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STOMATOGENESIS IN GLEICHENIA GIGANTEA, DICRANOPTERIS LINEARIS VAR. MONTANA AND D. SPLENDIDA (GLEICHENIACEAE)

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SUMMARY

This is the first ever study of the development of stomata in *Gleichenia gigantea* Wallich ex Hook. (subg. *Diplopterygium*), *Dicranopteris linearis* (Burm. f.) Underw. var. *montana* Holttum and *D. splendida* (Hand.-Mazz.) Tagawa in detail. In these ferns, as in many polypodioid members, the polocytic stomata far outnumber the mesoperigenous anomocytic type.

INTRODUCTION

There are three reasons that have prompted us to undertake a reinvestigation into the structure of stomata in the gleichenioid ferns. These are: firstly, the desire to resolve the controversy about the structure of mature stomata in these plants; secondly, to ascertain the pathway of development of stomata in them; and thirdly, to reassess the interrelationship between the Gleicheniaceae and the Polypodiaceae on the basis of stomatogenesis.

Kondo (1962) reported the occurrence of polocytic (his 2A type) stomata in the Gleicheniaceae, while Van Cotthem (1970) observed diacytic and anomocytic stomata in them. Jarrett (1980), who presumably was unaware of the differences between their observations, rejected the affinities between the Gleicheniaceae and Polypodiaceae, on the basis of Van Cotthem's (l.c.) data on stomata, and few other properties.

MATERIAL AND METHODS

Material of *Gleichenia gigantea* (US-D14/70), *Dicranopteris linearis* var. *montana* (US-D40/78) and *D. splendida* (US-T80/78) was collected from Darjeeling. Small pieces of lamina at various stages of development were fixed in a mixture of absolute alcohol and glacial acetic acid (3 : 1) and stored in 70% alcohol. Temporary aceto-carmine mounts of epidermal peels were made. Epidermal peels stained with Sudan IV in 70% alcohol were also examined. Illustrations were made with the aid of a POM (India) drawing apparatus. Herbarium specimens of the three species (bearing the numbers mentioned against them) are deposited at the Pteridology Herbarium, Department of Botany, Kalyani University. The terminology adopted by Sen & Hennipman (1981) is adopted here. The taxonomy is in accordance with Holttum (1959).

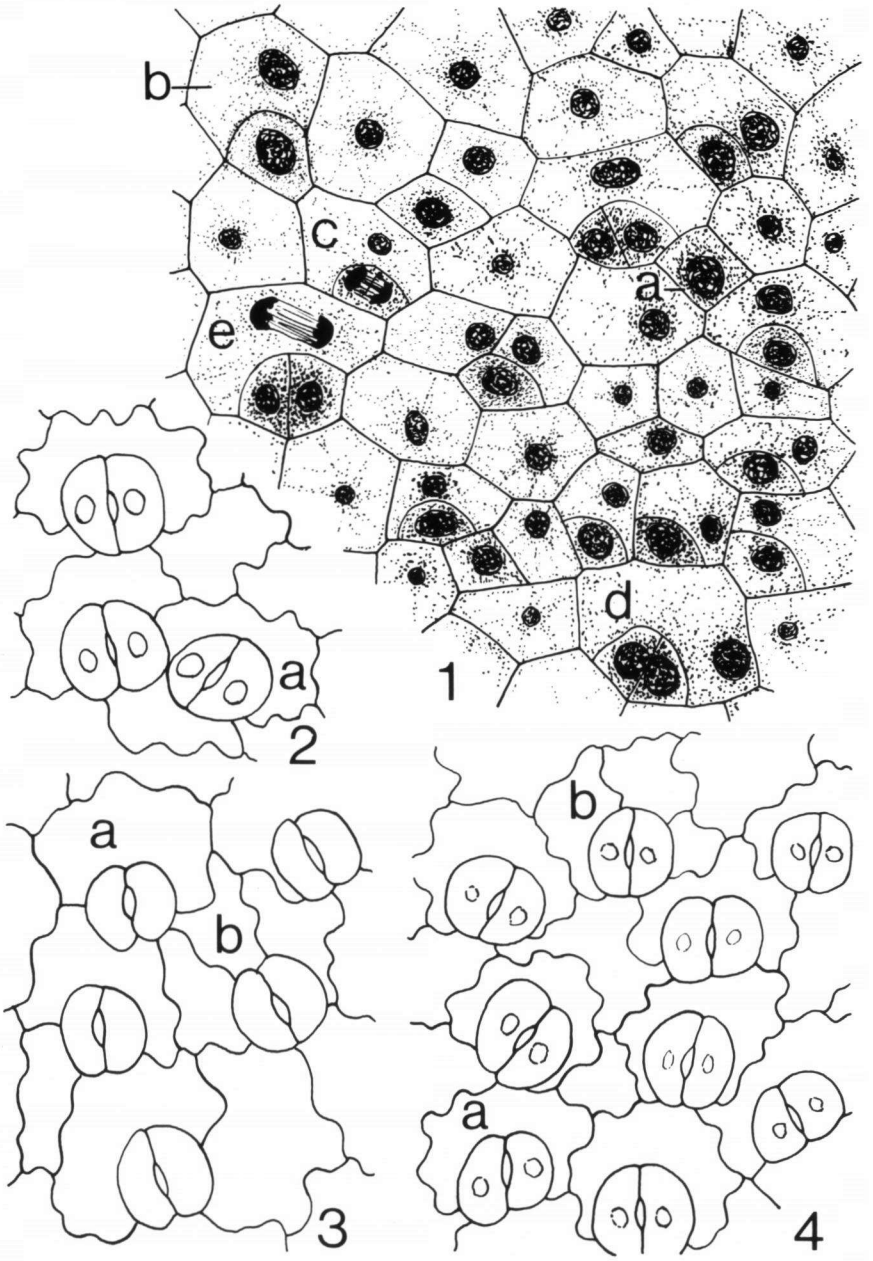

Fig. 1–4. Stomatogenesis and stomata in Gleicheniaceae. – 1. *Dicranopteris linearis* var. *montana*. Polocytic and mesoperigenous anomocytic stomata in stages of development; × 800. – 2. *Gleichenia gigantea*. Mature stomata; × 250. – 3. *Dicranopteris splendida*. Mature stomata; × 250. – 4. *Dicranopteris linearis* var. *montana*. Mature stomata; × 250.

OBSERVATIONS

In all the species studied the stomata occur only on the abaxial surface of the frond. The guard cells with their long axis lying almost parallel to the veins, are in the same level with the epidermis. The stomatal meristemoids are almost isodiametric to polygonal and uninucleate (fig. 1, a). They are distinguishable from the neighbouring protoderm cells by their smaller size, denser cytoplasm and conspicuous nucleus. The meristemoids appear in succession during a considerable period of growth of the frond. In *Dicranopteris splendida* occasionally, however, in certain regions of the lamina they may appear simultaneously and form a contiguous group of stomata without having any ordinary epidermal cell between them. A stomatal meristemoid undergoes an anticlinal division by a curved wall and forms two unequal cells (fig. 1, b). The smaller daughter cell with its dense staining cytoplasm end prominent nucleus acts as a guard-cell mother cell, and is nearer to the distal end of the frond. It soon undergoes division by a wall at right angles to the wall of the first division of the meristemoid, and forms a pair of guard cells, which through differential expansion gradually acquire characteristic shapes (fig. 1, c, d & e). Meanwhile the intercellular substance between the guard cells swells, and the guard cells separate from one another in their median parts forming a stomatal pore (figs. 2, 3 & 4). The larger daughter cell formed by the subdivision of the stomatal meristemoid acts as the initial of the subsidiary cell (fig. 1, b). In most cases this initial cell enlarges and directly becomes a subsidiary cell (figs. 2, a; 3, a; 4, a). It surrounds the proximal end of the guard cell and forms a polocytic stoma. Occasionally, however, the initial of the subsidiary cell instead of directly enlarging as a subsidiary cell undergoes one or more anticlinal divisions to produce two or more subsidiary cells (fig. 1, e). Following such division or divisions, the newly formed daughter cells adjust themselves in such a way that it becomes no longer possible to ascertain their polocytic nature in the mature state (figs. 3, b; 4, b). The two or more enlarging subsidiary cells at the proximal end of the guard cells resemble the other epidermal cells in morphological appearance and the stomata become anomocytic (figs. 3, b; 4, b). In these three taxa, therefore, the stomata are mesoperigenous in origin: the surrounding cell (in case of polocytic type) or cells (in case of anomocytic form) adjacent to the proximal pole of the guard cells are ontogenetically related to the guard-cell mother cell, but those adjacent to the distal pole are in no way related to the stomatal meristemoid.

In the fully grown frond of all the species, the polocytic stomata far outnumber the mesoperigenous anomocytic type. In no taxon the occurrence of a diacytic stoma (pair of guard cells enclosed by a pair of subsidiary cells whose common wall is at right angles to the guard cells) could be confirmed. In *Dicranopteris splendida* only occasionally a mature stoma gave a deceptive look of a diacytic stoma due to differential adjustment of the epidermal cells. Another interesting feature is that sometimes twin stomata occur in *Gleichenia gigantea* (fig. 2).

DISCUSSION

In the mature fronds of the gleichenioid ferns, it has already been noted elsewhere that the polocytic stomata far outnumber the mesoperigenous anomocytic type. But these types of stomata follow the same sequence of development. The only difference in them is that in the anomocytic type the initial of the subsidiary cell undergoes one or more divisions and that the newly formed daughter cells are not distinct from other epidermal cells in morphological aspects. The anomocytic type of stomata occurring in the gleichenioids should not be equated with the anomocytic type occurring in the lycopods, *Ophioglossum* and its allies, since the anomocytic type of stomata in these plants are ontogenetically different. Here the surrounding cells of the pair of guard cells are not ontogenetically related to the guard-cell mother cell, i.e., they are perigenous in origin (= haplocheilic).

The recent work of Sen and Hennipman (1981) has shown that some polypodioid taxa (e.g. *Polypodium amamianum, P. polypodioides, Sellignea feei, Crypsinus ebenipes, Drynaria parishii* and *Microgramma heterophylla*) are characterized by polocytic and mesoperigenous anomocytic stomata. It is, therefore, not possible to distinguish these polypodioid ferns from the gleichenias on the basis of stomatal structure or stomatogenesis. A large number of the polypodioid species develop copolocytic stomata in addition to the polocytic and anomocytic stomata. Interestingly the copolocytic stomata and the other specialized types like the cyclocytic, cocyclocytic, pericytic, copericytic, desmocytic and codesmocytic types which occur in many polypodioid ferns are conspicuously absent in the Gleicheniaceae. Though stomata have long been a subject of study and have been successfully utilized in taxonomy and phylogeny of many plants, yet the stomatal similarities between the Gleicheniaceae and Polypodiaceae do not mean that these families are phyletically related. Phyletic conclusions based entirely on a single feature, such as stomatogenesis, might mislead.

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