

# The endothecium — a neglected criterion in taxonomy and phylogeny?

A. R. A. NOEL\*

## ABSTRACT

A method has been devised for the screening of the endothecium in flowering plants, principally with a view to describing the cell wall thickening. A scheme of nomenclature and coding has been proposed, which permits a more detailed and unambiguous recording of endothelial variety than was hitherto possible. There is some evidence that this structural variation could have taxonomic and phylogenetic significance.

## RÉSUMÉ

### L'ENDOTHÉCIUM, UN CRITÈRE NÉGLIGÉ EN TAXONOMIE ET PHYLOGÉNIE?

Une méthode d'observation détaillée de l'endothécium chez les phanérogames a été établie, principalement en vue de décrire l'épaississement de la cloison cellulaire. L'établissement d'une terminologie et d'une codification, qui permet de distinguer la variation de l'endothécium de façon plus détaillée et moins ambiguë que jusqu'à présent, a été proposé. Il semble que cette variation structurale pourrait avoir une portée taxonomique et phylogénétique.

The study of anther structure has for a long time been overshadowed by the considerable advances in systematic and historical palynology and by the more recent work on the biology of the tapetum and pollen. Although there have been numerous applications of the external morphology of the stamen to taxonomic problems, the wealth of variety in anther wall histology is still incompletely explored or exploited.

One such source of variety is the structure of the mature endothecium, the so-called hypodermal fibrous layer. The most comprehensive studies of the characteristic wall thickening patterns in this tissue were made by Purkinje (1830), Chatin (1870), Le Clerc du Sablon (1885) and Kuhn (1908). Kuhn appreciated the need to consider the three dimensional aspects of the endothelial cell and identified six cell types on a basis of their wall thickening. The value of the endothecium in taxonomy was investigated by Dormer (1962) and Nordenstam (1978), with reference to the Asteraceae, by Arora & Tiagi (1977) in the Apiaceae and by Eyde (1977) in the Onagraceae. In these families wall thickening patterns were shown to have some diagnostic potential. Nevertheless, Davis (1966) had concluded that the endothecium appeared to have no taxonomic value, although in her extensive review she usually recorded only whether 'fibrous' thickenings were present or not.

It is the intention of this contribution to show that the range of structural diversity in the endothecium is much greater than was previously described. A comprehensive system of description and nomenclature will be developed in order that the systematic potential of endothelial features can be better assessed.

## MATERIALS AND METHODS

Preparations of the endothecium were made from both fresh material stored in formalin-propionic-acetic acid or 70% ethanol, and from dried herbarium specimens. Voucher specimens are preserved at the Natal University Herbarium (NU) in Pietermaritzburg, together with pickled material. So far over five hundred taxa have been examined.

Mature stamens were maintained for 15 mins in 60% aqueous lactic acid at 95° C. They were then mounted on a slide in glycerine jelly after opening the loculi and flattening the walls. A varying degree of maceration took place: sometimes the epidermis was removable in a sheet and often the endothelial cells were readily separable. Some large anthers, such as *Bruguiera gymnorrhiza* (L.) Lam. required up to 2 hrs heating. Herbarium material may need preliminary boiling in water, although this was not usually necessary. The samples described were from the central region of the loculus wall: the connective and specialized areas such as the stomium were not included.

The wall thickenings were examined and photographed with Nomarski interference contrast optics in a Reichert Univar microscope.

## GENERAL FEATURES OF THE ENDOTHECIUM

It is not proposed to consider the development or homology of the fibrous layer: this has been done by Eames (1961) and Davis (1966). It is sufficient to point out that the wall of the anther loculae varies in thickness and complexity, but that in most species at maturity comprises only an epidermis and endothecium, the ephemeral middle layers and tapetum making no effective contribution. The endothelial cells may be more or less isodiametric, broadly fusiform or elongated to varying degrees, and lying paralleled or normal to the epidermal surface. The orientation is usually related in a specific way to the long axis of the anther. There is a considerable range in cell size, the tangential width in *Euphorbia hirta* L. and *Plectranthus laxiflorus* Benth. being only 10.0

\* Department of Botany, University of Natal, P.O. Box 375, Pietermaritzburg 3200, South Africa.

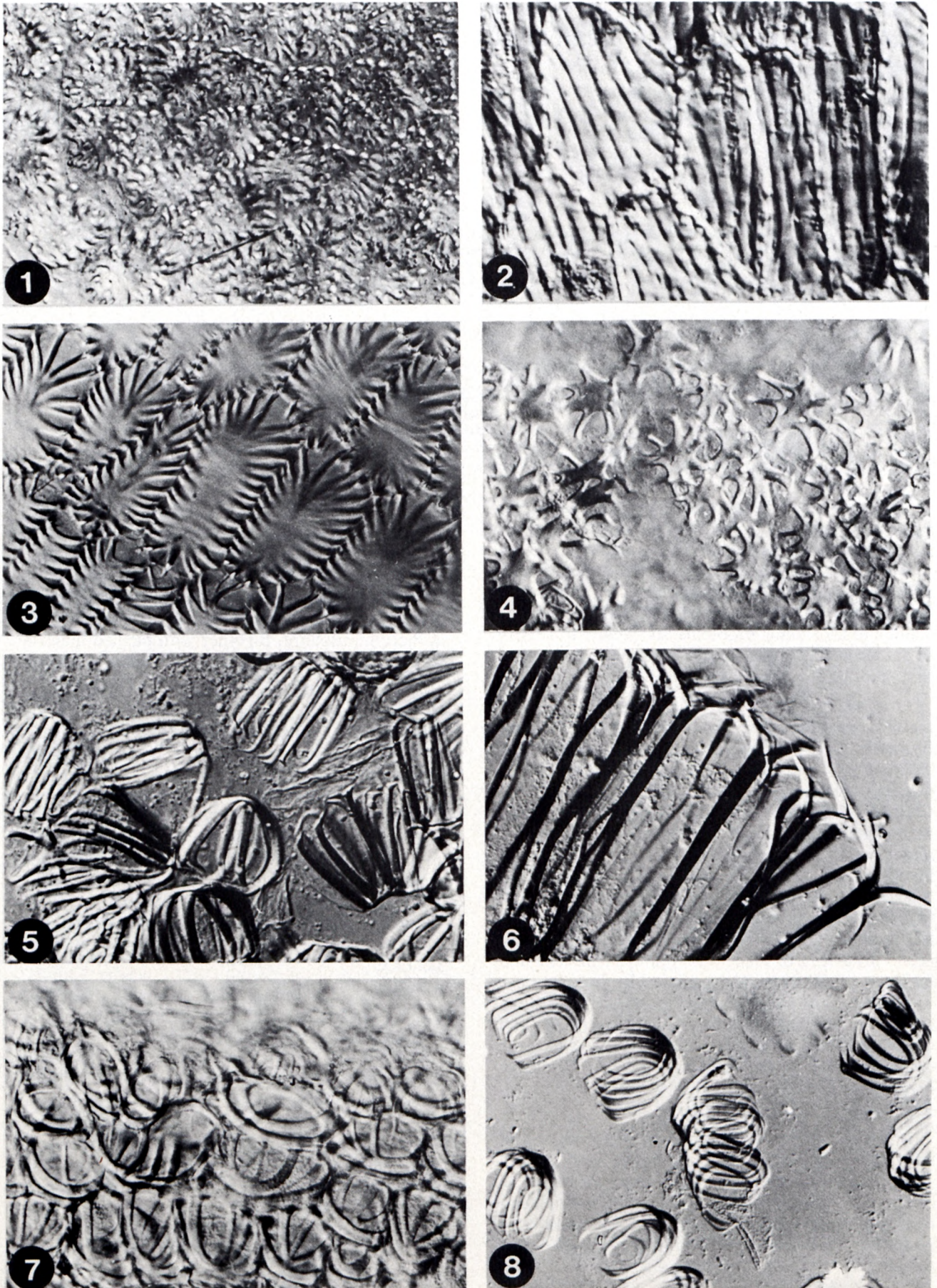


FIG. 1.—Endothelial wall thickening in: 1, *Commicarpus plumbagineus*; 2, *Ochna natalitia*; 3, *Burnatia enneandra*; 4, *Valeriana capensis*; 5, *Polygala virgata*; 6, *Lilium candidum*; 7, *Hermannia gerrardii*; 8, *Cephalalaria natalensis*; (all  $\times 800$ ).

and 12.5  $\mu\text{m}$  respectively, whereas that of *Tradescantia virginiana* L. was found to exceed 100  $\mu\text{m}$ .

#### CELL WALL THICKENING

The few studies that have been made of the development of the characteristic wall thickenings (Heslop-Harrison, 1968; De Vaal, 1978) indicate that secondary, orientated cellulose deposition takes place in a manner very similar to that which occurs during the differentiation of primary xylem elements. It is interesting to note that when no secondary wall deposition takes place, such as in *Erica oatesii* Rolfe, *Galopina circaeoides* Thunb. and *Philippia evansii* N.E. Br., all walls are quite thin. When thickening does occur, it is usually highly localized, in a pattern representing a high degree of specific organization. Only rarely are all walls equally and heavily thickened: one example is in the giant anthers of *Hydnora solmsiana* Dinter. Another uncommon type, where all walls show heavy reticulate thickening, occurs in *Chironia baccifera* L.

It is convenient to consider these thickenings in isolation from the rest of the wall and cell of which they are a part, admittedly an artificial approach. It then becomes possible to identify patterns of thickening and to recognize the components of variety, to which can be ascribed a name and a numerical code. For example, the inner tangential cell wall alone may be completely and heavily thickened or, alternatively, the thickening may be restricted to more or less of the centre of the wall. This thickening may be termed the 'base plate'. The presence of circular or lenticular unthickened regions characterize a 'perforate' plate, e.g. *Commicarpus plumbagineus* (Cav.) Stanl. (Fig. 1.1), *Ochna natalitia* (Meisn.) Walp. (Fig. 1.2) and *Clematis brachiata* Thunb. Absence of continuous thickening from around the margins of the tangential wall, so that the plate appears suspended, can be designated tympanate (*Burnatia enneandra* Micheli, Fig. 1.3) or with still further reduction, in isodiametric cells, palmate (*Valeriana capensis* Thunb., Fig. 1.4) and in elongate cells, rachial. The plate may eventually consist of no more than an anastomosis of strands running into the anticlinal walls. In an entirely different kind of thickening, 'polygonal', only the rims of the tangential walls are affected and the more or less angular rings of adjacent cells lie edge to edge to form a net. At least 11 states of the feature 'base plate' may be distinguished, the 300 series in Table 1. This tangential view of the endothelial cells is the most readily observed, and the thickening pattern, in conjunction with cell size and shape shows a large amount of potentially useful variation.

Thickening of the anticlinal walls usually takes the form of riblike extensions of the base plate. Diversity arises from the number, spacing, thickness and cross sectional profile (round to D shaped, as opposed to being obviously flattened). The ribs vary in length, in *Pelargonium luridum* (Andrs.) Sw. consisting of little more than triangular teeth fringing the plate. Alternatively the ribs fork and join to make a stout reticulum. In some more or less

symmetrical cells the ribs seem to arise from radiate thickenings of a large, thin, somewhat scalloped plate, giving a very characteristic type which may be called 'foliate', as in *Crinum moorei* Hook. f. The opposite extreme is represented by the lobster pot or ptenoid type in *Polygala virgata* Thunb. (Fig. 1.5), in which the symmetrical cell is enclosed by a cage of strands originating in a basal plexus and curving over to partially reinforce the outer tangential wall.

An interesting feature is the mode of termination of the ribs, either at the junction of the anticlinal wall with the outer tangential wall, or after turning across this outer wall. If the ribs are confined to the anticlinal wall, they may end in a flat top with pointed extensions on each side, the 'serif' type as shown by *Lilium candidum* L. (Fig. 1.6). If the ribs are very closely spaced, accentuated serifs can join laterally, forming in effect the rim of a basket, such as in *Hermannia gerrardii* Harv. (Fig. 1.7). Three variants 'sans-serif' are possible, rounded, knobbed or tapered to a point. The extent to which the ribs continue across the outer tangential wall varies from a slight incurving, when the centre region of the wall is left unsupported, to a complete traverse and even continuation down the opposite side of the cell.

The absence of continuous thickening of the inner tangential wall, that is the absence of base plate, has a profound effect on the pattern, and presumably mechanical consequences, of the thickening of the rest of the cell. The simplest and commonest of these patterns consists of a series of unconnected U-bars, involving the inner tangential and anticlinal walls only (*Cephalaria natalensis* Kuntze, Fig. 1.8). The profile of the U may be sharply angular or rounded, wide with relatively short ribs or narrow, with long ribs. These ribs show the same variety of ending as described previously: they may also show more or less regular branching, the effect of which is that the outer tangential wall may have many more ribs or rib endings than does the inner tangential wall. If one, or even both of the ribs of a U continues across the outer tangential wall and down the opposite side of the cell, without joining the ascending ribs on that side, a pseudo-annular pattern results, as exemplified by *Diclis rotundifolia* (Hiern) Hilliard & Burt, *Oenothera biennis* L. (Fig. 2.1), *Oxalis semiloba* Sond. or *Wahlenbergia zeyheri* Eckl. & Zeyh. Two further important related types are 'annular', with true rings (*Ipomoea ficifolia* Lindl., Fig. 2.2) and 'helical' (*Acalypha peduncularis* E. Mey., Fig. 2.3, and *Rinorea natalensis* Engl., Fig. 2.4). Helically thickened cells vary greatly in size, shape, number of gyres and strand thickness, and may even show double or opposed helices. The ends of the helix may be closed by spiral reinforcement of the anticlinal walls (*Aloe kraussii* Bak., Fig. 2.5). Although the names are self explanatory, considerable care is needed in practice, to discriminate between these plateless types of thickening. This is not difficult if maceration has effectively isolated the cells, but may be so with an intransigent endothecium overlain by a thickened epidermis. Furthermore, cells with pseudo-annular, annular and helical thickening, can intergrade locally, so that one may encounter a short helical section within an annularly thickened cell.

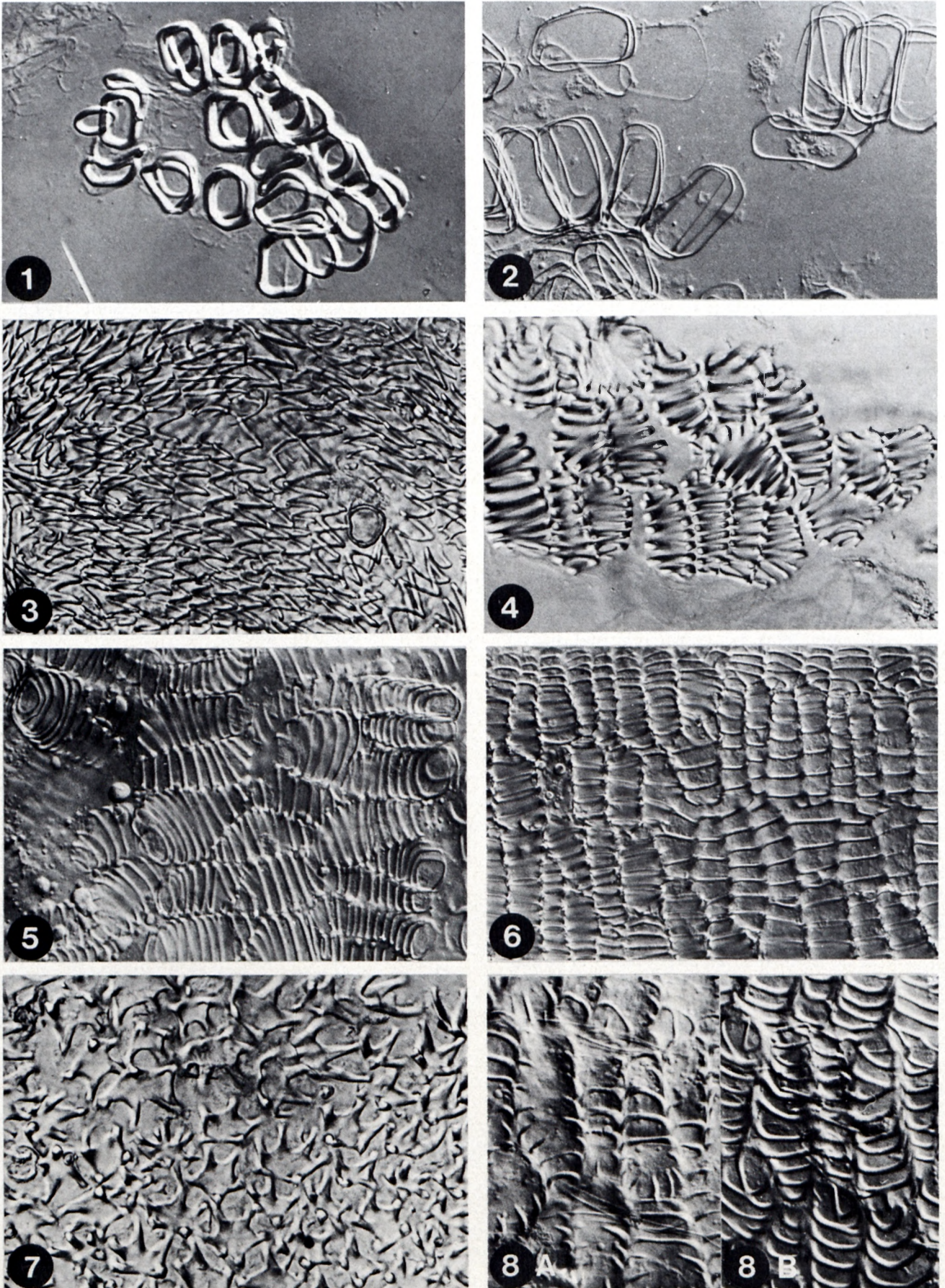


FIG. 2.—Endothecial wall thickening in: 1, *Oenothera biennis*; 2, *Ipomoea ficifolia*; 3, *Acalypha peduncularis*; 4, *Rinorea natalensis*; 5, *Aloe kraussii*; 6, *Piper capense*; 7, *Rorippa nasturtium-aquaticum*; 8, *Dianthus basuticus*—a, inner tangential and b, outer tangential views of the same field; (all  $\times 800$ ).

TABLE 1.—Summary and coding of endothelial characters

Cell character	Numerical code and character state				
<i>Cell size</i> <sup>1</sup>	111 Large: > 75 µm	112 Medium 25–75 µm	113 Small: < 25 µm		
<i>Shape</i>	121 ± Isodiametric	122 Rectangular	123 Fusiform	124 Vertical	
<i>Wall thickening</i>	201 Absent	202 Present: all walls solid	203 Present: all walls reticulate	204 Present: localized	
<i>Base plate</i>	311 Absent	312 Thin	313 Thick		
<i>Proportion</i>	321 Entire	322 > ½ (Tympante)	323 < ½ (Palmate or rachial)	324 Anastomosis	325 Polygonal
<i>Perforation</i>	331 Imperforate	332 Small and few	333 Large		
<i>Ribs: Pattern</i>	411 U	412 Pseudo-annular	413 Annular	414 Helical	415 Doubly Helical
<i>No per cell</i>	421 < 6	422 > 5 < 14	423 > 14		
<i>Spacing</i>	431 Wide (> twice rib width)	432 Close (< twice rib width)			
<i>Branching</i>	441 Absent	442 Present			
<i>Length</i>	451 Short (< ⅔ cell height)	452 Long (> ⅔ cell height)	453 Overtopping		
<i>Profile</i> <sup>2</sup>	461 Angular	462 Rounded			
<i>Section</i> <sup>2</sup>	471 D to round	472 Flattened	473 Thin, tapering		
<i>Tip</i>	481 Serif	482 Rounded	483 Knobbed	484 Pointed	

<sup>1</sup>Length in tangential view<sup>2</sup>In rib or ring

## TISSUE PATTERNS

The cell wall features described above contribute to an overall tissue pattern, which in a preparation of an extensive area of the loculus wall may be very striking, and for some purposes, sufficiently diagnostic. For these a separate set of descriptions may be applied, such as 'daisy field' for the small palmate pattern of *Piper capense* L. (Fig. 2.6) or 'scalariform' the pattern in *Rorippa nasturtium-aquaticum* (L.) Hayek (Fig. 2.7). Usually there will be an inner and an outer tangential view which differ considerably from one another, as in *Dianthus basuticus* Burt Davy (Fig. 2.8 A & B.) However, these patterns are not sufficiently sensitive and each can be derived from more than one cell type. There are also a number of other features which can be recorded from the same preparation, such as the presence of druses, wall thickening in the connective and in the epidermis, and cuticular sculpturing but these are insufficiently explored.

## CONCLUSIONS

Table 1 summarises the variation in endothelial wall thickenings so far recognized. It incorporates a code, so that the aggregate states of this feature can readily be scored for a large sample of taxa. Although this scheme is tentative, it is nevertheless clear that much more structural variety exists than has been reported previously and that it is susceptible to systematic description. The illustrations of Kuhn (1908) and other early writers were too diagrammatic and in numerous subsequent contributions to plant embryology, even where anther development has been described and figured, the endothelial wall thickenings have usually been inadequately represented. It is known (De Vaal, 1978) that the wall thickenings attain their final form

only late in the development of the anther, and it is possible that many stylized illustrations were based on immature cells.

The observations described here are presented as material for a study of structural variation: it is premature to comment on their taxonomic and phylogenetic significance. There are indications of constancy at the generic level, or even through larger groups such as the Asteraceae. There is also a discernible trend of the presence of a base plate and heavy lateral thickening through the Magnoliidae and Ranunculidae (*sensu* Takhtajan), a view which corroborates that of Eyde (1977). It is also apparent that a connection between endothelial type and anther function is less direct than might be anticipated.

## ACKNOWLEDGEMENTS

I wish to thank M. Brand, B. Emmanuel, I. Harper, D. Noel, P. Page and D. Tunnington for technical assistance. I also acknowledge the generous support of the CSIR for this and related projects.

## REFERENCES

- ARORA, K. & TIAGI, B., 1977. The role of the endothecium in the identification of Umbellifers. *Curr. Sci.* 46: 531.  
 CHATIN, G. A., 1870. *De l'anthere*. Paris.  
 DAVIS, F. L., 1966. *Systematic embryology of the Angiosperms*. New York: Wiley.  
 DE VAAL, J., 1978. *Studies in the cell wall development in the endothecium of Bulbine frutescens (L.) Willd.* M.Sc. thesis, University of Natal, Pietermaritzburg.  
 DORMER, K. J., 1962. The fibrous layer in the anthers of Compositae. *New Phytol.* 61: 150–153.

- EAMES, A. J., 1961. *Morphology of the Angiosperms*. New York: McGraw-Hill.
- EYDE, R. H., 1977. Reproductive structures and evolution in *Ludwigia* (Onagraceae). 1. Androecium, placentation, merism. *Ann. Mo. bot. Gdn* 64: 644-655.
- HESLOP-HARRISON, J., 1968. The emergence of pattern in the cell walls of higher plants. *Develop. Biol. Suppl.* 2: 118-150.
- KUHN, E., 1908. *Über den Wechsel der Zelltypen Endothecium der Angiospermen*. Ph.D. diss., University of Zurich. Zurich: Leeman.
- LE CLERC DU SABLON, M., 1885. Recherches sur la structure et la déhiscence des anthères. *Annls Sci. nat. Bot. sér.* 7,1: 97-134.
- NORDEMSTAM, B., 1978. Taxonomic studies in the tribe Senecioneae (Compositae). *Opera Bot.* 44: 3-83.
- PURKINJE, J. E. 1830. De cellulis antherarum fibrosis nec non de granorum pollinarium formis. *Commentatio Phytotomica*. Vratislaviae: Gruesonil.