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Notes on the ovule and partially pachychalazal seed of *Operculicarya decaryi* H. Perrier (Anacardiaceae) from Madagascar

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Abstract. The ovule of *Operculicarya decaryi* H. Perrier, a member of the tribe Spondiadeae, is anatropous, bitegmic and crassinucellar. It is also characterized by a funicular knee and a plate of meristematic cells, the hypostase *s. l.* Owing to a prominent knob formed by the inner part of the ovary wall and pericarp respectively, the ovule and seed are U-shaped. During seed ontogeny a secondary extension of the chalaza, including the hypostase *s. l.*, results in a partially pachychalazal seed. The seed-coat displays a dark brown saddle-like patch, i. e., the external manifestation of the tanniniferous hypostase, and an amphicribral raphal vascular bundle. Structurally the seed is not only similar to that of other members of the tribe Spondiadeae, but also resembles that of several taxa within the tribes Anacardieae and Rhoeae. The well-developed cuticular layer on the inner surface of the inner integument, and the deposits of tannin in the seed-coat are probably part of the micromorphological survival strategy of this xerophytic tree.

Key words: Anacardiaceae; Cuticular layer; Hypostase; *Lannea*; Seed-coat; Spondiadeae.

Introduction

The genus *Operculicarya* H. Perrier (Anacardiaceae - tribe Spondiadeae) is one of several flowering plant genera endemic to Madagascar (Malagasy Republic). *Operculicarya decaryi* H. Perrier, one of the four species (Capuron, 1975; Perrier de la Bâthie, 1946), is a deciduous, much branched, small, shrub-like tree with very small compound leaves. It is a xerophyte occurring on limestone-derived soils along rocky slopes in the arid, southern part of Madagascar. Although the species was described more than 40 years ago, details of its flower and fruit morphology have not been known until recently (Von Teichman and Hardy, 1992).

Corner (1976) emphasized the taxonomic significance of seed morphological characters in the dicotyledons. Seed-coat structure in the Anacardiaceae, with emphasis on its taxonomic value for the characterization of taxa and their phylogenetic affinities, was recently reviewed by Von Teichman (1991a, b). Despite the proven taxonomic value of seed characters in the Anacardiaceae, detailed information currently available is limited to a very small fraction of the about 60-80 genera. In the present paper, the structure of the ovule and young seed of *Operculicarya*, especially the seed-coat, is described for the first time. The work on *Operculicarya* forms part of a comprehensive survey of the seed structure of the Anacardiaceae.

Materials and Methods

Female floral buds, flowers and fruits at different stages of development were collected from a female tree of *Operculicarya decaryi* growing in the display glass house of the National Botanic Gardens, Pretoria.

Details of the voucher specimens, the preparation and staining of the 2-3 μm glycol methacrylate sections correspond to those described for the pericarp of *Operculicarya decaryi* (Von Teichman and Hardy, 1992).

Results

Since the only specimen of *Operculicarya decaryi* in Pretoria is female, its fruit development is parthenocarpic. Therefore mature seeds were not available for the present study. However, vestigial seeds (Fig. 1A) with structurally well-developed seed-coats, are present in fruits collected six weeks after anthesis. Consequently these functionally useless seeds contained no embryos.

The unilocular ovary contains a single, pendulous and anatropous ovule suspended more or less apically from the ovary wall near the future outer border of the operculum (Fig. 1B). The ovule is U-shaped, slightly laterally compressed, bitegmic and crassinucellar, with the funicle characterized by a funicular knee. Dissections and study of serial sections of the ovule at anthesis reveal the following additional features (Fig. 2):

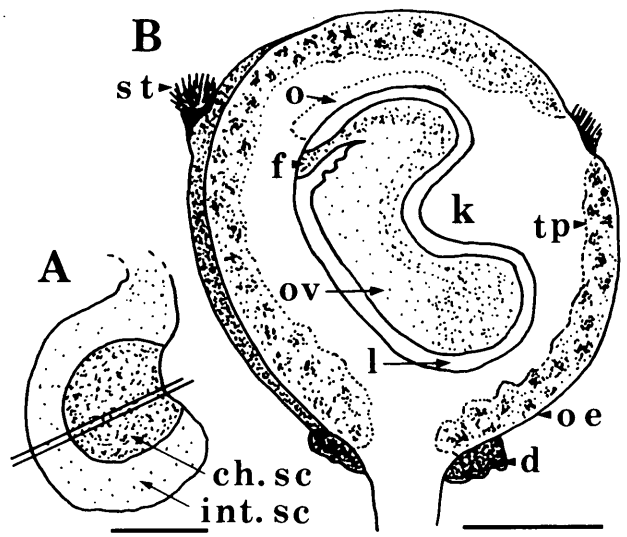

Fig. 1. Lateral view of vestigial seed (A) and longitudinal section of the unilocular ovary (B), showing in A the chalazal (ch. sc) and integumentary (int. sc) parts of the seed-coat, while the double line denotes the position of the transverse section illustrated in Fig. 3. In B the orientation of the ovule is shown, with d: disc; f: funicle; k: knob of inner part of ovary wall; l: ovary locule; o: position of future operculum; oe: outer epidermis; ov: ovule; st: stigma; tp: outer, tanniniferous parenchyma layers of ovary wall. Scale bar in A=1 mm; in B=0.5 mm.

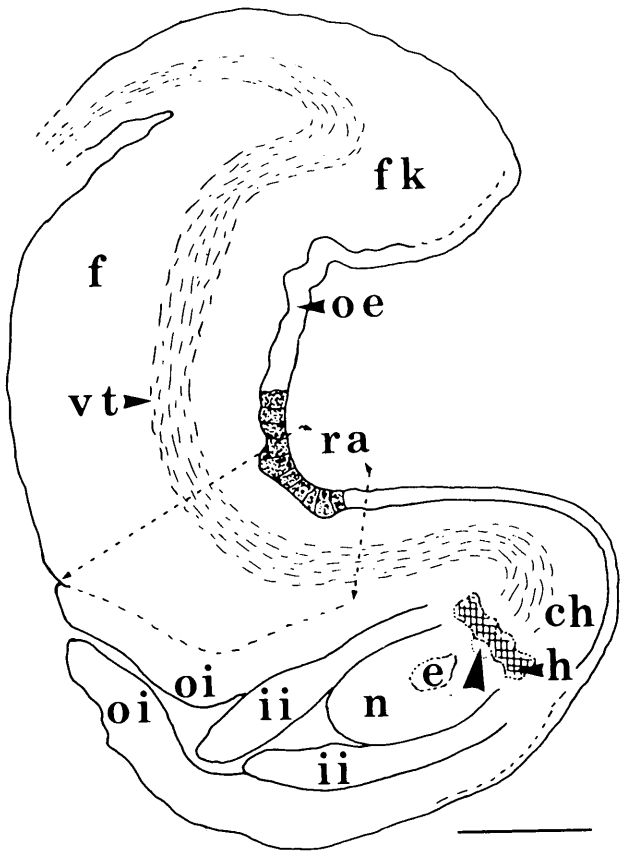

Fig. 2. Longitudinal section of the ovule at anthesis providing the details of the ovule shown in Fig. 1B. ch: chalaza; e: embryo sac; f: funicle; fk: funicular knee; h: hypostase *s. l.*; large arrow head: hypostase *s. s.*; ii: inner integument; n: nucellus; oe: outer epidermis which is partially tanniniferous; oi: outer integument; ra: raphe; vt: vascular tissue. Scale bar=150 μm.

(1) The outer epidermis is partly tanniniferous - especially on the raphal side, these tanniniferous cells manifest externally as brown specks.
(2) An outer, and a relatively well-developed inner integument, each up to four cell layers thick.
(3) A plate of meristematic cells, about three to four cell layers thick, exists in the chalazal-nucellar tissue; these cells represent the hypostase *s. l.*; they are rich in cytoplasm, exhibit large nuclei and are engaged in cell division.
(4) A very weakly developed hypostase *s. s.*, represented by a few cells with slightly thickened cell walls adjacent to the "hypostase *s. l.*". (The

distinction made in the hypostase is explained in the discussion.)

(5) A characteristic knob of the inner part of the ovary wall projects deeply into the ovary locule thus influencing the shape of the ovule and future seed.

In *Operculicarya decaryi* the chalaza with accompanying hypostase *s. l.*, undergoes significant secondary extension. Six weeks after anthesis the young, bent, light brown seed exhibits a darker brown saddle-like patch on the seed-coat (Fig. 1a). This is the partial pachychalaza.

Transverse sections of the young seed-coat, cut near the transition of the raphal and chalazal/integumentary parts (Fig. 3), show that the contribution of the raphe towards the formation of the seed-coat is very small, whereas the chalaza and especially the integuments contribute significantly to its development. Six weeks after anthesis, the outer epidermis of the young seed-coat is distinctly tanniniferous (Fig. 3A & B). This manifests externally as the light brown coloration. Both the outer and inner integument become thinner at the antiraphal side, the former four to five and the latter one cell layer broad (Fig. 3B).

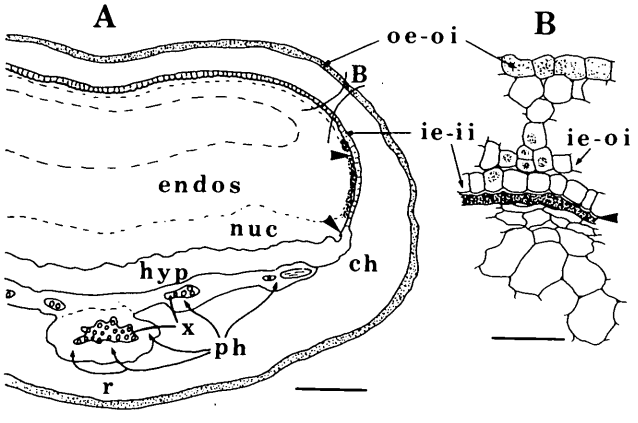

Fig. 3. Transverse section of a part of the seed-coat near to the transition of the raphal and chalazal/integumentary parts (A) and magnification of a small portion of the integumentary seed-coat (B). ch: chalaza at the transition to the outer and inner integument; endos: endosperm-like tissue; hyp: hypostase; ie-ii: inner epidermis of the inner integument; ie-oi: inner epidermis of outer integument; oe-oi: outer epidermis of the outer integument; ph: position of phloem; r: raphe; x: xylem. The arrow heads indicate the position of the cuticular layer. Scale bar in A=150 μm; in B=40 μm.

The outer and inner integument merge into the chalazal tissue (Fig. 3A) and the inner integument is continuous with the periphery of the hypostase *s. l.* The latter consists of contiguous, tanniniferous parenchyma cells up to seven layers thick. These tanniniferous cells of the hypostase *s. l.*, manifest externally as the dark brown saddle-like patch, i. e., the chalazal part of the seed-coat, or the partial pachychalaza.

The main bundle of the raphe is distinctly amphicribral, while several vascular branches reach towards the hypostase *s. l.*, (Fig. 3A). Noteworthy is the presence of a well-developed cuticular layer adjacent to the inner side of the inner integument (Fig. 3B). This very probably consists of the cuticles on adjoining surfaces of the inner integument and the nucellar epidermis. The nucellus becomes squashed at the antiraphal side, while endosperm-like remnants are also present. From previous detailed ontogenetic studies of seeds of closely related taxa (Von Teichman, 1991a & b), one can infer that the main structural difference between the young and mature seed-coat concerns a possible secondary impregnation of the cell walls of the hypostase *s. l.*, cells. However, this can only be confirmed once fully developed mature seeds become available.

Discussion and Conclusions

The recognition of a hypostase *s. s.*, and *s. l.*, in the ovule of the Anacardiaceae is suggested by Von Teichman (1988). In *Operculicarya decaryi,* as in other taxa of the Anacardiaceae, the hypostase *s. s.*, comprises a small group of chalazal-nucellar cells, adjacent to the embryo sac. These cells do not participate in the formation of the seed-coat. On the contrary, the hypostase *s. l.*, which initially may be a group of cells or a cell-plate, (lying adjacent to the hypostase *s. s.*, see Fig. 2), is usually characterized by being meristematic and containing tanniniferous deposits during the early stages of its ontogeny. Being an integral part of the chalaza, it naturally takes part in its secondary extension during the development of the chalaza in the partially or fully pachychalazal seeds. Therefore the hypostase *s. l.*, forms a significant part of the chalazal seed-coat, consisting of contiguous, more or less angular, relatively small, tanniniferous and thin-walled parenchyma cells. The cell walls of the latter may undergo further differentiation, i. e., a secondary impregnation

with lipid, i. e., cutin; callose or lignin (Von Teichman, 1991a, b).

The pronounced knob of the inner part of the ovary wall and resultant U-shaped ovule and seed render *Operculicarya decaryi* quite distinct from other members of the tribe Spondiadeae, particularly *Lannea discolor* (Sond.) Engl., a taxon to which it is otherwise obviously very closely related (Von Teichman and Hardy, 1992). On the other hand, the seed-coat anatomy of the young partially pachychalazal seed of *Operculicarya decaryi* is not only similar to that of *Lannea discolor* and other related taxa of the tribe Spondiadeae, but also, particularly with regard to the structure of the raphal vascular bundle and hypostase *s. l.*, to the "typical" seed-coat of the Anacardiaceae (Von Teichman, 1991b). In the latter paper it is indicated that the extended chalaza (as pachychalaza or partial pachychalaza), with the hypostase *s. l.*, also typifies the seed of certain other taxa of the Anacardiaceae, namely of the tribes Anacardieae, i. e., *Mangifera indica* L. as well as *Protorhus longifolia* (Bernh.) Engl. and *Rhus lancea* L. fil. of the tribe Rhoeae (Robbertse *et al.*, 1986; Von Teichman, 1991a, b). However in contrast to *Operculicarya decaryi*, both *Mangifera indica* and *Protorhus longifolia* are characterized by a pachychalazal ovule. These are presently the only pachychalazal ovules occurring in the Anacardiaceae.

In addition to some obvious macromorphological xerophytic adaptations displayed by *Operculicarya decaryi* (especially growth form), the anatomy of its fruit and seed presents a structural development that probably ensures the survival of this rare and endangered species in its harsh arid environment. These micromorphological adaptations include the extensive internal cuticular layer in the mature exocarp *s. s.*, the cuticular layer in the seed-coat, as well as the abundance of tanniniferous substances in both pericarp and seed-coat. It is hoped that the two papers on *Operculicarya decaryi* (the present one and Von Teichman and Hardy, 1992) will not only assist in the elucidation of the taxonomy of the family, but will also increase our knowledge of this endangered species.

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馬達加斯加島所產漆樹科 *Operculicarya decaryi* H. Perrier 之胚珠及部份厚合點型種子之註記

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Operculicarya decaryi H. Perrier 隸屬於漆樹科 Spondiadeae 族。其胚珠爲直生型，具雙珠被及厚珠心。胚珠的特色在於有一珠柄膝狀突及一由分生細胞所構成的承珠盤 (hypostase)。胚珠及種子均呈 U 字型，乃是由於子房及果皮內壁上一明顯的隆起所造成。在種子發生過程中，源自合點(包含承珠盤在內)的二次衍生物，造成種子爲部份厚合點型。種皮上可見一種脊維管束及一塊馬鞍狀褐色斑，後者係由單寧化的承珠盤增生而來。從種子構造方面而言，本種不僅與 Spondiadeae 族其他種相近，也與 Anacardieae 及 Rhoeae 兩族一些種類相似。胚珠內珠被之內表面具有發育良好的角質層及種皮內有單寧的沉積，這二點可能多少與此旱生樹木在微形態上發展出的適應策略有關。