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OVULE AND SEED OF XANTHOPHYLLUM (POLYGALACEAE)

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SUMMARY

The ovule primordia of *Xanthophyllum* are trizonate and the outer integument is completely of subdermal origin. Due to a different post-fertilization development the variation in seed coat morphology is considerable. Primitive features of the *Xanthophyllum* seed are thick endosperm with foliaceous cotyledons, a well-developed palisade layer and a thick mesophyll layer.

INTRODUCTION

The genus *Xanthophyllum* Roxb. comprises 93 species of shrubs and trees, nearly exclusively confined to Southeast Asia and Malesia. Though sometimes referred to as a separate family Xanthophyllaceae (Gagnepain, 1908; Cronquist, 1981), the genus is included in the Polygalaceae by Van der Meijden (1982), who follows Chodat's (1896) subdivision of the family in three tribes, viz. Polygaleae, Moutabeae and Xanthophylleae. The ovule of the Polygalaceae is anatropous, crassinucellate and sometimes provided with a long exostome (Davis, 1966). The endotestal seed coat consists of a palisade layer, a mesophyll layer and an epidermis and is mostly provided with hairs (Netolitzky, 1926; Corner, 1976). Rodrigue (1893) recognized the differences in testa structure within the family, and her classification of seed coats, adopted by Corner (1976), can be summarized as follows: (a) seed coats two cell layers thick (including *Polygala vulgaris*); (b) seed coats more than two cell layers thick (including *Polygala chamaebuxus*); (c) undifferentiated seed coats (including *Xanthophyllum* and some other genera with indehiscent fruits). Verkerke & Bouman (1980) showed that, within *Polygala,* differences in ovule ontogeny culminate in a reduction of the mesophyll layer of the testa in *P. vulgaris*.

Chodat (1890–1893) regarded the flower of *Xanthophyllum* as the most primitive of the family, and his pupil Jauch (1918) suggested that the parietal placentation of *Xanthophyllum* is more primitive than the axial placentation of the other genera. On the other hand, *Xanthophyllum* is regarded as a derived taxon in the Polygalaceae by Van der Meijden (1982). This author distinguishes 8 monophyletic groups of species and emphasizes the variation in testa structure within the genus. The present study was undertaken to compare the ontogeny of ovule and seed of

Xanthophyllum with other genera of the family and also to clarify the differences in testa structure between the monophyletic groups of the genus. For brevity, these groups are indicated by their group-number as proposed by Van der Meijden (1982) as follows:

group 1	Subgenus *Brunophyllum* (5 spp.)
group 2	Subgenus *Macintyria* (1 sp.)
group 3	Subgenus *Grandiflorum* (1 sp.)
group 4	Subgenus *Triadelphum* (5 spp.)
group 5	Subgenus *Coriaceum* (1 sp.)
group 6	Subgenus *Exsertum* (3 spp.)
group 7	Subgenus *Xanthophyllum* sect. *Xanthophyllum* (16 spp.)
group 8a	Subgenus *Xanthophyllum* sect. *Eystathes* subsect. *Jakkia* (47 spp.)
group 8b	Subgenus *Xanthophyllum* sect. *Eystathes* subsect. *Eystathes* (14 spp.)

MATERIAL AND METHODS

Alcohol material of flowers and seeds of *Xanthophyllum arnottianum* Wight, *X. affine* Korth. ex Miq. and *X. fragrans* C.T. White, slides of *X. venosum* King and ripe dried seeds of other species were received from Dr. R. van der Meijden and Dr. W. van Heel, Rijksherbarium, Leiden.

Group 1: *X. chartaceum* Meijden: Malaya, FRI 8933; *X. obscurum* A.W. Bennett: Borneo, Kostermans 10187; *X. papuanum* Whitmore ex Meijden: New Guinea, Versteegh BW 4871. – Group 2: *X. octandrum* (F. Muell.) Domin: Queensland, Hyland 8321. – Group 3: *X. fragrans* C.T. White: Queensland, Hyland 7747 (alcohol material). – Group 4: *X. ellipticum* Korth. ex Miq.: Sarawak, Anderson 29857. – Group 5: *X. ramiflorum* Meijden: Sarawak, Anderson 12894. – Group 6: *X. amoemum* Chodat: Malaya, FRI 16687; *X. stipitatum* A.W. Bennett: Borneo, Schut K.14. – Group 7: *X. arnottianum* Wight: South India, van Heel 1216 (alcohol material); *X. affine* Korth. ex Miq.: Borneo, Hallier 2224 (alcohol material). – Group 8a: *X. venosum* King: Malaya, FRI 1877 (slides); Malaya, KEP 98718. – Group 8b: *X. ngii* Meijden: Malaya: KEP 78252; *X. sylvestre* (Lour.) S. Moore: Thailand, Kostermans 742.

Alcohol material was dehydrated by means of an ethanol/normal butyl alcohol series, embedded in glycol metacrylate, sectioned at 5 µm with glass knives and stained with the PAS reaction (Feder & O'Brien, 1968). Ripe seeds obtained from the herbarium were soaked for three days in a detergent mixture (Alcorn & Ark, 1953), washed with water and fixed in Allen's modified Bouin's fluid (Johansen, 1940). In addition, hard testa structures were cleared in a mixture of glacial acetic acid and hydrogen peroxide (Berlyn & Miksche, 1976). For SEM studies alcohol material was dehydrated with dimethoxymethane (Gersterberger & Leins, 1978) and critically point-dried with liquid CO_2, gold/palladium sputter-coated for 3 min. and photographed by means of a Cambridge Stereoscan Mark 2A. The following stains were used for specific colour tests: Phloroglucinol-HCl, Sudan IV, ruthenium-red and IKI.

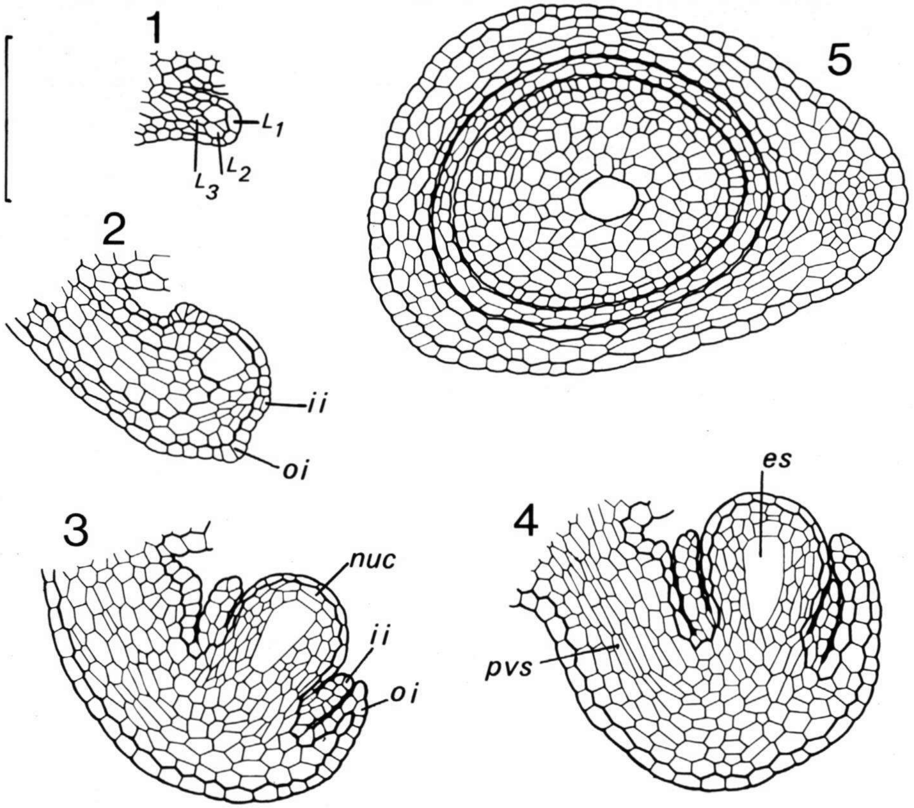


Fig. 1–5. *Xanthophyllum arnottianum*. — 1–4: Successive stages of ovule development in longitudinal sections. L_1: dermal tunica layer, L_2: subdermal tunica layer, L_3: corpus, ii: inner integument, oi: outer integument, nuc: nucellus, es: embryo sac, pvs: provascular strand. — 5: Almost mature ovule in cross section. In all figures the measure bar represents 100 μm, unless indicated otherwise.

OBSERVATIONS

Pre-fertilization development (figs. 1–6)

Xanthophyllum arnottianum has a unilocular gynoecium with a parietal placentation and usually four ovules. The ovule primordium is trizonate and is initiated by periclinal divisions in the third layer, the outer two layers initially divide only anticlinally (fig. 1). The subdermal archesporial cell soon divides into a megaspore mother cell and a primary parietal cell (fig. 2). The megaspore mother cell forms a linear tetrad of megaspores of which the chalazal megaspore enlarges and forms the embryo sac. By periclinal divisions in the second and third layer the ovule becomes thicker and gradually curves anatropically. The primary parietal cell divides repeatedly

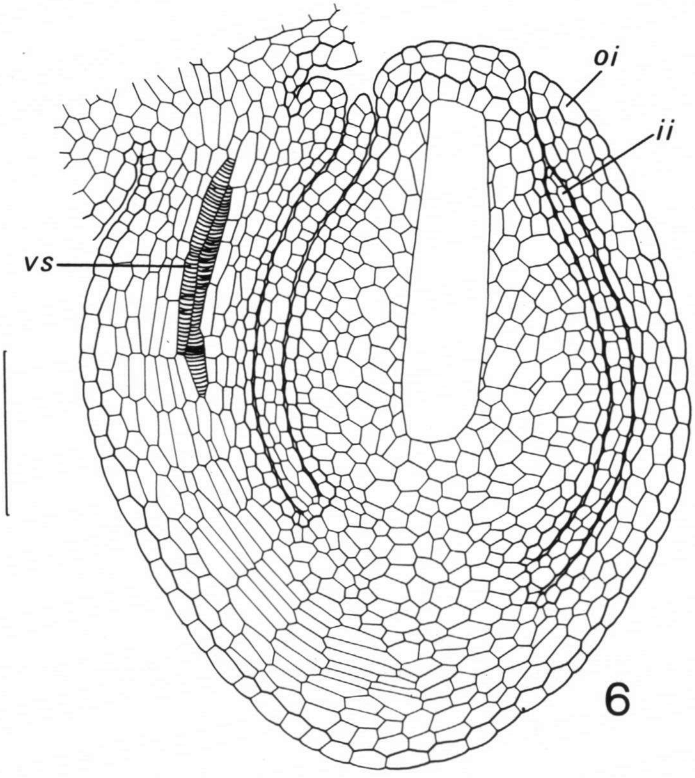


Fig. 6. *Xanthophyllum arnottianum.* Mature ovule in longitudinal section. vs: vascular strand.

to form a row of up to 6 parietal cells, but the dermal cells that cover the top of the nucellus initially only divide anticlinally. Prior to the formation of the parietal tissue, the inner integument is initiated in the dermal tunica layer by oblique or periclinal divisions in two adjacent cells; the primordium is ring-shaped (fig. 2). Shortly after the initiation of the inner integument, the outer integument is initiated in the subdermal layer; its primordium appears as a three cells thick incomplete ring at the anti-raphal side (figs. 2, 3, 15). As the curvature of the ovule is nearly 180°, the outer integument overgrows the inner integument and provascular tissue develops in the raphe (fig. 4).

In a mature ovule (figs. 5, 6) the nucellus is rather thick, and much of the parietal tissue is resorbed by the growing embryo sac; a small dermal cap has developed. The inner integument remains two cell layers thick and does not cover the top of the nucellus; hence it does not participate in the micropyle. The outer integument is 4–5 cells thick and has now also developed at the raphal side; it has not formed a dermal top and the subdermal tissue reaches up to the cleft-shaped micropyle. This results, when viewed in exact median longisection, in the top of the nucellus seemingly not

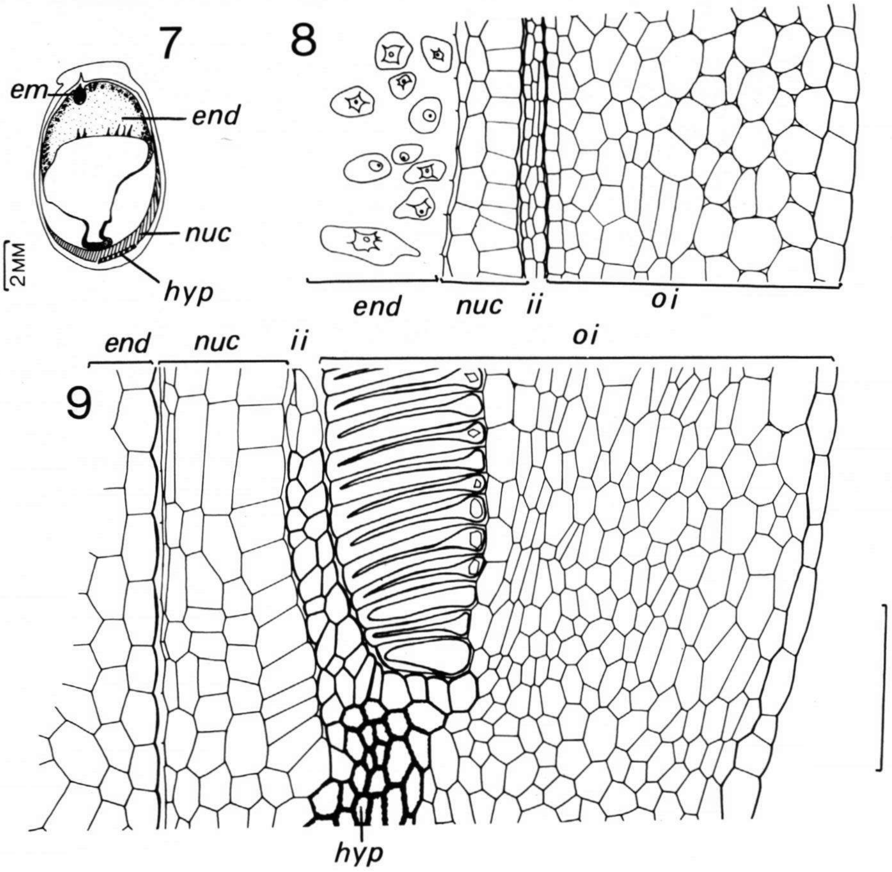


Fig. 7–9. *Xanthophyllum venosum*. Successive stages of seed development in longitudinal section; figs. 7 and 8 at the onset of cell wall formation in the endosperm; fig. 9 of a ripe seed at the chalazal connection of the integuments. em: embryo, end: endosperm, hyp: hypostase.

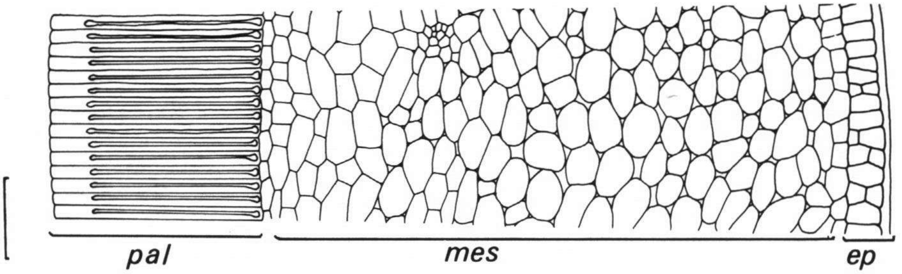
being covered by the outer integument. The raphe is 11–13 cells thick and contains vascular tissue. The chalaza is rather massive and is provided with provascular strands.

The pre-fertilization development of *X. venosum* is very similar to that of *X. arnottianum*.

Post-fertilization development

Xanthophyllum venosum (figs. 7–9)

After fertilization the ovule enlarges greatly. The nucellus, which has no distinct cuticle, is gradually resorbed from the inside as the nuclear endosperm develops and persists in the ripe seed as a thin layer of crushed cells. Most endosperm nuclei become concentrated in the chalazal region of the embryo sac and a large vacuole



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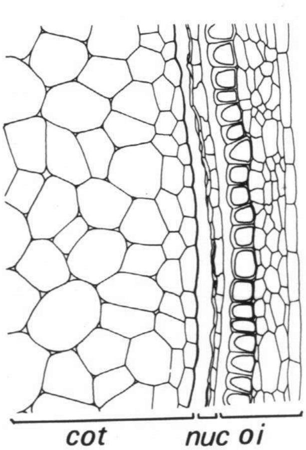

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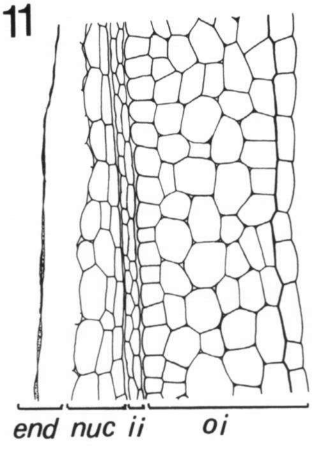

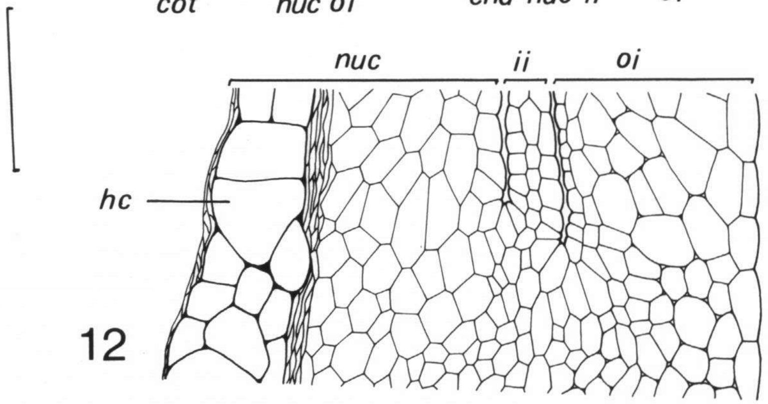

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Fig. 10. *Xanthophyllum fragrans*. Mature seed coat in cross section. pal: palisade layer, mes: mesophyll layer, ep: thickened epidermis. — Fig. 11–13. *X. arnottianum*. Successive stages of testa development in longitudinal section; figs. 11 and 12 of developing testa, fig. 12 at the chalazal connection of the integuments; fig. 13 of ripe seed coat. cot: cotyledon, hc: hypertrophic cell.

develops (fig. 7). As the seed ripens, cell wall formation in the endosperm starts in the micropylar region at the periphery of the embryo sac (figs. 7, 8). Somewhat later the embryo starts expanding and in the ripe seed the two semiglobose cotyledons are only surrounded by a relatively thin layer of cellular endosperm; but in the chalazal region the endosperm is thicker. The embryo and endosperm are rich in fatty substances.

Initially, the inner integument remains 2–3 cells thick (fig. 8), but eventually it becomes crushed, and in the ripe seed it persists only in the chalazal region, where its cells have slightly thickened walls (fig. 9). The outer integument ultimately forms the protective layer of the seed coat; the cells of the inner epidermis elongate and become thick-walled. These palisade cells become 100 μm long and have a slender lumen with a proximal widening which sometimes contains a crystal (fig. 16). The distal ends of the palisade cells slightly separate from each other and this causes a rupture of the primary cell wall (figs. 19, 20). The palisade layer remains unlignified. The development of the palisade layer is similar to that in *Polygala vulgaris* (Verkerke & Bouman, 1980). When the palisade layer has formed, cells in the chalazal region adjacent to the nucellus start thickening, their walls becoming prominently pitted (fig. 9). In the ripe seed this layer of thick-walled cells forms the hypostase, a protective layer of the seed where the palisade layer is interrupted. The mesophyll layer thickens and becomes up to 10 cells thick (figs. 8, 9); it consists of parenchymatic cells and is provided with several tracheary elements which result from the post-chalazal branching of the single amphicribral raphal strand. The epidermis of the testa consists of flattened isodiametrical cells and contains no stomata. The ripe seed, measuring 11.5 by 12 mm, is pale brown, glabrous and globular. The hilum forms a white spot 4 mm in diameter which strongly contrasts with the rest of the testa.

Xanthophyllum fragrans (fig. 10)

Compared with *X. venosum*, the ripe seed of *X. fragrans* shows some striking differences. The foliaceous cotyledons are enveloped by a copious endosperm; both are rich in fatty substances. The nucellar epidermis is still recognizable but there is no trace of the inner integument. The seed coat has in general the same build-up as that of *X. venosum*, but the palisade cells are much longer, 260 by 20 μm, and the outer epidermis of the testa consists of elongated cells with thickened distal walls which are not lignified and measure 50 by 20 μm. The seeds are light brown, glabrous and somewhat triangular in outline, measuring 18 by 13 mm. Like *X. venosum*, the hilum strongly contrasts with the rest of the testa.

Xanthophyllum arnottianum (figs. 11–13)

In this species the seed development is completely different from that of the two preceding species. After fertilization little nuclear endosperm develops; it remains as a thin layer at the periphery of the expanding embryo sac and does not become cellular. In the ripe seed no endosperm can be traced and the two semiglobose cotyledons completely fill up the embryo sac. The cells of the embryo are loaded with starch grains but poor in fatty substances. In the chalazal part of the nucellar tissue large hypertrophic cells are formed. In the ripe seed these cells and a thin outer layer of the nucellus can be found, but no trace of the inner integument is visible. In the outer integument, the inner epidermis elongates slightly and the walls faintly thicken, but no true palisade cells are formed (fig. 20). The mesophyll becomes 4–5 cells thick and intercellular spaces originate. The raphal vascular strand branches in the chalaza and forms many amphicribral strands of which some extend to the micropyle. However, in the ripe seed the mesophyll is much compressed, the chalazal region, which can be up to 20 cells thick; excepted. In contrast to the seed coats of *X. venosum* and *X. fragrans*, a hypostase is not developed.

Variation in the seed anatomy of Xanthophyllum (fig. 14)

The seeds of the eight groups are very different, and in group 1 even differences between species do occur. Due to the common pre-fertilization development, the seeds show basically the same build-up. The differences in seed structure are caused by a differential post-fertilization development.

Endosperm and cotyledons. — There is a considerable variation in the relative sizes of cotyledons and endosperm between the different groups. Cotyledons can be thin, foliaceous (groups 2, 3, 4, 6); or thicker, with lateral cleavages (group 1) to semi-globose (groups 5, 7, 8a, 8b). The amount of endosperm decreases as the embryo enlarges (groups 1, 5, 8a, 8b) and in group 7 mature seeds contain no endosperm at all. In all groups both endosperm and embryo contain fatty substances and are poor in starch, with the exception of groups 5 and 7 where the cells of the thick cotyledons (and in group 5 also the cells of the endosperm) are loaded with starch grains but are poor in fatty substances.

Palisade cells. — The length of the palisade cells of the testa varies between 10 and 270 μm. In group 1 much elongated and less elongated palisade cells may occur. In group 7 no proper palisade layer is formed. In all groups but group 7 a hypostase is formed.

Mesophyll. — The mesophyll of the testa is rather thick in groups 1, 2, 3, 4, 6, 8a, 8b, and ranges from 200 μm (group 6) up to 700 μm (group 3). It contains vascular bundles resulting from the postchalazal branching of the raphal vascular strand, and consists of parenchymatic cells with many intercellular spaces. In *X. papuanum* and *X. obscurum* (group 1) the mesophyll adjacent to the palisade layer consists of a laminated layer of crushed cells which is 100–300 μm thick. In this layer many vascular bundles, mainly consisting of vessel members (measuring 18 by 420 μm) with helical and scalariform wall thickenings, and occasional tracheids (measuring 10 by 300 μm) with helical wall thickenings have developed (fig. 17). The laminated layer can be regarded as an additional protective structure of the seed coat. The outer part of the mesophyll in these species consists of parenchymatic tissue which contains many large and sclerotic, isodiametrical idioblasts 80 μm in diameter. However, in *X. chartaceum* (also group 1) no differentiation of the mesophyll is apparent, and the palisade layer is much thicker than that of the other species studied (fig. 14). The mesophyll is much thinner in groups 5 and 7.

Epidermis. — The epidermis of the testa generally consists of flattened isodiametrical cells; no stomata were observed. In groups 2 and 3 the epidermis has elongated and the distal wall has thickened; Van der Meijden (1982) therefor regarded the seed coats of these groups as three-layered. All seeds investigated were glabrous.

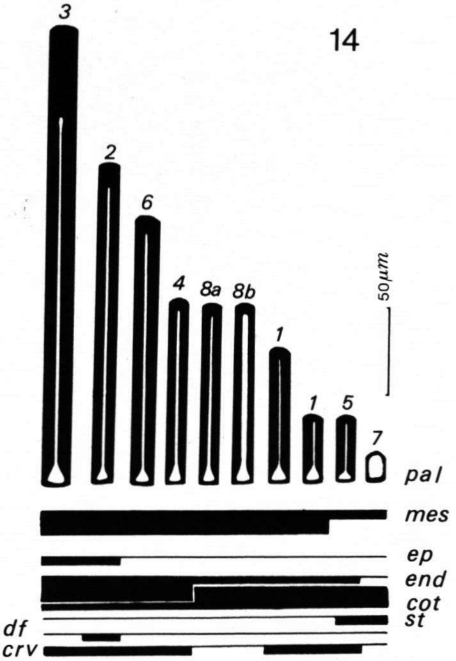


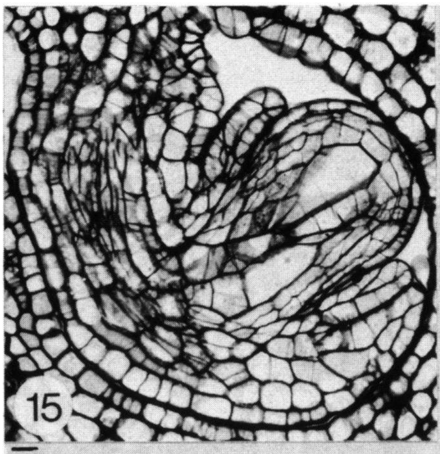
Fig. 14. Variation in the seed anatomy and character states of two other selected anatomical characters between the monophyletic groups of *Xanthophyllum*, indicated by their group number. Palisade cells are on scale; presence of other characters is indicated by a black horizontal bar, of which the thickness is proportional to the abundance of that character. pal: palisade cell, mes: mesophyll layer, ep: thickened epidermis, end: endosperm, cot: cotyledons, st: starch grains abundantly present, df: dehiscent fruit, crv: coarsely reticulate leaf venation.

DISCUSSION

The early ovular ontogeny is very similar in all species studied; however, due to a different post-fertilization development the variation in seed structure is unusual for the genus level. As Van der Meijden (1982) has pointed out, this variation had not been recognized in previous studies. In *Xanthophyllum*, the palisade layer, which is the protective layer of the polygalaceous seed, shows a trend towards reduction both in length (in groups 1, 5, 7) and in wall thickening (group 7). A hypostase develops in all groups but group 7. The mesophyll is reduced in thickness in groups 5 and 7. According to Van der Meijden (1982), in group 8b only *X. ngii* has a thickened mesophyll layer, but my observations indicate that of this group also *X. sylvestre* has a 200 µm thick mesophyll layer.

Another reduction trend is represented by the amount of endosperm, which can be large (groups 2, 3, 4, and 6) to small (groups 1, 5, 8a, 8b) or lacking (group 7). A correlated trend towards large cotyledons is present, ranging from foliaceous cotyledons towards the thick, semiglobose cotyledons of group 7. In general, the embryo and endosperm are rich in fatty substances, but in two groups with a reduced testa and thick semiglobose cotyledons (groups 5 and 7) starch is abundantly present and fatty substances are scarce.

In his revision of the genus Van der Meijden (1982: 33) designated the 'two-layered, outer layer thin' and the 'cotyledons thick' condition as possible plesiomorphic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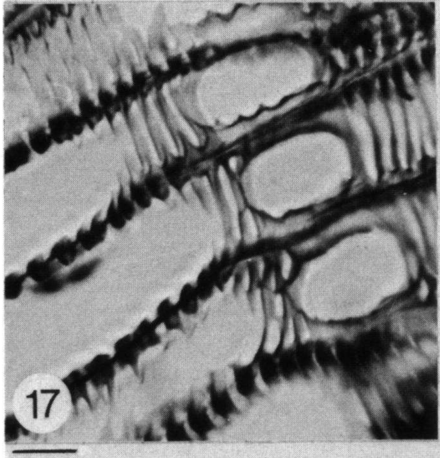
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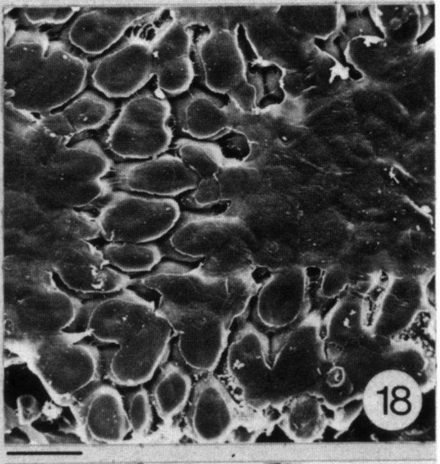
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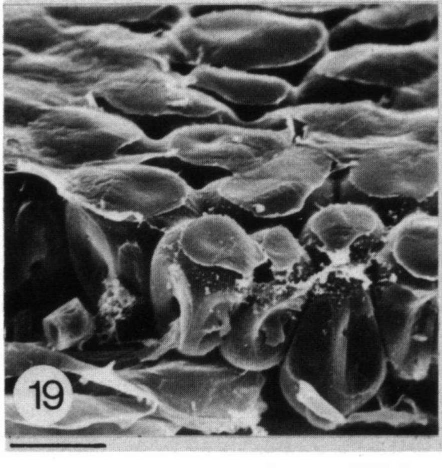
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character states of testa and embryo, respectively. However, the present author has come to a different conclusion after a microscopical investigation of the available material. The data presented in figure 14 enable a designation of the original combination of seed characters of the genus, and I consider the thick endosperm with foliaceous cotyledons, the fully developed palisade layer and the thick mesophyll layer without a thickened epidermis as primitive features of the *Xanthophyllum* seed. In group 7 the aberrant post-fertilization development leads to a neotenic seed with weakly developed palisade cells and a much compressed mesophyll layer. The thickened outer epidermis of the testa in group 2 can be understood as an adaptation to the dehiscence of the fruit (fig. 14). According to Van der Meijden (1982) the irregular dehiscence of the fruit wall in this group suggests a derivation from an indehiscent fruit type. Vascular tissue in the mesophyll can contribute greatly to the firmness of the seed coat in group 1. The testal tracheary elements form a meshwork of bundles, and hence are different from the solitary tracheoidal idioblasts associated with leaf mesophyll venation, which are, according to Dickison (1973), characteristic of all *Xanthophyllum* species but reach their greatest development in the less coriaceous species belonging to the subgenera *Macintyria* (group 2) and *Brunophyllum* (group 1).

The derived status of group 7 is also supported by data from the leaf anatomy of *Xanthophyllum* (fig. 14). Dickison (1973) noted a trend toward increased leaf-coriaceousness, culminating in the subgenus *Xanthophyllum* section *Xanthophyllum* (group 7). Van der Meijden (1982) distinguishes three types of leaf venation, viz. (a) a coarsely reticulate (groups 1, 2, 3, 4, 5, 6), (b) a finely reticulate (groups 8a, 8b) and (c) a scalariform (group 7). The author suggests that the coarsely reticulate venation (fig. 14) represents the plesiomorphic character state in *Xanthophyllum*.

The present study reveals some data which are in favour of the speculated hybrid origin of group 3 (Van der Meijden, 1982). Although formed in an indehiscent fruit, the seeds have a thickened outer epidermis like one of the presumed parental species *X. octandrum* (group 2). Furthermore, the exceptional length of the palisade cells (fig. 14) may again be interpreted as another '*gigas*' character of this group. Van der Meijden (1982) also speculated about the hybrid origin of *X. ramiflorum*, the single species of group 5. The author assumed that the parental species would belong to group 4 and group 7 or 8b. The present study shows that the seeds of groups 7 and 5 have more in common than those of groups 8b and 5. Hence it can be concluded that the assumed parental species of *X. ramiflorum* could be in groups 4 and 7.

As data of dispersal and germination of seeds are scarce, one can only speculate about the adaptive value of the differences between the seeds of the groups, but

Fig. 15. *Xanthophyllum arnottianum*. Developing ovule in longitudinal section. — Fig. 16. *X. venosum*. Outside of palisade layer after removing of mesophyll, showing proximal widening of lumina. — Fig. 17. *X. papuanum*. Vessel members in mesophyll of testa. — Fig. 18. *X. venosum*. Inside of palisade layer, showing rupture of primary cell wall. — Fig. 19. *X. arnottianum*. Inside of reduced palisade layer, showing slightly elongated palisade layer and rupture of primary cell wall. — Fig. 20. *X. venosum*. Cross section of palisade layer. Measure bar represents 10 μm in LM micrographs (figs. 15, 17) and SEM photographs (figs. 16, 18–20).

there are indications that the fat-rich seeds with foliaceous cotyledons and thick seed coats might belong to a different seedling type than the starch-rich seeds with semiglobose cotyledons and a reduced testa (Van der Meijden, 1983; De Vogel, 1980).

The ontogeny of ovule and seed of *Xanthophyllum* resembles that of *Polygala* (Verkerke & Bouman, 1980) in the trizonate ovulum primordium, the dermally initiated inner integument, the crassinucellate nucellus, the anatropous ovule and the development of the seed coat. However, there are some minor differences. In *Xanthophyllum* the outer integument is subdermally initiated from the very start, and hence it does not have a dermal top. Only a small dermal cap has developed and the inner integument does not form an endostome. The raphe is thicker and the chalaza is more massive than in *Polygala*, but compared with the more primitive representative *P. chamaebuxus*, the extension of the subdermal mesophyll layer and the size of the ripe ovule are very similar. The ripe seed of *Xanthophyllum* is light brown, exarillate, glabrous and provided with a well-developed hypostase. The hypostase protects the seed in the chalazal region, which enlarges about 40 times after fertilization in *Xanthophyllum* (in *Polygala* only four times).

In the genus *Polygala* an overall reduction of subdermal tissue in the outer integument appears. In *P. chamaebuxus* subdermal activity starts when the dermal top of the outer integument is four cells long. A delayed and restricted subdermal activity reduces the occurrence of the mesophyll layer in the more derived representative *P. vulgaris* (Verkerke & Bouman, 1980). As the outer integument in angiosperms is originally of subdermal origin (Bouman, 1974) the completely subdermal outer integument of *Xanthophyllum* can be regarded as more primitive than that of *Polygala*.

The present study indicates that the ovular ontogeny and seed coat development of *Xanthophyllum* shows many similarities with that of *Polygala*, and supports the placement of *Xanthophyllum* in the Polygalaceae. Rodrigue's (1893) conclusion that within the Polygalaceae the genera with indehiscent fruits have seeds with a reduced testa is incorrect; her description of *Xanthophyllum* must have been based on a representative of group 7.

The present establishment of primitive features of the *Xanthophyllum* seed enables comparison with seeds of other genera of the family. The question whether the seed of *Xanthophyllum* is to be regarded as primitive in the Polygalaceae can as yet not be answered; this must await the results of investigations of other genera (Verkerke, in preparation).

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