BIOLOGIA PLANTARUM (PRAHA)

8 (1) : 36—52, 1966

Morphology and Function of the Endoplasmic Reticulum

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Received, February 9, 1965

Abstract. Comparison with the findings in the cells of other plants and animals showed that the endoplasmic reticulum in the root apex of *Fagopyrum* has the same general character and function as in other biological objects, i.e. in secretory processes and especially in this case in the transport of the substances produced. Detailed studies of the morphology and activity of the endoplasmic reticulum showed some functional differences which are characteristic for this object. The endoplasmic reticulum participates apparently in the transport of the mass of known but functionally and nomenclatorically controversial formations which here are called dense bodies. Dense bodies exist in *Fagopyrum* in a considerable amount as compared to other objects. Frequent contact of the dense bodies with the ends of the endoplasmic reticulum, contact with the endoplasmic reticulum passing through the plasmodesm, accumulation of the dense bodies along the cell wall and in proximal distance of the plasmodesms and intensive staining of some plasmodesms was observed. The dense vacuoles in this object represent dilated spaces of the endoplasmic reticulum which apparently have the function of reservoirs of the dense mass. The endoplasmic reticulum in the calyptra cells appears to participate in the formation of the cell walls. This object differs hereby from others, where the participation of the Golgi apparatus has been observed in this function.

On the basis of studies of the morphological relationship between the classical and the electron microscopical Golgi apparatus it was observed in animal and plant cells that the endoplasmic reticulum and the substances contained in its structures or in the derived vacuoles can also participate in the formation of net-like and other structures of the classical Golgi apparatus, which can be impregnated with silver or osmium (Hršel 1965b).

It was, therefore, the purpose of this communication to clarify the properties and functions of the endoplasmic reticulum of *Fagopyrum* at a simultaneous comparison with the observations on other plant objects and in the animal cell. The material and method have been described in previous papers (Hršel 1956a, b, c). Besides fixation with $KMnO_4$ fixation with formol-OsO_4 (Sitte 1958) and OsO_4 buffer solution (pH 7·2) was used.

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Morphology of the Endoplasmic Reticulum

Endoplasmic reticulum in the animal cell. The endoplasmic reticulum morphologically is not as constant structure as the Golgi apparatus (SJÖSTRAND 1956). In the animal cell the endoplasmic reticulum is described as a system of membranes, consisting of tubuli, cisternae and vesicles (see PALADE 1956b). For various types of cells the elements of the endoplasmic reticulum are given in various ratios and arrangements. The tubuli and cisternae are usually connected by anastomoses and branches so that they form the reticular system in the whole cell. Reticular structures have been observed in rat liver cells, in guinea pig seminal cells etc. (PALADE 1956b, FAWCETT and ITO 1958). The cisternae are usually oriented parallelly and are often close to the nucleus (e.g. Nissels substance in neurons and systems of the endoplasmic reticulum in pancreas cells, PALADE 1956b etc.). In some cases concentrical circular formations ("Nebenkern") arise in the vicinity of the nucleus in healthy and pathological cells. They were found in the oocytes of the mollusc *Spissula solidissima* (yolk nucleus, REBHUN 1956), in the salivary glands of *Chironomus* and in the hypophysis cells of a rat stimulated with oestrogens (ref. see HAGUENAU 1958), in mouse hepatoma cells (FAWCETT and ITO 1958) and others (ref. see NIKLOWITZ 1962).

The nuclear envelope also belongs to the structures of the endoplasmic reticulum and their relationship was observed in the form of extensions of the endoplasmic reticulum from the nuclear envelope into the cytoplasm (WATSON 1955 etc.).

The endoplasmic reticulum exists in two forms: 1) Membranes covered with ribosomes ("rough surfaced form"). For this form the name "ergastoplasma" taken over from light microscopy is also used (ref. see HAGUENAU 1958). 2) Smooth membranes (smooth surfaced form, ref. see PALADE 1956b). The parallelly arranged cisternae in the vicinity of the nucleus are formed by the rough surfaced type. The nuclear envelope of rat (PALADE 1955a) and guinea pig pancreas cells (PALADE and SIEKEVITZ 1956) has been described to carry ribosomes, i.e. rough surfaced. The smooth surfaced form exists in cells mostly in the reticular form as tubuli, cisternae and vesicles (PALADE 1956b, FAWCETT and ITO 1958). It was observed in all cells in various quantities. It exists predominantly on the cell periphery. In seminal cells and in all cells having an intensive lipid metabolism the smooth surfaced form of the endoplasmic reticulum dominates considerably over the rough surfaced form (PALADE 1956b).

In guinea pig pancreas cells both membrane forms have been observed, i.e. the smooth surfaced and the rough surfaced form which continuously pass into each other (PALADE and SIEKEVITZ 1956). In a similar way the extension of the endoplasmic reticulum from the rough surface nuclear envelope appears as the smooth surfaced form in cells of the Reuber tumour in studies of the electron microscopical localization of enzymes (NOVIKOFF, ASSNER, GOLDFISCHER and HEUS 1962). These cases indicate that a common membrane system is concerned rather than two separate forms.

Endoplasmic reticulum in the plant cell. The endoplasmic reticulum in plant cells contains similar elements as that in animal cells, i.e. tubular structures and cisternae connected by branches and ana-

stomoses and vesicles. In young cells, e.g. in the root meristeme of *Pisum sativum*, the endoplasmic reticulum has a net-like structure (SITTE 1958). A similar arrangement of freely placed tubuli and cisternae positioned in various directions was observed in the apical area of *Fagopyrum* (Fig. 4 and 5). A parallel arrangement of membranes was found mostly in the peripheral parts of the cytoplasm in contrast to the animal cells. It was observed in the root meristeme of *Pisum sativum* (SITTE 1958), *Zea mays* (WHALEY, MOLLENHAUER and KEPHART 1959), in wheat embryo (SETTERFIELD, STERN and JOHNSTON 1959, HRŠEL, WOLFOVÁ and MOHELSKÁ 1961) and in the meristeme filamentous cells of the *Datura stramonium* apex (HOHL 1960) and in young cells of the *Allium cepa* calyptra (FALK 1962). This arrangement occurs also in some conducting elements, e.g. in young cells of the metaxyleme of *Allium cepa* root cells (FALK 1962). In the sieve tubes of *Metasequoia glyptostroboides* branches in repose phloem the tubular elements of the endoplasmic reticulum are similarly organized (KOLLMAN and SCHUMACHER 1961, 1962). The cisternae in the endoplasmic reticulum in the pith cells and the parenchrymatic phloem cells have the same orientation (KOLLMANN and SCHUMACHER, 1961, 1962). In the root meristeme of *Fagopyrum* the parallel arrangement of cisternae is found in the dermatogene below the apex in the cells, where dense vacuoles are differentiated (Fig. 6).

Parallel membranes of the endoplasmic reticulum exist in plant objects also under the influence of pathogenic factors. They were found in the root meristeme of *Sinapsis alba* and in the apical point of *Elodea canadensis* exposed to anoxibiotic conditions (WRISCHER 1960), in the gland cells of *Drosophyllum luisitanicum* in an object, wilting for 105 min (SCHNEPF 1961) and in centrifugated root meristeme cells of *Pisum sativum* (BOUCK 1963).

Concentrical circular formations consisting of parallel membranes ("Nebenkern") were also observed in plant objects. They occur in intact cells of some special objects, as well as in cells of objects exposed to pathogenic factors. In intact cells they were described as formations analogous to "yolk nucleus" in scutellum cells of the young *Triticum vulgare* embryo (HRŠEL, WOLFOVÁ and MOHELSKÁ 1961). Similar formations were found in the cytoplasm of the egg cells of *Lilium candidum* (HRŠEL, unpublished results). In young sieve tubes of the root apex of *Allium cepa* concentrical formations similar to the "Nebenkern" are also formed (FALK 1962). At the leaf base of the *Tropeolum majus* embryo an endoplasmic reticulum organized into concentrical formations was observed during germination swelling (NOUGAREDE 1963b).

Under pathological conditions similar concentrical formations were observed after experimentally caused anoxia in the root meristeme cells of *Hyacinthus orientalis* (GAVAUDAN, POUSSEL and GUYOT 1960) and under similar conditions also in the root meristeme cells of *Sinapsis alba* (WRISCHER 1960). After the effect of centrifugation on the root meristeme cells of *Pisum sativum* similar formations, "whorls" were found (BOUCK 1963).

Cluster-like formation composed of membranes of the endoplasmic reticulum were observed in the root meristeme of *Zea mays* (WHALEY, MOLLENHAUER and KEPHART 1959). Similar formations were found occassionally in the root meristeme cells of *Fagopyrum* below the apex (Fig. 7).

In other cells the endoplasmic reticulum is composed of finely branched

anastomosing membranes. It was observed in the root meristeme cells of *Pisum sativum* (SITTE 1958) and is shown in the microphotographs of the root meristeme of *Lens culinaris* (CAPORALV 1959, Pl. I). A similar finely branched anastomosing net is formed by the endoplasmic reticulum in the differentiating cells of the root calyptra of *Allium cepa* (FALK 1962). In some sieve tubes of *Metasequoia glyptostroboides* branches the endoplasmatic reticulum occurs as a tubulous branched net (KOLLMANN and SCHUMACHER 1962). The branched forms later decompose to vesicles. The same arrangement of the endoplasmic reticulum was observed in the root meristeme cells of *Fagopyrum*, where the formation of canalicule-like forms of dense vacuoles is assumed (Fig. 8) (see HRŠEL 1965b).

The root meristeme of *Triticum vulgare* contains different structures of the endoplasmic reticulum in the peribleme, the so-called "specially reticulated" forms which are very rich in anastomoses so that they a have sponge-like character (BUVAT and MOUSSEAU 1960). These authors found the fundaments of vacuoles in this type. The same structure of the endoplasmic reticulum was found rarely in the meristeme cells of the root meristeme of *Fagopyrum* (Fig. 9) without the observed relationship to the vacuoles. An endoplasmic reticulum of this type (similar to accumulated bubbles), communicating widely in some cases with the nuclear envelope, was observed in the root meristeme of *Zea mays* in mechanically damaged cells close to the cutting area during excision (MOLLENHAUER, WHALEY and LEECH 1960).

Structures of the endoplasmic reticulum composed predominantly of vesicles were observed in the differentiated cells of the leaf of *Elodea canadensis* (BUVAT 1958, 1961), in cells of the root calyptra of *Allium cepa* (FALK 1962), in the sieve tubes of *Metasequoia glyptostroboides* (young branches) (KOLLMANN and SCHUMACHER 1962) and in differentiating xyleme cells in *Cucurbita maxima* petioles (ESAU 1963a). In the root apex of *Fagopyrum* the vesicular structure of the endoplasmic reticulum was found in the cells of the conducting elements and of the calyptra (Fig. 10 and 11). Gradual vesiculation of the differentiating conductive elements (Fig. 13, compare with Fig. 12, representing a young cell from the apex area) or of calyptra cells (Fig. 14) was also observed. In cells of the conducting elements appearance of spontaneous (Fig. 13, see HRŠEL, MOHELSKÁ and WOLFOVÁ 1964) and in calyptra cells of gradual vesiculation of the originally net-like structure of the endoplasmic reticulum were observed.

To the structures of the endoplasmic reticulum belongs also the nuclear envelope. The nuclear envelope of the interkinetic nucleus communicates with the endoplasmic reticulum, the so-called extensions, which were described in most plant objects studied with the electron microscope (for references see BUVAT 1963 and others, Fig. 12, 13 and 19). The extensions and discontinuities of the nuclear envelope are characteristic for the apical areas of the studied objects, i.e. for young cells (see LEECH, MOLLENHAUER and WHALEY 1963). One of the proofs for the nuclear envelope being a component of the endoplasmic reticulum is its fragmentation and blending with the other elements of the endoplasmic reticulum during mitosis in the root meristeme of *Allium cepa* and *Zea mays* (PERTER and MACHADO 1960, WHALEY, MOLLENHAUER and LEECH 1960).

The tubular forms of the endoplasmic reticulum in plant cells pass through

the walls from cell to cell by help of special connections, the so-called plasmodesms (Fig. 12 and 13) which have been thoroughly studied in several papers (for references WHALEY, MOLLENHAUER and LEECH 1960, BUVAT 1963, KOLLMANN and SCHUMACHER 1963 and others).

Connection of the endoplasmic reticulum with the plasmalemma was also found in young leaves of *Dactylis glomerata* (POUX, unpublished results, see BUVAT 1963). A different tube containing endoplasmic reticulum was observed in cotton embryo (JENSEN 1963).

The endoplasmic reticulum exists in two forms in plant cells as well as in animal cells: 1) membranes covered by ribosomes ("rough surfaced") and 2) smooth membranes without ribosomes ("smooth surfaced") (for references see SITTE 1958, BUVAT 1958, 1961 and 1963 and others).

The rough surfaced endoplasmic reticulum which can be observed after fixation with OsO_4 is present in all cells in different quantities and arrangement depending on the function in the cell or the age of the cell.

The membranes of this form deposited in various directions as well as parallel were observed in the root meristeme of *Allium cepa* (BUVAT and CARASSO 1957) and in young leaves or the root meristeme of *Zea mays* (HEITZ 1957) and *Pisum sativum* (SITTE 1958). In cells of the root meristeme of *Fagopyrum* this form of the endoplasmic reticulum is present in various arrangements as elsewhere in the meristeme cells (Fig. 15 and 16).

In some plant objects as well as in animal objects the rough surfaced form predominates, in others the smooth surfaced form is present in greater quantity.

The rough surfaced endoplasmic reticulum was observed very frequently towards the end of embryogenesis in the cells of the young leaf bases of *Tropeolum majus* (NOUGARÉDE 1963a). In the growing root filaments of *Zea mays* and *Tradescantia albigora* the rough surfaced form of the endoplasmic reticulum predominates or is present exclusively (SIEVERS 1963b). In cells of the carnivorous plant *Drosophyllum luisitanicum* a strongly developed rough surfaced endoplasmic reticulum in parallel arrangement was observed after feeding with albumin (SCHNEPF 1963).

The parallel arrangement of this form was observed in the root meristeme cells of *Sinapsis alba* and in the vegetative peak of *Elodea canadensis* at oxygen deficiency (WRISCHER 1960), in the gland cells of *Drosophyllum luisitanicum* during wilting (SCHNEPF 1961) and is shown in germinating embryos of *Triticum* (SETTEFIELD, STERN and JOHNSTON 1959), in the cells of young *Tropeolum majus* leaves during the investigation of dehydration accompanying maturing of the seed (NOUGARÈDE 1963a) (Fig. 9).

The rough surfaced form in parallel arrangement was also observed with *Fagopyrum* (Fig. 15). A very close parallel arrangement of these membranes was observed in the cells of the centrifuged *Pisum sativum* root (BOUCK 1963).

The vesicular structure of the rough surfaced endoplasmic reticulum, formed by decomposition of the originally net-like structures, was found in cells of the root calyptra of *Allium cepa* (FALK 1962). Rough surfaced vesicles of the same origin occur in cells of the leaf bases of the *Tropeolum majus* embryo dehydrated during maturing of the seed (NOUGARÈDE 1963a).

It has not been usually studied in plant cells to which form of the endoplasmic reticulum the nuclear envelope belongs. In cells of the root meristeme of *Pisum sativum* ribosomes were observed in the area of the pores and annula

of the nuclear envelope. This corroborates the assumption that the nuclear envelope of plant cells is (at least locally) covered with ribosomes (SITTE 1958). In the nuclear envelope of the gland cells of *Drosophylum*, on the other hand, no ribosomes were found in these places, however, in the opinion of the author the envelope is still sparcely covered with ribosomes (SCHNEPF 1960). According to the demonstrated microphotographs of the nuclear envelope in the cells of the root meristeme of *Cucumis sativa* (PEVELING 1961); and the cells of the root meristeme of *Fagopyrum* (Fig. 16) studied in this work, the nuclear envelope appears to belong to the rough surfaced form of the endoplasmic reticulum in plant as well as in animal cells.

The endoplasmic reticulum in the smooth surfaced form was observed in the apical point and the leaf primordia of *Elodea canadensis* (BUVAT 1958). The endoplasmic reticulum in which vacuoles form is also smooth surfaced, e.g. in the root meristeme of *Triticum vulgare* (BUVAT and MOUSSEAU 1960, BUVAT 1961, 1962, 1963, POUX 1962). The parallel tubular structures of the endoplasmic reticulum found in the sieve tubes of the phloem in *Metasequoia glyptostroboides* branches also belongs to this form (KOLLMANN and SCHUMACHER 1961). The smooth surfaced endoplasmic reticulum or that sparcely covered with ribosomes occurs in unstimulated gland cells of *Drosophylum luisitanicum* (SCHNEPF 1960) and in the fungus *Neurospora crassa* (SHATTIN and TATUM 1959), in *Allomyces macrogynus* (BLONDEL and TURIAN 1960, PRÉVOST-MONNOT 1960) and in the alga *Himanthalia lorea* (BERKALOFF 1963).

The possibility of the transition of the rough surfaced into the smooth surfaced form and vice versa in one continuous membrane element has also been observed in plant cells. Microphotographs of the endoplasmic reticulum in cells of the *Allium cepa* root meristeme (BUVAT and CARASSO 1957) indicate the possibility for transition of one form into the other (LANCE 1958, BUVAT 1963). The rough surfaced form cannot be differentiated from the smooth surfaced form in some cases (BUVAT 1963). In young leaves of *Anthoxanthum odoratum* the membranes of the endoplasmic reticulum, where vacuoles are formed, appear to be without ribosomes, and segments attached to them are rough surfaced (POUX 1961). In the fungus *Allomyces macrogynus* a change of the endoplasmic reticulum from the smooth to the rough surfaced form was observed during the differentiation of the gametes (PRÉVOST-MONNOT 1960).

It follows from these observations that the endoplasmic reticulum in the plant like in the animal cell is a structure changing morphologically considerably according to the differentiation and function of the cell in the organism in contrast to the Golgi apparatus (Fig. 1). The changes through which the endoplasmic reticulum passes can be approximately classified as follows: net-like structures predominate in young embryonic cells (Fig. 1a) parallel structures in differentiated cells, which are functionally oriented in a certain direction and in cells under the effect of physiological changes or pathophysiological interferences, where it is necessary to supplement deficient or decomposed proteins of the substance (Fig. 1b). Branched and later vesicular structures are present in cells which are highly specialized or degenerate (Figs 1c, d). The rough surfaced form predominates, especially in the parallel arrangement in cells, where intensive protein formation can be expected (Fig. 1e). In cells of rapidly growing organisms or tissues the ribosomes sparsely

attach the membranes of the endoplasmic reticulum. The smooth surfaced form occurs at sites where certain compounds are transported or deposited, e.g. in sieve-tubes and membranes where vacuoles are formed and in lipid synthesis.

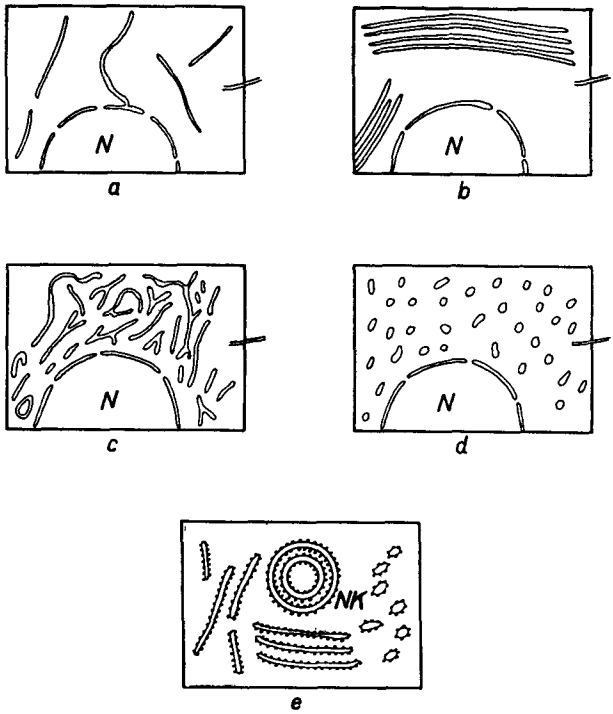

Fig. 1. Diagram of the morphological changes of the endoplasmic reticulum in the plant cell during differentiation.
a) Freely-placed membrane elements in various directions and extensions from the nuclear membrane in the young cell in the apical area.
b) Parallel arrangement of membranes in the active cell.
c) Branched structures in a fully differentiated cell.
d) Vesicular structure in the differentiated cell.
e) Various variants of the rough surfaced form of the endoplasmic reticulum. NK = "Nebenkern".

The existence of the endoplasmic reticulum in the smooth surfaced form in the apical point of *Elodea canadensis* (BUVAT 1956) will probably be connected with the intensive production of lipids, similarly as in animal cells (PALADE 1956b), which, however, in the plant cell serve the formation of the membrane systems of the chloroplasts in the differentiating leaf cells. This is indicated by the intensive staining of the vegetative peaks of other objects with sudan black e.g. in *Triticum vulgare* and *Oryza sativa* (HRŠEL 1956, 1958).

In the systems of the endoplasmic reticulum both forms, rough surfaced and smooth surfaced, cannot be separated occasionally. These forms may both be present in a common membrane structure or one form passes into the other during differentiation according to the requirements of the organism and the functional orientation of the cell. The endoplasmic reticulum is

a structure reflecting most sensitively age, functional and physiological state of the cell.

Function of the Endoplasmic Reticulum

Endoplasmic reticulum in the animal cell. Manifestations of the activity of the endoplasmic reticulum in the animal cell were observed in many cases. In the exocrinic cells of the guinea-pig pancreas inside the cavities of the endoplasmic reticulum granula were observed which are different from the zymogenic granula formed under participation of the Golgi apparatus (PALADE 1956a). The author assumes that the granula in this case are formed under participation of ribosomes adhering to the membranes of the endoplasmic reticulum. In other objects, e.g. in rat liver cells, a homogeneous finely granulated substance was found in the small cavities within the tubuli or cisternae. The surface of the membranes around the cavity is usually smooth surfaced (HAGUENAU 1958). In the endoplasmic reticulum of the liver cells of the Morris 5123 hepatoma and in several other objects a nucleoside phosphatase activity was observed. The activity of the same enzyme was also detected in the nuclear envelope, so that this structure is not identical with the structures of the endoplasmic reticulum only morphologically but also functionally (NOVIKOFF, GOLDFISCHER and HEUSS 1962).

The properties and function of the endoplasmic reticulum in the animal cell are explained by the authors who studied its structure and function as follows: the endoplasmic reticulum is a branched vacuolar system (PORTER 1955); it is the intracytoplasmic transport system (PALADE 1955b), it participates in secretory processes (PALADE 1956a); it participates actively in the synthesis of proteins for secretory purposes (PALADE and SIECHEVITZ 1956); it is affected by or participates in differentiation processes, it is the segregation apparatus of the cell (PALADE 1956b); it is important for the synthesis of secretory products (SJÖSTRAND 1956). The organized ergastoplasm (rough surfaced endoplasmic reticulum) is in relation to differentiation rather than to growth and is connected with synthesis of special secretes (HAGUENAU 1958). Formation of secretory products is effectuated in the ergastoplasm (OBERLING 1959). In the cisternae of the endoplasmic reticulum secretory products are formed in granular shape, doubtlessly under the participation of the ribosomes (WOHLFARTH-BOTTERMANN 1963).

Endoplasmic reticulum in the plant cell. The observed functional manifestations of the endoplasmic reticulum in the plant cell can be classified into two groups. Into the first group belongs the separation of the vesicular elements as in the Golgi apparatus, or their fusion with the endings of the tubuli or cisternae (Fig. 2a). At the ends of these membranes vesicular dilatations were observed in the root meristeme of *Zea mays* or vesiculae in the closest vicinity (WHALEY, MOLLENHAUER and KEPHART1959.) In the coleorhiza of *Zea mays* and in the cotyledons of the oil plants *Brassica napus* and *Sinapis alba* formation of so-called spherosomes was observed from the separated vesicular elements of the endoplasmic reticulum and their transformation into lipid drops (FRAY-WYSSLING, GRIESHABER and MÜHLETHALER 1963). In the circular elements of the endoplasmic reticulum in the mother cells of *Lilium candidum* separation of the vesicles from the endings of the membrane formations into the cytoplasm was also observed (HRŠEL

unpublished results). In contrast to the preceding objects no striking vesicular endings with light contact or separating light vesicles were observed in the endoplasmic reticulum of the root meristeme cells of *Fagopyrum* (see Figs 4, 5 . . . etc.). Studies of the synergids in the mature megagametophyte of the cotton plant showed irregular very dark dense bodies in the cytoplasm which are connected with the ends of the endoplasmic reticulum (JENSEN 1963). Similar dense bodies (Fig. 18, 19, 20 etc.) occur in large amount in *Fago-*

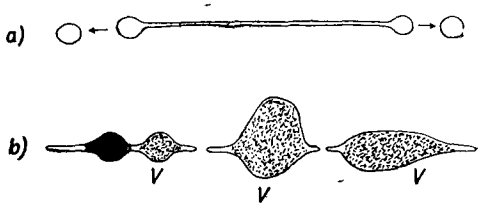

Fig. 2. Diagram of the function of the endoplasmic reticulum in the plant cell.
a) Separation and fusion of vesicular elements.
b) Deposition of a substance inside the cisternae of the dilated endoplasmic reticulum and formation of vacuoles *(V)*.

pyrum about 0·5 mm below the apex in the cells of the central cylinder or in its close vicinity. Here as well contact of these bodies with the ends of the endoplasmic reticulum was found (Fig. 20). This contact appears to be spontaneous in some cells (Figs. 18 and 19). Besides this appearance, accumulation of dense bodies was observed in some cells along of cell walls (comp. SITTE 1958) at the sites where systems of plasmodesms occur (Figs. 22 and 23). Contact of the dense bodies with the tubular element of the endoplasmic reticulum, passing through the plasmodesm, was also observed frequently (Figs. 21a, b). The cells in which dense bodies were found in large quantities have a characteristic appearance already in the light microscope (Fig. 24) and at small magnification in the electron microscope (Fig. 19 and 21b) and their cytoplasm can easily be differentiated from the cytoplasm of cells in the area of the apical point, which do not contain any dense bodies or only in small quantities like the cell of other objects (Fig. 17).

In the other group of functional manifestations of the endoplasmic reticulum secretion or transport and accumulation of various substances in the lumen of the endoplasmic reticulum is similar to that in the animal cell. These substances were observed either directly inside the lumen of the endoplasmic reticulum or in the dilated spaces, i.e. in the vacuoles (Fig. 2b) (see HRŠEL 1965a).

1) Substances inside the endoplasmic reticulum.

These substances are formed here either directly or they are transported by the endoplasmic reticulum. This appearance was observed in cells of the endosperm of *Hordeum vulgare*, where the formation of granula, containing proteins and lipids, was observed under participation of the endoplasmic reticulum, when the plants were exposed to low light intensity (BUTTROSE FREY-WYSSLING and MÜHLETHALER 1960). In the synergids of cotton the possibility of formation of the so-called filiform material in the endoplasmic reticulum was also observed as in animal cells secreting mucus (JENSEN 1963).

The rough surfaced endoplasmic reticulum in the gland cells of *Drosophyllum luisitanicum* apparently plays an important role in digestion by forming proteolytic enzymes as well as by taking up decomposed substances (SCHNEPF 1963). In secretion in the septal nectaria of *Gasteria trigona* the endoplasmic reticulum is assigned a certain role, which through the plasmodesm participates in the intracellular transport of substances (SCHNEPF 1964a). In the cells of the cynthial nectaria of *Euphorbia pulcherrima* the possibility of the participation of the endoplasmic reticulum in secretion was observed probably in the transport of substances within and between the cells, since its development attains the highest point at the start of secretion and decreases again after termination (SCHNEPF 1964b).

Studies of the plasmodesms and of the endoplasmic reticulum passing through the plasmodesms in secretory processes in the glandular epithelial cells of the active nectarium of *Gasteria trigona* did not show changes in their structure, although the transport of secretes is assumed also between cells (SCHNEPF 1964a). In contrast the internal channel of some plasmodesms of the whole plasmodesm in *Fagopyrum* cells in the medial area below the apex appear remarkably dark (Figs. 25a, c, d and 27) as compared to other plasmodesms (Figs. 25a, b and 26). Dense bodies accumulate occasionally in the vicinity of the plasmodesm (Figs. 21a, b, 22 and 23). Also in the light microscope some intensively stained plasmodesms can be observed (Fig. 24).

In the calyptra cells of the root apex of *Fagopyrum* accumulation of a dark substance of uncertain origin was observed in the intercellular space neighbouring the plasmalemma. The largest quantity of the dark substance is accumulated in the vicinity of the plasmodesms (Fig. 28).

2) Vacuoles.

In the first studies of the ultrastructure of the animal cell the endoplasmic reticulum of the usual appearance was designated as a "vacuolar system" (PORTER 1955). In the endoplasmic reticulum of plants extensive dilatations are frequently formed from small cavities and from these dilatations a genuine vacuolar system is formed which is characteristic of the plant cell (BUVAT 1957, 1958 and others). In the vacuoles substances of liquid to solid character are accumulated. The vacuoles are stained with different intensity after fixation with $KMnO_4$, OsO_4 according to their chemical composition and density of the content.

During secretion the secretory products accumulate in certain places of the endoplasmic reticulum which are also transformed to vacuoles (BUVAT 1961). The relationship of the vacuoles to the secretory processes was observed in the electron microscope in the glandular cells of *Drosophyllum luisitanicum* (SCHNEPF 1960). The author assumes that part of the secretes gets into the vacuoles and is deposited there. Similarly, the vacuoles of the gland cells of *Pinguicula vulgaris* fixed with $KMnO_4$ are considered to be the storage site of mucoid substances. The mucoid substances form a brown precipitate with $KMnO_4$ in vitro (VOGEL 1960). Intensified vacuolization was observed when the glandular cells of *Drosophyllum luisitanicum* are feed casein or albumin for a considerable time (SCHNEPF 1963).

The dense vacuoles in the root meristeme cells of *Fagopyrum* lead in lumen of the endoplasmic reticulum (HRŠEL 1961, 1965a, b). As most other vacuoles the dense vacuoles are also formed in its dilatations (HRŠEL 1965a, b). The dense

vacuoles, as in the preceding objects can be considered as reservoirs of compounds of secretory character, i.e. of dense massive material, stained intensively after fixation with $KMnO_4$ and OsO_4 (see HRŠEL 1965a).

Discussion

The endoplasmic reticulum was studied in the root meristeme cells of *Fagopyrum* from the morphological and functional point of view at simultaneous comparison with other objects and with animal cells. A similar arrangement of the endoplasmic reticulum was found as in other objects, i.e. freely distributed or net-like and parallel arranged cisternae and tubuli in younger and fully active cells, branched to vesicular forms in specialized cells, e.g. in older calyptra cells and in cells of some conductive elements (Fig. 1). For the cells of the root apex of *Fagopyrum* the following functional indications and properties of the endoplasmic reticulum and of the structures connected with it directly are characteristic and in a certain way different from other plant objects: the frequent contact of the dense bodies with the ends of the endoplasmic reticulum, the contact of the dense bodies with the ends of the endoplasmic reticulum passing through the plasmodesm, accumulation of dense bodies in the areas of the cell walls and especially in the immediate vicinity of the plasmodesms and intensive staining of some plasmodesms. The dense bodies belong to the group of the well-known but functionally and nomenclatorically undefined formations present in different quantity in the cytoplasm of the usual plant objects studied hitherto (see HRŠEL 1965c). The character of the cytoplasm of *Fagopyrum* cells in which the activity of the dense bodies becomes manifest (Figs. 18, 19, 21b, 27) and of the cytoplasm of young cells inactive in this sense where the dense bodies are rare Fig. 17 and 26) is very different. The strikingly increased quantity of dense bodies in active cells can be observed already in the light microscope where they appear as small dark spheroids (Fig. 24). The content of the dense bodies and of the dense vacuoles (see HRŠEL 1965a) has the following similar properties under the electron microscope: intensive staining after fixation with $KMNO_4$ and OsO_4 and relationships to the structures of the endoplasmic reticulum. The dense vacuoles, like those of other objects, have the possible function of reservoirs in which the transported substance accumulates, i.e. in this case the dense mass.

According to the observations mentioned the following reconstruction of the function of the endoplasmic reticulum in the *Fagopyrum* root apex cells appears most probable:

The dense bodies produced by the dictyosomes (see HRŠEL 1965c) fuse and are resorbed by the ends of the endoplasmic reticulum. The dense mass of the bodies thus gets into the intracisternal and intratubular spaces, it is transported by the cell or accumulates in the dilated spaces and forms dense vacuoles. The dense mass is again excreted in the ends of the endoplasmic reticulum into the same dense bodies which separate from the end of the endoplasmic reticulum. In the same way the dense mass probably passes also through the endoplasmic reticulum from the cell into the plasmodesma cell. The passing of the dense mass from cell to cell can also be observed in the light microscope on the same material processed for electron microscopic

purposes. The dense mass is probably transported in the mentioned way to the areas of the plant where it is required (Fig. 3).

Another ultrastructural manifestation of the function of the endoplasmic reticulum is the finding of accumulation of the dark mass in the intercellular spaces in the vicinity of the plasmodesms of the calyptra cells. In the cells

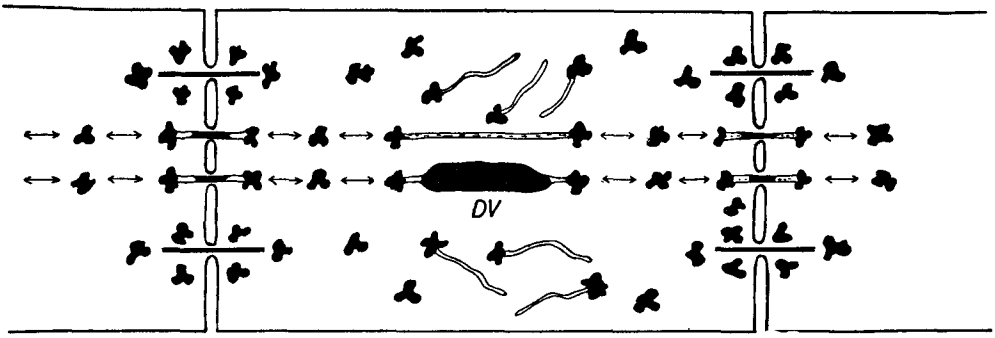

Fig. 3. Reconstruction of the assumed transport of dense material by dense bodies in the endoplasmic reticulum in the cell and between the cells in the root apex of *Fagopyrum*. *DV* — dense vacuole.

of the calyptra and in the root hairs of *Zea mays* (MOLLENHAUER, WHALEY and LEECH 1961, SIEVERS 1963a) and in the root apex of *Avena sativa* (GÜNTHER 1962) the participation of the vesicles of the Golgi apparatus in the formation of the cell walls by fusion with the plasmalemma was observed. This function of the Golgi apparatus was not observed in *Fagopyrum* (see HRŠEL 1965c). In the calyptra cells of *Fagopyrum*, on the other hand, accumulation of a dark mass was observed in the intercellular space in the near distance of the plasmodesms, not observed in other objects. The endoplasmic reticulum can apparently participate in the formation of the cell wall. The dark substance is excreted into the intercellular spaces through the plasmodesm which are probably adjusted to this purpose so that the substance passing through remains in the intercellular spaces. It is not clear whether the substance is formed directly in the endoplasmic reticulum or whether it is produced by the Golgi apparatus and only transported by the endoplasmic reticulum.

According to the studies of the endoplasmic reticulum in *Fagopyrum* and in agreement with the observations of other authors on other objects, the endoplasmic reticulum participates in certain secretory processes, like the Golgi apparatus. In *Fagopyrum* it apparently has the main function in the transport of secreted substances.

Acknowledgement

For assistance in this work I am indebted to Mrs. B. Wolfová, Dr. H. Mohelská, Ing. V Drahoš and to workers from the Institute Apparatus Technique, Czechoslovak Academy of Sciences, and to Miss J. Veverková.

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Fig. 4. Freely placed elements of the endoplasmic reticulum in the cells of the apical area of *Fagopyrum*. N = nucleus. Fixation with $KMnO_4$. Embedded in araldite. Magn. 22 000×.

Fig. 5. Net-like structures in a younger cell below the apex. Object and method the same. Magn. 26 000×.

Fig. 6. Parallel arrangement of membranes. Dtto. Magn. 25 000×.

Fig. 7. Cluster formation. Dtto. Magn. 22 000×.

Fig. 8. Branched elements. Dtto. Magn. 21 000×.

Fig. 9. Special reticulated elements. Dtto. Magn. 24 000×.

Fig. 10. Vesicular structures of the endoplasmic reticulum in a conducting cell. Dtto. Magn. 21 000×.

Fig. 11. Vesicular structure of the endoplasmic reticulum in an older calyptra cell. Dtto. Magn. 22 000×.

Fig. 12. Young cell in the apical area with an extension of the nuclear envelope (arrow). N = nucleus, PL = Plasmodesm, CW = cell wall. Dtto. Magn. 24 000×.

Fig. 13. Cell from the central part below the apex with starting spontaneous vesiculation of the endoplasmic reticulum during differentiation into conducting elements. The prolonged structures are released and gain vesicular appearance. See Fig. 12. N = nucleus, PL = Plasmodesm, CE = cell wall. The arrow indicates the extension of the nuclear envelope. Dtto. Magn. 23 000×.
(From HRŠEL, MOHELSKÁ and WOLFOVÁ 1964.)

Fig. 14. Gradual vesiculation of the endoplasmic reticulum in a calyptra cell. The cell contains also elongated membranes. The arrow indicates formation of vesicular structures. N = nucleus. Dtto. Magn. 21 000×.

Fig. 15. Parallel arrangement of membranes of rough surfaced form. DV = dense vacuole. Same materiel. Fixation with OsO_4 (PALADE), embedded in methacrylate. Magn. 39 000×.

Fig. 16. The same. N = nucleus, NL = nucleolus, NM = nuclear membrane. The arrow indicates the rough surfaced endoplasmic reticulum. Same object, fixation with formol-OsO_4, embedded in methacrylate. Magn. 44 000×.
(From HRŠEL, JURÁKOVÁ and BENEŠ 1960.)

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Fig. 17. Endoplasmic reticulum in the cell in the apical area without dense bodies. Same object, fixation with $KMnO_4$, embedded in araldite. Magn. 22 000×.
Fig. 18. Endoplasmic reticulum in the cell below the apex. Endoplasmic reticulum in contact with dense bodies. (Arrows.) Compare with Fig. 17. The same. Magn. 21 000×.
Fig. 19. Complete view of the cell from the area below the apex. Endoplasmic reticulum in contact with dense bodies. The arrows indicate the extensions of the nuclear envelope. N = nucleus. Dtto. Magn. 16 000×.
Fig. 20. Contact of the dense bodies with the ends of the endoplasmic reticulum at larger magn. Dtto. Magn. 24 000×.
Fig. 21a. Contact of dense bodies with the ends of the endoplasmic reticulum passing through the plasmodesm. Dtto. Magn. 34 000×.
Fig. 21b. Complete view of part of the cell containing a large quantity of dense bodies. The arrow indicates contact of dense bodies with the ends of the endoplasmic reticulum passing through the plasmodesm. N = nucleus. Dtto. Magn. 23 000×.
Fig. 22. Accumulation of dense bodies in the area of the cell wall in the near distance of the plasmodesms. N = nucleus. Dtto. Magn. 23 000×.
Fig. 23. Accumulation of dense bodies in the area of the cell wall. N = nucleus, V = vacuole, P = Plastide. Dtto. Magn. 22 000×.
Fig. 24. Area of the central cylinder below the apex in the light microscope. The dense bodies are visible as small black spheroids. In the black framed spaces are visible the transitions of the dense bodies from cell to cell on a transverse cut through the walls. The arrows indicate dark coloured plasmodesms. N = nucleus. Dtto. Magn. 1 500×.
Fig. 25a. Small magnification in the electron microscope. A simple arrow indicates widened dark-coloured plasmodesms, double arrows normal plasmodesms. Dtto. Magn. 8 500×.
Fig. 25b. Normal appearance of the plasmodesms at larger magnification. Dtto. Magn. 24 000×.
Fig. 25c, d. Dark-coloured plasmodesms. Compare with Fig. 25b. Dtto. Magn. 24 000×.
Fig. 26. Large magnification of a normal plasmodesm. Arrow inside a darker channel. Dtto. Magn. 42 000×.
Fig. 27. Large magnification of dark plasmodesms, through which apparently passes the mass of the dense bodies, the dark channel is dilated and intensively stainable (arrow). Dtto. Magn. 42 000×.
Fig. 28. Area of the calyptra cells in the space of the cell wall. PL = Plasmodesm, CW = cell wall. The arrows show the deposition of the dark mass in the intracellular space. Dtto. Magn. 32 000×.

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I. HRŠEL, Ústav experimentální botaniky, ČSAV, Praha: **Morfologie a funkce endoplazmatického retikula.** — Biol. Plant. **7** : 36—52, 1966.

Srovnáváním s nálezy v buňkách jiných rostlin a živočichů se ukázalo, že endoplazmatické retikulum ve všeobecných rysech v kořenové špičce u *Fagopyrum* má stejný charakter a funkci jako v jiných biologických objektech, tj. při sekrečních pochodech a speciálně v tomto případě při transportech produkovaných substancí. Podrobné studium morfologie a činnosti endoplazmatického retikula ukázalo některé zvláštnosti ve funkci, které jsou příznačné pro tento objekt. Endoplazmatické retikulum se patrně zúčastňuje při transportu hmoty dobře známých, ale funkčně a nomenklatoricky sporných útvarů, které jsou zde nazývány hustými tělísky. Hustá tělíska se proti jiným objektům vyskytují u *Fagopyrum* ve značném množství. Byl pozorován častý dotyk hustých tělísek se zakončeními endoplazmatického retikula, dotyk s endoplazmatickým retikulem procházejícím plazmodesmy, hromadění hustých tělísek v blízkosti plazmalemmy a plazmodesmů a intenzívní barvitelnost některých plazmodesmů. Husté vakuoly představují v tomto objektu dilatované prostory endoplazmatického retikula, které mají patrně

funkci reservoirů husté hmoty. Endoplazmatické retikulum v buňkách calyptry se podle pozorování také podílí při stavbě buněčných stěn. Tím se tento objekt liší od jiných objektů, kde byla pozorována pouze účast Golgiho aparátu při této funkci.

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При сравнении с клетками других растений и животных оказалось, что эндоплазматический ретикул имеет в корневом окончании у *Fagopyrum* в общих чертах тот же характер и функцию, что и в других биологических объектах, т. е. в процессах секреции и специально, в данном случае, при транспорте продуктов обмена веществ. Подробное изучение морфологии и деятельности эндоплазматического ретикула выявило некоторые функциональные особенности характерные для данного объекта. Эндоплазматический ретикул как видно участвует при транспорте хорошо известных, но по функции и номенклатуре неясных образований, здесь называемых густыми тельцами. Густые тельца по сравнении с другими объектами встречаются у *Fagopyrum* в значительном количестве. Наблюдалось очень частое соприкосновение густых телец с окончаниями эндоплазматического ретикула, соприкосновение с эндоплазматическим ретикулом проходящим плазмодесмы, накопление густых телец по близости плазмалеммы и плазмодесм и интенсивная окрашиваемость некоторых плазмодесм. Густые вакуоли в этом объекте представляют пространства эндоплазматического ретикула, имеющие, повидимому, функцию резервуаров густого вещества. Эндоплазматический ретикул в клетках калиптры по наблюдениям также участвует при образовании клеточных стенок. Этим данный объект отличается от других, у которых наблюдалось лишь участие аппарата Гольджи при этой функции.