, on the other hand, did swell when treated with water but was unchanged by treatment with alcohol. Since the grana swelled in water they would be composed of a substance similar to that of the stroma. Furthermore, since they appeared hollow after extraction