

## Features of Foliar Epidermis and Stomata in Some Euphorbiaceae Subfamily Oldfieldioideae

Raju, Vatsavaya S.

(Department of Botany, Kakatiya University, Warangal-506 009, India)

### ABSTRACT

The features of foliar epidermis and stomata are studied in nine genera representing all the four tribes of the subfamily Oldfieldioideae of the family Euphorbiaceae. On both sides of the leaf, the cuticle is generally smooth with more or less straight epidermal anticlinal walls. The epidermal cells are polygonal and their size varied with species on both sides. The costal cells are either distinct (*Dissiliaria*, *Oldfieldia*, etc.) or indistinct (Caletieae). In the taxa examined, the stomata are confined to the abaxial epidermis and diffusely orientated except in Caletieae. They are basically of brachyparacytic type; however, they are anomocytic in *Androstathys* and of a special type in *Mischodon*. A systematic consideration of these features showed that they are not only useful in revealing relationships within the subfamily but also of aid in the classification.

### INTRODUCTION

Raju and Rao (1977) have reviewed the earlier work on the foliar epidermis and stomata in the family Euphorbiaceae. That and a survey of the recent literature reveal the obvious gap in the knowledge of foliar epidermis and stomata of somewhat recently constituted and interesting subfamily Oldfieldioideae of the family Euphorbiaceae.

The Oldfieldioideae were recognized as a separate subfamily by Köhler and Webster (Webster, 1967) because of their special pollen and some other distinctive features. It was constituted with taxa out of the two traditional subfamilies, namely, Phyllanthoideae and Euphorbioideae/Crotonoideae, or from the biovulate Euphorbiaceae.

According to Webster (1975), the subfamily Oldfieldioideae consists of four tribes and 21 genera. It is the objective of the present paper to assess how far this subfamily and its tribal groupings are natural in terms of foliar epidermis and stomata.

### MATERIAL AND METHODS

The present study takes up the examination of only the mature foliar epidermis and stomata in nine genera which represent all the four tribes of the subfamily Oldfieldioideae (Webster, 1975). The names of the taxa examined, along with their sources, are given in Table 1. The methodology and terminology adopted here are the same as followed in the work of Raju and Rao (1977).

## RESULTS

### 1. Cuticle and epidermis

a) Cuticle : Generally smooth though feeble striations, similar to those found in the subfamily Phyllanthoideae (Rao and Raju, 1988) occur. They are usually prominent near the stomata or in costal cells (e.g. *Oldfieldia* – Fig. 1F; *Petalostigma* – Fig. 1K; *Dissiliaria* – Fig. 2A).

b) Epidermis : *Anticlinal walls* : The adaxial anticlinal walls are straight in all the taxa except *Mischodon* (Fig. 1I) where they are slightly undulate. The abaxial cell walls are also straight but for *Dissiliaria* (Fig. 1L) and *Androstachys* (Fig. 1H) where they are slightly sinuous or arched (Table 1).

*Cell shape* : Predominantly polygonal in all.

*Cell-size* : The cells vary in their size considerably. They are largest in the adaxial side ( $60.0 \times 45.0 \mu\text{m}$ ) as well as the abaxial side ( $46.8 \times 33.6 \mu\text{m}$ ) in *Pseudanthus* whereas smallest in the adaxial side in *Picrodendron* ( $20.0 \times 14.0 \mu\text{m}$ ) and on the abaxial side in *Petalostigma* ( $15.2 \times 10.0 \mu\text{m}$ ).

*Costal cells* : They are distinct in *Dissiliaria*, *Oldfieldia* (Fig. 1D, F) and *Picrodendron* while indistinct in Caletieae. However, they are distinct abaxially in others, e.g. *Androstachys* and *Austrobuxus* (Table 1).

### 2. Stomata

a) Distribution : The stomata are present only in the lower epidermis in the species examined (Table 2). They are usually confined to the intercostal areas (e.g. *Androstachys*, *Picrodendron*); but, in Caletieae, they occur along two narrow strips on either side of the midrib and slightly inner to the margins abaxially (Fig. 2C).

b) Orientation : The stomata are diffusely orientated in most cases, but arranged parallel to the midrib and margins in Caletieae (Fig. 2C).

c) Frequency of stomata and stomatal index : Highest number of stomata per sq mm area are found in *Androstachys* (c. 223) and lowest in *Austrobuxus* (74). Abaxially, the stomatal index in the subfamily is lowest in *Petalostigma* (5.70) and highest in *Dissiliaria* (20.00) (see Table 2).

d) Average size of stomata : Within the subfamily (Table 2), the stomata are smallest in *Mischodon* ( $24.0 \times 14.0 \mu\text{m}$ ) and largest in *Pseudanthus* ( $36.0 \times 33.2 \mu\text{m}$ ).

e) Morphology of guard cells : A cuticular rim/dome is present above the guard cells in several taxa, especially in the tribe Caletieae. The poles of the guard cells are slightly elevated (e.g. *Micrantheum*) or not so. In all the taxa, the poles of the guard cells are exposed; the radial walls are very much thickened (Fig. 1 B,C; Fig. 2E, Q), so also the outer stomatal ledge (Fig. 1C; Fig. 2B, E, Q, R).

f) Basic stomatal type : The stomata are basically brachyparacytic : *Austrobuxus* (Fig. 1B, C), *Dissiliaria* (Fig. 1L) and *Oldfieldia* (Fig. 1E) of Hyaenancheae, *Petalostigma* (Fig. 1K) of Petalostigmatae and *Picrodendron* (Fig. 2G) of Picrodendreae. However, they are of anomocytic type in *Androstachys* (Fig. 1H) and of special type in *Mischodon*.

Table 1. Features of cuticle and foliar epidermis in some Euphorbiaceae-Oldfieldioideae

TAXON	CUTICLE		EPIDERMIS						SOURCE
	Intercostal cells*		Costal cells						
	Ad	Ab	Ad	Ab	Ad	Ab	Ad	Ab	
Tribe: HYAENANCHEAE Subtribe: Mischodontinae 1. <i>Mischodon zeylanicus</i> Thw.	Sm	Sm	Stra, SI Sin	Stra, SI Sin	22.0×16.0	22.0×12.8	SI dist	SI dist	KRV Subramanyam et al. s.n., South India
Subtribe: Paivaesuinac 2. <i>Oldfieldia somatensis</i> (Chiov.) Milne-Redh.	Sm	Sm	Stra	Stra	38.0×28.0	30.0×15.2	Dist	Dist	Gathii 129, Kenya
Subtribe: Dissiliarinae 3. <i>Austroboxus swinhii</i> (Beuzev. & white) Airy-Show	Sm	Sm	"	"	39.6×34.8	27.0×26.0	"	"	JB Williams s.n., NSW, Australia
4. <i>Dissiliaria baloghitoides</i> F. v. Muell. ex baill.	Stri	Stri	"	SI Sin	NC	26.4×20.0	"	"	JB Williams s.n., Old., Australia
Tribe: PETALOSTIGMATEAE 5. <i>Androstachys johnsonii</i> Prain	Sm	Sm	"	Stra, Arch	24.0×18.0	20.0×09.2	"	"	LE Codd 8375, Transwaal, South Africa
6. <i>Petalostigma quadriloculare</i> F. v. Muell.	"	Stri	"	"	30.0×20.8	15.2×10.0	"	"	GJ White s.n., NSV, Australia
Tribe: CALETIEAE 7. <i>Micranthemum ericoides</i> Desf.	"	Sm	"	Stra	52.0×34.8	50.0×24.0	Indist	Indist	JB Williams s.n., NSW, Australia
8. <i>Pseudanthus ovalifolius</i> F. v. Muell.	"	"	"	"	60.0×45.0	46.8×33.6	"	"	HJ Wisman s.n., NSW, Australia
Tribe: PICRODENDREAE 9. <i>Picrodendron baccatus</i> (L.) King & Orban	"	"	"	"	20.0×14.0	21.2×14.8	SI dist	SI dist	FTG, Florida, USA

\*Predominantly polygonal in shape on either side in all taxa.  
 Ab: Abaxial; Ad: Adaxial; Arch: Arched; Dist: Distinct; Indist: Indistinct; NC: Not calculated because of limited material; Sin: Sinuous; SI: Slightly; Sm: Smooth; Stra: Straight; Stri: Striated; FTG: Fairchild Tropical Botanic Garden; Qld: Queensland; NSW: New South Wales.

Table 2. Features of foliar stomata in some Euphorbiaceae-Oldfieldioideae

TAXON	Stomatal Frequency (Sq. mm)		Stomatal index		Average stomatal size ( $\mu$ m)	Type of Stomata(%)			Stomatal abnormalities			
	Ad	Ab	Ad	Ab		P	ANO	Cy	C <sub>1</sub>	C <sub>2</sub>	C <sub>3</sub>	SG
Tribe: HYAENANCHEAE												
Subtribe: Mischodoninae												
1. <i>Mischodon zeylanicus</i>	-	NC	...	NC	24.0×14.0	NC	NC	NC	-	-	-	-
Subtribe: Paivacusinae												
2. <i>Oldfieldia somalensis</i>	-	NC	...	NC	28.0×26.0	99.0	1.0	-	-	+	+	+
Subtribe: Dissiliariinae												
3. <i>Austrobuxus swatini</i>	-	74	...	14.60	30.0×26.0	96.0	2.0	2.0	-	-	-	-
4. <i>Dissiliaria batoghioides</i>	-	122	...	20.00	32.4×22.0	99.0	1.0	-	-	+	-	-
Tribe: PETALOSTIGMATEAE												
5. <i>Androstachys johnsonii</i>	-	C.223	...	14.50	22.0×23.0	-	100	-	-	+	-	-
6. <i>Petalostigma guadriloculata</i>	-	100	...	5.70	24.0×25.2	99.5	0.5	-	-	-	-	-
Tribe: CALETIEAE												
7. <i>Micrantheum ericoides</i>	-	C.159	...	17.30	29.2×22.8	85.0	15.0	-	+	+	+	+
8. <i>Pseudanthus ovalifolius</i>	-	NC	...	NC	36.0×33.2	NC	NC	NC	-	+	-	-
Tribe: PICRODENDREAE												
9. <i>Picrodendron baccatum</i>	-	153	...	14.90	24.8×16.0	98.0	2.0	-	-	+	-	-

Ab; Abaxial; Ad; Adaxial; ANO: Anomocytic; C<sub>1</sub>, C<sub>2</sub>, C<sub>3</sub>: Superposed, parallel and obliquely placed contiguous stomata, respectively; Cy: Cyclocytic; NC : Not calculated Decease of limited material; P: Paracytic; SG: Single guard-celled stomata, + : Present; - : absent.

Sometimes, late divisions in one or both the subsidiaries of brachyparacytic stomata has led to the alterations in the basic type as in *Picrodendron* (Fig. 2G).

g) Stomatal abnormalities : Parallel type of contiguous stomata (Raju and Rao, 1977) are the most frequent (Fig. 2N); superposed and obliquely placed ones do occur as in *Micranthemum*. Arrested stomatal development and other stomatal abnormalities are rather infrequent (Table 2; Fig. 2L-P). Plasmodesmata of type I (Raju and Rao, 1983) occur in *Dissiliaria* (Fig. 2R).

## DISCUSSION

The following is the discussion on the bearing of foliar epidermis and stomata, in the light of evidence from allied disciplines, in the classification of Euphorbiaceae subfamily Oldfieldioideae and all its four tribes (Webster, 1975). However, some of the conclusions drawn are tentative since the representative taxa studied are not exhaustive.

### 1. Hyaenancheae

Being split-up into four subtribes, it is the largest tribe within Oldfieldioideae (Webster, 1975). It includes those biovulate genera which have pollen of *Aristogeitonia* subtype (Punt, 1962) or *Tetracoccus* type (Köhler, 1965). However, Webster (1975) has left out *Androstachys* and *Paradytpetes* of Hutchinson's (1969) tribe Hyaenancheae. Except Hyaenanchinae, the other three subtribes are considered here for a taxonomic discussion.

a) *Mischodontinae* : Of the five genera included, *Mischodon* Thwaites is a monotypic taxon from Sri Lanka and (?) southern India (Raju, 1984). In it, the stomata are confined to the lower epidermis with plenty of prismatic crystals in the veins.

Although *Mischodon* resembles the other members of the tribe in its pollen, it is somewhat isolated in other respects. For instance, it has a special type of stomata (present study), the vessels are exclusively solitary though the wood conforms to the un-named group of the Phyllanthoideae of Metcalfe and Chalk (1950).

*Mischodon*, together with *Dissiliaria* and *Longetia*, was assigned to *Dissiliariinae* by Pax and Hoffmann (1922). Such a treatment appears unjustified because *Mischodon* has smaller epidermal cells (Table 1), special type of stomata and deciduous hairs, whereas *Dissiliaria* and *Austrobuxus* have larger epidermal cells (Table 1), typical brachyparacytic stomata and well-developed persistent hairs (Rao and Raju, 1985). So, Webster (1975) seems to be justified in keeping the subtribe *Mischodontinae* for *Mischodon*, distinct from *Dissiliariinae* Pax & Hoffmann. However, the other genera of the subtribe (Webster, 1975) are to be investigated to understand their further relationships.

b) *Paivaesinae* : It has four genera, among which is the type genus *Oldfieldia* Benth. (*Paivaesusa* Welw. ex Hook.) from tropical Africa with estimated four species. While Hutchinson (1969) treated *Oldfieldia* in *Bischoffieae*, Köhler (1965) has named after it the subtribe *Oldfieldiinae*, the tribe *Oldfieldieae* and the subfamily *Oldfieldioideae*. Later, Webster (1967) has

validated the subfamily name (*Oldfieldioideae* Köhler & Webster, J. Arnold Arb. **48**: 308. 1967).

As regards the relationship between *Oldfieldia* and *Bischofia*, the former differs from the latter in digitately compound leaves with the leaflets showing brochidodromous venation (Raju, 1981), stomata on the lower epidermis only, straight anticlinal walls, presence of uniseriate hairs and no epidermal idioblasts. Moreover, the pollen grains of *Bischofia* do not conform to the *Tetracoccus* type (cf. Köhler, 1965) and the wood is of *Tetracoccus* type (Metcalf and Chalk, 1950). Hence, a direct relationship between these two genera appears unlikely. Probably they represent different subfamilies as has been opined and treated by Webster (1975).

c) *Dissiliariaceae*: *Longetia* and *Dissiliaria* were the original members of Pax and Hoffmann's (1922) *Dissiliariaceae*. Hutchinson (1969) has treated them in the tribe *Hyaenancheae* which was not split-up further.

Besides *Longetia* and *Dissiliaria*, this subtribe (Webster, 1975) has two more genera, namely *Choriceras* and *Austrobuxus*. According to Airy-Shaw (1973), *Longetia* is congeneric to *Austrobuxus*, in which case, the subtribe will have only three genera. However, Webster (1975) maintains these two as distinct. Unless more materials of these are available for study, this issue cannot be discussed here.

Both *Austrobuxus* and *Dissiliaria* have simple hypostomatic leaves with brachyparacytic stomata and distinct costal epidermal cells. The wood conforms to the un-named group of Metcalf and Chalk (1950) or group C of Bamber (1974) and the pollen grains belong to *Aristogeiton* type of Punt (1962) or *Longetia* type of Köhler (1965). But, they differ: The trichomes are uniseriate in *Austrobuxus* whereas they are uniseriate, stellate and glandular in *Dissiliaria* (Rao and Raju, 1985). The fibres are exclusively of type II in *Austrobuxus* whereas of type I and II occur in *Dissiliaria* (Bamber, 1974).

*Dissiliaria* is certainly isolated within *Oldfieldioideae* concerning its trichomes (Rao and Raju, 1985). In this regard, it resembles certain members of *Acalyphoideae* and *Crotonoideae*. Perhaps here it is relevant to note that, according to Metcalf and Chalk (1950: 1231), the wood of *Dissiliaria* has more in common with the subfamily *Crotonoideae* (incl. *Acalyphoideae*) rather than with group A or B of the *Phyllanthoideae*.

## 2. *Petalostigmateae*

The subtribe *etalostigmatinae* of Pax and Hoffmann (1922) and Köhler (1965) with *Petalostigma* was raised to the status of a tribe by Webster (1975). However, Webster (1975) added to it the anomalous genus *Androstachys*.

Addition of *Androstachys* to *Petalostigmateae* certainly makes it heterogeneous from the point of view of foliar epidermis, stomata, trichomes and venation or otherwise. First, *Petalostigma* has stomata of brachyparacytic type which is typical of woody *Euphorbiaceae* (Raju, 1981) whereas *Androstachys* has anomocytic stomatal type, which is uncommon amongst the *Euphorbiaceae* (Raju, 1981). Although the leaves are tomentose beneath in both, it is formed of short, stout and non-coiled unicellular hairs in *Petalostigma* and of long, linear, coiled hairs in

*Androstachys* (Rao and Raju, 1985). Second, the pollen of *Petalostigma* belongs to Aristogeitonia type (Punt, 1962) or Tetracoccus type (Köhler, 1965). Third, even though both have wood belonging to the un-named group of Phyllanthoideae, *Androstachys* has small, exclusively solitary vessels and uniseriate rays and fibres with distinctly bordered pits (cf. Metcalfe and Chalk, 1950). Fourth, they hail from two different continents: *Androstachys* belongs to south east Africa and Malagasy while *Petalostigma* comes from Australia and New Guinea. Therefore, the affinities between *Androstachys* and *Petalostigma* are perhaps illusory.

### 3. Caletieae

This is entirely an Australian tribe with four genera. A species each of *Micrantheum* and *Pseudanthus* have been studied here.

The taxa of Caletieae constitute a natural group with specialized habit and leaf external and internal morphology which are perhaps associated with their geographic location and endemism.

The plants have small ericoid leaves with straight epidermal anticlinal walls and sunken stomata occurring along narrow strips and orientated parallel to the midrib. The epidermal cells are large, nearly two times larger than in any other Oldfieldioideae studied (Table 1).

### 4. Picrodendreae

The tribe is monogeneric with the isolated monotypic neotropical genus, *Picrodendron* Planch. Until recently, it was included in the family Picrodendraceae Small. Fawcett and Renale (1917) and later Webster (1967) suggested a possible relationship between *Picrodendron* and the Euphorbiaceae. To this effect, Webster (1975) has brought this genus into the fold of Euphorbiaceae-Oldfieldioideae. This was upheld by Hayden (1977) after assessing its affinities with alleged relatives based on wood and leaf anatomical features.

Interestingly, the foliar epidermal features and stomata (Tables 1 and 2) and trichomes (Rao and Raju, 1985) characteristic of *Picrodendron* are shared by other members of the Oldfieldioideae. The African genus *Oldfieldia* with which *Picrodendron* was associated for sometime has in common the features such as compound leaves, hypostomatic leaflets, brachyparacytic stomata and simple hairs. However, the trifoliately compound leaves are found in *Celaenodendron* and *Piranhea* of the subtribe Paivaesusinae of Hyacnancheae. A study of their taxa in close proximity with *Picrodendron* perhaps reveal the truth whether *Picrodendron* has to be treated along with the other compound-leaved Oldfieldioideae (as an advanced subtribe of Hyacnancheae – cf. Hayden *et al.*, 1984) or retained in a separate tribe as has been earlier done by Webster (1975).

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### Explanation of Figures

**Fig. 1.** Leaf in surface view in Euphorbiaceae—Oldfieldioideae.

A–C: *Austrobuxus*: A, B—Adaxial and abaxial epidermises. C—stomatal complex enlarged.

D–F: *Oldfieldia*: D, E—Adaxial and abaxial epidermises. F—costal cells with cuticular striations.

G, H: *Androstachys*: Adaxial and abaxial epidermises.

I: *Mischodon*: Adaxial epidermis.

J, K: *Petalostigma*: Adaxial and abaxial epidermises.

L: *Dissiliaria*: Abaxial epidermis.

cd—cuticular dome; cl—cuticular (stomatal) ledge; hb—hair base; g—guard cell (present below the cuticular dome).

**Fig. 2.** Features of epidermis and stomata in Euphorbiaceae—Oldfieldioideae.

A–C: *Micrantheum*: A, B—Adaxial and abaxial epidermises. C—Arrangement of stomata in relation to the leaf margin.

D, E, J, N, O: *Pseudanthuus*: D, E—Adaxial and abaxial epidermises. J—Adaxial epidermis in TS.

N, O—Parallel and obliquely placed contiguous stomata.

F, G: *Picrodendron*: Adaxial and abaxial epidermises.

H: *Androstachys*: Prismatic crystals in the epidermis.

I: *Austrobuxus*: A prismatic crystal in the epidermal cell.

K, L: *Petalostigma*: K—Adaxial epidermis in TS. L—stomatal complex with one guard cell and aperture undifferentiated.

M, P: *Oldfieldia*: M—Single guard-celled stoma. P—Oblique contiguous stomata.

Q, R: *Dissiliaria*: Q—Cuticular striations radiating from the guard cells. P—Plasmodesmatal type— I cf—cuticular flange(s).

Fig. 1

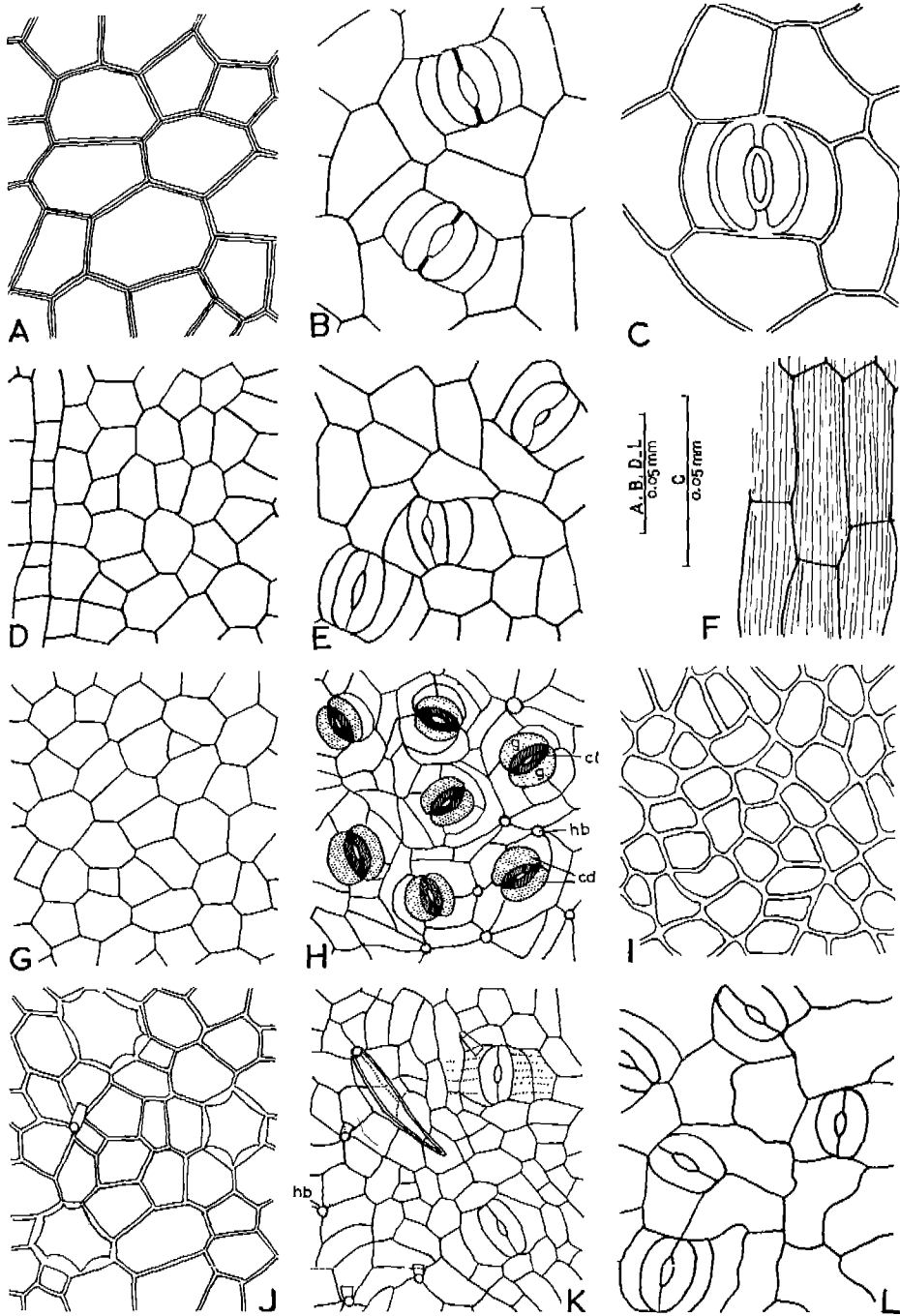


Fig. 2

