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Lipotubuloids – Structure and Function

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1. Introduction

In the 19th and 20th centuries these structures were called „elaioplasts" according to Wakker (1888) who introduced this term with regard to nucleus-size lipid bodies present in *Vanilla planifolia* leaf epidermis which strongly refracted light. Since they are clearly visible under light microscope (Fig. 1A,B) they became the focus of interest in those days and were described in about 120 mono- and dicotyledonous plant species. Also in our laboratory "elaioplasts" were for the first time observed in 12 *Gentiana* species (Kwiatkowska, 1959, 1961) and in *Dahlia variabilis* (Kwiatkowska, 1963).

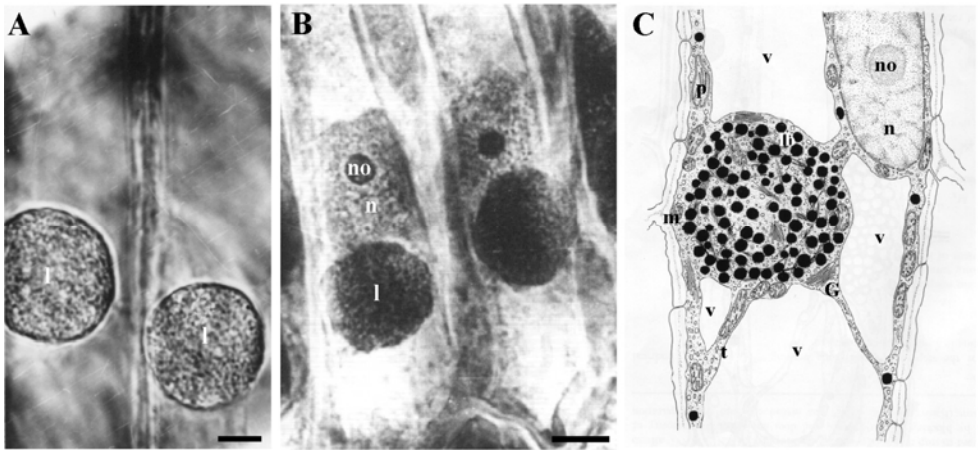

Fig. 1. *Ornithogalum umbellatum* "elaioplast" (lipotubuloid); A – in a living cell; B - after OsO_4 fixation; C – a scheme of epidermis cell with lipotubuloid; G – Golgi apparatus, l – lipotubuloid, lb – lipid bodies, m – mitochondrion, n – nucleus, no – nucleolus, p – plastid, t – tonoplast, v - vacuole; bars: 10 µm.

In 1883 Schimper introduced the term plastids which has been widely accepted since then. Among plastids, which are cell organelles containing double phospholipid bilayer, there are those producing lipids, i.e. elaioplasts which this term actually means. However, they are totally different from Wakker's "elaioplasts", the latter not being plastids in the contemporary meaning of this term. This was unequivocally proved by EM observations of

"elaioplasts" in *Ornithogalum umbellatum* ovary and stipule epidermis described by Raciborski (1895) and Kwiatkowska (1966). Their ultrastructure indicates that they are specific cytoplasm domains (Fig. 2) (Kwiatkowska, 1971a, 1971b, 1972a). They do not have their own membrane but invaginating into vacuoles are surrounded by a tonoplast (Fig. 1C).

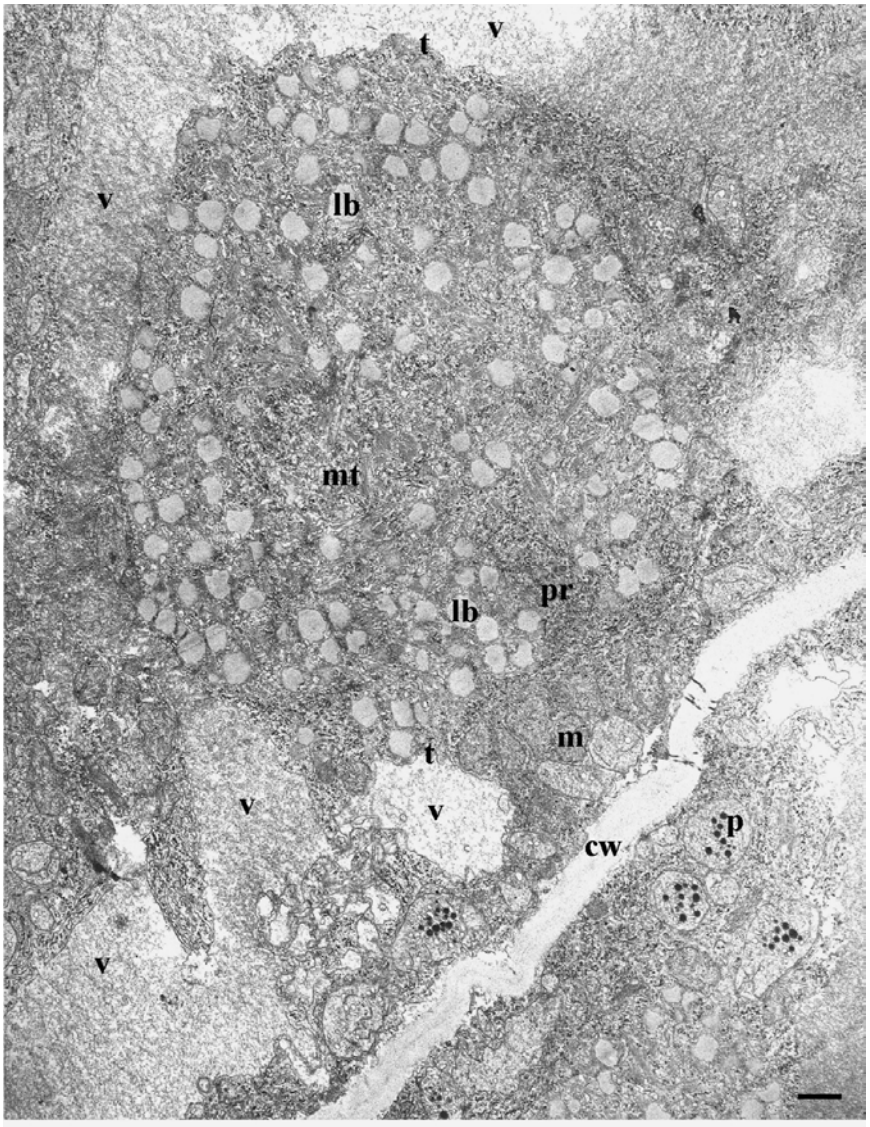

Fig. 2. *O. umbellatum* lipotubuloid. Electronogram from the ovary epidermis fixed in freshly prepared mixture of OsO_4 and glutaraldehyde; cw – cell wall, lb – lipid body, m – mitochondrion, mt – microtubules, p – plastid, pr – polyribosomes, t – tonoplast; v – vacuole; bar: 0.3 µm.

Elaioplasts are mainly filled with aggregates of osmiophilic granules identified as lipid bodies (Kwiatkowska, 1973a) and surrounded by a phospholipid half unit membrane characteristic only of these structures (Yatsu & Jacks 1972). Differences in the structure and thickness of lipid mono- and bilayer were revealed only after fixation of *O. umbellatum* epidermis in freshly prepared mixture of OsO_4 and glutaraldehyde (Kwiatkowska, 1973a).

Lipid bodies of plants are covered with proteins, oleosins, which prevent their merging during oil seed germination (Huang, 1996; Hsieh & Huang, 2004). It was shown that the amount of oleosins in a cell determined the size of lipid bodies (Siloto et al., 2006).

O. umbellatum lipid bodies are entwined by microtubules adhering to their surfaces and running in different directions forming a basket-like structure around them (Fig. 3).

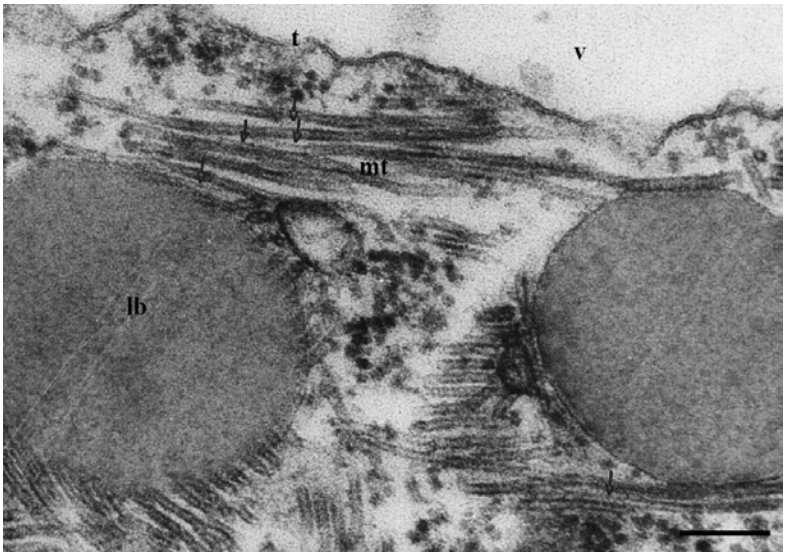

Fig. 3. *O. umbellatum* lipid bodies surrounded by a half unit membrane, entwined by microtubules; arrows indicate actin filaments; lb – lipid body, mt – microtubules, t – tonoplast, v – vacuole; bar: 0.1 µm (Kwiatkowska et al., 2005).

Beside lipid bodies and microtubules in this domain there are numerous ribosomes, ER cisternae and vesicles as well as few mitochondria, microbodies and Golgi structures and also autolytic vacuoles later during development.

In order to emphasis that the structures observed in *O. umbellatum* are not plastids a term lipotubuloids has been coined, it reflects the fact that they are rich in lipids and microtubules (Kwiatkowska, 1971a, 1971b, 1972a). Lipotubuloids were first reported in *O. umbellatum*, however recently they have also been identified in *Haemanthus albiflos* (Fig. 4) (Kwiatkowska et al., 2010), where they were previously described as "elaioplasts" by Politis (1911) and Tourte (1964, 1966). These structures are also present in *Vanilla planifolia, Funkia Sieboldiana* and *Athaea rosea* (Kwiatkowska et al., 2011a) in which they were previously called "elaioplasts" by Wakker (1888), Zimmermann (1893), Wałek-Czernecka & Kwiatkowska (1961), respectively.

All the above mentioned lipotubuloids contain the same organelle (Fig. 4) which implies that their presence there is not accidental but results from a functional relationship between them and lipid bodies. The main difference consists in stability of microtubules, those in *O. umbellatum* are markedly more stable, probably due to the polysaccharide layer covering them, than the others (Kwiatkowska, 1973b).

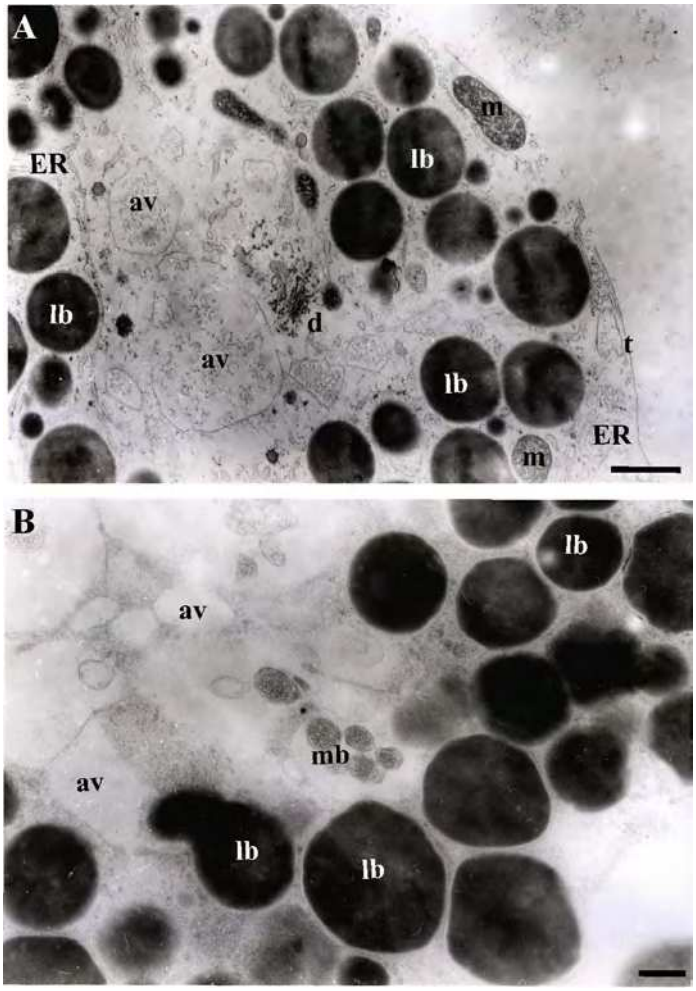

Fig. 4. Fragments of *Haemanthus albiflos* lipotubuloid with various organelles (A) and moreover with microbodies (B); av – autolytic vacuole, d – dictyosome, ER – endoplasmic reticulum, lb – lipid bodies, m – mitochondria, mb – microbodies, t – tonoplast; bars: 1 μm (A), 0.6 μm (B) (Kwiatkowska et al., 2010).

In the case of *H. albiflos* lipotubuloids become visible only after preincubation in 15 μm taxol with microtubule stabilizing buffer (100 mM PIPES, 1 mM $MgCl_2$, 5 mM EGTA) pH 7.2 for 2 h prior to fixation in the freshly prepared mixture of 2.5% glutaraldehyde and 1%

OsO_4, followed by postfixation in 1% OsO_4 (Fig. 5). The presence of tubulin around lipid bodies was confirmed by the immunogold method with the α anti-tubulin antibody (Kwiatkowska et al., 2010).

In the case of *V. planifolia, F. Sieboldiana and A. rosea* lipotubuloids were fixed according to the same procedure but without taxol preincubation. α anti-tubulin antibody application also gave positive results: gold grains were localized around lipid bodies of lipotubuloids in these plants.

Contrary to *O. umbellatum* lipotubuloids, microtubules in the other species were mostly observed in cross-sections near lipid bodies, no microtubules between lipid bodies, characteristic of *O. umbellatum*, were noted. This might be the result of poorer stability of these microtubules as varying stability of microtubules even in the same cell (Kwiatkowska et al., 2011c) is a well known phenomenon resulting, among others, from post-translational tubulin modifications (PTM) such as acetylation, tyrosination, polyglutamylation, polyglycylation, phosphorylation, palmitoylation (Verhey & Gaertig, 2007; Hammond et al., 2008; Fukushima et al., 2009). Nevertheless, we think that it is fully justified to call the structures present in *H. albiflos, V. planifolia, F. Sieboldiana A. rosea* lipotubuloids.

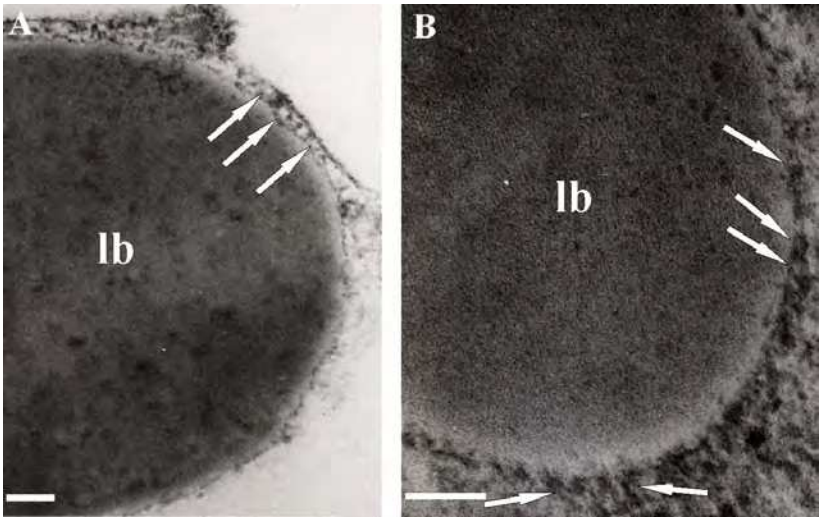

Fig. 5. *H. albiflos* lipid bodies entwined by microtubules (A,B) in cross and longitudinal sections (white arrows); lb – lipid bodies; bars: 0.1 µm (Kwiatkowska et al., 2010).

It is highly probable that among "elaioplasts" which are not plastids described in other species further lipotubuloids will be identified. Due to that old papers concerning "elaioplasts" are listed in literature and a table presenting families in which "elaioplasts" were described is included (Table. 1)

The main subject of our work have been lipid bodies and microtubules in *O. umbellatum* lipotubuloids which are most stable during fixation for EM. We returned to them after 30 years (during which we concentrated on *Chara* spermiogenesis) due to the development of new methods and new ideas concerning lipid bodies.

Family	References
Monocotyledoneae	
Dioscoreaceae	Politis, 1911
Iridaceae	Politis, 1911; Faull, 1935
Liliaceae	Zimmermann, 1893; Raciborski, 1895; Politis, 1911; Guillermond, 1922; Wóycicki, 1929; Weber, 1955; Thaler, 1956; Tourte, 1964, 1966; Kwiatkowska, 1966
Orchidaceae	Wakker, 1888; Zimmermann, 1893; Raciborski, 1895; Politis, 1911; Faull, 1935
Dicotyledoneae	
Anacardiaceae	Guttenberg, 1907 in Linsbauer, 1930
Campanulaceae	Górska-Brylass, 1962
Compositae	Beer, 1909
Cucurbitaceae	Riss, 1918
Gentianaceae	Kwiatkowska, 1959, 1961
Malvaceae	Politis, 1911; Luxenburgowa, 1928; Wałek-Czernecka & Kwiatkowska, 1961
Orobanchaceae	Bidermann, 1920
Pirolaceae	Bidermann, 1920

Table 1. Examples of plant family of mono- and dicotyledonous class in which "elaioplasts" have been identified.

2. Lipid bodies – Biogenesis and lipid synthesis

Lipid bodies (lipid droplets, oil bodies, spherosomes) are organelles commonly present in plants, animals and some Prokaryote. For many years they were treated only as the source of energy, however during the last decade they were shown to play a role in lipid homeostasis and to contain numerous proteins involved in signal transductions as well as proteins transiently stored or degraded (Martin & Parton, 2005; Cermelli et al., 2006; Welte, 2007; Fujimoto et al., 2008). Moreover, they became the focus of interest because disturbances in their functioning cause many serious dieses in humans and animals such as obesity, diabetes, atherosclerosis, cardiovascular disease, allergic inflammation, arthritis, mycobacterial infections, bacterial sepsis, acute respiratory distress syndrome (Bozza et al., 2009). Lipid bodies are also important for plant productivity and biotechnology (Baud & Lepiniec, 2010; Lu et al., 2011).

Cytological studies with the use of light and electron microscopy combined with autoradiography and immunocytochemistry might significantly elucidate lipid bodies biogenesis and function as well as their interactions with other cell organelles. Lipotubuloids which contain an enormous number of lipid bodies and microtubules are especially suitable experimental material.

Biogenesis of lipid bodies is one of cytological controversies. Some scientists believe that they are formed in cytoplasm as naked droplets (Lung & Weselake, 2006) which are later surrounded by a half unit membrane, others suggest that both ER membranes take part in their biogenesis (Robenek et al., 2011). However, the most common hypothesis is based on

old ultrastructural observations (Frey-Wyssling et al., 1963) of plant cells which indicate that ER contributes to lipid bodies formation resulting from the accumulation of lipids between leaflets of a phospholipid bilayer (Fujimoto et al., 2008; Ducharme & Bickel, 2008; Guo et al., 2009; Ohsaki et al., 2009).

In *O. umbellatum* lipotubuloids lipid bodies are formed in the latter way. This process can be observed in the lipotubuloids enlarging due to *de novo* formation of lipid bodies during intensive ovary epidermis growth (Kwiatkowska, 1971b). Ovary epidermis cells are characterized by intensive growth without mitotic divisions leading to their 30-fold (by 3000%) enlargement (Fig. 6). It is also closely correlated with lipotubuloid growth (correlation coefficient 0.98) which indicates the important role played by these structures in cells (Kwiatkowska et al., in prep.).

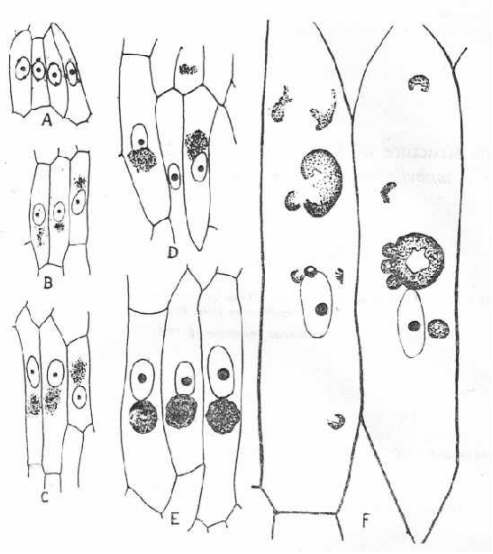

Fig. 6. *O. umbellatum* ovary epidermis and lipotubuloid development (Kwiatkowska, 1971b)

Forming lipid bodies first appear as a gap (Fig. 7A) then change into a lens-like structure grey in color (Fig. 7B,C) . Later it enlarges and becomes greatly osmiophilic, due to that the phospholipid half unit membrane which surrounds it is poorly visible as a thinner and lighter structure than a bilayer membrane (Fig. 7E-G). It appears very clearly later on around mature spherical lipid bodies which are filled with less osmiophilic and more homogenic substance (Fig. 7I,J) as well as in structures which are transient forms between forming and mature lipid bodies (Fig. 7H); these transient forms are connected with ER. However, mature lipid bodies are not linked with ER directly, but through microtubules which are adjacent to ER at one end and to lipid bodies at the other.

The immunogold technique revealed single or aggregated gold grains indicating the presence of diacylglicerol acyltransferase 1 and 2 (DGAT1 and DGAT2) in the specific rough ER regions and which means that these enzymes are synthesized in ER bound ribosomes (Fig. 8) (Kwiatkowska et al., 2011b).

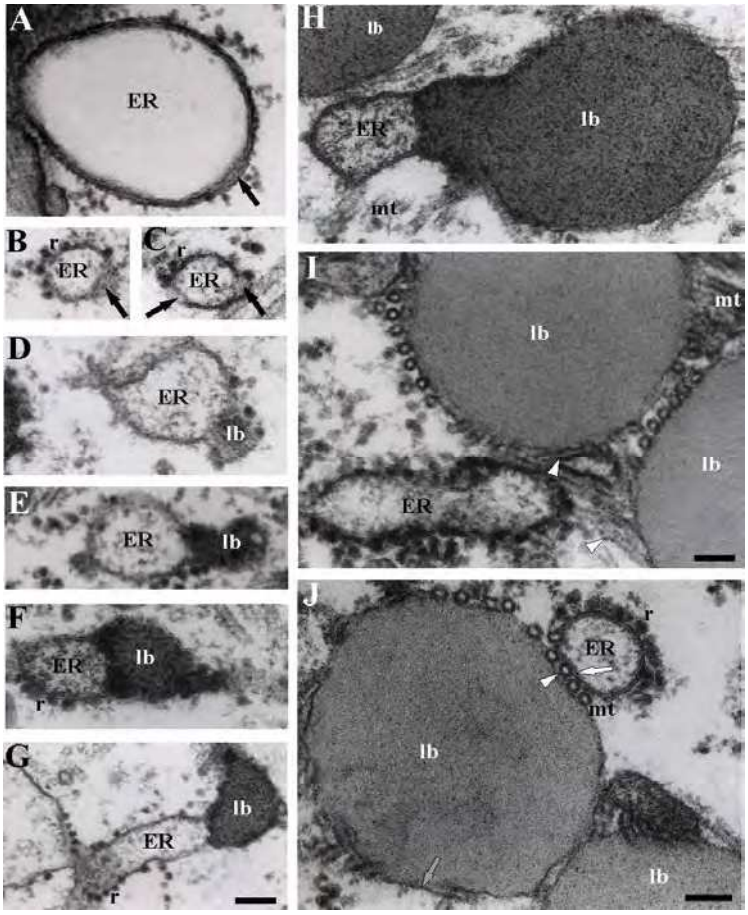

Fig. 7. Biogenesis of lipid bodies in *O. umbellatum* lipotubuloids; A - early step of lens-like structure formation (arrow); B,C - accumulation of electron-clear substance between two leaflets of ER membrane (arrows); D-H - enlargement of nascent lipid body; I,J - matured lipid bodies. Connection between lipid bodies and ER by microtubules (white arrow heads); ER - endoplasmic reticulum, lb - lipid body, mt – microtubules, r – ribosomes, white arrow - ER membrane bilayer, gray arrow - lipid body monolayer; bars: 50 nm (A-F, H,I), 100 nm (G), 50 nm (J), (Kwiatkowska et al., 2011b).

More gold grains indicating DGAT1 and DGAT2 were observed in characteristic swollen regions surrounded by thinner membranes at the ends or sides of ER cisternae (Fig. 9).

These pictures seem to present lipid bodies *in statu nascendi*. They suggest that during their formation enzymes are transported from ER to the surface of lipid bodies. These pictures correspond to gold grains localization indicating DGAT1 and DGAT2 situated at the outside zone of mature lipid bodies (Fig. 10). Thus it seems possible that the last stage of lipid synthesis, transformation of DAG into TAG, can take place in mature lipid bodies similarly as in adipocytes and COS7 fibroblast (Kuerschner et al., 2008).

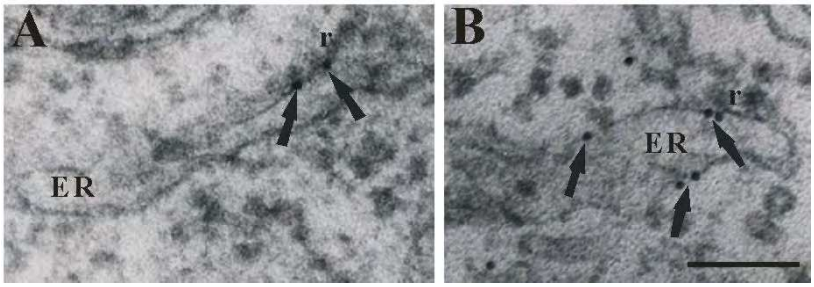

Fig. 8. 10 nm gold grains (arrows) indicating DGAT2 presence near ribosomes on ER in *O. umbellatum* lipotubuloid (A,B); ER – endoplasmic reticulum, r – ribosomes; bar: 100 nm, (Kwiatkowska et al., 2011b).

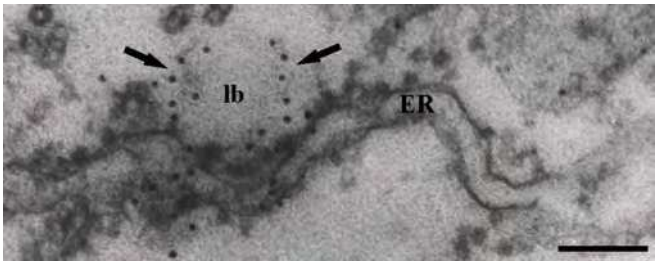

Fig. 9. Swelling ER cisternae surrounded with a membrane thinner that ER bilayer with gold grains indicating DGAT2 presence (arrows) in *O. umbellatum* lipotubuloid; ER – endoplasmic reticulum, lb – lipid body; bar: 100 nm, (Kwiatkowska et al., 2011b).

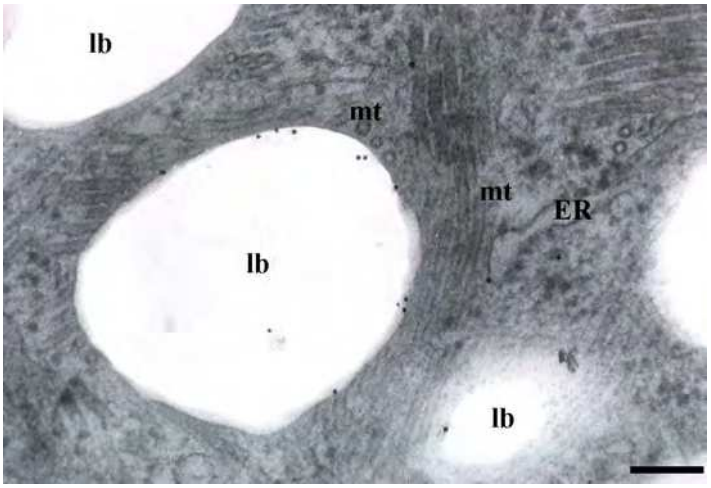

Fig. 10. Mature lipid bodies in *O. umbellatum* lipotubuloid; 10 nm gold grains indicating DGAT2 presence; sections after hydrogen peroxide treatment to remove osmium; ER – endoplasmic reticulum, lb – lipid body, mt - microtubules; bar: 100 nm (Kwiatkowska et al., 2011b).

Buers et al. (2009) also observed that in macrophages freeze-fracture replica immunogold method revealed DGAT2 on lipid bodies surfaces. To the best of our knowledge our results of immunogold research revealing DGAT1 and DGAT2 on the surfaces of lipid bodies in *O. umbellatum* lipotubuloids are the only such results to date in plants. In the case of *O. umbellatum* lipotubuloids autoradiographic studies with ^{3}H-palmitic acid at the ultrastructural level (Kwiatkowska et al., 2011b) directly prove that lipid synthesis does take place at the outside of mature lipid bodies (Fig. 11B-J).

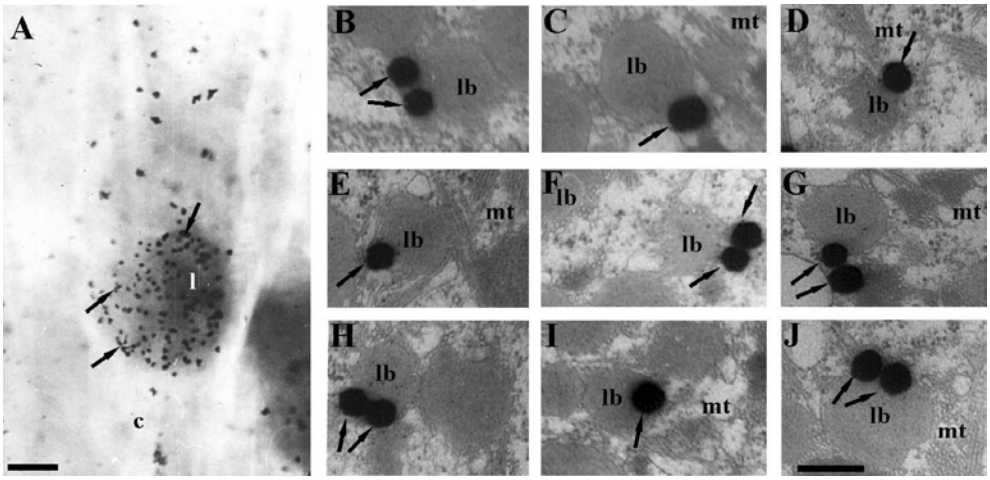

Fig. 11. *O. umbellatum* lipotubuloid autoradiograms after 2 h ^{3}H-palmitic acid incorporation; A - light microscope picture of a lipotubuloid labeled with silver grains (arrows); B-J – electronograms of silver grains localized at the half unit membrane/core border of lipid bodies (arrows); c – cytoplasm, l – lipotubuloid, lb – lipid bodies, mt – microtubules; bars: 10 µm (A), 0.2 µm (B-J), (Kwiatkowska et al., in prep.).

Autoradiographic labeling disappears after lipid extraction with lipid solvents which shows that this precursor becomes incorporated into lipids. It is most clearly seen on light microscope pictures of autoradiograms where lipotubuloids are literally sprinkled with autoradiographic grains (Fig. 11A) which disappear completely after lipid extraction. These pictures bring to the mind the term intuitively proposed by Wakker (1888) – "elaioplasts" which means - producing fat.

Silver grains and gold grains resulting from autoradiographic and immunogold reactions, respectively are co-localized at the surface of mature lipid bodies at the half unit membrane/core border which clearly indicate their contribution to lipid synthesis contrary to lipid bodies *in statu nascendi* in which lipid synthesis is connected directly with ER (see above).

Recent studies with immunogold reaction and 20 nm colloidal gold coupled with anti-lipase antibodies have shown the presence of lipase near lipid bodies surfaces (Fig. 12) (Kwiatkowska et al., in prep.). Similar lipase localization in *Ricinus communis* was observed by Eastmond (2004) with the use of immunogold method. Lipase is probably responsible for the disappearance of selective labeling of lipotubuloids incubated for 2 h in ^{3}H-palmitic acid and postincubated for 6 h in the non-radioactive medium (Kwiatkowska, 2004). The mature lipid bodies are approximately of the same size (0.1-0.4 µm) during ovary development in

spite of active lipid synthesis due to the dynamic balance between lipid synthesis and lipolysis, however the number of lipid bodies in lipotubuloids which grow significantly, increases (Kwiatkowska et al., 2007). Thus the fact that lipid bodies do not enlarge cannot be treated as an unequivocal proof that lipid synthesis does not occur in them.

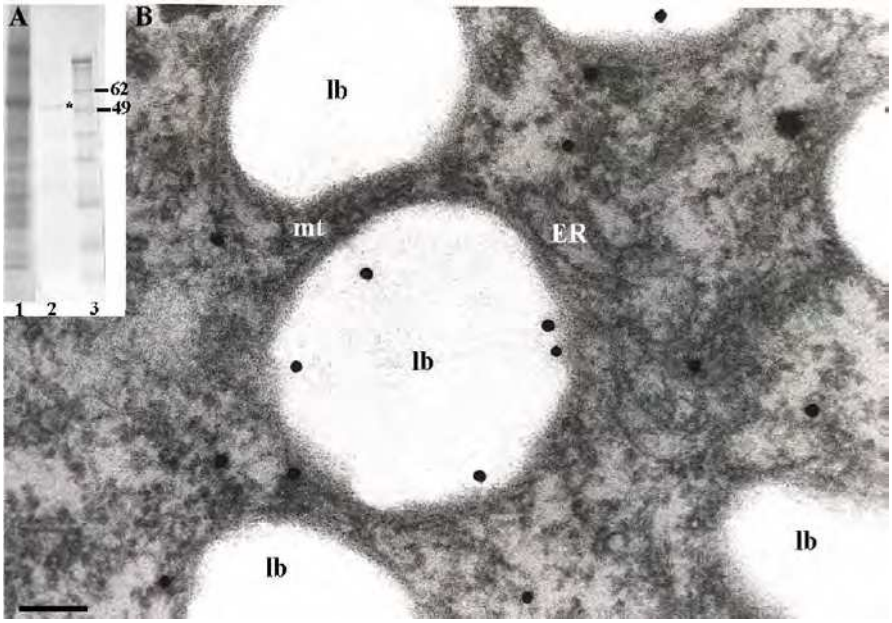

Fig. 12. Immunodetection of lipase in *O. umbellatum* ovary epidermis; A - Western blot analysis; line 1 – SDS-PAGE electrophoretic separation of the ovary epidermis extract; line 2 – Western blotting of the ovary epidermis extract probed with the anti-human lipase antibody; line 3 – molecular mass standards and their weights in kDa; B – lipid bodies with 20 nm gold grains indicating lipase presence; ER – endoplasmic reticulum, lb – lipid bodies, mt – microtubules; bar: 100 nm (Kwiatkowska et al., in prep.).

3. Microtubules and lipotubuloid movement

Microtubules as cytoskeleton elements are mostly involved in movement. Lipotubuloids are characterized with very specific and dynamic movement (Kwiatkowska, 1972a). It consists of sometimes very dynamic rotation with varying speed, direction and axis as well as progressive movement (Fig. 13). Lipotubuloid progressive movement depends on cyclosis, it stops when cytoplasm movement is arrested with dinitrophenol (DNP) which blocks ATP synthesis. Rotation, however, persists for some time after DNP application which suggests that it is autonomous, independent of cytoplasm movement. Also the fact that peripheral speed of the rotating lipotubuloid reaches 31.4 μm/s and is 6.2 times faster than the maximum speed of cytoplasmic motion (Kwiatkowska, 1972a) proves the above suggestion.

The question arises what is the connection between microtubules and lipotubuloid movement. One thing seems certain, microtubules which join lipid bodies create one structure able to move as a unity despite not having its own membrane.

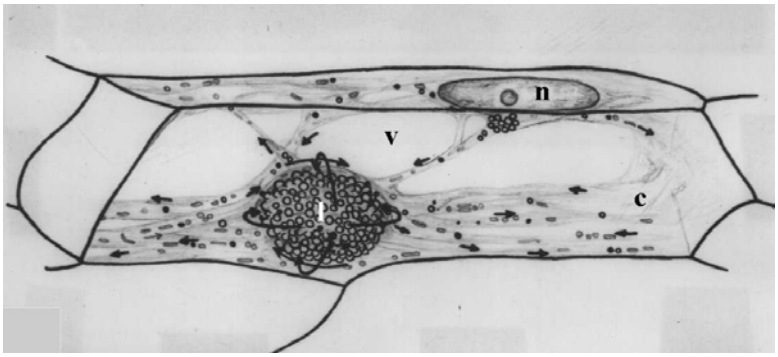

Fig. 13. A scheme of a lipotubuloid in an epidermal cell of *O. umbellatum* stipule which has turned around (several times) within 10-12 s, changing its direction and axis without a change in cellular location; c – cytoplasm, l – lipotubuloid, n – nucleus, v – vacuole, long arrows – the direction of lipotubuloid rotation, short arrows – direction of cytoplasm movement (Kwiatkowska et al., 2009).

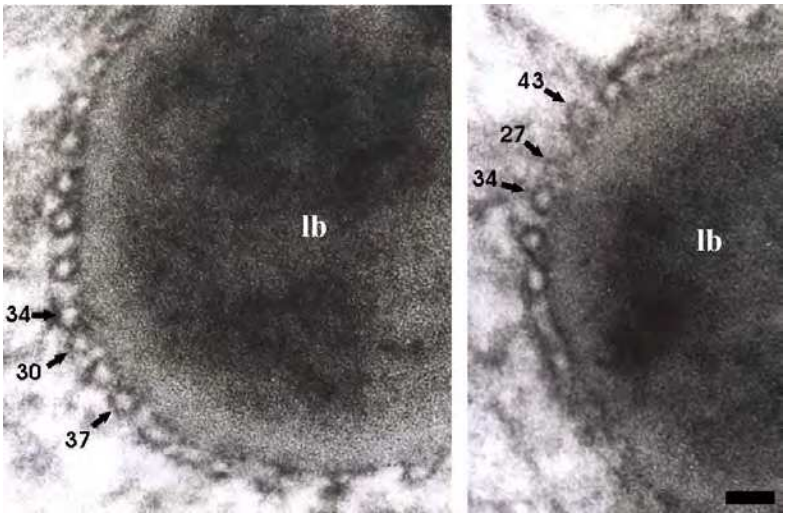

Fig. 14. Fragments of *O. umbellatum* lipid body surrounded with microtubules differing in width; lb – lipid bodies, numbers denote microtubule diameters in nm; bar: 50 nm (Kwiatkowska et al.,2009).

Moreover, it turned out that microtubules of lipotubuloids differ in diameter (Fig. 14), two populations were revealed: wide (43-58 nm) and narrow (24-39 nm). In the lipotubuloids in the ovary epidermis which move less dynamically the number of wide microtubules is smaller (Kwiatkowska et al., 2006) than in the fast-moving lipotubuloids present in stipule (Kwiatkowska et al., 2009). The microtubule diameter depends on the varying number of protofilaments which form them, the bigger the number the greater the diameter (Fig. 15A). Regardless of the above correlation, analyses of microtubule cross-sections revealed that with the same number of filaments (e.g. 10, 11, 12) two microtubule populations were

observed both in the control and after DNP removal while under DNP influence only one middle-sized population was present (Fig. 15B). It was also shown that the number of microtubule protofilaments in the control, under DNP influence and after its removal was stable. Analysing wall structure of microtubules varying in size but formed from the same number of protofilaments it was revealed that these changes depended on varying tubulin monomer sizes as well as different distances between them (Fig. 16).

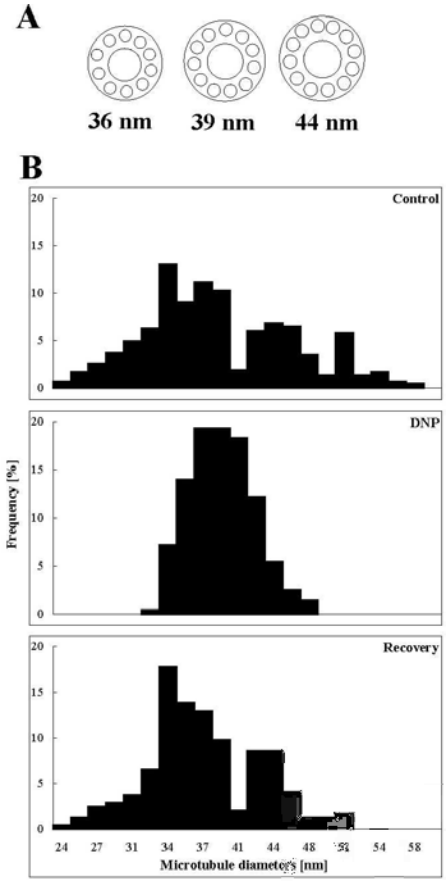

Fig. 15. A – A scheme of microtubules whose width depends on the number of filaments; B - a graph presenting two microtubule populations in the control and after DNP removal, and one microtubule population after DNP application (Kwiatkowska et al., 2009).

In the wider microtubules both these parameters are greater and *vice versa* (Kwiatkowska et al., 2009). All the above proves flexibility of microtubules *in vivo* depending on their functional status. The fixation method used by us makes it possible to "freeze" the microtubule structure in the *in vivo* state due to quick OsO_4 penetration as was shown by Omoto & Kung (1980). Other authors observed microtubule flexibility *in vitro* (Nogales et al., 1999; Li et al., 2002; Pampaloni & Florin, 2008).

In *O. umbellatum* lipotubuloids, apart from microtubules, there are also short actin filaments which were observed in ultrastructural pictures (Fig. 3) (Kwiatkowska et al., 2005). A hypothesis has been put forward that interaction of actin filaments with microtubules may determine the transformation of wide microtubules into narrow ones and *vice versa* (Kwiatkowska et al., 2009). Microtubules of varying sizes were observed *in vitro* as a result of tubulin co-sedimentation in the presence of actin and myosin Va (Cao et al., 2004).

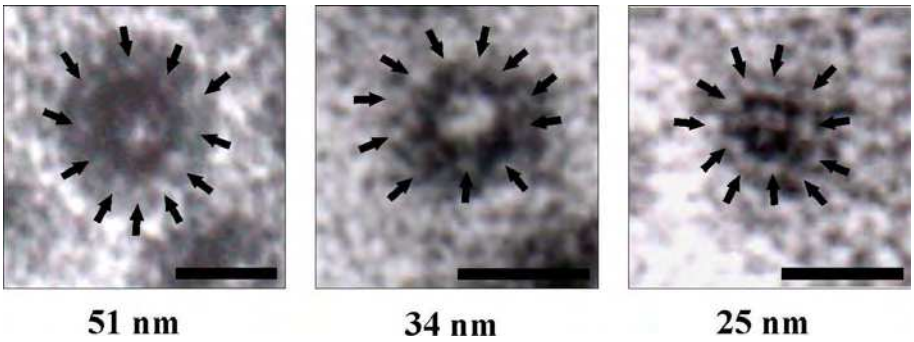

Fig. 16. Microtubules different in size consisting of the same number of protofilaments; visible differences in monomer sizes (arrows) and in distances between them; bars: 25 nm (Kwiatkowska et al., 2009).

We also suppose that changes in lipotubuloid microtubule sizes might the driving force of their autonomic rotation.

It is worth stressing that the rotary-progressive lipotubuloid movement plays an important role in substance exchange between them and a cell. This is supported by the results concerning the involvement of intracellular motion in spreading various substances in a cell (Verchot-Lubicz & Goldstein, 2010).

4. Microtubules and lipid synthesis in mature lipid bodies

Autoradiographic ultrastructural studies with the use of ^{3}H-palmitic acid showed that incorporation of this precursor into lipids took place at the site of microtubule adhesion to the half unit membrane (Fig. 11B-J) thus a hypothesis has been put forward that these two structures cooperate in lipid synthesis (Kwiatkowska, 2004). It is supported by the fact that after short radioactive incubation microtubules are labeled first while lipid bodies as late as after 2 h (Kwiatkowska et al., 2011b). Thus it can be assumed that microtubules take up lipid precursors, including radioactive particles, and transmit them to the incorporation site.

The immunogold labeling showed that gold grains, indicating the presence of two enzymes: DGAT1 and DGAT2 as well as of phospholipase D also indispensable for lipid synthesis (Andersson et al., 2006), were present at microtubule walls (Fig. 17, 18) (Kwiatkowska et al., 2011b). The results concerning phospholipase D correspond to these of the co-sedimentation assay in which microtubules decorated with phospholipase D were observed (Gardiner et al., 2001; Gardiner et al., 2003; Dhonukshe et al., 2003).

On the basis of autoradiography and immunogold labeling a hypothesis may be put forward that microtubules take an active part in lipid synthesis as transmitters of precursors

and enzymes to their respective destinations. Valuable proofs of microtubule involvement in lipid synthesis come from research with their inhibitors. Pacheco et al. (2007) observed that colchicine or taxol similarly blocked lipid body formation, being the reaction to inflammation, in mouse monocytes.

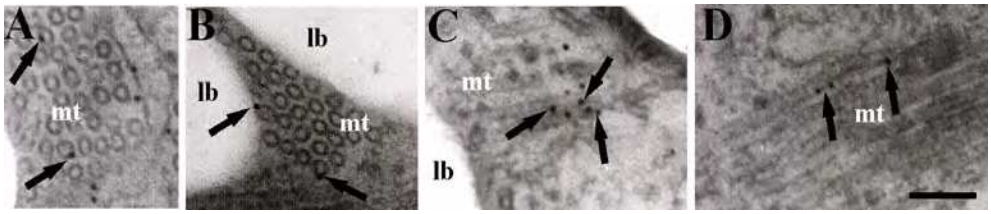

Fig. 17. *O. umbellatum* microtubules in cross (A,B) and longitudinal sections (C,D) with 10 nm gold grains at the surface indicating the presence of DGAT2 (arrows); lb – lipid bodies, mt – microtubules; bar: 100 nm (Kwiatkowska et al., 2011b).

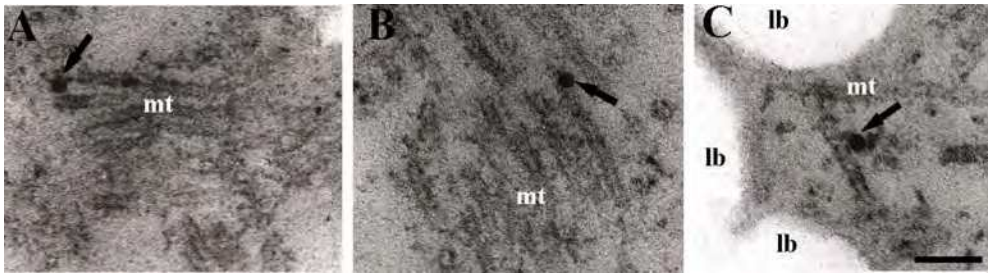

Fig. 18. *O. umbellatum* microtubules in longitudinal sections (A-C) with 20 nm gold grains at the surface indicating the presence of phospholipase D (arrows); lb – lipid bodies, mt – microtubules; bar: 100 nm (Kwiatkowska et al., 2011b).

Recently a similar experiment has been carried out on *O. umbellatum* lipotubuloids, which were incubated for 6 h in propyzamide which is known to induce microtubule degradation (Nakamura et al., 2004; Sedbrook et al., 2004). It turned out that it induced partial microtubule disintegration and changed their structure by forming on their walls dark deposits visible in EM. Most probably they make microtubules lose their transmitting abilities, this leads to the blockade of new lipid synthesis which is reflected by inhibited incorporation of ^{3}H-palmitic acid into lipotubuloids. This seems to be the decisive proof of microtubule role in lipid synthesis (Kwiatkowska et al., 2011b).

We believe that in the case of lipotubuloids of other plants they may also function as transmitters of different substances to lipid bodies, however this issue needs further research.

Up till now there has been no research proving a similar role of microtubules in lipid synthesis in other organisms, although microtubules surrounding single lipid bodies, not organized into lipotubuloids, were observed in *Marchantia paleacea* (Galatis et al., 1978), *Lactuca sativa* (Smith, 1991) and in red alga *Gelidium robustum* (Delivopoulos, 2003). Small sizes and great lability of microtubules probably make observation of more common structural and functional correlation between microtubules and lipid bodies impossible.

As it was mentioned earlier lipotubuloids are rich in ribosomes and rough ER in the form of cisternae and vesicles. No detailed research concerning their functioning was conducted but it easily visible that ribosomes are actively involved in translation as they form numerous polysomes (Fig. 2). Since formation of new lipid bodies and lipid synthesis involve a whole enzymatic system and many regulatory factors active ER and ribosomes in lipotubuloids are indispensable.

Other structures such as mitochondria, microbodies surrounded with single lipid bi-layers (glyoxysomes and peroxysomes) as well as Golgi structures are less numerous and have not been studied in detail so far. It is believed that lipid bodies cooperate with other organelles as "gregarious" organelles (Goodman, 2008). Mitochondria and microbodies are in close contact with lipid bodies. Due to synaptic connections (Binns et al., 2006) there is correlation between release and oxidation of lipid acids resulting from lipolysis (Goodman, 2008; Fujimoto et al., 2008; Guo et al., 2009). Moreover, mitochondria may supply energy and NADPH which make lipid synthesis and lipid bodies biogenesis possible (Walter & Farese, 2009).

Golgi structures which are very dynamic organelles may be involved in microtubule polymerization as many authors believe (Chabin-Brion et al., 2001; Efimov et al., 2007; Kodani & Sutterlin, 2009). On the other hand, COPI (Beller et al., 2008) and COPII complexes (Soni et al., 2009) produced by Golgi structures are evolutionary conserved regulators of lipid homeostasis.

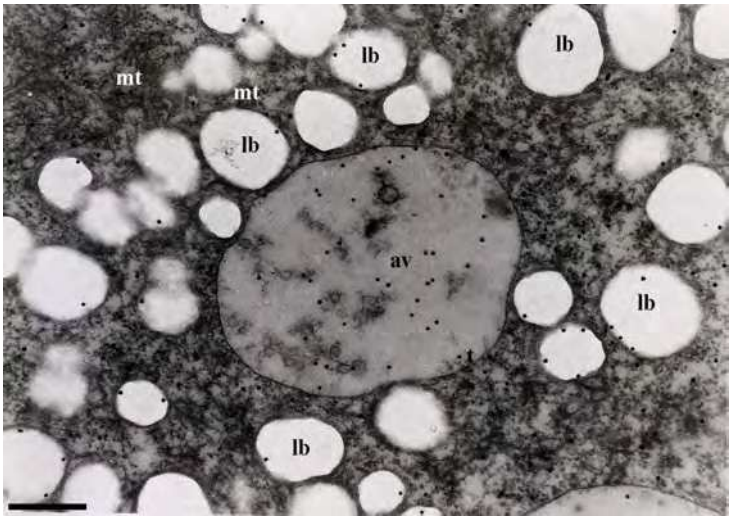

Fig. 19. An autolytic vacuole (av) after immunogold reaction for lipase in *O. umbellatum* lipotubuloid; lb – lipid bodies, mt – microtubules, t – tonoplast; bar: 500 nm (Kwiatkowska et al., in prep.).

At the final stage of lipotubuloid development autolytic vacuoles appear prior to microtubule disappearance leading to disintegration of lipotubuloids into separate lipid bodies (Fig. 6). These vacuoles are surrounded with a tonoplast and contain fragments of membranes and cell structures which is characteristic of autolytic vacuoles. Immunogold labeling revealed in them numerous gold grains indicating the presence of lipase (Fig. 19)

(Kwiatkowska et al., in prep.). The above observation supports earlier results of cytochemical assays revealing lipase and acid phosphatase in lipotubuloids (Kwiatkowska, 1971b). Triggering of autolysis during dynamic metabolism was also observed in animal cells (Dong & Czaja, 2011).

5. Lipotubuloids and cuticle synthesis

It is known that cuticle are produced by epidermis cells which may dedicated more than 50% of their metabolites to this structure (Suh et al., 2005). In the case of *O. umbellatum* lipotubuloids incubated for 2 h in ^{3}H-palmitic acid and postincubated for 6 h in the non-radioactive medium autoradiographic grains first assembled over lipotubuloids become scattered all over a cell (tangential section) (Fig. 20).

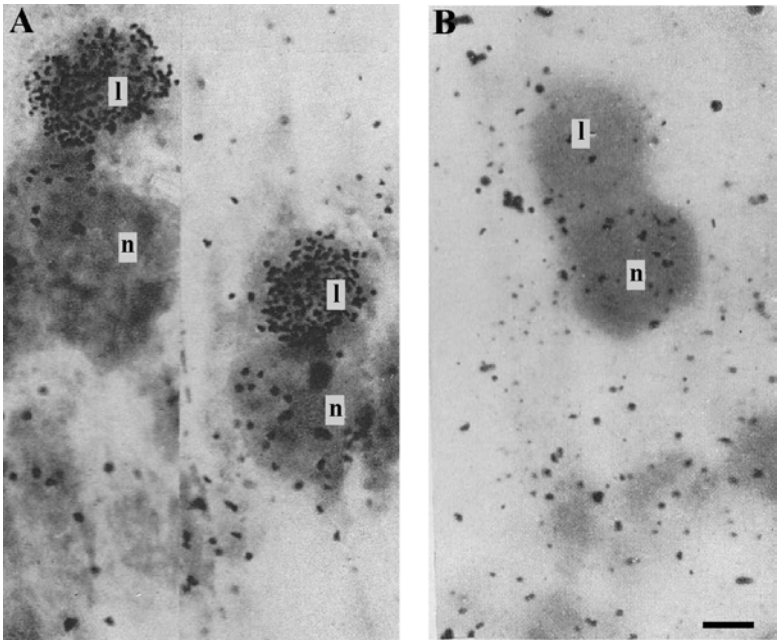

Fig. 20. *O. umbellatum* light microscope autoradiograms; A – silver grains aggregated over lipotubuloids after 2 h incubation in ^{3}H-palmitic acid; B – scattered silver grains after 2 h incubation in ^{3}H-palmitic acid followed by 6 h postincubation in non-radioactive medium - cells in tangential section; l – lipotubuloid, n – nucleus; bar: 10 µm (Kwiatkowska, 1972b).

After postincubation the number of autoradiographic grains falls by about 70% which means that a great amount of lipids was metabolized during 6 h. The remaining autoradiographic grains do not disappear after lipid extraction but their number drops (Tab. 2). Cell radioactive parts insoluble in solvents are visible on the epidermis cross section at the site corresponding to a cuticular layer from Bird's (2008) cuticule scheme (Fig. 21). Thus it seems very probable that there are cutins insoluble in lipid solvents. This part of scattered autoradiographic grains which disappeared after lipid extraction may correspond to waxes which are easily dissolved in organic solvents (Kwiatkowska et al., in prep.). A hypothesis

has been put forward that about 30% of lipids from lipotubuloids turn into cuticle. A question arises if this transformation takes place in lipotubuloids or in other cell compartments and the lipids from lipotubuloids are only building blocks. This problem is worth elucidating since many recent results indicate its great importance with regard to economical and biotechnological issues (Heredia et al., 2009; Dominguez et al., 2011). Cutin is the most ubiquitous biopolymer in biosphere (Heredia, 2003). We are planning to take up this question soon.

Labeled area	Incubation in ^{3}H-palmitic acid	Incubation in ^{3}H-palmitic acid after lipid extraction	Incubation in ^{3}H-palmitic acid and 6 h post-incubation in non-radioactive medium	Incubation in ^{3}H-palmitic acid and 6 h post-incubation in non-radioactive medium after lipid extraction
Whole Cell	294 ± 14	4 ± 0.8	102 ± 5	19 ± 0.9
Lipotubuloid	240 ± 9	1 ± 0.5	12 ± 0.4	3 ± 0.8
The rest of cytoplasm and nucleus	54 ± 1.8	3 ± 0.9	90 ± 11	16 ± 1.1

Table 2. Number of silver grains over particular compartments of *O. umbellatum* ovary epidermis cell after incubation in ^{3}H-palmitic acid under different experimental conditions ± SE.

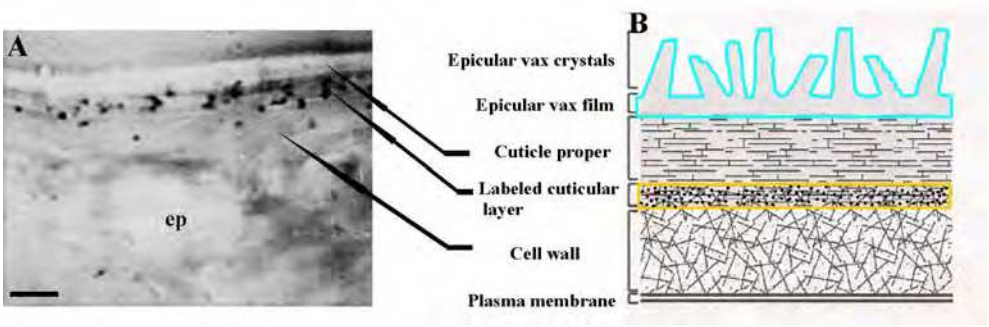

Fig. 21. A - Cross-section of *O. umbellatum* ovary epidermis (ep); autoradiogram after 2 h incubation in ^{3}H-palmitic acid, 6 h postincubation in the non-radioactive medium and after extraction in the lipid solvent; silver grains localized in the cuticular layer (Kwiatkowska et al., in prep.); B – a scheme of cuticle according to Bird (2008 - modified); bar: 5 µm.

6. Conclusions

Lipotubuloids are a very specific, dynamic, complicated set of metabolically active (although seemingly static) lipid bodies containing DGAT and lipase which cooperate with microtubules and other organelles. A lipotubuloid is somewhat independent in a cell which is reflected by its capability for autonomous rotary movement, however, it is closely correlated with the development of the ovary epidermis and cuticle synthesis during seed

formation in a fruit. Studies concerning these structures may further elucidate lipid metabolism and their functional relation with a cell and its organelles.

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8. References

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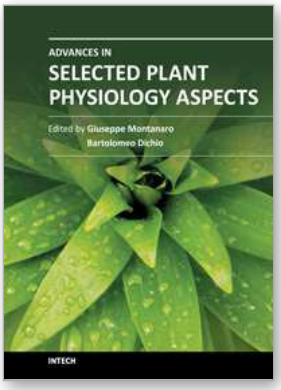

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The book provides general principles and new insights of some plant physiology aspects covering abiotic stress, plant water relations, mineral nutrition and reproduction. Plant response to reduced water availability and other abiotic stress (e.g. metals) have been analysed through changes in water absorption and transport mechanisms, as well as by molecular and genetic approach. A relatively new aspects of fruit nutrition are presented in order to provide the basis for the improvement of some fruit quality traits. The involvement of hormones, nutritional and proteomic plant profiles together with some structure/function of sexual components have also been addressed. Written by leading scientists from around the world it may serve as source of methods, theories, ideas and tools for students, researchers and experts in that areas of plant physiology.

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