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Ontogeny of Stoma in Plants

Before illustrating the ontogeny of stomatal complex it may be useful to have a precise definition of the following terms which are used in this essay. The definitions are in accordance with **Pant (1965).**

i. Stoma: It includes the pore and two guard cells.

ii. Stomatal complex/stomatal apparatus: It includes a stoma and the adjoining subsidiary cells. It also includes a stoma and the neighbouring epidermal cells when subsidiary cells are not distinguishable.

iii. Stomatal meristemoid: It refers a protoderm cell whose first or consecutive divisions lead to the formation of guard cells of a stoma. Marginal meristems produce marginal initials that in turn form the abaxial and adaxial leaf epidermal layers. The marginal initials undergo anticlinal divisions and subdivisions. The derivative cells form protoderm cells. Some specialized protodermal cells transform into stomatal meristemoid.

iv. Meristemoid: It refers the cells that are the derivatives of stomatal meristemoid and retain the capacity for further divisions.

v. Guard cell initial/guard cell mother cell (gcmc): It refers a meristemoid whose bisection results in the formation of two sister guard cells'.

vi. Mesogene: It refers to the subsidiary cells that have a common origin with guard cells, that is, the subsidiary cells and the two guard cells are the derivative cells of same meristemoid.

vii. Perigene: It refers to the subsidiary cells that have a different origin from guard cells. The cells that form subsidiary cells occur around the meristemoid that forms guard cells.

Stomatal meristemoid, by several divisions, forms a stoma. The meristemoid is usually isodiametric or polygonal in shape and possesses a single conspicuous nucleus with denser cytoplasm. Usually the stomatal meristemoids are initiated between the mature stomata (e.g. gymnosperms and angiosperms).

Sometimes their origin is acropetal (e.g. stem of Psilotum); basipetal origin is observed in Lycopodiales, Convolvulaceae, Rubiaceae etc. while simultaneous differentiation is observed in Erythrina, a member of Leguminosae. The differentiation of a stomatal meristemoid and its subsequent divisions leading to the formation of a stoma vary from group of plants.

The classifications proposed by Metcalfe and Chalk and Stebbins and Khush take no account of the ontogeny of stomata. It is now evident that mature stomatal pattern does not reveal the ontogenetic relationship between guard cells and subsidiary cells. Subsidiary cells may be perigene, mesogene or may be mesogene and perigene in a stomatal complex. Accordingly a new classification is proposed by Pant based on the ontogenetic relationship of subsidiary cells and guard cells.

Pant classified stomata into following types:

(I) Mesogenous: A stomatal complex is said to be mesogenous where all subsidiary cells or a single ring-like subsidiary cell have a common origin with the guard cells, that is, the same meristemoid gives rise to subsidiary cells and guard cells.

Pant recognizes the following four subtypes in mesogenous:

(a) Tetralabrate: The meristemoid is more or less rectangular in shape and has four cutting faces. The four sides of meristemoid cut off four mesogene subsidiary cells in a spiral sequence depicted in diagram as 1-1, 2-2, 3-3 and 4-4. All cells enclose a central guard cell initial. The initial divides and forms two guard cells.Example: Lactucaviscosa

(b) Trilabrate (= cruciferous): The meristemoid has three cutting faces. Each side divides by anticlinal division in a spiral sequence that is depicted in diagram in numericals. All cells enclose a central guard cell initial that divides to form two guard cells. Example: Beta vulgaris, Sedum spurium and Daturastramonium etc.

(c) Dolabrate: The meristemoid has two parallel cutting faces. It is of three types:

i. Mesoparacytic (= rubiaceous): The meristemoid divides by two successive parallel divisions and the resulting cells enclose the central guard cell mother cell (gcmc). The gcmc divides to form a pair of guard cells by a wall that is parallel to the wall formed earlier. Example: Ricinuscommunis, Phaseolus vulgaris etc.

ii. Mesodiacytic: The meristemoid divides by two successive parallel divisions and the resulting cells enclose the gcme. The gcmc divides to form a pair of guard cells by a wall that is at right angles to earlier division. Example: Ocimumbasilicum an Asteracanthalongifolia.

iii. Pyrrosia type: The stomatal meristemoid divides to form two cells by anticlinal wall. One of the two cells forms a single encircling mesogene cell. The other cell divides by a curved periclinal wall. Two cells thus formed, one is 'planoconcavemesogene subsidiary cell which appears annular in surface view'. Example: Pyrrosia lingua.

The other is gcmc and it is hemispherical and dome shaped. The gcmc remains attached to the outer periclinal wall by its flat outer side. The gcmc divides to form a pair of guard cells by a wall that is at right angles to the wall that formed first in the meristemoid.

(d) Unilabrate: The meristemoid divides by a curved periclinal wall to form a subsidiary cell that encloses a dome shaped gcmc. The subsidiary cell is annular as observed in surface view. It is to note that there occurs no anticlinal division in unilabrate type. The gcmc divides to form a pair of guard cells by a wall that is at right angles to the wall that formed first in the meristemoid. Example: Anemia and Schizaea.

(II) Perigenous:

A stomatal complex is said to be perigenous where the subsidiary cells and guard cells do not have a common origin. The subsidiary cells originate from cells that lie around the

meristemoid. Meristemoid divides symmetrically to form two daughter guard cells (Fig. 12.16G). Example: Psilotum, Selaginella, Isoetes, Ginkgo, Cucurbitaceae, Nymphaeaceae and Lemnaceae etc.

(III) Mesoperigenous:

A stomatal complex is said to be mesoperigenous where one stomatal meristemoid gives rise to one mesogene subsidiary cell and gcmc that divides symmetrically resulting two daughter guard cells. The rest of subsidiary cells are perigene and originate from cells lying around the meristemoid.

i. Plagiogyria type: The meristemoid divides by anticlinal division into a large cell and small cell. The partition wall is curved. The smaller cell is gcmc. Gcmc divides to form a pair of guard cells by a wall that is perpendicular to the first division of meristemoid. A single mesogene subsidiary cell girdles the three sides of the stoma. Perigene subsidiary cell occurs on the fourth side of stoma. Ex. Plagiogyria japonica.

ii. Tetracentron type: The meristemoid divides by anticlinal wall into two cells among which one is gcmc. Gcmc divides to form a pair of guard cells by a wall that is parallel to the wall formed in the first division of meristemoid.Example: Tetracentronsinensis and Trochodendronaralioides.

iii. Ranunculus type: The meristemoid divides to form two daughter cells among which one is the gcmc. Gcmc divides to form a pair of guard cells. The partition wall in gcmc has no relation to the first wall of meristemoid. The wall may be at any angle other than perpendicular and parallel.Example: Ranunculus, Delphinium and Nigella.

Florin (1933) proposed the following two stomatal patterns based on origin:

(a) Haplocheilic: In haplocheilic stoma two guard cells originate from a common meristemoid. The meristemoid functions directly as guard mother cell (GMC). There occurs no division in the meristemoid before its transformation to GMC. GMC and guard cells influence the neighbouring protodermal cells to divide and form subsidiary cells. So in this type of stomatal complex the subsidiary cells are perigene. Ex. Ephedra. Haplocheilic stoma is similar to perigenous stoma of Pant.

(b) Syndetocheilic: In syndetocheilic stoma the stomatal meristemoid undergoes a number of divisions resulting in the formation of GMC and subsidiary cells that adjoin the guard cells. So in this type of stomatal complex the subsidiary cells are mesogene. Ex. Welwitschia. Syndetocheilic stoma is similar to mesogenous stoma of Pant.

Florin and Pant recognized perigenous stomata as distinct type. But Payne (1979) regards that there exists no perigenous stoma. It is evident that a protodermal cell undergoes either equal or unequal division to form daughter cells. In equal division the number of protodermal cells increases. A protodermal cell when undergoes unequal division, is destined to form meristemoid.

This finds support due to the fact that unequal cells resulted from unequal division exhibit differential staining. There occurs no truly perigenous stoma in which a protodermal cell directly serves as GMC. In this sense a stoma is either mesogenous or mesoperigenous.

Payne proposed the following classification of stomata based on 'the manner of production and division of the GMC:

i. Diameristic:

A stoma is said to be diameristic where GMC divides with a wall formed at right angles relative to the wall that cuts it off from its meristemoid. Meristemoid divides repeatedly resulting two or more subsidiary cells which are parallel to each other

They enclose a central GMC. GMC divides to form two guard cells and the cell wall is formed at right angle to long axes of subsidiary cells. At maturity the stomatal complex consists of a pair of guard cells and a pair of subsidiary cells, the long axes of which are at right angles to each other. . Example: mesogenous stoma of Lamiaceae and mesoperigenous stomata of monocots and Caryophyllaceae.

ii. Parameristic:

A stoma is said to be parameristic where GMC divides with a wall parallel to the wall that cuts it off from its meristemoid. Meristemoid divides thus forming two cells. One of the daughter cells becomes the first lateral subsidiary cell.

The other daughter cell again divides in such a way that the resulting cell wall curves to meet both ends of the cell wall that is formed in the first division. Among the two cells thus formed one becomes the second lateral subsidiary cell.

These two divisions enclose GMC. GMC divides parallel to the long axes of subsidiary cells. Thus a mature stoma exhibits a pair of guard cells enclosed by a pair of lateral subsidiary cells. The long axes of guard cells and subsidiary cells are parallel to each other. Example: mesogenous stoma of Rubiaceae and mesoperigenous stoma of Liriodendron.

iii. Anomomeristic:

A stoma is said to be anomomeristic where GMC divides with a wall formed at any angle relative to the wall that cuts it off from its meristemoid. Meristemoid divides to form GMC. GMC in turn divides to form a pair of guard cells the partition wall of which has no definite orientation in relation to the wall that formed GMC. Example: mesoperigenous stoma of Ranunculus.

Florin's work(on the investigation of the development of leaves in gymnosperm**) revealed two types of development:**

(1) Perigenous and the adult appearance of stoma is termed as haplocheilic, and

(2) Mesogenous and the adult appearance is termed as syndetocheilic.

Later in 1965 and onwards, Pant, followed by other workers, revised ontogenetic terminology. Pant did not subdivide the perigenous group.

Mesogenous group is subdivided into four subgroups and mesoperigenous group is subdivided into three types in Pant's classification. Later van Cotthem followed by other workers, reviewed the whole subject thoroughly and proposed additional terminology.

They subdivided the perigenous group. The study of stomatal ontogeny gained much prominence due to the fact that mature stomata which appear alike may have different developmental pathway. This aspect is to be considered while assessing the phylogenetic position of a species based on stoma.