Origin and structure of Ubisch bodies in *Pinus sylvestris*

JOHN R. ROWLEY, BJÖRN WALLIS

Botany Department, University of Stockholm, S-106 91 Stockholm, Sweden

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ABSTRACT

In *Pinus sylvestris* Ubisch bodies are produced repeatedly, and each crop is formed at a distinct phase in the secretory cycles of tapetal cells. While each production has a Ubisch body wall similar to the then current state of the exine with regard to thickening and ornamentation, the survivors of previous productions do not change. Examples of all the structurally different Ubisch body wall forms can be seen when terminally, at the time of pollen shedding, the relict Ubisch bodies become spatially concentrated on the minimal surface area of the senescent cells of the tapetum. In angiosperms after one or a few periods of initiation Ubisch bodies may remain in association with the surface of tapetal cells where the Ubisch body wall undergoes changes like those of the maturing pollen exine. We conclude that as a consequence of Ubisch body detachment from the plasma membrane of tapetal cells there is in *Pinus sylvestris* no updated information for modification of the wall and the Ubisch body wall remains static.

Key words: Ubisch bodies, orbicules, tapetum, morphogenesis, sporopollenin, receptors, glycolyx

INTRODUCTION

Ubisch bodies have a long history of observation and from the earliest publication by Rosanoff (1865) they were recognized to be associated with the tapetum and to have a composition like the exine of pollen grains. They have been given many names but the two most used are **orbicules** (Erdtman et al. 1961) and Ubisch bodies (Kosmath 1927). Kosmath's suggestion was in honor of Professor Ubisch for her contribution

to information on the occurrence and character of these intriguing structures. There are many reviews covering various aspects of Ubisch body structure and development (Rowley 1962, 1963, Heslop-Harrison 1963, Carniel 1963, 1971, Roland 1967, Risueño et al. 1969, Christensen et al. 1972, Rowley and Skvarla 1974, Rodriguez-Garcia 1978, Reznickova and Willemse 1980, Audran 1981, El-Ghazaly and Jensen 1986). It was seen from a comparison of Ubisch bodies in *Poa*, *Degeneria* and *Cryptomeria* (*Pinaceae*) that their ornamentation could be as specific as that on the surface of the pollen grains (Rowley et al. 1959); implicating the involvement of plasma membrane receptors, similar to the receptors for the exine, for sporopollenin accumulation in these bodies. Rowley and Erdtman (1967), Risueño et al. (1969), and Horner and Lersten (1971) observed sites of continuity between the plasma membrane of tapetal cells and the membrane around the core globule ("pro-orbicule", "pro-Ubisch body", "lipid-like cores of orbicules") of Ubisch bodies. There is little information concerning formation of the core globule, its release from the cytoplasm, and the way it becomes coated by plasma membrane and its glycocalyx. We have given special attention to those points in our studies of early stages in formation of Ubisch bodies.

Our observations of Ubisch bodies are part of a more comprehensive study of development of microsporangia in *Pinus sylvestris* starting with a stage before meiosis in microspore mother cells. We are interested in the mechanisms whereby the tapetal cells produce and excrete material to be utilized in the formation of the sporopollenin of microspore walls, walls of Ubisch bodies, and other coatings present in the sporangium. We have made collections several times each day during the period of growth and development of microsporangia in order to ascertain the degree of coordination of tapetal cell cycles with stages of meiosis and subsequent events in microspores.

The collections were made over nine years and these annual replicates were crucial for our interpretation of the production of Ubisch bodies in *P. sylvestris*.

MATERIALS AND METHODS

Male strobili of *Pinus sylvestris* were sampled from mid April until dehiscence of microsporangia. Collecting was alternated between eight trees located on or near the university campus and an island in the archipelago of Stockholm.

Wafers 0.5 mm thick were cut from strobili, and immersed in one of the fixatives in use on the day of the fixation. A wafer was then divided

by pulling into three sectors of two to four microsporangia each. These were transferred to one of the fixatives described in Walles and Rowley Rowley (1982) and Rowley and Walles (1985a, b). Illustrations for this report draw upon material prepared from five of these fixation mixtures. They are briefly characterized here and numbered for notation in the figure legends.

1. The Karnowsky mixture of 2.5% glutaraldehyde (GA) and 7.5% paraformaldehyde in 0.06 M phosphate buffer (pH 7.2) used with or without dilution. Some of these fixations included 1% caffeine, 2% tannic acid (GURR, mole. wt. ca 1,200 or a low molecular weight preparation from Mallinckrodt Inc. St. Louis, MO: No. AR-1764).

2. GA (1%) in 0.025 M sodium cacodylate-HCl buffer (pH 7.4).

3. GA (1%) in 0.075 or 0.05 M s-collidine buffer (pH 7.4).

4. Luft's ruthenium red method as used by Latta et al. (1975). Small sectors of strobili were kept in 1% GA in 0.02 M sodium cacodylate buffer (pH 7.2-7.4, 20°C) for 3-10 days. The sectors were then transferred to 2% GA in 0.02 M buffer plus 500 ppm ruthenium red (pH 7.4, 20°C, 1 h), rinsed in three changes of the buffer, and immersed in a mixture of 2% OsO₄ in 0.02 M buffer plus 500 ppm ruthenium red (pH 7.4, 20°C, 3h).

5. Hepler's potassium ferrocyanate method. Sectors of strobili were fixed in 2% GA in 0.5 M cacodylate buffer (pH 7.4) containing 5 mM CaCl₂, washed in buffer, post-fixed in a mixture of 1% OsO₄ with 0.8% K₃Fe(CN)₆, and poststained enblock with 2% uranyl acetate (Hepler 1981).

RESULTS

INITIATION OF UBISCH BODIES

In *P. sylvestris* the core globule of an Ubisch body originates from a manifold-like structure, into which cisternae of rough endoplasmic reticulum (rER) open and deposit material (Figs. 1-3). The globule being filled is in effect a secretory manifold within the ground cytoplasm but in contact with the plasma membrane distally. Fig. 5 reveals a key shaped Ubisch body being expelled but still attached to the tapetal cell plasma membrane at the base of the "beak" (cf. Fig. 18f). The Ubisch bodies in Fig. 6a-c are in various states of release from the "filling site" of the rER-manifold. These sites appear as crypts in the cell surface. Such crypt-like profiles are also seen in Figs. 4, 8, 11, 14 and 17.

The immature Ubisch body leaves the cytoplasmic cavation in such a way that one sector of the globule acts as a hinge or fulcrum. The bottom face of the Ubisch body is heavily coated by plasma membrane glycocalyx (Fig. 4). If we imagine Ubisch bodies divided into four sectors,

PLATE I

Fig. 1. Part of tapetal cell, providing a survey of serral globules (U) consisting of manifold-like structures connected to cisternae of rER (arrows). Glycocalyx (G). Fixation: No. 4. Scale bar: 1 μ m. Fig. 2. Detail of Ubisch body core globule (U), rER (arrows), and surface glycocalyx (G) of tapetal cell. Fixation: No. 4. Scale bar: 0.5 μ m. Fig. 3. Core globule (U) of future Ubisch body. The micrograph is like Fig. 2 but shows plasma membrane coating (arrow) over core globule. Fixation: No. 4. Scale bar: 0.5 μ m. Fig. 4. Ubisch body (U) in crypt at tapetal cell (T) surface. Glycocalyx of tapetal cell (G). Fixation: No. 4. Scale bar: 0.5 μ m

PLATE II

Fig. 5. Ubisch bodies formed between metaphase I and the introduction of nexine in microspores tend to have a long "beak" region constituting the last portion of the body to be detached (arrow) from the tapetal cell plasma membrane. The bald spot under the beak is indicated by asterisks like in Fig. 18 e-g. There is a multitude of detached components of Ubisch body walls (DC) in the tapetal cell coating. Fixation: No. 5. Scale bar: 0.5 μ m. Fig. 6 a-d. Details from the surface of an individual tapetal cell (T). The Ubisch bodies being released in Figs. 6a and b have two profiles of minimal wall thickness (arrows). In Fig. 6c the Ubisch body is associated with a poorly defined crypt. In Fig. 6d the Ubisch body is orientated in such a way that it shows some of the "beak" region (arrow). The tapetal cell coating contains many examples of fragments of detached coating of Ubisch bodies (DC). Fixation: No. 5. Scale bar: 0.5 μ m

PLATE III

Fig. 7. Microspore tetrad period. Tapetal cell (T) surface coating has many holes (asterisks) left by extruded Ubisch bodies (U). Much of the wall material has been extracted because of the preparation technique used. Microspore (E) surface shows exine-template for sexine (S) but no nexine (cf Fig. 8). Fixation: No. 1. Scale bar: 0.5 μ m. Fig. 8. A later stage than Fig. 7. The Ubisch body (U) wall material is preserved because of impregnation with sporopollenin. The thin site of a body is marked by an asterisk. Microspores have lamellae of the nexine (N), here shown at the future aperture site, where there is little or no template for the sexine. Fixation: No. 1. Scale bar: 0.5 μ m

PLATE IV

Fig. 9. Same locule as in Fig. 7 but here the fixation included ruthenium red. The core globule was contrasted by the section stain. The surface coating of tapetal cells was better preserved when ruthenium red was included in the aldehyde fixative (cf. Fig. 7). Fixation: No. 4. Scale bar: 100 μ m. Fig. 10. Same locule as in Fig. 8 but here the fixation included ruthenium red. There is no improvement in preservation of the Ubisch body wall after the time of nexine initiation. The surface coating (arrow) of tapetal cells (T) is improved by use of ruthenium red. Fixation: No. 4. Scale bar: 0.5 μ m. Fig. 11. Tapetal cells and associated Ubisch bodies six days before the shedding of pollen. The Ubisch body wall has lost stain acceptance. The last Ubisch bodies to be produced have a thick wall, are generally regular in shape, and are coated by short spinules, like the one marked by an asterisk. Fixation: No. 1. Scale bar: 1 μ m

PLATE V

Fig. 12. Tapetal cell (T), Ubisch bodies and a microspore (M) just after the tetrad period. The lamellated nexine (N) of the apertural region and portions of inflated sacci (Sa) are

PLATE I

PLATE II

PLATE III

PLATE IV

PLATE VI

PLATE VIII

strongly stained like the walls of Ubisch bodies. The Ubisch body wall is irregular. One Ubisch body (U) shows a beak (arrow) and two thin wall regions marked with a star and an asterisk. Fixation: No. 1 (with caffeine). Scale bar: 1 μ m

PLATE VI

Fig. 13. Tapetal cell (T) and three Ubisch bodies, all with "beaks". Two of them show thin parts of the wall (asterisks) just below the beak (cf. Fig. 18 e-f). Fixation: No. 3. Scale bar: 0.5 μ m. Fig. 14. Detail from the outer part of a tapetal cell with a thick surface coating (G) at a period early in a secretory cycle. An Ubisch body (U) is partly released from the cytoplasm. The coating of tapetal cells is loaded with discarded Ubisch body wall material (DC). Fixation: No. 4. Scale bar: 0.5 μ m

PLATE VII

Fig. 15. Just prior to the first microspore mitosis. The exine, Ubisch body wall, and extratapetal lamellation readily accept stain during this period. There are a variety of Ubisch bodies although those most prominent are aligned at the surface of the tapetal cell. They are more or less spheroidal and coated by spinules. The microspore has a conspicuous cap region (S) and nexine (N) lamellations over the aperture (A). Fixation: No. 1 (with tannic acid). Scale bar: 5 μ m

PLATE VIII

Fig. 16. Persisting Ubisch bodies accumulated on the diminished surface of a senescent tapetum during the period just before pollen shedding. The bodies of the most recent crop (marked by asterisks) have thick walls, short spinules, and tend to be symmetrical. Early productions have a long beak and relatively thin wall (arrows). Examples of intermediate crops with irregularly thickened walls are circled. Fixation: No. 1. Scale bar: 5 μ m. Fig. 17. Ubisch bodies form before the surface coating on tapetal cells is lost during the cyclic differentiation into hypersecretion. Before being lost the glycocalyx coating of tapetal cells becomes riddled by the cavities of departed Ubisch bodies. In this figure two Ubisch bodies are partly out (arrows) of the tapetal cell surface coating. Fixation: No. 2. Scale bar: 0.5 μ m

three of these are coated but unevenly and the forth and last to be separated during the export sequence has a gap in the coating and also a beak located above the gap. The beak is quite distinctive in several different crops of Ubisch bodies. It varies from a short almost imperceptible protrusion to a half a micrometer long handle-like extension and both length and shape are specific for several periods of production. In the early formed Ubisch bodies these beaks are considerably elongated, like handles, so that the entire body is like a Pharaonic sceptre (Figs. 5 and 8). The drawing in Fig. 18f and g is based upon Ubisch bodies produced near the first mitosis possessing relatively short "beaks" (Fig. 12). Ubisch

bodies produced following the first mitosis are more symmetric than earlier and have a beak zone that is hardly detectable. Some of these late formed Ubisch bodies are marked by asterisks in Fig. 16 and one is so marked in Fig. 11.

STABILIZATION OF THE GLYCOLALYX OF THE UBISCH BODY WALL

The glycocalyx coating on Ubisch bodies was sensitive to fixation, dehydration, and other aspects of chemical and solvent preparation for TEM until the nexine appeared, presumably as an indication of the earliest occurrence of sporopollenin in the preexine and wall of Ubisch bodies. Figs. 7 and 8 are from a tetrad stage. After lamellae of the nexine are evident, the Ubisch body wall remains thick regardless of the conditions of preparation (Fig. 8). At a stage where there is a preexine but no nexine (Fig. 7) the Ubisch body coating is mostly lost during preparation for TEM unless special attention is given to the use of fixation methods that stabilize carbohydrate components of glycocalices. The Ubisch body in Fig. 9, from material of the same stage as Fig. 7, was preserved by the addition of ruthenium red to the aldehyde, buffer rinse, and osmium tetroxide portions of the fixation procedure. Similar results were obtained with other special fixatives. The material in Figs. 5 and 6 is from telophase II in microspore mother cells and an appreciable amount of glycocalyx coating material on Ubisch bodies was retained after use of a potassium ferrocyanate fixation method (Hepler 1981).

After accumulation of sporopollenin, as indicated by the presence of nexine-lamellae, no improvement in preservation of the wall of Ubisch bodies was obtained with addition of ruthenium red (Fig. 10, cf. Fig. 8) but retention of the coating matrix on tapetal cells remained substantially better.

STAIN ACCEPTANCE OF THE WALL OF UBISCH BODIES

Stain acceptance by the Ubisch body-wall changes during maturation of microsporangia. Stain acceptance was low prior to the appearance of the nexine, even when a coating of considerable depth was preserved, as after fixation with ruthenium red (Fig. 9). Staining was greatly elevated during intervals of increases in thickness of the exine (Figs. 12, 13, 15). These intervals extend through the first mitosis of the microspore, following the stage in Fig. 15. Thereafter stain acceptance declines in both the exine and wall of Ubisch bodies going from moderate (e.g., Fig. 16) to very weak staining a few days before the pollen grains were shed (Fig. 11). Examples of three levels of stain acceptance are exhibited together in Figs. 9-11. The high contrast in the Ubisch body core globule in Fig. 9 was a common,

although not invariable, result of the ruthenium red-osmium procedure. The globular centrum of the Ubisch body in Fig. 10 is contrasted about the margin following fixation with ruthenium red but to a much lower degree than in Fig. 9.

THE GLYCOLALYX AROUND UBISCH BODIES

The glycocalyx coating of Ubisch bodies is thin in two regions. There is little glycocalyx in the zone below the broad beak. This is where

Fig. 18. Diagram showing model for origin and morphogenesis of Ubisch bodies. The plasma membrane-glycocalyx is symbolized by line-baring. a-c — Three stages in the filling up of the core globule (c-g) of future Ubisch bodies by material from rER cisternae. The position of the globule is at the cell surface and an extending part is covered by the plasma membrane. d-e — When core globules start to protrude from the formative crypt, plasma membrane-glycocalyx occurs at the bottom of the crypt. Arrows indicate direction of rotation. f-g — Nearly free and entirely free Ubisch bodies. The lower surface of the beak is variously coated by plasma membrane-glycocalyx before the Ubisch body is separated from the tapetal cell surface. There is little coating on the zone rotated past the cell surface (stars). There is no coating at the pivotal area (asterisk) of the rotation

the surface of the cavated tapetal cell cytoplasm remains in contact with the Ubisch body until its final detachment. This zone is denoted by asterisks in Figs. 5, 8, 12, 13 and 18e-g. Opposite the subbeak bald zone there are variable numbers of this sites. Their number and distinctness is greatest during intervals of microspore exine thickening; examples are shown in Figs. 6b, 8, 10 and 13. The region involved in this nonuniform accumulation of plasma membrane-glycocalyx is indicated by a star in Fig. 18d-g. In these sketches the glycocalyx is thin over the entire anti-beak region on the immature Ubisch bodies and free Ubisch body in Fig. 18g. In Fig. 12 thin zones are marked by an asterisk and a star on an Ubisch body sectioned in a way favorable to show both beak and anti-beak regions in profil.

In Fig. 6b. thin places in the wall are marked by arrows on the Ubisch body, which has been rotated out from its cavation-mould. The thick glycocalyx coatings at "top" and "bottom" of Ubisch bodies can be appreciated from those bodies that still partly remain in connection with their cavations (Figs. 6a-c).

PERIODS OF PRODUCTION OF UBISCH BODIES

Tapetal cells repeatedly enter into periods of hypersecretory activity followed, until a terminal stage near maturity of pollen grains, by differentiation to a largely meristematic-like condition. The core-globules become coated with glycocalyx by the tapetal cell plasma membrane only during an interval early in each secretory cycle.

Structurally the production of Ubisch bodies is uniform for each cycle with respect to length of beak, extent of subbeak and antibeak bald zones, general thickness of the wall initiating glycocalyx, and surface ornamentation. Three distinct forms are illustrated in Figs. 8, 13, and 14 for a stage of very early nexine formation and two periods of exine thickening on free microspores respectively. Ubisch bodies formed in each cycle are to some extent distinct and in several cycles the form is exceptionally distinctive. The current production of Ubisch bodies is dominant during each cycle. Most of them migrate into the locule leaving characteristic gaps in the glycocalyx of the tapetal cell, e.g., Figs. 5, 7, and 17. The greater part of Ubisch bodies leave no permanent record. A few Ubisch bodies of each cycle are sequestered, perhaps because of their location in the lateral space between tapetal cells or because they formed late in a cycle.

It is only at the terminal stage of pollen grain development, when Ubisch bodies are no longer being formed and when the surface area of the ageing tapetum is progressively restricted, that all the different forms of Ubisch bodies are concentrated in space and readily observed in al-

most any section passing through the inner surface of tapetal cells. At that time the last formed production is no longer more common than Ubisch bodies from the many other cycles.

DISCUSSION

Studies giving attention to Ubisch bodies throughout pollen grain formation in angiosperm taxa reveal modification in Ubisch wall structure commensurate with, although simpler than, exine development in microspores. The Ubisch bodies apparently remain attached to the plasma membrane of tapetal cells. In some dicots, e.g. *Vinca* (Cousin 1979), a lamellation forms ("pellicule", Cerceau-Larrival and Roland-Heydacker 1976) between the unit membrane of the plasmalemma and Ubisch bodies. In the grasses the "pellicule" consists of a network of thin rods followed, at a specific phase of development, by a fibrillar layer (e.g., El-Ghazaly and Jensen 1986). Banerjee (1967) recovered both sheet and net forms of this pellicule with attached Ubisch bodies after destruction of anther cells using the hot acid acetolysis method of Gunnar Erdtman. Thus in the angiosperms there are some taxa producing plasma membrane coated cores for Ubisch bodies that undergo a sequence of development mirroring the exine of microspores and these bodies are both persistent and spatially fixed to a pellicule over the surface of tapetal cells.

It is a pattern differing in fundamental respects from what we find for *Pinus sylvestris*. Perhaps the most significant distinction pertains to the detachment of Ubisch bodies in *Pinus* from the plasma membrane of tapetal cells. As a consequence, we infer, most Ubisch bodies migrate into the locus and are delivered to microspores. We have observed many successive productions of Ubisch bodies each with a characteristic wall form similar to the exine of microspores for each period of development. Ubisch bodies of *P. sylvestris* receive the plasma membrane code for development during the interval of initiation but are then detached and "frozen" at that stage since they receive no updated information for modification.

In *P. sylvestris* the production of Ubisch bodies occurs during the initial phases of the many secretory cycles in the microsporangium. Following the interval of Ubisch body production the rate of material export from tapetal cells increases greatly resulting in partial reduction of the glycocalyx surface coating and apparently the loss of most of the Ubisch bodies. The cytoplasm of tapetal cells returns to a meristematic-like condition with a renewal of the cell surface glycocalyx. When a new cycle of secretion commences Ubisch bodies are again formed.

Presumably the glycocalyx coating of Ubisch bodies includes receptors

for sporopollenin. Disregarding the variable ornamentation at the surface of the wall the coating is nonuniform in thickness over the central granule of the Ubisch bodies. Our explanation for this has to do with the mode of release of Ubisch bodies from the tapetal cell cytoplasm and cell surface. The sequence of morphogenesis is presented diagrammatically in Fig. 18.

The earliest Ubisch body form to persist in the mature microsporangium is produced at the time of nexine formation in the microspore tetrad. It seems reasonable to suppose that a few of this form survive because at this stage the Ubisch body wall is endowed with sporopollenin. No substructure was apparent in sections of either the wall of Ubisch bodies or the nexine from that period of development through maturity. Progression toward a structureless amorphous-like exine appearance in ultrathin sections is a change typical of exines in general after a certain level of development is reached; it is a modification considered to coincide with accumulation of sporopollenin. Before that the glycocalyx coating of Ubisch bodies showed a pronounced filamentous "wall" substructure. That substructure had a character similar to the glycocalyx of the plasma membrane of tapetal cells during the period of production of the Ubisch body-like structures. Sporopollenin is added to the Ubisch body wall as shown by the observation that it, like the exine, goes through a "protosporopollenin" interval followed by a decrease in reactivity to stain. We found, that the early preexine and Ubisch body wall required special stabilization methods to prevent their loss during TEM preparation. One of the most acceptable tests for polyuridine containing polysaccharides (Foster 1981), ruthenium red, was a favourable method for stabilization of the delicate wall of the material mentioned.

It appears now more admissible than earlier to consider that sporopollenin could be recycled during development. It is evident that on living pollen grains the exine is greatly modified during germination (cf. review in Rowley and Rowley 1986) and that the exine does not achieve its renowned resistance until after, at least, a brief period of storage (Bailey 1960, Southworth 1974, Pierart et al. 1981, Rowley et al. 1981, Kress 1986). According to the results of Pierart et al. (1981), elevated temperature is a reason for the increased polymerization level of sporopollenin occurring during storage.

We find it possible that the Ubisch body with its "wall" of sporopollenin may be a kind of temporary packaging of sensitive material for transport through the locular sap, which presumably contains exocellular enzymes (e.g., Herdt et al. 1978). The "wall" might in addition provide a means of identifying certain exported substance employing a plasma membrane glycocalyx compatible with the microspore system.

Many different Ubisch body forms occur in micrographs present in the papers by Dickinson (1970) and Dickinson and Bell (1972, 1976a, b) describing development of the microsporangia and pollen grains of *Pinus banksiana*. The results of our studies are in agreement with the observations of Willemse (1971) on *P. sylvestris*, i.e., that the core globule forms in association with rER and that on leaving the cytoplasm Ubisch bodies can pass through the wall-like coating of tapetal cells. Ubisch bodies of several different forms are apparent in his illustrations.

Our results suggest the following explanations for stain acceptance before, during, and after the so called **protosporopollenin** interval of exine development. That period begins after initiation of the nexine, apparently the beginning of sporopollenin accumulation. Before nexine initiation there was no or an inadequate supply of sporopollenin precursors, and the glycocalyx receptors for sporopollenin were consequently extracted and lost by the chemical methods of preparation for TEM. After the nexine forms, sporopollenin stabilizes the glycocalyx receptors. At this "protosporopollenin" time stain acceptance is high, because, we reason, there is sufficient sporopollenin to prevent extraction of glycocalyx molecules but not so much as to prevent entry of stain. Later in development stain acceptance diminishes, because, we reason, glycocalyx molecules are so effectively encapsulated in sporopollenin that penetration of stain is restricted.

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Powstawanie i struktura ciał Ubischa u Pinus sylvestris

Streszczenie

U *P. sylvestris* ciała Ubischa powstają wielokrotnie i każda grupa ciał tworzy się w odrębnej fazie cyklu wydzielniczego komórek tapetum. Ściany ciał Ubischa, które powstały w tym samym czasie, są podobne pod względem grubości i urzeźbienia do istniejącej wtedy egzyny; powstałe wcześniej nie zmieniają się. Przykłady wszystkich, różnych strukturalnie form ścian ciał Ubischa mogą być widoczne w czasie rozsiewania pyłku, pozostałe ciała Ubischa są skupione na minimalnej powierzchni starzejących się komórek tapetum. U okrytozalążkowych, po jednym lub kilku okresach inicjacji, ciała Ubischa mogą pozostawać w związku z powierzchnią tapetum, gdzie ich ściana przechodzi przemiany takie, jakie zachodzą w egzynie dojrzewającego pyłku. Wnioskujemy, że u *Pinus sylvestris* w konsekwencji oderwania się ciał Ubischa od błony plazmatycznej komórek tapetum, ściany ciał Ubischa pozostają niezmienione i nie ma, jak dotąd, informacji na temat ich modyfikacji.