VELAMEN IN TERRESTRIAL MONOCOTS

II.† Ontogeny and Morphology of Velamen in the Amaryllidaceae with a Discussion on the Exodermis in Amaryllidaceae and the Liliaceae

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Goebel (1922) listed a few plants of Amaryllidaceae possessing velamen. Dutt (1954) reported velamen in two species of *Crinum*. Deshpande (1955) observed velamen in a few members of Amaryllidaceae. Very recently Mulay and Deshpande (1959) published an account of the ontogeny and morphology of velamen in the Liliaceae.

Materials and Methods

Material was collected from the different botanical gardens in India and during the botanical excursions of Birla College. Roots of *Agapanthus africanus* were kindly made available to the author by Dr. Hecht of the State College of Washington. The author is thankful to Dr. Hecht for the same.

Usual procedures of dehydration, embedding and staining were followed.

Observations

Names of the plants and number of velamen layers are given in the following table.

Name of the plant	Number of velamen layers
1. *Agapanthus africanus* (L.) Hoff. ..	5–7
2. *Alstroemeria aurantiaca* Don. ..	1
3. *Amaryllis belladona* Linn. ..	1
4. *Clivia miniata* Regel. ..	4–5
5. *Crinum latifolium* Linn. ..	4–5
6. *Crinum moorei* Hook. F. ..	3
7. *Eucharis grandiflora* Planch. Lind.	1
8. *Haemanthus coccineus* Linn. ..	1
9. *Narcissus tazetta* Linn. ..	1
10. *Zephyranthes tubispatha* Herb. ..	1

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The fact that the velamen is protodermal in origin has now been well established in the recent literature on velamen contributed by Mulay *et al.*

The velamen in these species varies from 1–7 layers (*see* table above). It is characterised by fine fibrillar thickenings as in *Crinum, Agapanthus* and *Clivia* (Text-Figs. 1 and 2) and slightly thick bands as in *Haemanthus, Zephyranthes* and *Amaryllis* (Text-Fig. 3). In addition to these fibrillar thickenings, the walls of the velamen cells are pitted. In *Crinum latifolium* and *Agapanthus africanus* these pits appear as cross-pits (Text-Fig. 6). Nature of these thickenings and pits is clearly revealed under crossed nicols. In longitudinal section velamen cells appear elongated along the root axis. The velamen of *Agapanthus* and *Crinum* has identical features.

Exodermis is clearly seen taking its origin from 2 or 3 prominent centrally placed cells which could be taken as periblem initials (Text Fig. 7), in such species as *Ruscus hypophyllum, Polygonatum oppositifolium, Sansevieria thyrsiflora* and many other members of the Liliaceae and in *Amaryllis belladona, Eucharis grandiflora, Zephyranthes tubispatha* of the Amaryllidaceae where the periblem is distinct. The cells flanking the periblem initials first undergo anticlinal and then periclinal divisions each cell thus forming three cells arranged one above the other (Text Fig. 7). Of these three cells the one toward the cap forms a uniseriate layer which is the exodermis; the central one undergoes periclinal divisions to form the cortex; and the cell toward plerome, undergoing only anticlinal divisions, forms a uniseriate layer which becomes the endodermis.

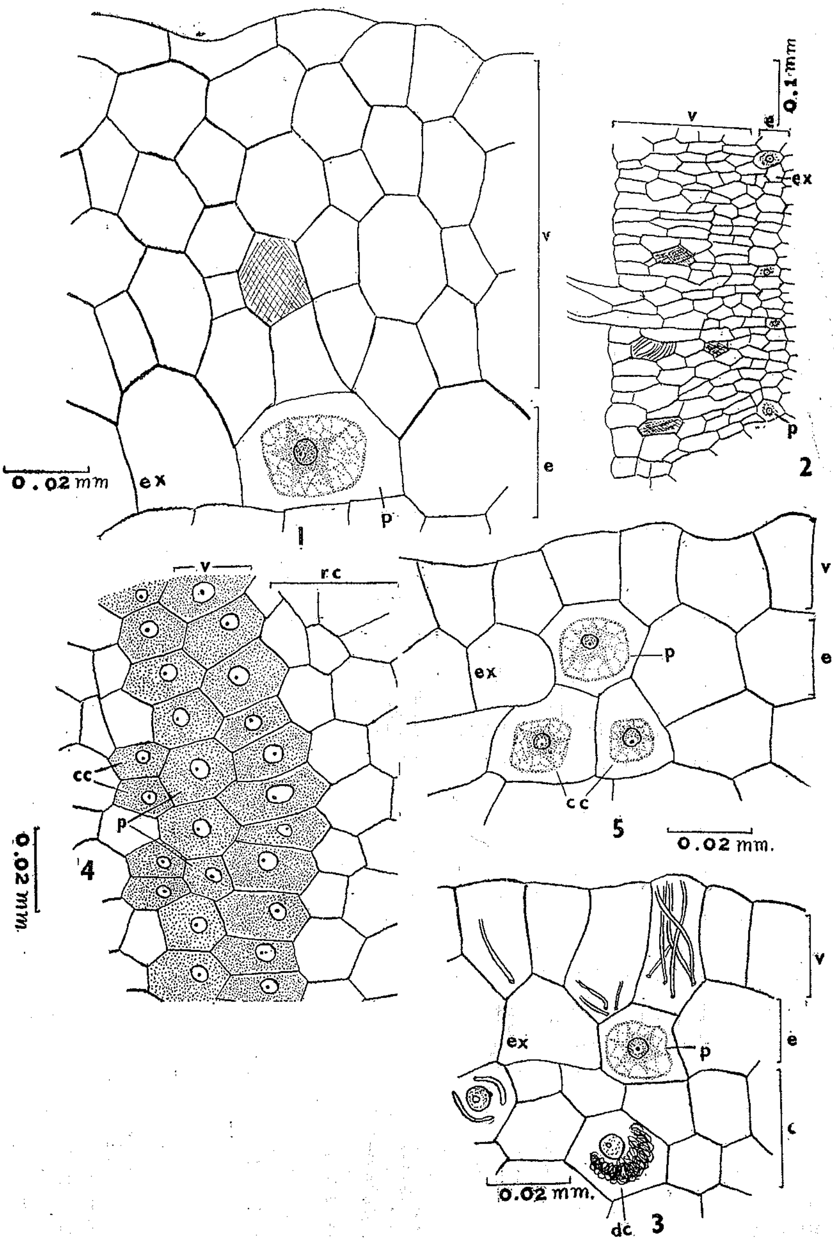
Next the origin of the exodermis may be considered in species where there are no distinct periblem initials. In such cases there is a common group of initials, for the cap, protoderm and the cortex. This condition is seen in *Tupistra clarkei, Hemerocallis flava* and *Aspidistra lurida* of the Liliaceae and *Agapanthus africanus, Haemanthus coccineus, Crinum latifolium* and *Clivia nobilis* of the Amaryllidaceae. In such plants the following observations suggest rather definitely that the exodermis is initiated within the cortical zone:

1. Bordering the common group of initials, there are three or four cells, more prominent than the others; of these, the cell lying nearest the plerome, forms the endodermis and the one nearest and just beneath the protoderm, the exodermis.

2. It would seem very unlikely that the exodermis would be formed from the protoderm since periclinal divisions within this tissue result in the formation of velamen (Pl. XVII, Fig. 1); furthermore, the velamen has never been known to give rise to the exodermis.

It would therefore appear that the exodermis is ontogenetically related to the cortex and not to the protoderm.

The exodermis in all the species studied, uniformly showed the following features: It is a uniseriate layer. It delimits the cortex from



TEXT-FIGS. 1–5. Portion of root of *Agapanthus africanus* in transverse section showing fibrillar thickenings. *v* = velamen; *e* = exodermis; *ex* = exodermal cell; *p* = passage cell; Fig. 2. Same of *Clivia nobilis*. Fig. 3. Portion of root of *Amaryllis belladona* in transverse section showing banded thickenings. A few cortical cells digesting mycrorrhizal fungus. A few velamen cells also show fungal hyphae. *v* = velamen; *p* = passage cell; *dc* = digestive cell; *e* = exodermis; *ex* = exodermal cell; *c* = cortex. Fig. 4. Portion of the root of *Haemanthus coccineus* in transverse section showing early stages of the complimentary cells, passage cell and velamen. *v* = velamen ; *rc* = root cap; *p* = passage cell; *cc* = complimentary cells. Fig. 5. Portion of the root of *Haemanthus coccineus* in transverse section showing the mature region. *cc* = complimentary cells; *v* = velamen; *p* = passage cell; *ex* = exodermal cell; *e* = exodermis.

the velamen, and it consists of long exodermal cells and short passage cells (Pl. XVII, Fig. 2). The exodermal cells are the dead cells and their outer tangential walls are thick and striated. Passage cells possess protoplasmic contents and usually thin outer tangential walls. Occurrence of pits is quite common on the exodermal cell-walls. Radial walls are thick or thin and taper towards the cortex. The meristematic cell from which the passage cell is formed also gives rise to one or two complimentary cells, toward the cortex (Text-Figs. 4 and 5). These latter are living cells and have some of the features as the passage cells.

Discussion

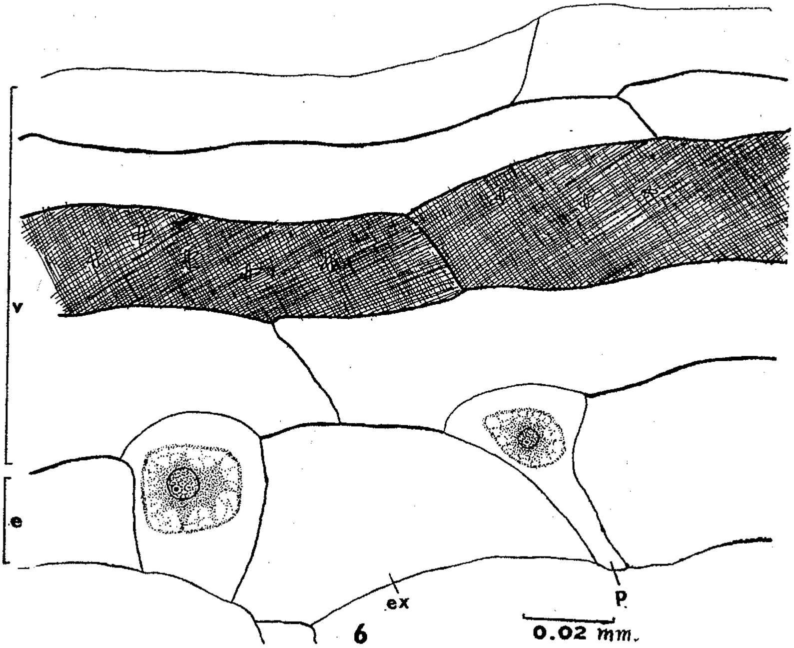
The presence of fibrillar thickenings in addition to pits on the cell walls of the velamen of the Amaryllidaceae species clearly indicate a structural advance over the velamen of the Liliaceae which is charactersised by pits only (Mulay and Deshpande, 1959). The velamen of *Hemerocallis fulva* of the Liliaceae shows thickening fibrils which are to some extent similar to the fibrillar thickenings observed in *Agapanthus africanus* and *Crinum latifolium*. The latter two species have identical structure. All the above three species, *i.e.*, *Hemerocallis fulva* of the Liliaceae, *Crinum* and *Agapanthus* of the Amaryllidaceae show multiperforate plates in the metaxylem (Pl. XVII, Fig. 3).

Haberlandt (1914) has stated that the outer tangential walls of the exodermis are thick but never pitted. On the other hand in the present investigation pits have been observed in the walls of the exodermal cells of the species of the Liliaceæ and the Amaryllidaceae. Occurrence of pits on the exodermal walls of the epiphytic orchids is quite common as has been demonstrated in the structure of exodermis in *Eria nana* A. Rich. and *Coelogyne barbata* Lindl. ex Griff. (Mulay *et al.*, 1958).

There is no consensus of opinion concerning the use of the terms 'exodermis' and 'hypodermis'. Both the terms are used individually to describe several different tissues, and many a times are used synonymously.

The outermost cortical layer next to the epidermis was described as 'hypodermis' by Jorgensen* (1878), Sachs (1882), De Bary (1884) and Sielder* (1892). Mez* (1896) designated it as a 'sclerosed layer' and described it as a characteristic of Bromeliaceous roots. Kroemer (1903) used the term 'intercutis' to include both exodermis and the

* Quoted by Krauss (1949).



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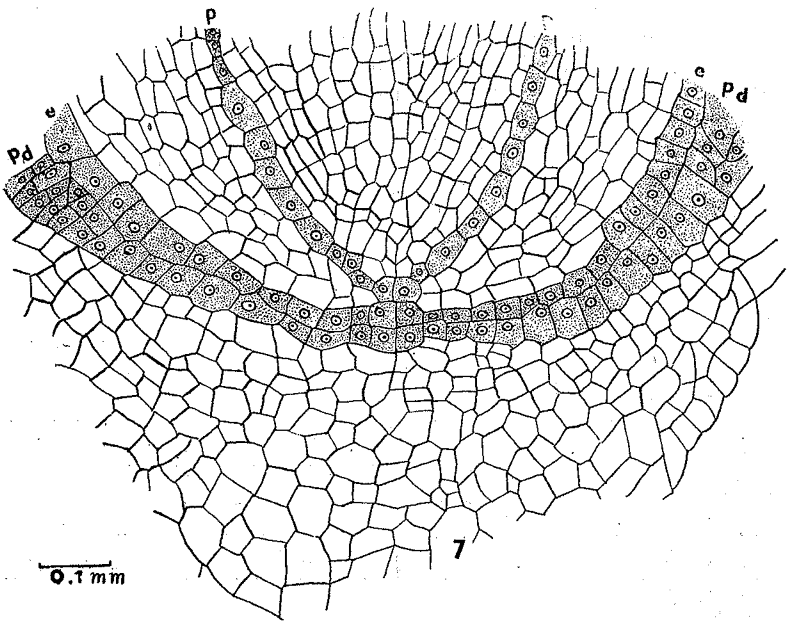

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TEXT-FIGS. 6–7. Fig. 6. Portion of the root of *Crinum latifolium* in l.s. showing cross pits and fibrillar thickenings. *v* = velamen; *p* = passage cell; *ex* = exodermal cell; *e* = exodermis. Fig. 7. Median longitudianl section of the root apex of *Sansevieria thyrsiflora* showing the origin of exodermis. Stippled cells at the apex show apical construction. *pd* = protoderm; *e* = exodermis; *p* = pericycle.

outer cortex. Holm (1915) in describing secondary roots of *Ananas* named the outermost layer of the cortex as ' exodermis '.

The term ' hypodermis ' is still being applied to the subepidermal cortical layers in general anatomical literature. Some authors distinguish hypodermis of root under the special name ' exodermis ', while Hayward (1938), Eames and MacDaniels (1947) and Williams (1947) maintain that such an exodermis as described above is merely a type of hypodermis. Van Fleet (1950) discusses the histochemical and morphological relationship between hypodermis and endodermis, and believes the hypodermis to be the mirror image of the endodermis. According to the recent observations of Mulay *et al.* supported by the findings of the present investigations, it is the exodermis and not the hypodermis which is the counterpart and mirror image of the endodermis. All the authors who designate exodermis as hypodermis or by any other term do not seem to have taken into consideration the ontogeny of this particular tissue. According to Meyer (1940) the earlier authors studied only the morphological and functional aspect but never investigated the ontogeny and thus failed to recognise the exodermis as having a distinct origin. Her ontogenetical studies revealed that the exodermis is formed from the cortically initiated zone. Meyer's stand on this tissue has been justified by Engard (1944) who concludes from his work on orchid roots, that the term exodermis for the designation of this layer is correct. The histogenetic origin of both exodermis and the endodermis can be traced to the periblem or cortically initiated zone, its outer limiting layer forming the exodermis and inner limiting layer forming the endodermis. Engard (1944) further opines that the term ' hypodermis ', described by many earlier authors, refers to the spatial relationship with epidermis and does not show any ontogenetic relation with the cortex. This has been pointed out by Krauss (1949) also.

The following are the facts emerging out from a careful comparison of the exodermis with the endodermis, as observed in the present study and by Mulay *et al.*:

1. Both originate from the periblem or the cortical initiation zone, the exodermis forming outer limit and the endodermis the inner limit of the cortex.

2. Both form uniseriate layers, resulting from anticlinal divisions.

3. Both have cells with suberised walls with occasional individual passage cells.

4. Exodermal cells have thick outer tangential walls while endodermal cells have thick inner tangential walls. The walls of the passage cells in both the layers are thin.

5. Sometimes casparian strips which normally occur in endodermal cells may be found in exodermal cells.

6. The occurrence of passage cells in the endodermis is usually in groups of two or three. Groups of two or three passage cells have also been observed in the exodermis.

Thus, a comparative study of these two tissues shows the justification for the use of the term ' exodermis ' for the outer limiting layer of the cortex, which lies beneath the velamen.

Summary

1. The velamen in the Amaryllidaceae is characterised by fibrillar and banded thickenings and thus is more specialised than the velamen in the Liliaceae which has pits only.

2. Ontogenetically the exodermis is related to the endodermis.

3. The exodermis is a uniseriate layer delimiting cortex from the velamen.

4. A thorough comparison of the endodermis with that of exodermis indicates that the use of the term ' exodermis ' for the outer limiting layer of the cortex is justified.

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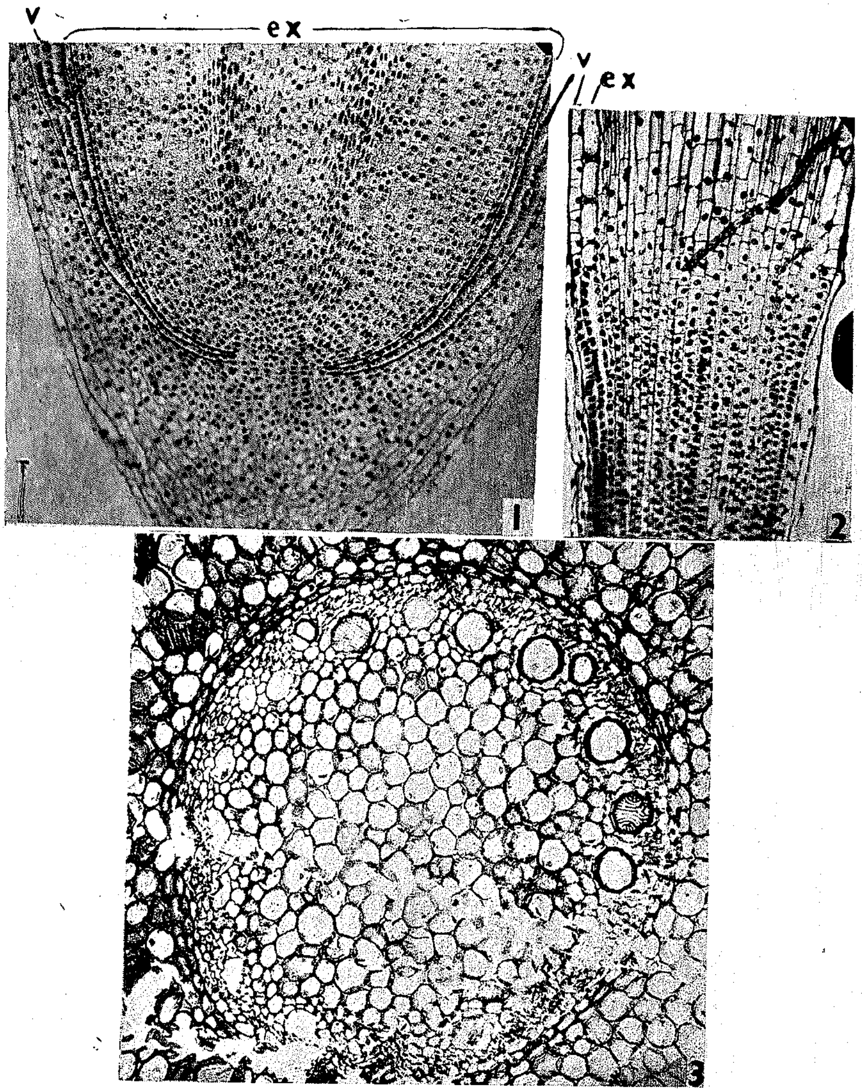
EXPLANATION OF PLATE XVII

FIG. 1. Median longitudinal section of the apical region of *Aspidistra lurida* showing the formation of exodermis and velamen. *v* = velamen; *ex* = exodermis. At the apex is a group of common initials. Retouched portion shows velamen and the exodermis, ×200.

FIG. 2. L.S. behind the root apex of *Haemanthus coccineus* showing differentiation of exodermis into long and short cells. Note that short cells have prominent nuclei and the long cells without them. External to exodermis is velamen in early stages showing nuclei, ×195.

FIG. 3. T.S. root of *Hemerocallis fulva* showing multiperforate metaxylem vessels, ×200.



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FIGS. 1–3