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The Tapetum: Its Form, Function, and Possible Phylogeny in *Embryophyta*

By

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Abstract: It appears that the tapetum is universally present in land plants, even though it is sometimes difficult to recognize, because it serves mostly as a tissue for meiocyte/spore nutrition. In addition to this main function, the tapetum has other functions, namely the production of the locular fluid, the production and release of callase, the conveying of P.A.S. positive material towards the loculus, the formation of exine precursors, viscin threads and orbicules (= Ubisch bodies), the production of sporophytic proteins and enzymes, and of pollenkitt/tryphine. Not all these functions are present in all land plants: *Embryophyta.* Two main tapetal types are usually distinguished in the *Spermatophyta*: the secretory or parietal type and the amoeboid or periplasmodial type; in lower groups, however, other types may be recognized, with greater or lesser differences. A hypothetical phylogenesis of the tapetum is proposed on the basis of its morphological appearance and of the nutritional relations with meiocytes/spores. The evolutionary trends of the tapeta tend towards a more and more intimate and increasingly greater contact with the spores/pollen grains. Three evolutionary trends can be recognized: 1) an intrusion of the tapetal cells between the spores, 2) a loss of tapetal cell walls, and 3) increasing nutrition through direct contact in narrow anthers.

In their early developmental stages, the anthers produce a tapetum between the sporogeneous tissue and the anther wall; the general opinion now is that the tapetal cells are of parietal origin; both the tapetal cells and the sporogeneous cells have developed originally from the same subepidermal tissue (FOSTER & GIFFORD 1959, ECHLIN 1971 a). The tapetum is of considerable physiological significance because all the nutritional material entering the sporogeneous cells/microspores/pollen grains passes or originates from it (MAHESWARI 1950, DICKINSON 1982). In addition, during certain periods of pollen development, it accumulates substantial quantities of reserve compounds (e.g. starch and/or protein crystals in

plastids, HESLOP-HARRISON 1972; lipid droplets and masses in- and outside the plastids, HESSE 1978a; soluble polysaccharides in the vacuoles, PACINI & FRANCHI 1983). These stored substances successively disappear during and after the tapetum degeneration, but several characters of mature pollen grains, which are of considerable interest in pollination, depend just on these substances. Not only is the tapetum ontogeny, form and function reviewed, but also some new insights regarding the relationships between the microspores/pollen grains and the tapetum itself are presented as well as new ideas on the hypothetical phylogeny of the tapetum types.

The Tapetum Types

Usually two main tapetum types are distinguished in the angiosperms: 1. The secretory (or parietal or glandular or cellular) tapetum, and 2. the amoeboid (or invasive or "genuine" periplasmodial) tapetum (GOEBEL 1905, SCHNARF 1929). It should be stressed that these two main types are variously subdivided by several authors using different criteria. A key (Table 1) to the tapetum subtypes corresponding with the descriptions in Fig. 2 and Table 6 is presented.

The characters of the tapetum types vary, especially after meiosis during tapetum degeneration, and the differences can become blurred: e.g. CARNIEL (1963) points out that a "secondary" (= "false" sensu CARNIEL) periplasmodium can arise from both a cellular or a "primary" ("real") periplasmodial tapetum. Some authors have based their classifications on the number and ontogeny of the nuclei in the tapetal cells (WUNDERLICH 1954, CARNIEL 1963, BUSS & LERSTEN 1975, D'AMATO 1977). An enumeration of all tapetum types reported in literature is nearly impossible. Basically, this great diversity, however, can be reduced to the two main types. To date it is known that a parietal tapetum is characteristic for 175 angiosperm families, 88% of which are dicots. An exclusively amoeboid tapetum has been found and described in 32 angiosperm families, only 14 of which are dicots. Both tapetum types are present in 12 families. The tapetum character of c. 177 families is unknown (Table 2) (see also DAVIS 1966).

The role of the tapetum types with respect to the produced material is different: All the substances produced by the secretory tapetum reach the microspores/pollen grains via the locular fluid (PACINI & JUNIPER 1979b). In contrast, in the amoeboid tapeta, the cytoplasm adheres closely to the microspores (DICKINSON & POTTER 1976, HORNER & PEARSONS 1978, PETTITT 1979a, b, SHEFFIELD & BELL 1979, BELL 1981, OWENS & DICKINSON 1983, PACINI & JUNIPER 1983), although it should be stressed again that in later developmental (i.e. degeneration) stages, the resulting substances do not allow a distinction between the former amoeboid or secretory

Table 1. Dichotomic key for tapetum subtypes. The numbers refer to the drawings of these tapetum types in Fig. 2

Tapetal cells with or without walls and more or less retaining their shape	Tapetal cells with persistent walls	Tapetal cells surrounding the loculus	**1**
		Tapetal cells enclosing spores whose walls lignify at the end of their life and become elaters	**2**
		Tapetal cells more or less enclosing spores and retaining a thin wall till degeneration; elaters present or not	**4**
	Tapetal cells lacking walls (except the outer tangential one) after tetrad stage and surrounding the loculus (parietal tapetum)	Many microspores/pollen grains in a cross section of the anther	**5**
		Few microspores/pollen grains (5–12) in a cross section of the anther. Monoaperturate pollen grains, pores oriented towards tapetum	**8**
Tapetal cells not retaining their shape loosing their walls	Tapetal cells loose their walls and intrude only after a transient parietal phase	Tapetal cell cytoplasms do not fuse	**6**
		Tapetal cell cytoplasms fuse to form a real periplasmodium	**7** p.p.
	Tapetal cells may loose their walls at different stages but their cytoplasms fuse immediately	Tapetum (amoeboid tapetum in ferns) enclosing iso-, micro- or megaspores	**3**
		Tapetum (amoeboid tapetum in angiosperms) enclosing microspores/pollen grains	**7** p.p.

Table 2. Tapetum types in the angiosperm families (according to DAVIS 1966, with some modifications and additions). The amoeboid tapetum is well represented in the monocots, while the parietal tapetum dominates by far in the dicots. Note the rather large number of families with unknown tapetum characters

Tapetum character	Families of Dicots	Monocots
Parietal tapetum	154	21
Amoeboid tapetum	14	18
Both types in the same family	11	1
Presumably parietal tapetum	13	2
Angiosperm families investigated	**192**	**42**
	234	
Families not yet investigated	177	

tapetum. It should also be pointed out that in secretory tapeta, the cells are polarized both in structure and function, while the cells of the amoeboid tapeta are not. The inner and the outer tangential faces of the secretory tapetum differ in their capacity to release certain substances, e.g. the outer tangential face is apparently not concerned with material secretion (with the possible exception of orbicules). The polarity of the tapetum cells is also expressed by the intercellular tapetal space (radial cell faces) through which secretion also takes place (PACINI & JUNIPER 1979b): a gradient from the outer to the inner face of the tapetum cells exists with respect to the timing of cell wall solution, and the production and the release of the various stored substances. Conversely, no polarity is found on the cell surface of the amoeboid tapeta (MEPHAM & LANE 1969, LOMBARDO & CARRARO 1976, DICKINSON & POTTER 1976, ROLAND-HEYDACKER 1979, PACINI & JUNIPER 1983), even if (e.g. in *Arum italicum*) two zones are temporarily evident in the periplasmodium: one zone just surrounds the microspores (with polyribosomes, microtubules, vesicles and few dilated ER cisternae), while the other zone (with nuclei, mitochondria, plastids, small vacuoles, ribosomes) does not (PACINI & JUNIPER 1983)*.

* In some species, the secretory tapetum cells are of different sizes and are present in the same microsporangium region ("dimorphic tapetum" according to VIJAYARAGHAVAN & RATNAPARKHI 1973, and GUPTA & NANDA 1978a, b), but this dimorphism is probably only a morphological character, no proof exists that it is correlated to the tapetum function. Furthermore, the interpretation of some tapetal cytoplasmic elements differs: MEPHAM & LANE (1969) defined the amoeboid tapetum plasmamembrane surrounding the microspores of *Tradescantia bracteata* as if the spores were in a vacuole: the tapetal plasmamembrane appears retracted from the exine (Fig. 7 in MEPHAM & LANE 1969).

In both tapetum types, the produced substances are either "ready-made" (Table 3: the locular fluid, the callase, the PAS-positive content, partly the sporophytic proteins) or become polymerized after their release (the exine precursors, the viscin threads, the culture sac, the orbicules, the pollenkitt/tryphine substances, and partly the sporophytic proteins). As already mentioned above, the mode of nutrition in the two main tapetum types is quite different: The locular fluid (locular sap according to SUNDERLAND & al. 1984), which mostly occurs only in the secretory tapetum, represents an infiltrating medium between the sporophyte and the developing gametophytes. This intermediate fluid, which vehiculates nutritients, is extremely reduced in volume or even absent in amoeboid tapeta and in some particular parietal ones. The nutrition of meiocytes/microspores/pollen grains therefore takes place indirectly in secretory tapeta and directly in amoeboid tapeta.

The advantages or disadvantages of the two main tapetum types can be seen as follows: The main advantage of amoeboid tapeta is that nutrition can take place without the locular fluid as an intermediate, while the main disadvantage is that this can only take place in small anthers with few microspores/pollen grains per locule. In contrast, the main advantage of the secretory tapetum is that the anthers may be large with many microspores/pollen grains per locule, while its main disadvantage is the need of water inside the locule to protect against dehydration and to transfer nutrients via the locular fluid. To maintain a cavity full of fluids for periods ranging from a few days up to some months, even if protected by anther walls, corolla and calyx, is not easy, especially for plants in arid areas. Thus it could be expected that water plants possess parietal tapeta, but this is not the case. On the contrary, parietal tapeta are common in plants growing in dry habitats whilst amoeboid tapeta are common in monocots growing in wet habitats (with the only exception of the *Typhaceae*). According to SCHNARF (1929), DAVIS (1966), and DAHLGREN & CLIFFORD (1981), of 18 monocot families found predominantly in wet habitats only one is known to have a parietal tapetum, while in monocot families occuring in predominantly dry habitats, the converse is found, i.e. only one out of 10 checked families has an amoeboid tapetum. In the dicots, the situation is similar to that in the monocots, but is not as significant.

The tapetum degeneration process takes place in different ways. On the one hand, some residual substances are formed, which are later found mostly on or near the pollen surface (e.g. tryphine-pollenkitt coatings originating from the lipid production by the plastids and from particular other cell organelles: CARNIEL 1971, DUNBAR 1973, HESSE 1978a, 1979a, b, 1980; PACINI & CASADORO 1981). This type of tapetum degeneration process may vary greatly in detail; the percentage amount of active,

synthesizing organelles especially depends on the mode of pollination or other ecophysiological conditions. The systematic position of the plants concerned, does not indicate the mode of tapetum degeneration process, at least not in the lower taxonomic categories. On the other hand, the tapetum may degenerate without leaving or hardly leaving any residue: the pollen surface is nearly free of tapetal derivates, while the degenerated tapetum material itself remains enclosed within tapetal membranes. This feature is especially predominant in several strictly wind-pollinated taxa (Hesse 1980, 1984a, and unpublished).

The beginning of the tapetum degeneration is also very variable. In taxa with amoeboid tapeta as in *Tradescantia bracteata* (Mepham & Lane 1969), *Rhoeo discolor* (Albertini & al. 1981, Souvré & Albertini 1982), *Rhoeo spathacea* (Nanda & Gupta 1977), *Arum italicum* (unpublished results of our own), and *Helianthus annuus* (Horner & Pearson 1978) tapetum degeneration only begins after the first haploid mitosis division has taken place. In secretory tapeta, degeneration may take place between the stage of microspore release and the first haploid mitosis, as in *Pinus banksiana* (Dickinson & Bell 1976), *Helleborus viridis* (Echlin & Godwin 1968), *Beta vulgaris* (Hoefert 1971), *Sorghum bicolor* (Christensen & al. 1972), *Allium cepa* (Risueño & al. 1969), *Lilium longiflorum* and *L. henryi* (Heslop-Harrison & Dickinson 1969); but in *Olea europaea* (Pacini & Juniper 1979b), *Citrus limon* and *Prunus avium* (our unpublished data), however, it occurs after the first haploid mitosis.

Tapetum Origin, Form, and Function

Although the nourishing function of the tapetal cells probably starts after the differentiation of the anther tissues, it has at the beginning a low rate because the microspore mother cells/meiocytes are encased in a callosic wall and the tapetum cells are also enveloped by a mostly cellulosic wall. Later on, however, the flow of nutrients increases, as all the tapetum cells loose their walls and the callose disappears. The callosic wall is formed during the prophase between the pectocellulosic wall and the plasmalemma. Due to its very low permeability it acts as a molecular filter between the sporophyte and the gametophyte (Heslop-Harrison & Mackensie 1967, Southworth 1971). Isolated meiocytes develop in a simple culture medium from the early prophase until the tetrad stage (Ito & Stern 1967); this means that during this period the tapetum has very little influence on the meiocytes. In the "successive" type a new callosic wall is formed after the first meiotic division separating the dyads and after the second division the spores from one another. In the "simultaneous" type of microspore ontogenesis, no walls are laid down until the second meiotic division has been completed.

WILLIAMS & HESLOP-HARRISON (1979) have shown that in the tapeta of *Rhoeo spathacea* (amoeboid) and *Lilium longiflorum* (secretory), RNA synthesis follows a very similar pattern, and massive protein synthesis starts at the very beginning of the microspore period, just in anticipation of the final maturation of the anther, when the main transfer of tapetal material to the pollen grains takes place. This activity ends at the tapetal degeneration period, when some of the degeneration products are the last nutritive substances available to the pollen grains. A similar process of RNA transient accumulation also occurs in the parietal tapetum of *Hyoscyamus niger* during microsporogenesis (RAGHAVAN 1981).

Nutrients are absorbed by spores and pollen grains mainly via the apertures or the minor exine foramina, but a certain amount may pass through the little channels and lamellae separating the exine molecular units (ROWLEY & FLYNN 1971, PETTITT 1976, ROWLEY 1981, ROWLEY & al. 1981).

The roles commonly ascribed to gymnosperm and angiosperm tapeta, aside from their essential role in nutrition, are presented in Table 3, and should be compared with the former, much shorter lists given in MASCARENHAS (1975) and WALLES & ROWLEY (1982); the occurrence of the same functions in *Bryophyta* and *Pteridophyta* is described only if known. Functions typical of only one kind of tapetum are also reported:

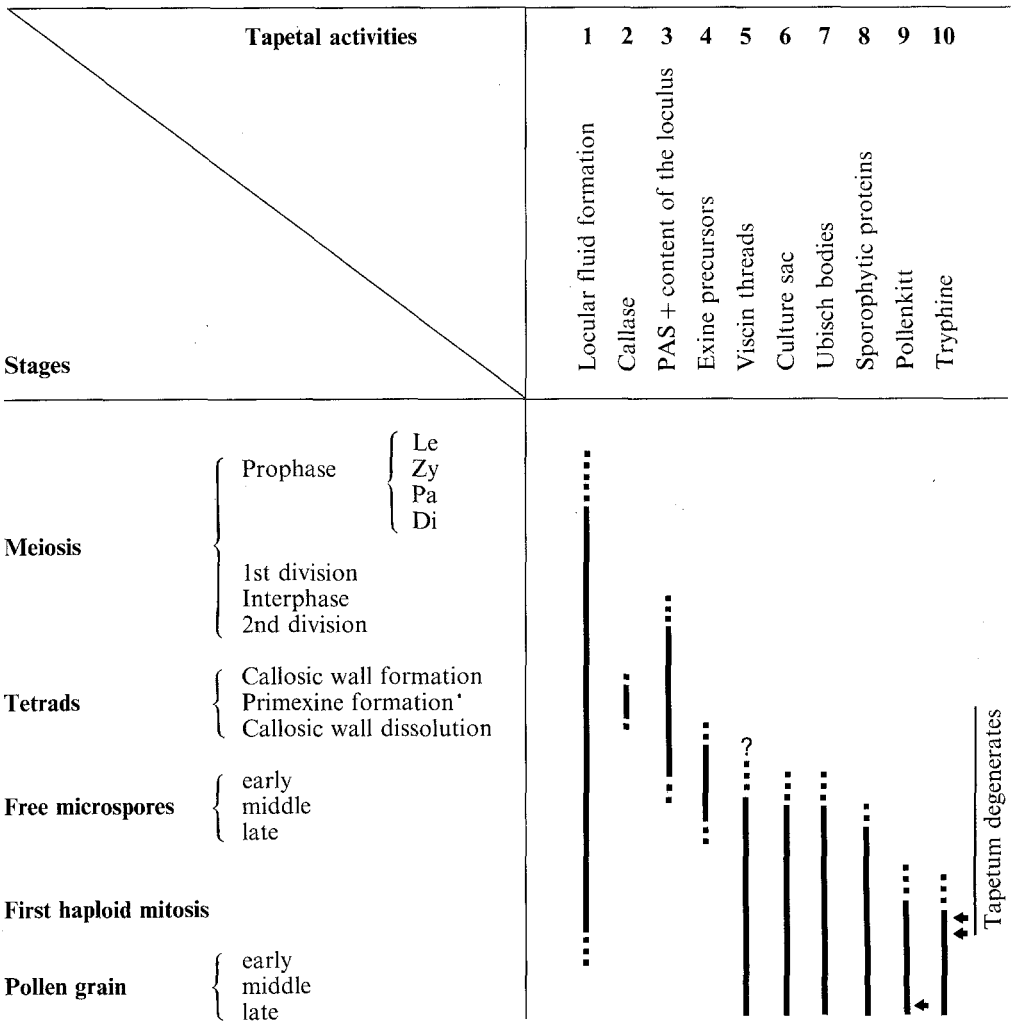
1. Formation of the locular fluid: a poorly known substance only known to occur in secretory tapeta. In the angiosperms the locular cavity increases in size during the anther development; the locular fluid is continually supplied by the tapetum at least until it starts to degenerate (PACINI & FRANCHI, unpublished).

2. Production and release of callase: This enzyme depolymerizes the callosic walls of the tetrads (MEPHAM & LANE 1969, IZHAR & FRANKEL 1971, STIEGLITZ 1977) and the microspores are released. The tapetum then becomes very active and has a multiple function (see below 3. until 10.). Interestingly, cytochemical methods do not reveal callose encapsulating the sporocytes and spores in mosses and ferns (WATERKEYN & BIENFAIT 1971, BIENFAIT & WATERKEYN 1976). On the contrary, in gymnosperms a thin callosic wall is present around the microspores/tetrads in *Larix europaea*, and a thick one in *Ephedra sinica* (ROSSI, pers. comm.).

3. Conveyance of PAS-positive material into the locule: It is present in the tapetal vacuoles from the second meiotic division onward, until the early microspore stage in some gymnosperms and angiosperms (DICKINSON 1970, HIDEUX & ABADIE 1980/81, GORI & FERRI 1982, GORI 1982, PACINI & FRANCHI 1983).

4. Formation of exine precursors: Whilst there is a broad consensus on the role exerted by the tapetum producing exine precursors, e.g. carotenes and carotenoid esters in angiosperms (ECHLIN 1971b, DICKINSON 1976a),

Table 3. Tapetal activities during pollen grain development in *Spermatophyta*. Tapetal activities are staggered in time; 1 and 2 are not present in the ripe anther/pollen grains, 3 is absorbed by microspores, the other persist being polymerized or deposited on anther/pollen grains surfaces. The arrows indicate the main deposition periods



very little information is available on the formation of the exine in ferns (PETTITT 1979a, b). It was confirmed recently that the intervention of the tapetum builds up at least some exine layers (LUGARDON 1978, PETTITT 1979a). BROWN & LEMMON (1980) in a paper on spore wall formation in a moss state: "Of considerable interest is the occurrence of exine papillae

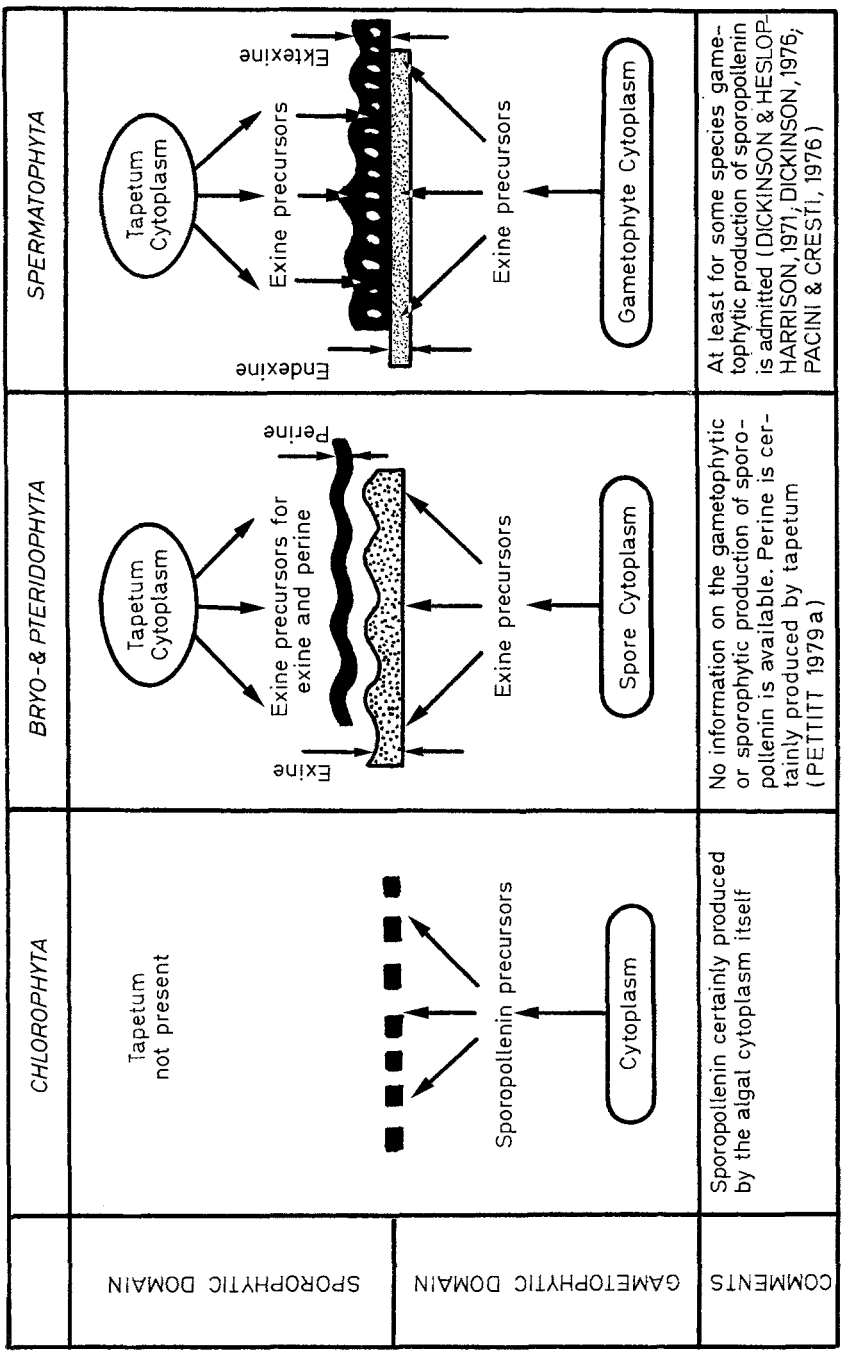


Fig. 1. The origin of sporopollenin in *Euphyta* (*Chlorophyta, Bryophyta, Pteridophyta,* and *Spermatophyta*)

which arise late in the spore wall development and cannot be correlated with any internal spore activity. Studies on the role of the tapetum in moss spore wall development are certain to provide much useful information". An additional, very elaborate layer ("perine" or "perispore" according to BOWER 1935) is superimposed on the fern exine; it is produced by the tapetum cytoplasm (KONAR & KAPOOR 1974, PETTITT 1979a, LUGARDON 1978). According to LUGARDON (1978) both the cytoplasm of the spores and the cytoplasm of the tapetum participate in the making of the exospore as well as in the making of the exine, but the exact amount required for each layer is not known (Fig. 1).

A sporopollenin layer, continuous or forming rods, is also found around cell walls (often spores) of some moulds and green algae (BROOKS & SHAW 1971, 1978, BURCZYK & HESSE 1981, HONEGGER & BRUNNER 1981, GOOD & CHAPMAN 1978; SIMONS & al. 1982, DE VRIES & al. 1983): in these examples of often unicellular organisms, sporopollenin precursors are without doubt produced by the cytoplasm itself.

It should be borne in mind that the intervention of the microspore cytoplasm may play a role in the formation of some inner layers of the exine, at least in some angiosperms (DICKINSON & HESLOP-HARRISON 1971, DICKINSON 1976 b, PACINI & CRESTI 1976). MEPHAM & LANE (1969) and MEPHAM (1970) consider that in *Tradescantia bracteata*, exine precursors are secreted by the microspore itself but the polymerization seems to be controlled by the sporophyte. Fig. 1 summarizes our knowledge on the origin and the disposal of sporopollenin in Green Algae, Bryo- and Pteridophyta, and Spermatophyta.

5. Formation of viscin threads, i.e. long, flexible, fragile sporopollenin ropes or strands on the surface of pollen tetrads or single pollen grains coalesced with the exine itself. They occur in the *Onagraceae*, in some *Ericaceae*, and in a few *Caesalpiniaceae* (SKVARLA & al. 1976, HESSE 1981a, b, 1984b). Although they are extremely similar to the exine with respect to their ultrastructure, staining reactions etc., their exact ontogeny is not yet known. ROWLEY & al. (1983) maintained, that the viscin threads are connected with the locular wall: The viscin threads would not act then as pollen-connecting fibres for transferring the "pseudo-pollinia" by pollinating animals.

6. For the formation of an acetolysis-resistant membrane, the so-called "culture sac": It invests the tapetum and, after its degeneration, the developing microspores in some *Asteraceae* (HESLOP-HARRISON 1969), in *Acacia* (KENRICK & KNOX 1979), in *Pinus* (DICKINSON 1970, WILLEMSE 1971) and most probably also in other gymno- and angiosperms. Recently PETTITT (1979 b) found a similarly organized layer in the fern *Botrychium lunaria*.

7. For the formation of orbicules (Ubisch bodies): These sporopollenin bodies occur mostly on the inner (tangential and/or radial) cell walls of the tapetum cells (CARNIEL 1967, ECHLIN 1971b, PACINI & JUNIPER 1979b, AUDRAN 1979, 1981). Their shape and dimension are species-specific; some lack the pro-orbicular core, which is seen as most representative for orbicules (CHRISTENSEN & al. 1972, DUNBAR 1973, ROWLEY & SKVARLA 1976, DICKINSON 1976b, HESSE 1985). The orbicules have been reported up to now only in association with parietal tapeta. Sometimes, in gymnosperms (NILSSON & al. 1977, PACINI & FRANCHI unpublished), they appear to adhere to the exine surface, whilst in angiosperms all similar observations remain unproven. Probably analogous bodies are also found in ferns (LUGARDON 1981). BROWN & LEMMON (1984) however report that in *Andreaea rothii* degenerated tapetal cells are coated "by an electron-dense material similar to the perine of spores"; in mosses, orbicules seem to be lacking. The orbicules should be seen merely as sporopollenin concretions homologous with the exinous sporopollenin; they neither act as sporopollenin surplus nor as a sporopollenin intermediate or for storage nor – as is sometimes supposed – as pollenkitt (HESLOP-HARRISON & DICKINSON 1969, ECHLIN 1971b, HESSE 1985).

8. For the formation of sporophytic proteins and enzymes; these are deposited next to the aperture regions (PACINI & JUNIPER 1979a, PACINI & al. 1981) or preferably in the interaperturate areas (HESLOP-HARRISON & al. 1973, HESLOP-HARRISON 1975). Enzymes of sporophytic origin have also been detected in the perine of some Pteridophyta (PETTITT 1979a, b).

9. For the formation of tryphine, which in contrast to pollenkitt (see below), is comprised of a mixture of hydrophobous and hydrophilous substances often containing cytoplasmic elements (degenerated organelles); in practice it is difficult to distinguish between tryphine and pollenkitt, as at the beginning of material deposition, lipid pollenkitt lumps are often intermingled with some cytoplasmic hydrophilic derivatives (now called tryphine), while later on only the lipids form an oily pollen surface layer, representing the classical "pollenkitt". The tryphine, best investigated to date in some *Brassicaceae*, is deposited outside the pollen grains (ECHLIN 1971a, DICKINSON & LEWIS 1973a, b; AUDRAN & BATCHO 1981). It is not only responsible for the variable stickiness of the pollen surface (mostly due to its lipid components), but very probably contains several enzymatic substances as well. After the rupture of the tapetal protoplasts apparently caused by plasmalemma breaks (*Raphanus*: DICKINSON & LEWIS 1973b), the cytoplasmic content is released into the loculus. At first the cell organelles are still present, degenerating only later to form the tryphine coating.

10. Formation of pollenkitt, an hydrophobic, oily layer containing mainly lipids and carotenoids. The tapetal cell organelles (mostly the

plastids, perhaps other organelles, too) form lipid masses (DUNBAR 1973, HESSE 1978a, PACINI & CASADORO 1981); hydrophilic components for the formation of "tryphine" are practically absent. The lipid masses are deposited outside the mature pollen grains just before they are released (HESLOP-HARRISON 1968a, ECHLIN 1971a, HESSE 1978b, 1979b, 1980, 1981b). It should be stressed that pollenkitt is not absent in any of the anemophilous angiosperms investigated so far. At least a small amount is produced by the anther tapetum. Tiny droplets of lipid material are mostly placed on the exine surface or in exine caves, while larger masses remain inside the degenerating cytoplasm. These distribution modes may, therefore, be interpreted as an "inactivation" procedure of the pollenkitt production in anemophilous angiosperms, as e.g. in the *Betulaceae, Fagaceae, Salicaceae*, and *Poaceae* (HESSE 1978b, 1979b, 1980, and unpublished). In contrast to the angiosperms, in which pollenkitt is universally present it is totally lacking in the gymnosperms (HESSE 1984a).

The Tapetum's Influence on Pollen Grain Shape and Size

Independently of the tapetum type, nutrients can be absorbed over the entire spore or pollen grain surface (both the poral and the interporal areas) (ROWLEY & FLYNN 1971, PETTITT 1976, ROWLEY 1976, 1981, ROWLEY & al. 1981). If spores or pollen grains, however, are gathered in dyads, tetrads, polyads or massulae, the absorbing external surface of each grain is progressively reduced, and in the massulae there are single grains or tetrads which are completely enclosed inside the massula itself, without direct contact with the tapetum (COCUCCI & JENSEN 1969). On the other hand, however, the inner exine walls, or sometimes the intine itself, of joined grains are generally reduced or even discontinuous so that nutrients may pass easily through and ensure the nutrition of inner spores/pollen grains (COCUCCI & JENSEN 1969, LINSKENS & SUREN 1969, NIEZGODA & al. 1983, ZAVADA 1983). This also ensures a synchronous pollen development (HESLOP-HARRISON 1968b).

Families with "clumped" pollen are listed in Table 4, and the respective tapetum type is reported. The parietal tapetum is by far the most dominant. Obviously it is more successful in nourishing "clumped" pollen, but in some taxa additional features may occur: The often multilayered parietal tapetum of some *Asclepiadaceae* does not loose its walls, e.g. in *Asclepias curassavica* (LINSKENS & SUREN 1969), *Pergularia daemia* (VIJAYARAGHAVAN & SHUKLA 1981), and *Calotropis procera* (DAN DICKO-ZAFIMAHOVA & AUDRAN 1981). Another interesting feature occurs in some *Annonaceae, Balsaminaceae, Convolvulaceae, Gentianaceae, Mimosaceae, Loranthaceae, Onagraceae, Plumbaginaceae, Rhizophoraceae* (LERSTEN 1971), *Myrsinaceae, Sterculiaceae, Flacourtiaceae* (ENDRESS & VOSER

Table 4. List of angiosperm families which form pollen dyads, tetrads, polyads or massulae. For each family the presence of monads and the known tapetum type is also reported (data mainly from SCHNARF 1929, ERDTMAN 1952, and DAVIS 1966; some data are integrated from KENRICK & KNOX 1979[1], from PETTITT 1981[2], and from our own investigation[3]). The presence of a certain character is indicated by x; if two or more types are present, the prevalent one is denoted by xx; uncertain data of tapetum types are indicated by a question-mark

	Monads	Dyads	Tetrads	Polyads	32-Massulae	Tapetum	
						parietal	amoeboid
Agavaceae	xx		x			x	
Annonaceae	xx	x[3]	x			x	
Apocynaceae	xx		x			x	
Araceae	xx		x				x
Asclepiadaceae			xx		xx	x	
Begoniaceae	xx		x			x	
Berberidaceae	xx		x			x	
Bignoniaceae	x		x				x
Bromeliaceae	xx		x			x	
Caesalpiniaceae	xx		x			x	xx
Chlaenaceae	x					?	?
Clethraceae	xx		x			x	
Cornaceae	xx		x			x[3]	
Cucurbitaceae	xx		x			x	
Cynomoriaceae			x?			?	?
Datiscaceae	xx		x			?	?
Droseraceae	x		xx			x	
Empetraceae			xx			?	?
Ericaceae	x		xx			x	
Gentianaceae	xx		x			xx	x
Goodeniaceae	xx		x			x	
Guttiferae	xx		x			x	
Hydrocharitaceae	x		x[2]				x
Juncaceae			xx			x	
Lactoridaceae			xx			?	?
Marcgraviaceae	xx		x			x	
Mimosaceae	x		x	xx	x	x	x[1]
Monimiaceae	xx		x			x	
Myrothamnaceae			xx			?	?
Nepenthaceae			xx			?	?
Nympheaceae	xx		x			x	
Oenotheraceae	xx		x			x[3]	
Orchidaceae	x		x		xx	x	
Pedaliaceae	xx		x			x	
Philydraceae	xx		x			x	
Podostemaceae	xx	x				x	
Proteaceae	xx		x			x	
Pyrolaceae	xx		x			x	
Rubiaceae	xx		x			x	
Sapindaceae	xx		x			x	
Saxifragaceae	xx		x			x	
Scheuchzeriaceae		x					x
Solanaceae	xx		x			xx	x
Thurniaceae			x			?	?
Tiliaceae	xx		x			x	
Typhaceae	x		x			x	
Velloziaceae	x		x			x	
Winteraceae			x			x	x

1975), and *Orchidaceae-Epidendroideae* (DRESSLER 1981): the anthers can be septate, so that each locule is divided into small subloculi, thus resulting in a closer contact between the tapetum and the pollen grains as the tapetum also cover the septa. In some of the cited angiosperm families, pollen grains are loose but in the case of "clumped" pollen each sublocule is completely filled ensuring an intimate contact with the tapetum (KENRICK & KNOX 1979). A similar feature also occurs in pteridophyta groups, for example in the micro- and megasporangia of *Isoetes* sp., *Psilotum triquetur, Tmesipteris tannensis, Equisetum limosum*, and *Selaginella spinulosa* (GOEBEL 1905, BOWER 1959).

Another unusual pollen grain shape is present in some seagrasses (*Hydrocharitaceae, Posidoniaceae, Cymodoceaceae, Zosteraceae*) with thread-like pollen (ERDTMAN 1952, ZAVADA 1983): the tapetum is always amoeboid (DAVIS 1966, DUCKER & al. 1978, PETTITT 1981). The particular shape, their elongated form, the inaperturate condition, and the sometimes enormous length obviously require that the tapetum be in close contact with entire grains in order to ensure uniform nutrition.

Tapetum Types in Land Plants and Their Possible Evolution

Although BOWER (1959) states that the tapetum is not a constant in all sporangia and anthers of land plants and "sometimes it is not differentiated at all, a condition which holds through the *Bryophyta*", other authors recognize the occurrence of this tissue in the *Bryophyta* (PAOLILLO 1964, 1969; EYMÉ & SUIRE 1971; JENSEN & HULBARY 1978; BROWN & LEMMON 1980, 1982, 1984), whilst some use the terms "nutritive cells" (KELLEY & DOYLE 1975), "elater mother cells" (INOUÉ & SHIMAMURA 1981), or "spore sac layer cells" (MUELLER 1974). GOEBEL (1905), however states that "the idea of the tapetal cells is not morphological, but is only functional" because "the significance of the tapetum is nutritive". In our opinion, the tapetum is a constant for sporangia and anthers: it is a specialized tissue for spore nutrition and probably the source of sporopollenin precursors; it must be present in all groups of land plants, even if only for a very short time or if it is (especially in lower plants) difficult to recognize.

A short note on hypothetical phylogenetic trends of the tapetum in sporangia and anthers of land plants was given by PACINI & FRANCHI (1982a); the present paper aims to broaden this concept*. We regard the less specialized cells as representing the most ancient type of the tapetum: they should neither loose their walls, nor should they undergo further differentiation surrounding the locular cavity until degeneration. This

* One should bear in mind the characters of the various tapetum types/subtypes as given in Table 1 and 6.

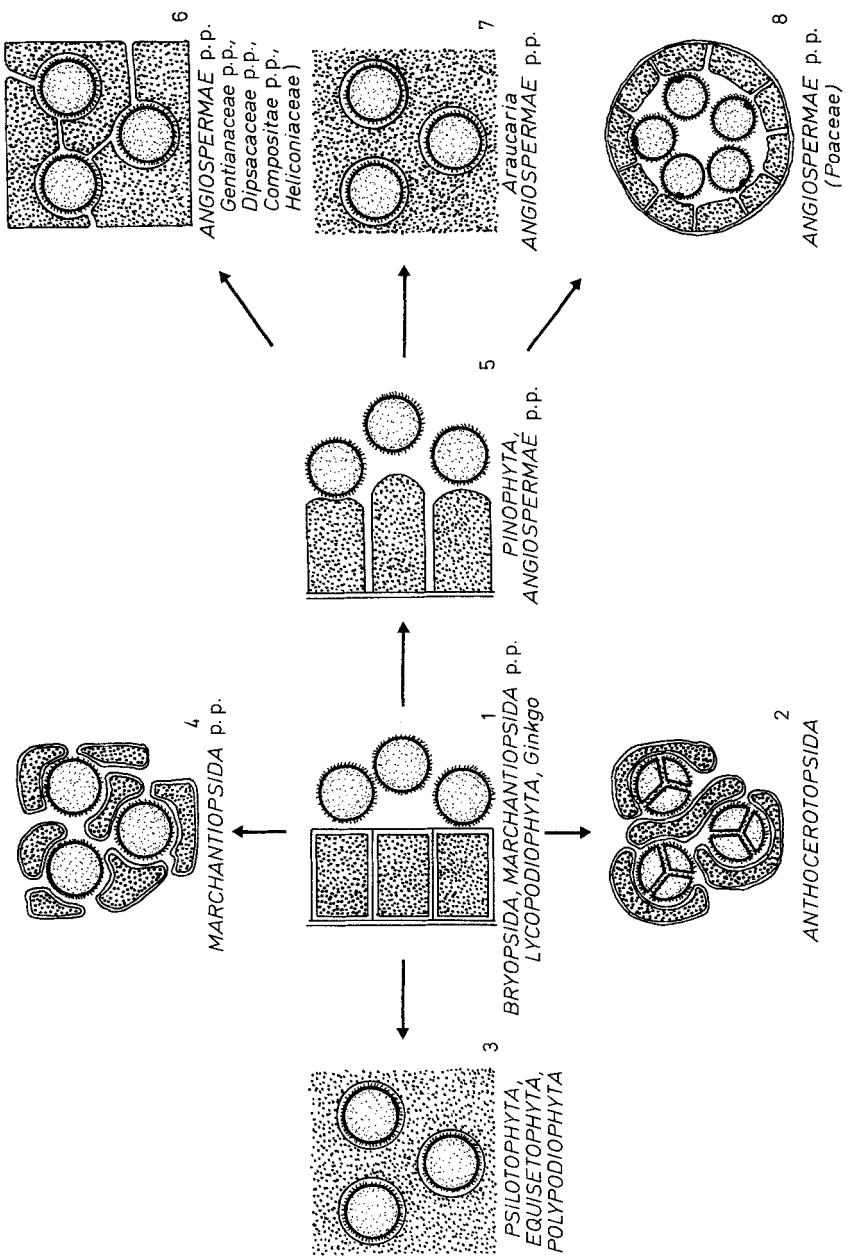


Fig. 2. Hypothetical phylogenesis of most of the tapetum types, based only on extant taxa. The tapeta are shown in their most active trophic phase; for details and the numbering refer to the text

kind of tapetum is present in the *Bryopsida, Marchantiopsida* p.p., and *Lycopodiophyta* (COULTER & al. 1910, FOSTER & GIFFORD 1959, JENSEN & HULBARY 1978, BROWN & LEMMON 1980, 1982, BROWN & al. 1982, BUCHEN & SIEVERS 1976, 1978) (Fig. 2/1). Due to the persisting cell walls, the passage of nutrients and of other material to the loculus is rather slow. Nevertheless a peculiar loculus type is present in mosses in the shape of a hollow cylinder, covered on both sides by the tapetum and containing two or three rows of spores in cross section (JENSEN & HULBARY 1978); this feature seems to facilitate spore nutrition.

From this ancestral type, some important modifications exist, mainly by the intrusion of tapetum cells into the loculus. In *Anthocerotopsida*, the tapetum cells, arranged in cylindrical rows, do not loose their walls, and surround the spores, which are arranged in tetrads. After the exine formation, the tapetum cell walls become thicker evidently by means of lignification, and are transformed into elaters (VAN THIEGHEM 1884, SCHUSTER 1966, PACINI & FRANCHI unpublished) (Fig. 2/2). Further more, in some *Marchantiopsida*, the tapetal cells also intrude retaining their walls and their shape, but only in some examples they are transformed into elaters, whilst in others they maintain their nutritive function surrounded only by a thin wall, until their degeneration (KELLEY & DOYLE 1975, INOUÉ & SHIMAMURA 1981) (Fig. 2/4). Apart from the role of the elaters in spore dispersal, these modifications of the tapetum should be interpreted as a first step towards a more active spore nutrition, due to the direct contact between the spores and the tapetal cells.

The maximal contact between the spores and the surrounding sporophyte occurs when the tapetal cells lose their walls during intrusion (BILDERBACK 1978, SHEFFIELD & BELL 1979, PETTITT 1979a) and fuse to form a real periplasmodium (Fig. 2/3), for example, in *Psilotophyta* (FOSTER & GIFFORD 1959, SPORNE 1962), *Equisetophyta* (FOSTER & GIFFORD 1959), also in the *Osmundales, Ophioglossales* (COULTER & al. 1910, FOSTER & GIFFORD 1959), *Filicales* (MANTON 1950, SHEFFIELD & BELL 1979), *Salviniales* (COULTER & al. 1910, KONAR & KAPOOR 1974) and *Marsileales* (BILDERBACK 1978), i.e. all the orders of the *Polypodiophyta*. This intrusion generally starts during the late meiotic prophase (FOSTER & GIFFORD 1959, KONAR & KAPOOR 1974). In *Psilotum nudum*, however, tapetum cells are already intermingled with spore mother cells when the archesporial tissue starts to differentiate (FOSTER & GIFFORD 1959). For a better understanding of the tapetum modifications in the Spermatophyta, it is necessary to examine the "female" tapetal features: Interestingly, a counterpart of the anther tapetum occurs around the megasporangia/embryo sacs, the ovular tapetum. Heterosporic genera of the *Lycopodiophyta* and *Polypodiophyta* (e.g. *Selaginella, Isoetes, Marsilea, Salvinia*) exhibit the same tapetum type in mega- and microsporangia. In

the *Spermatophyta*, which are all heterosporic, the tapetum is always present around the developing male gametophyte, and sometimes also around the female ones. In the ovules of the *Pinatae*, the tapetum, usually called "spongy tissue" (SINGH 1978) is – with some exceptions – generally present. This tissue, besides its nutritive role, also forms an ornamented exine wall around the megaspore and the developing gametophyte (SINGH 1978, SINGH & OWENS 1981, OWENS & al. 1982). The "spongy tissue" sometimes looses its walls, while sometimes it also forms an acetolysis-resistant wall (SINGH 1978), and the formation of Ubisch bodies is also reported (SINGH & OWENS 1981). In the angiosperms – generally in sympetalous plants with unitegmic and tenuinucellate ovules – a tapetum also surrounds the embryo sac: usually it is called endothelium or "integumentary tapetum" (KAPIL & TIWARI 1978), and only has a nutritive function not forming sporopollenin. Although the integumentary tapetum is absent from the primitive superorders of the dicotyledons and perhaps from all of the monocotyledons, it is present in the highly evolved groups and can thus be regarded as an advanced feature (KAPIL & TIWARI 1978), its systematic distribution within the angiosperms is not yet clear. Although our knowledge of the ovular tapetum is limited, it is probably represented by a type similar to Fig. 2/5, i.e. an intermediate form between a parietal type similar to Fig. 2/5 and a type similar to Fig. 2/6. Significantly the ovular tapetum in the *Spermatophyta* is mostly parietal and only sometimes looses its cell walls, the anther tapetum of these groups is similarly dominated by the parietal type. From this, it can be concluded, that the genetic information for the tapetum (sub-)type in both ♀ and ♂ floral parts is similar.

In contrast to the ovular tapetum with its limited versatility, the anther tapeta show a number of modifications, all directed towards more active microspore nutrition. The first significant modification of the ancestral tapetum type in the *Spermatophyta* (the secretory one with walls: Fig. 2/1) occurs when the parietal tapetum looses its inner tangential and radial walls (Fig. 2/5) during the microspore/tetrad stage. This kind of tapetum is the most widespread in the *Spermatophyta* (SINGH 1978 and DAVIS 1966). The loss of these walls leads to more efficient and direct nutrition, allowing the release of vesicles (exocytosis) and of substances with polymerization tendency into the locule*.

According to the present investigations another intermediate type between a real periplasmodium and a strictly cellular tapetum exists in

* The only known exceptions are found in some members of the *Asclepiadaceae* (Fig. 2/1). The nutrition is nevertheless efficient, as the pollen mass fills the entire locule and remains in direct contact with the multilayered tapetum, and the cell walls inside the massulae are reduced (LINSKENS & SUREN 1969, VIJAYARAGHAVAN & SHUKLA 1976, DAN DICKO-ZAFIMAHOVA & AUDRAN 1981).

most angiosperms, well represented in Fig. 2/6. After meiosis the cell walls not only disintegrate but the protoplasts fuse to form a "false" periplasmodium (Carniel 1963, Hesse 1984a and unpublished). This tapetum modification, found only after careful study of all developmental stages, has given rise to controversial views, e.g. in *Larix* (Singh: plasmodial, Chwirot 1980: parietal tapetum). Only a few exceptions are known: while *Ginkgo* has a real cellular, parietal tapetum (unpublished investigations of our own), *Araucaria columnaris* has a limited periplasmodium, formed by a few cells (Hodcent 1965).

The only known example for direct contact between the tapetum and each microspore, at least during the free pollen period, is found in some *Poaceae* (Rowley 1964, Christensen & al. 1971, Christensen & Horner 1974, Colhoun & Steer 1981) (Fig. 2/8): the anthers are elongated and narrow, and in cross section only few microspores are arranged in a single circular layer closely adhering to the tapetal cells (Sunderland & al. 1984). After the formation of the exine and the intine, the grains rotate so that their single pore is closest to the locular side of the tapetal cells (Rowley 1964). After this, a further polarization of the pollen grains takes place: the pore remains facing the tapetum, and the starch engorgement process starts from the poral area and continues from there (Christensen & Horner 1974). In some examples of cytoplasmic male sterility, the tapetal cell walls remain very thin most probably failing in their nutritive role (e.g. in maize, Colhoun & Steer 1981).

A direct contact between the tapetal cells and all the microspores/pollen grains cannot occur if the anthers are large and broad: the microspores in the middle of the locule lack direct tapetal contact. If the tapetal cells remain in situ, there should be a highly efficient nutrient diffusion towards the inner locular parts to ensure a uniform nutrition of the microspores. If not, some grains might have a delayed development. Specialized tapetal features (e.g. multilayered, multinucleate or dimorphic tapeta with different degeneration times and rates: Bonnet 1912, Carniel 1963, Davis 1966, Vijayaraghavan & Ratnaparkj 1973) may provide a greater amount of substances to the loculus but may fail to ensure uniform nutrition. The possible solution to this problem is to move around the microspores/pollen grains inside the locule. This hypothesis (Pacini & Franchi 1981, 1982a, b) is based only on morphological evidence and still remains to be proved. On the other hand, if the tapetal cells intrude into the locule, intimate contact is ensured and maintained. This "spermatophytic" amoeboid tapetum is derived from a secretory tapetum lacking cell walls: although morphologically similar to the amoeboid tapetum of lower plants, it has a different phylogenetic origin (see Figs. 2/3, 2/7, and 3) and intrudes into the locule at a later stage.

The cells of the amoeboid tapetum intrude into the locule after loosing

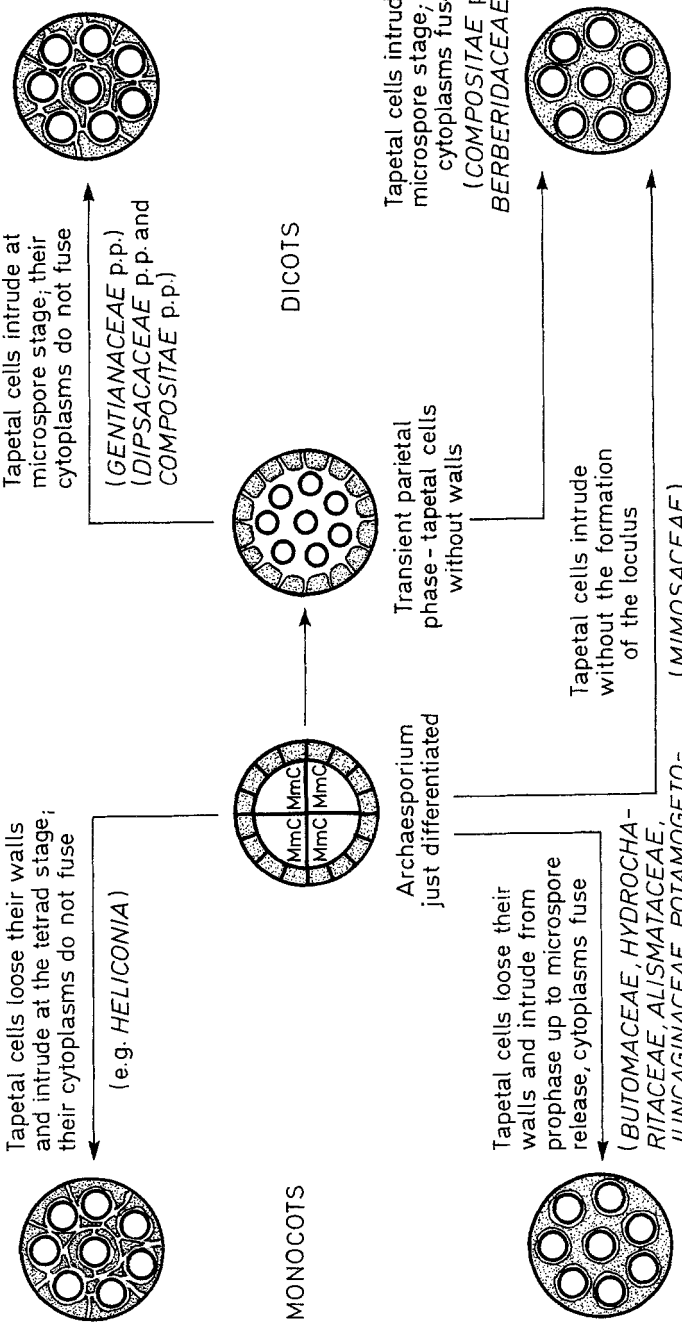


Fig. 3. Semischematic representation of developmental stages of the angiospermic amoeboid tapetum. The tapetum is represented by a dotted (cytoplasm) area. MmC = microspore mother cells. Further explanations in the text

Table 5. Time of intrusion of amoeboid

Dicots	*Berberidaceae*	*Mahonia aquifolium*
	Mimosaceae	*Acacia conferta*
	„	*A. iteaphylla*
	„	*A. subulata*
	Gentianaceae	*Gentiana acaulis*
	Compositae	*Adenostemma rugosum*
	„	*Vernonia elaegnifolia*
	„	*Elephantopus scaber*
	„	different species of tribe *Astereae*
	„	different species of tribe *Inuleae*
	„	*Cosmos pipinnatus*
	„	*Helianthus annuus*
Monocots	*Butomaceae*	*Butomus* sp.
	„	*Limnocaris* sp.
	Hydrocharitaceae	*Hydrocharis* sp.
	„	*Stratioides* sp.
	„	*Thalassia hemprichii*
	„	*Halophila stipulacea*
	„	*Thalassodendron ciliatum*
	Alismataceae	*Alisma* sp.
	„	*Sagittaria* sp.
	Juncaginaceae	*Triglochin* sp.
	Potamogetonaceae	*Potamogeton* sp.
	Najadaceae	*Amphibolis antarctica*
	„	*Ouvirandra* sp.
	Araceae	some species
	„	*Arum italicum*
	Heliconiaceae	*Heliconia* sp.
	Zingiberaceae	*Amomum dealbatum*
	Costaceae	*Tapeinochilos ananassae*
	Commelinaceae	*Gibasis karwinshkiana*
	„	*G. venustula*
	„	*Rhoeo spathacea*
	„	„
	„	*Tradescantia* sp.
	„	*T. bracteata*
	Sparganiaceae	*Sparganium* sp.
	Typhaceae	*Typha* sp.
	Pandanaceae	*Pandanum parvum*

their cell walls, while the plasmalemma is reorganized (PACINI & JUNIPER 1983). The intrusion process takes place at different developmental stages. Especially in amoeboid tapeta, there are family- or even genus-specific differences of the intrusion timing. It may start in late diplotene (as e.g. in *Rhoeo spathacea*) or even in late microspore stage as in the *Butomaceae* and *Alismataceae* immediately before pollen mitosis (Table 5). In the

tapeta into the loculus in angiosperms

early microspores	Roland-Heydacker (1979)
"	Kenrick & Knox (1979)
"	"
"	"
"	Lombardo & Carraro (1976)
"	Pullaiah (1979a)
"	"
"	"
"	Pullaiah (1978)
"	Pullaiah (1979b)
"	Dickinson (1982)
"	Horner & Pearson (1978)
early/mid vacuolate microspores	Maheshwari (1950)
tetrad stage	"
microspore release	"
"	"
tetrad stage	Pettitt (1981)
2nd meiotic division	"
interphase	Ducker & al. (1978)
2nd meiotic division	Maheswari (1950)
microspore release	"
"	"
1st and/or 2nd meiotic division	"
"	Ducker & al. (1978)
2nd meiotic division	Maheswari (1950)
tetrad stage	"
2nd meiotic division/tetrad	Pacini & Juniper (1983)
"	Stone & al. (1979)
early tetrad	Sachar & Arora (1983)
dyad stage	Stone & al. (1979)
tetrad stage	Owens & Dickinson (1983)
late tetrad/early microspore stage	"
"	Nanda & Gupta (1977)
pachytene	Williams & Heslop-Harrison (1979)
late diplotene	Maheshwari (1950)
late tetrad stage/early microspore	Mepham & Lane (1969)
"	Maheshwari (1950)
tetrad stage	"
"	Cheah & Stone (1975)
late prophase I	

monocots, the intrusion stage commonly occurs during meiosis or the tetrad stage, while in the dicots it generally starts at the microspore stage, preceded, interestingly, by a transient parietal phase. After the intrusion, the tapetum cytoplasms usually fuse or, more rarely, remain intact. If the tapetal cells intrude before the release of the microspore the tapetal cytoplasm directly surrounds the microspores; this is found especially in

the monocots. Conversely, only a few dicots behave similarly, e.g. some *Acacia* species (KENRICK & KNOX 1979), while in some *Berberidaceae* and *Asteraceae* (Fig. 3) the tapetum intrudes after a transient parietal phase (HORNER & PEARSON 1978). After their intrusion the tapetal cells often fuse to form a real periplasmodium, which is in this respect similar to those of lower plants. In some angiosperm families, there is an intermediate form between a parietal tapetum without cell walls and a real periplasmodium (each protoplast remains as an individual) (*Gentianaceae*: LOMBARDO & CARRARO 1976; *Dipsacaceae*: JUEL 1915, CHIARUGI 1927; *Asteraceae*: DICKINSON & POTTER 1976, CHIARUGI 1927, TISCHLER 1915; *Heliconiaceae*: STONE & al. 1979) (Figs. 2/6 and 3). Unfortunately, this interesting modification has been rather neglected in literature; its characters, ontogenesis and – especially – its exact distribution in the angiosperms should be carefully studied, especially with respect to the occurrence of a possibly widely similar subtype in the gymnosperms.

In 207 angiosperm families, the tapetum type is a strict family character (Tab. 2), and the amoeboid tapetum occurs mostly in monocots. The occurrence of both tapetum types, however, has been found in at least 12 (either primitive or advanced) families: *Caesalpiniaceae, Caprifoliaceae, Chenopodiaceae, Droseraceae, Euphorbiaceae, Gentianaceae, Haemodoraceae, Helleboraceae, Lauraceae, Solanaceae, Vitaceae, Winteraceae* and (the only monocot family) the *Zingiberaceae**. SPORNE (1973) in his short note comparing the tapetum types and some primitive/advanced structure characters in vegetative and reproductive organs of dicots, states that the secretory tapetum is primitive, whilst the amoeboid type is advanced. The presence of a certain tapetum type is evidently also linked with further reproductive parameters e.g. locule diameter, pollen shape or dry/wet habitats. Although there is no unequivocal proof that the secretory type is strictly primitive, it would appear that SPORNE's suggestion is correct. Although it cannot be denied that some tapetum types have evolved independently in the higher orders, the switching from one type to another within families or genera should be interpreted as being a significant evolutionary trend.

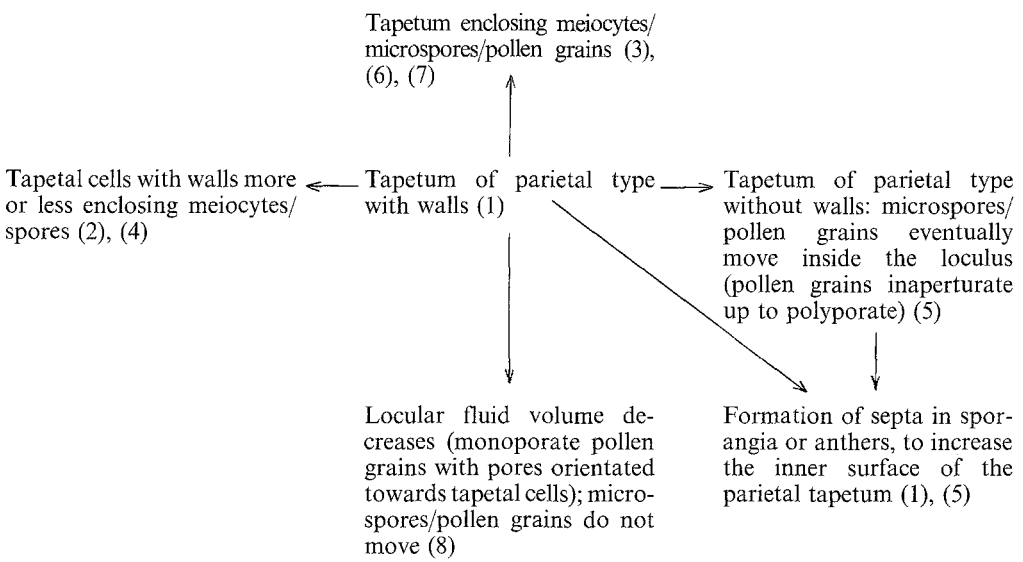
Conclusions

The occurrence of an anther tapetum is universal in all land plants (mosses, ferns, and *Spermatophyta*) even if it is difficult to recognize and even if referred to with different names by different authors. The possible main function of the tapetum is to nourish the microspores/pollen grains during their development. Beside this, there are several other functions

* Mostly one type predominates, e.g. the secretory type in the *Chenopodiaceae* (LAKSHMANAN & DULCY 1982).

which are staggered in time; some of them are not present in all taxa. The strictly secretory (= parietal) tapetum, because of its overall occurrence in the *Bryophyta* and the *Lycopodiophyta*, and because of its rather ineffective trophic function, is regarded as being the most primitive type (Fig. 2/1). All the other tapetum types have been derived from this

Table 6. Tapetum (sub-)types derived from the parietal type, facilitating nutrition of spores/microspores/pollen grains. The numbers refer to those in Table 1 and Fig. 2



"primitive" type tending towards more efficient nutrition. The possible derivations from the ancestral type are summarized in Table 6, and the hypothetical tapetum phylogenesis is given in Fig. 2. Based on this, the amoeboid tapetum can be considered as being much more advanced than the parietal one. This view agrees with SPORNE's (1973) conclusions that the occurrence of some primitive characters in dicot families are correlated with a secretory tapetum. HAECKEL's well known axiom "ontogeny is a summary of phylogeny" is once again supported by the existence of amoeboid tapeta (Fig. 3) whose intrusion into the locule takes place after a transient parietal phase.

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