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DEVELOPMENT OF THE SEED OF TRICHILIA GRANDIFOLIA OLIV. (MELIACEAE)

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SUMMARY

The ovule of *Trichilia grandifolia* is bitegmic, anatropous and crassinucellate with a massive chalaza and thick outer integument. After fertilisation a pachychalaza develops which ultimately constitutes about 2/3 of the bulk of the seed. The integuments form the remaining part of the seed coat. The outer integument is strongly multiplicative and becomes much thicker than the inner one, which in the mature seed can be distinguished as a thin, crushed layer. The whole sarcotestal seed coat contains a plexus of vascular bundles in the inner layer of the outer integument and of the pachychalaza. Along the raphal side no distinct inner integument can be discerned in part of the ovules and pre-raphe bundles run towards the top of the inner integument. A derived condition of the seed is indicated.

1. INTRODUCTION

As a supplement of the systematic studies of GROENENDIJK & DE WILDE (1981), the seed development of *Trichilia grandiflora* was studied.

The seeds of Meliaceae are very variable, they may be large, with or without an aril, sarcotesta, or pachychalaza, or winged, or small and reduced in drupaceous fruits (CORNER 1967). The outer epidermis is a palisade layer or unspecialised, and is sometimes provided with stomata. The inner layer of the outer integument is sometimes a thin crystal layer. When an exotegmen exists (sclerotised cells of the outer layer of the inner integument) it typically consists of longitudinally oriented, lignified and pitted fibres.

According to Corner, the primitive meliaceous seed exhibited the following characteristics:

1. A massive construction.
2. A red funicular aril, perhaps also exostomal.
3. A thick testa with black or red cuticle or epidermal walls, with stomata, and with the endotesta as a layer of crystal cells.
4. An exotegmen with ribbon-like sclereids as in Celastraceae.
5. Endosperm present.

The genus *Trichilia* is very large and characterised by a considerable variation in seed coat structure and in the nature of the aril. Exarillate species also occur.

Trichilia grandifolia is remarkable on account of its very large complicated seeds (GROENENDIJK & DE WILDE 1981). Because of this complicated seed structure, the following study was undertaken.

2. MATERIAL AND METHODS

The material of *Trichilia grandifolia* Oliver was collected at São Tomé by Mr. W. C. S. Heemskerk, Ms. E. M. C. Groenendijk and Dr. J. J. F. E. de Wilde. Sections were cut by the standard microtome techniques and by hand.

The following stains were used for specific colour tests: phloroglucinol-HCl, Sudan IV, ruthenium red and JKJ.

3. OVULE STRUCTURE AND EARLY SEED DEVELOPMENT

The two fruit locules of *Trichilia grandifolia* each contain two bitegmic, anatropous, crassinucellate and suspended ovules. When the ovule is about 1 mm in diameter (*fig. 1*), the strongly vascularised chalazal part is about as long as the tegumentary part. The raphe bundle is very massive. The outer integument (o.i.) is already much thicker than, and protrudes beyond, the inner integument (i.i.). In the base of the o.i. postchalazal bundles begin to develop. During the early stages of seed development (*figs. 2* and *3*) the embryo sac (e.s.) resorbs the central chalazal tissue, as a result of which it becomes partly surrounded by the integuments and partly by the chalaza. In this way a pachychalaza is formed and as a result the seed coat has a dual origin. Both the pachychalaza and the o.i. are

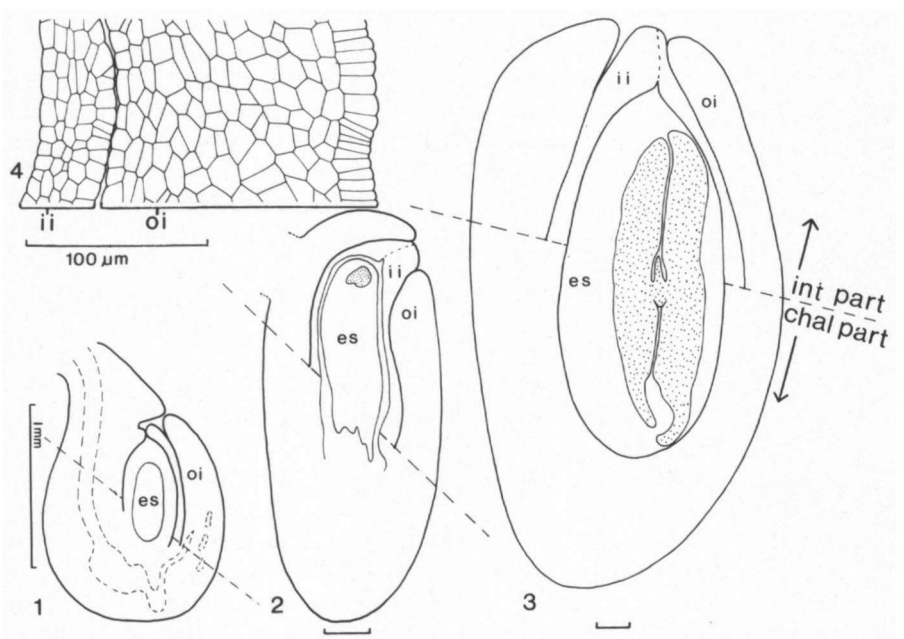
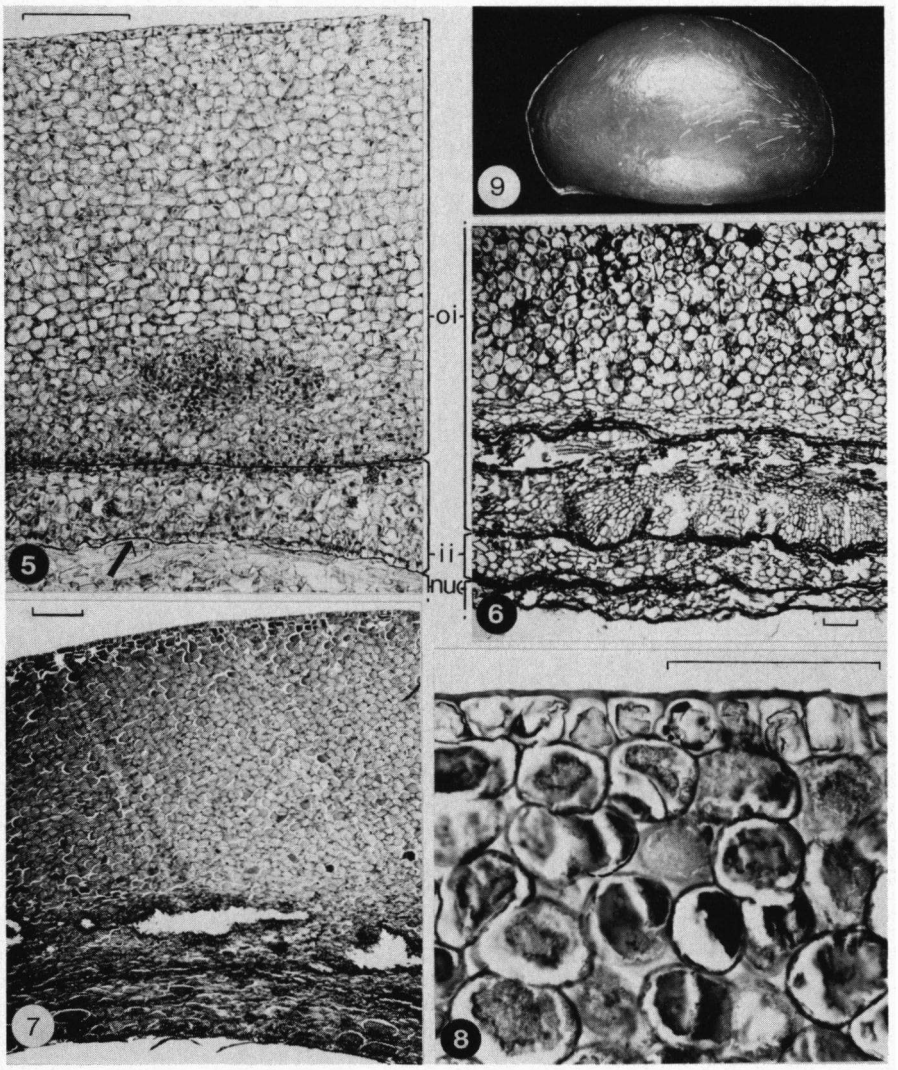


Fig. 1. l.s. of mature ovule with vascular bundles in the chalaza; fig. 2, 3: l.s. of early stages of developing seeds (scale indicators: 1 mm); fig. 4: l.s. of i.i. and o.i. of mature ovule (corresponding with *fig. 1*). oi = outer integument, ii = inner integument, es = embryo sac, int = integumentary, chal = chalazal.



Figs. 5, 6, 7, 8: photomicrographs of the seed coat. Fig. 5: l.s. of developing seed coat with vascular bundle; arrow points at nucellar cuticle; fig. 6: l.s. of inner side of seed coat shortly before maturity with plexus of vascular bundles; fig. 7: t.s. of developing seed coat at the chalazal side; fig. 8: l.s. of outer part of sarcotesta; fig. 9: photograph of mature seed (all scale indicators: 100 μm).

strongly multiplicative and increase considerably in thickness (*figs. 5, 7*). In the o.i. the middle layers, but especially the inner layers, show periclinal divisions. The outer layer remains one-layered during the whole seed development. In the inner layers crystals are formed mainly around the vascular bundles. Parallel with these developments postchalazal bundles gradually develop along the

whole length of the o.i., mainly in its inner layers (*figs. 5, 11*). The whole seed coat thus becomes vascularised.

The i.i. is also somewhat multiplicative but it remains thinner than the o.i. The cells of the outer layer are somewhat longitudinally stretched in the direction of the long axis of the seed. Crystals, amongst which star-shaped ones occur. Also very large idioblasts (tannin cells?) are present.

The nucellus has a rather thick cuticle (*fig. 5*) which in later stages, together with the nucellar tissue, becomes inconspicuous.

The endosperm becomes cellular at a rather early stage and is never abundant.

The seed exhibits another singular character: In part of the ovules and developing seeds at the raphal side the pachychalaza extends (almost) to the micropylar level and as a result there is here no, or a hardly discernible, i.i. (*figs. 1, 10* and *11*) Pre-raphe bundles run to the micropyle and enter the top of the i.i. (*fig. 10*). This situation seems to be variable, because sometimes a short i.i. is visible at the raphal side.

4. LATER DEVELOPMENTAL STAGES AND MATURE SEED STRUCTURE

The chalazal part of the seed becomes progressively somewhat larger than the tegumentary part, so that the mature seed is markedly pachychalazal. Two-thirds of its bulk is formed by the chalaza and only about one-third of its length is covered by derivatives of the integuments.

The o.i. is very multiplicative and by the gradual crushing of the tissue at both sides of the vascular bundles these come to lie in a rather thin layer at the inside of this integument (*fig. 6*).

The inner side of the chalaza is further resorbed by the e.s. so that the vascular bundles also come to lie in the innermost layers.

Both the chalaza and the o.i. thus form the sarcotesta, at the inside of which a plexus of vascular bundles exists. The sarcotestal cells become slightly thick-walled and rounded with intercellular spaces between them. The cell contents show a great affinity to biological stains.

The outer walls of the cells of the epidermal layer of the seed are slightly thickened and pectinous (*fig. 8*). Stomata have not been observed and there is no trace of an aril. The i.i. also becomes crushed but it persists in the ripe seed and closes the exostome-opening (foramen). Shortly before maturity the walls of the middle layers of the i.i. become locally thick-walled and pitted, but in the fully mature seed the pits are not discernible any longer. These thick-walled cells are lignified.

In the chalazal part of the seed the embryo comes to lie against the plexus of vascular bundles which give imprints on the surface of the embryo. Therefore this part of the embryo assumes a rougher appearance (*fig. 12*). In the tegumentary part of the seed the crushed i.i. lies between the embryo and the vascular bundles, so that this part of the embryo remains smoother (*fig. 12*).

The thickness of the mature seed coat varies from a few mm in the micropylar region to about 10 mm at the chalazal side. Nucellus and endosperm remnants

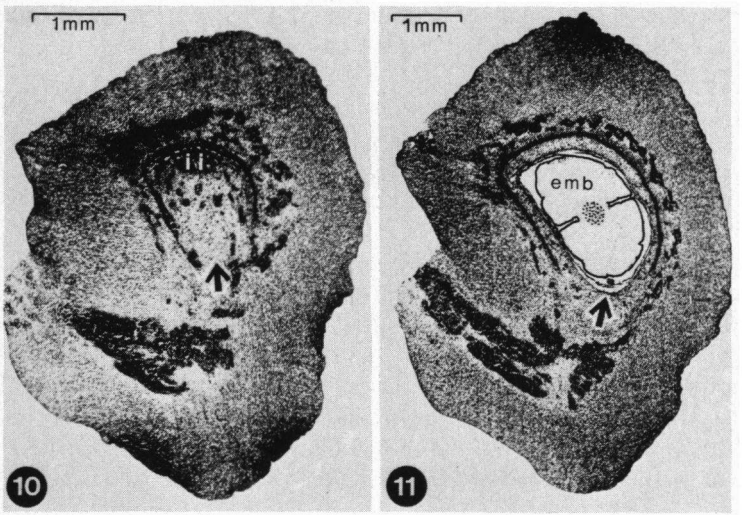


Fig. 10 and 11: t.s. of developing seeds: i.i. missing at the raphal side, arrows indicate place where i.i. is lacking.
Fig. 10: upper part of the i.i. with vascular bundles; fig. 11: level of the young embryo, with ii forming incomplete ringwall.

are not discernible in the mature seed.

The compound raphe bundle with different anastomosing bundles is surrounded by groups of tannin cells. All vascular bundles in the seed are more or less amphicribral and contain elements with spiral or annular thickenings or pitted walls.

The embryo contains both oil and starch, has planoconvex cotyledons (*figs. 12, 13*) and oil glands, strongly reacting with Sudan IV. *Fig. 13* shows the

Fig. 12: photograph of embryo showing the smooth tegumentary and the rough chalazal part; fig. 13: the two cotyledons separated and shown from the inside with radicle and plumule.

cotyledons separated with the small radicle and plumule lying inside them.

The mature seed is 7–10 cm long and cream-coloured (*fig. 9*).

5. DISCUSSION

The remnants of a sclerotised tegmen and the occurrence of crystals in the inner layer of the o.i. are characters which still fit in with the general seed structure found in Meliaceae.

The pachychalazal specialisation in *Trichilia grandiflora* is a new example of the coincidence of a large seed size with pachychalazy and a strong vascularisation. According to Corner the expansion of the chalaza is associated with an extensive vascular supply. Evidently these vascular bundles play a role in the transport of nutrients to the large embryo. The pre-raphe bundles to the top of the i.i. and the absence of the i.i. at the raphal side must possibly also be considered in this context. In this train of thought vascular bundles arise where they are needed. Corner described pre-raphe bundles in the Meliaceous genus *Dysoxylon*.

The rough part of the embryo described by GROENENDIJK & DE WILDE 1981 corresponds with the pachychalaza, and the smooth part with the tegumentary part of the seed. The pachychalaza, the lack of endosperm, the strongly multiplicative integuments, the very large seed, the sarcotesta, the pre-raphe bundles and perhaps also the loss of an aril indicate a derived condition of the seed of *Trichilia grandifolia*.

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