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Ontogeny, Structure and Differentiation of anther Tapetum in *Celsia Coromandeliana*

By

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With 2 Figures

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Summary

The ontogeny of the anther wall in *Celsia coromandeliana* VAHL. has been investigated. The primary parietal layer divides to form two secondary parietal layers — the outer one segments to form the endothecium and the middle layer whereas the inner one directly forms a part of the tapetum toward the wallward side. The remainder of the tapetum lining the sporogenous mass is derived from the connective tissue. The tapetum, thus, has dual origin. Tapetal cells derived from the parietal layer are isodiametric whereas those derived from cells of the connective are radially elongated and even show variation in size. Further two or three cells of the connective that span the two tapetal populations show characteristic elongation. It is concluded that the anther tapetum in *C. coromandeliana* has not only dual origin but also reveal polymorphism. The factors controlling the stimulation of connective to differentiate and then to re-differentiate as tapetum are not yet clear.

Zusammenfassung

Es wurde die Ontogenie der Antherenwand von *Celsia coromandeliana* VAHL. untersucht. Die sich teilende primäre Parietalschicht bildet zwei sekundäre Parietalschichten; die äußere wird zum Endothecium und zur Zwischenschicht, während die innere unmittelbar den zur Antherenwand hin liegenden Teil des Tapetums bildet. Der übrige Teil des Tapetums, das dem sporogenem Gewebe aufliegt, stammt aus dem Connectiv. Das

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Tapetum hat somit zweifachen Ursprung. Die aus der Parietalschicht hervorgegangenen Tapetumzellen sind isodiametrisch, während die aus dem Connectiv gebildeten radial gestreckt sind und in ihrer Größe variieren. Weitere zwei oder drei Zellen des Connectivs, die die beiden Tapeten verbinden, sind charakteristisch verlängert. Es wird geschlossen, daß das Tapetum der Antheren von *C. coromandeliana* nicht nur zweifachen Ursprungs ist, sondern Polymorphismus aufweist. Die Faktoren, die das Connectiv zur Differenzierung anregen und dann zu dessen Rückdifferenzierung zum Tapetum führen, sind noch nicht bekannt.

(Editor)

1. Introduction

In the *Scrophulariaceae*, little work has been done on the development of anther wall layers — with particular reference to tapetum (see MAHESHWARI 1950, WUNDERLICH 1954, FOSTER & GIFFORD 1959, DAVIS 1966). The tapetum, in majority of the angiosperms, is presumed to be derived from the inner parietal layer. ESAU 1965, PERIASAMY & SWAMY 1966, however, reported dual origin for anther tapetum. In *Celsia coromandeliana*, the development, structure and differentiation of anther tapetum toward the wallward and connective sides, has been investigated.

2. Material and Methods

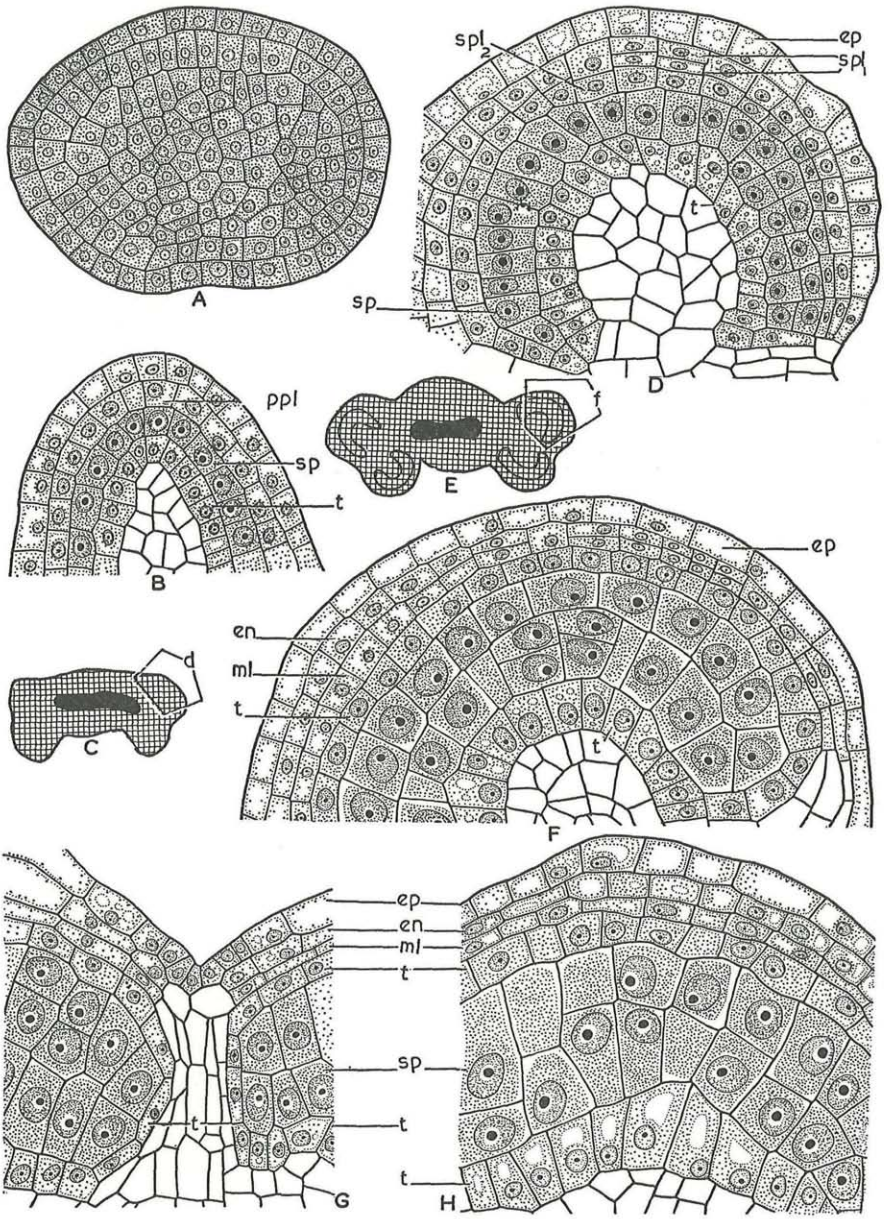
Buds and flowers of *Celsia coromandeliana* VAHL. were collected from the Yamuna banks, Delhi, and fixed immediately in acetic-acid ethanol or Carnoy's fluid. The material was dehydrated in alcohol-xylene series

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Fig. 1. *Celsia coromandeliana*, Development of anther wall and dual origin of the tapetum. (en = endothecium, ep = epidermis, ml = middle layer, ppl = primary parietal layer, sp = sporogenous layer, spl_1, spl_2 = secondary parietal layers, t = tapetum). — A: Undifferentiated anther; ×540. — B: Transverse section of an anther lobe showing epidermis, primary parietal layer (ppl) and sporogenous layer (sp.) The tapetum toward the connective has differentiated whereas toward the epidermis it has not yet formed; ×540. — C, E: Transections of anthers at various stages of development; ×54. — D: Portion marked *d* in C magnified to show epidermis, some cells of secondary parietal layer (spl_1) divide periclinally to form endothecium and middle layer. The spl_2 directly acts as the tapetum; ×540. — F: Portion marked *f* in E magnified to show four wall layers-epidermis, endothecium, middle layer and tapetum. Some of the sporogenous cells show periclinal divisions; ×540. — G: Parts of adjacent sporangia showing the elongating connective cells bridging the gap between the tapetal layers derived from inner wall layer and the connective cells which have re-differentiated as tapetum; ×540. — H: Portion of anther lobe. The tapetum toward the inner side is derived from the cells of the connective and are of different sizes; ×540.

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and embedded in paraffin wax. Sections were cut between 4 and 6 microns, and stained with either safranin or iron-alum haematoxylin with fast green as counterstain. The callose was localized by aniline blue-UV fluorescence test (JENSEN 1962).



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3. Observations

3.1. Development of anther wall layers: The pre-archesporial anther, in transection, is somewhat oval and consists of homogenous mass of cells surrounded by a well defined epidermis (Fig. 1A). As development proceeds, the hypodermal plate of archesporial cells differentiates in each corner, which can be distinguished by dense cytoplasm and prominent nuclei. Each archesporial cell cuts off a primary parietal cell toward the epidermis and a primary sporogenous cell toward the inside (Fig. 1B). The cells of the primary parietal layer divide periclinally resulting in two secondary parietal layers (spl_1 & spl_2; Fig. 1C, D). The inner layer (spl_2) matures directly into the tapetum (Fig. 1E, F), whereas the outer layer (spl_1) segments to form the middle layer and the endothecium (Fig. 1F). There is no further increase in the number of wall layers which including the epidermis remains four. The anther wall at maturity comprises epidermis, endothecium, middle layer and tapetum (Fig. 1G, H). The sporangia are horse-shoe shaped (Fig. 2A), and the connective vascular bundle is massive with well developed xylem and phloem. The epidermis initially keeps pace with the enlarging anther but later its cells get flattened and become wavy (Fig. 2C, D). The tapetal cells at first are uninucleate (Fig. 2B, E) but later become binucleate (Fig. 2F).

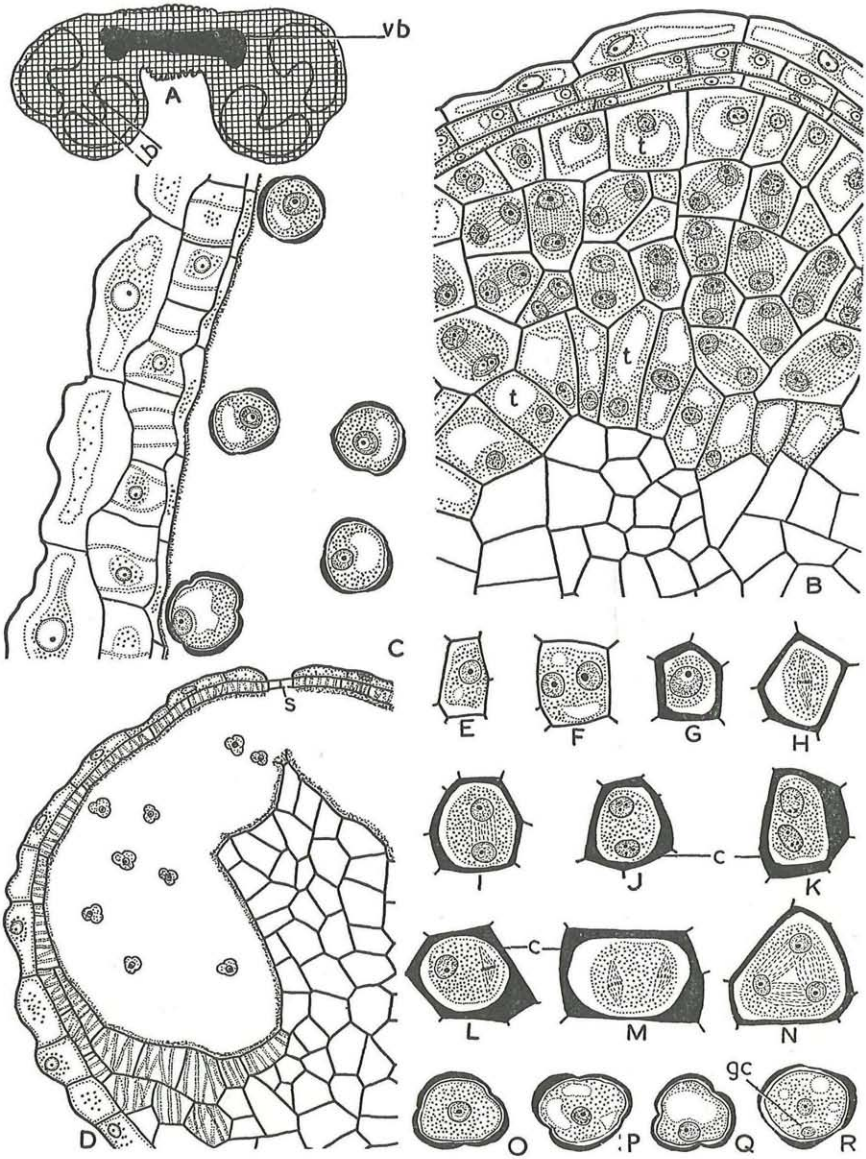
The cells of the primary sporogenous layer, meanwhile, by several mitotic divisions, give rise to a mass of sporogenous cells which ultimately differentiate into microspore mother cells. At uninucleate stage of the pollen grains, the endothecium acquires fibrous thickenings on their radial

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Fig. 2. *Celsia coromandeliana*, Microsporogenesis and male gametophyte (c = callose, gc = generative cell, s = stomium, t = tapetum, vb = vascular bundle). — A: Transverse section of anther showing well developed vascular bundle. The four sporangia are horse-shoe shaped with broad connective; ×60. — B: Portion marked *b* in A enlarged to show 4-wall layers. The tapetal cells towards the inner side is derived from the cells of the connective and show radial elongation and size variation as compared to the one derived from parietal layer; ×600. — C: Transection of anther at an older stage revealing elongated epidermis, fibruos endothecium, compressed middle layer and degenerated tapetum. The pollen grains have smooth exine; ×600. — D: Transverse section of a portion of an anther showing persistent epidermis, endothecium, degenerated tapetum and one-celled pollen grains. The stomium (s) is well developed; ×140. — E, F: Uni-, and bi-nucleate tapetal cells; ×600. — G—M: Meiosis in microspore mother cells. Copious deposition of callose surrounds the meiocytes; ×600. — N: Tetrahedral tetrad; ×600. — O—Q: Uninucleate pollen grains. The nucleus lies initially in the middle (Fig. 0) but vacuolation in pollen cytoplasm (Fig. P) pushes the nucleus to one side as seen in figure Q; ×600. — R: Two-celled pollen grain. The generative cell (*gc*) is adpressed towards the wall; ×600.

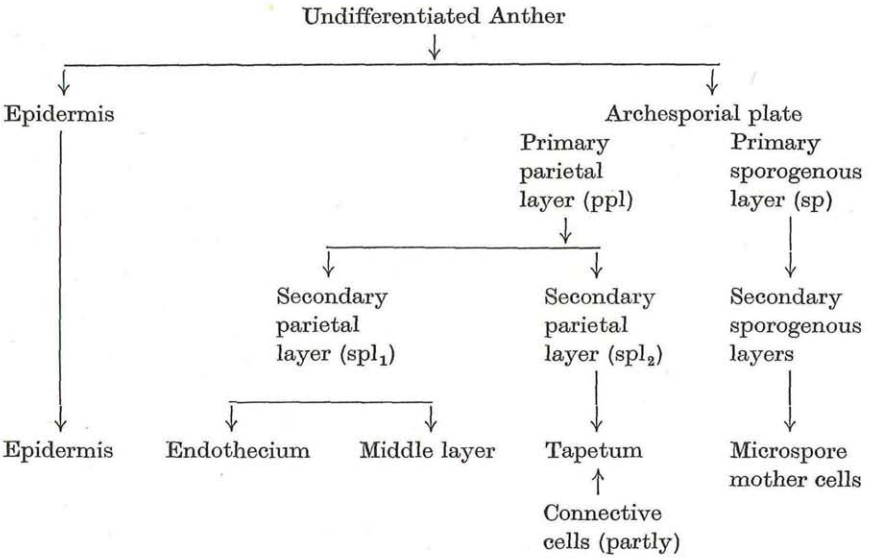
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walls, the middle layer is compressed and the tapetum degenerates (Fig. 2C). The tapetum toward the connective is early to organise and to degenerate as compared to the tapetum derived from the inner secondary parietal layer. One or two layers of a few connective cells develop fibrous thickenings (Fig. 2D). The anther wall, at the time of dehiscence, consists only of the epidermis and the fibrous endothecium (Fig. 2D).



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The following chart summarises the development of the anther wall which follows the Dicotyledonous type (DAVIS 1966):



3.2. Dual origin and polymorphism in anther tapetum: A row of uninucleate cells toward the connective becomes conspicuous with prominent nuclei and dense cytoplasm, at the stage when the sporogenous and primary parietal layers are formed (Fig. 1B). The inner secondary parietal layer (spl_2) which remains undivided (Fig. 1D) forms only a part of the tapetum toward the wallward side (Fig. 1F), whereas the cells of the connective abutting the spore mother cells form the remainder of the tapetal population. The tapetum, thus, has dual origin.

The tapetal cells derived from the connective tissue are strikingly different from those derived from the parietal layers. The former have radially elongated cells and even show variation in size among themselves, whereas the latter have small and quadrangular cells (Fig. 1D, F, H). The connective cells that span the two tapetal populations — the tapetum derived from secondary parietal layer (spl_2) and that derived from the connective cells — also show characteristic elongation (Fig. 1G) and behave as tapetum. The tapetum in this taxon, therefore, exhibits polymorphism.

3.3. Microsporogenesis and male gametophyte: During meiosis, the meiocytes enlarge, become rounded and are surrounded by a thick layer of callose (Fig. 2G). Meiosis in the microspore mother cells (Fig. 2H—N) results in the formation of either tetrahedral or decussate microspore tetrads. The pollen grains are tricolpate with thick exine and thin intine

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(Fig. 2O—Q). In the young spore, the nucleus is centrally situated and embedded in a dense cytoplasm (Fig. 2O). As the pollen attains maturity one or two large vacuoles are formed and the nucleus is pushed to the periphery (Fig. 2P, Q). The nucleus of the microspore divides to form a large vegetative and a small generative cell (Fig. 2R). At the time of dehiscence of anther, the cells of the partition wall sequestering the microsporangia break down. The adjacent pollen sacs become confluent and pollen grains are shed through the stomium (Fig. 2D).

4. Discussion

4.1. Callose around meiocytes: Heslop-Harrison 1964 considers that callose layer secreted around the microspore mother cells isolates the meiocytes from the surrounding diploid tissue to achieve nuclear independence. Present work on *Celsia coromandeliana* is in agreement with the above view. Callose is secreted around the microspore mother cells during the meiotic divisions and persist until the formation of microspore tetrads.

4.2. Tapetal polymorphism: Recently dimorphic anther tapetum has been reported in *Alectra thomsonii* (Vijayaraghavan & Ratnaparkhi 1973). Many genera of the *Acanthaceae* and *Labiatae* also reveal such type of tapetum (Maheshwari 1950). In the above taxa the tapetal cells derived from parietal layer are smaller and rectangular while those derived from connective cells are larger, and a few of them are even palisade-like. Such a feature is also met with in *Celsia coromandeliana*. The cells of the connective on either side of the sporangium that bridge the two tapetal populations exhibit characteristic elongation. The morphology of tapetal cells at the time of span are different from the rest of the tapetal populations. The tapetal cells derived from the connective interestingly also exhibit various morphological dimensions. The tapetum, thus, exhibits polymorphism in *Celsia coromandeliana*.

4.3. Tapetal cells toward connective-differentiation and re-differentiation: Many workers presumed that the tapetum is always the product of parietal layer because tapetal cells once formed, exhibit morphological homogeneity in their (a) nuclear behaviour, (b) cytoplasmic constituents and (c) histochemical reactions. Esau 1965, Periasamy & Swamy 1966, however, conjecture that the tapetum on the inner side arises from cells of the connective. Vijayaraghavan & Ratnaparkhi 1973, have shown dual origin and dimorphic anther tapetum in *Alectra thomsoni*. The tapetum derived from the parietal layer does not completely encircle the sporogenous mass and tapetal population towards the connective is derived from the cells of the connective closest to the inner side of the sporogenous mass. No sterilization of the sporogenous tissue toward the connective is observed. The ontogeny of the tapetum in *C. coromandeliana* agrees with that of *A. thomsoni* and thus has dual origin.

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Ontogenetically the cells which abut the inner surface of the sporogenous tissue, initially differentiate as the connective cells and then re-differentiate as the tapetum. These connective cells, once stimulated and destined to act as tapetum exhibit not only cytological synchrony but also histochemical homogenity with the rest of the tapetal population irrespective of its ontogeny — parietal or connective. Whether these two populations derived from different sources also exhibit the same ultrastructural details remains to be investigated. No ultrastructural ontogeny of the tapetal cells exists (ECHLIN 1971). It is not yet clear whether the factors controlling the stimulation of connective cells-impinging upon the gametophytic tissue-to re-differentiate as tapetum arise intrinsically in the connective tissue or directed by the juxtaposed meiocytes. It will, however, be interesting to investigate the biochemical reportiere of these cells derived from the connective, to reveal polymorphism and destined to act as tapetum.

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