STUDIES ON SEEDS WITH RUMINATE ENDOSPERM

V. Seed Development and Rumination in Two Genera of the Rubiaceae

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Received September 17, 1964

(Communicated by Professor T. S. Sadasivam, F.A.S.C.)

INTRODUCTION

The occurrence of a well-defined rumination of the endosperm in the Rubiaceae has been mentioned for several genera of the family by Schumann (1897) and the character has also been employed in the taxonomic segregation of certain taxa of the family. Studies concerning the various aspects of the phenomenon of rumination in the family have been lacking, except for the few casual observations made by Fagerlind (1937). Very recently, an account of the development of rumination in Tarenna asiatica of the family has been given by Periasamy and Parameswaran (1964).

MATERIAL AND METHODS

The present study covers seven species of Psychotria and one of Randia. Table I gives particulars regarding the nature, collection and other aspects of the materials.

Herbarium materials were obtained from the ‘Herbarium Collegii Presidentiae Madrasensis’. The methods of study are the same as has been described in a previous paper of this series (Periasamy, 1962 a).

OBSERVATIONS

Psychotria congesta; P. dalzellii; P. elongata; P. sepens; P. reevesii; P. macrocarpa; P. bisulcata.

Ovule.—One, anatropous, unitegmic, tenuinucellate and basally attached ovule in each carpel of the bicarpellate and bilocular ovary.

Post-fertilization development.—In P. congesta, P. dalzellii and P. elongata, either only one or both the ovules may develop into mature seeds. If only one seed develops, the seed becomes almost spherical (Figs. 1-3); if both the seeds develop, the seeds become somewhat hemispherical with a flat

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ventral surface and a convex dorsal surface (Figs. 4–6). In *P. reevesii*, *P. serpens*, *P. macrocarpa* and *P. bisulcata*, both the seeds develop to maturity; the ventral surface is flat and the dorsal surface is convex with five furrows.

### Table I

<table>
<thead>
<tr>
<th>Name of the plant</th>
<th>Nature of material</th>
<th>Name of collector</th>
<th>Place of collection</th>
</tr>
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<tr>
<td><em>Psychotria bisulcata</em> W. and A.</td>
<td>Herbarium material</td>
<td>E. Govindarajalu and B. G. L. Swamy, 2346</td>
<td>Banathirtham, S. India,</td>
</tr>
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<td></td>
<td></td>
<td>P. F. Fyson 6250, 1743</td>
<td>Yercaud, S. India</td>
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<tr>
<td><em>P. congesta</em> Hook. f.</td>
<td>„</td>
<td>P. F. Fyson 1892, 2845; 4257, 1863</td>
<td>Ootacamund, S. India,</td>
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<td></td>
<td>„</td>
<td>L. G. Sedgewick 3383</td>
<td>Kodaikanal, S. India,</td>
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<td><em>P. dalzellii</em> Hook. f.</td>
<td>„</td>
<td>P. F. Fyson 6762</td>
<td>Jog Falls, S. India</td>
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<td>E. Govindarajalu and B. G. L. Swamy 2439</td>
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<td><em>P. elongata</em> Hook. f.</td>
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<td>C. E. Brown 6410; P. F. Fyson 6940</td>
<td>Coonoor, S. India</td>
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<td></td>
<td>„</td>
<td>Tang Chang Chang 3956</td>
<td>Foochow, Fukien Province, China</td>
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<td><em>P. macrocarpa</em> Hook. f.</td>
<td>Herbarium material</td>
<td>E. Govindarajalu and B. G. L. Swamy 2439</td>
<td>Banathirtham, S. India</td>
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<tr>
<td><em>P. reevesii</em> Wall.</td>
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<td>Tang Chang Chang 3826</td>
<td>Foochow, Fukien Province, China</td>
</tr>
<tr>
<td><em>P. serpens</em> L.</td>
<td>„</td>
<td>Tang Chang Chang 3826</td>
<td>„</td>
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<tr>
<td><em>Ranlac malabarica</em> Lamk.</td>
<td>Freshly fixed</td>
<td>Author</td>
<td>Tambaram, S. India</td>
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</table>
in *P. reevesii* (Figs. 7–9), three furrows in *P. serpens* (Figs. 10–12), and two furrows in *P. macrocarpa* (Figs. 13–15) and *P. bisulcata* (Figs. 16–18).

Seed development is of the massive chalazal type (see Periasamy, 1962 b). As a result of the pronounced chalazal growth, the seed elongates at the base and the integumentary portion as well as the young quiescent endosperm are carried towards the apex of the seed (Fig. 19). The single unbranched vascular strand of the ovule becomes extended from the funicle up to the base of the seed along the median plane at the ventral side. Simultaneously with the growth in length of the seed, the cross-sectional area of the seed also increases (Fig. 20). Meanwhile, the cells of the epidermal layer divide anticlinally and enlarge excessively. The activity of the epidermis and the inner layers leads to the formation of infoldings of the epidermal layer into the inner layers (Figs. 20, 21). The infoldings develop first at the dorsal side of the seed and afterwards along the lateral and also the ventral side (Figs. 20, 25).

In *P. congesta*, *P. dalzellii* and *P. elongata*, the tissues which laterally flank the vascular trace grow excessively towards the ventral side; as a result, the vascular bundle is pushed deep into the tissues of the seed (Fig. 20). Ultimately, a deep furrow is formed along the median plane of the seed at the ventral side, and the vascular trace becomes situated at the tip of the furrow (Figs. 3, 6, 25–27). This ventral furrow is deeper in seeds that develop singly in a fruit than in seeds which develop as a pair. In *P. reevesii*, *P. serpens*, *P. macrocarpa* and *P. bisulcata*, the median ventral furrow is not formed and hence the vascular trace lies at the surface of the seed (Figs. 9, 12, 15, 18, 28–31).

The infoldings of the epidermal layer are confined to the basal portion of the seed which develops by the activity of the chalaza in *P. congesta* and *P. dalzellii* (Fig. 19); the comparatively small apical region, which develops by the activity of the integumentary portion, is devoid of any infolding (Figs. 19, 22). The situation in the other species cannot, however, be ascertained due to paucity of younger stages of seed development.

In *P. congesta*, *P. dalzellii* and *P. elongata*, the infoldings of the epidermal layer are connected to each other in the form of a network at the surface of the seed (Figs. 1, 2, 4, 5, 24), and they extend to varying depths towards the interior (Figs. 3, 6, 25, 27). In *P. reevesii*, the infoldings form a broad network at the ventral face of the seed (Fig. 7) but develop mainly along five longitudinal furrows at the dorsal side (Figs. 8, 9, 28); infoldings, which connect these longitudinal furrows with each other, also develop in an irregular
manner (Fig. 7). In *P. serpens*, the ventral face of the seed has very few infoldings (Fig. 10) and at the dorsal face they are confined to three longitudinal furrows (Figs. 11, 12, 29). In *P. macrocarpa*, the seed becomes three-lobed because of two wide dorsal depressions and the infoldings of the epidermal layer are very weakly developed in a few places at the dorsal face (Figs. 15, 30). In *P. bisulcata*, except for the three-lobed condition of the seed, there are no infoldings of the epidermal layer of the seedcoat (Figs. 18, 31) and the seed is non-ruminate.

![Diagram of seed structures](image)

Figs. 1-18. Structure of the mature seed in six species of *Psychotria*—comparative representation; magnifications approximately uniform. Thick line in the top row and thick dot in the bottom row indicate vasculature.

In all the species, except *P. congesta*, the epidermal layer does not divide periclinally so that it remains single-layered at the external surface of the seed, but appears two-layered at the infolded portions (Figs. 26, 31). In *P. congesta*, periclinal divisions occur in the infolded portion of the epidermis so that it becomes more than two-layered at these regions (Figs. 23, 24).

Active growth of the endosperm tissue in volume commences only after the seed has enlarged nearly to its mature size, and the infoldings of the epidermal layer are fully formed. Gradually, the endosperm replaces all the inner layers that surround it, but leaves intact the epidermal layer with its infoldings. Hence, in the mature seed, the seedcoat is single-layered and its infoldings make the endosperm ruminate (Figs. 23–30). In *P. dalzellii* and *P. elongata*, the cells of the mature seedcoat are filled with dark brown
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contents (Figs. 26, 27). In the other species, the cells of the seedcoat are thin-walled and devoid of stainable contents (Figs. 23–25, 28–31).

In all the species, the inner portion of the fruit wall develops into a hard endocarp with heavily lignified cells. In *P. reevessii*, *P. serpens*, *P. macrocarpa* and *P. bisulcata*, the inner surface of the stony endocarp is parallel to the external surface of the seeds, so that it appears as if the external contour of the seed is limited and determined by the internal surface of the endocarp (Figs. 28–31). In all the species, abundant druses and raphides accumulate in the fleshy portion of the fruit wall external to the stony endocarp.

Raphides are also found in the apical portion of the seedcoat which develops from the integumentary part in *P. congesta* and *P. dalzellii*; this portion is massive and sclerotic (Fig. 22) but some of the cells are thin walled and contain raphides.

*Randia malabarica*

*Ovule.*—Many, hemianatropous, unitegmic, tenuinucellate ovules in each locule of the bicarpellate, bilocular ovary. The ovules are attached to the swollen axile placentum. The placental tissue grows in between the ovules and surrounds their ventral half, giving the appearance of a second integument (Fig. 32). In the placental tissue, several cells are filled with brownish contents.

*Post-fertilization development.*—The tissue of the ovule as well as that of the placenta becomes actively meristematic after fertilization. In the ovule, the tissues show a centrifugal growth around the young endosperm (Fig. 32). Longitudinal growth of the seed is brought about by the chalazal part as well as by the integumentary part, so that the quiescent endosperm comes to occupy a position somewhere in the middle of the seed (Fig. 33). Therefore, the development has to be considered as the massive chalazal type.

The cells of the epidermal layer of the seed enlarge markedly in comparison to the actively meristematic inner layers and the placental tissue; gradually, the epidermis becomes thrown into shallow, irregular folds and undulations; the placental tissue fills in the irregular spaces caused by the irregular contour of the external surface of the seed (Fig. 33).

It cannot be said with certainty, whether the irregular surface of the seed arises because of the irregular growth of the tissues of the seed itself, or is caused by the irregular growth of the placental tissue which tightly surrounds the young seed. However, it is observed, that in those places
where the seed is not surrounded by the placental tissue, the surface of the seed does not become as irregular as in those places where it is so surrounded (Fig. 33).

During further development, the cells of the epidermal layer enlarge excessively, and their inner tangential walls and the inner halves of the radial walls are alone lignified, leaving the outer tangential walls and the portion of the radial walls immediately abutting on it unthickened (Fig. 34). In the mature seed the thickenings become massive with pit canals in the inner tangential wall; the unthickened portions of the cell walls disorganise (Fig. 35).

The placental tissue surrounds the seed except for a small portion at the dorsal surface; its cells are thin-walled but many become filled with brownish contents (Fig. 36). Finally, the entire tissue becomes somewhat pulpy and the mature seeds lie embedded in it.

The endosperm is cellular. It remains quiescent and of small volume until the seed has enlarged nearly to its mature size (Figs. 32, 33). After that, the endosperm grows rapidly in volume and replaces all the surrounding tissues of the seed except the epidermal layer which serves as the mature seed-coat and whose irregular surface makes the endosperm ruminate (Fig. 36). The cells of the mature endosperm are thin-walled and contain fatty reserves (Figs. 35, 36).

The inner portion of the ovary wall becomes lignified as a stony endocarp. The lignified cells of the endocarp contain one simple crystal in each. Raphides are deposited in the fleshy portion of the ovary wall external to the stony endocarp.

**DISCUSSION**

A discussion of the phenomenon of rumination in the angiosperms in regard to its developmental aspects, and a classification of the rumination types, have been made in a previous publication (Periasamy, 1962 b). The discussion here will, therefore, be confined only to those features that are characteristic of seed development and rumination in the Rubiaceae.

In the two genera of Rubiaceae studied at present, and in *Tarenna asiatica* (Periasamy and Parameswaran, 1964), rumination is of the *Spigelia* type (Periasamy, 1962 b), and the seeds show a massive chalazal growth. *Tarenna asiatica* and *Randia malabarica* have a certain amount of integumentary growth also, and in these, the infoldings or undulations of the seed coat are formed both at the chalazal and integumentary portions of the seed. In
Psychotria congesta and P. dalzellii, which show a very pronounced rumination, chalazal growth is very massive with very little growth of the integumentary portion, and the rumination infoldings are also confined to the chalazal portion alone. The nature of the chalazal activity has not been studied in the other species of Psychotria. It would, however, be interesting to investigate the chalazal activity in the species Psychotria elongata, P. reevesii, P. serpens and P. macrocarpa, which show a gradually decreasing degree of rumination, and in P. bisulcata which is non-ruminate, and see whether there is a decrease or not of the amount of chalazal growth correspondingly with the degree of rumination. Such a study may perhaps throw more light on the relation between chalazal growth and rumination (see Periasamy, 1962 b), since Psychotria is a rare genus which shows a pronounced degree of rumination in some of its species and a complete absence of it in the others through a gradual series of intergrading forms. The pattern of rumination also shows an interesting series of graded variations. In P. congesta, P. dalzellii and P. elongata, the rumination furrows of the infoldings form a network as seen on the surface of the seed and in this respect resemble Spigelia splendens and S. anthelmia (Dahlgren, 1922) of the Loganiaceae. In P. reevesii, the infoldings are formed mainly along five longitudinal furrows at the dorsal side, and in P. serpens, along three. In P. macrocarpa, the rumination is so mild as to escape notice unless observed critically and it is interesting to note that Gamble (1921) has described this as having ruminate endosperm. Thus, in this taxonomically difficult genus, rumination affords valuable help for segregation of species, and it may prove to be so in other taxa of the family with ruminate endosperm, if they are adequately investigated in regard to the various aspects of this character.

In all the investigated plants of the Rubiaceae, all the infoldings or undulations of the rumination do not penetrate to the same depth into the endosperm surface, but are much variable in the different regions of the seed. This situation is in contrast to that seen in Ervatamia heyneana, Voacanga grandifolia (Periasamy, 1963), Spigelia splendens and S. anthelmia (Dahlgren, 1922), which have also a Spigelia type of rumination, but in which all the infoldings of rumination penetrate more or less uniformly to the same depth. The cells of the mature seed coat do not acquire any thickening of their cell walls in Psychotria. In P. dalzellii and P. elongata, the cells of the seed coat become filled with dark brown contents as in Tarenna asiatica (Periasamy and Parameswaran, 1964). Wall thickening of the seedcoat in Randia mala- bàrìca is just the reverse of what is seen in Tarenna asiatica. In Tarenna asiatica, the outer tangential and the radial walls bordering upon it alone
become lignified whereas in *Randia malabarica*, it is the inner tangential and the radial walls bordering upon it that are thickened. Netolitzky (1926) has designated the former as the Resedaceous type of thickening and the latter as the Ericaceous type of thickening.

The behaviour and significance of the placental tissue, which grows around the ovules in *Randia malabarica* and *Tarenna asiatica*, has been discussed in a previous paper (Periasamy and Parameswaran, 1962).

**SUMMARY**

The unitegmic, tenuinucellate ovules of *Psychotria* and *Randia* show after fertilization a massive chalazal growth which is more pronounced in the former than in the latter. In *Psychotria*, the epidermis forms deep or shallow infoldings into the inner layers that grow around the young, quiescent endosperm; the infoldings are confined to the chalazal part alone and are absent in the integumentary part. In *Randia malabarica*, the epidermis forms shallow and irregular undulations both in the chalazal and the integumentary parts.

The endosperm remains quiescent and of small volume during the early stages of seed development. When the seed has attained nearly its mature size, the endosperm grows rapidly in volume and attains a ruminate configuration by replacing all the surrounding tissues of the seed except the epidermis which, with its infoldings or undulations, serves as the mature seed coat. *Psychotria* shows a graded variation from a pronounced degree of ruminination in *P. congesta* to complete absence of ruminination in *P. bisulcata*, through a gradually decreasing series represented by *P. dalzellii*, *P. elongata*, *P. reevesii*, *P. serpens* and *P. macrocarpa*. The cell walls of the mature seed coat do not become thickened in *Psychotria*, but in *Randia malabarica*, they acquire an Ericaceous type of lignification.

**ACKNOWLEDGEMENT**

I offer my thanks to the University Grants Commission for the award of a senior research fellowship during the tenure of which this paper was prepared for the press. My thanks are also due to Prof. B. G. L. Swamy for his kind interest and encouragement.

**REFERENCES**


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Schumann, K. .. "Floral anatomy and embryology of *Tarenna asiatica*," 1964 (in press).


**EXPLANATION OF PLATES**

**PLATE XIX**

**FIGS. 19–25. Psychotria congesta**

**FIG. 19.** L.S. of young seeds with portion of ovary wall at an early stage after fertilization; note restriction of infoldings to the basal chalazal part, ×28.

**FIG. 20.** T.S. of seed at a slightly later stage than Fig. 19, ×58.

**FIG. 21.** Enlarged view of portion of T.S. of young seed showing infoldings of the epidermis into the inner layers, ×280.

**FIG. 22.** T.S. through apex of young seed; note absence of infoldings of epidermal layer; white areas represent cells which later on become lignified, ×103.

**FIG. 23.** Portion of T.S. of mature seed, ×50.

**FIG. 24.** Tangential L.S. of mature seed just below the surface, ×12.

**FIG. 25.** T.S. of fruit with mature seed, ×14.

**FIG. 26.** *Psychotria elongata*. T.S. of mature seed, ×11.

(CH, chalaza; EN, endosperm; V, vascular strand.)

**PLATE XX**

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FIGS. 32-36. Randia malabarica

Fig. 32. T.S. of young seed with placental tissue soon after fertilization, × 73.

Fig. 33. L.S. of young seed at about the same stage as Fig. 32, ×26.

Fig. 34. Portion of T.S. of immature seed showing thickening of epidermal layer, × 150.

Fig. 35. Same as Fig. 34, in mature seed, ×220.

Fig. 36. T.S. of mature seed with placental tissue, ×40.

(EN, endosperm; EM, embryo; EP, epidermis; IL, inner layers; PT, placental tissue.)