STUDIES IN THE DISEASES OF *MANGIFERA INDICA* LINN.

V. The Structure and Development of Lenticels in the Mango Fruits

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Introduction

Mangoes have recently received much attention in India and various diseases of the mango fruit are being investigated. The role of fruit lenticels as passages of infecting organisms has been emphasized by several workers (Kidd and Beaumont, 1925; Baker and Heald, 1932 and others) from time to time. The 'black-tip' disease of mango fruit recently reported (Das Gupta and Verma, 1939) seems to be frequent in orchards situated near brick kilns. If the gases emanating from the kilns have any direct effect on the fruits, the role of lenticels as channels of gaseous exchange may not be insignificant. It is for these reasons that the present investigation has been carried out.

The term 'lenticel' was originally adopted by De Candolle for such structures occurring on stems of flowering plants. In structural details the lenticels of fruits and stems differ. The layer of cambium cells invariably present in lenticels of the stem is usually lacking in the mango and other fruits. Nevertheless the same term may be applied in the fruits as a matter of convenience. Clements (1935) has used the term 'lenticel' in the case of pomes of *Pyrus Malus* and has rightly pointed out that the use by some workers of the names like fruit 'spots', 'dots', or 'pits' to denote lenticels of fruits involves a certain amount of confusion. These terms are liable to be misunderstood since the same expressions have often been employed by plant pathologists to indicate symptoms of certain fruit diseases. The pome being morphologically a stem structure the use of the term 'lenticel', in the author's opinion, is still more justified. In the case of true fruits such as mangoes, the essential structure of the lenticels is the same as in pomes of *Pyrus Malus* and therefore in the present paper the term 'lenticel' has been retained and refers to the small spots seen on the skin of healthy mango fruits. Lenticels without the characteristic cambium, designated as 'ventilating pits', have been reported in petioles of members of the Cyatheaceæ and the Marattiaceæ by Haning (ex. Haberlandt, 1914), but for reasons stated above Haning's terminology need not be followed for fruits.

Material and Methods

Three varieties of mango fruits, namely *safeda*, *dasehri* and *bambai*, were selected for study. Fruits in various stages of development starting from the youngest stage to the very mature one were collected from

Begum Bagh and Sikandarbagh orchards, Lucknow, during the months of March, April and May 1941. Epidermal peelings of these fruits were made in order to study the stomatal and lenticel structures in surface view. The peelings were made by treating small pieces of fruits with strong nitric acid and potassium chlorate for 12–24 hours, depending upon the stage of maturity of fruits. The soft part including the entire mesocarp was thus macerated and by shaking the treated pieces in water in a test-tube the epidermal peelings separated neatly from the rest of the tissue. The peelings were then treated with strong ammonia solution, washed in water and mounted in glycerine. Pieces of fruits were also embedded in paraffin and microtomed to help in the study of the structure of mature and developing, as well as open and closed lenticels. The open and closed lenticels were ascertained by the technique followed by Clements (1935) for *Pyrus Malus*. The fresh fruits were dipped in a solution of methyl blue at room temperature (30° C.) and later transferred to a cold chamber at 15° C. for about 24 hours. In so doing the skin of the fruit contracts and the lenticels are subjected to a mild expansion without being ruptured. The coloured solution passes through the open lenticels which show a halo of the dye while the closed lenticels remain uncoloured.

The number of lenticels, closed and open, was ascertained in all the three varieties of fruits by direct counts.

Structure of Lenticels

The lenticels appear as minute specks on the skin of fruits. The spots are of different sizes in the three varieties of mango. They are bigger in *bambai* than in *safeda* and *dasehri*, the last having the smallest spots among the three. The apparent colour of the lenticels ranges from light to dark brown and is often brick red as in *safeda*.

In surface view, as seen in peelings of the epidermis of mature fruits under the microscope, the lenticel region shows an opening of an irregular form surrounded by much divided subsidiary (of stomatal origin) and epidermal cells which radiate from the opening in all directions (Pl. VI, Figs. 1, 2, 3).

In vertical sections the lenticel apertures are seen as breaks in the epidermis (Text-figs. 1, 2 and 3). Below the opening a number of hypodermal cells are loosely packed, the number depending upon the size of the lenticels. These hypodermal cells are filled with a tannin-like substance to which the apparent colour of the lenticels is due. In fruits having larger lenticels the hypodermal cells seem to radiate from the opening. This is due to the pulling force acting on the hypodermal cells during the stretching of the epidermis as the fruit matures and grows in size. Below the hypodermal cells are ordinary parenchymatous cells of the pericarp. Unlike lenticels of stems of angiosperms, the lenticels in mango fruits do not show any sign of development of a cambium under the loosely packed hypodermal cells, and in this respect differ from them. As already stated, it is the absence of this cambium that should evoke difference of opinion as to the validity and correctness of the use of the term 'lenticel' (primarily employed to describe the lenticels of stems of angiosperms) for such structures on fruits.

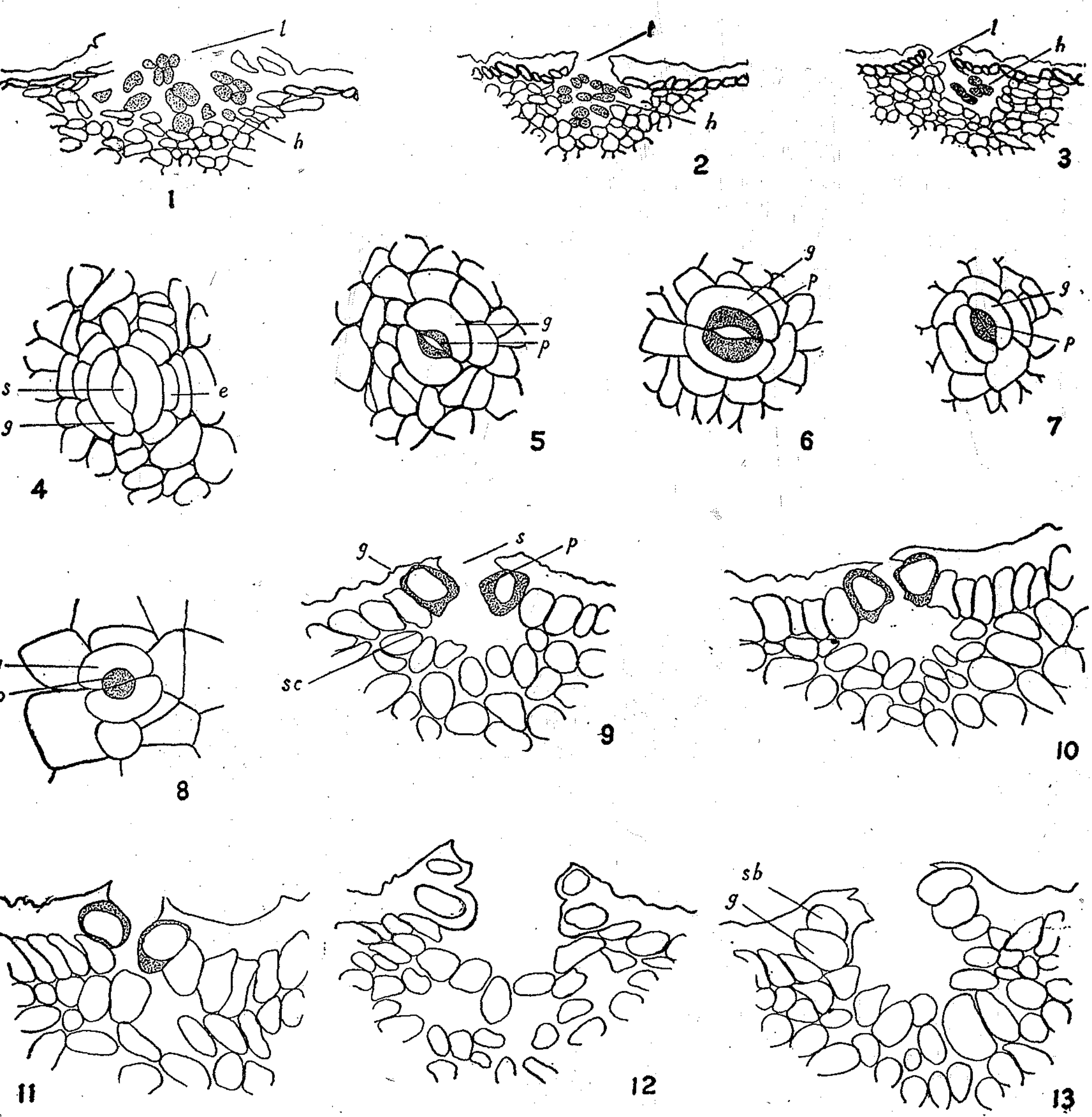
Development of Lenticels

Lenticels which occur invariably on the skin of mature mango fruits are, however, not percievable when the fruits are very young. An examination of the epidermal peelings of fruits of this age reveals that the skin bears a number of stomata, but no lenticels are found.

The stomatal apparatus consists of two large guard cells with a substomatal chamber below and a stomatal pore above (Text-figs. 4–11). The guard cells have their walls thin on the side away from the pore while round the latter the wall is very thick, forming a thickened poral rim. The poral rim is much more clear in surface view when the stomatal pore is closed than when it is open. In the region of the poral rim the guard cells have projecting cuticular ridges which in a section appear as horn-like cuticular projections from the guard cells and partly overarch the stomatal pore (Text-figs. 9–11).

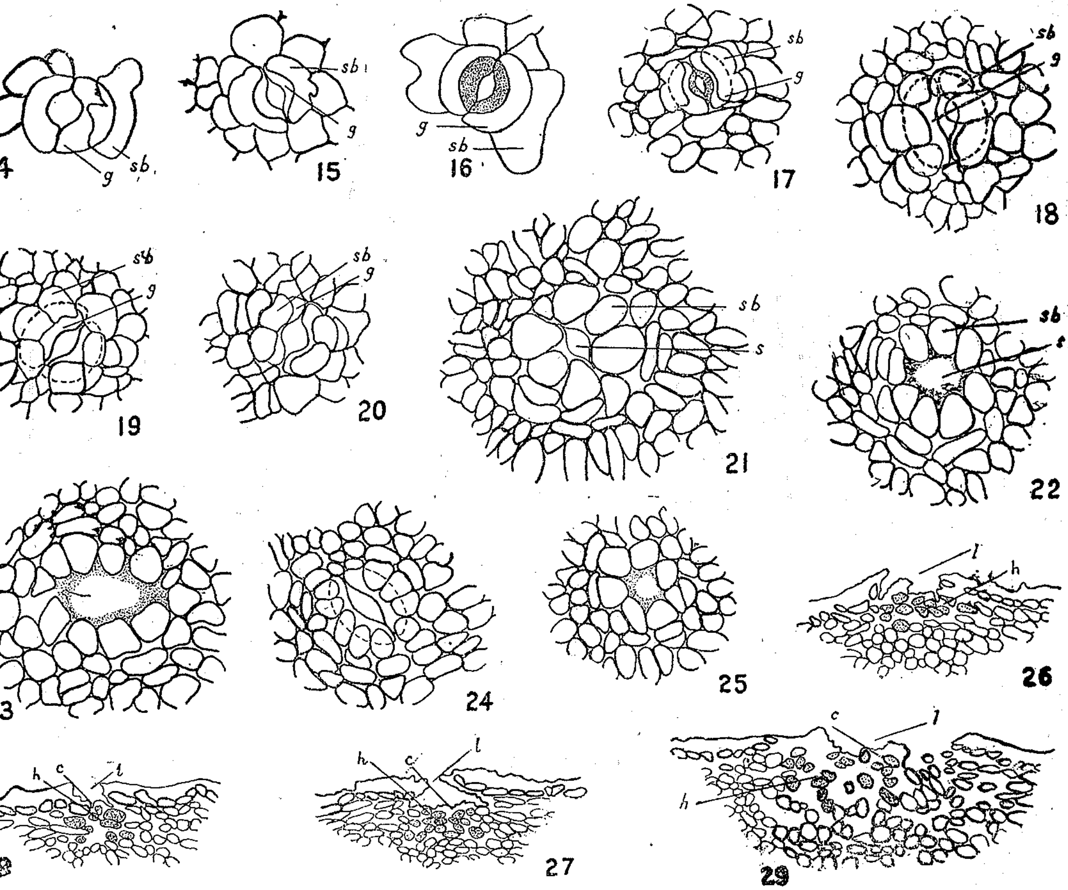
Subsidiary cells which usually accompany guard cells in many angiosperms seem to develop, in the case of mango fruits, after the guard cells are fully distinct. In very young stages of the fruit the guard cells are surrounded by ordinary epidermal cells (Text-figs. 4–8), but later on an enlarged cell appears on the lateral side of each guard cell. Thus on the side of each guard cell appears a lateral subsidiary cell. No polar subsidiary cells have been found to develop in this case. As the fruits grow the lateral subsidiary cells begin to overarch the guard cells (Text-figs. 14–17). Each subsidiary cell then divides transversely into three or sometimes four cells, which further overarch the guard cells (Text-figs. 18–20, and Pl. VI, Figs. 4–6). This type of subsidiary cells has also been reported in some angiosperms (Bandulska, 1924, 1926) and the Benettitales (Florin, 1933). In vertical sections of the stomata at this stage the guard cells are seen to be superposed by the subsidiary cells (Text-figs. 12, 13).

The first step in the development of lenticels is the permanent opening of the guard cells. The lateral subsidiary cells further divide and completely overarch the guard cells leaving only the stomatal pore. In surface view these cells lie round the pore (Text-figs. 21–25). By further division the subsidiary cells merge into the adjoining epidermal cells and in so doing they spread radially from the stomatal pore, probably under the force caused by the stretching of the epidermis as the fruits mature (Pl. VI, Figs. 1–3). Due to the stretching of the epidermis on all sides, the pore is widened and forms the lenticel aperture. At the same time the hypodermal cells below the substomatal chamber undergo change, under the same influence, which creates intercellular spaces among them (Text-figs. 1–3). The hypodermal cells get a deposit of tannin-like substance to which the colour of the lenticels, in surface view, is due. The number of hypodermal cells taking part depends on the size of the lenticels. Thus the least number is involved in *dasehri*, where the lenticels are the smallest, and the largest in *bambai* where the lenticels are the biggest among the three varieties studied. During these changes the guard cells of the stomata remain intact for quite a long time and can be recognised particularly in surface view. The shape and form of the guard cells do not, however, remain the same



Text-Figs. 1–13.—Figs. 1–3. Lenticels in vertical sections. *l*, lenticel aperture; *h*, loosely packed hypodermal cells. 1. *bambai*; 2. *safeda*; 3. *dasehri*. ×94. Figs. 4–8. Stomata in surface view. *s*, stomatal pore; *g*, guard cells; *e*, epidermal cell; *p*, poral rim. 4–5. *bambai*; 6–7. *safeda*; 8. *dasehri*. ×375. Figs. 9–11. Same in vertical sections. *sc*, substomatal chamber. 9. *bambai*; 10. *safeda*; 11. *dasehri*. ×375. Figs. 12–13. Same when guard cells are overarched by subsidiary cells (*sb*). 12. *bambai*; 13. *safeda*. ×375.

when seen in a vertical section. It is to be pointed out here that all the stomata in a fruit do not develop into lenticels. In such cases the guard cells shrivel and the pore becomes permanently closed and as the fruit enlarges they can be seen lying somewhat disorganised among the developing lenticels.



Text-Figs. 14–29.—Figs. 14–25. Stages in development of lenticels from stomata, as seen in surface view. *s*, stomatal pore; *g*, guard cell; *sb*, subsidiary cell. 14, 21, 22. *bambai.* ×375. 17, 18. *bambai.* ×240. 15, 19. *safeda.* ×240. 23. *safeda.* ×375. 16. *dasehri.* ×375. 20, 24, 25. *dasehri.* ×240. Figs. 26–28. Vertical sections of closed lenticels. *l*, lenticel aperture; *h*, hypodermal cells; *c*, cuticle. 26. *bambai;* 27. *safeda;* 28. *dasehri.* ×84. Fig. 29. *bambai.* A partially closed lenticel in vertical section. ×84.

As the fruits grow some of the lenticels become closed, while the rest remain open. Closed and open lenticels were ascertained by the technique followed by Clements (1935) for apples and described above. The closing of the lenticels has been found to occur by the development of a layer of cuticle on the outermost layer of the hypodermal cells. The extent of development of this layer of cuticle determines the complete or partial closure of the lenticels. In fully closed lenticels, the cuticle develops over the whole length of the hypodermal cells (Text-figs. 26–28), while in partly closed ones the cuticle does not cover some of the hypodermal cells (Text-fig. 29). Lenticels, in which the cuticle does not at all cover the hypodermal cells, are regarded as open (Text-figs. 1–3).

Distribution of Lenticels in Mature Fruits

It was thought desirable to note the distribution of lenticels, closed and open, on the surface of the fruits. For this purpose a piece of graph paper divided in square centimeters was spread over the surface of the fruit and by pricking a needle through the paper, the four corners of the squares were marked off on the skin of the fruit. These squares were then completed on the skin of the fruit with ink and direct counts of lenticels in these areas were made under a magnifying lens. Counts were made for the total number of lenticels, both open and closed, per unit area in the basal and apical halves of the fruit, and also for open and closed lenticels separately, in any region of the fruit. The unit area taken was 9 sq. cms. in order to cover sufficient surface. Twelve fruits of each variety were taken and in each fruit different regions of the halves were covered in counting the number of lenticels.

Table showing the number and distribution of lenticels per 9 sq. cms. in mature fruits

Variety of Fruit	Total number of lenticels both open and closed		Number of open lenticels	Number of closed lenticels
	Basal half	Apical half		
safeda ..	190–198	240–248	25–36	160–172
dasehri ..	190–196	260–266	35–40	150–215
bambai ..	70–79	100–120	65–81	7–11

It will be noticed from the above table that the total number of lenticels in *bambai* is the least, while there is no marked difference between *safeda* and *dasehri*. It is also evident that lenticels are more numerous in the apical half of the fruit than in the basal half. In *safeda* and *dasehri* more of the lenticels are closed than open, while the reverse is the case in *bambai*.

Conclusion

It is evident from the foregoing observations that the skin of the mature mango fruit has numerous lenticels which look like tiny spots to the naked eye. In structure, there is a general correspondence with the lenticels found on stems of angiosperms, although there are differences in details. In the first instance, the fruit lenticels are comparatively very small in size, the number of hypodermal cells involved being just a few. The hypodermal cells do not characteristically radiate from the lenticel opening in all cases as is the case with stem lenticels. Another important difference is the absence of the cambium cells below the hypodermal cells in fruit lenticels, while in lenticels of stem the cambium is conspicuously developed (Haberlandt, 1914). It is the absence of this cambium that has led to the discussion on the correctness or otherwise of the use of the term 'lenticel' in the case of fruits.

It has been found that the lenticels in mango fruit develop from stomata as also observed by several other workers (Zschokke, 1897, Tetley, 1930, Clements, 1935) for apples. In the development of the lenticel from the stoma it has been observed that the lateral subsidiary cells of the guard cells play an important role. The subsidiary cells, having divided transversely into several cells, gradually overarch the guard cells leaving only the stomatal pore which is now permanently open. It is the stomatal pore that forms the lenticel aperture which widens up rather irregularly under the stretching force of the enlarging fruit. Under the same influence the subsidiary cells along with the epidermal cells radiate from the pore in all directions, giving the lenticel region a characterstic appearance in surface view. At the same time some of the hypodermal cells below the substomatal chamber get loosely arranged and develop deposits of tannin which gives the brown colour to the lenticel. The overarching of guard cells by subsidiary cells has been observed before in leaves of angiosperms (Bandulska, 1924, 1926) and the Benettitales (Florin, 1933), but has not been reported for fruits so far in author's knowledge. In mature fruits some of the lenticels become closed by the development of cuticle on the outermost layer of hypodermal cells, while others remain open.

A study of the number and distribution of lenticels shows that certain varieties (*safeda* and *dasehri*) have more lenticels per unit area than others (*bambai*), and also that they are more in the apical half of the fruit than in the basal half. As regards the open and the closed lenticels it has been found, that in *safeda* and *dasehri* more of the lenticels are closed than open, while reverse is the case in *bambai*.

Summary

The structure and development of lenticels in mango fruits have been described. The lenticels have been found to develop from stomata which alone are present in young fruits. The stomata become permanently open and the guard cells are gradually overarched by lateral subsidiary cells which divide and merge into the cells of the epidermis. As a result of the stretching, to which the epidermal cells of the enlarging fruit are subjected, the stomatal pore also enlarges, forming the lenticel aperture, from which the subsidiary and the epidermal cells seem to radiate. The hypodermal cells below the stomatal pore also come under the influence of stretching and become loosely arranged in rows radiating from the pore. Their walls become brown. The cambium, a usual feature below the hypodermal cells in stem lenticels, is absent in the lenticels of mango fruits. In the

mature fruit some of the lenticels become fully or partly closed by a complete or partial development of a layer of cuticle over the hypodermal cells.

All the stomata do not develop into lenticels. Lenticels are more numerous in the apical half of the fruit than in the basal half.

ACKNOWLEDGMENT

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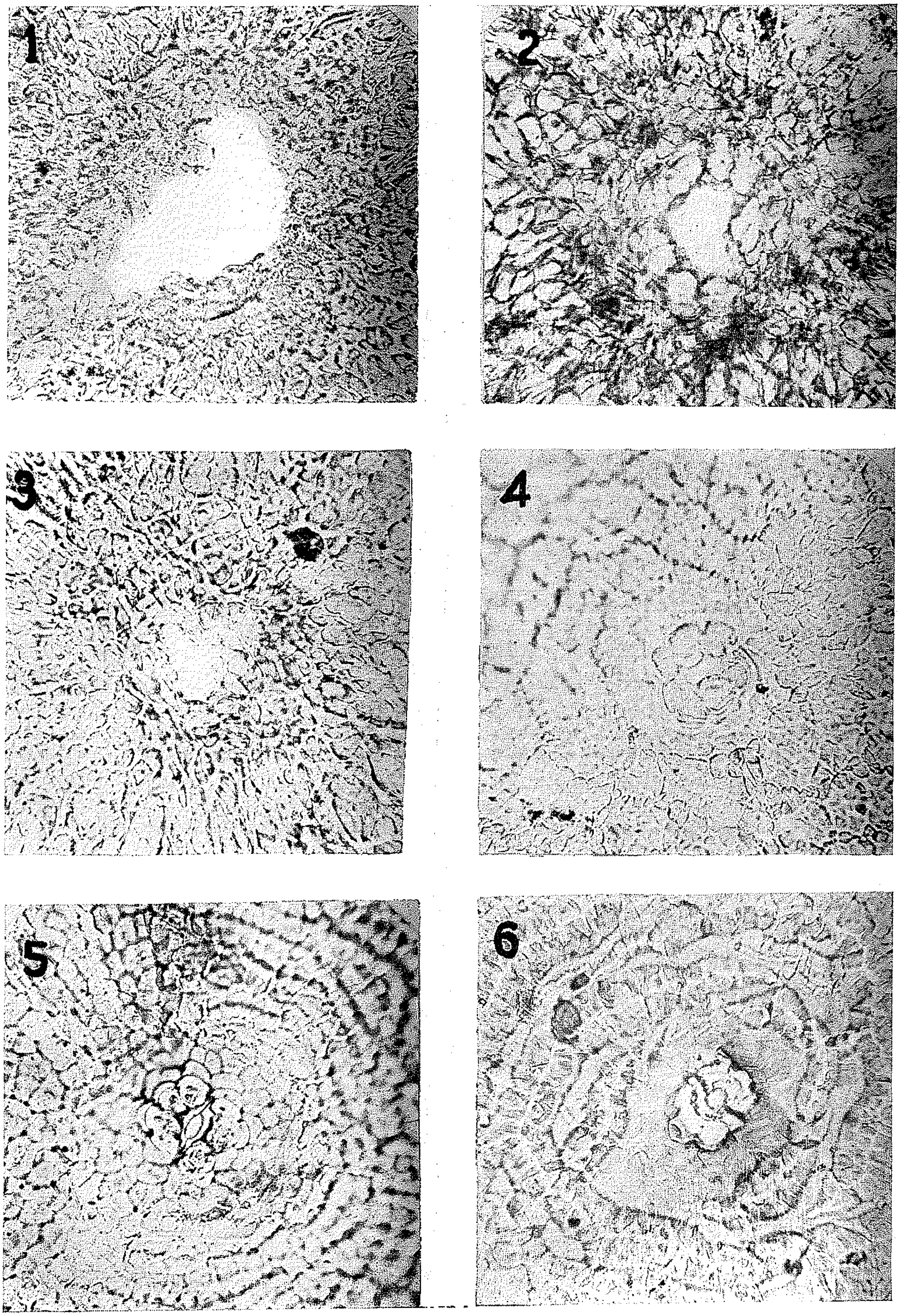
EXPLANATION OF PLATE VI

Figs. 1–3. Lenticels in surface view. (1) *bambai*, (2) *safeda*, (3) *dasehri*. All ×200.

Figs. 4–6. Surface view of stomata overarched by the lateral subsidiary cells. (4) *bambai*, (5) *safeda*, (6) *dasehri*. All ×200.



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