

THE BOTANICAL REVIEW

VOL. 64

JULY-SEPTEMBER 1998

No. 3

Orbicules in Angiosperms: Morphology, Function, Distribution, and Relation with Tapetum Types

SUZY HUYSMANS

*Laboratory of Plant Systematics
Botanical Institute
K.U.Leuven
Kard. Mercierlaan 92
B-3001 Heverlee, Belgium*

GAMAL EL-GHAZALY

*Palynological Laboratory
Swedish Museum of Natural History
Roslagsvägen 101
S-104 05 Stockholm, Sweden*

AND

ERIK SMETS

*Laboratory of Plant Systematics
Botanical Institute
K.U.Leuven
Kard. Mercierlaan 92
B-3001 Heverlee, Belgium*

I. Abstract/Résumé	241
II. Introduction	242
III. Tapetum	242
A. Types	243
B. Development	243
C. Functions	243
D. General Distribution in Angiosperms	243
IV. Orbicules	244
A. Discovery and Early Days of Orbicule Research	244
B. Definition and Terminology	244

Copies of this issue [64(3)] may be purchased from the NYBG Press,
The New York Botanical Garden, Bronx, NY 10458-5125 USA. Please
inquire as to prices.

C. Morphology and Composition	245
D. Origin and Development	245
1. Determination of Sporopollenin Deposition on Pro-orbicules	247
E. Function	247
1. Orbicules as a Transport Mechanism for Sporopollenin	247
2. Temporary Packaging of Sensitive Material for Transport through Locular Sap	248
3. By-products of Tapetal Cell Metabolism	248
4. Associated with Pollen Dispersal	248
5. Role in Degradation of Tapetal Cells	249
6. Prevention against Osmosis and Collapse of Developing Microspores	249
F. A Distinctive Micromorphological Character?	249
G. Intraspecific Variation	250
H. Orbicules in the Fossil Record	251
I. Do Orbicules Cause Allergy?	251
V. Distribution of Orbicules in Angiosperms	252
A. Presence of Orbicules	252
B. Secretory Tapeta without Orbicules	259
C. Why No Orbicules in Taxa with an Amoeboid Tapetum?	259
VI. Comments on Dahlgrenogram	263
A. Correlation with Tapetum Types	263
VII. Future Research	263
VIII. Acknowledgments	264
IX. Literature Cited	264

I. Abstract

Orbicules, or Ubisch bodies, are sporopollenin particles lining the inner tangential and sometimes also the radial tapetal cell walls. They occur only in species with a secretory tapetum. The surface ornamentation of orbicules and pollen of the same species is often strikingly similar. Although orbicules were discovered more than a century ago, these structures remain enigmatic since their function is still obscure. Proposed hypotheses about their possible function are discussed. We also deal here with topics such as the possible allergenicity of orbicules and their representation in the fossil record. The use of orbicule characters for systematics is reviewed.

The distribution of orbicules throughout the angiosperms, based on a literature review from the first report until today, is shown in a list with 314 species from 72 families. Those species found in the literature without orbicules are presented together with their tapetum type. We plotted this information on a dahlgrenogram to visualize the distribution of orbicules. Orbicules occur in all subclasses of the angiosperms. Their occurrence is not correlated with certain modes of pollination or habitats.

Résumé

Les orbicules, ou corps d'Ubisch, sont des particules de sporopollénine couvrant la surface intérieure tangentielle et parfois la surface radiale des cellules du tapétum. On ne les trouve que dans les espèces possédant un tapétum sécréteur. L'ornementation superficielle des orbicules et celle du pollen d'une même espèce est souvent remarquablement similaire. Malgré le fait que les orbicules ont été découvert il y a plus d'un siècle, ces structures restent énigmatiques et leur fonction est toujours méconnue. Les hypothèses proposées concernant la fonction éventuelle des orbicules sont commentées dans cet article. Nous avons également

traité des sujets tels que les éventuels effets allergènes des orbicules ainsi que leur présence dans les strates fossiles. L'utilisation de caractères orbiculaires dans la systématique est analysée.

Nous présentons une liste de 314 espèces appartenant à 72 familles possédant des orbicules, sur base d'une analyse de la littérature à partir de la première observation jusqu'au présent. Pour les espèces rapportées dans la littérature qui ne possèdent pas d'orbicules, nous présentons aussi leur type de tapétum. Nous avons projeté cette information sur un Dahlgrenogramme afin de visualiser la distribution des orbicules. Nous les retrouvons dans toutes les sous-classes des angiospermes. Leur présence n'est pas corrélée avec certains modes de pollinisation ou avec divers types d'habitat.

II. Introduction

Orbicules, or Ubisch bodies, were discovered more than a century ago by Rosanoff (1865). Up to now these minute structures, covering the inner surface of most secretory tapeta, remained enigmatic and therefore highly attractive to botanists concerned with anther structure, pollen development, and sporopollenin synthesis.

In a recent overview Pacini and Franchi (1993) listed 33 species from 22 angiosperm families with secretory tapetum and orbicules (references from 1971 to 1993). From the early days of orbicule research two other lists of taxa with presence/absence of orbicules were published. Von Ubisch (1927) investigated 20 taxa from 14 families and Kosmath independently reported in the same year on 69 taxa from 35 families.

The lack of any recent summary about the distribution of orbicules throughout the angiosperms encouraged us to review the literature from the very first report (Rosanoff, 1865) until December 1996. Papers published since 1970 were traced by a literature search in BIOSIS on the keyword "orbicule?". Earlier articles and additional papers (e.g., sometimes the term "Ubisch bodies" was used instead of "orbicules") were found mainly by unraveling reference lists. The extensive bibliography of stamen morphology and anatomy (Lynch & Gregory, 1996) proved to be a useful source of additional references. All papers under "Tapetum" in the subject index were checked for information about orbicules.

We restricted this review to the angiosperms; for information on gymnosperms (e.g., Ueno, 1960a, 1960b; Yamazaki & Takeoka, 1962; Audran, 1981; Rowley & Wallis, 1987) and lower plants (ferns: e.g., Lugardon, 1981; mosses: e.g., Zajac, 1995) we refer to specialized literature.

The aim of the present paper is threefold: (1) to give a concise state of knowledge about tapetum and orbicules, (2) to enumerate the taxa where orbicules were reported to be present or certified absent, and (3) to visualize the systematic distribution of orbicules throughout the angiosperms by plotting the information on a dahlgrenogram. We also document the oft-suggested correlation between the presence of orbicules and tapetum types by comparing this dahlgrenogram with the distribution of tapetum types.

III. Tapetum

The anther tapetum is a highly specialized tissue. It is the innermost cell layer of the anther wall in all Spermatophyta and it plays a crucial role in the development of both microspores and orbicules. We only mention some basic points here that are necessary for a better understanding of what follows on orbicules.

A. TYPES

Since Goebel (1901) two main tapetal types are recognized: the secretory (a.k.a. parietal, glandular, or cellular non-syncytial) tapetum and the amoeboid (a.k.a. syncytial invasive or periplasmoidal) tapetum. In secretory tapeta the cells remain in situ until their degeneration, while in amoeboid tapeta the tapetal protoplasts move into the loculus, forming a periplasmodium that is in direct contact with the developing microspores. The distinction between these two main types has become less evident (e.g., Rowley et al., 1992). Many subtypes have been recognized (Pacini et al., 1985) and transitional types have been described (for references, see Hesse & Hess, 1993). Secretory tapeta are believed to be the most primitive type from which all other types, tending toward more efficient nutrition, are derived (Sporne, 1973; Pacini et al., 1985).

B. DEVELOPMENT

The tapetum is essentially of parietal origin, irrespective of the type of anther wall formation (Davis, 1966). Periasamy and Swamy (1966), however, suggested the dual origin of tapetum in angiosperms: from the parietal layer in the outer regions of the locules and from the connective tissue toward the inner half of the locules. Other studies suggest that tapetum could arise from the sporogenous tissue as well (Bhandari, 1971).

Tapetal cells pass through a number of cycles of secretory activity and redifferentiation, which is rather unusual for plant cells (Rowley, 1993). The behaviour and ultrastructure of tapetal cells through their lifetime is quite variable for different species and of course determined by the type of tapetum. References of ontogenetic studies of tapetum can be found in, e.g., Bhandari, 1984, and Suarez-Cervera & Seoane-Camba, 1986.

C. FUNCTIONS

Tapetal cells have an essential nutritive role for the developing microspores. Several other functions were suggested by Pacini et al. (1985), such as the production and release of callase to dissolve the callosic envelope around the tetrads, the production of other sporophytic proteins, the formation of sporopollenin precursors, the formation of tryphine, pollenkitt, and viscin threads. Secretory tapeta in addition produce orbicules and the locular fluid (Pacini et al., 1985).

D. GENERAL DISTRIBUTION IN ANGIOSPERMS

Secretory tapeta are characteristic of 175 (+ 15 presumably) angiosperm families, 88% of which are dicots. Amoeboid tapeta have been found in 32 angiosperm families, of which 14 are dicots. Both types of tapetum occur together in 12 families. Surprisingly, the tapetum type of ca. 177 families is still unknown (Pacini et al., 1985, after Davis, 1966, with modifications). According to Davis (1966), there are 21 families where both tapetum types occur together. A current review of tapetum information in the monocotyledons, is forthcoming from Furness and Rudall (this issue).

The distribution of the two main tapetum types in angiosperms was shown on dahlgrenograms: for dicots by Dahlgren (1991), and for monocots by Dahlgren and Clifford (1982) and Dahlgren et al. (1985).

IV. Orbicules

A. DISCOVERY AND EARLY DAYS OF ORBICULE RESEARCH

The historical literature, from the first report in 1865 by Rosanoff up to the 1920s, concentrates mainly on anatomy and morphology of the anther, and often more specifically the tapetum.

Rosanoff (1865: 447) observed a granular membrane completely enveloping the mature massulae in the Mimosaceae. Between this membrane and the microspores is an empty space with more granules, or "Körnchen und Tröpfchen" (grains and droplets), as Rosanoff called them. Rosanoff also found out that these granules are resistant to concentrated sulfuric acid and thus give the same reaction as cuticula.

In his carefully illustrated study on anther anatomy of many species from different plant families, Chatin (1870) distinguished three layers in the anther wall, of which the innermost may reduce to granules. Chatin's figures indicate that these granules most likely correspond to orbicules.

In the 1920s, several botanists studied the anther tapetum. Their attention was drawn to the minute particles between tapetum and pollen grains. Mascré (1922) reported for Boraginaceae that tapetal cells are cutinised towards the locule. It seems that the cutinised layer by Mascré corresponds to orbicules arranged between the tapetal cells and the pollen grains. Schnarf (1923) mentioned the presence of "kugelige Verdickungen" (spherical thickenings) on the adaxial side of the secretory tapetum cells in *Lilium martagon*. These structures remained intact even after total destruction of the tapetal cells.

The first paper illustrated with light microscopic pictures was written by Krjatchenko (1925). He studied the activity of mitochondria and described the development of granules on the inner surface of the tapetal cells in *Lilium croceum*. Krjatchenko suggested that they develop from lipid droplets secreted by the tapetal cells, and that the droplets possibly originate from mitochondria.

Von Ubisch (1927) and Kosmath (1927) independently published a list of taxa with and without orbicules; the structures were called "Plättchen" (plates) by von Ubisch (1927) and "kutikulaähnliche Tapetumzellmembran" (cuticula like tapetal cell membrane) by Kosmath (1927). Both scientists did experiments with several chemicals and stains to elucidate the nature of the structures. Since these particles showed the same reaction as the pollen exine and because they developed synchronously with the pollen wall, von Ubisch concluded that they must be homologous with the exine. Both authors stressed that these particles are restricted to and a general feature of secretory tapeta. Von Ubisch observed a cavity in the center of the particles and Kosmath reported interspecific size differences.

B. DEFINITION AND TERMINOLOGY

Contrary to what the literature says, Kosmath (1927) did not coin the term "Ubisch granules" because of the contribution of von Ubisch. As far as we could trace, it was Rowley (1962) who introduced the term "Ubisch body." The term "orbicules," proposed by Erdtman and coworkers (1961: 9), was defined as "small granules spread over the exine surface in certain gymnosperms." In Japanese literature they are often called "con-peito-grains," referring to star-shaped cookies made for special occasions (J. Rowley, pers. comm.). In his first papers on the topic, Heslop-Harrison (1968a, 1968b) used the term "plaques." Later, in 1971, he rejected "Ubisch bodies" in favor of "orbicules" since they were not discovered by von Ubisch.

Another, carefully formulated early definition was presented by Rowley (1963). He defined Ubisch bodies as extra-exinous objects having a role in exine establishment. This definition is consistent with the previously published ideas of Rowley et al. (1959), Chambers and Godwin (1961), and Heslop-Harrison (1962). Form and perhaps also origin of orbicules was reported to be variable.

Skvarla and Larson (1966: 1123) referred in their definition to the parallelisms with the exine: "Ubisch bodies are small bodies of sporopollenin resembling the form of pollen exines of the species in which they occur."

Other authors distinguished between Ubisch bodies and orbicules (Madjd & Roland-Heydacker, 1978; Abadie & Hideux, 1979). According to them, Ubisch bodies are hollow and have a surface structure comparable to the respective pollen exine, while orbicules are massive spherical structures that can deform; both do consist of sporopollenin. In the present paper the two terms are considered synonyms.

C. MORPHOLOGY AND COMPOSITION

Orbicules are most variable in both shape and size. Size is ranging from 0.14 μm in *Rondeletia odorata* (Rubiaceae; Huysmans et al., 1997) and 0.15 μm in *Saxifraga cymbalaria* var. *huetiana* (Saxifragaceae; Abadie & Hideux, 1979) to 15 μm in *Quararibea* (Bombacaceae; Nilsson & Robyns, 1974). Generally they are less than 5 μm in diameter.

Frequently, remarkable similarities between the surface structure of orbicules and the respective pollen exine have been reported (grasses: Rowley et al., 1959; *Quararibea*: Nilsson & Robyns, 1974; *Sorghum*: Christensen et al., 1972; *Triticum*: El-Ghazaly & Jensen, 1986; *Lilium*: Clément & Audran, 1993a; *Platanus acerifolia*: Suarez-Cervera et al., 1995), although this is not always true (El-Ghazaly & Nilsson, 1991; Huysmans et al., 1997).

To our knowledge, orbicules have almost never been found in taxa with an amoeboid tapetum, *Gentiana acaulis* being the only exception (Lombardo & Carraro, 1976b). Most angiosperms with a secretory tapetum produce orbicules, mainly on the inner tangential, and to a lesser extent on the radial walls of tapetal cells (e.g., El-Ghazaly & Jensen, 1986; Huysmans et al., in prep.). Sometimes, however, orbicules are found all around the tapetal cell membranes (e.g., in *Primula obconica*: Stevens & Murray, 1981).

Orbicules are resistant to acetolysis and react similarly to the exine with different histochemical stains, thus providing ample evidence for sporopollenin composition of the orbicule wall. El-Ghazaly and Jensen (1987) found for both orbicule walls and pollen exines of *Triticum aestivum* an intense staining for acidic and neutral polysaccharides and for unsaturated lipids, while the structures stained moderately for proteins. Suarez-Cervera et al. (1995), working on *Platanus acerifolia*, showed that the central part of the orbicules stains positively for lipids, glycoproteins, and acidic and neutral polysaccharides during all stages of maturation. A detailed cytochemical investigation of *Lilium* orbicules was published by Clément and Audran (1993a, 1993b).

D. ORIGIN AND DEVELOPMENT

There have always been questions about tapetal cells being the site of origin for orbicules and about which organelles in the tapetal cells could give rise to pro-orbicules. A concise review of the origin of orbicules is provided by Bhandari (1984).

According to Krjatchenko (1925), in *Lilium croceum* "une substance grasseuse" (a granular substance) is formed at tetrad stage by the mitochondria of the tapetal cells and is excreted

through the plasmalemma to form a dented locule surface. Heslop-Harrison (1962) adopted this idea in his paper on the origin of tapetal particles in *Silene pendula* and *Cannabis sativa*. Organelles that have the dimensions of mitochondria and show "occasionally sufficient evidence of cristae" were believed to be the site of origin for orbicules (Heslop-Harrison, 1962: 1069). This interpretation was reconsidered by Heslop-Harrison and Dickinson (1969) on the basis of evidence from other studies (Carniel, 1967; Rowley & Erdtman, 1967; Echlin & Godwin, 1968a). Rowley and Erdtman (1967), for instance, thought the word "mitochondria" in Krjatchenko (1925) should read as "lysosomes" to explain the source of orbicules.

Skvarla and Larson (1966) interpreted orbicules to represent sporopollenin deposition upon membranes aggregated at the tapetal surface. They believed that these membranes are derived from ruptured microspores since in *Zea mays* cytoplasmic organelles and cytomembranes are always suspended in the locular fluid. One year later, however, Carniel (1967: 500) gave evidence for an intracellular development of Ubisch bodies in *Oxalis*: "Contrary to the current opinion they are not located on the outside of the inner cell wall but on its inside." In 1971 Carniel stressed in his work on *Eleocharis* that only mature Ubisch bodies become free as a result of tapetal protoplast degeneration.

The endoplasmic reticulum of tapetal cells as site of origin for orbicules was first mentioned by Echlin and Godwin (1968a). This has been confirmed for *Allium cepa* (Risueño et al., 1969). Risueño et al. (1969) observed endoplasmic reticulum elements, dispersed through the cytoplasm from the nuclear membrane to areas in the vicinity of the plasmalemma, producing electron-dense bodies with characteristics similar to those of the central core of the sporopollenin granules.

Risueño et al. (1969) discussed the three hypotheses published at that time about the origin of orbicules. These hypotheses can be summarized as follows:

1. They are formed both in the cells of the tapetum and in the locule of the pollen sac (Rowley et al., 1959).
2. They originate solely in the tapetum through modification of certain cytoplasmic organelles (Heslop-Harrison, 1962).
3. They are formed exclusively in the locule without invoking tapetal cell regulation, from membrane complexes derived from abortive microspores (Skvarla & Larsson, 1966).

In our opinion, Risueño et al. (1969) did not distinguish consistently between the formation of the pollen exine and Ubisch bodies. They assumed Ubisch bodies to be a main source of sporopollenin precursors for the exine (as we discuss in greater detail in the next section).

Tapetal endoplasmic reticulum as site of origin for orbicules has since then also been proposed by Reznickova and Willemse (1980), Herich and Lux (1985) for *Lilium*, El-Ghazaly and Jensen (1986) for *Triticum aestivum*, Chen et al. (1988) for *Anemarrhena asphodeloides*, and El-Ghazaly and Nilsson (1991) for *Catharanthus roseus*.

The development of orbicules is studied mostly in the shadow of pollen ontogenetic investigations. In few papers on the subject, pro-orbicules were believed to appear between the tapetal plasmalemma and the degenerating walls of the tapetal cells (Horner & Lersten, 1971; Christensen et al., 1972; Steer, 1977). In *Avena* (Steer, 1977) and *Sorghum* (Christensen et al., 1972), lipid droplets appear on tapetal plasmalemma depressions after loss of the cell wall of the inner facing tapetal cell surfaces. No morphological evidence was found for the intracytoplasmic formation of pro-orbicules. The timing of pro-orbicule formation varies slightly between the different species: from early stages of meiosis II in *Avena* (Steer, 1977) to late tetrad stage in *Sorghum* (Christensen et al., 1972) to microspore release from the tetrads in *Citrus* (Horner & Lersten, 1971).

In most papers, however, pro-orbicule formation is considered to be intra-tapetal (e.g., Echlin & Godwin, 1968a; El-Ghazaly & Jensen, 1986). Suarez-Cervera et al. (1995) believed the so-called "grey bodies" in the tapetal cytoplasm to be the progenitors of the Ubisch bodies (references are given for different species). The next question, then, is how they pass the tapetal plasmalemma. In *Triticum* it is shown that a membrane is formed around the pro-orbicule as it approaches the plasmalemma. After fusion of these membranes, the pro-orbicules are released (El-Ghazaly & Jensen, 1986).

1. Determination of Sporopollenin Deposition on Pro-orbicules

Sporopollenin accumulation in higher plants essentially takes place simultaneously in the primexine of developing microspores and on the surface of the pro-orbicules (e.g., Christensen et al., 1972; El-Ghazaly & Jensen, 1986). Rowley and Skvarla (1974: 445) stated that "the specific form of the Ubisch body wall, which is identical with the pollen exine surface, is determined by a plasma membrane-glycocalyx."

In monocots the orbicular wall seems to develop on a specific reticulate pattern (= glycocalyx). For example, Rowley and Skvarla (1974) reported a plasma membrane glycocalyx on pro-orbicules of *Phleum pratense*, El-Ghazaly and Jensen (1985) in *Triticum*, and Reznickova and Willemsse (1980) and Clément & Audran (1993a) in *Lilium*. The coat of the pro-orbicules, which appears to guide the deposition of sporopollenin, stains positively for polysaccharides and proteins, similar to the pollen wall (Rowley, 1976; Rowley & Dahl, 1982; El-Ghazaly & Jensen, 1987).

E. FUNCTION

Why should the (secretory) tapetum develop any sporopollenin wall at all and why should it form mainly on the inner tangential surface of the tapetal cells? Echlin (1971) and Bhandari (1984) reviewed the early literature on the different hypotheses that have been proposed to attribute a function to orbicules. We summarise these views here and report on additional findings in the past 20 years. The list of suggested possible functions of orbicules is long, and none of them is satisfactorily proved.

1. Orbicules as a Transport Mechanism for Sporopollenin

Orbicules represent a transport mechanism for sporopollenin between the tapetum and the developing microspores and thus take active part in sporoderm formation. The idea that orbicules might contribute to the development of the exine was first raised by Maheshwari (1950). Protoplasmic strands were observed in *Poa annua* by Rowley (1962) extending from the tapetum to the spinules on the pollen exine. Banerjee and Barghoorn (1971) showed in some grasses that spinules of orbicules are in contact with those on the pollen exine through strands of sporopollenin, indicating a track for the possible transfer of substrate from the tapetal cells to the exine. In *Triticum*, microfilaments are observed occasionally connecting orbicule spinules with the microspore wall (El-Ghazaly & Jensen, 1986). Banerjee and Barghoorn (1971: 127) found in some grasses, immediately prior to anther dehiscence, some depolymerisation of the mature sporopollenin, "possibly caused by secretion from the centrum of the Ubisch bodies." In the same study it is observed that a large number of new spinules are produced at pollen maturity, apparently by the orbicules. This would suggest an important role for orbicules in sporoderm formation in grasses.

This idea is shared by Risueño et al. (1969) for *Allium cepa*. They observed that orbicules become part of mature exines and thus actively take part in the formation and development of the pollen exine. In *Soja* some orbicules become nail-shaped and are found in the tectum perforations of the pollen grains (Madjd & Roland-Heydacker, 1978). The authors carefully suggested a possible participation of the orbicules in the construction of the pollen exine. Robertson (1984) mentioned that orbicules of *Rhigozum trichotomum* (Bignoniaceae) become intimately bound to the exine after being released into the thecal fluid. He added that the orbicules are stripped of the osmiophilic layers which appear to be incorporated into the sporoderm. Polowick and Sawhney (1993) indicated that in *Lycopersicon esculentum* (Solanaceae) the orbicule surface may also provide material for the exine. Abadie et al. (1981) mentioned contact between orbicules and exine in *Turgenia latifolia* and *Hydrocotyle mexicana* (Apiaceae). An additional argument to strengthen this hypothesis might be the observation that the exine initially develops on the side facing the tapetum, and thus facing the orbicules (Gorzynski, 1935).

A number of authors follow a hypothesis that is in contradiction to the former one—namely, that there is no direct relationship between orbicules and exine development (Carniel, 1967; Rowley & Erdtman, 1967; Heslop-Harrison & Dickinson, 1969). A fact corroborating this idea is that sporopollenin synthesis associated with the tapetum begins before sporopollenin accumulation in the exine in *Silene pendula*, *Lilium longiflorum*, and *Oxalis* spp. Furthermore, orbicules are not universally present, not even in all taxa with secretory tapeta (see Table II) so they cannot have such a general function as exine construction.

2. Temporary Packaging of Sensitive Material for Transport through Locular Sap

This hypothesis was suggested by Rowley and Wallis (1987) in their work on *Pinus sylvestris*. The locular fluid probably contains exocellular enzymes (see Herdt et al., 1978) against which the sporopollenin wall of the orbicules forms an effective barrier.

3. By-products of Tapetal Cell Metabolism

Some researchers hold that orbicules have no specific function; they are nothing more than a by-product of tapetal cell metabolism. Heslop-Harrison (1968b) stated that orbicules cannot be considered to act as a temporary storage of sporopollenin material because they are neither eliminated nor eroded during exine growth after callose dissolution. Heslop-Harrison (1968b) simply regarded orbicules as by-products of the tapetum (see also Echlin & Godwin, 1968a; Dickinson & Bell, 1972).

Christensen et al. (1972) mentioned that the orbicule wall formation could be regarded as a vestigial capacity of the tapetum because, phylogenetically, this layer once was active sporogenous tissue. Hesse (1986) also referred to the homology between the sporogenous tissue and the anther tapetum to explain the highly similar genetic information for formation of sporopollenin in both tissues. Indeed, analogies between orbicules and the respective ektexine are not restricted to few unrelated species but are, in fact, common in higher plants.

4. Associated with Pollen Dispersal

Heslop-Harrison (1968a, 1968b) was the first researcher to suggest that orbicules are associated with pollen dispersal forming a non-wettable locule surface from which pollen can easily

detach. Keijzer (1987b) tested Heslop-Harrison's hypothesis on anthers of *Lilium* hybrid cv. 'Enchantment'. He removed the pollen grains and pollenkit from a dehisced anther and then detached the tapetal membranes on the inner tangential endothecium wall together with the orbicules. Afterwards pollen and pollenkit was reattached to this reduced pollen sac. Under extremely wet circumstances (98% relative humidity), most of the pollen did fall out of the anther whereas intact anthers did not lose their pollen. Both types of dehisced anthers reclosed under these wet conditions. In our opinion this is not a proof of the validity of the hypothesis. On the contrary, this experiment only proves that the removal of orbicules changes the sticking properties of the pollen to the locule wall—or perhaps that, as formulated in an abstract by the same author (Keijzer, 1984), in natural circumstances the lack of orbicules leads to the removal of the pollen grains by rain.

An observation in favor of this hypothesis is that during the shrinkage of the locule wall at dehiscence, the orbicules approach each other, creating a more continuous layer. This was also observed by Heslop-Harrison and Dickinson (1969) in *Lilium longiflorum*.

5. Role in Degradation of Tapetal Cells

The idea that orbicules might actively participate in lysis and degradation of tapetal cells has been suggested by Rowley and Erdtman (1967). They mentioned that orbicules are probably incidental in a tapetal digestive system that uses acid hydrolases. Herich and Lux (1985) observed in *Lilium henryi* that the orbicules get connected with the tapetal plasmalemma and then become lytically active. They could not elucidate which part of the orbicules is lytically active and enzymatic studies were promised.

6. As Prevention against Osmosis and Collapse of Developing Microspores

In some species, material (sporopollenin precursors) passing from the secretory tapetum to the microspores is generally deposited on the pro-orbicules to form the sporopollenin wall of the orbicules. Polymerisation of this excess of material will decrease the risk of high concentrations of sporopollenin precursors in contact with the developing microspores (El-Ghazaly & Jensen, 1986; El-Ghazaly & Nilsson, 1991).

F. A DISTINCTIVE MICROMORPHOLOGICAL CHARACTER?

The possible taxonomic value of orbicules has been repeatedly stressed (Heslop-Harrison, 1962; Rowley, 1963; Banerjee, 1967; Carniel, 1971). Banerjee (1967) argued for the use of orbicules as a criterion in the taxonomy of grasses since their size, shape, and abundance vary by species. Despite this awareness, few studies have been published where the systematic importance of orbicule characters was investigated. The work of Ueno (1959, 1960a, 1960b) in gymnosperms was pioneering in this respect. To our knowledge, the combined pollen and orbicule morphological investigation in Bombacaceae (Nilsson & Robyns, 1974) was the first of its kind in angiosperms. Later the taxonomic applicability of orbicules has been demonstrated in Chloanthaceae, generally included in the Verbenaceae (Raj & El-Ghazaly, 1987) and in the genus *Euphorbia* (El-Ghazaly, 1989; El-Ghazaly & Chaudhary, 1993). In many cases pollen morphological similarity between species is also reflected in their orbicules. However, conflicting results may occur. In a recent paper (Huysmans et al., 1997) character states of orbicules were delimited in the Cinchonoideae—Rubiaceae on the basis of SEM ob-

servations. Evidence is given that, at least in this group, orbicule characteristics are systematically useful on generic or tribal level.

Striking analogies between orbicules and the respective sexine seem to be common in higher plants (Hesse, 1986). The similarities are not only macromorphological but also in the finest micromorphological characters of the structural elements in orbicules and the respective sexines (e.g. Rowley & Skvarla, 1974; El-Ghazaly & Jensen, 1986, 1987). These parallels are explained by Hesse (1985) as being rooted in the homology of tapetum and sporogenous tissue.

G. INTRASPECIFIC VARIATION

The occasionally observed intraspecific variation in orbicules contradicts the above-mentioned possible taxonomic value of these structures. Two main types of intraspecific variation can be distinguished: (1) different kinds of orbicules in one species or (2) not all specimens of the same species produce orbicules.

Hesse (1986) pointed out that different kinds of orbicules can occur in a single species. In *Delonix elata*, for instance, large, elongated, curved, and sculptured orbicules are found together with tiny, globular, or ovoid orbicules. In *Euphorbia palustris*, Hesse (1986) distinguished type A and B orbicules, respectively with and without central core. Shape and size is variable in both types. A and B orbicules occur together in time and space. We feel hesitant to accept this delineation because tangential sections on the periphery of orbicules with a central core will also appear as coreless. Hesse (1986) concluded that, at least in *Euphorbia*, they represent another orbicule generation; the different orbicule-characters are presumably due to different gene expressions during the stages of microsporogenesis. Cerceau-Larrival et al. (1981) found in *Saxifraga cymbalaria* both disc-shaped and spherical orbicules. The spherical orbicules originate later in the ontogeny than the disc-shaped ones.

Fusion of single orbicules (= derived from one pro-orbicule) may occur forming "complex" orbicules. These complex orbicules may be composed of few single orbicules as in *Helleborus foetidus* (Echlin & Godwin, 1968a), *Euphorbia* (Hesse, 1986), *Cinchona pubescens*, and *Luculia pinceana* (Huysmans et al., 1997). In the latter two rubiaceaceous species, the orbicule cores seem to remain intact (Huysmans et al., 1997). In *Lilium* some sporopollenin globules fuse, forming "a second generation of orbicules" (Reznickova & Willemse, 1980).

In *Turgenia latifolia* and *Hydrocotyle mexicana* (Apiaceae) a double orbicular secretion is observed (Abadie et al., 1981). The secretory tapetum of *Turgenia latifolia* produces micro-orbicules (0.25 μm) and macro-orbicules (5 μm) that are without central core. Orbicules in *Hydrocotyle mexicana* have a lipidic core and macro-orbicules also exhibit a non-sporopollenin body surrounded by an acetolysis-resistant sheath. The tapetum of *Hydrocotyle mexicana* is of the intermediary type.

Examples of species where not all specimens produce orbicules are found only in the vast amount of literature on both genetic and cytoplasmic male sterility (see reviews by, inter alia, Edwardson, 1970; Laser & Lersten, 1972; Kaul, 1988). Many authors report irregularities in the tapetum. Ontogenetic disturbance in the structure and/or function of the tapetum leads to male sterile pollen (Gifford & Foster, 1989: 566).

Few examples are given to illustrate the possible differences between orbicules in fertile and sterile lines of the same species. In a comparative study on the tapetal behaviour in male fertile and male sterile *Iris pallida*, Lippi et al. (1994) found no orbicules at all in the sterile clone. In the male fertile line the inner anther surface was completely covered by orbicules.

The same pattern was observed for *Zea mays* (Colhoun & Steer, 1981) and *Beta vulgaris* (Hoefert, 1971).

Moussel et al. (1992) worked on *Vicia faba* and found for the fertile line that 14 out of 30 stamens had membranous formations (MFs) that give rise to pro-orbicules. In the other 16 stamens orbicules were not formed but the MFs moved in the anther cavity and became fixed on the ectoaperture edges of the microspores. In the sterile line only eight stamens on 26 produced orbicules and the number of MFs formed was more abundant. Exine formation was characterized by an exaggerated development of the different pollen wall layers. The authors advanced the following model to explain the observations: the MFs participate either in pro-orbicule synthesis in the tapetal glycolyx or in building the tectum ornamentation by moving through the anther cavity loaded with sporopollenin. In male sterile lines many of the MFs are used for the abundant exine development, thus restricting the orbicule number.

Male sterility can affect orbicule formation in other ways too, such as through differences in size or wall ornamentation.

Keijzer and Cresti (1987) compared anther tissue development in male sterile *Aloe vera* and male fertile *Aloe ciliaris*. In the sterile line tapetal development and breakdown were normal; one of the visible deviations, however, was the presence of some large orbicules, which is in conflict with the model proposed by Moussel et al. (1992). Young et al. (1979) studied anther and pollen development in male sterile intermediate wheatgrass plants. They found different expressions of male sterility including orbicular wall malformations. De Vries and Ie (1970) noted that male sterility did not necessarily affect orbicule formation. They looked at anther tissue and pollen grains of cytoplasmic male sterile and fertile wheat (*Triticum aestivum*) for possible differences in cytoplasmic structures. Orbicules were observed in the anthers of both male sterile and fertile plants, with no visible differences.

El-Ghazaly and Jensen (1990) and El-Ghazaly (1990) studied the effect of a gametocide on the development of the pollen wall and noted that the orbicules were smaller in size and with thinner walls than those in untreated anthers.

H. ORBICULES IN THE FOSSIL RECORD

Spores with adhering orbicules are known from as early as the Devonian (Emsian; ± 370 million years ago) (Taylor, 1990). Most accounts on fossil orbicules are from Mesozoic (Cretaceous) seed plants (e.g., Taylor & Alvin, 1984; Osborn et al., 1991; Serbet & Stockey, 1991; Archangelsky & Taylor, 1993). Fossil orbicules are also found in pteridosperm pollen organs (e.g., Taylor, 1976; Stidd, 1978). A comparison between fossil orbicules and tapetal membrane systems and those of extant plants can be found in Taylor, 1976.

On the basis of presence of orbicules in lycopods and bryophytes, Pacini et al. (1985) regarded the secretory tapetum as the most primitive. This hypothesis is corroborated by the presence of orbicules early in the fossil record.

I. DO ORBICULES CAUSE ALLERGY?

The allergenicity of pollen grains has long been the subject of extensive research. The question whether orbicules also contain allergens was first raised by Davis (1967). Orbicules of allergenic species dispersed into the atmosphere may act as a very effective vector to bring allergens to susceptible individuals. Indeed, the orbicules are often much more numerous than

pollen grains and small enough to pass easily through the pores of most protective masks (Miki-Hirosige et al., 1994) and airfilters.

We give just some recent examples of immunocytochemical studies that pay attention to orbicules as well. For a detailed account we refer to the specialized biomedical literature. Intracellular localization of the two major allergens in rye-grass anthers (*Lolium perenne*) using specific monoclonal antibodies after anhydrous fixation showed no labeling on the orbicules or in the tapetal cells (Taylor et al., 1994). Yet, in a previous study on the same species, glycoproteins were found on the orbicules and in the anther locule (Vithanage et al., 1982). The major allergen responsible for Japanese cedar pollinosis is also found in the respective orbicules and on the tapetal materials remaining in the young anther, using both monoclonal and polyclonal antibodies produced from the protein (Miki-Hirosige et al., 1994). It is assumed that some of the allergenic protein is produced in the tapetum and localized in the orbicules and pollen wall during maturation, and that the rest of the allergenic protein is produced in the Golgi apparatus in the mature pollen grain (Miki-Hirosige et al., 1994). In a first paper on the possible allergenicity of *Betula* orbicules (El-Ghazaly et al., 1995), using the nitrocellulose membrane test on samples collected on Burkard tapes, it is shown that a large number of very small spots (ca. 4 μm) become visible on the nitrocellulose membrane. These are caused by small particles that cross-react with the polyclonal *Bet v* rabbit antibody. Because of their small size and since the time of appearance is simultaneous with the occurrence of pollen in the air, it is assumed that these small particles are orbicules.

V. Distribution of Orbicules in Angiosperms

A. PRESENCE OF ORBICULES

Our literature search resulted in a list of 314 species from 72 families reported to have orbicules (Table I). Although we aimed to search as exhaustively as possible, we realise that the present list is still incomplete because information is published in very diverse research fields, which complicates tracing. We would like to encourage readers to inform us about additional findings, either personal or from papers we overlooked.

Papers discussed in section IV.A are not included in Table I. Davis (1966: 14) listed 19 families in which orbicules have been recorded. Eleven of these are not in Table I: Amaranthaceae, Amaryllidaceae, Aristolochiaceae, Cuscutaceae, Cyclanthaceae, Linaceae, Molluginaceae, Olacaceae, Pedaliaceae, Portulacaceae, and Rhamnaceae. In the embryological descriptions of the respective families (Davis, 1966) only scarce information is given on orbicule occurrence. Since no specific references are given, this information is not included in Table I.

To visualise this information on a classification system, we have chosen to plot it on a dahlgrenogram (Dahlgren, 1989) (Fig. 1). Although we considered using the well-known "angiosperm-tree" by Chase et al. (1993) for this purpose, we ultimately decided that a convenient overview would be nearly impossible, given the fact that the tree with dicots and monocots on family level fills several pages. Moreover, information on presence or absence of tapetum types is so far only plotted on dahlgrenograms. All things considered, a dahlgrenogram was the obvious choice for presenting our data on orbicule distribution. We think the dahlgrenogram still is one of the most interesting tools for demonstrating the distribution of characters even if some classificatory insights are changed and evolutionary relationships are less univocal.

For localization of the families and assessment of their relative size, we followed Dahlgren (1989a, 1989b) for dicotyledons and Dahlgren and Clifford (1982) and Dahlgren et al. (1985) for monocotyledons.

(Text continues on p. 259)

Table I
Taxa of flowering plants reported to have orbicules.

Taxa	Subject of research	Illustrations	References
MAGNOLIOPSIDA			
Acanthaceae (Lamiales)			
<i>Elytraria acaulis</i> (L.f.) Lindau	Embryol.	Draw.	Johri & Singh, 1959
Annonaceae (Annonales)			
<i>Anaxagorea brevipes</i> Benth.	P + t devel.	TEM	Gabarayeva, 1995
Apiaceae (Araliales)			
<i>Artemisia squamata</i> L.	O-morphol.	SEM, TEM	Cerceau-Larrival & Roland-Heydacker, 1976
<i>Daucus carota</i> L.	O-morphol.	SEM, TEM	Cerceau-Larrival & Roland-Heydacker, 1976
<i>D. littoralis</i> Sibth. & Sm.	O-morphol.	SEM, TEM	Cerceau-Larrival & Roland-Heydacker, 1976
<i>Eryngium palmatum</i> Pancic & Vis.	O-morphol.	SEM, TEM	Cerceau-Larrival & Roland-Heydacker, 1976
<i>Hydrocotyle mexicana</i> Cham. & Schtdl.	O-histochem., o-devel., o-ultrastruc.	SEM, TEM	Abadie et al., 1981
<i>Smyrniun perfoliatum</i> L.	Pollenkitt	TEM	Weber, 1991
<i>Trachymene pilosa</i> Sm.	P + t devel.	Draw., SEM, TEM	Cerceau-Larrival et al., 1981
<i>Turgenia latifolia</i> Hoffm.	O-histochem., o-devel., o-ultrastruc.	SEM, TEM	Abadie et al., 1981
"	P + t devel.	Draw., SEM, TEM	Cerceau-Larrival et al., 1981
Apocynaceae (Gentianales)			
<i>Catharanthus roseus</i> G. Don	T + o devel.	LM, TEM	El-Ghazaly & Nilsson, 1991
" (= <i>Vinca rosea</i> L.)	P + t + o ultrastruc., histochem.	Draw., SEM, TEM	Cousin, 1979
"	P + t devel.	Draw., SEM, TEM	Cerceau-Larrival et al., 1981
Austrobaileyaaceae (Annonales)			
<i>Austrobaileya maculata</i> C.T. White	P-devel.	SEM, TEM	Zavada, 1984
Berberidaceae (Ranunculales)			
<i>Nandina domestica</i> Thunb.	P + t devel.	Draw.	Kamelina & Touchina, 1982
Betulaceae (Fagales)			
<i>Betula pendula</i> Roth	Immunochem.	SEM, TEM	El-Ghazaly et al., 1995
Bignoniaceae (Lamiales)			
<i>Pyrostegia ignea</i> Presl	T-devel.	Draw., LM	Gupta & Nanda, 1978
<i>P. venusta</i> Miers	T-histochem.	LM	Gupta & Nanda, 1972
<i>Rhigozum trichotomum</i> Burch.	P + o devel.	LM, SEM, TEM	Robertson, 1984
<i>Tecoma stans</i> (L.) H.B. & K.	T-histochem.	LM	Gupta & Nanda, 1972
"	T-devel.	Draw., LM	Nanda & Gupta, 1978
Bixaceae (Malvales)			
<i>Bixa orellana</i> L.	Embryol.	Draw.	Chopra & Kaur, 1965
Bombacaceae (Malvales)			
<i>Quararibea</i> Aublet. (61 spp.)	P + o morphol.	LM, SEM, TEM	Nilsson & Robyns, 1974
Caesalpiniaceae (Fabales)			
<i>Delonix elata</i> Gamble	O-morphol.	SEM, TEM	Hesse, 1986
Cannabaceae (Urticales)			
<i>Cannabis sativa</i> L.	O-ultrastruc.	TEM	Heslop-Harrison, 1962
Capparidaceae (Capparales)			
<i>Capparis spinosa</i> L. (as "var. <i>inermis</i> ")	T + o ultrastruc.	LM, SEM, TEM	Gori & Lorito, 1988

Table I (continued)

Taxa	Subject of research	Illustrations	References
Caryophyllaceae (Caryophyllales)			
<i>Silene dioica</i> (L.) Clairv.	P + t devel., cytochem.	Draw., LM, TEM	Audran & Batcho, 1981
<i>S. pendula</i> L.	O-ultrastruc.	TEM	Heslop-Harrison, 1962
Chenopodiaceae (Caryophyllales)			
<i>Beta vulgaris</i> L. (normal)	CMS	TEM	Oryol & Golubeva, 1985
"	T-devel.	TEM	Hoefert, 1971
Chloanthaceae (see Verbenaceae)			
Convolvulaceae (Solanales)			
<i>Ipomoea alba</i> L.	O-general	LM	Traverse, 1991
<i>I. purpurea</i> Roth*	P + o histochem.	LM	Waterkeyn & Bienfait, 1971
<i>I. rubro-caerulea</i> Hook., cv.	P + o histochem.	LM	Waterkeyn & Bienfait, 1971
Degeneriaceae (Magnoliales)			
<i>Degeneria vitiensis</i> L.W.Bailey & A.C.Sm.	P + o morphol., p-devel.	Draw., LM, TEM	Dahl & Rowley, 1965
Dialypetalanthaceae (Gentianales)			
<i>Dialypetalanthus fuscescens</i> Kuhl.	Taxonomy	LM, SEM	Piesschaert et al., 1997
Ericaceae (Ericales)			
<i>Arbutus unedo</i> L.	T-general	Draw., LM, SEM, TEM	Pacini, 1990
<i>Calluna vulgaris</i> (L.) Hull	Pollenkitt	TEM	Hesse, 1979
"	Sp architect., p + o ultrastruc.	SEM, TEM	Hesse, 1985
<i>Erica herbacea</i> L.	Pollenkitt	TEM	Hesse, 1979
Euphorbiaceae (Euphorbiales)			
<i>Euphorbia</i> L. (9 spp.)	P + o morphol.	LM, SEM	El-Ghazaly, 1989
<i>Euphorbia</i> L. (60 spp.)	O-morphol.	SEM	El-Ghazaly & Chaudhary, 1993
<i>E. palustris</i> L.	O-morphol.	SEM, TEM	Hesse, 1986
<i>E. pulcherrima</i> Willd.ex Klotzsch	P + t histochem.	LM	Rudrammiyappa & Amigeri, 1985
<i>Mercurialis annua</i> L.	Pollination	LM	Lisci et al., 1994
Eupomatiaceae (Annonales)			
<i>Eupomatia laurina</i> R.Br.	O-morphol.	SEM, TEM	Hesse, 1986
Fabaceae (Fabales)			
<i>Soja hispida</i> Moench = <i>Glycine max</i> Merr.	T-devel., histochem.	TEM	Madjd & Roland-Hejdacker, 1978
<i>Vicia faba</i> L.	P + t devel.	Draw., SEM, TEM	Cerceau-Larrival et al., 1981
"	CMS	Draw., TEM	Moussel et al., 1992
Fagaceae (Fagales)			
<i>Quercus robur</i> L.	T-ultrastruc.	Draw., TEM	Rowley, 1993
Flacourtiaceae (Violales)			
<i>Caloncoba echinata</i> Gilg	Embryol. anther	Draw.	Endress & Voser, 1975
Gentianaceae (Gentianales)			
<i>Exacum</i> L.	P + t devel. & morphol.	Draw., LM, SEM	Sankara Rao & Chinnappa, 1983
<i>Gentiana acaulis</i> L.	T-devel.	TEM	Lombardo & Carraro, 1976b
Hamamelidaceae (Hamamelidales)			
<i>Hamamelis virginiana</i> L.	Pollenkitt	LM, SEM, TEM	Hesse, 1981
Lamiaceae (Lamiales)			
<i>Lavandula dentata</i> L.	P-devel.	TEM	Suarez-Cervera & Seoane-Camba, 1986

Table I (continued)

Taxa	Subject of research	Illustrations	References
Magnoliaceae (Magnoliales)			
<i>Liriodendron chinense</i> Sarg.	T-devel.	TEM	Ru-Wen & Zeng-Fang, 1995
<i>Magnolia delavayi</i> Franch.	P + o devel.	—	Gabarayeva, 1991
<i>Michelia fuscata</i> Blume	P + t devel.	—	Gabarayeva, 1986
Mimosaceae (Fabales)			
<i>Acacia conferta</i> A.Cunn. ex Benth.	P + t devel., cytochem.	LM, SEM	Kenrick & Knox, 1979
<i>A. ieaphylla</i> F.Muell. ex Benth.	P + t devel., cytochem.	LM, SEM	Kenrick & Knox, 1979
<i>A. paradoxa</i> Chiov.	P-devel.	Draw., SEM, TEM	Fitzgerald et al., 1993a
<i>A. subalata</i> Vatke	P + t devel., cytochem.	LM, SEM	Kenrick & Knox, 1979
<i>Prosopis juliflora</i> DC.	O-devel.	LM, TEM	Vijayaraghavan & Chaudry, 1993
Monimiaceae (Laurales)			
<i>Austromathaea elegans</i> L.S.Sm.			D. Foreman, pers. comm.
<i>Daphnandra repandula</i> F.Muell.			D. Foreman, pers. comm.
<i>D. micrantha</i> Benth.			D. Foreman, pers. comm.
<i>Doryphora sassafras</i> Endl.			D. Foreman, pers. comm.
<i>Steganthera macooria</i> (Bailey) Endress			D. Foreman, pers. comm.
Moringaceae (Capparales)			
<i>Moringa oleifera</i> Lam.	Embryol.	Draw.	Puri, 1941
Myrtaceae (Myrtales)			
<i>Eucalyptus melliodora</i> A.Cunn. ex R.T.Baker & H.G.Sm.	Embryol.	Draw.	Davis, 1968
Nymphaeaceae (Nymphaeales)			
<i>Nymphaea colorata</i> Peter	T-ultrastruc.	LM, TEM	Rowley et al., 1992
"	T-ultrastruc.	Draw., TEM	Rowley, 1993
<i>N. mexicana</i> A. Gray	T-developm.	LM, TEM	Gabarayeva & El-Ghazaly, 1997
Oleaceae (Oleales)			
<i>Olea europaea</i> L.	T-devel.	Draw., TEM	Pacini & Juniper, 1979
Oxalidaceae (Linales)			
<i>Oxalis acetosella</i> L.	P + o histochem.	LM	Waterkeyn & Bienfait, 1971
<i>O. rosei</i> Knuth			Banerjee & Barghoom, 1970
<i>Oxalis</i> L. (4 spp.)	O-devel.	LM, TEM	Carniel, 1967
Paeoniaceae (Paeoniales)			
<i>Paeonia tenuifolia</i> L.	T-devel.	TEM	Marquardt et al., 1968
Phytolacaceae (see Stegnospermataceae)			
Platanaceae (Hamamelidales)			
<i>Platanus acerifolia</i> Willd.	P + o devel., histochem.	SEM, TEM	Suarez-Cervera et al., 1995
Polygalaceae (Polygalales)			
<i>Securidaca longepedunculata</i> Fresen.	P + t devel.	Draw., LM, SEM, TEM	Coetzee & Robbertse, 1985
Polygonaceae (Polygonales)			
<i>Fagopyrum giraldii</i> (Damm. & Diels) Haraldson			L.-P. Ronse Decraene, pers. comm.
<i>F. esculentum</i> Moench.			L.-P. Ronse Decraene, pers. comm.
<i>F. snowdenii</i> (Hutch. & Dandy) S.-P. Hong			L.-P. Ronse Decraene, pers. comm.
<i>F. tataricum</i> (L.) Gaertn.			L.-P. Ronse Decraene, pers. comm.
<i>Oxygonum sinuatum</i> (Meisn.) Dammer			L.-P. Ronse Decraene, pers. comm.
<i>Polygonum tenue</i> Michx.			L.-P. Ronse Decraene, pers. comm.
<i>P. kelloggii</i> Greene			L.-P. Ronse Decraene, pers. comm.

Table I (continued)

Taxa	Subject of research	Illustrations	References
Primulaceae (Primulales)			
<i>Primula obconica</i> Hance	T-ultrastruc., t-histochem.	TEM	Stevens & Murray, 1981
Ranunculaceae (Ranunculales)			
<i>Caltha palustris</i> L.	O-ultrastruc.	Draw., LM, SEM, TEM	Cheng & Lin, 1980
<i>Ficaria ranunculoides</i> Moench	P + o devel.	LM, TEM	Roland, 1967
<i>Helleborus foetidus</i> L.	P + o + t devel., ultrastruc.	TEM	Echlin & Godwin, 1968a, 1968b, 1969
<i>Nigella damascena</i> L.	Embryol.	Draw., LM	Vijayaraghavan & Marwah, 1969
"	Techniques	LM	Bhandari & Kishori, 1971
"	T + o devel., histochem.	LM	Bhandari & Kishori, 1973
<i>Pulsatilla chinensis</i> (Bunge) Regel	T-devel., histochem.	LM	Mu et al., 1988
Rosaceae (Rosales)			
<i>Prunus avium</i> L. cv. Stella & Durone I di Vignola	P + t devel.	LM, TEM	Pacini et al., 1986
Rubiaceae (Gentianales)			
14 spp. from 12 genera	O-morphol.	SEM, TEM	Huysmans et al., 1997
<i>Catesbaea spinosa</i> L.			S. Huysmans, unpubl.
<i>Coccocypselum guianense</i> K.Schum.			S. Huysmans, unpubl.
<i>Erihalis vacciniifolia</i> Benth. & Hook.f.			A. Igersheim, pers. comm.
<i>Exostema</i> (Pers.) Bonpl.			A. Igersheim, pers. comm.
<i>Gonzalagunia panamensis</i> (Cav.) K.Schum.			S. Huysmans, unpubl.
<i>Hamelia patens</i> Jacq.			S. Huysmans, unpubl.
<i>Hoffmannia giesbreghtii</i> Hemsl.			S. Huysmans, unpubl.
<i>Mitriostigma axillare</i> Hochst.			S. Huysmans, unpubl.
<i>Paederia foetida</i> L.			S. Huysmans, unpubl.
<i>Pentas lanceolata</i> (Forssk.) Deflers			S. Huysmans, unpubl.
<i>Serissa foetida</i> Lam.			S. Huysmans, unpubl.
<i>Strumpfia maritima</i> Jacq.	General morphol.	—	Igersheim, 1993
Rutaceae (Rutales)			
<i>Citrus limon</i> (L.) Burm.f.	P + o devel.	LM, TEM	Horner & Lersten, 1971
Salicaceae (Salicales)			
<i>Populus nigra</i> L.	Pollenkitt	TEM	Hesse, 1979
<i>P. tremula</i> L.	P-devel.	LM, TEM	Rowley & Erdtman, 1967
Saxifragaceae (Saxifragales)			
<i>Saxifraga clusii</i> Gouan	T + p devel.	TEM	Abadie & Hideux, 1983
<i>S. cymbalaria</i> L. var. <i>huetiana</i> (Boisson) Engl. & Irmsch.	T + o devel., histochem.	SEM, TEM	Abadie & Hideux, 1979
"	P + t devel.	Draw., SEM, TEM	Cerceau-Larrival et al., 1981
"	P + o ultrastruc.	Draw., TEM	Abadie et al., 1987
<i>S. sempervivum</i> C.Koch	T + p devel.	TEM	Abadie & Hideux, 1983
<i>S. stolonifera</i> Curtis	P + o ultrastruc.	Draw., TEM	Abadie et al., 1987
<i>Saxifraga</i> L. (6 spp.)	Sp. polymerization	SEM, TEM	Hideux & Abadie, 1986
Scrophulariaceae (Lamiales)			
<i>Antirrhinum majus</i> L.	T-devel.	TEM	Lombardo & Carraro, 1976a
Simmondsiaceae (Euphorbiales)			
<i>Simmondsia chinensis</i> C.K.Schneid.	A-devel.	LM, SEM, TEM	Chaudhry & Vijayaraghavan, 1995

Table I (continued)

Taxa	Subject of research	Illustrations	References
Solanaceae (Solanales)			
<i>Lycopersicum esculentum</i> Mill.	T-devel.	SEM, TEM	Polowick & Sawhney, 1993
<i>L. peruvianum</i> Mill.	T-general	Draw., LM, SEM, TEM	Pacini, 1990
"	P-devel., p-ultrastruc.	TEM	Pacini & Juniper, 1984
<i>Petunia hybrida</i> Hort. ex Vilm.	P + t devel.	Draw., SEM, TEM	Cerceau-Larival et al., 1981
Stegnospermataceae (Caryophyllales)			
<i>Stegnosperma halimifolium</i> Benth.	Embryol.	Draw.	Kamelina & Proskurina, 1985
Tiliaceae (Malvales)			
<i>Tilia platyphyllos</i> Scop.	P-ultrastruc.	LM, TEM	Chambers & Godwin, 1961
<i>T. europaea</i> L.	P-ultrastruc.	LM, TEM	Chambers & Godwin, 1961
Urticaceae (Urticales)			
<i>Parietaria judaica</i> L.			Pacini & Franchi, unpubl.
<i>P. officinalis</i> L.	O-general	—	Franchi & Pacini, 1981
<i>Urtica dubia</i> Forssk.	O-general	—	Franchi & Pacini, 1981
Verbenaceae (Lamiales)			
9 sp., 8 genera	O-morphol.	SEM	Raj & El-Ghazaly, 1987
LILIOPSIDA			
Alismataceae (Alismatales)			
<i>Echinodorus cordifolius</i> (L.) Griseb.	T-ultrastruc.	Draw., TEM	Rowley, 1993
"	P-devel.	TEM	El-Ghazaly & Rowley (in press)
Alliaceae (Asparagales)			
<i>Allium cepa</i> L.	O-devel.	TEM	Risueño et al., 1969
<i>A. sativum</i> clone Piemonte	Histochem.	LM, TEM	Gori, 1982b
Anthericaceae (Asparagales)			
<i>Anemarrhena asphodeloides</i> Bunge	O-devel.	TEM	Chen et al., 1988a
"	T + o ultrastruc.	TEM	Chen et al., 1988b
Asparagaceae (Asparagales)			
<i>Asparagus officinalis</i> L. subsp. <i>officinalis</i>	P + t ultrastruc.	SEM, TEM	Gori, 1982a
Asphodelaceae (Asparagales)			
<i>Aloe ciliaris</i> Haw.	A-devel., CMS	LM, SEM, TEM	Keijzer & Cresti, 1987
<i>A. vera</i> (L.) Burm. f.	A-devel., CMS	LM, SEM, TEM	Keijzer & Cresti, 1987
<i>Gasteria verrucosa</i> Duval	O-funct.	Draw., LM, SEM, TEM	Keijzer, 1987b
Centrolepidaceae (Poales)			
<i>Centrolepis aristata</i> (R.Br.) Roem. & Schult.	P-devel.	SEM, TEM	Rowley & Dunbar 1996
Convalariaceae (Asparagales)			
<i>Ophiopogon japonicus</i> Ker Gawl.	T + o devel.	TEM	Liu et al., 1992
Cyanastraceae (Asparagales)			
<i>Cyanastrum cordifolium</i> Oliv.			Furness & Rudall (this issue)
Cyperaceae (Cyperales)			
<i>Eleocharis palustris</i> R.Br.	O-devel.	TEM	Carniel, 1971
<i>E. palustris</i> group	P-devel., histochem.	SEM, TEM	Dunbar, 1973
Hyacinthaceae (Asparagales)			
<i>Ledebouria socialis</i> (Baker) Jessop	Sp-architec.	TEM	Hess & Frosch, 1994
Iridaceae (Liliales)			
<i>Iris pallida</i> Lam.	T-devel., CMS	LM, SEM, TEM	Lippi et al., 1994
Lanariaceae (Asparagales)			
<i>Lanaria lanata</i> Druce			Furness & Rudall (this issue)

Table I (continued)

Taxa	Subject of research	Illustrations	References
Liliaceae (Liliales)			
<i>Lilium henryi</i> Baker	O-funct.	LM, SEM, TEM	Heslop-Harrison, 1968b
"	O-devel.	SEM, TEM	Heslop-Harrison & Dickinson, 1969
"	Sp-chem.	—	Shaw, 1971
"	O-ultrastruc., o-funct.	TEM	Herich & Lux, 1985
<i>L. hybrid</i> cv. Enchantment	T + o devel.	Draw., TEM	Reznickova & Willemse, 1980
"	P + o devel.	SEM	Reznickova et al., 1980
"	P + o devel.	—	Reznickova & Willemse, 1981
"	O-funct.	Draw., LM, SEM, TEM	Keijzer, 1987b
"	O-histochem.	Draw., LM, TEM	Clément & Audran, 1992
"	O-histochem., o-ultrastruc.	Draw., LM, TEM	Clément & Audran, 1993a
"	O-histochem., o-ultrastruc.	Draw., LM, TEM	Clément & Audran, 1993b
"	O-histochem.	TEM	Clément & Audran, 1993c
<i>L. longiflorum</i> Thunb.	O-funct.	LM, SEM, TEM	Heslop-Harrison, 1968b
"	O-devel.	SEM, TEM	Heslop-Harrison & Dickinson, 1969
<i>L. martagon</i> L.	T-morphol.	Draw., LM	Schnarf, 1923
"	P + o histochem.	LM	Waterkeyn & Bienfait, 1971
<i>L. regale</i> E.H.Wilson, cv.	P + o histochem.	LM	Waterkeyn & Bienfait, 1971
Orchidaceae (Orchidales)			
<i>Doritis pulcherrima</i> Lindl. ^b	P-devel.	LM, SEM, TEM	Wolter et al., 1988
Philesiaceae (Asparagales)			
<i>Lapageria rosea</i> Ruiz & Pav.			Furness & Rudall (this issue)
Phormiaceae (Asparagales)			
<i>Dianella tasmanica</i> Hook.f.			Furness & Rudall (this issue)
Poaceae (Poales)			
<i>Avena sativa</i> L.	T-devel.	LM, TEM	Steer, 1977
"	O-devel.	Draw.	Ogorodnikova, 1986
<i>Dactylis glomerata</i> L.	O-morphol.	SEM	Banerjee, 1967
"	T-general	Draw., LM, TEM, SEM	Pacini, 1990
<i>Lolium perenne</i> L.	Immunochem.	SEM, TEM	Vithanage et al., 1982
"	P + t ultrastruc.	LM, TEM	Pacini et al., 1992
"	Immunochem.	TEM	Taylor et al., 1994
<i>Oryza sativa</i> L.	T-ultrastruc.	TEM	Nishiyama, 1970 ^c , 1976 ^d
"	Morphogenesis	SEM	Takeoka et al., 1989 ^d
<i>Phleum pratense</i> L.	O-morphol.	SEM	Banerjee, 1967
"	O-devel.	TEM	Rowley & Skvarla, 1974
<i>Poa annua</i> L.	P-ultrastruc.	TEM	Rowley et al., 1959
"	Sp-ultrastruc.	Draw., TEM	Rowley, 1962
"	O-devel.	Draw., TEM	Rowley, 1963
<i>Saccharum spontaneum</i> L.	P-devel.	LM, SEM, TEM	Roques & Feldmann, 1996
<i>Secale cereale</i> L.	O-devel.	Draw.	Ogorodnikova, 1986
<i>Sorghum bicolor</i> Moench	P + o devel.	Draw., LM, SEM, TEM	Christensen et al., 1972
"	CMS, t-ultrastruc.	LM, SEM	Overman & Warmke, 1972
<i>Spartina patens</i> Muhl.	O-morphol.	SEM	Banerjee, 1967

Table I (continued)

Taxa	Subject of research	Illustrations	References
<i>Triticum aestivum</i> L.	CMS, p-ultrastruc.	TEM	De Vries & Ie, 1970
"	P + o devel.	TEM	El-Ghazaly & Jensen, 1985
"	P + o devel.	Draw., LM, TEM	El-Ghazaly & Jensen, 1986
"	O-devel.	Draw.	Ogorodnikova, 1986
"	P + o histochem.	LM, TEM	El-Ghazaly & Jensen, 1987
<i>T. turgidum</i> L. var. <i>durum</i> × <i>Agropyron intermedium</i> (Host) P.Beauv.	T-devel., CMS	LM, TEM	Young et al., 1979
<i>Zea mays</i> L.	P-devel.	TEM	Skvarla & Larson, 1966
"	O-morphol.	SEM	Banerjee, 1967
Trilliaceae (Dioscoreales)			
<i>Trillium kamschaticum</i> Ledeb.	P-devel.	LM, TEM	Takahashi, 1987
Uvulariaceae (Liliales)			
<i>Disporum smilacinum</i> A.Gray	P-devel.	SEM, TEM	Takahashi & Sohma, 1979
<i>Tricyrtis latifolia</i> Maxim.			Furness & Rudall (this issue)

* Family assignment follows Mabberley (1993) for dicotyledons and Dahlgren et al. (1985) for monocotyledons, except *Lanaria*, which follows Dahlgren (1989a).

^b A, anther; architec., architecture; chem., chemistry; CMS, cytoplasmic male sterility; cytochem., cytochemistry; devel., development; embryol., embryology; funct., function; histochem., histochemistry; immunochem., immunochemistry; morphol., morphology; o, orbicule; p, pollen; sp, sporopollenin; t, tapetum; ultrastruc., ultrastructure.

^c Draw., drawing; LM, light microscopy; SEM, scanning electron microscopy; TEM, transmission electron microscopy.

^d The same species is reported in the literature both with and without orbicules (cf. Tables I & II). It is therefore not included in Figure 1.

^e In the text of the cited reference the occurrence of orbicules is stated, although included figures are not convincing at all. The authors are also more cautious in the figure captions ("maybe Ubisch bodies": p. 81). This report is considered doubtful.

^f Original paper was not seen; information was extracted from English abstract.

^g Intracellular macro-orbicules, however, are observed in the tapetal cells.

B. SECRETORY TAPETA WITHOUT ORBICULES

Although it is generally accepted that orbicules are a general feature of secretory tapeta, few taxa have been traced with a secretory tapetum but without orbicules. Table II presents an overview of all negative observations we came across. We only mention references where the absence of orbicules is explicitly stated. The tapetum type of the respective species is also given, to enable the reader to interpret the information correctly. Nowhere is a hypothesis given to explain this absence.

C. WHY NO ORBICULES IN TAXA WITH AN AMOEBOID TAPETUM?

We found in the literature only one exception to the generally accepted rule that the presence of orbicules does not coincide with an amoeboid tapetum. According to Lombardo and Carraro (1976b), *Gentiana acaulis* has an amoeboid tapetum and also orbicules.

Bhandari (1984: 82) wrote the following about this question: "The lack of Ubisch bodies in the periplasmoidal tapetum might also indicate the presence of some system of direct utilization of sporopollenin precursors during pollen wall formation."

(Text continues on p. 262)

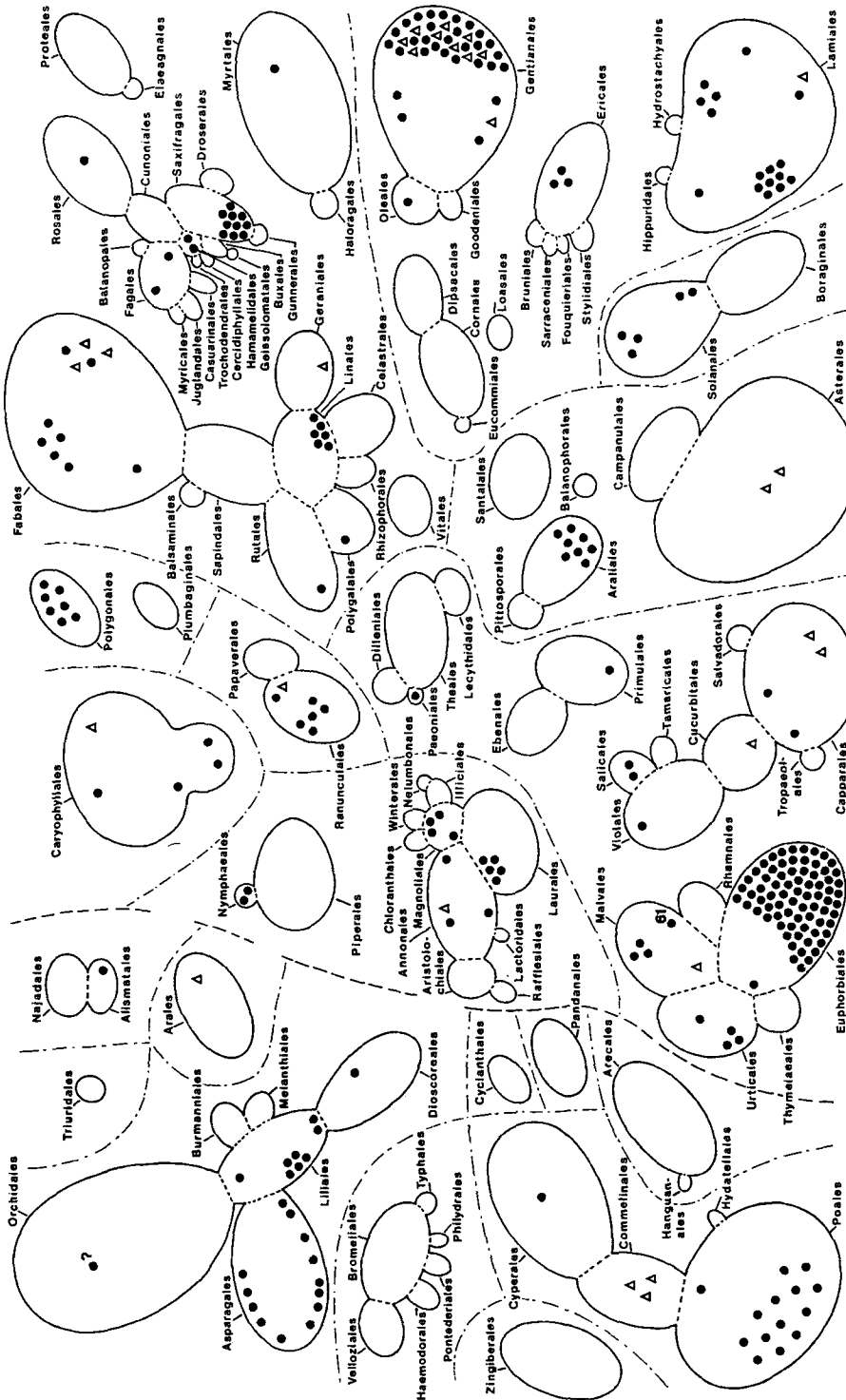


Fig. 1. Information in Tables I and II plotted on dahlgrenogram (Dahlgren, 1989a) to visualise the current knowledge of the distribution of orbicules in the angiosperms. Key: ●, species with orbicules; △, species without orbicules; ●?, doubtful observation of orbicules.

Table II
Taxa of flowering plants reported not to have orbicules.

Taxa ^a	Tapetum type ^b	References
MAGNOLIOPSIDA		
Annonaceae*		
<i>Asimina triloba</i> Dunal	S-A	Gabarayeva, 1992, 1993
Asclepiadaceae		
<i>Calotropis procera</i> (Ait.) Ait. f.	Inter	Cerceau-Larrival et al., 1981; Audran & Dicko-Zafimahova, 1992
Asteraceae		
<i>Cosmos bipinnatus</i> Cav.	A	Gupta & Nanda, 1972
<i>Helianthus annuus</i> L.	A	Gupta & Nanda, 1972
Berberidaceae*		
<i>Mahonia aquifolium</i> Nutt.	A	Roland-Heydacker, 1979
"	A	Cerceau-Larrival et al., 1981
Brassicaceae		
<i>Brassica oleracea</i> L.	S	Murgia et al., 1991
<i>Raphanus</i> L.	?	Dickinson, 1976
Cactaceae		
<i>Cereus jamacaru</i> DC.	S	Gupta & Nanda, 1972
Convolvulaceae*		
<i>Ipomoea purpurea</i> Roth ^c	?S	Godwin et al., 1967
Cucurbitaceae		
<i>Cucurbita pepo</i> L.	S	Ciampolini et al., 1993; Pacini & Franchi, 1993
Fabaceae*		
<i>Lens culinare</i> medik.	S	Biddle, 1979
<i>Pisum sativum</i> L.	S	Biddle, 1979
<i>Ulex europaeus</i> L. ^d	S	Misset & Gourret, 1984
Geraniaceae		
<i>Geranium robertianum</i> L.	S	Weber, 1996
Lamiaceae*		
<i>Rosmarinus officinalis</i> L.	S	Jiménez et al., 1996
Malvaceae		
<i>Hibiscus rosa-sinensis</i> L.	A	Gupta & Nanda, 1972
Rubiaceae*		
<i>Bouvardia ternifolia</i> Schldl.	?	S. Huysmans, pers. obs.
<i>Capirona decorticans</i> Spruce	S?	S. Huysmans, pers. obs.
<i>Ganguelia gossweileri</i> (S. Moore) Robbr.	?	Robbrecht et al., 1996
<i>Gardenia ternifolia</i> Schum. & Thonn. subsp. <i>jovis-tonantis</i> (Welw.) B. Verdc.	?	S. Huysmans, pers. obs.
<i>Gouldia terminalis</i> (Hook. & Arn.) Hillebr.	S?	Huysmans et al., 1997
<i>Mitriostigma axillare</i> Hochst.	?	Tomas Hansson, unpubl.
<i>Multidentia crassa</i> (Hiern) Bridson & Verdc.	S?	S. Huysmans, pers. obs.
<i>Psychotria kirkii</i> Hiern	S?	S. Huysmans, pers. obs.
<i>Simira rubescens</i> (Benth.) Bremek. ex Steyerm.	?	Huysmans et al., 1997

Table II (continued)

Taxa	Tapetum type	References
LILIOPSIDA		
Araceae		
<i>Arum italicum</i> Mill.	A	Pacini & Juniper, 1983
Commelinaceae		
<i>Rhoeo discolor</i> Hance	A	Cerceau-Larrival et al., 1981
<i>Rhoeo spathacea</i> (Sw.) Stearn	A	Nanda & Gupta, 1977
<i>Tradescantia virginiana</i> L.	A	Tiwari & Gunning, 1986
Orchidaceae	S ^c	Pacini & Franchi, 1993

^a Family assignment follows Mabberley (1993) for dicotyledons and Dahlgren et al. (1985) for monocotyledons. *, other taxa in same family known to have orbicules (see Table I).

^b S, secretory tapetum, A, amoeboid tapetum, Inter, intermediary tapetum.

^c The same species is reported in the literature both with and without orbicules (cf. Tables I & II). It is therefore not included in Figure 1.

^d Intracellular macro-orbicules, however, are observed in the tapetal cells.

^e Orchids are among the few taxa with a secretory tapetum and a strong entomophilous syndrome that lack orbicules entirely (Pacini & Franchi, 1993). For information on tapetum in orchids, also see Chardard, 1971; Wolter et al., 1988; and Fitzgerald et al., 1993b.

The absence of orbicules in amoeboid tapeta indeed tests the hypothesis that implicates an active role for orbicules in the development of the pollen exine—an attributed function that awaits definitive proof.

In their work on the development of the amoeboid tapetum in *Tradescantia*, Tiwari and Gunning (1986b) found membrane-bound granules during tetrad stage which they considered to be analogous to the tapetal pro-orbicules in secretory tapeta. Since their amount and dimensions were not so obvious as in secretory tapeta, Tiwari and Gunning (1986b: 112) suggest “that in the plasmodial tapetum the machinery for transferring tapetally-synthesized sporopollenin to the spore-wall is efficient enough to limit the extent of formation of orbicules as by-products.” The same authors posed the question of whether the limited occurrence of the granules is a manifestation of the amoeboid tapetum’s capacity to overproduce sporopollenin or an evolutionary relic of the secretory tapetum (if the amoeboid type is considered to be more evolved than the secretory type, see section III.A.). Comparable structures were not yet reported for other amoeboid tapeta.

Experiments with colchicine treatments on anthers from species with an amoeboid tapetum yielded very interesting results concerning orbicules. Microtubules next to the tapetal plasma membrane were observed in different stages of development (Pacini & Keijzer, 1989; Tiwari & Gunning, 1986a, 1986c, 1986d). When the formation of these microtubules was blocked by colchicine treatments in anthers of *Tradescantia virginiana*, a species with an invasive syncytial tapetum, the plasmodium formation was inhibited (Tiwari & Gunning, 1986c). The spatial regulation of sporopollenin deposition was disrupted, which resulted in the formation of orbicules on the outside of the plasma membranes of tapetal cells. Similar effects of colchicine treatments were observed in the anthers of *Canna*, which has a nonsyncytial invasive tapetum normally without orbicules (Tiwari & Gunning, 1986). This work provided an experimental basis for the observation that sporopollenin polymerisation in an ordered form only takes place on extracellular lipidic surfaces. In the invasive amoeboid tapetum of *T. virginiana*, cell fusion during normal development indeed removes all such surfaces.

Table III

Summary of Tables I and II: number of families and species with and without orbicules.

		Orbicules present	Orbicules absent
Dicots	Families	53	13
	Species	275	24
Monocots	Families	19	3
	Species	39	4
Total	Families	72	16
	Species	314	28

VI. Comments on Dahlgrenogram

In Table III we summarize the information of Tables I and II and Figure 1.

Fig. 1 demonstrates that the presence of orbicules is not restricted to a particular subclass or any other higher-level systematic group. The families with orbicules are spread over the system without a clear distribution pattern. Remarkably, the presence and absence of orbicules sometimes occur in the same family (Annonaceae, Berberidaceae, Fabaceae, Lamiaceae, Rubiaceae).

Suarez-Cervera et al. (1995: 81) speculated: "Perhaps their presence [orbicules] together with pollen grains, especially anemophilous, will also allow us to relate them with a system for a better dispersion of these pollen grains by the wind." From Figure 1 no such correlation with certain pollination syndromes could be deduced.

A. CORRELATION WITH TAPETUM TYPES

When we superimpose our dahlgrenogram on dahlgrenograms showing the distribution of tapetum types—namely, those of Dahlgren (1991) for dicots and Dahlgren and Clifford (1982) and Dahlgren et al. (1985) for monocots—there is indeed a very strong correlation: Orbicules do not occur in families with a dominant occurrence of an amoeboid tapetum. We found only two exceptions to this rule: Bignoniaceae and Alismataceae.

Both the Bignoniaceae and Alismataceae were shown to have an amoeboid tapetum; Davis (1966) confirms this. However, in Bignoniaceae four species are known to have orbicules, and in Alismataceae one. A recent study of tapetal development in *Echinodorus cordifolius* (Alismataceae) (El-Ghazaly & Rowley, in press), however, showed that tapetal cells remain secretorial until microspores are released from the callose envelope. At that time tapetal cells start to intrude into the locules and surround the microspores. Orbicules were clearly observed at tetrad stages only. This again illustrates that developmental studies are necessary to determine the true nature of the tapetum.

VII. Future Research

Many questions about origin, function, and morphological variation of orbicules remain. Only little of our knowledge is based on proven facts, the rest is based on hypotheses. Pro-

gress in understanding these fascinating structures can only be made by applying advanced techniques, assuring a more reliable fixation of the delicate tapetal tissues (e.g., rapid freeze-substitution). By autoradiography and isotope labeling, sporopollenin precursors can be traced and their route and destination can be determined during development.

The orbicule wall has the same biochemical composition as the pollen wall and is also ultrastructurally very similar. It is therefore a model to study sporopollenin biosynthesis in comparison with the pollen exine since orbicules are acellular structures, independent of cytoplasmic control (Clément & Audran, 1993b).

Any interpretation involving the control of exine morphology must also explain or be compatible with orbicule formation. Since orbicules are tapetal in origin, their existence severely tests models involving direct mediation of pollen wall form from the gametophyte (Rowley & Skvarla, 1974).

To make progress on the possible taxonomic value of orbicules it is necessary to have an idea about the overall morphological variation on a high systematic level. With the information available today it appeared impossible to recognize orbicule types on angiosperm level. More detailed SEM-observations of orbicules in situ are needed to reach this goal.

VIII. Acknowledgments

The first author holds a grant from the IWT and her research is financially supported by the research project N° G.0143.95 from the Fund for Scientific Research (F.W.O.). A travel grant from F.W.O. enabled S. Huysmans to discuss the final manuscript in Stockholm with G. El-Ghazaly and also with John Rowley, whose enthusiasm and expertise greatly stimulated finalisation of the paper. Thanks are due to Louis Ronse De Craene for translating the French abstract.

IX. Literature Cited

- Abadie, M. & M. Hideux. 1979. L'anthere de *Saxifraga cymbalaria* L. ssp. *huetiana* (Boiss.) Engl. et Irmsch. en microscopie électronique (M.E.B. et M.E.T.). 1. Généralités. Ontogénèse des orbicules. Ann. Sci. Nat. Bot. 13(1): 199–233.
- & ———. 1983. Les anthères de *Saxifraga clusii* Gouan et de *Saxifraga sempervivum* C.Koch. Quelques phases de l'ontogénèse des cellules tapétales et sporales. Ann. Sci. Nat. Bot. 13(5): 71–95.
- , M.-T. Cerceau-Larrival & F. Roland-Heydacker. 1981. Quelques aspects de la production des tapis dans les anthères de deux ombellifères: *Turgenia latifolia* (L.) Hoffm. et *Hydrocotyle mexicana* Cham. et Schlecht. Ann. Sci. Nat. Bot. 13(2–3): 149–162.
- , M. Hideux & J. R. Rowley. 1987. Ultrastructural cytology of the anther. II. Proposal for a model of exine considering a dynamic connection between cytoskeleton, glycolemma and sporopollenin synthesis. Ann. Sci. Nat. Bot. 13: 1–16.
- Archangelsky, S. & T. N. Taylor. 1993. The ultrastructure of in situ *Clavatipollenites* pollen from the early Cretaceous of Patagonia. Amer. J. Bot. 80: 879–885.
- Audran, J.-C. 1981. Pollen and tapetum development in *Ceratozamia mexicana* (Cycadaceae): sporal origin of the exinic sporopollenin in Cycads. Rev. Palaeobot. Palynol. 33: 315–346.
- & M. Batcho. 1981. Cytochemical and infrastructural aspects of pollen and tapetum ontogeny in *Silene dioica* (Caryophyllaceae). Grana 20: 65–80.
- & L. D. Dicko-Zafimahova. 1992. Aspects ultrastructuraux et cytochimiques du tapis staminal chez *Calotropis procera* (Asclepiadaceae). Grana 31: 253–272.
- Banerjee, U. C. 1967. Ultrastructure of the tapetal membranes in grasses. Grana Palynol. 7: 365–377.
- & E. S. Barghoorn. 1970. The structure of the Ubisch bodies (orbicules) and their control on mature exine pattern of grass pollen grains. Maize Genet. Coop. Newsl. 44: 46–47.

- & ———. 1971. The tapetal membranes in grasses and Ubisch body control of mature exine pattern. Pages 126–127 in J. Heslop-Harrison (ed.), *Pollen development and physiology*. Butterworths, London.
- Bhandari, N. N.** 1971. Embryology of the Magnoliales and comments on their relationships. *J. Arnold Arbor. Harv. Univ.* 52: 1–39, 285–304.
- . 1984. The microsporangium. Pages 53–121 in B. M. Johri (ed.), *Embryology of angiosperms*. Springer-Verlag, Berlin.
- & **R. Kishori.** 1971. Ubisch granules on tapetal membranes in anthers; rapid selective staining by spirit blue. *Stain Techn.* 46: 15–17.
- & ———. 1973. Development of tapetal membrane and Ubisch-granules in *Nigella damascena*—A histochemical approach. *Beitr. Biol. Pflanzen* 49: 59–72.
- Biddle, J. A.** 1979. Anther and pollen development in garden pea and cultivated lentil. *Canad. J. Bot.* 57: 1883–1900.
- Brummitt, R. K. & C. E. Powell.** 1992. *Authors of plant names*. Royal Botanic Gardens, Kew.
- Carniel, K.** 1963. Das antherentapetum. Ein kritischer überblick. *Österr. Bot. Z.* 110: 145–176.
- . 1967. Licht- und elektronenmikroskopische untersuchung der Ubischkörperentwicklung in der gattung *Oxalis*. *Österr. Bot. Z.* 114: 490–501.
- . 1971. Zur kenntnis der Ubischkörper von *Heleocharis palustris*. *Österr. Bot. Z.* 119: 496–502.
- Cerceau-Larrival, M.-T. & F. Roland-Heydacker.** 1976. Ontogénie et ultrastructure de pollens d'Om-bellifères. *Tapis et corps d'Ubisch*. *C.R. Acad. Sci. Paris* 283: 29–32.
- , **M. Abadie, L. Albertini, J.-C. Audran, A. Cornu, M.-T. Cousin, L. Dan Dicko-Zafimahova, G. Duc, I. K. Ferguson, M. Hideux, S. Nilsson, F. Roland-Heydacker & A. Souvre.** 1981. Relations sporophyte-gamétophyte: Assise tapétale-pollen. *Ann. Sci. Nat. Bot. Paris* 13: 69–92.
- Chambers, T. C. & H. Godwin.** 1961. The fine structure of the pollen wall of *Tilia platyphyllos*. *New Phytol.* 60: 393–399.
- Chardard, R.** 1971. Infrastructure des cellules tapetales, des microsporocytes et des grains de pollen de quelques Orchidacées. *Ann. Univ. ARERS* 9: 154–178.
- Chase, M. W., D. E. Soltis, R. G. Olmstead, D. Morgan, D. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, M. J. Donoghue, W. D. Clark, M. Hedrén, B. S. Gaut, R. K. Jansen, K.-J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. Strauss, Q. Xiang, G. M. Plunkett, P. S. Soltis, S. Swensen, L. E. Eguiarte, G. H. Jr. Learn, S. C. H. Barrett, S. Graham, S. Dayanandan, V. A. Albert.** 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbcl*. *Ann. Missouri Bot. Gard.* 80: 528–580.
- Chatin, A.** 1870. L'Anthère. Recherches sur le développement, la structure et les fonctions de ses tissus. J-B. Baillière et fils, Paris.
- Chaudhry, B. & M. R. Vijayaraghavan.** 1995. Structure and development of anther, pollen and exinal connections in joboba (*Simmondsia chinensis*). *Proc. Indian Nat. Sci. Acad.*, B61, 3: 199–208.
- Chen, Z.-K., F.-H. Wang & F. Zhou.** 1988a. On the origin, development and ultrastructure of the orbicules and pollenkitt in the tapetum of *Anemarrhena asphodeloides* (Liliaceae). *Grana* 27: 273–282.
- , ——— & ———. 1988b. The ultrastructural aspect of tapetum and Ubisch bodies in *Anemarrhena asphodeloides*. *Acta Bot. Sin.* 30: 1–5.
- Cheng, P.-C. & M.-I. Lin.** 1980. Cytological studies on the stamen of *Caltha palustris* L. 1. Anther and filament morphology, ultrastructural studies of their cuticle and orbicule. *Natl. Sci. Council. Monthly* 8: 1113–1140. (Chinese, Engl. abstract).
- Chopra, R. N. & H. Kaur.** 1965. Embryology of *Bixa orellana* Linn. *Phytomorphology* 15: 211–214.
- Christensen, J. E., H. T. Horner Jr. & N. R. Lersten.** 1972. Pollen wall and tapetal orbicular wall development in *Sorghum bicolor* (Gramineae). *Amer. J. Bot.* 59: 43–58.
- Ciampolini, F., M. Nepi & E. Pacini.** 1993. Tapetum development in *Cucurbita pepo* (Cucurbitaceae). *Pl. Syst. Evol. Suppl.* 7: 13–22.
- Clément, C. & J.-C. Audran.** 1992. Apports de la cytochimie à la connaissance des orbicules dans l'an-thère de *Lilium* (Liliacées). I. Le coeur orbiculaire. *Bull. Soc. bot. Fr., Lettres Bot.* 139: 369–376.
- & ———. 1993a. Cytochemical and ultrastructural evolution of orbicules in *Lilium*. *Pl. Syst. Evol. Suppl.* 7: 63–74.

- & ———, 1993b. Orbicule wall surface characteristics in *Lilium* (Liliaceae). An ultrastructural and cytochemical approach. *Grana* 32: 348–353.
- & ———, 1993c. Electron microscope evidence for a membrane around the core of the Ubisch body in *Lilium* (Liliaceae). *Grana* 32: 311–314.
- Coetzee, H. & P. J. Robbertse. 1985. Pollen and tapetal development in *Securidaca longepedunculata*. *S. Afr. J. Bot.* 51: 111–124.
- Colhoun, C. W. & M. W. Steer. 1981. Microsporogenesis and the mechanism of cytoplasmic male sterility in maize. *Ann. Bot.* 48: 417–424.
- Cousin, M.-T. 1979. Tapetum and pollen grains of *Vinca rosea* (Apocynaceae). *Grana* 18: 115–128.
- Dahl, A. O. & J. R. Rowley. 1965. Pollen of *Degeneria vitiensis*. *J. Arnold Arbor.* 46: 308–323.
- Dahlgren, G. 1989a. An updated angiosperm classification. *Bot. J. Linn. Soc.* 100: 197–203.
- , 1989b. The last dahlgrenogram. System of classification of the dicotyledons. Pages 249–260 in *The Davis and Hedge Festschrift*. Edinburgh University Press, Edinburgh.
- , 1991. Steps toward a natural system of the dicotyledons: Embryological characters. *Aliso* 13: 107–165.
- Dahlgren, R. M. T. & H. T. Clifford. 1982. *The monocotyledons: A comparative study*. Academic Press, London.
- , ——— & P. F. Yeo. 1985. *The families of the monocotyledons. Structure, evolution and taxonomy*. Springer-Verlag, Berlin.
- Davis, G. L. 1966. *Systematic embryology of the angiosperms*. John Wiley & Sons, New York.
- , 1967. The anther tapetum, Ubisch granules and hay fever. *Austral. J. Sci.* 30: 235–236.
- , 1968. Floral morphology and the development of gametophytes in *Eucalyptus melliodora* A. Cunn. *Austral. J. Bot.* 16: 19–35.
- De Vries, A. Ph. & T. S. Ie. 1970. Electron-microscopy on anther tissue and pollen of male sterile and fertile wheat (*Triticum aestivum* L.). *Euphytica* 19: 103–120.
- Dickinson, H. G. 1976. The deposition of acetolysis-resistant polymers during the formation of pollen. *Pollen Spores* 18: 321–334.
- & P. R. Bell. 1972. The role of the tapetum in the formation of sporopollenin-containing structures during microsporogenesis in *Pinus banksiana*. *Planta* 107: 205–215.
- Dunbar, A. 1973. Pollen development in the *Eleocharis palustris* Group (Cyperaceae). *Bot. Not.* 126: 197–254.
- Echlin, P. 1971. The role of the tapetum during microsporogenesis of angiosperms. Pages 41–61 in J. Heslop-Harrison (ed.), *Pollen development and physiology*. Butterworths, London.
- & H. Godwin. 1968a. The ultrastructure and ontogeny of pollen in *Helleborus foetidus* L. I. The development of the tapetum and ubisch bodies. *J. Cell Sci.* 3: 161–174.
- & ———, 1968b. The ultrastructure and ontogeny of pollen in *Helleborus foetidus* L. II. Pollen grain development through the callose special wall stage. *J. Cell Sci.* 3: 175–186.
- & ———, 1969. The ultrastructure and ontogeny of pollen in *Helleborus foetidus* L. III. The formation of the pollen grain wall. *J. Cell Sci.* 5: 459–477.
- Edwardson, J. R. 1970. Cytoplasmic male sterility. *Bot. Rev. (Lancaster)* 36: 341–420.
- El-Ghazaly, G. 1989. Pollen and orbicule morphology of some *Euphorbia* species. *Grana* 28: 243–259.
- , 1990. A comparison of pollen wall development in normal and gametocide treated plants of *Triticum aestivum*. *Bull. Soc. Bot. Fr.* 137: 65–70.
- & R. Chaudhary. 1993. Morphology and taxonomic application of orbicules (Ubisch bodies) in the genus *Euphorbia*. *Grana suppl.* 2: 26–32.
- & W. A. Jensen. 1985. Studies of the development of wheat (*Triticum aestivum*) pollen. III. Formation of microchannels in the exine. *Pollen Spores* 27: 5–14.
- & ———, 1986. Studies of the development of wheat (*Triticum aestivum*) pollen. I. Formation of the pollen wall and ubisch bodies. *Grana* 25: 1–29.
- & ———, 1987. Development of wheat (*Triticum aestivum*) pollen. II. Histochemical differentiation of wall and Ubisch bodies during development. *Amer. J. Bot.* 74: 1396–1418.
- & ———, 1990. Development of wheat (*Triticum aestivum*) pollen wall before and after effect of a gametocide. *Canad. J. Bot.* 68: 2509–2516.

- & S. Nilsson. 1991. Development of tapetum and orbicules of *Catharanthus roseus* (Apocynaceae). Pages 317–329 in S. Blackmore & S. H. Barnes (eds.), Pollen and spores. Systematics Association Special Vol. 44. Clarendon Press, Oxford.
- & J. R. Rowley. In press. Tapetum and microspore development in *Echinodorus cordifolius* (Alismataceae). *Nordic J. Bot.*
- , Y. Takahashi, S. Nilsson, E. Grafström & B. Berggren. 1995. Orbicules in *Betula pendula* and their possible role in allergy. *Grana* 34: 300–304.
- Endress, P. K. & P. Voser. 1975. Zur androeciumanlage und antherenentwicklung bei *Caloncoba echinata* (Flacourtiaceae). *Pl. Syst. Evol.* 123: 241–253.
- Erdtman, G., B. Berglund & J. Praglowski. 1961. An introduction to a Scandinavian pollen flora. Almqvist & Wiksells, Uppsala.
- Fitzgerald, M. A., D. M. Calder & R. B. Knox. 1993a. Character states of development and initiation of cohesion between compound pollen grains of *Acacia paradoxa*. *Ann. Bot.* 71: 51–59.
- , ——— & ———. 1993b. Secretory events in the freeze substituted tapetum of the orchid *Pterostylis concinna*. *Pl. Syst. Evol. Suppl.* 7: 53–62.
- Franchi, G. G. & E. Pacini. 1981. Gli orbicoli: Formazione, morfologia e loro significato. *Giornale Botanico Italiano* 115: 133 (Italian).
- Furness, C. A. & P. J. Rudall. The tapetum and systematics in monocotyledons. *Bot. Rev.* 64: 201–239.
- Gabarayeva, N. I. 1986. The development of the exine in *Michelia fuscata* (Magnoliaceae) in connection with the changes in cytoplasmic organelles of microspores and tapetum. *Bot. Zhurn. S.S.S.R.* 71: 311–322 (Russian).
- . 1991. The ultrastructure and development of exine and orbicules of *Magnolia delavayi* (Magnoliaceae) in the tetrad and the beginning of posttetrad periods. *Bot. Zhurn. S.S.S.R.* 76: 10–19 (Russian).
- . 1992. Sporoderm development in *Asimina triloba* (Annonaceae). I. The developmental events before callose dissolution. *Grana* 31: 213–222.
- . 1993. Sporoderm development in *Asimina triloba* (Annonaceae). II. The developmental events after callose dissolution. *Grana* 32: 210–220.
- . 1995. Pollen wall and tapetum development in *Anaxagorea brevipes* (Annonaceae): Sporoderm substructure, cytoskeleton, sporopollenin precursor particles, and the endexine problem. *Rev. Palaeobot. Palynol.* 85: 123–152.
- & G. El-Ghazaly. 1997. Sporoderm development in *Nymphaea mexicana* (Nymphaeaceae). *Pl. Syst. Evol.* 204: 1–19.
- Gifford E. M. & A. S. Foster. 1989. Morphology and evolution of vascular plants. Ed. 3. W. H. Freeman, New York.
- Godwin, H., P. Echlin & B. Chapman. 1967. The development of the pollen grain wall in *Ipomoea purpurea* (L.) Roth. *Rev. Palaeobot. Palynol.* 3: 181–195.
- Goebel, K. 1901. Organographie der pflanzen. 1. Auflage.
- Gorzynski, T. 1935. Untersuchungen über kleistogamie. IV. Entwicklung der archesporgewebe und der befruchtungsvorgang bei *Cardamine chenopodiifolia* Pers. *Acta Soc. Bot. Polonice* 12: 257–274.
- Gori, P. 1982a. An ultrastructural investigation of microspores, pollen grains and tapetum in *Asparagus officinalis*. *Phytomorphology* 32: 277–284.
- . 1982b. Accumulation of polysaccharides in the anther cavity of *Allium sativum*, Clone Piemonte. *J. Ultrastruct. Res.* 81: 158–162.
- & M. Lorito. 1988. An ultrastructural investigation of the anther wall and tapetum in *Capparis spinosa* L. var. *inermis*. *Caryologia* 41: 329–340.
- Gupta, S. C. & K. Nanda. 1972. Occurrence and histochemistry of the anther tapetal membrane. *Grana* 12: 99–104.
- & ———. 1978. Studies in the Bignoniaceae. I. Ontogeny of dimorphic anther tapetum in *Pyrostegia*. *Amer. J. Bot.* 65: 395–399.
- Herdt, E., R. Stüttfeld & R. Wiermann. 1978. The occurrence of enzymes involved in phenylpropanoid metabolism in the tapetum fraction of anthers. *Cytobiologie* 17: 433–441.
- Herich, R. & A. Lux. 1985. Lytic activity of Ubisch bodies (orbicules). *Cytologia* 50: 563–569.

- Heslop-Harrison, J.** 1962. Origin of exine. *Nature* 195: 1069–1071.
- . 1968a. Pollen wall development. *Science* 161: 230–237.
- . 1968b. Tapetal origin of pollen-coat substances in *Lilium*. *New Phytol.* 67: 779–786.
- . 1971. The pollen wall: Structure and development. Pages 75–98 in J. Heslop-Harrison (ed.), *Pollen development and physiology*. Butterworths, London.
- & **H. G. Dickinson.** 1969. Time relationships of sporopollenin synthesis associated with tapetum and microspores in *Lilium*. *Planta* 84: 199–214.
- Hess, M. W. & A. Frosch.** 1994. Subunits of forming pollen exine and Ubisch bodies as seen in freeze substituted *Ledebouria socialis* Roth (Hyacinthaceae). *Protoplasma* 182: 10–14.
- Hesse, M.** 1979. Entwicklungsgeschichte und ultrastruktur von pollenkitt und exine bei nahe verwandten entomo- und anemophilen angiospermen: Salicaceae, Tiliaceae und Ericaceae. *Flora* 168: 540–557.
- . 1981. Pollenkitt und viscin threads: their role in cementing pollen grains. *Grana* 20: 145–152.
- . 1985. Hemispheric surface processes of exine and orbicules in *Calluna* (Ericaceae). *Grana* 24: 93–98.
- . 1986. Orbicules and the ektexine are homologous sporopollenin concretions in Spermatophyta. *Pl. Syst. Evol.* 153: 37–48.
- Hesse, M. & M. W. Hess.** 1993. Recent trends in tapetum research. A cytological and methodological review. *Pl. Syst. Evol. Suppl.* 7: 127–145.
- Hideux, M. & M. Abadie.** 1986. Ontogenetic constraints on function in pollen of some *Saxifraga* L. species. Pages 35–48 in S. Blackmore & I. K. Ferguson (eds.), *Pollen and spores: Form and function*. The Linnean Society, London.
- Hoefert, L. L.** 1971. Ultrastructure of tapetal cell ontogeny in *Beta*. *Protoplasma* 73: 397–406.
- Horner, H. T. Jr. & N. R. Lersten.** 1971. Microsporogenesis in *Citrus limon* (Rutaceae). *Amer. J. Bot.* 58: 72–79.
- Huysmans, S., G. El-Ghazaly, S. Nilsson & E. Smets.** 1997. Systematic value of tapetal orbicules: A preliminary survey of the Cinchonoideae (Rubiaceae). *Canad. J. Bot.* 75: 815–826.
- Igersheim, A.** 1993. The character states of the Caribbean monotypic endemic *Strumpfia* (Rubiaceae). *Nordic J. Bot.* 13: 545–559.
- Jiménez, J. L. U., P. H. Fernández, M. G. Schlag & M. Hesse.** 1996. Pollen and tapetum development in male fertile *Rosmarinus officinalis* L. (Lamiaceae). *Grana* 34: 305–316.
- Johri, B. M. & H. Singh.** 1959. The morphology, embryology and systematic position of *Elytraria acaulis* (Linn.f.) Lindau. *Bot. Not.* 112: 227–251.
- Kamelina, O. P. & N. G. Tutchina.** 1982. A contribution to the embryology of the non-investigated taxa. II. The development of the anther and pollen grains in *Nandina domestica* (Berberidaceae). *Bot. Zhurn. S.S.S.R.* 67: 1459–1468. (Russian)
- & **O. B. Proskurina.** 1985. On the embryology of *Stegnosperma halimifolium* (Stegnospermataceae). Distribution of the embryological features in Caryophyllales. *Bot. Zhurn. S.S.S.R.* 70: 721–730. (Russian)
- Kaul, M. L. H.** 1988. Male sterility in higher plants. Springer-Verlag, Berlin.
- Keijzer, C. J.** 1984. Pollen dispersal and the function of the orbicules. *Acta Bot. Neerl.* 33: 244.
- . 1987b. The processes of anther dehiscence and pollen dispersal. II. The formation and the transfer mechanism of pollenkitt, cell-wall development of the loculus tissues and a function of orbicules in pollen dispersal. *New Phytol.* 105: 499–507.
- & **M. Cresti.** 1987. A comparison of anther tissue development in male sterile *Aloe vera* and male fertile *Aloe ciliaris*. *Ann. Bot.* 59: 533–542.
- Kenrick, J. & R. B. Knox.** 1979. Pollen development and cytochemistry in some Australian species of *Acacia*. *Austral. J. Bot.* 27: 413–427.
- Kosmath, L. von.** 1927. Studien über das antherentapetum. *Österr. Bot. Z.* 76: 235–241.
- Krjatchenko, D.** 1925. De l'activité des chondriosomes pendant le développement des grains de pollen et des cellules nourricières du pollen dans *Lilium croceum* chaix. *Rev. Gén. Bot.* 37: 193–211.
- Laser, K. D. & N. R. Lersten.** 1972. Anatomy and cytology of microsporogenesis in cytoplasmic male-sterile angiosperms. *Bot. Rev. (Lancaster)* 38: 425–450.

- Lippi, M., F. Cimoli, E. Maugini & G. Tani. 1994. A comparative study of the tapetal behaviour in male fertile and male sterile *Iris pallida* Lam. during microsporogenesis. *Caryologia* 47: 109–120.
- Lisci, M., C. Tanda & E. Pacini. 1994. Pollination ecophysiology of *Mercurialis annua* L. (Euphorbiaceae), an anemophilous species flowering all year round. *Ann. Bot.* 74: 125–135.
- Liu, N., F. Wang & Z. Chen. 1992. Fine structure of tapetal cells and Ubisch bodies in the anther of *Ophiopogon japonicus*. *Acta Bot. Sin.* 34: 15–19.
- Lombardo, G. & L. Carraro. 1976a. Tapetal ultrastructural changes during pollen development. I. Studies on *Antirrhinum maius*. *Caryologia* 29: 113–125.
- & ———. 1976b. Tapetal ultrastructural changes during pollen development. III. Studies on *Gentiana acaulis*. *Caryologia* 29: 345–349.
- Lugardon, B. 1981. Les globules des Filicinées, homologues des corps d'Ubisch des Spermatophytes. *Pollen Spores* 23: 93–124.
- Lynch, A. H. & M. Gregory. 1996. A bibliography of stamen morphology and anatomy. Pages 272–336 in W. G. D'Arcy & R. C. Keating (eds.), *The anther: Form, function and phylogeny*. Cambridge University Press.
- Mabberley, D. J. 1993. *The plant book, a portable dictionary of the higher plants*. Cambridge University Press, Cambridge.
- Madjd, A. & F. Roland–Heydacker. 1978. Sécrétions et dégénérescence des cellules du tapis dans l'anthere du *Soja hispida* Moench, Papilionaceae. *Grana* 17: 167–174.
- Maheshwari, P. 1950. Introduction to the embryology of angiosperms. McGraw-Hill, New York.
- Mascré, M. 1922. Sur l'étamine des Boraginées. *C.R. Acad. Sci. Paris* 175: 987–988.
- Marquardt, H., O. M. Barth & U. von Rahden. 1968. Zytophotometrische und elektronenmikroskopische beobachtungen über die tapetumzellen in den antheren von *Paeonia tenuifolia*. *Protoplasma* 65: 407–421.
- Miki-Hirosige, H., S. Nakamura, H. Yasueda, T. Shida & Y. Takahashi. 1994. Immunocytochemical localization of the allergenic proteins in the pollen of *Cryptomeria japonica*. *Sex. Pl. Reprod.* 7: 95–100.
- Misset, M. T. & J. P. Gourret. 1984. Accumulation of smooth cisternae in the tapetal cells of *Ulex europaeus* L. (Papilionoideae). *J. Cell Sci.* 72: 65–74.
- Moussel, B., C. Moussel & J.-C. Audran. 1992. La stérilité mâle nucléo-cytoplasmique chez la féverole (*Vicia faba* L.). IX. Fonctionnement du tapis et formations membranaires chez les génotypes fertiles. Incidence du dysfonctionnement du tapis sur l'ontogénèse de l'exine des microspores stériles. *Grana* 31: 25–48.
- Mu, X., F. Wang & W. Wang. 1988. Development and histochemical observations of tapetum and peritapetal membrane in anther of *Pulsatilla chinensis*. *Acta Bot. Sin.* 30: 6–13.
- Murgia, M., M. Charzynska, M. Rougier & M. Cresti. 1991. Secretory tapetum of *Brassica oleracea* L.: Polarity and ultrastructural features. *Sex. Pl. Reprod.* 4: 28–35.
- Nanda, K. & S. C. Gupta. 1977. Development of tapetal periplasmodium in *Rhoeo spathacea*. *Phytomorphology* 27: 308–314.
- & ———. 1978. Studies in the Bignoniaceae. II. Ontogeny of dimorphic anther tapetum in *Tecomma*. *Amer. J. Bot.* 65: 400–405.
- Nilsson, S. & A. Robyns. 1974. Pollen morphology and taxonomy of the genus *Quararibea* s.l. (Bombacaceae). *Bull. Jard. Bot. Nat. Belg.* 44: 77–99.
- Nishiyama, I. 1970. Male sterility caused by cooling treatment at the young microspore stage in rice plants. Part 6. Electron microscopical observations on normal tapetal cells at the critical stage. *Proc. Crop Sci. Soc. Jap.* 39: 474–479.
- . 1976. Male sterility caused by cooling treatment at the young microspore stage in rice plants. Part 13. Ultrastructure of tapetal hypertrophy without primary wall. *Proc. Crop Sci. Soc. Jap.* 45: 270–278.
- Ogorodnikova, V. F. 1986. The genesis and ultrastructure of the sporopollenin wall of tapetal cells in grasses. *Bot. Zhurn. S.S.S.R.* 71: 1366–1371. (Russian)
- Oryol, L. I. & E. A. Golubeva. 1985. The effect of x and z alleles on ultrastructure of anthers and the mechanism of cytoplasmic male sterility in sugar beet. *Genetica* 21: 1002–1011. (Russian)

- Osborn, J. M., T. N. Taylor & P. R. Crane.** 1991. The ultrastructure of *Sahnia* pollen (Pentoxylales). *Amer. J. Bot.* 78: 1560–1569.
- Overman, M. A. & H. E. Warmke.** 1972. Cytoplasmic male sterility in *Sorghum*. II. Tapetal behavior in fertile and sterile anthers. *J. Hered.* 63: 227–234.
- Pacini, E.** 1990. Tapetum and microspore function. Pages 213–237 in S. Blackmore & R. B. Knox (eds.), *Microspores, evolution and ontogeny*. Academic Press, London.
- & **G. G. Franchi.** 1993. Role of the tapetum in pollen and spore dispersal. *Pl. Syst. Evol. Suppl.* 7: 1–11.
- & **B. E. Juniper.** 1979. The ultrastructure of pollen-grain development in the olive (*Olea europaea*). 2. Secretion by the tapetal cells. *New Phytol.* 83: 165–174.
- & ———. 1983. The ultrastructure of the formation and development of the amoeboid tapetum in *Arum italicum* Miller. *Protoplasma* 117: 116–129.
- & ———. 1984. The ultrastructure of pollen grain development in *Lycopersicon peruvianum*. *Caryologia* 37: 21–50.
- , **G. G. Franchi & M. Hesse.** 1985. The tapetum: its form, function, and possible phylogeny in Embryophyta. *Pl. Syst. Evol.* 149: 155–185.
- , **L. M. Bellani & R. Lozzi.** 1986. Pollen, tapetum and anther development in two cultivars of sweet cherry (*Prunus avium*). *Phytomorphology* 36: 197–210.
- , **P. E. Taylor, M. B. Singh & R. B. Knox.** 1992. Development of plastids in pollen and tapetum of rye-grass, *Lolium perenne* L. *Ann. Bot.* 70: 179–188.
- Periasamy, K. & B. G. L. Swamy.** 1966. Morphology of the anther tapetum in angiosperms. *Curr. Sci.* 35: 427–430.
- Piesschaert, F., E. Robbrecht & E. Smets.** 1997. *Dialypetalanthus fuscescens* Kuhl. (Dialypetalanthaceae): The problematic taxonomic position of an Amazonian endemic. *Ann. Missouri Bot. Gard.* 84: 201–223.
- Polowick, P. L. & V. K. Sawhney.** 1993. Differentiation of the tapetum during microsporogenesis in tomato (*Lycopersicon esculentum* Mill.), with special reference to the tapetal cell wall. *Ann. Bot.* 72: 595–605.
- Puri, V.** 1941. The life-history of *Moringa oleifera* Lamk. *J. Indian Bot. Soc.* 20: 263–284.
- Raj, B. & G. El-Ghazaly.** 1987. Morphology and taxonomic application of orbicules (Ubisch bodies) in Chloanthaceae. *Pollen Spores* 29: 151–166.
- Reznickova, S. A. & M. T. M. Willemse.** 1980. Formation of pollen in the anther of *Lilium*. II. The function of the surrounding tissues in the formation of pollen and pollen wall. *Acta Bot. Neerl.* 29: 141–156.
- & ———. 1981. The formation of sporopollenin-containing structures in the anther of *Lilium*. *Bot. Zhurn. S.S.S.R.* 66: 1155–1165. (Russian)
- , **A. C. Van Aelst & M. T. M. Willemse.** 1980. Investigation of exine and orbicule formation in the *Lilium* anther by scanning electron microscopy. *Acta Bot. Neerl.* 29: 157–164.
- Risueño, M. C., G. Giménez-Martín, J. F. López-Sáez & M. I. R.-García.** 1969. Origin and development of sporopollenin bodies. *Protoplasma* 67: 361–374.
- Robbrecht, E., S. Huysmans & E. Figueiredo.** 1996. The generic status of *Oxyanthus gossweileri* (Rubiaceae) from Angola. *S. Afr. J. Bot.* 62: 17–22.
- Robertson, B. L.** 1984. Tapetal cell changes and sporoderm development in *Rhizogonum trichotomum* (Burch.). *Ann. Bot.* 53: 803–810.
- Roland, F.** 1967. Différenciation du sporoderme chez *Ficaria ranunculoïdes* Moench. Observation et évolution de "corps d'Ubisch." *Pollen Spores* 9: 415–425.
- Roland-Heydacker, F.** 1979. Aspects ultrastructuraux de l'ontogénie du pollen et du tapis chez *Mahonia aquifolium* Nutt. (Berberidaceae). *Pollen Spores* 21: 259–278.
- Roques, D. & P. Feldmann.** 1996. Développement de l'anthère et du grain de pollen chez une espèce sauvage apparentée à la canne à sucre (*Saccharum spontaneum*). *Canad. J. Bot.* 74: 788–795.
- Rosanoff, S.** 1865. Zur kenntniss des baues und der entwicklungsgeschichte des pollens der Mimosaceae. *Jahrb. Wiss. Bot.* 4: 441–450.
- Rowley, J. R.** 1962. Nonhomogeneous sporopollenin in microspores of *Poa annua* L. *Grana Palynol.* 3: 3–19.

- . 1963. Ubisch body development in *Poa annua*. Grana Palynol. 4: 25–36.
- . 1976. Dynamic changes in pollen wall morphology. In I. K. Ferguson & J. Muller (eds.), The evolutionary significance of the exine. Linn. Soc. Symp. Ser. 1: 39–66.
- . 1993. Cycles of hyperactivity in tapetal cells. Pl. Syst. Evol., Suppl. 7: 23–38.
- Rowley, J. R. & A. O. Dahl. 1982. Similar substructure for tapetal surface and exine “tuft”-units. Pollen Spores 24: 5–8.
- & A. Dunbar. 1996. Pollen development in *Centrolepis aristata* (Centrolepidaceae). Grana 35: 1–15.
- & G. Erdtman. 1967. Sporoderm in *Populus* and *Salix*. Grana Palynol. 7: 518–567.
- & J. J. Skvarla. 1974. Plasma membrane-glycocalyx origin of Ubisch body wall. Pollen Spores 16: 441–448.
- & B. Walles. 1987. Origin and structure of Ubisch bodies in *Pinus sylvestris*. Acta Soc. Bot. Poloniae 56: 215–227.
- , N. I. Gabarayeva & B. Walles. 1992. Cyclic invasion of tapetal cells into loculi during microspore development in *Nymphaea colorata* (Nymphaeaceae). Amer. J. Bot. 79: 801–808.
- , K. Mühlethaler & A. Frey-Wyssling. 1959. A route for the transfer of materials through the pollen grain. J. Biophys. Biochem. Cytol. 6: 537–538.
- Rudramuniyappa, C. K. & B. G. Annigeri. 1985. Histochemical observations on the sporogenous tissue and tapetum in the anther of *Euphorbia*. Cytologia 50: 39–48.
- Ru-Wen, F. & Y. Zeng-Fang. 1995. Ultrastructure and development of the tapetum in *Liriodendron chinense* (Hemsl.) Sarg. Chinese J. Bot. 7: 133–138.
- Sankara Rao, K. & C. C. Chinnappa. 1983. Studies in Gentianaceae. Microsporangium and pollen. Canad. J. Bot. 61: 324–336.
- Schnarf, K. 1923. Kleine Beiträge zur Entwicklungsgeschichte der Angiospermen. IV. Über das Verhalten des Antherentapetums einiger Pflanzen. Österr. Bot. Z. 72: 242–245.
- Serbet, R. & R. A. Stockey. 1991. Taxodiaceous pollen cones from the Upper Cretaceous (Horseshoe Canyon Formation) of Drumheller, Alberta, Canada. Rev. Palaeobot. Palynol. 70: 67–76.
- Shaw, G. 1971. The chemistry of sporopollenin. Pages 305–348 in J. Brooks et al. (eds.), Sporopollenin. Academic Press, London.
- Skvarla, J. J. & D. A. Larson. 1966. Fine structural studies of *Zea mays* pollen. I. Cell membranes and exine ontogeny. Amer. J. Bot. 53: 1112–1125.
- Sporne, K. R. 1973. A note on the evolutionary status of tapetal types in dicotyledons. New Phytol. 72: 1173–1174.
- Steer, M. W. 1977. Differentiation of the tapetum in *Avena*. I. The cell surface. J. Cell Sci. 25: 125–138.
- Stevens, V. A. M. & B. G. Murray. 1981. Studies on heteromorphic self-incompatibility systems: The cytochemistry and ultrastructure of the tapetum of *Primula obconica*. J. Cell Sci. 50: 419–431.
- Stidd, B. M. 1978. An anatomically preserved *Potoniaea* with in situ spores from the Pennsylvanian of Illinois. Amer. J. Bot. 65: 677–683.
- Suarez-Cervera, M. & J. A. Seoane-Camba. 1986. Ontogénese des grains de pollen de *Lavandula dentata* L. et évolution des cellules tapétales. Pollen Spores 28: 5–28.
- , J. Marquez & J. Seoane-Camba. 1995. Pollen grain and Ubisch body development in *Platanus acerifolia*. Rev. Palaeobot. Palynol. 85: 63–84.
- Takahashi, M. 1987. Development of omniaperturate pollen in *Trillium kamschaticum* (Liliaceae). Amer. J. Bot. 74: 1842–1852.
- Takahashi M. & K. Sohma. 1979. Pollen wall formation and tapetum in *Disporum smilacinum* A. Gray (Liliaceae). Sci. Rep. Tôhoku Univ. Ser. IV (Biol.) 37: 273–281.
- Takeoka, Y., K. Ogawa, T. Kawai & T. Wada. 1989. Scanning electron microscopic observations on morphogenesis of the panicle and spikelet in rice plants. Jap. J. Crop Sci. 58: 119–125.
- Taylor, P. E., I. A. Staff, M. B. Singh & R. B. Knox. 1994. Localization of the major allergens in ryegrass pollen using specific monoclonal antibodies and quantitative analysis of immunogold labeling. Histochem. J. 26: 392–401.
- Taylor, T. N. 1976. The ultrastructure of Schopfipollenites: orbicules and tapetal membranes. Amer. J. Bot. 63: 857–862.

- . 1990. Microsporogenesis in fossil plants. Pages 121–145 in S. Blackmore & R.B. Knox (eds.), *Microspores: Evolution and ontogeny*. Academic Press, London.
- . & K. L. Alvin. 1984. Ultrastructure and development of Mesozoic pollen: Classopollis. *Amer. J. Bot.* 71: 575–587.
- Taylor, P. E., I. A. Staff, M. B. Singh & R. B. Knox. 1994. Localization of the two major allergens in rye-grass pollen using monoclonal antibodies and quantitative analysis of immunogold labelling. *Histochem. J.* 26: 392–401.
- Tiwari, S. C. & B. E. S. Gunning. 1986. An ultrastructural, cytochemical and immunofluorescence study of postmeiotic development of plasmoidal tapetum in *Tradescantia virginiana* L. and its relevance to the pathway of sporopollenin secretion. *Protoplasma* 133: 100–114.
- Traverse, A. 1991. Giant Ubisch bodies and other “throwaway sporopollenin” as sources of information. *Curr. Sci.* 61: 678–681.
- Ubisch, G. von. 1927. Kurze mitteilungen zur entwicklungsgeschichte der antheren. *Planta* 3: 490–495.
- Ueno, J. 1959. Some palynological observations of Taxaceae, Cupressaceae and Araucariaceae. *J. Inst. Polyt. Osaka, D*, 10: 75–87.
- . 1960a. On the fine structure of the cell walls of some gymnosperm pollen. *Biol. J. Nara Women's Univ.* 10: 19–25.
- . 1960b. Studies on pollen grains of Gymnospermae. *J. Inst. Polyt. Osaka, D*, 11: 109–136.
- Vijayaraghavan, M. R. & B. Chaudhry. 1993. Structure and development of orbicules in the tapetum of *Prosopis juliflora* (Leguminosae, Mimosoideae). *Phytomorphology* 43: 41–48.
- . & K. N. Marwah. 1969. Studies in the family Ranunculaceae—Microsporangium, microsporogenesis and Ubisch granules in *Nigella damascena*. *Phyton* 13: 203–209.
- Vithanage, H. I. M. V., B. J. Howlett, S. Jobson & R. B. Knox. 1982. Immunocytochemical localization of water-soluble glycoproteins, including Group 1 allergen, in pollen of ryegrass, *Lolium perenne*, using ferritin-labelled antibody. *Histochem. J.* 14: 949–966.
- Waterkeyn, L. & A. Bienfait. 1971. Primuline induced fluorescence of the first exine elements and Ubisch bodies in *Ipomoea* and *Lilium*. Pages 108–127 in J. Brooks, P. R. Grant, M. D. Muir, P. van Gijzel & G. Shaw (eds.), *Sporopollenin*. Academic Press, London.
- Weber, M. 1991. The transfer of pollenkitt in *Smyrniium perfoliatum* (Apiaceae). *Ann. Bot.* 68: 63–68.
- . 1996. The existence of a special exine coating in *Geranium robertianum* pollen. *Intl. J. Pl. Sci.* 157: 195–202.
- Wolter, M., C. Seuffert & R. Schill. 1988. The ontogeny of pollinia and elastoviscin in the anther of *Doritis pulcherrima* (Orchidaceae). *Nordic J. Bot.* 8: 77–88.
- Yamazaki, T. & M. Takeoka. 1962. Electron microscopic investigations of the fine details of the pollen grain surface in Japanese gymnosperms. *Grana Palynol.* 3: 3–12.
- Young, B. A., J. Schulz-Schaeffer & T. W. Carroll. 1979. Anther and pollen development in male-sterile intermediate wheatgrass plants derived from wheat x wheatgrass hybrids. *Canad. J. Bot.* 57: 602–618.
- Zajac, K. 1995. Ultrastructural features of secretory tapetum in the capsule of the moss *Ceratodon purpureus* (Hedw.) Brid. *Phytomorphology* 45: 31–37.
- Zavada, M. S. 1984. Pollen wall development of *Austrobaileya maculata*. *Bot. Gaz.* 145: 11–21.