

# EPIDERMAL STRUCTURE AND DEVELOPMENT OF STOMATA IN *EPHEDRA FOLIATA* BOISS.

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## SUMMARY

The epidermal structure of the leaf and stem of *Ephedra foliata* Boiss. is described. The epidermis of internodes and leaves shows longitudinal rows of cells and stomata. In the nodes and the leaf bases the stomata are irregularly orientated. The subsidiary cells are perigene and the development of stomata is typically haplocheilic.

## INTRODUCTION

Various descriptions of the ontogeny of stomata in the living gymnosperms are available. These include accounts of the haplocheilic development of stomata in certain conifers by Florin (1931), in *Gnetum gnemon* and *G. ula* by Maheshwari and Vasil (1961), and in three species of *Cycas* and *Ginkgo biloba* by Pant and Mehra (1964). Syndetocheilic development of stomata has been reported in *Gnetum gnemon* and *Welwitschia mirabilis* by Takeda (1913*a, b*, respectively). A genus of modern gymnosperms whose stomatal ontogeny remains uninvestigated is *Ephedra*. Accordingly, in the present paper the authors have described the development of stomata in the common Indian species, *E. foliata*. The material was collected from a plant cultivated in the Botanical Garden of the Allahabad University.

## RESULTS

### *The adult epidermis*

The epidermis of mature internodes is ridged and consists of longitudinally elongated epidermal cells (Figs. 1 and 3) which tend to be in rows parallel to the long axis of the stem. The size of the epidermal cells varies considerably but those of the nodal region tend to be shorter and are often wider than long. The epidermal bands above the ridges are non-stomatiferous and are of somewhat larger cells with papillae on their surface. The form and size of the papillae is very variable, e.g. in the ridges of the internodes of the plant a papilla may usually appear as a short local bulge of a cell where its cuticle is thickened but just above a node, usually on its side which faces a leaf, the papillae tend to be more elongated becoming long tapering and hair-like near the leaf base (Fig. 4). Their rounded tips are directed downwards and occasionally somewhat swollen. Cauline stomata are usually confined to the furrows. In the internodes the stomata are typically placed in longitudinal rows and those of adjacent rows are often alternating (Fig. 1). In the nodal region the stomata may be irregularly or even transversely orientated (Figs. 4 and 5). The stomatal index is 22.

Some of the cells of the upper (adaxial) epidermis of a leaf (Figs. 10 and 11) are

papillate, but near the leaf base practically every cell is papillate (Fig. 11) and there are also a few long papillae at the tip of the leaf (Figs. 12 and 13). Papillae of the foliar epidermis are usually directed upwards towards the tip of the leaf. They are normally inserted at or near the distal end of each epidermal cell. Stomata occur on both sides

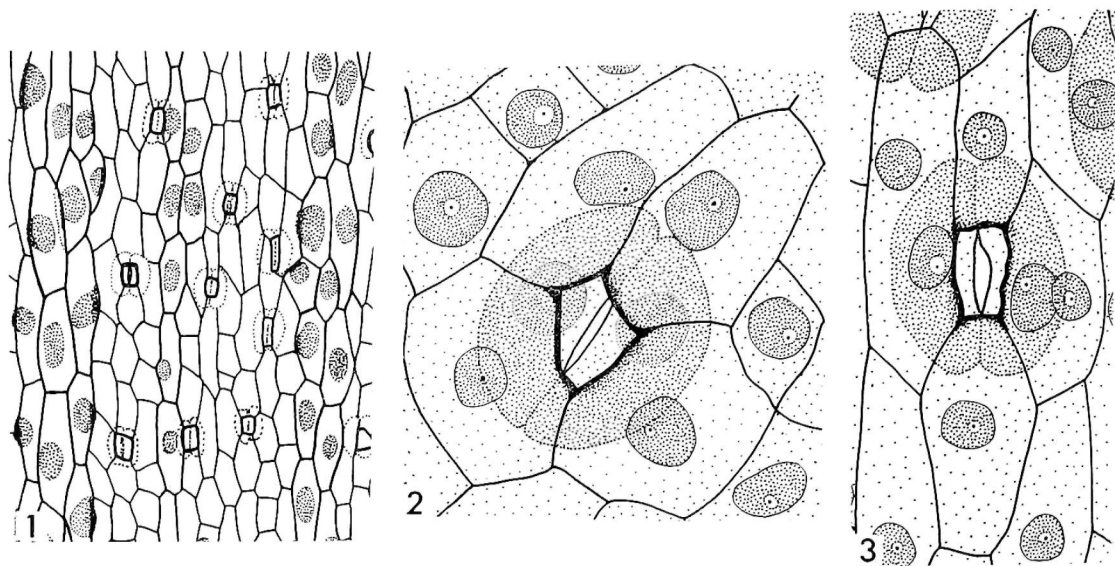
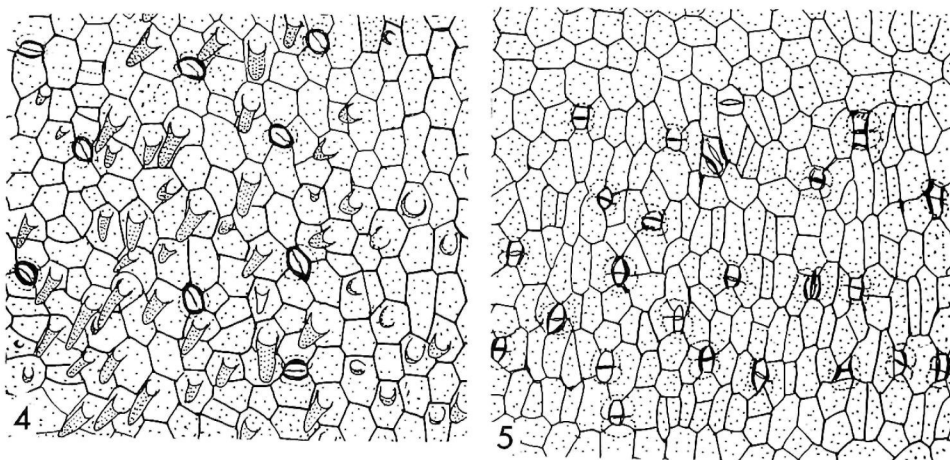


Fig. 1. Cuticle of an internode showing somewhat larger papillate cells over the ridges and an intervening stomatiferous area in the region of a furrow.  $\times 100$ .

Figs. 2 and 3. Mature stomata from a leaf base and an internode, respectively. Guard cell outlines, which are overlapped by subsidiary cells, are shown by dotted lines. The centripetal sides of subsidiaries are thickened and somewhat papillate. The subsidiaries in Fig. 2 are irregular but those in Fig. 3 are differentiated into two polars and two laterals. Fig. 2,  $\times 750$ ; Fig. 3,  $\times 600$ .



Figs. 4 and 5. Cuticles from the lower extremity of an internode and a node, respectively. The epidermal cells tend to be shorter and the stomata are irregularly or transversely orientated. Both  $\times 125$ .

of the leaf but their number decreases steadily towards the base where there are practically none on the upper side. Stomata occur almost up to the leaf apex (Figs. 12 and 13). Foliar stomata are longitudinally orientated over the lamina but near the leaf base they tend to be irregularly placed.

The structure of the mature stomata of *Ephedra* is well known (cf. Thompson, 1912; Pearson, 1929; Florin, 1933). In *E. foliata* the guard cells are  $36\text{--}57\ \mu$  long  $\times$   $10\text{--}21\ \mu$  wide (mean  $45 \pm 2 \times 17 \pm 3\ \mu$ ). The stomata are usually evenly spaced but they may be occasionally contiguous in the stems as well as in the leaves (Fig. 9). The guard cells are generally surrounded by four but sometimes five and rarely more, rather slightly specialized subsidiaries which differ from the ordinary epidermal cells only in having the sides towards the stomatal pore slightly thickened and often somewhat papillate. The four subsidiaries of the stomata in the internodes and leaves are usually differentiated into two polars and two laterals but there is no such differentiation in the stomata of the nodes and the leaf bases (Fig. 2). The stomatal index in the middle region of the upper epidermis is 18 and that of the lower is 24.

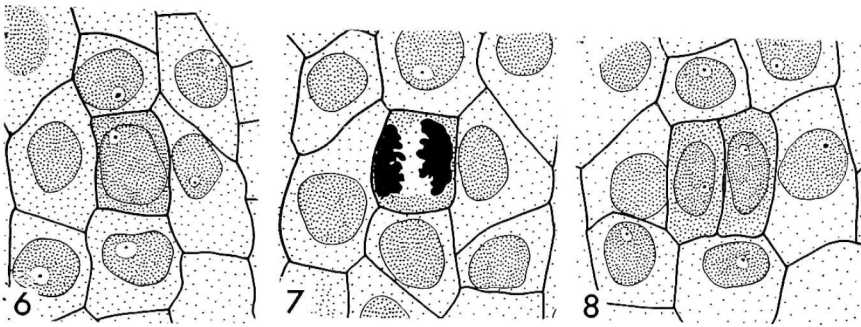


Fig. 6. Protoderm cells of a stem near apex showing a stomatal meristemoid (darker stippled).  $\times 750$ .

Fig. 7. Epidermis of a stem near apex showing a meristemoid at anaphase.  $\times 750$ .

Fig. 8. Epidermis of a young stem showing freshly formed guard cells without the intervening pore.  $\times 750$ .

The cuticle of the stems and leaves, prepared by macerating them with Schulze's fluid, shows clear cell outlines and longitudinal striations or cutin folds. The striations are especially clear on the surface of marginal cells of the leaf lamina, over the cells of the ridges of the stem and on the surface of papillae.

The epidermal structure of the leaves and stems of *E. foliata* resembles that of many species of *Cordaites*. Besides showing a general similarity in having stomatiferous and non-stomatiferous bands lying parallel to the long axis, the stomata of *Ephedra foliata* resemble those of *Cordaites borassifolius*, *C. angulosostratus*, *C. mansfieldi*, *C. serpens*, *C. principalis* and others in having similar, poorly specialized, subsidiary cells (Harms and Leisman, 1961; Pant and Verma, unpublished) which tend to be papillate on the side of the stomatal pore. Indeed, the epidermal structure of *Ephedra foliata* and *Cordaites* leaves is so similar that it may be cited as an additional argument in support of the cordaitean affinities of *Ephedra* (Eames, 1952; Pant, 1957).

#### *Development of stomata*

Epidermal peels of young portions of the stems and leaves were stained in acetocarmine. They show short, irregularly placed, isodiametric, polygonal cells with straight anticlinal walls and, here and there among them, meristemoids (guard cell mother cells) may be distinguished by their deeper stain and rectangular shape (Fig. 6). The nucleus of a meristemoid divides only once (Fig. 7) and usually a longitudinally placed wall

subsequently partitions it into two cells. This results in the formation of two guard cells which are at first small, flush with the surface and without an intercellular gap between them (Fig. 8). The subsidiaries are formed by protoderm cells which happen to surround the meristemoid. Protoderm cells, other than the meristemoids, may also divide but they

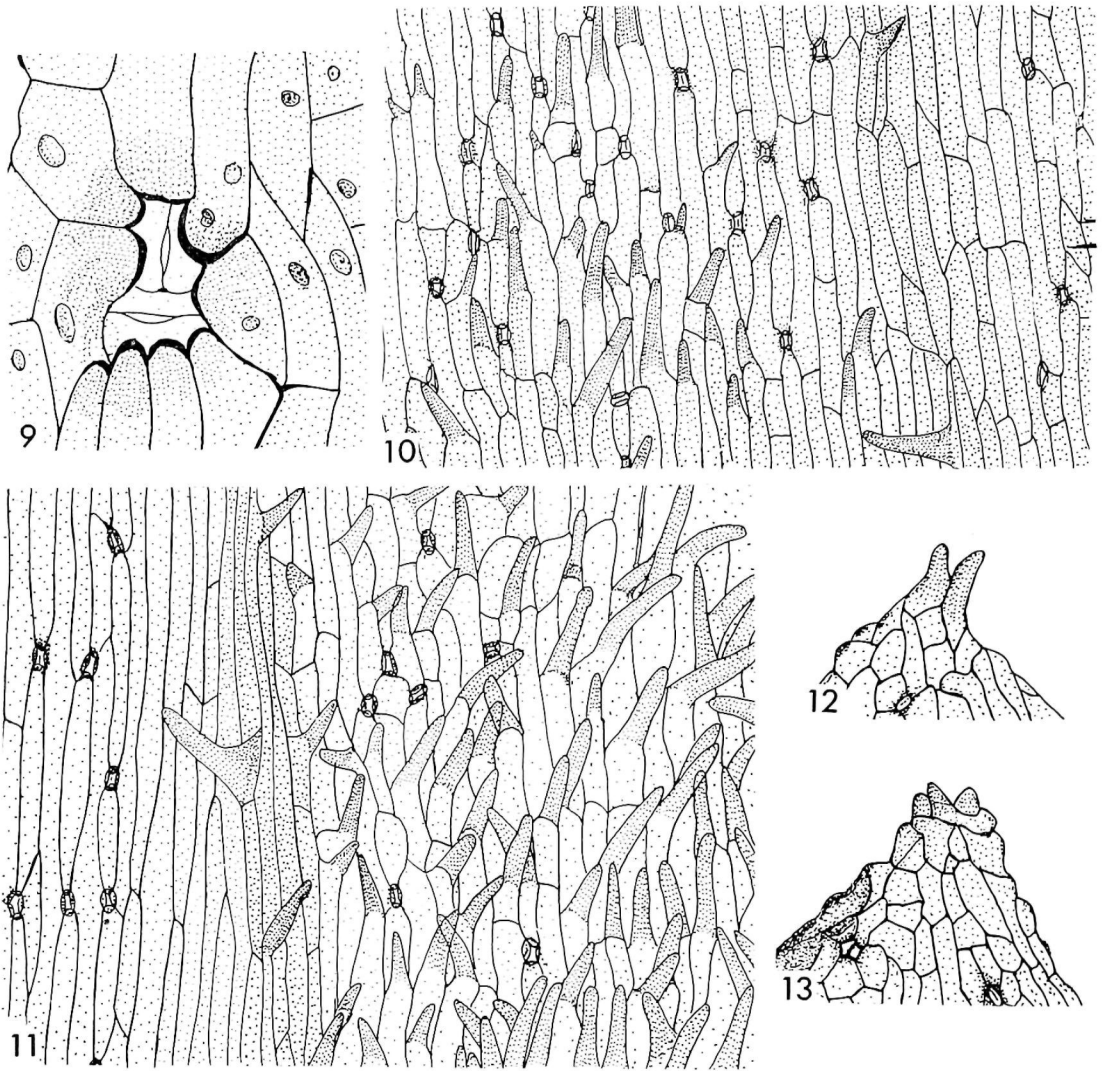


Fig. 9. Two contiguous stomata from near the apex of a leaf.  $\times 200$ .

Figs. 10 and 11. Cuticles from the middle and basal parts, respectively, of leaves. Non-papillate portions, on the right in Fig. 10 and on the left in Fig. 11, represent the cuticle of the upper surface. The lower side shows papillate epidermal cells. The frequency of stomata on the lower side is higher in the middle region (Fig. 10) than near the base (Fig. 11) but the papillae are more numerous and larger in the basal part than in the middle region. Both  $\times 125$ .

Figs. 12 and 13. Cuticles from the apices of leaves showing larger papillae in cells at their tips. Note the occurrence of stomata up to very near the apex. Both  $\times 125$ .

generally form transverse walls and their daughter cells develop into ordinary epidermal cells. The meristemoids of the leaf base and nodal epidermis may divide in any direction. As the subsidiary cells enlarge and mature they grow over the guard cells. The guard cells ultimately become kidney shaped and a stomatal pore appears between them.

## CONCLUSION

This study of the development of stomata in *Ephedra foliata* shows that its guard cell mother cells and subsidiaries do not develop from an immediately preceding common parent cell and thus confirms their haplocheilic nature (Florin, 1933) which, hitherto, was concluded merely from the appearance of the adult stomatal apparatus.

## ACKNOWLEDGMENTS

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