

# MORPHOLOGY OF THE ANTHER TAPETUM OF ANGIOSPERMS

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**T**HE anther tapetum of angiosperms is presumed to be the tissue that serves for the nutrition of the microsporogenous cells during the development of the latter into the microspores. Although it is not yet known how exactly this function is discharged, the functional aspect of tapetum is evident from the following facts: (1) The tapetum invariably exhibits characteristic and profound morphological changes, and gradually undergoes degeneration during the time of sporogenesis. (2) As a rule, the tapetum completely surrounds the mass of sporogenous tissue and hence any nutritive substance needed for the latter must necessarily pass through the tapetum.

Since the basic phenomenon that underlies the concept of tapetum as a separate morphological entity, is its functional role, this aspect of the tapetum has received much of the attention of investigators. On the other hand, the morphological aspect of the tapetum has not been looked into with critical enquiry, and whatever information that is available is most often physiologically oriented. Thus we see that the nuclear behaviour, the cytoplasmic configuration, the time of degeneration, its role in the nutrition of the sporogenous tissue, etc., are features that are usually described not only in ontogenetic accounts of tapetum of individual species but also in reviews and books (Maheshwari, 1950; Wunderlich, 1954). However, the one important aspect of tapetum that perhaps has, more than anything else, influenced its morphological aspect, is the remarkably uniform physiological behaviour of its constituent cells. The tapetum, therefore, appears to constitute a single, indivisible unit. This physiological homogeneity has obviously led to the assumption also of a morphological homogeneity. Since in most of the angiosperms the cells of the innermost of the wall layers derived from the primary parietal tissue function as tapetal cells, the 'normal' type of tapetum of angiosperms is invariably considered to be the product of only the innermost wall layer.

Although a concept of morphological homogeneity has by and large pervaded and influenced most of the investigations on ontogeny of the anther, instances are not lacking where the supposed homogeneity is said to be absent, and a morphological duality reported to be

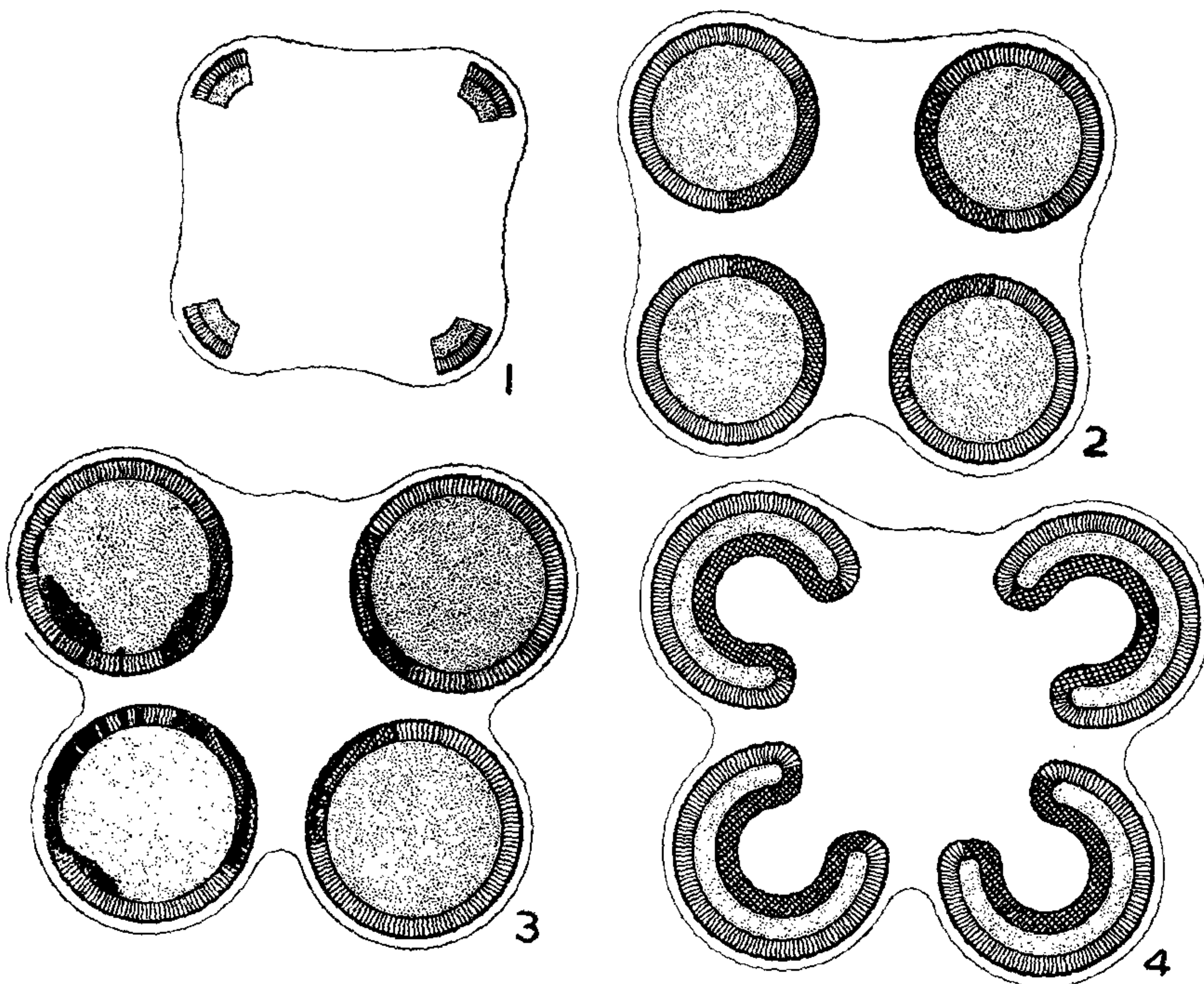
present (Boke, 1949; Maheshwari, 1950; Periasamy, 1955; Periasamy and Swamy, 1959, 1964; Budell, 1963; Periasamy and Parameswaran, 1965). The few instances of such reports, however, have failed to influence and modify the older and widespread morphological concept. Thus, Steffen and Landmann (1958), who have discussed the morphology and variations of the anther tapetum of angiosperms, state that the 'normal' type of tapetum, that obtains in a majority of angiosperms and forms their type I, develops from the derivatives of the parietal cell. Similarly, their types II and III are also assumed to be morphologically homogeneous, the former being a sterilization product that arises by a periclinal division of the secondary archesporium, and the latter by a peripheral or a random sterilization of the archesporial cells.

First, let us consider the sequence of ontogeny of the 'normal' tapetum of angiosperms. As stated by Periasamy and Swamy (1964), the archesporium, which must be looked upon as the initials of the microsporangium, divides periclinally to give rise to the outer, primary parietal tissue, and the inner, primary sporogenous tissue. Although in some species the archesporium differentiates as a single longitudinal row of cells in each of the four corners of the anther primordium, in most species it appears to differentiate as a plate of more than two or three cells in width. In either case, the primary parietal tissue abuts on the external face alone of the primary sporogenous tissue and does not extend to the lateral and inner faces (Fig. 1). During subsequent ontogeny both the primary parietal tissue, and the primary sporogenous tissue, undergo developmental changes with accompanying multiplication of cells. These changes bring about marked modifications in the initial configuration of the two tissues, not only in relation to one another but also with respect to the anther as a whole. Anticlinal and periclinal divisions in both the tissues result in the development of a variable number of wall layers and the formation of a massive sporogenous tissue (except where it is uniseriate). The sporangium as a whole bulges out to varying extent depending upon the massiveness of the sporogenous tissue and the degree of development of the extrasporangial tissues of the connective region. During the process of bulg-



ing out, the wall layers derived from the parietal tissue extend as an arc along the outer face of the sporangium (Figs. 2-4), the greater

not been reported, nor is there any possibility of such an occurrence. Even in *Cananga odorata* (Periasamy, 1955) in which the sporo-



FIGS. 1-4. Figs. 1-3. Successive stages in the development of the 4 microsporangia in the anther. Fig. 4. Mature anther showing intrusion of connective tissue into the microsporangia. All figures diagrammatic. Parietal tissue and tapetum derived from it single-hatched; tapetum derived from connective cross-hatched; sporogenous tissue stippled.

the bulging the wider being the arc (see also Periasamy and Swamy, 1964). Nevertheless, even a superficial examination of the cellular readjustments involved in the growth pattern of the sporangium would show that whatever be the extent of the wall tissue complex, it does not extend to the inner face of the sporangium towards the connective, a feat which requires the girdling of the wall layers around the sporogenous tissue by 180° on its either arm. Such a feat can be accomplished only by extensive sliding or intrusive growth of the cells or cell layers of the wall tissue; so far such a growth pattern of ontogeny has

genous tissue forms a uniseriate row, and hence requires a minimum extension of the wall layers to engirdle the sporogenous tissue, a careful study of the ontogeny reveals that none of the wall layers does so extend to the side towards the connective. Such being the case even in the instance of a uniseriate sporogenous tissue, in plants which have a plate of archesporium and a massive sporogenous tissue it would be an ontogenetic improbability for any of the wall layers to extend to the inner face of the sporangium, diametrically opposite to the position of origin of the primary parietal tissue.



From the foregoing considerations it may safely be concluded that in the angiosperms, the wall layers derived from the primary parietal tissue do not extend fully around the sporogenous tissue and especially fail to cover its inner face towards the connective. The tapetum as a rule arises from the innermost of the wall layers although in certain instances more than one layer may be regularly or irregularly involved (Wunderlich, 1954). In any case, the tapetum that results from the wall layers would represent only that particular portion which abuts on the outer face of the sporogenous tissue and does not account for the whole of the tapetum that covers the sporogenous tissue all around. Therefore a certain part of the tapetum situated towards the inner face of the sporogenous cell mass must necessarily arise from a tissue that does not morphologically belong to the wall layers, and consequently is not a derivative of the primary parietal tissue. Indeed, the tapetum towards the inner face arises from the derivative cells of the connective that initially abutted on the archesporium. Thus, morphologically, the tapetum has a dual origin, partly from the wall layer or layers and partly from the cells of the connective, the relative proportion of the two depending upon the configuration of the sporangium in relation to the connective (Figs. 3, 4).

In spite of the morphological duality, it is true, as stated already, that the entire tapetum becomes in most plants remarkably homogeneous in regard to its cellular alignment as a single layer, the size and structure of its individual cells, and their cytological and physiological behaviour. However, instances are not altogether lacking in which the morphological duality is indicated also by differences in arrangement, size and behaviour of the different parts of the tapetum. In a majority of plants belonging to the Acantheaceae and other Bicarpellatae (Maheshwari, 1950), the tapetal cells on the inner face elongate radially to a marked extent in comparison to those on the outer face. In *Tarenna asiatica* (Periasamy and Parameswaran, 1965), the tapetum on the outer face consists of a single layer of regularly aligned cells, but on the inner face it comprises more than one layer of irregularly arranged cells, and a careful study of the ontogeny reveals that the differences in configuration correspond to differences in morphology. Such structural and physiological differences within the tapetum, either in its fully formed state or during ontogeny, may be more widespread than what is

reported at present, if only critical studies, that are lacking, are made on the ontogeny of the anther and the tapetum.

Apart from the relatively lesser number of instances of the visible expression of the morphological duality, of the tapetum, the homogeneity that bears no indication of such duality, attained in most angiosperms, must be looked upon as an instance of analogy and an example of how plants can fulfil their functional needs through diverse morphological and morphogenetic pathways. This would naturally be disconcerting to morphologists who may like to have such a homogeneous and compact tissue as the tapetum to be also morphologically homogeneous, in order that the importance of morphology be all-pervading without being minimised when it comes in face with the functional aspects. In fact it is this deeply rooted sense of the importance of morphology that may have been responsible for perpetuating the idea that the tapetum is a morphologically homogeneous tissue, but facts speak otherwise in this regard.

Within the major plant groups the sporangium exists in several levels of specialization (see also Periasamy and Swamy, 1964), from a condition in which it consists of nothing more than a spore mass, to a complex one, in which the spore mass is associated with structures that serve for the nutrition, protection and controlled distribution of the spore mass. It is generally believed that these structural associates have resulted from the setting apart, or what is called sterilization, of a part of the spore mass for other functions. In other words, a division of labour sets in the morphologically homogeneous sporogenous mass. The exact stage in ontogeny at which the division of labour commences, however, varies widely. It may start after the sporogenous mass has attained its final number of cells, when some of them instead of developing the morphological characteristics of spores, develop into other structures such as tapetum and wall, or degenerate to contribute to the nutrition of those destined to mature as spores. The division of labour may also commence at earlier stages when cell multiplication in the sporangium has not yet ceased, so that either one or both the functionally-divided parts continue to divide further and multiply in cell number, during which process further division of labour may occur in one or both. In this trend of specialization, if we may consider that the earlier the division of labour sets in the more specialized the sporangium is, the extreme expression of specialization would be the begin-



ning of division of labour at the very first division of the sporangial initial or initials. Indeed, this is the case in the microsporangium of angiosperms, because the very first division of the archesporium, which must be viewed as the initial of the microsporangium, sets apart a parietal tissue that does not contribute anything to the sporogenous mass, and a sporogenous tissue which gives rise to the spores proper.

During the multiplication of cells of the parietal tissue, further division of labour takes place into tapetum and wall layers, the latter then segregating into the middle layer or layers and the endothecium. Although there may be some ontogenetic variation in the sequence of division of labour, in general it suggests that the tapetum is an earlier specialization than the endothecium. In fact, the tapetum is first seen at the pteridophytic level, whereas the endothecium emerges only in the angiosperms. As surmised by Periasamy and Swamy (1964), the emergence of endothecium, as the counterpart of the exothecium in gymnosperms, appears to be related to the isolation of the outermost layer as a mere 'skin' with very limited morphogenetic potentialities, in the fundamental organization of the plant body of the angiosperms as a whole.

In contrast to the parietal tissue, no subsequent division of labour takes place in the sporogenous tissue in the majority of angiosperms. However, there are instances where some of the sporogenous cells may, instead of functioning as spore mother cells, serve as sterile partitions or tapetal cells as in *Cananga odorata* (Periasamy and Swamy, 1959), and in the Gentianaceae and the Geraniaceae tapetum (type III of Steffen and Landmann, 1958). The unique case of the Cyperaceae in which even after meiosis, three spore nuclei of each tetrad degenerate and only one develops, may also be mentioned as a very late division of labour in the spore mass.

Hand in hand with the above-stated trends of specialization, the microsporangium of angiosperms has also become a sunken structure due to the loss of an individual stalk. This has done away with the necessity of production of a

complete and morphologically homogeneous wall all around the spore mass, because the tissue of the connective itself adequately serves this function toward the inner, sunken face (Periasamy and Swamy, 1964). With the loss of the wall toward the inner face, the production of the tapetum, which is a function of the wall layers, becomes also ceased, and the connective tissue, that replaces the wall here, naturally takes up also the function of giving rise to the tapetum in the concerned region. Thus, from a consideration of the phylogenetic modification of the microsporangium as well, it seems but natural that the tapetum toward the inner face of the sporangium of angiosperms should arise from cells of the connective and not from the wall layers.

It may therefore be concluded that the anther tapetum of angiosperms, although physiologically homogeneous in most instances, is morphologically heterogeneous, being derived in part from the parietal tissue toward the bulging, outer face of the sporangium, and in part from the cells of the connective toward the sunken, inner face.

1. Boke, N. H., "Development of the stamens and carpels in *Vinca rosea* L.," *Amer. J. Bot.*, 1949, **36**, 535.
2. Budell, B., "Untersuchungen der Antherentwicklung einiger Blütenpflanzen," *Z. Bot.*, 1963, **52**, 1.
3. Maheshwari, P., *An Introduction to the Embryology of Angiosperms*, McGraw-Hill Book Co., New York, 1950.
4. Periasamy, K., Studies in the Annonaceae Embryology of *Cananga odorata* and *Millettia wightiana*, Thesis, University of Madras, 1955.
5. — and Parameswaran, N., "A contribution to the floral morphology and embryology of *Tarenna asiatica*," *Beitr. Biol. Pflanzen*, 1965, **41**, 123.
6. — and Swamy, B. G. L., "Studies in the Annonaceae. 1. Microsporogenesis in *Cananga odorata* and *Millettia wightiana*," *Phytomorphology*, 1959, **9**, 251.
7. — and —, "Is the microsporangium of angiosperms wall-less?" *Curr. Sci.*, 1964, **33**, 735.
8. Steffen, K. and Landmann, W., "Entwicklungsgeschichtliche und cytologische Untersuchungen am Balkentapetum von *Gentiana cruciata* L. und *Impatiens glandulifera* Royle.", *Planta*, 1968, **50**, 423.
9. Wunderlich, R., "Über das Antherentapetum mit besonderer Berücksichtigung seiner Kernzahl," *Österr. bot. Z.*, 1954, **101**, 1.