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Ontogeny of the Anomocytic stoma—variations and modifications

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Abstract. Recent studies on the ontogeny of stomata in a number of plants have shown that the anomocytic stoma is not always perigenous or haplocheilic in origin as was previously believed but may be formed in a variety of ways. These are classified and reviewed in the present paper. The need to investigate ontogeny of this type of stoma in more plant groups is emphasized.

Keywords. Anomocytic; stoma; development.

1. Introduction

It is generally believed that the topography of the cells surrounding the guard cells is indicative of their mode of development. Metcalfe and Chalk (1950) have described the Anomocytic or irregular-celled type of stoma as one surrounded by a limited number of cells that are indistinguishable in size, shape or form from those of the remainder of the epidermis. Earlier Vesque (1889) named such stomata as " Ranunculaceous ", and cited the family Ranunculaceae as a typical example.

Prantl (1872) was perhaps the first to recognise two main ontogenetic types of stomata, the direct and the indirect types. In the direct type, the stomatal initial underwent only two divisions, cutting off a mesogene neighbouring cell during the first division and the two guard cells during the second division. In the indirect type, the initial divides three or more times to give rise to more than one mesogene neighbouring cells before forming the guard cells. A similar classification was suggested by Florin (1933) but he took into account the adult form of the stomata as well. However, his studies were based solely on gymnosperms. Of the two types (Florin 1933), in the haplocheilic type, the stomatal meristemoid divides once giving rise to the guard cells. The neighbouring cells are derived independently from the protoderm and are like ordinary epidermal cells. Thus the haplocheilic type of Florin corresponded to the anomocytic type of Metcalfe and Chalk topographically, and it came to be believed that all anomocytic stomata develop in the haplocheilic manner. A detailed investigation of the development of stomata in the Ranunculaceae itself (Auer 1952; Pant and Mehra 1964c) brought to light the fact that in this family the stomatal meristemoid first gives rise to a mesogenous neighbouring cell before forming the two guard cells.

Thus in the Ranunculaceae, the surrounding cells are not all perigenous in origin (as in the haplocheilic type) but one of them is mesogenous and the others are perigenous in origin. This type corresponds to the direct type of Prantl (1872) and has been called the mesoperigenous type by Pant and Mehra (1964c).

Other recent studies (see Fryns-Claessens and Van Cotthem 1973), have shown that the mature stomatal complex commonly known as the anomocytic type is not necessarily perigenous or haplocheilic in origin but may be the end product of several different types of ontogenetic pathways. Fryns-Claessens and Van-Cotthem (1973) recognised in the anomocytic stomata the perigenous and meso-perigenous modes of development but did not consider that this type of stoma may even be formed mesogenously. However, they have mentioned the development of cyclocytic stomata where 3 or 4 parallel subsidiaries are formed at first in the mesogenous manner. In these "radial, tangential and oblique divisions occur before, after or simultaneously with the formation of the guard cells "to form cyclocytic stomata surrounded by rings of subsidiary cells. In the present study not only cyclocytic but anomocytic stomata were also found to develop by such divisions.

A survey of recent literature has brought to light at least seven different ontogenetic types (and some sub types) giving rise to the anomocytic stoma. These are classified and reviewed hereunder (figure 1).

2. Ontogenetic types of anomocytic stomata

2.1. *Perigenous*

Here a protoderm cell becomes directly converted into the guard cell mother cell and divides only once to form the two guard cells (figure 1·1). The neighbouring cells are formed from cells which lie around the guard cells, either with or without divisions in them. *e.g.* conifers and cycads (Florin 1931, 1933); *Psilotum nudum* (Pant and Mehra 1963), *Ginkgo* and *Cycas* (Pant and Mehra 1964a), *Ephedra* (Pant and Mehra 1964b), *Lycopodium, Selaginella* and *Isoetes* (Pant and Mehra 1964d), *Pistia* and the Lemnaceae (Pant and Kidwai 1966a), Celastraceae (Pant and Kidwai 1966b), (Den Hartog and Baas 1978), *Nelumbo nucifera* (Gupta *et al* 1968), *Nymphoides* (Pant and Kidwai 1969), *Ophioglossaceae* (Pant and Khare 1969; Inamdar 1970), *Tmesipteris tannensis* (Pant and Khare 1971), *Clerodendrum phlomidis* (Kannabiran 1974); some rare early stomata in *Abrus precatorius* L. (Kannabiran 1975b), *Nepenthes* (Pant and Bhatnagar 1977), stomata in the outer epidermis of ovary wall in *Zornia* (Kannabiran 1975a) and *Azadirachta indica* (my unpublished observations). Fryns—Classens and Van Cotthem (1973) have designated this type as "Aperigenous".

2.2. *Mesoperigenous*

Here the neighbouring cells of the stomata have a dual origin, some being derived from the stomatal meristemoid and the others independently. In this type also there may or may not be further divisions in the neighbouring cells. Two types are distinguishable :—

A. With one division (Direct type of Prantl 1872; Unilabrate type of Ramayya and Rao 1968)—Here the stomatal meristemoid undergoes one division to form

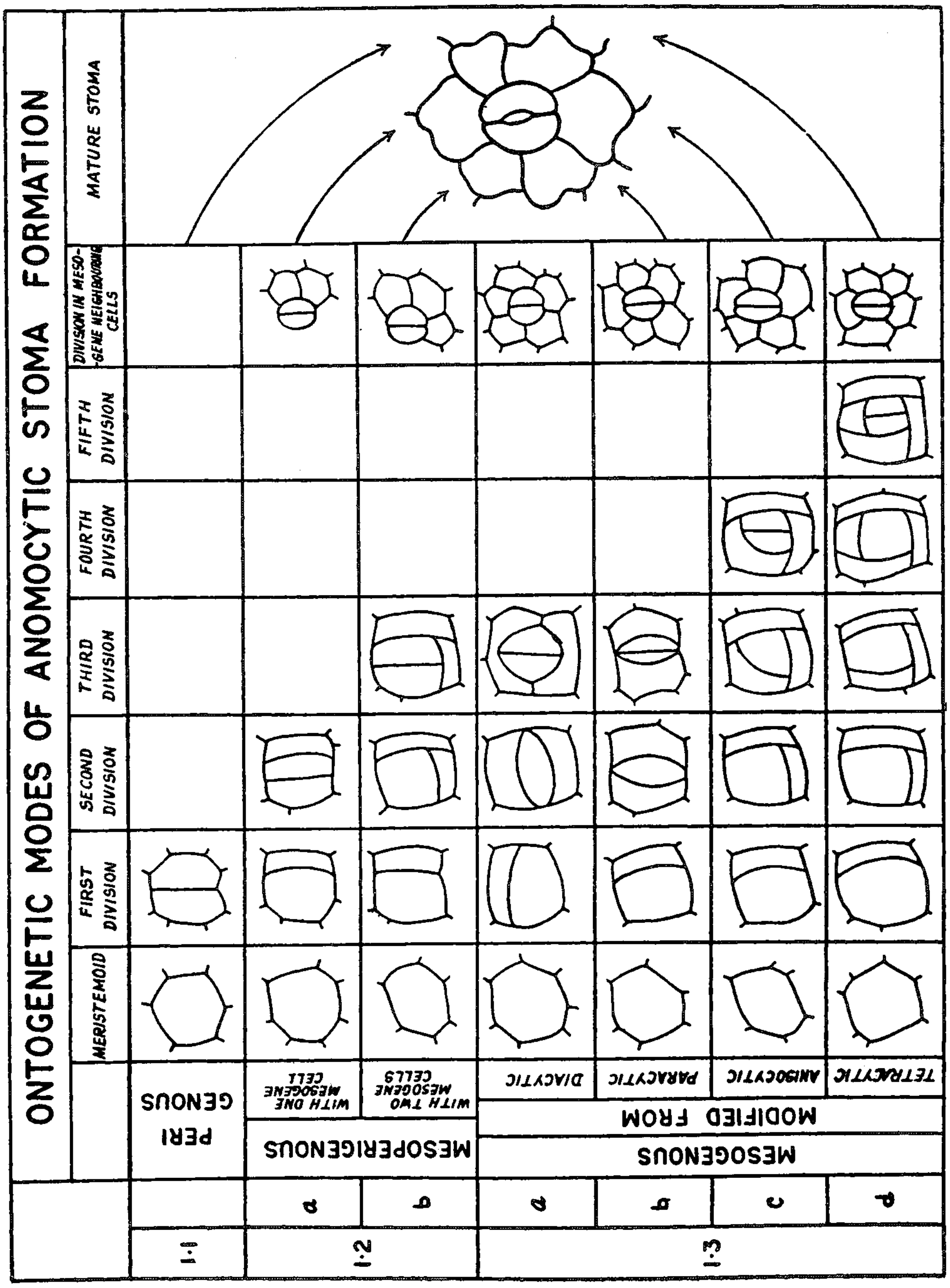

Figure 1. (*See caption in p. 252*)

one mesogene cell and then gets converted into the guard cells mother cell (figure 1.2a). Three subtypes can be distinguished although they may occur side by side on the same organ. Examples are only from taxa where they are predominant.

(a) Where the division in the guard cell mother cell is parallel to the first division (*Tetracentron* type of Pant 1965) e.g. *Tetracentron sinensis* and *Trochodendron aralioides* (Bondeson 1952); *Papaverceae* (Kidwai 1972).

(b) Where the second division is at right angles to the previously formed mesogene cell (*Plagiogyra* type of Pant 1965; Eupolo-meso-perigenous type of Fryns-Claessens and Van Cotthem 1973). e.g. many ferns (Kondo and Toda 1956), Cucurbitaceae (Pant and Banerjee 1965a) Caryophyllaceae (Pant and Kidwai 1968) and some stomata of *Anagallis arvensis* (Verma 1972).

(c) Where the second division is at angles other than 90° or 180°. Obviously this type is intermediate between type (a) and (b) (*Ranunculus* type of Pant 1965) e.g. *Ranunculus*, *Nigella* and *Delphinium* (Pant and Mehra 1964c), Onagraceae (Kidwai 1965), some stomata of *Anagalis arvensis* (Verma 1972) and some Vitaceae (my unpublished observations).

B. With two divisions (Dolabrate type of Ramayya and Rao 1968)—Here the stomatal meristemoid undergoes two divisions and forms two mesogene cells before forming the guard cells (figure 1.2b). The two mesogene cells are usually arranged in a 'L' shaped manner, i.e. at right angles to each other (called 'T' shaped arrangement by earlier authors). Clearly this is a type intermediate between the direct and indirect types of Prantl (1872) e.g. *Piper betle* (Pant and Banerjee 1965b), *Cucumis pubescens* and *Tagetes patula* (Ramayya and Rao 1968), *Gentiana* sp (Pant and Kidwai 1969), *Angiopteris evecta* (Pant and Khare 1969), *Lactuca sativa* (Pant and Kidwai 1972), *Marcgravia* (Fryns-Claessens and Van Cotthem 1973) and some stomata of *Leea* (my unpublished observations). In *Marcgravia*, as the four subsidiaries are orientated in a cross position to the pore, the authors have designated the stomata as "stauro-mesoperigenous". As in the unilabrate type, Ramayya and Rao (1968) have distinguished in this category three subtypes depending on the angle of division of the guard cell mother cell in relation to the second division of the meristemoid. (a) Parallel, (b) at right angles, (c) at other angles. As this type of development has been described from very few plants and all three subtypes are found mixed on the same surface of the leaves or other organs it is not possible to give separate examples for each subtype. Clearly more work needs to be done on this category of the anomocytic stoma.

2.3. *Mesogenous*

When all the cells surrounding the guard cells are formed from the same mother cell as the guard cells, usually by divisions taking place secondarily in the stomata which are originally formed from a dolabrate, trilabrate or tetralabrate initial. Four categories are distinguished. The terms diacytic, paracytic, anisocytic and tetracytic, though generally used for mature stomatal complexes are here used to describe transitory stages during ontogeny, merely to illustrate the topography of the various type during development.

(i) Modified from Diacytic type—When the young mesogene cells are formed in a diacytic manner i.e. at right angles to the two guard cells (figure 1.3a) and subsequently get modified by subdivisions to the anomocytic type e.g. some stomata in Verbenaceae (Pant and Kidwai 1964; Inamdar 1969), stomata on stems and peduncles of *Ocimum* sp. (Ramayya and Rao 1969).

(ii) Modified from paracytic type—The two young mesogene subsidiary cells are formed parallel to the guard cells (figure 1·3b). Later they divide and the stoma becomes anomocytic e.g. some stomata in Magnoliaceae (Pant and Gupta 1966), Oleaceae (Inamdar 1968), Amaryllidaceae (Shah and Gopal 1970), *Strychnos*, *Santalum* and *Dalbergia* (my unpublished observations).

(iii) *Modified from anisocytic type*—Here three surrounding cells are formed from a trilabrate initial (figure 1·3c) before the meristemoid forms the guard cells. At a later stage some or all of the neighbouring cells divide by anticlinal walls so that the stoma becomes surrounded by 4 to 6 or 7 subsidiary cells, indistinguishable from the other epidermal cells, e.g. some stomata of *Notonia grandiflora* (Pant and Verma 1963) *Peperomia pellucida* and *Piper betle* (Pant and Banerjee 1965b), *Crotalaria* (Shah and Gopal 1969) some Cruciferae (Pant and Kidwai 1967), *Canscora*, *Enicostema* and *Hoppea* (Pant and Kidwai 1969), Amaryllidaceae (Shah and Gopal 1970), *Bombax ceiba* (Kidwai 1974) and some stomata in *Leea* (my unpublished observations).

(iv) *Modified from tetracytic type*—When some of the four mesogene cells, formed from a tetralabrate initial (figure 1·3d) and surrounding the guard cells divide and give rise to an anomocytic stoma e.g. some stomata of Amaryllidaceae (Shah and Gopal 1970) and *Bombax ceiba* (Kidwai 1974).

3. Discussion

Developmental studies of different types of stomata in diverse plants have clearly shown that the form and arrangement of the subsidiary cells around the guard cells may not always indicate their actual mode of development. Among all the stomatal types, the anomocytic stomatal complex is perhaps the most interesting as it may be formed in one of at least seven ways (with several subtypes) which may be classified into the three broad categories of Pant (1965) viz. the perigenous, mesoperigenous and mesogenous types. Fryns-Classens and Van Cotthem (1973) have distinguished only the perigenous and mesoperigenous ontogenies for the anomocytic stoma though they have suggested the possibility of finding "other examples in the future".

The different modes of development ultimately resulting in the anomocytic type of stoma in the mature condition are closely related and depend on the number of asymmetric divisions a meristemoid undergoes before giving rise to the guard cell mother cell (figure 1). In the Onagraceae the stomata develop in the mesoperigenous unilabrate manner (Kidwai 1965), but in *Trapa*, the second division which partitions the guard cell mother cell is deferred till the mesogene cell becomes indistinguishable, and the development thus verges on the perigenous type. Fryns-Claessens and Van Cotthem (1973), suggest that such stomata are transitional between the aperigenous and the anomo-mesoperigenous types.

In a single family, Gentianaceae (Pant and Kidwai 1969), anomocytic stomata develop in three or four different ways viz. perigenous, mesoperigenous unilabrate mesoperigenous dolabrate and mesogenous trilabrate.

Metcalfe and Chalk (1950) have listed a number of families in which this type of stoma is predominant but their ontogeny is not known. Clearly there is need for developmental studies of stomata in plants showing the anomocytic type as by merely studying the mature epidermis, erroneous conclusions are likely to be drawn regarding their development, as Tomlinson (1974) has pointed out in the case of monocotyledons. According to Hallier (1905, 1912), the primitive type of stomatal apparatus in flowering plants is devoid of subsidiary cells (i.e. the anomocytic type in present day terminology). The question will naturally arise as to which developmental type of anomocytic stoma is primitive and which more advanced. With further work on the ontogeny in taxa showing this type of stoma, the question will perhaps be answered.

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Figure 1. Diagrammatic representation of the different ontogenetic modes of anomocytic stoma formation. The terms diacytic, paracytic, anisocytic and tetracytic, though generally used for mature stomata are here used to describe transitory stages during ontogeny, merely to illustrate their topography during development. 1·1 Perigenous; 1·2 Mesoperigenous (a) Unilabrate, (b) dolabrate. 1·3 Mesogenous (a) modified from diacytic, (b) modified from paracytic, (c) modified from anisocytic, (d) modified from tetracytic.