Epidermal Structure and Ontogeny of Stomata in some Verbenaceae

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ABSTRACT

The present paper deals with epidermal structure and development of stomata in 14 species of Verbenaceae. The epidermal cells are either polygonal, isodiametric, or elongated in various directions, and irregularly arranged. The anticlinal walls are thick, mostly sinuous, occasionally arched or straight. The surface of the cuticle shows parallel, rarely corrugated, striations. Some 12 types of eglan- dular and glandular trichomes, and foliar nectaries are noticed. The mature stomata are diacytic, anisocytic, paracytic, with a single subsidiary cell, anomocytic and perigenous. The development of anomocytic stomata is perigenous, while that of others is mesogenous or syndetocheilic type. Abnormalities noticed here include contiguous stomata, stomata with a single guard cell, and aborted guard cells.

INTRODUCTION

The family Verbenaceae comprises 98 genera and 2,614 or more species (Lawrence, 1963). The family is predominantly tropical or subtropical, although some species of Verbena extend into temperate regions. Some genus such as Phyla grow in marshy places. While others, Clerodendrum, Lantana, and Vitex, are xerophytic. Lianes are represented by species of Clerodendrum and Petrea. The family is important economically for teak wood (Tectona grandis L. f.). A number of genera including Callicarpa, Caryopteris, Clerodendrum, Duranta, Holmskioldia, Lantana, Petrea, Stachytarpheta, Verbena, and Vitex are cultivated in gardens as important ornamentals.

Metcalfe and Chalk (1950) pointed out that the stomata in the family Verbenaceae are mostly carophyllaceous (diacytic), occasionally rubiaceous (paracytic) or ranunculaceous (anomocytic). Pant and Kidwai (1964) reported all four types of stomata in the leaves of Phyla nodiflora Michx. As far as the author is aware no other report exists on stomatal ontogeny in the Verbenaceae. The present investigation, therefore, was undertaken with a view to fill in this gap in our knowledge.

MATERIALS AND METHODS

Material of the following 14 species was collected from plants growing wild and as ornamentals in the botanical gardens of the University campus: Citharexylum subserratum Sw., Clerodendrum fragrans R. Br., C. inerme (L.) Gaertn., C. phlomidis Linn. f., C. splendens G. Don, C. umbellatum var. speciosum Moldenke, Duranta plumieri Jacq., Gmelina arborea Roxb.,
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Holmskioldia sanguinea Retz., Lantana camara L. var. aculeata (L.) Moldenke, Petrea volubilis Linn., Stachytarpheta jamaicensis Vahl, Verbena venosa Gill. & Hook., and Vitex negundo Linn. Young and mature leaves were fixed in Farmer’s fluid (FAA) and subsequently stored in 70 per cent alcohol. For the study of developmental stages of stomata, temporary mounts of the epidermal peels stained with Delafield’s haematoxylin mounted in glycerine were examined.

Observations
Mature Epidermis

The leaves of Citharexylum subserratum, Lantana camara, Stachytarpheta jamaicensis, and Verbena venosa are amphistomatic, while those of other species are hypostomatic. The cells of the epidermis are polygonal, isodiametric, or elongated in various directions, and arranged irregularly. The epidermal cells have mostly sinuous, occasionally arched or straight, and thick, anticlinal walls. The surface of the cuticle shows mostly parallel and straight, rarely corrugated, striations radiating from the base of the hairs (Fig. 5 A and B) or stomata (Fig. 3 H and K).

Some 12 types of eglandular and glandular trichomes have been observed in the species investigated. They are: (I) E glandular trichomes; (i) simple unicellular (Figs. 5 B and 6 A); (ii) simple, unicellular, conical, silicified (Fig. 5 C); (iii) simple, conical, unicellular, surrounded by 8–10 cells at the base (Fig. 4 K); (iv) capitate eglandular, with a broad unicellular head (Fig. 7 H); (v) capitate eglandular, with 2-celled head (Fig. 7 I); (vi) capitate eglandular trichome, with long stalk and a unicellular excentric head (Fig. 4 J); (vii) simple filiform uniseriate (Figs. 1 N; 2 G; 3 J; and 7 E); (viii) simple filiform uniseriate with terminal silicified cell (Fig. 7 F); (ix) hooked trichome with terminal silicified cell (Fig. 7 G). (II) Glandular trichomes; (x) short-stalked capitate glandular (Fig. 4 G and H); (xi) peltate glandular (Figs. 1 I; 3 L; and 5 B); (xii) filiform peltate glandular trichome with compound foot, uniseriate filiform stalk of 4–6 cells and head of 4–8 cells (Fig. 7 D). Extra-floral nectaries have been observed in the species of Clerodendrum (Fig. 3 C) and Lantana (Fig. 4 I).

Mature Stomata

The great majority of the stomata are diacytic (Figs. 2 D, E, F; 4 D, E; 5 B, D, E; and 6 A); some are anisocytic (Figs. 1 J and 5 A, D), paracytic (Figs. 1 J and 3 E, K), anomocytic (Figs. 1 L, M; 2 D, E, F; 6 A, B; and 7 A, B, C), perigenous (Figs. 1 K and 3 F), and with a single subsidiary cell (Figs. 1 M; 2 E, F; 3 I, K; 5 D, E; and 6 A). Abnormal stomata with a single guard cell (Figs. 2 D; 3 G; 5 E; 6 A; and 7 C), contiguous stomata (Figs. 2 E; 5 E; 6 A; and 7 B, C), and stomata with unequal guard cells (Figs. 3 F, K; 5 A, D; and 6 B) are common. Abnormal stomata with a single guard cell, and contiguous stomata are either diacytic (Figs. 2 D; 5 E; and 6 A) or anomocytic (Figs. 2 E; 6 A; and
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FIG. 1. Duranta plumieri Jacq. (A–N X 690)

A. Meristemoid.
B. Meristemoid after first division forming a large rectangular cell and a small triangular one.
C. Formation of three subsidiary cells.
D. Second division of the meristemoid forming the second subsidiary cell (S₂); note the division in the central cell.
E. Final division of the meristemoid forming two guard cells and three subsidiary cells (S₁, S₂, and S₃).
F–G. Stages in the development of stomata with a single subsidiary cell.
H. Development of paracytic stomata.
I. Development of anomocytic stomata; note the peltate glandular hair.
J. Leaf epidermis showing anisocytic, paracytic stomata and stomata with a single subsidiary cell.
K. Perigenous stomata.
L. Anomocytic stoma.
M. Anomocytic stomata and stomata with a single subsidiary cell.
N. Simple uniseriate filiform trichome with compound foot.
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A. Stomatal meristemoid.
B. Meristemoids in different stages of development showing diacytic formation.
C. Formation of guard cells.
D. Leaf epidermis showing diacytic and anomocytic stomata; note abnormal diacytic stomata with a single guard cell.
E. Clerodendrum umbellatum var. speciosum Moldenke.
   Leaf epidermis showing diacytic and anomocytic stomata; note contiguous stomata (×440).
F–G. Clerodendrum fragrans R. Br.
F. Leaf epidermis showing diacytic and anomocytic stomata; note abnormal stomata with a single guard cell (×440).
G. Simple uniseriate filiform trichome with compound foot (×70)
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In *Gmelina arborea* four contiguous stomata have been observed. Occurrence of groups of from two to many stomata are frequent in *Gmelina arborea* and *Lantana camara*, occasional in the other species. Stomata with aborted guard cells have been noticed in the species of *Clerodendrum* (Fig. 3 H). In diacytic stomata the guard cells are sometimes obliquely oriented and not situated at right angles to the subsidiary cells. Pant and Kidwai (1964) regard such forms as transitional between caryophyllaceous and rubiaceous types.

Ontogeny of Stomata

The epidermal cells in a young leaf are polygonal, isodiametric, or elongated, and uninucleate with straight, arched, or sinuous walls. The stomatal initials are mostly triangular, rarely trapezoidal, and are distinguishable by their comparatively small size, relatively large nucleus, and dense staining properties (Figs. 1 A; 2 A; 3 A; 4 A; and 7 A). The meristemoids occur in a random fashion, sometimes between mature stomata. The development of different types of stomata is as follows: (i) In anisocytic stomata, the meristemoid (Fig. 1 A) divides unequally to form a small triangular cell in a corner and a large flat cell, which is more or less rectangular (Fig. 1 B). The large flat rectangular cell organizes into a first subsidiary cell (S1) (Fig. 1 D and E). The small triangular cell enlarges and divides by a wall intersecting the first to form a second subsidiary cell (S2) (Fig. 1 D). Then the triangular meristemoid divides again on the third side to give rise to a third subsidiary cell (S3) (Fig. 1 C). At this stage the central small triangular cell is surrounded by three subsidiary cells. It now functions as the guard mother cell, becomes rounded, and divides equatorially forming two guard cells which develop an intervening pore (Fig. 1 E and j). Thus, the meristemoid behaves very much like an apical cell with three cutting faces to produce three subsidiary cells in a spiral manner. Here it is always the smaller cell which remains meristematic and keeps on dividing repeatedly (see also Shanks, 1965; Pant and Banerji, 1965; Pant and Kidwai, 1967; Paliwal, 1967). The mature stomata are cruciferous and surrounded by three subsidiary cells (Figs. 1 J and 5 A, D). (ii) In diacytic stomata a septum is formed on one side of the protoderm cell forming two unequal cells (Figs. 2 B and 4 B). The smaller cell is lenticular, has a prominent nucleus, and dense cytoplasm. This functions as the meristemoid, while the larger one organizes into the first subsidiary cell. The meristemoid increases in size and becomes more or less circular in outline (Fig. 4 B). This cell divides by a curved wall to give rise to two unequal cells (Figs. 2 B and 4 C). The larger of these differentiates into the second subsidiary cell. Of these three cells in a row, the central is considerably smaller, but later enlarges and divides vertically at right angles to the earlier divisions giving rise to two guard cells. The mature stomata, thus, become diacytic (Figs. 2 D, E, F; 4 E; 5 B, D, E; and 6 A) surrounded by two subsidiary cells situated at right angles to the stomatal pore. (iii) In paracytic stomata the meristemoid divides into two unequal cells which are more or less rectangular
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**Fig. 3**

**A-J. Clerodendrum philomidis** Linn. f. (A-J × 440)

- **A.** Meristemoid after division forming two unequal cells.
- **B.** Linear triad.
- **C.** Leaf epidermis showing paracytic stomata and stomata with a single subsidiary cell and foliar nectary.
- **D.** Linear tetrad.
- **E.** Paracytic stoma.
- **F.** Anomocytic and perigenous stomata; note stomata with unequal guard cells.
- **G.** Abnormal stoma with a single guard cell.
- **H.** Stoma with aborted guard cells.
- **I.** Stoma with a single subsidiary cell.
- **J.** Simple uniseriate filiform trichome with compound foot.

**K-L. Clerodendrum inerme** (L.) Gaertn.

- **K.** Leaf epidermis showing paracytic, anomocytic, perigenous stomata and stomata with a single subsidiary cell; note stomata with unequal guard cells (× 440).
- **L.** Peltate glandular trichome (× 690).
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(Fig. 3 A). The larger rectangular cell differentiates into a first subsidiary cell while the smaller one divides again forming two unequal cells (Fig. 3 C). Of the three cells in a row, the central is smallest and becomes the guard mother cell, while the flanking cells develop into subsidiary cells. The guard mother cell divides vertically to form two guard cells which develop an intervening pore (Figs. 1 H and 3 D). The mature stomata are paracytic with two parallel flanking subsidiary cells (Figs. 1 J and 3 E, K). Sometimes the meristemoid divides to give rise to two unequal cells, of which the larger differentiates as the subsidiary cell, while the smaller becomes the guard mother cell which divides vertically to form two guard cells (Figs. 1 F, G and 3 B). The mature

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**Fig. 4**

*Lantana camara* L. var. *aculeata* (L.) Moldenke (A–K × 345)

A. Meristemoid.
B. Formation of the first subsidiary cell.
C. Formation of the second subsidiary cell.
D. Formation of two guard cells.
E. Leaf epidermis showing meristemoid in various stages of development giving rise to diacytic stomata.
F. Anomocytic stoma.
G–H. Short-stalked capitate glandular trichomes.
I. Foliar nectary.
J. Capitate eglandular trichome with long stalk, and a pear-shaped excentric unicellular head cell.
K. Simple conical unicellular trichome surrounded by 8–10 epidermal cells at the base.
Inamdar—Epidermal Structure and stoma has thus, only one subsidiary cell (Figs. 1 M; 3 I, K; 5 D, E; and 6 A). Rarely the single subsidiary cell is situated at right angles to the guard cells (Fig. 6 A). (iv) In anomocytic stomata the meristemoid directly becomes a guard mother cell without cutting off any subsidiary cells (Figs. 1 I; 2 B; 4 E; and 7 A). It divides vertically forming two equal guard cells which develop an intervening pore (Figs. 1 I; 2 B; 4 E; and 7 A). Sometimes, in anomocytic stomata, the surrounding adjacent epidermal cells divide and assume the

![Diagram of stomata](image-url)
form of subsidiary cells. Thus, the stomata becomes perigenous (Figs. 1 K and 3 F).

Since in anisocytic, diacytic, paracytic stomata, and stomata with a single subsidiary cell, the subsidiary cell or cells and the guard cells originate from the same initial, the development of the different types of stomata conforms to the syndetocheilic type of Florin (1931, 1933) or mesogenous type of Pant (1965). The development of anomocytic stomata is perigenous.

**FIG. 6.**


Leaf epidermis showing diacytic and anomocytic stomata; note simple unicellular trichome, contiguous stomata, and abnormal stomata with a single guard cell (X 320).

b. *Citharexylum subserratum* Sw.

Leaf epidermis showing anomocytic stomata; note stomata with unequal guard cells (X 220).

**DISCUSSION**

The stomata, in the family Verbenaceae, have been described as caryophyllaceous (diacytic), rubiaceous (paracytic), and ranunculaceous (anomocytic) by Metcalfe and Chalk (1950). Pant and Kidwai (1964) reported diacytic, paracytic, anisocytic, anomocytic, and some transitional types of stomata in *Phyla nodiflora* Michx. According to them in diacytic stomata, the encircling cell is present. Pant and Mehra (1963) have also described two encircling cells in *Asteracantha longifolia*. They pointed out that the meristemoid undergoes five successive divisions to give rise to two encircling cells and two subsidiary cells, with a lenticular guard mother cell in the middle. However, Paliwal is of the opinion that the encircling cells, which Pant and
Mehra (1963) have described, may perhaps be just ordinary epidermal cells which have changed their form due to the growth of the stomatal apparatus in their vicinity. During the course of present studies no such encircling cells are observed. The diacytic stomata, therefore, are formed as a result of three successive mitotic divisions of the meristemoid and not five (see also Paliwal, 1967).

The development of cruciferous type stomata has been described in *Sedum spurium* (Strasburger, 1866-7); *Cochlearia officinalis* (Tognini, 1897); *Bryophyllum calycinum* (Yarbrough, 1934); *Notonia grandiflora* (Pant and Verma, 1963); *Bupleurum tenue* (Gupta, Paliwal, and Gupta, 1965), and
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Cruciferae (Paliwal, 1967; Pant and Kidwai, 1967). The meristemoid behaves like an apical cell and cuts off subsidiary cells in a spiral sequence on its three sides. The divisions of the subsidiary cells have not been observed during the present studies.

Occurrence of different types of stomata on the same surface of a leaf have been observed in some species. A combination of different types of mature stomata has been reported earlier by Sen (1958), Pant and Kidwai (1964), Pant and Mehra (1964), Pant and Banerji (1965), Paliwal (1965), and Inamdar (1967, 1968).

The abnormal stomata with a single guard cell, contiguous stomata, stomata with aborted guard cells, and group of stomata are common. Such abnormalities have been described by Pant and Kidwai (1964) in Phyla nodiflora a member of Verbenaceae.

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