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The Classic Golgi Apparatus and Vacuoles

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Abstract: The dense vacuoles, considered to be the classic Golgi apparatus in the root meristem of *Fagopyrum*, were studied by the following methods: 1. Impregnation methods for the demonstration of the Golgi apparatus, 2. cytochemical methods, 3. electron microscopic methods in the light microscope and 4. the electron microscope. A comparison was made with the classic Golgi apparatus in animal cells in the light and electron microscope.

Dense vacuoles in *Fagopyrum* and also evidently in other plants, were taken for the classic Golgi apparatus on account of their morphological similarity to the Golgi apparatus in animal cells on impregnation with silver and osmium and their staining preperties with lipoid methods. Dense vacuoles differ from the classic Golgi apparatus in other chemical properties, such as content of phenol substances, etc. No formations were found in animal cells which were similar to dense vacuoles on investigating by electron microscopy. In the electron microscope dense vacuoles have the appearance of derivatives of the normal light vacuoles known in plant cells. They therefore belong to vacuome of plant cell and cannot be analogous to the classic Golgi apparatus in animal cells. Thus the use of the term Golgi apparatus for dense vacuoles is not well founded.

A comparison was made of fixation and impregnation used in the light microscope with fixation in the electron microscope. After fixation with permanganate, dense vacuoles have the same shape as after impregnation. After fixation with permanganate, they stain an intense black in the same way as after impregnation with silver and osmium. The form of the vacuoles is dependent on the fixation used. The comparison was made in the light microscope.

This study arose primarily as a result of three papers on the Golgi apparatus published in recent years. MILOVIDOV (1957), made a study of the vacuoles of the root meristem of *Fagopyrum* using the light microscope and identified the vacuoles containing phenol inclusions with the classic Golgi apparatus of animals. (Apparato reticolare interno.) PERNER (1958) and SITTE (1958), working with other plants, criticized the work of Milovidov from the aspect of electron microscope observations. In the electron microscope, these same authors found membrane structures in plant cells similar in structure to those found under the electron microscope in animal cells and which DALTON (1952) and authors after him denoted as the Golgi apparatus.

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Structures termed the Golgi apparatus in the light microscope and structures described as Golgi apparatus in the electron microscope have not been compared in plant cells. The root meristem of *Fagopyrum*, studied by MILOVIDOV (1957) in the light microscope, was selected for this purpose.

Historical Survey

In cytological work on material from the *Polygonaceae* family, which includes *Fagopyrum esculentum*, SUGIURA (1925) found a structure which: "looks like the Golgi apparatus although it is fixed with Farmer's fluid (with acetic acid)" in a karyological study of the tapetal cells of *Polygonum savatieri* NAKAI. He used iron haematoxylin as stain. He raised a query about calling them the Golgi apparatus and wrote about structures resembling the Golgi apparatus. In a karyological study of *Fagopyrum emerginatum* and *Fagopyrum cymosum*, JARETZKY (1928) also found deeply staining filamentous formations mainly lying close to the nucleus in the tapetal cells of the anther. He also used fixation with acetic acid (Flemming, Carnoy, Navašin) and staining with Heidenhein's iron haematoxalin. Jaretzky wrote: "It is evidently the Golgi apparatus as accepted by SUGIURA in *Polygonum savatieri*." JARETZKY considered that they served for the deposition of nutrients and as site of transit of nutrient substances to maternal pollen cells.

Finally, MILOVIDOV (1957) in the work mentioned above on the root meristem of *Fagopyrum esculentum* MOENCH and *Fagopyrum tataricum* GAERTN. (fixation with Navašin's Carnoy fluid, stained with iron haematoxylin) found vacuoles with inclusions of phenol compounds, which he termed classic Golgi apparatus, in addition to empty vacuoles. At the same time he was against using the term Golgi apparatus since he was dealing with a system of vacuoles. All three authors used methods employed for karyological purposes (fixation with Carnoy, Navašin) which are not usual for the demonstration of the Golgi apparatus, since they may disrupt the phospholipid structure of the Golgi apparatus due to the effect of acetic acid (PERNER 1958) and other components of the fixatives. Impregnation with silver and osmium, which are the classic methods used for the demonstration of the Golgi apparatus in animal cytology, were not employed in the above works of SUGIURA, JARETZKY or MILOVIDOV. This short review shows that the term Golgi apparatus was some time given to cytoplasmatic formations in plant cells detected after the use of methods not normally employed for its detection.

The inclusions in the vacuoles of the root meristem of *Fagopyrum* were later studied histochemically and by the electron microscope HRŠEL, JURÁKOVÁ and BENEŠ 1960, HRŠEL 1961a, HRŠEL 1961b). The cytochemical nature of the inclusions was investigated in these works and their vacuolar origin confirmed. In this object, the cells contain empty light vacuoles and vacuoles containing inclusions.

Results

1) The use of classical impregnation methods for the demonstration of the Golgi apparatus

In works (HRŠEL, JURÁKOVÁ and BENEŠ 1960, HRŠEL 1961a) using classical impregnation methods and their newer modifications for the demonstration of the Golgi apparatus in animal cells it was found that the vacuoles with inclusions ("dense vacuoles" of MANTON 1962) in the cells of the root meristem of *Fagopyrum* are impregnated with silver or osmium on using the method of Da Fano, Aoyama, Elftmann and Kolatschev (dermatogen and periblem under the shoot apex). The morphological appearance of the dense vacuoles is of two types: 1). the impregnated substance is massive and fills the entire vacuole, 2). the substance is concentrated round the edge of the vacuole leaving the centre empty. In both cases the vacuoles have a canalicular or spherical shape. The cells of the other parts of the root have vacuoles with fluid contents (light vacuoles) normally found in plant tissues.

2) The cytochemistry of dense vacuoles

Impregnation methods for the demonstration of the Golgi apparatus using silver and osmium have no histochemical value and are evidently based on the silver and osmium by lipids (BAKER 1953a).

Methods of Staining with Silver

The classical impregnation methods for the demonstration of the Golgi apparatus in animal cells with silver salts are based on a group of methods which depend on the use of silver salts as staining agents. They are of low specificity and if choosing and exactly adhering to a suitable procedure, they can be used to stain a number of cell structures (Golgi apparatus, mitochondria, vacuoles, chloroplasts, nucleus components, cell walls etc.). There are two main groups of methods of staining with silver:

a) Methods of staining argyrophil structures

They are based on staining with silver salts on adding reagents (Pearse 1953, 1960).

i) Impregnation methods for demonstration of the Golgi apparatus (Da Fano, Aoyama, Elftman)

(Fixation with formaldehyde and compounds of heavy metals, i.e. cobalte nitrate, cadmium chloride etc., impregnation with a solution of $AgNO_3$ and reduction with hydroquinone with sodium sulphite)

b) Methods of staining argentaffin structures

These methods are based on the reducing power of the substance in the tissue (PEARSE 1953, 1960).

i) Methods of staining with alkaline solutions of silver for showing up phenols and polysaccharides (argentaffin reaction)

(The tissue is fixed with various fixatives and stained with alkaline silver solution. Before staining, sections are oxidized with CrO_3, HIO_4, Lugol's solution etc.)

ii) The method of demonstrating ascorbic acid (staining at an acid pH)

(The tissue is fixed with acetic acid vapour, ethanol or ethanol and acetic

acid, and then impregnated with a solution of $AgNO_3$ with acetic acid or a solution of $AgNO_3$ with pH adjusted to between 2 and 2·5).

The dense vacuoles of *Fagopyrum* are argyrophil and argentaffin at the staining in alkaline silver solution. An exception is formed by the reaction for ascorbic acid, in which fine granules are stained which are not connected with the dense vacuoles (HRŠEL, JURÁKOVÁ and BENEŠ 1960).

c) Other methods

In the investigation of dense vacuoles a number of methods for the determination of lipids, phenols, polysaccharides, protein and nucleic acids, were used (HRŠEL, JURÁKOVÁ and BENEŠ 1960, HRŠEL 1961a). Cytochemical analysis showed that the demonstration of lipids was characteristic for dense vacuoles (staining with Sudan Black after fixation with Ca-formol etc.) and of phenols (coupling reaction, argentaffin reaction, staining with basic stains etc.). According to cytochemical study, the dense vacuoles in Fagopyrum probably contain lipids combined with phenols.

3) Study of dense vacuoles with electron microscopic methods under the light microscope

Sections of objects prepared for electron microscopy were also examined under the light microscope. Fixation with $KMnO_4$ and embedding in araldite were used. Fixation (2% $KMnO_4$ — 2 hours) and embedding were done by MOLLENHAUER's method (1959). In addition, a control test was made using impregnation of the object with 2% OsO_4 at 37° C for hours according to the classical Kolatschev method of demonstrating the Golgi apparatus, and embedding in araldite and metacrylate, or impregnation with silver by the method of Da Fano and embedding in araldite. For comparison, objects fixed in Palade's fixative, which is mainly used in the electron microscopy of animal objects (OsO_4 — veronal acetate buffer pH 7·2), and Navašin and Regaud fixative, normally used in the light microscope (fig. 3, 4), were also embedded in araldite. Navašin fixative is a nucleus fixative with a large amount of acetic acid and Regaud fixative is one of the most careful fixatives for mitochondria and cytoplasm.

Thick sections (1—5 μ) were transferred to glass slides with distilled water. After drying they were mounted in Canada Balsam and examined under the light microscope with and without phase contrast (Ultrathin sections were picked on the grid for electron microscopic study.) The cells of the dermatogen and periblem under the shoot apex were studied.

Examination of thick sections showed that the method for electron microscopy preserved the cells in very good condition. Proof of the excellent results of the method of fixation with $KMnO_4$ and embedding in araldite is illustrated by the preservation of plasmodesmata, which can be seen without difficulty under the light microscope and cannot be detected by any of the usual methods in sections of objects embedded in paraffin (Fig. 7, 9). Dense vacuoles ("classic" Golgi apparatus) are very well preserved (Fig. 9), they stain an intense black with $KMnO_4$ and have the same appearance as in paraffin sections (MILOVIDOV 1957). Light vacuoles have the same lobulated form with sharp bends which is characteristic for this fixation in the electron microscope (Fig. 7).

Objects fixed with potassium permanganate and embedded into paraffin and stained with haematoxylin do not show the advantages of fixation with $KMnO_4$, i.e. the preservation of plasmodesmata etc. The cause is evidently embedding in paraffin. Paraffin may cause shrinkage of tissue and other changes in the object even when using a good fixative.

With Regaud's fixative and Palade's fixative slight evidence of existing plasmodesmata was preserved (Fig. 4, 6). The results with these two methods of fixation are similar. According to the diameters of the intercellular spaces the cells appear swollen. All vacuoles are spherical. The spherical shape is evidently an artefact and arises as a result of the slow penetration of the fixing solution into the object. In objects fixed in this way there is a greater number of vacuoles than after fixation with $KMnO_4$, since artificial vacuoles are evidently formed due to prefixation changes as a result of the slow penetration of the fixative (Fig. 4, 6).

Objects impregnated with osmium by the method of Kolatschev for the Golgi apparatus do not show plasmodesmata between the cells. From the diameter of the intercellular spaces the cells are greatly shrunken. Dense vacuoles are canalicular in shape, light vacuoles are spherical (Fig. 5). Impregnation with silver by the method of Da Fano for the demonstration of the Golgi apparatus gives approximately the same results. Cells fixed with Navašin fixative do not show visible plasmodesmata either. The cells are greatly shrunken and the intercellular spaces are large. The contents of dense vacuoles are concentrated into granules which in places are joined together. The nuclei and nucleus structures are very clearly outlined as against the results of the previous fixatives. The appearance of the cells after this fixation in unstained sections shows that it is a nucleus fixative (Fig. 3).

Embedding into plastic material is much more careful than embedding into paraffin. The disadvantage is the relatively complicated and long processing of the sections. Moreover, the embedding of the object is more complicated than with the paraffin method. It is also a disadvantage that araldite cannot be removed from the section. The staining of these sections with microscopic stains is difficult.

4. Study of dense vacuoles by the electron microscope

The finding of vacuoles with inclusions (dense vacuoles) in *Fagopyrum* was confirmed by electron microscopy (HRŠEL, JURÁKOVÁ and BENEŠ 1960). Later, MANTON (1962) found so-called dense vacuoles with a homogeneous content in the epidermal cells of the meristem of *Anthoceros* in addition to light vacuoles with liquid contents in the subepidermal cells. Similar dense vacuoles containing phenol inclusions were also described by ESAU (1963) in the cells of the root meristem of *Vitis vinifera*. The dense vacuoles with inclusions in *Fagopyrum* have the same appearance as in *Vitis*. They have the form of canalicular or spherical formations which stain deeply after fixation with $KMnO_4$ (Fig. 10, 11, 13). Intense staining after fixation with $KMnO_4$ for electron microscopic purposes is good for differentiating dense vacuoles with preservation of membrane structure of other cell components. According to size, shape and staining after fixation with $KMnO_4$, dense vacuoles correspond to the formations observed in the light microscope (Fig. 5, 9). As in

the light microscope, they are of two types: 1) a deeply staining substance massively fills the entire vacuole (Fig. 10, 11) and 2) the substance is concentrated round the edge of the vacuole and the centre is empty or contains small inclusions (Fig. 13, 14). Elongated and canalicular vacuoles sometimes

Fig. 1.

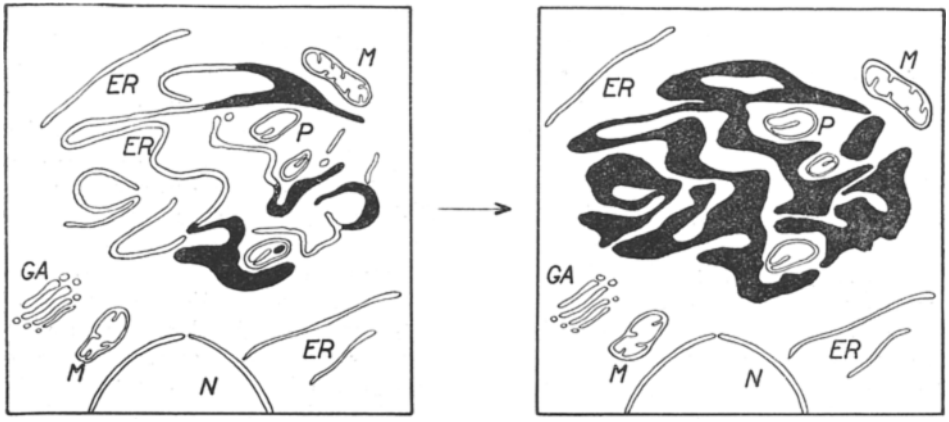

Fig. 1. Diagram of formation of dense vacuoles in endoplasmic reticulum.

open into fine endings which have the appearance of continuations of the endosplasmic reticulum (fig. 13). A relationship between endoplasmic reticulum and dense vacuoles had been observed previously (HRŠEL 1961b). Dense vacuoles arise: 1. by the storing of a dense substance in some parts of the endoplasmic reticulum. The cisternae of the endoplasmic reticulum enlarge by the accumulation of an electron microscopically dark, dense substance. In this way the canalicular form of dense vacuoles develop (Fig. 10, 11, 13). 2) In other cases, the flocculated contents of the vacuoles which were limited by a simple membrane (the tonoplast) were observed to contain small, dark, irregular inclusions (Fig. 12) which congregated at the edge of the vacuoles in the further stages of development and filled them partly or completely (Fig. 13, 14). In older vacuoles, the vacuolar membrane is not visible (Fig. 10,

Fig. 2.

Fig. 2. Diagram of formation of dense vacuoles (DV) by deposition of inclusions in light vacuoles.

11, 13, 14). Since the vacuoles develop by dilatation of the endoplasmic reticulum (BUVAT 1958), the vacuolar origin of the formations determined by the light microscope (MILOVIDOV 1957) is confirmed by the electron microscope. (Fig. 1, 2).

The Classic Golgi Apparatus in the Cells of Plants and Animals

Dense vacuoles in *Fagopyrum*, denoted by MILOVIDOV (1957) as classic Golgi apparatus of plant cells were compared morphologically, cytochemically and ultramicroscopically with the classic Golgi apparatus in animal cells because in animal cells (neurones) the Golgi apparatus was first described in the light microscope. Dense vacuoles have the following properties concordant with the classic Golgi apparatus in animal cells: 1) They have a canalicular and net-like appearance similar to that of the Golgi apparatus in nerve and other cells in the light microscope. In some cells we found half moon-like formations similar to the dictyosomes in animal cells. Dense vacuoles are often found in the space near the nucleus. 2) They can be impregnated with silver and osmium by the classical methods used in animal objects for demonstrating the Golgi apparatus. 3) They give positive results on using methods for the demonstration of lipids. The following properties are unusual: 1) Staining with iron haematoxylin after fixation with nucleus fixatives with a large mount of acetic acid. 2) The demonstration of phenol substances.

In addition to the morphological similarities between the Golgi apparatus in animal cells and dense vacuoles, both formations stain on using impregnation and lipid methods. This was evidently the reason why dense vacuoles were taken for the Golgi apparatus in plant cells and other objects and thus became the subject of dispute on the identity of the Golgi apparatus and the vacuolar system (Parat-Guilliermond vacuome theory). Other methods give different results. Dense vacuoles stain with alkaline silver solution but the animal Golgi apparatus does not. The reaction for ascorbic acid, which is negative in dense vacuoles, was used in some animal objects for the demonstration of the Golgi apparatus (ref. under HIRSCH 1939).

Methods of staining with silver salts, other than the impregnation method, show a different spectrum of affinity to dense vacuoles and the Golgi apparatus in animal cells.

The staining of dense vacuoles with iron haematoxylin after fixation with nucleus fixatives with large amounts of acetic acid is not the usual manner of demonstrating the Golgi apparatus in animal cells, since acetic acid destroys phospholipids. However, there are some methods for demonstrating the Golgi apparatus in which tissue was fixed with fixatives containing large amounts of acetic acid. Salazar, for instance, (ref. under HIRSCH 1939) used Bouin's fixation for demonstrating some components of animal Golgi apparatus. Moreover, the method of demonstrating ascorbic acid with silver salts (ref. under HIRSCH 1939) used for demonstrating the Golgi apparatus, is based on fixation with large amounts of acetic acid with ethanol. The fixation of dense vacuoles with nucleus fixatives with large amounts of acetic acid (Navašin) and embedding in paraffin certainly results in a certain diminution of the amount of stainable substance in the dense vacuoles, as determined by

comparing with fixative Ca-formol and embedding in water soluble waxes (HRŠEL, JURÁKOVÁ and BENEŠ 1960), but the vacuoles are not completely disrupted. Similar results were obtained on comparing Navašin's fixation with impregnation and fixation with $KMnO_4$ (Fig. 3, 5, 9). Staining with iron haematoxylin was used in some cases for demonstrating the Golgi apparatus of animal sex cells (MONNÉ 1948). The finding of phenols in dense vacuoles (HRŠEL, JURÁKOVÁ and BENEŠ 1960) is at variance with the cytochemical findings in the Golgi apparatus of animal cells, since, according to the literature, phenol substances have not been found in the Golgi apparatus of animal cells.

The chemical composition of the classic Golgi apparatus of animal cells is not always reported as the same. In the Golgi apparatus lipids (most) have been demonstrated, also mucoids, PAS positive material (GERSH 1949 etc. ref. under BAKER 1953b), cholesterol, protein and ascorbic acid (MONNÉ 1948, HIRSCH 1939, GERSH 1949).

It is evident that dense vacuoles differ in some of their cytochemical properties from the classic Golgi apparatus of animal cells. This could be due to a different chemical composition and other properties of the discutable classic Golgi apparatus in plant cells.

If we compare the ultrastructure of *Fagopyrum* root cells with that of animal cells after fixation with $KMnO_4$ and other fixatives we never find formations resembling the shape of dense vacuoles in the neurones of animal cells where the Golgi apparatus was first described. This shows that the ultrastructural and cytochemical character of *Fagopyrum* cell dense vacuoles and the classic Golgi apparatus of animal cells are definitely different. Evidently dense vacuoles in other plant objects examined under the light microscope were regarded as Golgi apparatus of plant cells. However, they are not a universal component of plant cell. Formations described in older works on plant material as the Golgi apparatus must be restudied, using electron microscopy and cytochemistry, since older methods, particularly impregnation, were not specific and could stain different structures in different objects. These results show that dense vacuoles cannot be considered to be the Golgi apparatus but belong to the vacuome of plant cells (MILOVIDOV 1957).

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IVAN HRŠEL, Ústav experimentální biologie a genetiky ČSAV, Praha: **Klasický Golgiho aparát a vakuoly.** — Biol. Plant. **7** : 136—145, 1965.

Husté vakuoly („dense vacuoles"), pokládané za klasický Golgiho aparát v kořínkovém meristému *Fagopyrum*, byly studovány 1. impregnačními metodami na důkaz Golgiho aparátu, 2. cytochemickými metodami, 3. elektronově mikroskopickými metodami ve světelném mikroskopu a 4. elektronovým mikroskopem. Bylo provedeno srovnání s klasickým Golgiho aparátem v živočišné buňce, ve světelném a elektronovém mikroskopu.

Morfologická podobnost, impregnovatelnost stříbrem a osmiem a barvitelnost lipidovými metodami jako u Golgiho aparátu živočišné buňky byly důvodem, že husté vakuoly byly označovány u *Fagopyrum* a patrně i v jiných rostlinných objektech za klasický Golgiho aparát. Dalšími chemickými vlastnostmi, např. obsahem fenolových sloučenin aj., se husté vakuoly od klasického Golgiho aparátu liší. Pod elektronovým mikroskopem nebyly nalezeny v živočišných buňkách žádné útvary podobné hustým vakuolám. Husté vakuoly se jeví pod elektronovým mikroskopem jako deriváty normálních světlých vakuol, známých v rostlinné buňce. Náleží tedy k vakuomu rostlinné buňky a nemohou být útvary analogické s Golgiho aparátem v živočišné buňce. Název Golgiho aparát je pro husté vakuoly neopodstatněný.

Byly srovnávány fixace a impregnace užívané v světelné mikroskopii s fixacemi v elektronové mikroskopii. Husté vakuoly mají po fixaci permanganátem stejný tvar jako po impregnaci. Barví se po fixaci permanganátem intenzívně černě jako po impregnaci stříbrem a osmiem. Tvar vakuol je závislý na užité fixaci. Srovnání bylo provedeno v světelném mikroskopu.

И. Гршел, Институт экспериментальной биологии и генетики, Институт экспериментальной ботаники ЧСАН, Прага: **Классический аппарат Гольджи и вакуоли.** — Biol. Plant. 7: 136—145, 1965.

Густые вакуоли («dense vacuoles»), считаемые классическим аппаратом Гольджи в корневой меристеме *Fagopyrum*, изучались: 1) импрегнационными методами доказательства аппарата Гольджи, 2) цитохимическими методами, 3) электронмикроскопическими методами в световом микроскопе, 4) электронным микроскопом. Осуществлено

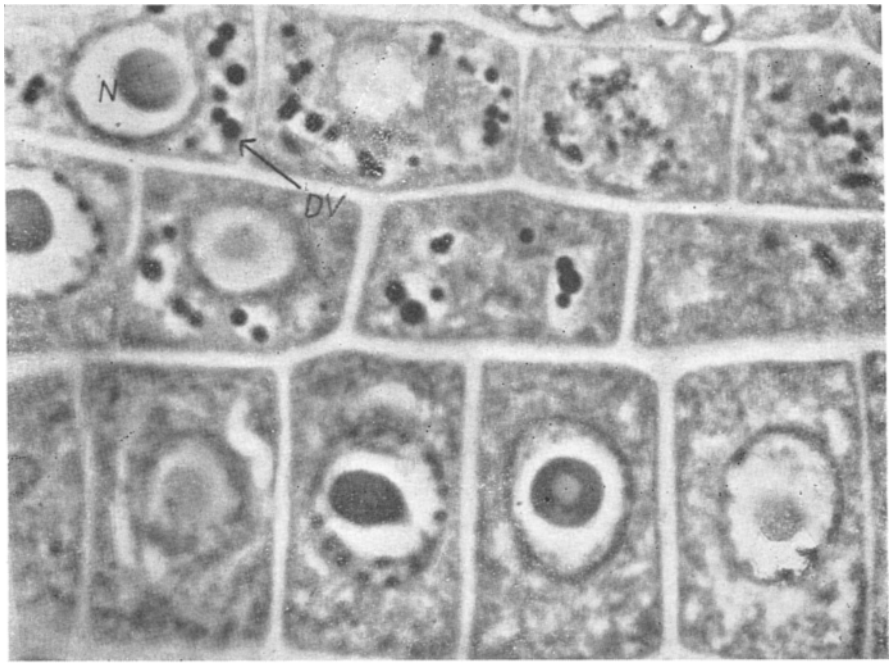

Fig. 3. Cells from area under growth apex of root of *Fagopyrum* in dermatogen. Dense vacuoles (DV) with inclusions. Nucleus (N). Fixation by Navašin, embedded in araldite. Light microscope, 2000×.

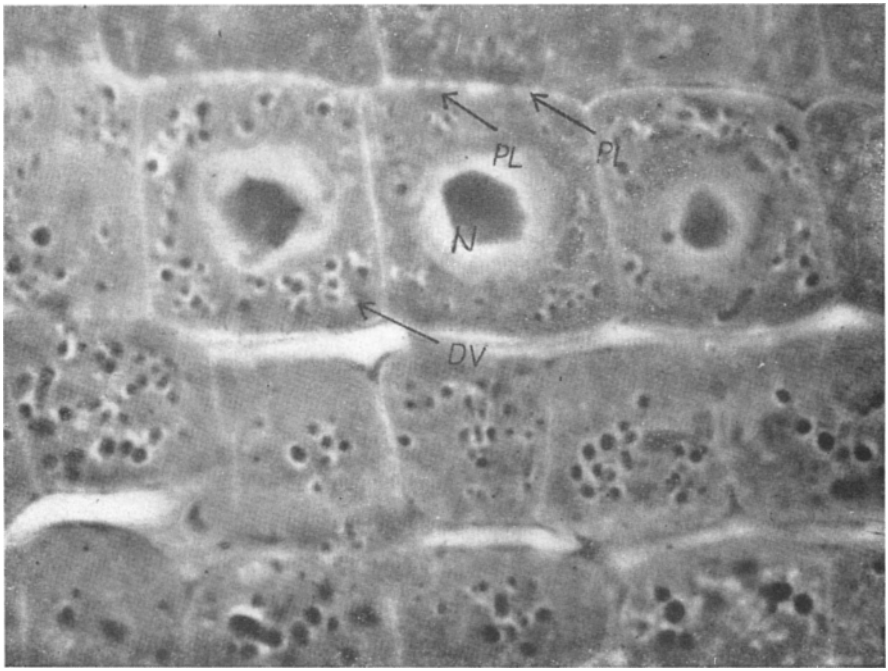

Fig. 4. The same. Spherical dense vacuoles (DV) with inclusions. Weakly indicated plasmodesmata (PL). Nucleus (N). Fixation by Regaud, embedded in araldite. Light microscope, 2000×.

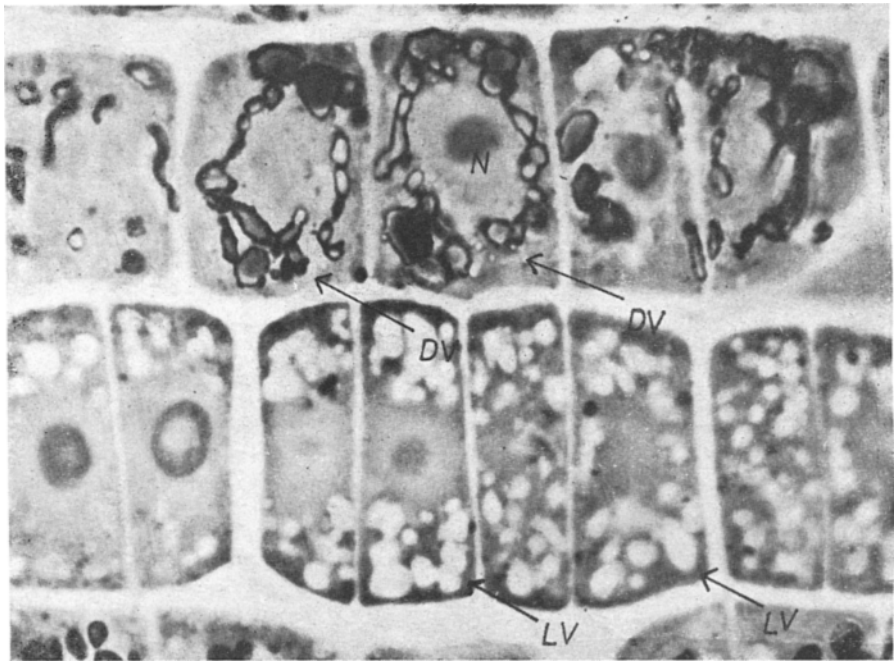

Fig. 5. The same. Dense vacuoles (DV) in the form of canaliculi. Classic Golgi apparatus. Light vacuoles (LV) spherical. Nucleus (N). Palade fixation (1% OsO_4 in buffer, pH 7·2), impregnation 48 hours in 2% OsO_4 at 37° C for Golgi apparatus by method of Kolatschev, embedded in araldite. Light microscope, Phase contrast. 2000×.

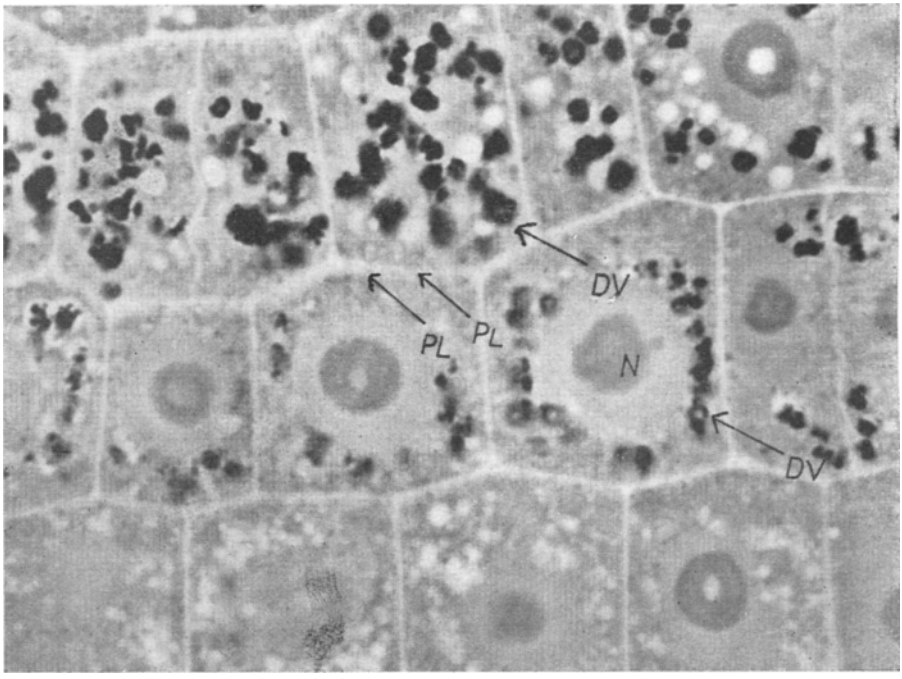

Fig. 6. The same. Dense vacuoles (DV) and light spherical vacuoles. Weakly indicated plasmodesmata (PL). Nucleus (N). Palade fixation (1% OsO_4 in veronal-acetate buffer pH 7·2), embedded in araldite. Light microscope, 2000×.

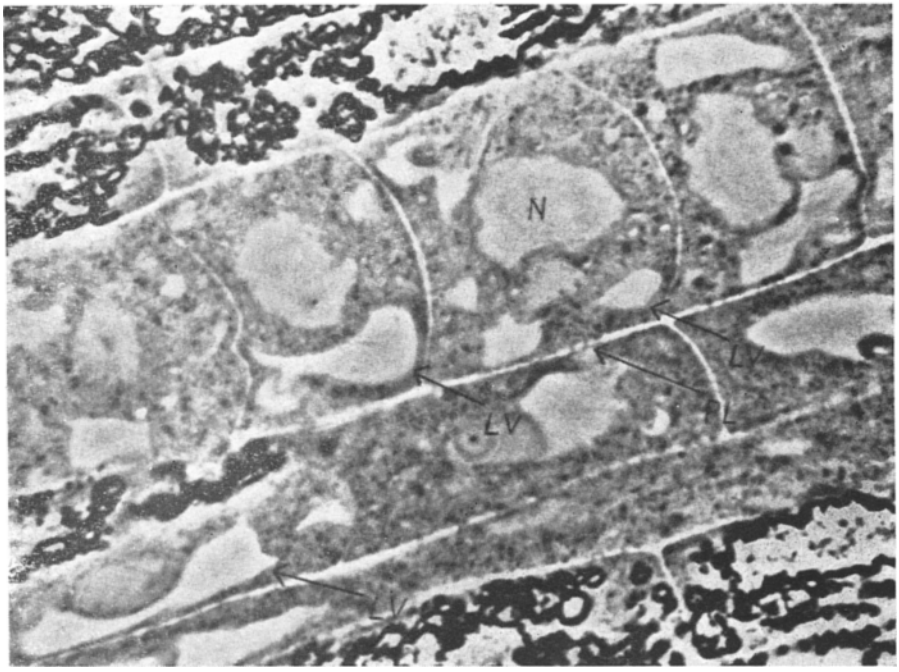

Fig. 7. Vacuolized cells in region of central cylinder about 0·5 mm. under growth apex of root. Light vacuoles lobulated. Definite plasmodesmata (PL). Nucleus (N). Fixation with 2% $KMnO_4$, embedded in araldite. Light microscope, 2000×.

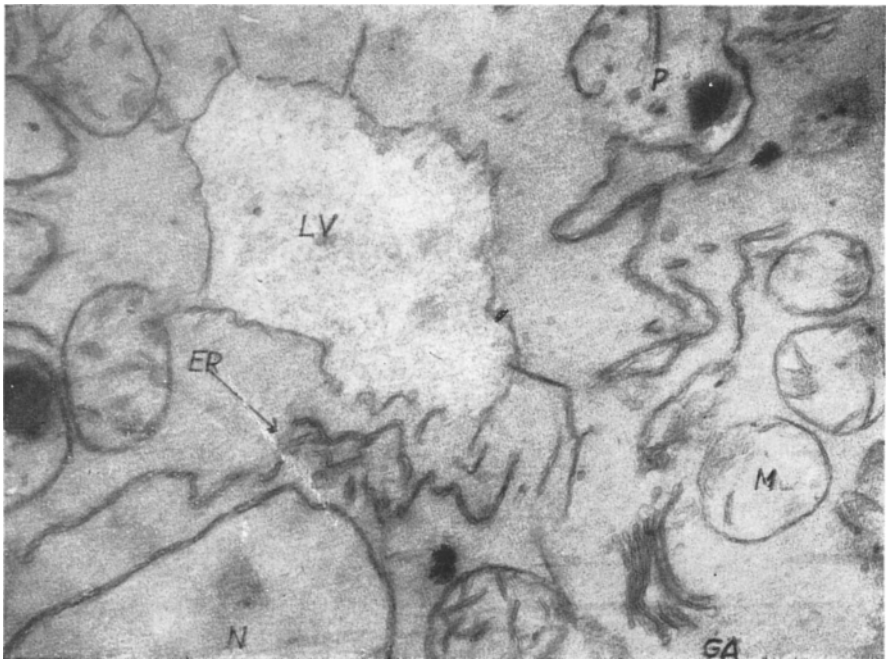

Fig. 8. The same. Part of cell. Light vacuole (LV), mitochondria (M), proplastid (P), endoplasmic reticulum (ER), Golgi apparatus (GA), nucleus (N). Fixation with 2% $KMnO_4$, embedded in araldite. Electron microscope, 23,000×.

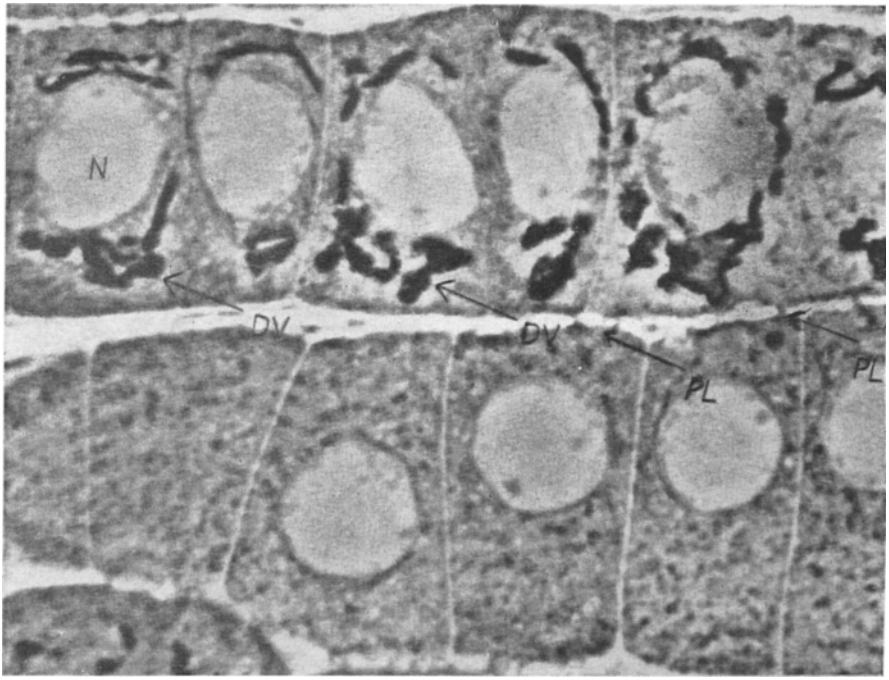

Fig. 9. Cells from area under growth apex of *Fagopyrum* root, dermatogen. Dense vacuoles (DV) in form of "classic Golgi apparatus", stained deep black with permanganate. Definite plasmodesmata (PL). Nucleus (N). Fixation with 2% $KMnO_4$, embedded in araldite, Light microscope, 2000×.

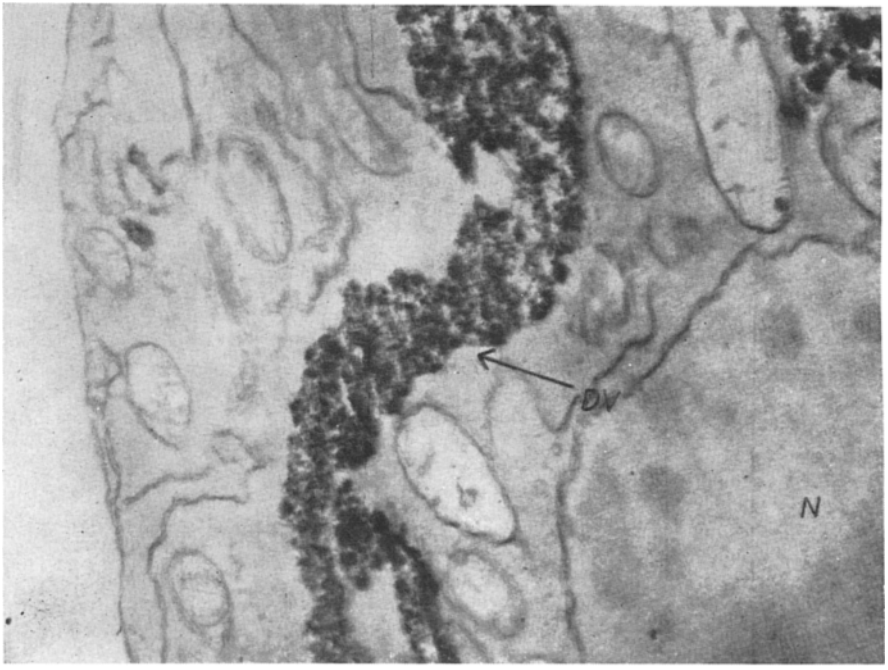

Fig. 10. The same. Part of cell. Dense vacuole (DV) in form of "classic Golgi apparatus", staining deep black with permanganate. Nucleus (N). Fixation with 2% $KMnO_4$, embedded in araldite. Electron microscope 19,000×.

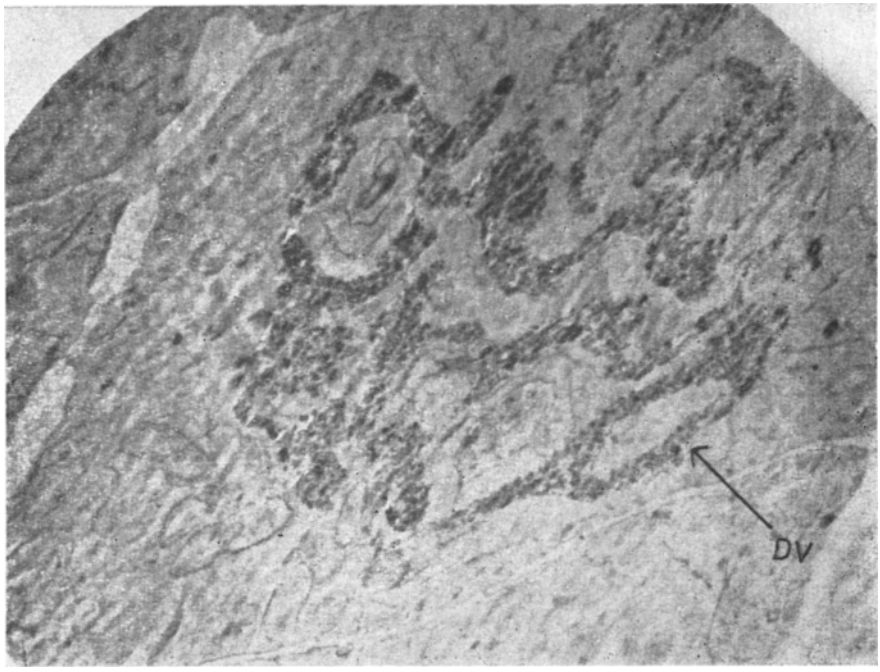

Fig. 11. The same. Dense vacuoles (DV) in form of "lcassical Golgi apparatus" (canaliculi, net work). Fixation with 2% $KMnO_4$, embedded in araldite. Electron microscope. 8000×

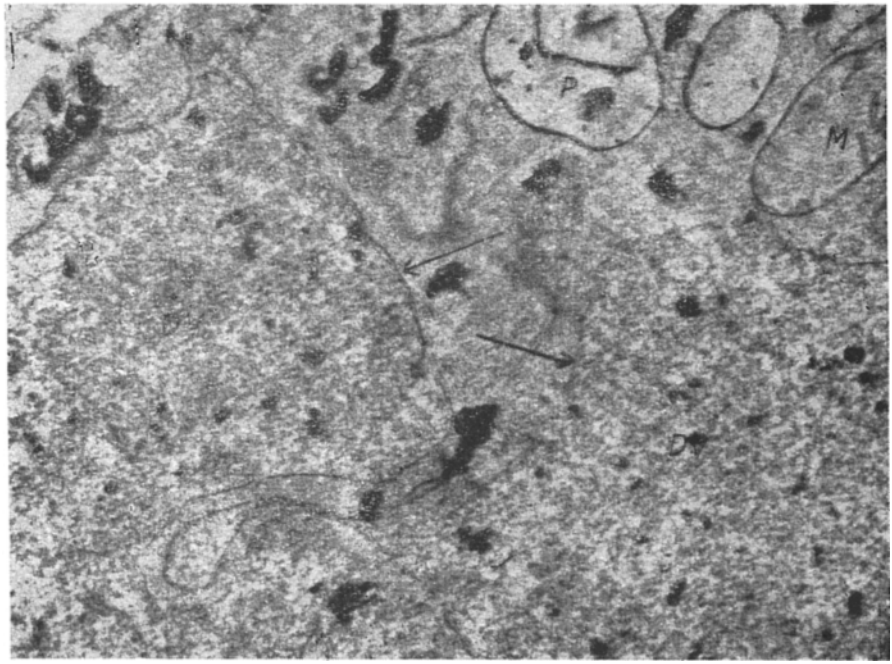

Fig. 12. The same. Dense vacuoles (DV) at beginning of transformation from light vacuoles. Small dark inclusions among contents of vacuoles. The arrow points to tonoplast membrane. Proplastid (P), mitochondria (M). Fixation with 2% $KMnO_4$, embedded in araldite. Electron microscope. 19,000×.

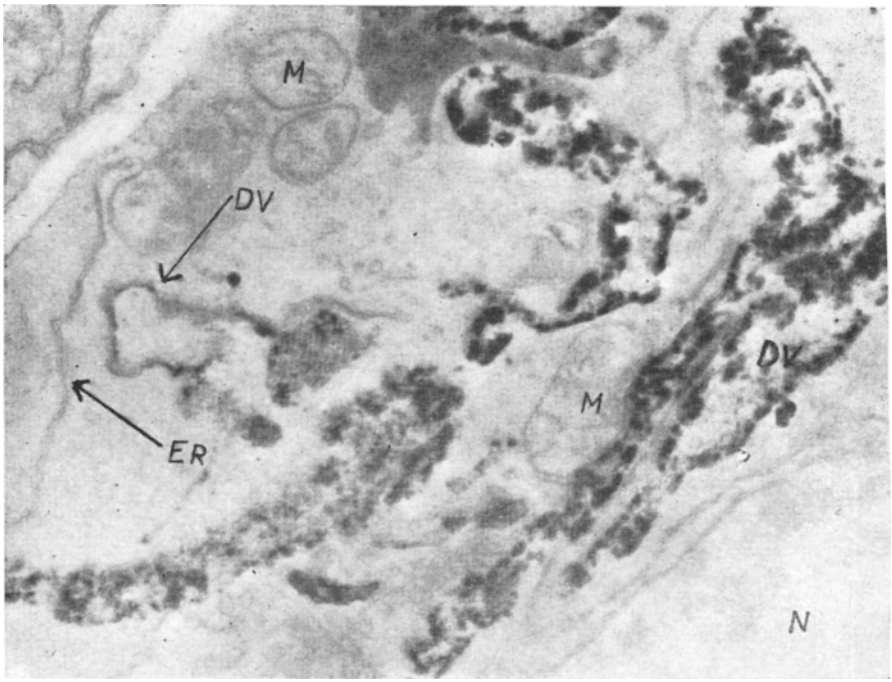

Fig. 13. The same. Dense vacuoles (DV) in relation to endoplasmic reticulum. The arrow (DV) indicates filamentous form of dense vacuole. Arrow (ER) endoplasmic reticulum. Mitochondria (M), nucleus (N). Fixation with 2% $KMnO_4$, embedded in araldite. Electron microscope. 19,000×.

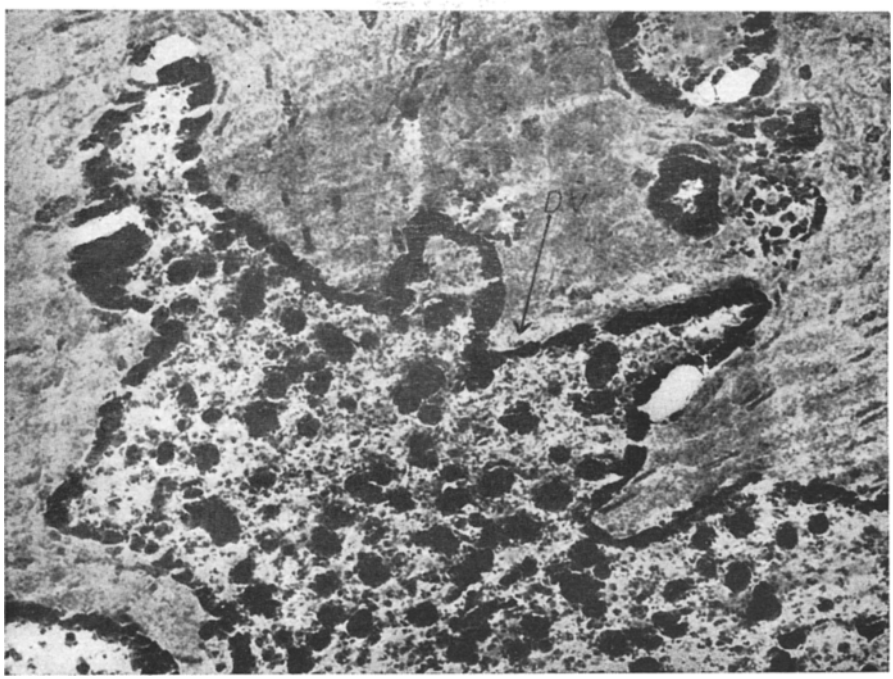

Fig. 14. The same. Dense vacuoles (DV) in form of formations bordered with dark material. Fixation with 2% $KMnO_4$, embedded in araldite. Electron microscope. 12,000×.
All photographs in the light microscope are made from non-stained sections without removing the araldite and mounted in Canada balsam.

сравнение с классическим аппаратом Гольджи в клетке животных, в световом и электронном микроскопах. Морфологическое сходство, способность к импрегнации серебром и осмием и окрашиваемость липидическими методами как у аппарата Гольджи животной клетки являлись поводом тому, что густые вакуоли обозначались у *Fagopyrum* и, повидимому, и у других растительных объектов классическим аппаратом Гольджи. Дальнейшими химическими свойствами, напр. содержанием фенольных соединений и др., густые вакуоли отличаются от классического аппарата Гольджи. Под электронным микроскопом не найдены в животных клетках никакие образования подобные густым вакуолям. Густые вакуоли являются под электронным микроскопом дериватами нормальных светлых вакуолей, известных в растительных клетках. Они принадлежат, следовательно, к вакуому и не могут быть образованиями аналогичными аппарату Гольджи в животной клетке. Название аппарат Гольджи для густых вакуолей не оправдано. Сравнивались фиксации и импрегнация, используемые в световом микроскопе, с фиксациями в электронной микроскопии. Густые вакуоли имеют после фиксации перманганатом одинаковую форму как и после импрегнации. Окрашиваются после фиксации перманганатом интенсивно черно, так же как и после имрегнации серебром и осмием. Форма вакуолей зависит от использованной фиксации. Сравнение проводилось в световом микроскопе.