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Reconstructions of stomata in Komlopteris Barbacka and Pachypteris Brongniart and their adaptation to climate

by M. BARBACKA, Budapest

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Abstract – The SEM investigation of stomata of *Komlopteris* BARBACKA and *Pachypteris* BRONGNIART supported the theory of adaptation of *Komlopteris* to a wet, tropical climate and swamp-like environment. This is contrary to the opinion of some authors who investigated *Komlopteris*-like leaves (before revision some of them were described as *Thinnfeldia)* as xeromorphic. The examination of stomatal structure in *Pachypteris* has suggested that this plant might have required different conditions. With 18 figures.

INTRODUCTION

The structure of stomata of *Komlopteris* (BARBACKA 1994a) leaves (before revision they were known under the name of *Thinnfeldia)* was interpreted by some authors (GOTHAN 1914, ANTEVS 1914) as being typical of xeromorphic plants in view of their thick cuticles and sunken guard cells.

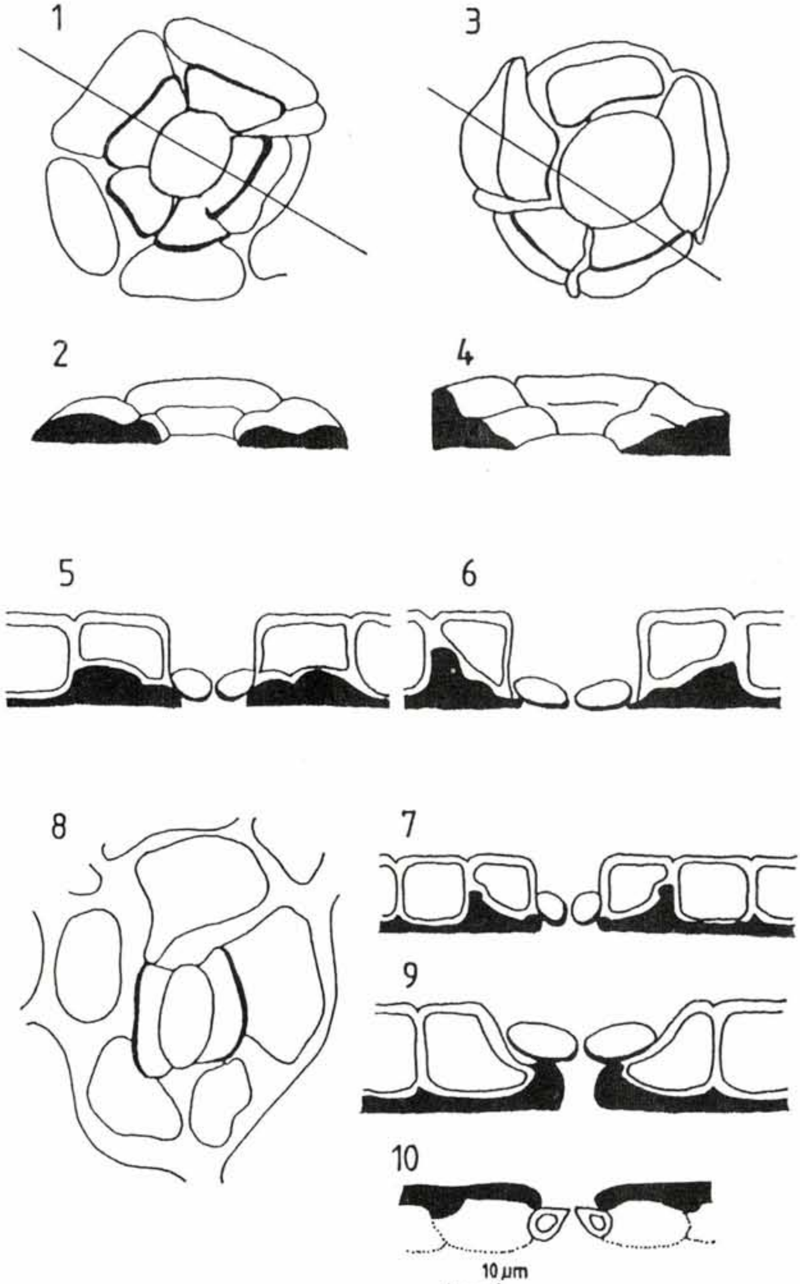
About 80 specimens of *Komlopteris* from the Mecsek Mountains (Southern Hungary) and several specimens of different species of *Pachypteris* from various localities were examined (one from the Mecsek Mountains, one from Georgia, and five from Steierdorf-Anina in Romania). Besides the morphological and cuticular differences between the two genera (Barbacka 1994a), the investigation of stomata in SEM shows that these genera might be adapted to different conditions.

RESULTS AND INTERPRETATION

The stoma of *Komlopteris* consists of 5-8 small subsidiary cells which form a regular ring around the stomatal pit. The inner (near the stomatal pit) and outer outlines of the ring create the characteristic thickenings which probably mark anticlinal walls of subsidiary cells (Figs 1-4). In different forms of leaves two different types of thickenings were observed. In the first one, the inner and outer anticlinal walls are very thick and the periclinal walls form a narrow, sunk line in between (Figs 1-2, 11). This type looks like a double concentric ring around the stomatal pit, the ring is interrupted by the radial anticlinal walls.

In the second type, there is no thickening around the stomatal pit, the periclinal walls are not sunken and the concave line is formed by the contact of the periclinal wall and an outer anticlinal wall (Figs 3-4, 12). In this case the ring is double too, but the outer one is narrower than the inner one. Generally speaking, stomata of *Komlopteris* were described as bowl-shaped with protruding outer margins and the guard cells situating at the bottom.

The character of the cuticle layer is better visible under SEM and shows, that on the outer surface of the cuticle stomata were marked only by holes with flat margins (Fig. 14). The inner surface, viewed from the mesophyll side, showed all epidermal structures and the outer margins of the rings formed by subsidiary cells appeared to be sunken into the epidermis. Consequently, the guard cells must have been situated near the surface of the leaves (Figs 5-6). The relatively broad stomatal pit allowed the large area of guard cell walls to make contact with their surroundings.



Figs 1-4. Types of stomata of *Komlopteris*: 1-2 = *K. nordenskioeldii* No BP 89.275.1., 3-4 = *K.* sp. No BP 89.301.1. Schematic drawing. – Figs 5-7. Transverse section of stomata in *Komlopteris*: 5 = *K. nordenskioeldii* No BP 89.275.1., 6 = *K.* sp. No BP 89.301.1., the type of stoma with well preserved guard cells, g = type with no preserved guard cells. – Fig. 8. Stoma of *Pachypteris banatica* No BMP-12, schematic drawing. – Fig. 9. Transverse section of stomata in *Pachypteris banatica*. –
Fig. 10. Transverse section of stomata of *Pachypteris dagincourtii* (after BARALE 1984: 10)

The recently examined species of different forms show, among other details, differences in the degree of cutinization on those parts of the guard cells which are found close to the stomatal pit. In some sorts of leaves those parts of the periclinal walls were not preserved, so the cutinization was probably weak. In other sorts of leaves large numbers of stomata possessed well cutinized parts of the guard cell's periclinal walls in the stomatal pit (Fig. 13). This was probably caused by unequal arrangement of guard cells towards the outer surface of the epidermis in different leaves and might depend on the position of the leaf in the plant and on external factors. The guard cells lying underneath the surface of the cuticle (Fig. 7) were probably less cutinised than those lying on the level of the surface, so they were destroyed by maceration or fell out.

The exposed guard cells in the stomata of *Komlopteris* may be related to adaptation of the plant to wet climate. The character of the climate in this area was shown by results of the geological and palynological examinations of the sediments in the Mecsek Mountains. (PAÁL-SOLT 1969), where *Komlopteris* is represented by a great number of leaves. According to them the type of the territory in the Mecsek Mountains was like a delta plain with swamps, marsh vegetation and fen forests (PAÁL-SOLT 1969).

Similar conditions were found in Scania in the type locality of *Komlopteris* [*K. nordenskioeldii* (NATHORST) BARBACKA, 1994a]. NATHORST (1878) mentioned in his monograph on this flora from Pålsjo the wet, tropical character of the climate in that territory, and the results of recent examinations confirmed his opinion (PIEŃKOWSKI 1991). In consequence, *Komlopteris* may be regarded as a representative of tropical fen.

The adaptation to environmental conditions of environment is not so clear in the case of *Pachypteris*. Based on observations of different species of *Pachypteris* it is clear that they possess two types of stomata. In one group [*P. major* (RACIBORSKI) REYMANÓWNA 1963, *P. lanceolata* BRONGN. sensu DOLUDENKO & SVANIDZE (1969), *P. desmomera* (SAPORTA) BARALE (1971), *P. daincourtii* (SAPORTA) BARALE 1984, *P.* cf. *lanceolata* BRONGNIART sensu VAN DER BURGH & VAN CITTERT (1984)] the stomata seem to be similar to those of *Komlopteris*. They were more or less regular, roundish in shape and the outer outlines of the subsidiary cells were protruded. Their similarity to stomata of *Komlopteris* is visible under a light microscope only, because subsidiary cells seem to form a double ring too. In fact, the lines which divided subsidiary cells into concentrical rings were formed by outlines of guard cells below the subsidiary cells and not, like in the case of *Komlopteris*, by contact of the cell walls of subsidiary cells. Because of this, their structure is different from bowl-shaped stomata in *Komlopteris*. The schematic drawing of transversal section of a stoma in *Pachypteris daincourtii* (SAPORTA) BARALE (BARALE 1984) suggests that the guard cells were probably small in stomata of that type (Fig. 10).

The second group of *Pachypteris* [*P. rhomboidalis* ETTINGSHAUSEN) NATHORST sensu DOLUDENKO (1971) *P. rhomboidalis* No BP 60.216.1.(Hung. Nat. Hist. Mus., Budapest), *P. banatica* (HUMML) DOLUDENKO (BARBACKA 1994b), *P. lanceolata* BRONGNIART sensu HARRIS (1964) *P. papillosa* (THOMAS et BOSE) HARRIS 1964], had stomata with irregular and large subsidiary cells (Figs 8-9). Looking from the mesophyll side they reflected the shape of a truncated pyramid with a protruding rim on the top around the stomatal pit (Figs 15-17). It was formed by thickly cutinised parts of guard cell walls. The guard cells, often well preserved, stronger cutinised than those of *Komlopteris*, were large, with extended poles (Figs 16-17). Their outer margins are often visible under the light microscope below the subsidiary cells and reach beyond the limits of the stomatal pit. The arrangement of guard cells suggests that they were sunken (Fig. 18). Looking from the outer surface, the cuticle was similar to that of *Komlopteris*, but the holes marking the stomata possesed bend edges (Fig. 18).

The proportions of the size of the stomatal pit and the subsidiary cells in *Pachypteris* differed from that of *Komlopteris*. While in *Komlopteris* the width of the stomatal pit ranged between 1/3 and 1/2 of the width of the whole stoma in transversal section, in *Pachypteris* it was about

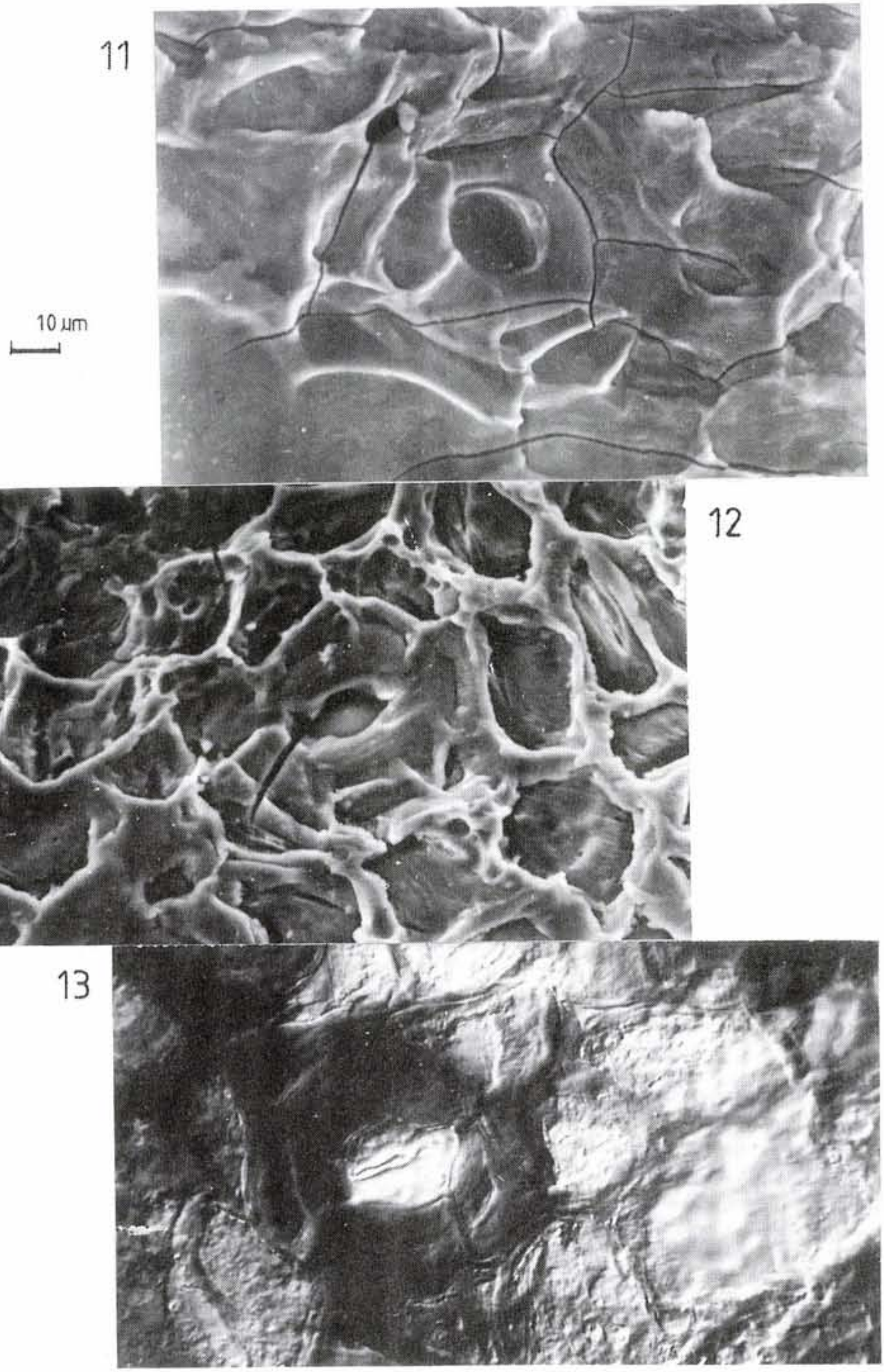


Fig. 11. The lower cuticle of *Komlopteris* from the Mecsek Mountains (*Komlopteris sp.* No. BP 89.353.1.) from the inside (type 1). – Fig. 12. Stoma of *Komlopteris sp.* (No. BP 89.358.1.) from the inside (type 2). – Fig. 13. Stoma of *Komlopteris sp.* (No. BP 89.301.1.)

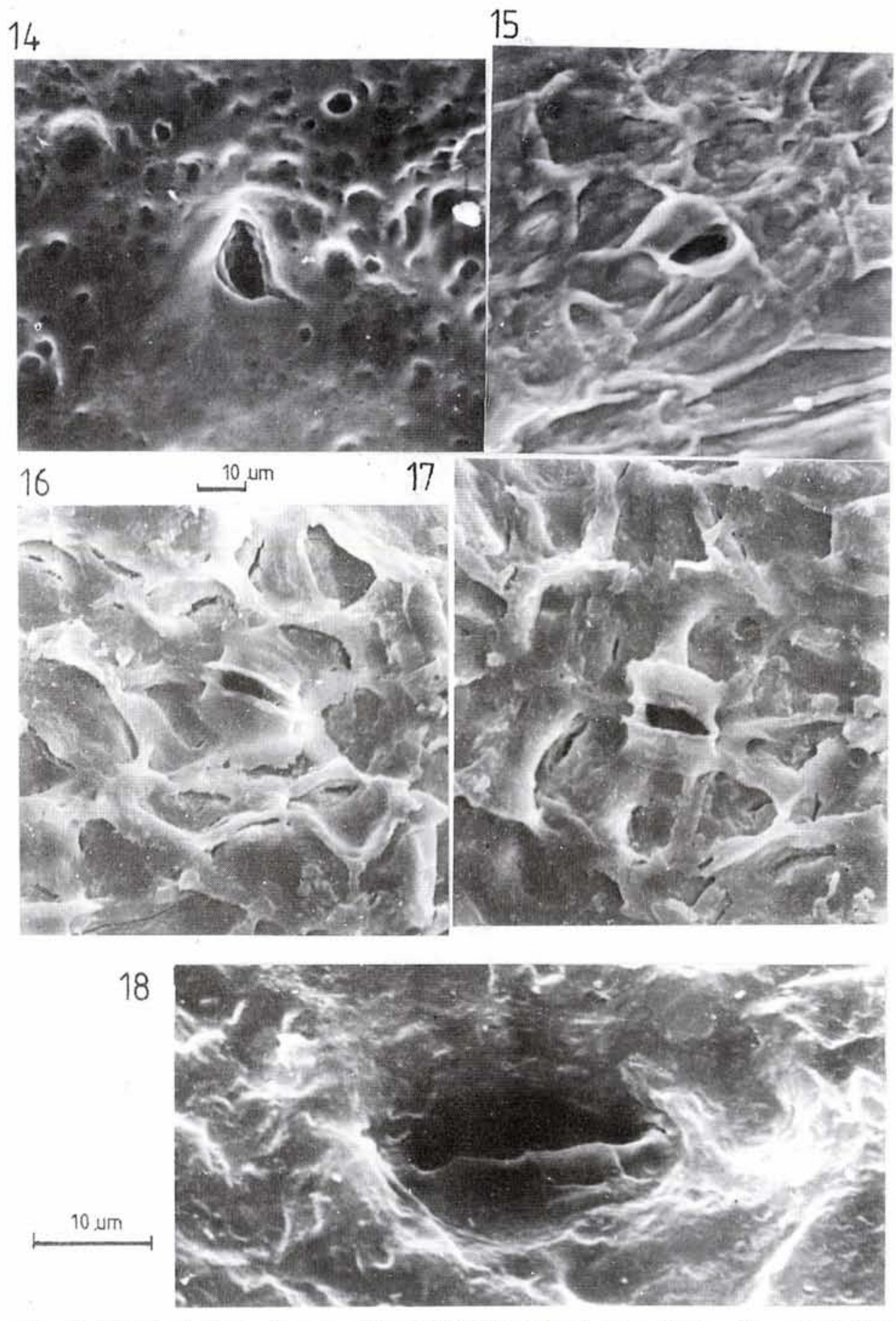


Fig. 14. Stoma of *Komlopteris sp.* (No. BP 89.353.1.) from the outside. – Figs 15-17. The lower cuticle of *Pachypteris banatica* from Mecsek Mountains, No. BMP-12, stoma from the inside. – Fig. 18. Stoma of *Pachypteris banatica* (No. BMP-12) from the outside

1/4 or less. Thus, in general, the guard cells of the stomata in *Pachypteris* were better protected than in *Komlopteris*. This might be due to adaptation to conditions different from that of *Komlopteris*.

The interpretation of adaptation of *Pachypteris* is not so evident as in the case of *Komlopteris*. The structure of stomata suggests a xeromorphic type, which is characteristic of halophytes as well, for instance *P. papillosa* HARRIS (HARRIS 1964). Undoubtedly the epidermis in *P. papillosa* is extremely well protected due to its thick cuticle and stomata furnished with papillae. However, considering that the territory of the Mecsek Mts. was of delta nature which occasionally might be flooded by salt water, *Pachypteris banatica* from this locality could possibly be a halophyte as well.

The explanation of the connection between the type of the stomata (regular or irregular) and the character of adaptation to environmental circumstances (xerophytic or halophytic) demand further examinations, but we cannot exclude the possibility that genus both ecological forms occur within one.

SUMMARY

The reconstruction of stomata in *Komlopteris* and *Pachypteris* involved an attempt to solve the question about the connection between cuticular structure and climatic conditions. In the case of the locality in Mecsek the plant remains preserved in both morphology and cuticular structure. The observations were based on real climatic data, the adaptations seem to be visible not only in the construction of the stomata, but also in the morphology of the leaves. The leaves in question were large with large pinnae and entire margins in *Komlopteris*, while in *Pachypteris* they were far smaller and often with dissected margins. Earlier investigations into the plant-climate relationship suggested an influence of the climate on morphological and cuticular features (CHALONER & CREBER 1990). Although the examination concerned mainly angiosperms and a younger age (Late Cretaceous), the observations of *Komlopteris* and *Pachypteris* from Mecsek suggest that similar considerations may be related to older floras as well.

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Author's address: Dr. MARIA BARBACKA
Department of Botany
Hungarian Natural History Museum
H-1088 Budapest, Könyves Kálmán krt. 40.
Hungary