

BENNETTITALEAN STOMATA

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ABSTRACT

Not only the topography, but also the size of stomata is fairly constant in the Bennettitales. Occasional departures from the typical dimensions were probably related to polyploidy. Specialized subsidiary cells, examined with SEM, formed a cupola over the guard cells. The ontogeny of syndetocheilic stomata as deduced from aborted apparatuses was mesogenous-tetralabrate. Distribution of compressed stomata on the margins of stomatal zones suggests higher concentration of a morphogen responsible for positional information near the veins and the direction of positional signals spreading from them. More orderly arrangement of stomata in the median portion of an intercostal zone is attributed to inhibitory action of developing meristemoids, while the differences in stomatal frequencies on the opposite margins of a stomatal zone were probably caused by microshades from the ribbed costae.

INTRODUCTION

BENNETTITALEAN stomata are of interest (i) as a clear-cut stomatal type, confined, among gymnosperms only to the Bennettitales (Cycadeoidales) with possible exception of *Gnetum*, (ii) as the first historical appearance of the paracytic morphotype and possibly also of the mesogenous ontotype, and (iii) as a manifestation of peculiar pattern of the cell differentiation.

Investigation of the bennettitalean stomata led Florin to his well-known classification of stomatal types. He distinguished "1. Primary type, in which an initial cell (Urmutterzelle) is functioning immediately as the mother cell of guard cells and is divided by a longitudinal wall into two; the lateral subsidiary cells are independent neighbours of the guard cell's mother cell or their derivatives. 2. Advanced type, which differs by that initial cell usually undergoes two divisions, the median of issuing cells is functioning as the guard cell's mother cell and is divided by a longitudinal wall into two guard cells while the lateral neighbour cells originate from the same initial cell and are immediately functioning as subsidiary cells or give rise to the latter by formation of longitudinal walls. For the first type, I propose now for the sake of brevity a term haplocheilic (simple-lipped) type, and for the second one — syndetocheilic (complex-lipped) type" (Florin, 1933, p. 14, translated from German). I cited these original designations to show that Florin had definitely

meant an ontogenic classification, though later it was applied as purely morphological for mature stomata. It was shown that both haplocheilic and syndetocheilic arrangements may arise either from mesogenous or from perigenous subsidiary cells (the latter terms also have been proposed by Florin). Pant and Mehra (1964) have questioned the mesogenous ontogeny of the bennettitalean (typical syndetocheilic) stomata and suggested an application of the term syndetocheilic to mature stomata only. However, in his later work Pant (1965a) recognized a possibility of the mesogenous dolabrate ontogenic type in the Bennettitales.

MORPHOLOGY

Apart from their uncertain ontogeny, the syndetocheilic stomata are fairly constant topographical character of the Bennettitalean epidermis as contrasted with considerable diversity of stomatal types in other gymnosperms and especially among angiosperms. There is, of course, a danger of circularity because we sometimes recognize the bennettitalean affinity of fossil leaves by their stomatal type only. For example, Ash (1976) has assigned *Eoginkgoites* to the Bennettitales in respect to syndetocheilic stomata of these "Ginkgoalean" leaves. By such a practice the constancy of stomatal characters can be exaggerated in the prejudice of the gross leaf morphology. However, the floral morphology in the Bennettitales is also far more constant than their vegetative characters.

In addition to topographical features, the size of stomata is surprisingly constant in the Bennettitales. Among the early Mesozoic Greenland bennettites, the length of guard cell thickenings is below 35 μm in 10 species, but in *Anomozamites hartzii* it is 50 μm (Harris, 1935). In the Early Cretaceous species from Primorye (Krassilov, 1967) this measure is: *Nilssoniopteris rhitidrachis*—27 μm , *N. robusta*—30 μm , *Zamites borealis*—36 μm , *Ptilophyllum bajulae*—30 μm , *Olozamites* sp.—22 μm , *Pterophyllum sutshanense*—22 μm , *Cycadolepis pterophylloides*—24 μm , while *Diclyozamites grossinervis* emerges with guard cell thickenings 40 μm long. It seems unlikely that any ecological factor was responsible for this departure from the long-standing norm. Other species, no doubt explained diverse environments but their stomatal dimensions were not affected. One can suggest polyploidy as a cause of unusually large stomata.

Stomata in the Bennettitales are typically arranged in short rows within intercostal bands and oriented perpendicular or oblique to the veins. Stomatal apparatus is composed of guard cells and a pair of subsidiary cells parallel to the aperture (paracytic). The subsidiary cells are usually specialized, i.e. they differ from the ordinary epidermal cells by either reduced size, or thickened cuticle, or less sinuous anticlinal walls or combination of these characters. In a few cases subsidiary cells are not specialized. There is no positive correlation between the degree of specialization and the order of arrangement of stomata. In fact, less specialized stomata are often more orderly distributed. In *Nilssoniopteris amurensis* (Novopokr.) Krassil. stomata are highly specialized with straight-walled and strongly thickened subsidiary cells, while the topography of stomatal bands is rather irregular (for general description see Krassilov, 1974). A few stomatal characters are more clearly seen in the electron micrographs (Pl. 1, figs. 1, 2) than in the light photographs. On the inner side of the cuticle, the thickened subsidiary cells are concave, forming a cupola over the guard cells. The border of a cupola are thick and sometimes continuous with one of the guard cell thickenings (Pl. 1, fig. 4, upper stoma). This suggests rather late separation of mature guard cell thickenings from the cuticle of subsidiary

cells. Poles of the guard cells never extend beyond the subsidiary cells. The guard cell thickenings fit the diameter of a cupola. They are spreading at the level of ordinary epidermal cells or alternatively folded up and hang on their poles well below the inner surface of a cuticle. The thickenings are semicircular in surface view and bean-shaped in side view (Pl. 1, fig. 2), with minutely dentate contour. The cuticle of subsidiary cells is internally smooth while in ordinary cells it is scabrate.

ONTOGENY

Pant (1965b) suggested that stomatal ontogeny can be deduced from the arrangements of cells in aborted apparatuses. A few aborted stomata were observed in *Nilssoniopteris amurensis* (Pl. 2, figs. 7-10). The whole aborted apparatus in Pl. 2, fig. 8 is slightly longer than an ordinary epidermal cell. It is divided by longitudinal walls into four narrow elongate cells of equal width. The median pair—guard cells—are spindle-shaped, thickened from pole to pole. Outer pair—subsidiary cells—are crescent-shaped, not thickened. In other cases the guard cells are more arched and somewhat depressed and the subsidiary cells are slightly thickened.

It can be surmised from this arrangement that mother cells of underdeveloped apparatuses experienced meristematic activity rather late, when epidermal cells nearly reached their mature size. The division into four cells was evidently instantaneous. Thus, the stomata were mesogenic tetralabrate. The thickening process spread discontinuously from guard cells to subsidiary cells. In normal stomata, the guard cell thickenings were probably formed in the early stage of development just after the initial division of a meristemoid. Later, during stretching stage, thickening was transferred to subsidiary cells while the guard cell poles remained unthickened. Aborted stomata were found in the portions of intercostal bands with comparatively low stomatal frequency.

Further abnormalities providing some evidence on the development of meristemoids are (i) stomata with encircling cells, (ii) contiguous stomata with common subsidiary cells, and (iii) compressed stomata with neighbouring subsidiary cells.

Occasional stomata have lateral encircling cells which are thickened and separated from subsidiary cells by incompletely developed wall always parallel to the guard cells (Pl. 1, fig. 6). In contiguous stomata which are exceedingly rare (about 1 per 9 sq mm) the guard cells of both apparatuses are parallel to each other. Adjacent stomata are normally separated by one or two unspecialized cells. Compressed stomata (Pl. 1, figs. 4, 5; Pl. 2, fig. 2) have no intervening cells or these are thickened like subsidiary cells. In respect to the thickening, the whole group of compressed stomata may be considered as a single unit subdivided by a series of parallel walls formed by unusually high activity of meristemoids.

MORPHOGENY

Plant epidermis is apparently an ideal object for developmental studies. However, actual possibilities of recognizing a pattern of cell differentiation produced by positional signals depend on the role of random variability of individual cells in determining the cell states (see Lewis *et al.*, 1977). Several observations in the cuticle of *Nilssoniopteris amurensis* have some bearing on this problem:

1. Costal stomata-free bands are often bridged by occasional stomata near the midvein.

2. Compressed stomata (see above) are developed mostly on the margins of stomatal zones.

3. Groups of compressed stomata on opposite sides of a costal zone are usually placed on the lines perpendicular to the costa (Pl. 1, fig. 3).

4. Laterally compressed stomata (or only one stoma in group of two or three) are usually reduced in size while under polar compression stomata are of normal size (Pl. 1, figs. 4, 5).

5. Stomata are more orderly arranged in the median part of the stomatal zone than on the margins.

6. Stomatal frequency is sometimes higher on one margin of a stomatal zone than on the other.

Explanation of these phenomena is conjectural and awaits further study. The bridging of stomata-free zones near the midvein is probably caused by a morphogen acting as positional signal for meristemoid

formation spreading laterally from the midvein as well as from the lateral veins. Higher concentration of a morphogen just near the veins explains also enhanced meristematic activity and production of the compressed stomata on the margins of stomatal zones. Groups of compressed stomata on the lines transversing the costae indicate the direction of a positional signal. In the regions of low stomatal frequency some meristemoids are aborted. If the random variability of individual cells is a basic factor determining distribution of meristemoids along the lines of positional signals, then the scarcity of contiguous stomata may be explained by strong inhibitory action of a meristemoid on adjacent cells. Inhibition in the direction perpendicular to the signals is suggested by the reduction of individual stomata in laterally compressed groups. Cells in the median portion of a stomatal zone are surrounded by developing meristemoids and the inhibitory control over distribution of meristemoids prevails here over the random variability. Hence the arrangement of stomata is more regular in the median part of a zone than along the margins. And finally, the differences on opposite sides of a stomatal zone may be related to microshades produced by strongly ribbed costae.

CONCLUSIONS

Florin's interpretation of the syndetocheilic stomata, though based on the topography of mature apparatuses only, were essentially correct. The mesogenous stomata arrived rather lately in the history of seed plants, the Bennettitales have been the first group developing this stomatal type as their most constant character. Subsidiary cells of the bennettitalean stomata have been even more specialized than it was revealed by the light microscopy. I believe that fossil cuticles are of some value not only in detecting the ontogenic type of stomata but also in the developmental studies in general. It is suggested that the cell states have been determined by the positional signals, the random variability, the inhibitory action of developing meristemoids and the micro-environmental heterogeneities.

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EXPLANATION OF PLATES

PLATE 1

Stomata of *Nilssoniopteris amurensis* (Novopokr.)
Krassil., SEM micrographs

1. Typical stoma showing guard cells with their semicircular thickenings and thin poles, cupped by concave subsidiary cells. $\times 1600$.
2. Side view of the guard cell thickening. $\times 1800$.
3. Stomatal bands separated by costal zone. Note the groups of compressed stomata on the lines traversing the costal zone. $\times 200$.
4. Laterally compressed stomata of unequal size. $\times 1000$.

5. Stomata of equal size compressed in the polar direction. $\times 600$.
6. Stoma with lateral encircling cells. $\times 800$.

PLATE 2

Stomata of *Nilssoniopteris amurensis* (Novopokr.)
Krassil., SEM micrographs

7. Portion of stomatal zone with aborted stoma in the centre. $\times 300$.
8. The same aborted stoma. $\times 1500$.
- 9, 10. Another aborted stoma. $\times 1000$ and 1600 .
11. A row of compressed stomata. $\times 600$.

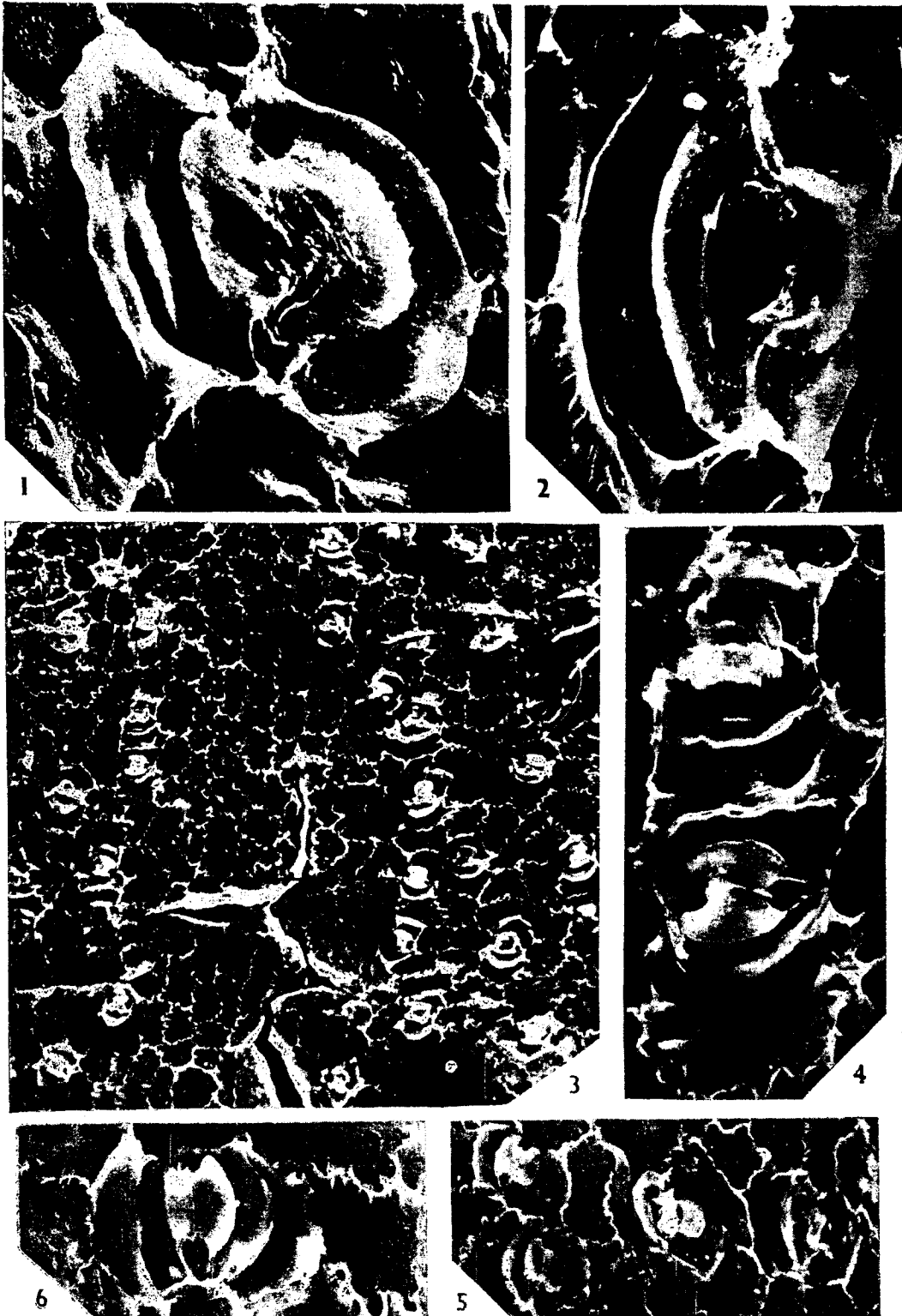


PLATE I

