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Comparative Study of the Pollen Wall Development in *Illicium floridanum* (Illiciaceae) and *Schisandra chinensis* (Schisandraceae)

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ABSTRACT: Pollen wall development of *Illicium floridanum* and *Schisandra chinensis* have been studied and compared. Both species have a similar reticulate exine, but their similarity occured to be only superficial. At early tetrad stage of both species the plasma membrane acquires a regularly invaginative profile, the distribution pattern of invaginations on the microspore surface corresponds to the future reticulate exine pattern. In the invaginative sites of the plasma membrane of both species fibrillar strands appear which are the auxiliary (phantom) structures. Further developmental process is different in both species. In *Illicium* sporopollenin accumulates around the auxiliary strands, localized in plasma membrane invaginations, resulting in the appearance of the reticulate sculpture of hollow tunnels on the surface of a microspore; this reticulate pattern becomes concave after lifting of the invaginated portions of the plasma membrane. In *Schisandra*, on the contrary, sporopollenin never accumulates in the location of the auxiliary fibrillar strands (these are sites of future lumina), but sporopollenin accumulations concentrate on the elements of the glycocalyx on the evaginated top (protruding sites) of plasma membrane. The latter are sites for columellae formation, and muri are constructed from the rows of columallae covered by tectum. Hence, the development of the exine in both species is different, and the inner structure of reticulate exine in *Illicium* differs from that of *Schisandra* - in spite of the very similar sculpture.

KEY WORDS: **Exine patterns, Auxiliary structures, *Illicium floridanum, Schisandra chinensis*.**

INTRODUCTION

The group of so-called primitive angiosperms (Magnoliidae) is of special interest in many aspects. Nevertheless, only several studies have been dedicated to the modes of sporoderm development (Meyer, 1977; Zavada, 1984 – *Austobaileya maculata* (Austrobaileyaceae); Gabarayeva, 1986a, b – *Michelia figo* (Magnoliaceae), 1987a, b, c – *Manglietia tenuipes* (Magnoliaceae); Waha, 1987 – *Asimina triloba* (Annonaceae); Gabarayeva, 1991a – *Magnolia delavayi* (Magnoliaceae), 1991b – Magnoliaceae; Rowley and Flynn, 1990-1991 – *Tambourissa* (Monimiaceae); Zhang and Chen, 1992 – *Magnolia denudata* (Magnoliaceae); Gabarayeva, 1992, 1993a – *Asimina triloba* (Annonaceae); Rowley and Vasanthy, 1993 – *Cinnamomum* (Lauraceae); Takahashi, 1994 – *Illicium religiosum* (Illiciaceae); Gabarayeva and Rowley, 1994 – *Nymphaea colorata* (Nymphaeaceae); Gabarayeva, 1995 – *Anaxagorea brevipes* (Annonaceae), 1996 – *Liriodendron chinense* (Magnoliaceae); Gabarayeva and El-Ghazaly, 1997 – *Nymphaea mexicana* (Nymphaeaceae); Kreunen and Osborn, 1999 – *Nelumbo* (Nelumbonaceae); El-Ghazaly *et al*., 2000 – *Magnolia* (Magnoliaceae); Gabarayeva *et al*., 2001 – *Nymphaea capensis* (Nymphaeaceae); Tsou and Fu, 2002 – *Annona* (Annonaceae); Gabarayeva *et al*., in press – *Cabomba aquatica* (Cabombaceae)).

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Our studies on Magnoliaceae, cited above, have shown that it should be expected a range of different morphogenetic modes leading to the resolving of similar morphological goals. For instance, several different types of endoplasmic reticulum (smooth endoplasmic reticulum, chain-mail reticulum, zebra-reticulum) were found during tetrad period, involved into the process of the formation of similar patterns of exine in Magnoliaceae species (Gabarayeva, 1991b, 1996, 1997). By analogy, we suggested different modes of development in the two Illiciaceae species under our study which have very similar reticulate pattern of the exine.

Our task in this study was to investigate in detail the sporoderm ontogeny in *Illicium floridanum* and *Schisandra chinensis* and to compare the both processes. Our aim was to show the possibility of the achievement of similar morphological structures in nature by different morphogenetic processes.

MATERIALS AND METHODS

Flower buds of *Illicium floridanum* Ellis and *Schisandra chinensis* (Turcz.) Baill. were collected from the glass-houses of the Komarov Botanical Institute (St.-Petersburg). The materials were fixed in 3% glutaraldehyde and 2.5% sucrose in O.1 M phosphate buffer (pH 7.3, 20℃, 24 h) and post-fixed in 2% osmium tetroxide (pH 7.4, 20℃, 1 h). After acetone dehydration the samples were embedded in mixture of Epon and Araldite. Ultrathin sections were stained with a saturated solution of alcoholic uranyl acetate and 0.2% aqueous lead citrate. Sections were examined with Hitachi H-600. Pollen grains for SEM study were air dried, transferred to stubs and sputter coated. Specimens were examined in Jeol JSM 35.

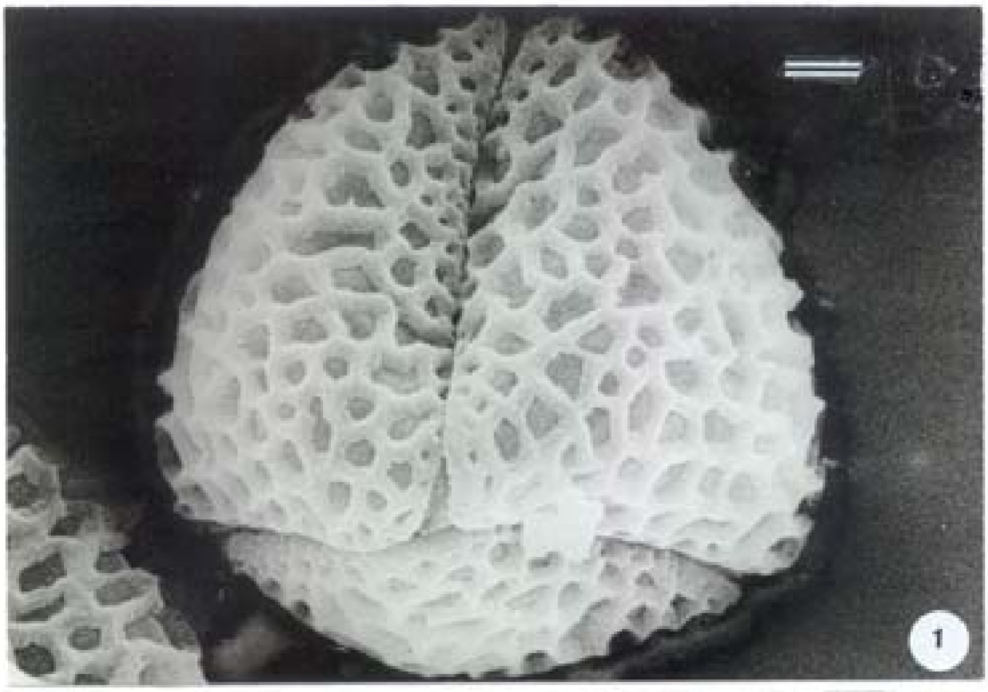
RESULTS

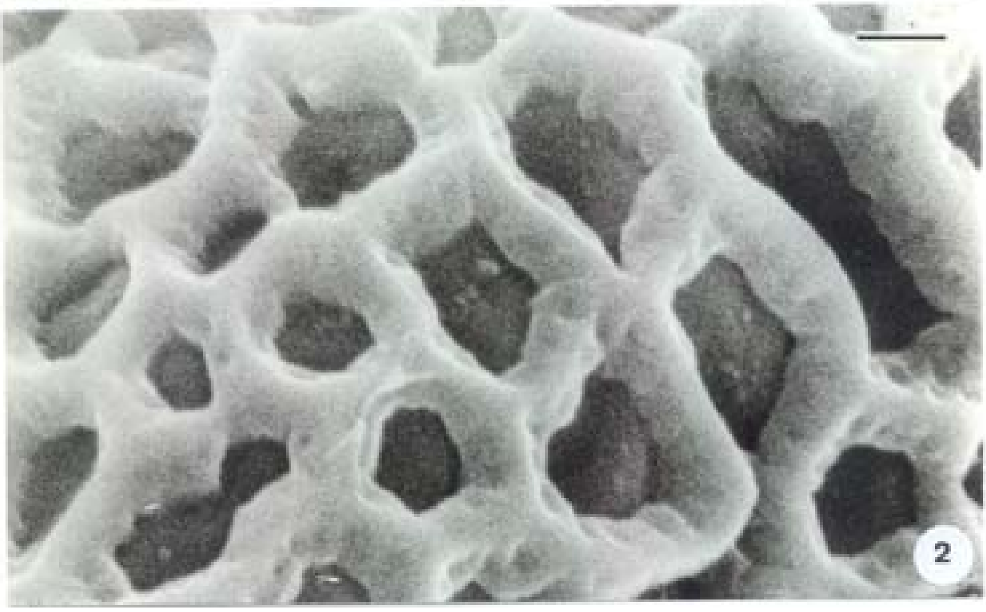
Sporoderm development in *Illicium floridanum*

Mature pollen grains have a reticulate pattern of exine (Figs. 1 & 2). Pollen grains are isopolar and tricolpate with fused furrows at both poles. The developmental process of this structure is rather complex and needs detailed analysis.

Early post-meiosis tetrad microspores are covered by a thick callose envelope, and their plasma membrane is rather even and lacked any signs of the glycocalyx (Fig. 3). Later the first generation of the glycocalyx appears on the surface of the plasma membrane as roundish dark contrasted units (Figs. 4 & 5). Dictyosomes and their vesicles, contained similar roundish units, are observed in the microspore cytoplasm. These first units of the glycocalyx are evidently excreted by Golgi vesicles. At the next developmental step this first generation of the glycocalyx disappers - probably has been engulfed in the process of endocytosis.

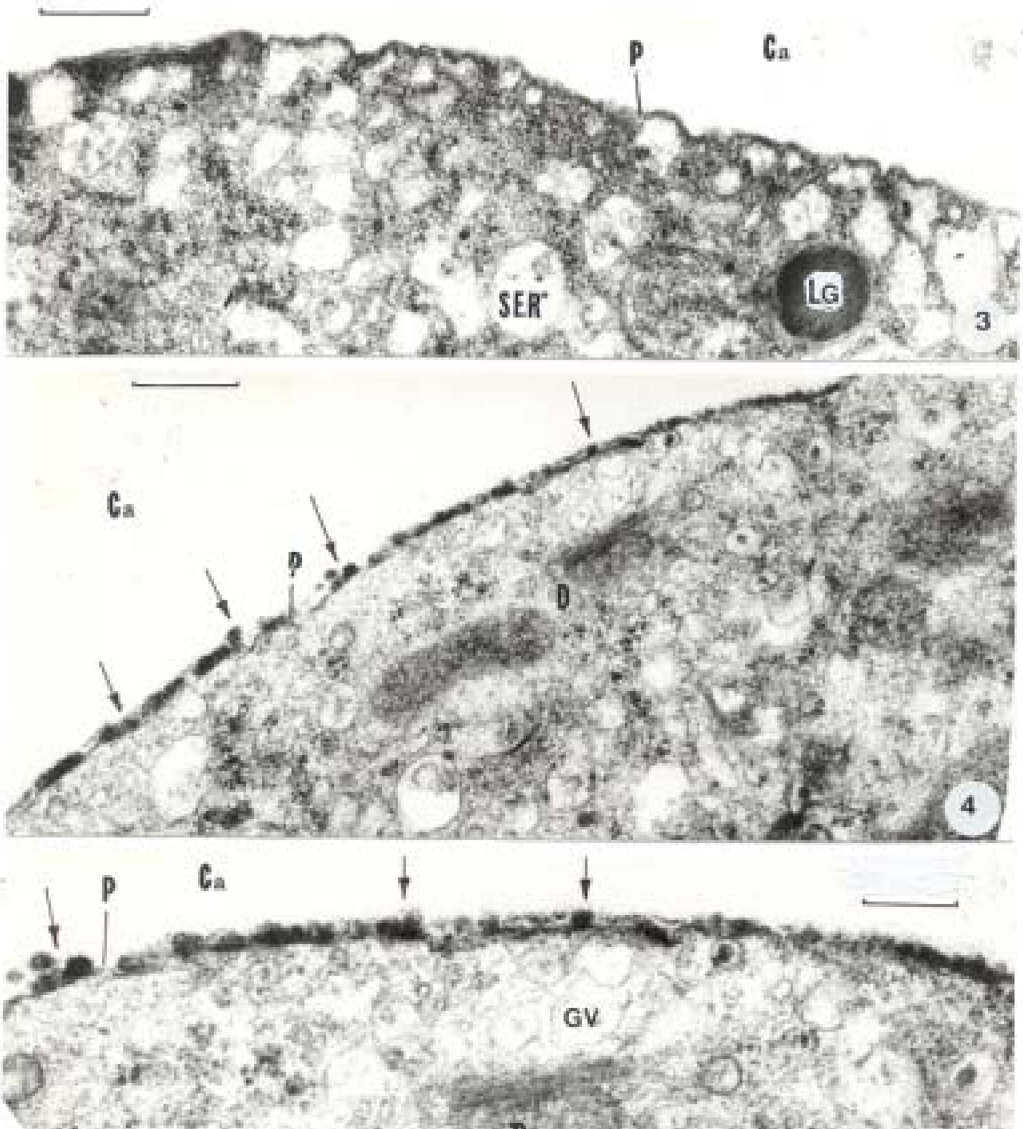
In young tetrad microspores the plasma membrane acquires a periodically invaginated profile. Thin fibrillar strands appear in invaginated regions (Figs. 6 & 7). They are rather long if sectioned longitudinally (Figs. 6 & 7), and they are narrow in cross section (Fig. 10). Being first thin, they become more pronounced later (Figs. 8 & 9). These fibrillar strands are auxiliary structure and play an important role in establishing of exine pattern, but they disintegrate in the later developmental stages.





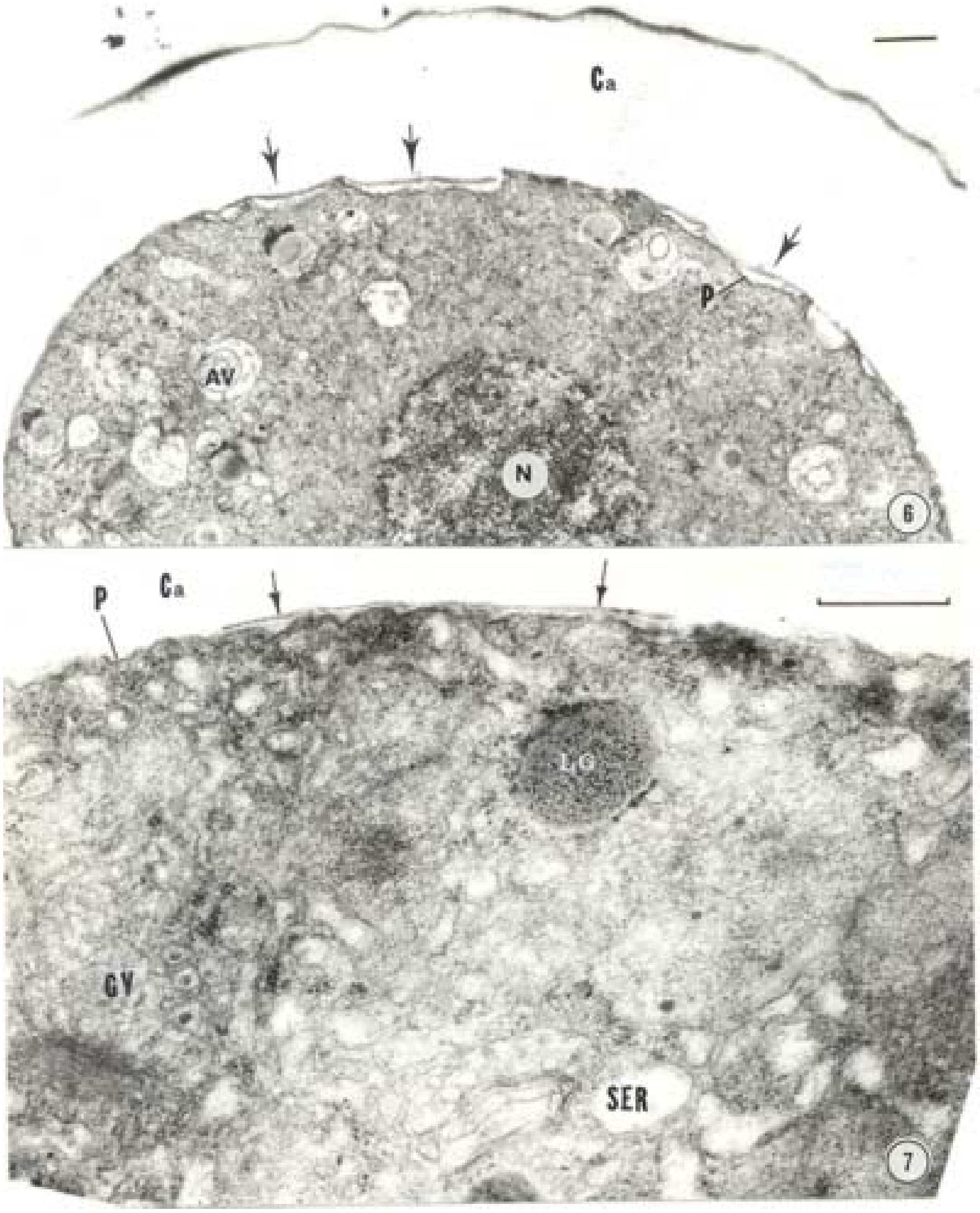
Figs. 1-2. Scanning electron micrographs of the mature pollen grain of *Illicium floridanum*. 1. A survey of a pollen grain. Bar = 2 µm. 2. Sculpture of the reticulate exine. Bar = 0.5 µm.

At middle tetrad stage the secondary generation of the glycocalyx appears between and around the fibrillar strands (Figs. 10-13). In Fig. 10 and in Figs. 13-15 the fibrillar strands are crossly sectioned, and the portions of the glycocalyx alternate with the auxiliary strands. In Figs. 11 & 12 the auxiliary fibrillar strands are longitudinelly sectioned. The microspore cytoplasm is abundant in Golgi vesicles. The auxiliary strands, as previously, are arranged to the invaginations of the plasma membrane and form a "network" around the microspore surface which corresponds to the future reticulate exine pattern (Figs. 6 & 8). Microfilaments are seen perpendicularly to the plasma membrane (Figs. 11 & 12).



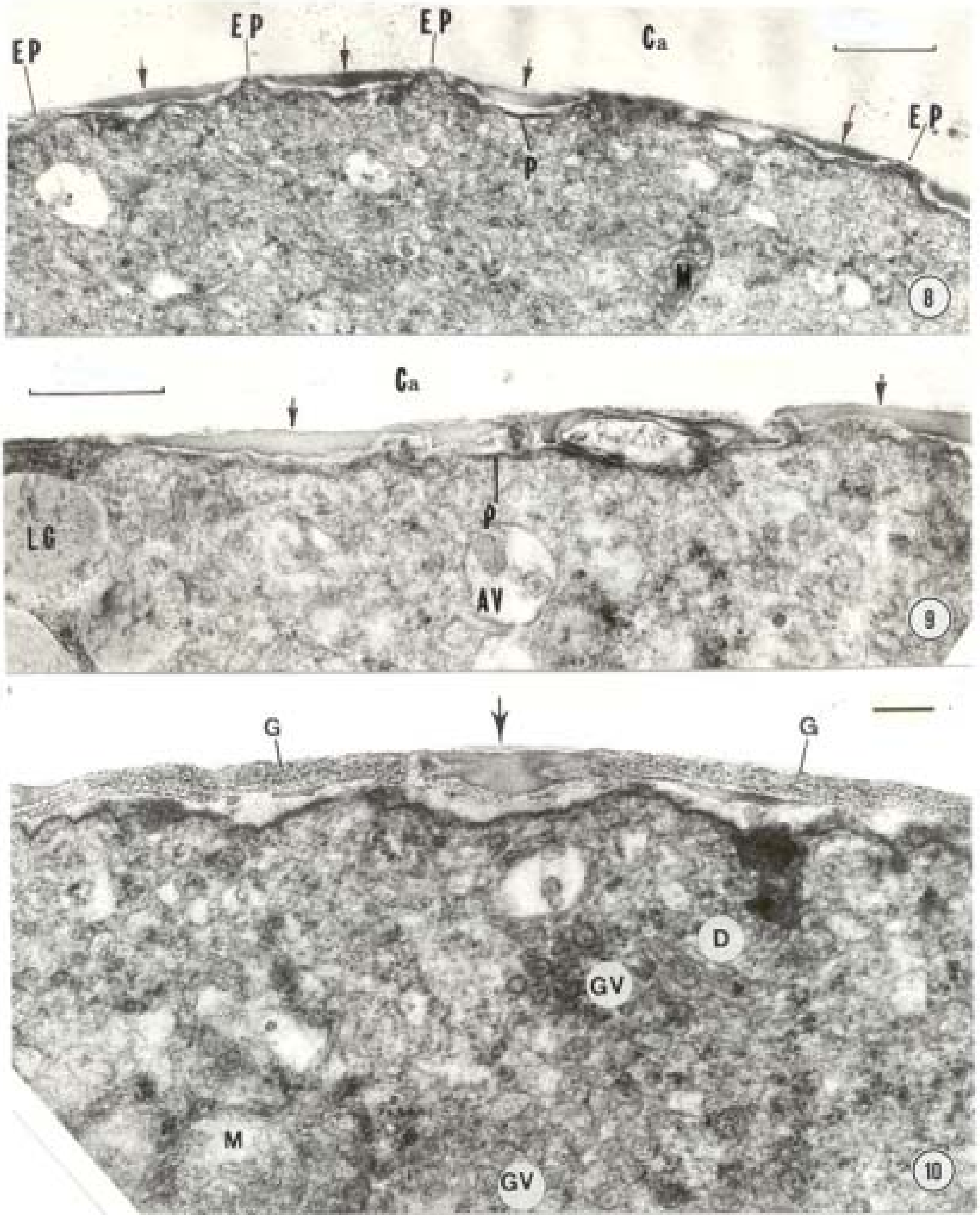
Figs. 3-5. Early tetrad microspores of *Illicium floridanum.* 3. Early post-meiosis tetrad microspore enveloped in the thick callose wall. There is no any signs of the glycocalyx on the surface of the plasma membrane. 4. The appearance of the roundish units of the glycocalyx (arrows) on the plasma membrane surface. 5. The magnified portion of fig. 4. (Ca: callose, D: dictyosome, GV: Golgi vesicles, LG: lipid globules, P: plasma membrane, Pl: plastid, SER: smooth endoplasmic reticulum). 3 & 4: Bar = 0.5 µm. 5: Bar = 0.25 µm.

At late tetrad stage abundant clusters of a dark contrasted lipoid substance, which are probably a sporopollenin precursor, accumulates on the plasma membrane and in the periplasmic space (Figs. 14 & 15). This process starts at previous stage, when small droplets of this substance are observed on the surface of the plasma membrane (Fig. 13). Sporopollenin precursor begins to accumulate around the auxiliary fibrillar strands (Figs. 14 & 15).



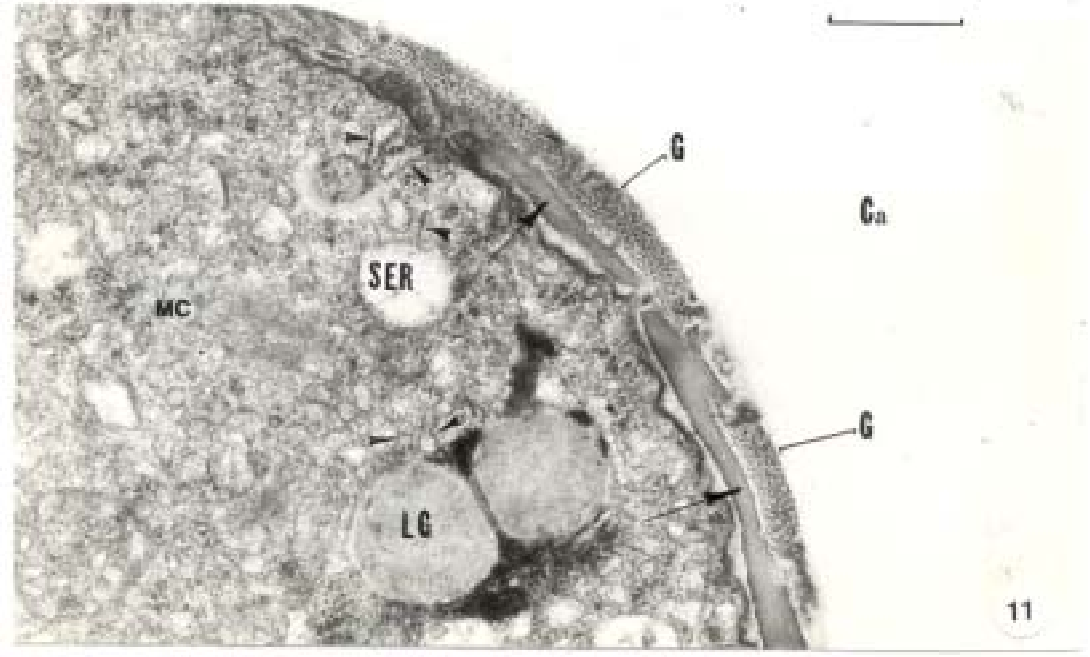
Figs. 6-7. Young tetrad microspore stage in *Illicium floridanum*. The appearance of long thin fibrillar strands alongside the plasma membrane, in its invaginations (arrows). The first generation of the glycocalyx disappeared. (AV: autophagic vacuole, Ca: callose, GV: Golgi vesicles, LG: lipid globule, N: nucleus, P: plasma membrane, SER: smooth endoplasmic reticulum). 6: Bar = 1 µm. 7: Bar = 0.5 µm.

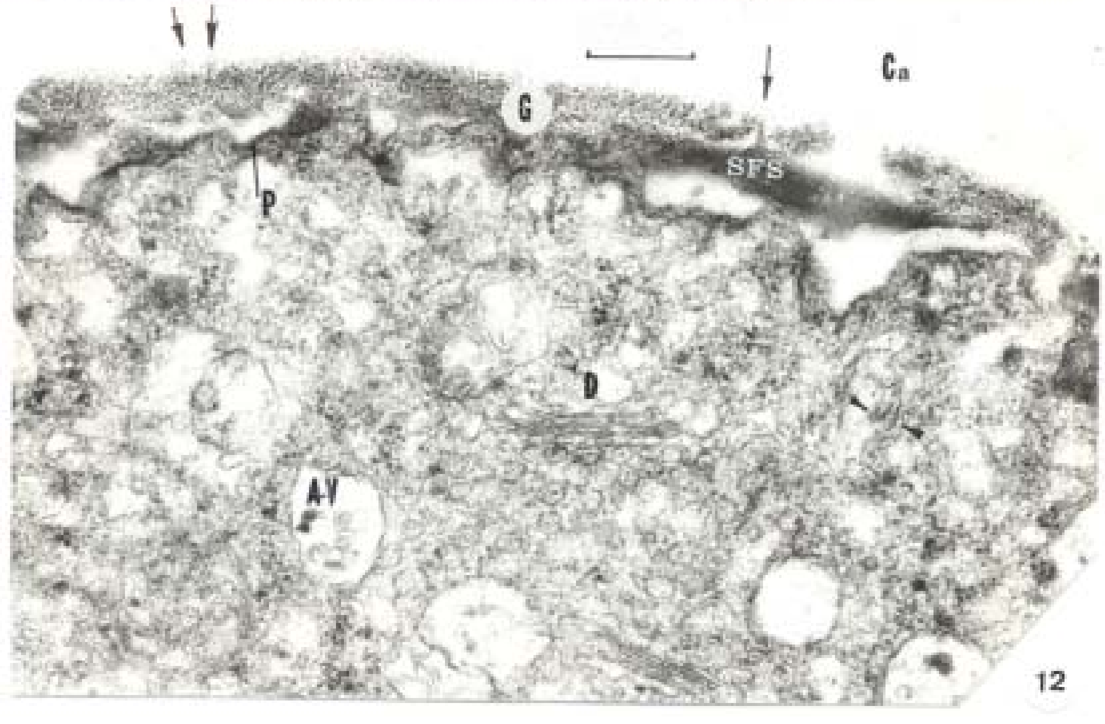
At young free microspore stage the auxiliary fibrillar strands disintegrate, and sporopollenin, which had been accumulated around these strands as around frame at previous stage, form a reticulate system of tunnels. These tunnels look as archs on cross sections (Figs. 16-19). These archs lean on the foot layer. At this stage the endexine is formed and consists of lamellae with white lines and granules of a fibrillar substance.



Figs. 8-10. The transition from young to middle microspore tetrad stage in *Illicium floridanum*. 8-9. The alternation of the invaginations and evaginations of the plasma membrane. The fibrillar strands (arows) are located in the invaginations (longitudinal sections through the strands). 10. Middle tetrad microspore stage. Cross section through a fibrillar strand (arrow). The plasma membrane underneath the strand is covered with the secondary generation of the glycocalyx (G). (AV: autophagic vacuole, Ca: callose, D: dictyosome, EP: evagination of the plasma membrane, GV: Golgi vesicles, LG: lipid globule, M: mitochondrion. P: plasma membrane). 8 & 9: Bar = 0.5 μm. 10: Bar = 0.2 μm.

At next stage the intine appears. Its inner profile is wavy. The archs of ectexine which are cross sections of hollow tunnels are very prominent (Fig. 19).

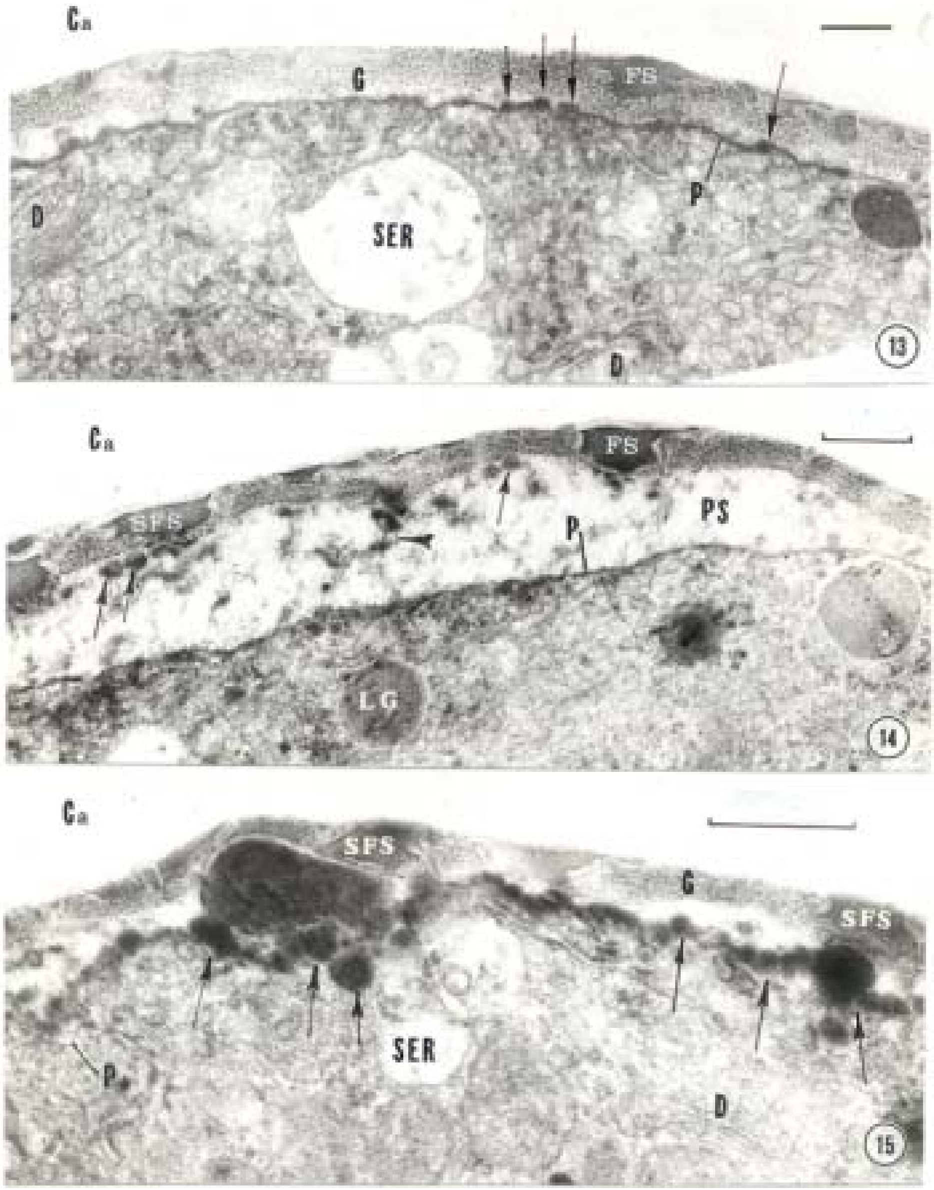




Figs. 11-12. Middle tetrad microspore stage in *Illicium floridanum*. 11. The glycocalyx (G) appears above and around the fibrillar strands (arrows). Arrowheads: microfilaments. 12. The glycocalyx surrounds the fibrillar strands (FS). The discrete, radially oriented units of the glycocalyx – tufts – are shown with arrows. (AV: autophagic vacuoles, Ca: callose, D: active dictyosome, LG: lipid globule, MC: microspore cytoplasm, P: plasma membrane, SER: smooth endoplasmic reticulum). 11 & 12. Bar = 0.5 µm.

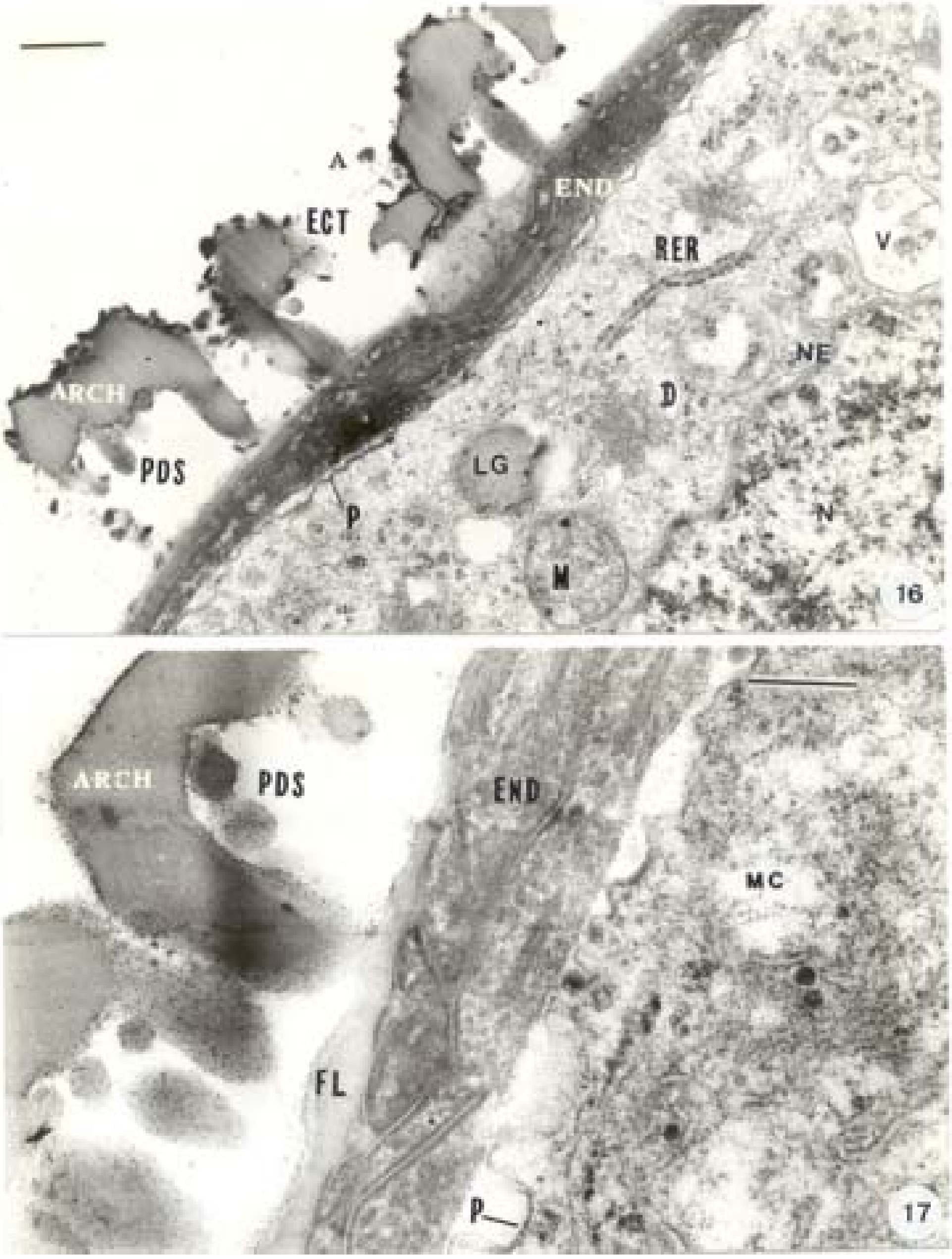
Sporoderm development in *Schisandra chinensis*

Mature pollen grains of *Schisandra* also have a reticulate pattern (Figs. 20 & 21), but, as we shall see below, the similarity is only superficial.



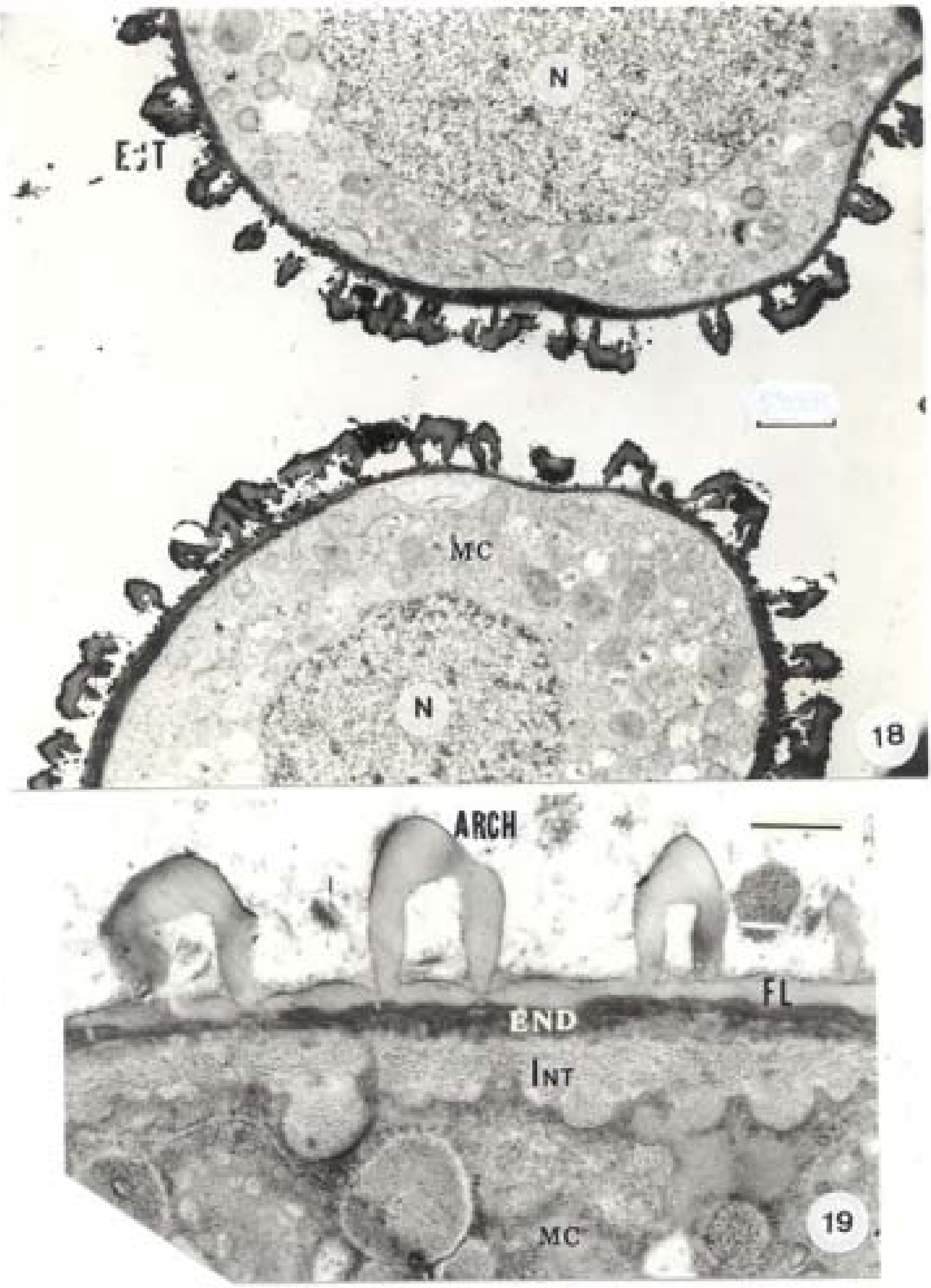
Figs. 13-15. The transition from middle to late tetrad microspore stage in *Illicium floridanum*. 13. The appearance of a dark contrasted lipoid substance on the surface of the plasma membrane (arrows). 14-15. Late tetrad microspore stage. Vast deposition of the dark contrasted lipoid substance on the plasma membrane and in the periplasmic space (arrows). The fibrillar strands (FS) become covered with the dark contrasted lipoid substance. A spiral of a binder element of the glycocalyx tuft is shown by arrowhead. (Ca: callose, D: dictyosome, FS: fibrillar strand, G: glycocalyx, LG lipid globule, P: plasma membrane, PS: periplasmic space, SER: smooth endoplasmic reticulum). 13: Bar = 0.25 µm. 14 & 15: Bar = 0.5 µm.

Young tetrad microspores have a wavy profile which resulted from exocytosis of many Golgi vesicles (Fig. 22). Somewhat later the plasma membrane forms deep invaginations in a way that invaginations and evaginations arranged alternately, and keeps this configuration (Figs. 23, 25, 26). A layer of the glycocalyx appears on the surface of the plasma membrane (Fig. 24).



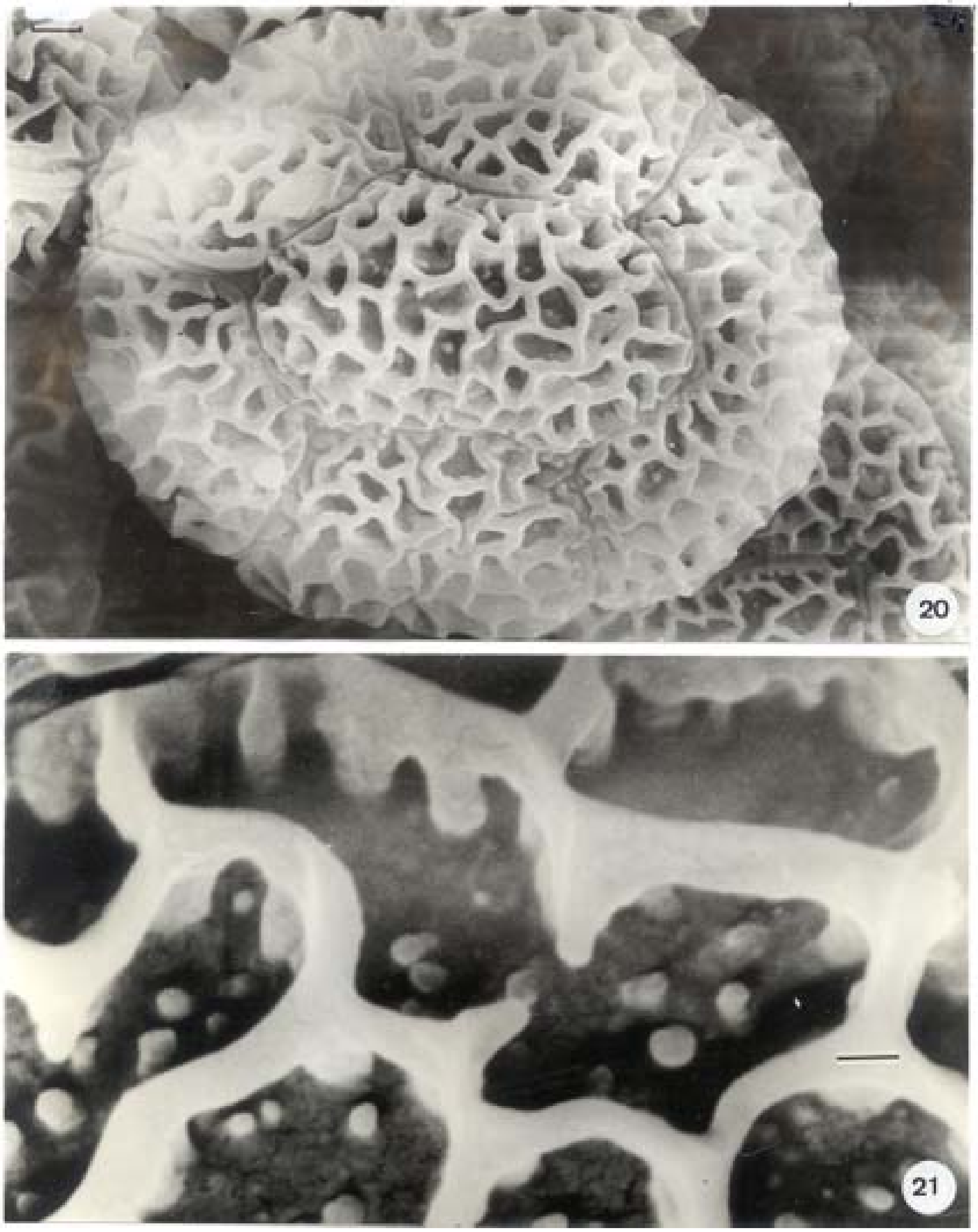
Figs. 16-17. Early free microspore stage in *Illicium floridanum*. Callose is disintegrated. The elements of the exine are seen on cross section as archs on the surface of the foot layer. These archs (ARCH) were formed around the fibrillar strands which are disintegrated now (place of disintegrated strands – PDS). The endexine is lamellated under the apertural site (A: aperture) and intermixed with granules in interapertural regions (END). (D: dictyosome, ECT: ectexine, FL: foot layer, LG: lipid globule, M: mitochondrion, MC: microspore cytoplasm, N: nucleus, NE: nucleus envelope, P: plasma membrane, RER: rough endoplasmic reticulum, V: vacuole) 16: Bar = 0.5 µm. 17: Bar = 0.25 µm.

At middle tetrad stage fibrillar strands appear above those portions of the glycocalyx which are located in the invaginated regions of the plasma membrane (Figs. 25 & 26). They are absent at the evaginative points, where the glycocalyx initiates to accumulate sporopollenin. The tetrad microspore cytoplasm is abundant in active dictyosomes (Fig. 25).



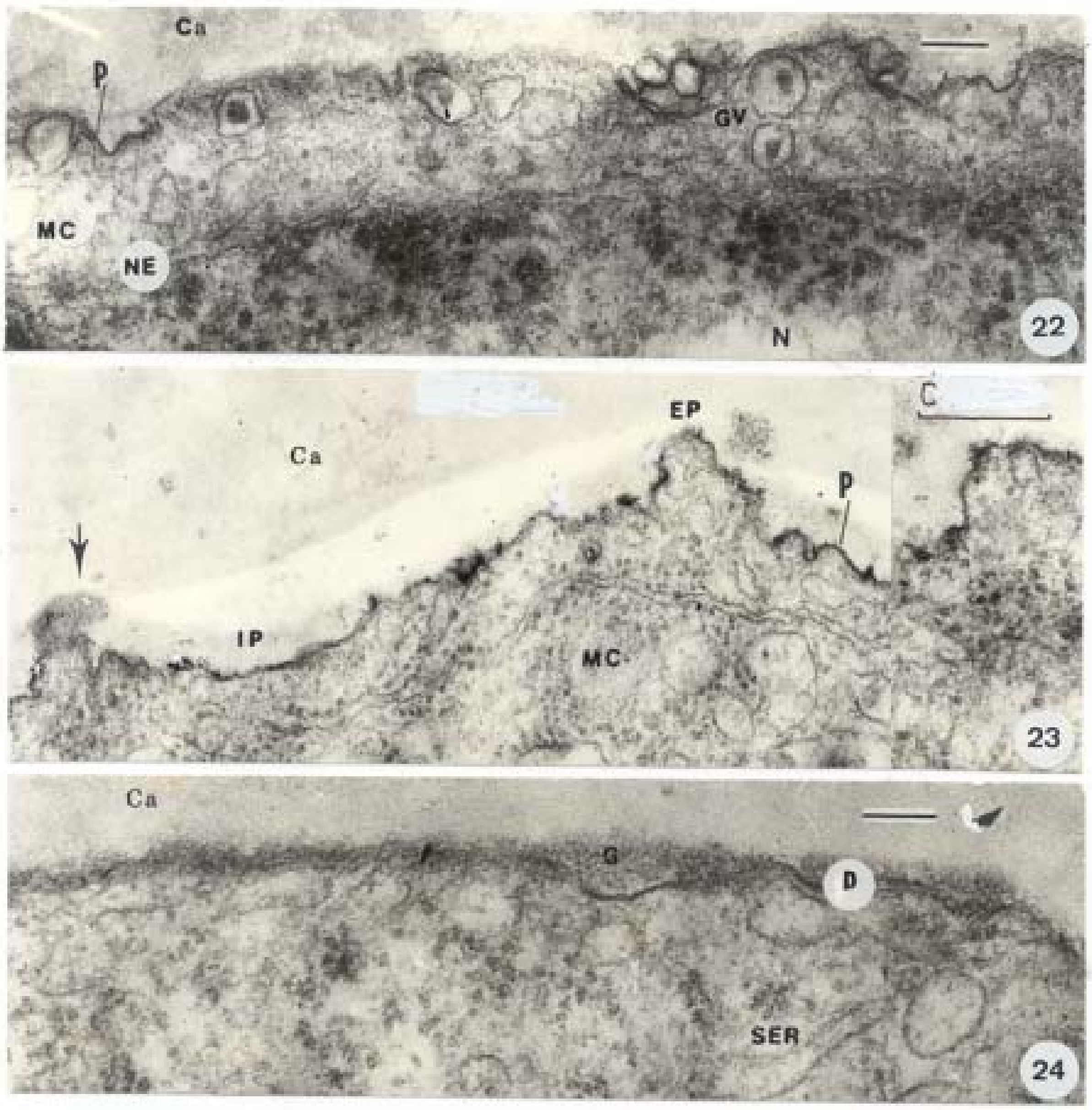
Figs. 18-19. Young free microspore (18) and the appearance of the intine (19) in *Illicium floridanum*. The elements of ectexine on cross section are seen as archs (ARCH). They are sections of hollow tunnels, the latter create reticulate pattern on the surface of pollen grain. (ECT: ectexine, END: endexine, FL: foot layer, Int: intine, MC: microspore cytoplasm, N: nucleus). 18: Bar = 2 µm. 19: Bar = 0.5 µm.

At late tetrad stage the glycocalyx located on the evaginated portions of the plasma membrane becomes especially prominent by virtue of sporopollenin accumulation (Fig. 27). These are actual sites where the procolumellae begin to form. The fibrillar strands, spreaded by the glycocalyx, occupy the places only above the invaginations of the plasma membrane – the places form the future lumina (Figs. 26 & 27). Many Golgi vesicles, lipid globules and autophagic vacuoles are seen in the microspore cytoplasm (Fig. 27).



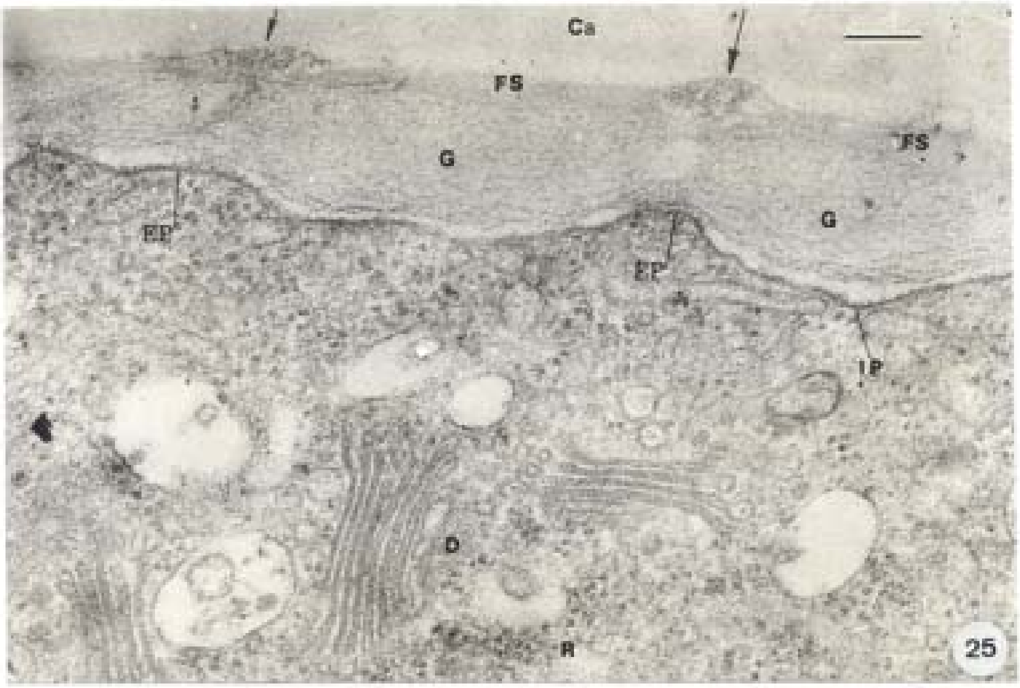
Figs. 20-21. Scanning electron micrographs of *Schisandra chinensis*. 20. A surwey of a pollen grain. 21. The reticulate sculpture of a pollen grain. 20: Bar = 1 µm. 21: Bar = 0.25 µm.

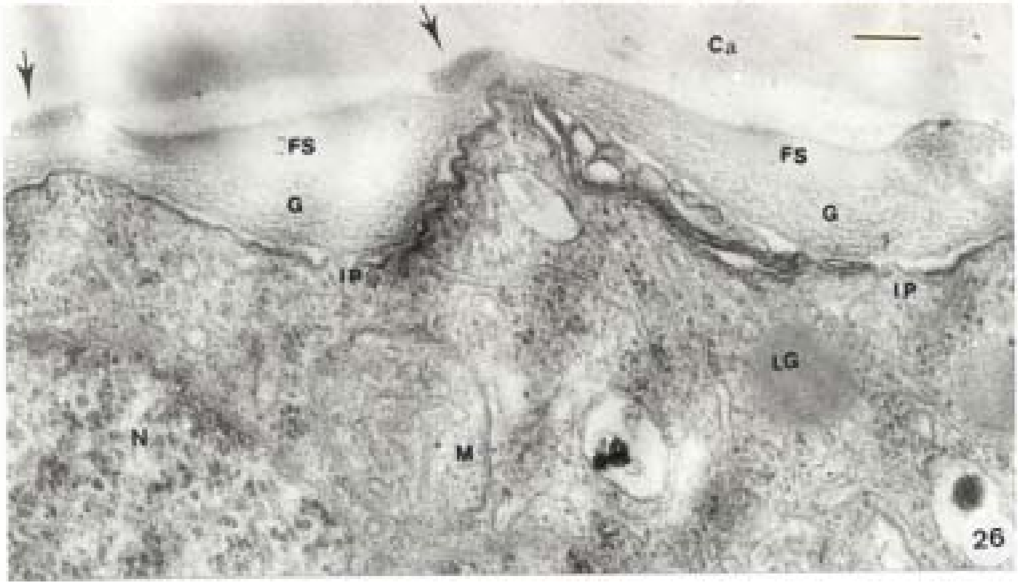
At late tetrad stage procolumellae are prominent on the evaginated tops of the plasma membrane evaginations. Between them, above invaginations, the fibrillar strands are observed (Fig. 28). Procolumellae and their enlarged protectal parts create a reticulate pattern on the surface of the microspore. The fibrillar strands occupy zones between the exine reticulum, in the places of the lumina.



Figs. 22-24. Early tetrad microspore stage in *Schisandra chinensis*. 22. There is still no signs of the glycocalyx on the surface of the plasma membrane, which will be excreted later by Golgi vesicles (GV). 23. The invaginative character of the plasma membrane in young tetrad microspore. The first signs of the glycocalyx on the cytoplasmic protrusions (arrow). 24. The appearance of the layer of the glycocalyx on the plasma membrane. (Ca: callose, EP: evagination of the plasma membrane. IP: invagination of the plasma membrane, MC: microspore cytoplasm, N: nucleus, NE: nuclear envelope, P: plasma membrane, SER: smooth endoplasmic reticulum). 22: Bar = 0.15 µm. 23: Bar = 0.3 µm. 24: Bar = 0.12 µm.

At young free microspore stage the columellae are completely formed (in section is seen only parts of them – Fig. 29). At this stage the endexine appears. It consists of several lamellae and dark contrasted granules.





Figs. 25-26. Middle tetrad microspore stage in *Schisandra chinensis.* The invaginative character of the plasma membrane is evident. The fibrillar strands (FS) are located only under the invaginations of the plasma membrane, above the glycocalyx (G), which covers all the surface of the plasma membrane. The glycocalyx located on the tops of evaginations begins to accumulate sporopollenin (arrows). (Ca: callose, D: dictyosome, EP: evagination of the plasma membrane, IP: invagination of the plasma membrane, LG: lipid globule, M: mitochondrion, N: nucleus). 25 & 26: Bar = 0.25 µm.

DISCUSSION

The reticulate exine patterns of *Illicium floridanum* and *Schisandra chinensis* pollen grains are very similar when investigated in scanning electron microscope, but this similarity is superficial. In essence, they are absolutely different. The reticulum of *Illicium floridanum* is

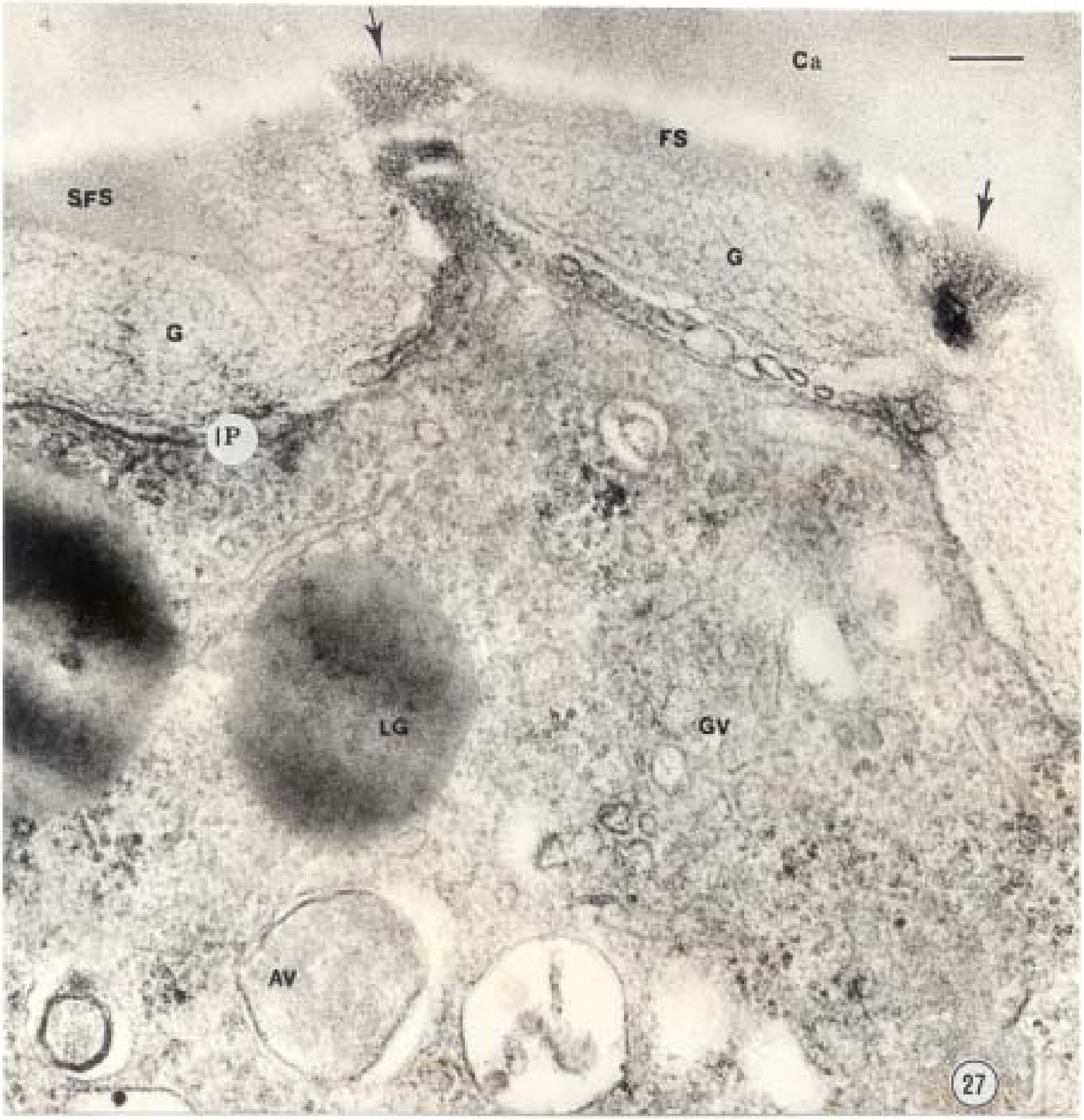


Fig. 27. Late tetrad microspore stage in *Schisandra chinensis*. The fibrillar strands (FS) which are seen above glycocalyx only under the invaginations, mark the sites of the future lumina The sites of the glycocalyx above evaginationed regions of the plasma membrane accumulate sporopollenin and acquire dark contrast of the future columellae (arrows). (AV: autophagic vacuole, Ca: callose, D: dictyosome, G: glycocalyx, GV: Golgi vesicle, IP: invagination of the plasma membrane, LG: lipid globule, P: plasma membrane). Bar = 0.12 µm.

the system of tunnels, whereas the reticulum of *Schisandra chinensis* is built of those columellae, partly covered by the tectum. As is seen from results, the ways of the development of the exine have much in common, but at the same time they are considerably different. Both species first develop the layer of the glycocalyx, consisting of separate entities – tufts (see Fig. 12). Then in both species the auxiliary structures appear - the fibrillar strands which are located in the invaginations of the plasma membrane. These auxiliary strands we call phantom structures, because, having accomplished their auxiliary role, they

Fig. 28. Late tetrad microspore stage in *Schisandra chinensis*. The formation of the procolumellae with distal widen tecta (arrows) on the evaginations of the plasma membrane. The fibrillar strands (FS), spreaded by glycocalyx, occupy the alternative invaginative sites. (Ca: callose, G: glycocalyx, IP: invagination of the plasma membrane, LG: lipid globule, R: ribosomes, SER: smooth endoplasmic reticulum). Bar = 0.25 µm.

disintegrate. Such phantom structures have already been observed during exine development in *Asimina triloba* (Gabarayeva, 1992). It is interesting to note that Takahashi (1989) observed similar strutures inside invaginations of the plasma membrane in *Caesalpinia*, which he has called radial structures (because of their asterisk form). In exine development of *Illicium floridanum* and *Schisandra chinensis* these phantom structures play different roles. As shown in results, in *Illicium* these fibrillar strands are the frame for sporopollenin accumulation around them, that results in the appearance of hollow tunnels (the archs in

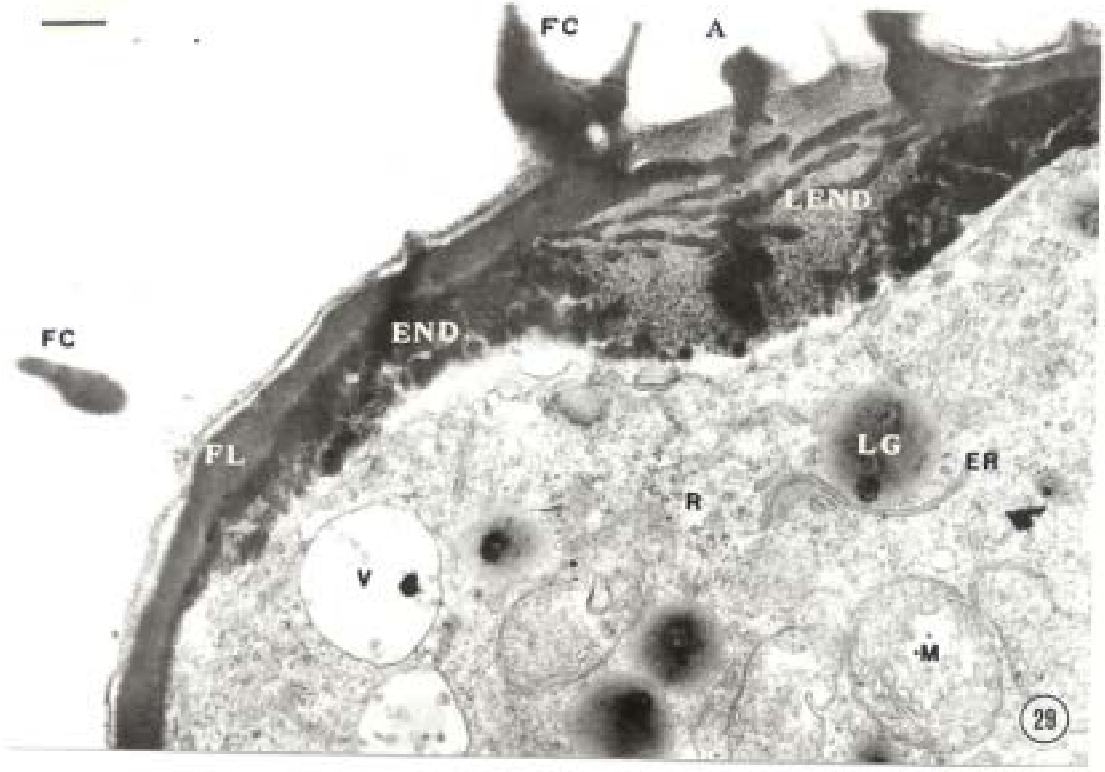


Fig. 29. Young free microspore in *Schisandra chinensis*. The formation of the endexine (END), the latter consists of lamellae (LEND: lamellae of the endexine), intermixed with granules. Under the aperture (A) the endexine is widen. Only fragments of columellae (FC) are seen in this section. (ER: cisterna of endoplasmic reticulum, FL: foot layer, LG: lipid globule, M: mitochondrion, R: ribosomes, V: vacuole). Bar = 0.25 μm.

sections). More strictly, sporopollenin accumulates on the receptors of the glycocalyx, the latter surrounds the strands of the fibrillar substance. On the contrary, in *Schisandra* in places where the strands are laid down (the invaginative regions of the plasma membrane) sporopollenin never accumulates: these are zones of future lumina. It is important that the glycocalyx underlying the fibrillar strands in invaginations in *Schisandra*, lacks evidently sporopollenin receptors. In *Schisandra,* sporopollenin accumulation is arranged only to those glycocalyx units which are located on the evaginative tops of the plasma membrane: such glycocalyx units are evidently supplied with sporopollenin receptors. The concept of sporopollenin receptors was discussed by Rowley and Skvarla (1993). On the whole, it is possible to say that the reticulate pattern in *Illicium* is formed on the invaginations of the plasma membrane, whereas in *Schisandra* it forms on the evaginations of it. In *Illicium floridanum* the convex muri appear as a result of lifting of the invaginative sites of the plasma membrane. The regular invaginative character of the plasma membrane profile plays an importante role in the formation of the reticulate pattern in both species. We called these movements of the plasma membrane macromovements (as distinct from micromovements - Gabarayeva, 2000); they create the preliminary reticulate pattern of the space conformation of the plasma membrane. These macromovements are evidently carried out with the help of microfilaments, the fragments of which were observed in our material. The importance of the invaginative character of the plasma membrane were reported earlier (Takahashi, 1989, 1995;

Takahashi and Skvarla, 1991). However, the question of what determines the space configuration of the plasma membrane is still open. Sheldon and Dickinson (1983) suggested that neither the spindle nor the cytoskeleton was involved in formation of the reticulate pattern of *Lilium*, and proposed that material was inserted into the plasma membrane to form contiguous plates. These plates then modify the properties of the membrane in a way that the evaginations that constitute the first stages of wall formation only develop between them. This is a very important observation, but we have not managed to see the formation of such plates near the plasma membrane in early development of *Illicium* and *Schisandra*. Dickinson and Sheldon (1986) also suggested that it was impossible to involve any organelles in the process of patterning, and that reticulate pattern of *Lilium* was generated by a mechanism of self-assembly operating at the plasma membrane. Skvarla and Rowley (1987) consider that receptors for future elements of exine appear directly on the plasma membrane before there is any indication of a primexine matrix. Our supposition was that receptors for sporopollenin accumulation are distributed through the glycocalyx (primexine matrix) layer by self-orientation, whereas the layer of the glycocalyx is formed by self-assembly (Gabarayeva, 1990, 1993b, 2000). The experimently simulated exines were received by Hemsley and his coauthors (Hemsley *et al.*, 2000). They suggest another possibility of formation of exine patterns by pure self-assembly from sporopollenin emulsion.

Takahashi (1994) in his paper on exine development of *Illicium religiosum* showed, however, that muri form on the evaginations of the plasma membrane. He considers that muri consist of columellae and tecta, the latter changes its configuration during free microspore period and acquire more convex form. But in Fig. 1, D and especially in Fig. 2, H, I of his paper (Takahashi, 1994) it is possible to see the same arch structures, as we observed in cross sections during exine development in *Illicium floridanum*. Archs in section view correspond to tunnels 3-dimentionally. Indeed, fractured exine in scanning electron microscope in Fig. 2, H in the Takahashi paper (1994) shows such tunnels. But Talakashi interprets the lateral sides of archs in sections as columellae, and the upper part of them as tecta. Our interpretation is that *Illicium floridanum* exine lacks descrete columellae and tecta, but consists of a system of hollow tunnels, forming around the auxiliary fibrillar strands: columella-like lateral elements of archs are seen only in sections, 2-dimentionally. Our point of view coinside with that of Walker (1976) who suggested that pollen of *Illicium* lacks columellae.

CONCLUSIONS

1. The reticulate patterns of *Illicium floridanum* and *Schisandra chinensis* seem very similar in scanning electron microscope, but ontogenetic study has shown that they are absolutely different.
2. The regular invaginative character of the plasma membrane profile plays an importante role in the formation of the reticulate pattern in both species.
3. On the whole, the reticulate pattern in *Illicium* is formed on the invaginations of the plasma membrane, whereas in *Schisandra* it forms on the evaginations of it.
4. In both species so-called phantom structures appear first – the fibrillar strands which later disintegrate.
5. In both species then glycocalyx appears on the suface of the plasma membrane, but in *Illicium* the units of the glycocalyx have sporopollenin receptors, whereas in *Schisandra* they have sporopollenin receptors only on the top of the plasma membrane evaginations.

6. In result, in *Illicium* sporopollenin accumulates on the glycocalyx *around* phantom strands (which later disappear), whereas in *Schisandra* sporopollenin accumulates exclusively on the glycocalyx *on the tops* of the plasma membrane evaginations.
7. As a consequence, in *Illicium* a reticulate system of hollow tunnels appears in the invaginations of the plasma membrane, but in *Schisandra* a reticulate pattern appears as series of semitectate columellae on the tops of the plasma membrane evaginations, whereas in places where phantom strands are located, sporopollenin never accumulates: these are places of future lumina.
8. The comparative study of sporoderm development in *Illicium floridanum* and *Schisandra chinensis* shows the importance of ontogenetic investigations for the interpretation of the mature exine structure.

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多花八角與中華五味子花粉壁發育的比較研究

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摘　　　　要

多花八角 (*Illicium floridanum*) 與中華五味子 (*Schisandra chinensis*) 花粉壁的發育過程在本文中加以研究並比較。兩種植物花粉都具有相似的網紋外壁，但它們的相似處僅在表面。在小孢子發育過程中四分小孢子時期的早期，原生質膜上都有一種具規則性凹陷的外表輪廓，這個表面凹陷的分佈型態與未來的花粉網紋外壁形態具一致性。而兩種植物的小孢子在原生質膜凹陷的位置內都會出現一種備用的 (幻像般) 纖維束構造，但在花粉外壁進一步的發育過程中逐漸出現了差異。多花八角花藥中孢粉素會圍繞著原生質膜凹陷處的纖維束沈積，導致小孢子表面形成中空隧道般的網紋雕刻，這種網紋形態在原生質膜凹陷部分隆起後卻變成凹陷狀。相反的，在中華五味子花藥中孢粉素不會堆積在纖維束周圍 (這個位置將會形成未來的網目中)，堆積卻集中在原生質膜上臘梅糖所形成的凸起頂端 (突起的位置上)。後者為圓柱體形成的位置，由於多列的圓柱體會被蓋頂層所覆蓋，而形成了網格。雖然多花八角與中華五味子具有相似的網紋外壁，但內部結構卻有差異，因此可見兩種植物的花粉外壁發育過程是不盡相同的。

關鍵詞：外壁型態、備用的構造、多花八角、中華五味子。

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