식물학회지 제30권 제2호
Korean J. Bot. 30(2) : 79~94(1987)

Epidermal Structure and Stomatal Types in Various Parts of Each Organ of *Kalanchoe*

Jeong, Woo-Gyu, Jin-Sung Kim, Chung-Suk Kim and Min-Wung Sung
(Department of Biology, Gyeongsang National University, Chinju)

*Kalanchoe*屬의 器官 部位別 表皮構造와 氣孔類型

鄭宇珪 · 金鎭聖 · 金鼎錫 · 成敏雄
(慶尙大學校 大學院 生物學科)

ABSTRACT

This study was carried out to investigate the epidermal structure, the stomatal types, the ontogeny of stomata in various parts of each organ of *K. blossfeldiana*, *K. kewensis*, and *K. tometosa* belonging to *Kalanchoe*. The epidermal cells were polygonal or isodiametric ones in the leaves, and mostly rectangular, tetragonal, and elongated ones in the other organs. The candelabrum-like, triradiate stellete trichomes in the aerial parts of all organs of *K. tomentosa* were found. The cuticular striations and square crystals of calcium oxalate in the epidermal cells of petals of *K. blossfeldiana* were observed. The great majority of the mature stomata in various parts of all the organs were commonly helicocytic types. This type was subdivided into three subtypes such as parahelicocytic, anomohelicocytic, and dianisocytic stomata on the basis of the division angle of the guard mother cells. Sometimes, the anisocytic type was found in most organs. This type was subdivided into three subtyes such as paranisocytic, anomoanisocytic, and dianisocytic stomata in the same way as the helicocytic type. A new stomataltype with anisocytic stoma within a girdle of four subsidiary cells of tetracytic type in the leaf of *K. kewensis* was firstly observed in the vascular plants. This type was termed the coaniso-tetracytic type. The anomomeristic pattern in the mesogenous category of stomatal types was found in various organs of all the material plants. Developmental mode of stomata was constant in all the parts of each organ within the same plant. The stomata was observed to be a few similar stomatal types in various parts of each organ within the same plant. The ontogeny of all the types is eumesogenous or mesogenous type. The ontogenetic type of stomata was mostly helico-eumesogenous type in all the organs of all the material plants. The mature stomata varied from organ to organ in regard of the number and arrangement of subsidiary cells.

INTRODUCTION

Strasburger(1866) reported the stomata in the leaves of *Sedum spurium*. Vesque (1889) regarded stomata as cruciferous on the basis of stomatal development in Cruciferae. Mecalfe and Chalk (1950) introduced the terminology of anisocytic for the cruciferous stomata on the basis of structure and orientation in *Crassula muscosa*, *S. spurium*, and many other plants. They pointed out that the stomata in members of the Crassulacae were nearly always surrounded by a girdle of three subsidiary cells. Several workers reported on stomatal ontogeny in *Bryophyllum*, *Kalanchoe*, *Sedum*, and *Aeonium* that the stomata were the anisocytic types usually possessing three to six subsidiary cells (Yarbrough, 1934; Inamdar and Patel, 1970; Korn, 1972; Sachs and Benouaiche, 1978). The subsidiary cells were formed by spiral series of cell division, the last of which produced two guard cells. Payne (1970) classified the anisocytic types possessing a girdle or helix of three or more subsidiary cells named by other workers into two types, helicocytic type with a helix of four or more subsidiary cells and anisocytic type with three subsidiary cells. Jeong and Sung (1985b) used the terminology of Stevens and Martin (1978) derived from the combination of the types of mature stomata with the stomatal ontogeny types. Jeong *et al.* (1986) subdivided a helicocytic type of Payne (1970) into three subtypes such as parahelico-eumesogenous, anomohelico-eumesogenous, and diahelico-eumesogenous stomata. The study on epidermal structure, stomatal types and ontogeny of stomata has mostly been carried out to investigate the leaves of many plants untill now. However, this study on various parts of each organ in the same plant was rarely performed by only a few workers (Stebbins and Kush, 1961; Inamdar and Bhatt, 1972; Shah and Kothari, 1975).

In Classulace, the stomatla types and stomatal ontogeny in the leaves have been worked up in many plants by many workers (Weiss, 1865; Strasburger, 1866; Yarbrough, 1934; Mecalfe and Chalk, 1950; Payne, 1970; Korn, 1972; Shah and Benouaiche, 1978; Jeong and Sung, 1985 a, b; Jeong *et al.*, 1986; Jeong and Kim, 1986). However, the studies except that of Inamdar and Petal (1970) were reported only on the leaves of this family. Therefore, the authors made a comparative study of the epidermal structure, the stomatal types, and the ontogeny of stomata in various parts of all the organs except for the roots of *Kalanchoe*. *K. blossfeldiana*, *K. kewensis*, and *K. tomentosa* chosen out of plants belonging to *Kalanchoe*. The reason for the choice of them is that they are available in Korea. The subtypes of helicocytic and anisocytic types, anomomeristic pattern in the mesogenous type, and coaniso-tetracytic types were found in this paper. Besides, the results in accordance with the purpose of this study were reported in this paper.

MATERIALS AND METHODS

Materials of *Kalanchoe blossfeldiana*, *K. kewensis*, and *K. tomentosa* were chosen out of plants grown as ornaments in the green house of Gyeongsang National Uviversity campus. They were sand-cultured with Hoagland solution under natural conditions for five months from March to July, 1983. The investigated organs were leaves, stems, peduncles, pedicels, bracts, sepals, petals, ovaries, stamens, and styles. The epidermal peels of young and mature organs were taken off fresh organs by pardermal hand section. These peels were stained with saffranin and mounted in the glycerine water on slide glass. Their epidermal structure, mature stomata, and ontogenetic types of stomata were observed and microphotographed with Olympus Universal Research Microscope of Vanox Model AD-1. The size of guard cell pairs and the number of stomata per square milimeter on the leaves were measured. The photographs were then copied onto the tracing paper. The terminology used here was according to Cotthem (1970) as well as Stevens and Martin(1978).

RESULTS

Epidermal structure. Epidermal structure of various parts in each organ was not shown to be very diffenent. However, without regard to each organ, the shape of epidermal cells differed in accordance with the external shape of various parts in each organ of all material plants. They were wider and shorter in relatively wide or thick organs such as the leaves, stems, and peduncles but more narrow and longer in relatively slender organs such as pedicels, stamens, and styles (Figs. 7, 8, 12, 14, 15, 21, 24; Table 1). Without regard to each organ the epidermal cells were polygonal or isodiametric cells in the lamina of leaves, bracts, and sepals (Figs. 12-14, 15, 23, 27, 32-36, 40, 42, 43), and were rectangular, pentagonal or tetragonal cells in other organs(Figs. 21-28, 33). These cell walls were thick, and arched or sinuous in the laminas, bracts, and sepals (Figs. 7, 8, 12, 14, 15). The nature of sinuous was more prominent in the petals and ovaries of *K. blossfeldiana* (Figs. 19, 20). The cell walls in the stems, peticles, peduncles, and pedicle were straightened(Figs. 21, 22, 26, 31) and arranged commonly parallel to the long axis of these organs. The subsidiary cells were commonly thin and arched in all the organs. The size of subsidiary cells was smaller than that of epidermal cell (Figs. 23-27).

Candelabrum-like, triradiate stellate hairs consisted of a three-barched terminal body(TC) formed by three needle-like cells, a rounded basal cell(BC), and three to four stalk cells(SC) between them. Candelanbrum-like, biradiate hairs consisted of a two-branched terminal body formed by two needle-like cells, a stalk with three or four cells, and a basal cell. These hairs rose from epidermis, and tufted on aerial parts in all organs of *K. tomentosa*(Figs. 16, 17). The cuticular striations were more prominent in the patels of *K. blossfeldiana*(Figs. 18). The square crystals of calcium oxalate were more prominent in the petal of *K. blossfeldiana*(Fig. 13). The rough surface of epidermis in all the organs of *K. tomentosa* was observed(Figs. 14, 35). The guard cells of this plant were more rounded than those of the two other plants(Figs. 14, 35)

Distribution of stomata. The leaves, bracts, and sepals were amphistomatic. On them, the stomata were unevenly distributed in the epidermis. On the stems, peticles of leaves, peduncles, pedicels, and ovariers, the stomata were uniformly distributed in the epidermis and generally oriented in the direction of the long axis of these organs(Figs. 21, 22). The number of stomata was greater on the epidermis of leaves and bracts than on the epidermis in the other organs. In the leaves the number of stomata was different in each species. That of stomata was greater on the lower surface than on the upper surface, but the stomatal number on two surfaces of leaves was not shown to be very different. The largest number of stomata was 48.8/mm^2 on the

Table 1. Epidermal struc ure and stomatal types in various parts of each organ of Kalanchoe *PO: Polygonal· IS: Isodiametric; EL: Elongated: TE: Tetragonal; HEX: Hexagonal; RE: Rectangular; PE: Pentagonal; LR: Lomg Rectangular· AR: Arched; ST: Straight; SI: Sinuous; MS: More Sinuo s; VD: V rious Direction; CP: Common Parallel; H: Helicocytic(PH: Parahelicocytic, AH: Anomohelicocytic, DH: Dfahelicocytic); A: Anisocytic(PA: Paranisocytic, AA: Anomoanisocytic, DA: Dianisocytic); CAT: Coaniso-tetracytic; Ra: Rarely; SO: Sometimes; Non: Nonobserved.

Species	Organs	Epidermal cells		Stomata	
		Shape	Walls	Arrangement	Types(Subtypes)
K. blossfeldiana	Leaf	PO or IS	AR	VD	H(PH Ra AH) Ra A(PA)
	Bract	PO or EL	AR	VD	H(PH Ra DH) Ra A(PA)
	Petiole	TE or RE	ST	CP	H(PH Ra AH) So A(PA Ra DA)
	Stem	TE or HEX	ST	CP	H(PH Ra AH, DH) So A(PA Ra DA)
	Peduncle	TE or PE	ST	CP	H(PH Ra AH) So A(PA Ra AA)
	Pedicel	TE or RE	ST	CP	H(PH) Ra A(PA)
	Sepal	RE or Is	SI or Is	VD	H(PH RA AH) Ra A(PA)
	Petal	RE or LR	MS	CP	H(PH Ra AH, DH) So S(PA Ra AA, DA)
	Ovary	RE or LR	MS	CP	H(PH Ra AH) So A(PA)
	Stamen	LR	ST	Non	
	Style	LR	ST	Non	
K. kewensis	Leaf	PO or Is	ARr or STt	VD	H(PH Ra AH, DH) Ra A PA), CAT
	Bract	Po or IS	AR or ST	VD	H(PH) Ra A(PA)
	Petiole	RE or HEX	ST	CP	H(PH Ra DH) Ra A(PA)
	Stem	RE or HEX	ST	CP	H(PH Ra AH) So A(PA)
	Peduncle	RE	ST	CP	H(PH) Ra A(PA)
	Pedicel	RE	ST	CP	H(PH)
	Sepal	RE or TE	SI or AR	VD	H(PH Ra AH) Ra A(PA)
	Petal	LR or RE	SI	CP	H(PH Ra AH, DH) Ra A(PA)
	Ovary	LR or RE	SI	CP	H(PH) Ra A(PA)
	Stamen	LR	ST	Non Non	
	Style	LR	ST or SI	Non	
K. tomentosa	Leaf	PO or HEX	AR or ST	VD	H(PH) Ra A(PA)
	Petiole	PO or TE	ST	VD	H(PH)
	Epiphyl ous bud	PO or TE	AR or ST	VD	H(PH)
	Stem	TE or HEX	ST	CP	H(PH) So A(PA)

*Reproduction bud in one base of leaf

Table 2. Distribution and size of stomata on the upper and lower surfaces 30 of the leaves in *kalanchoe*

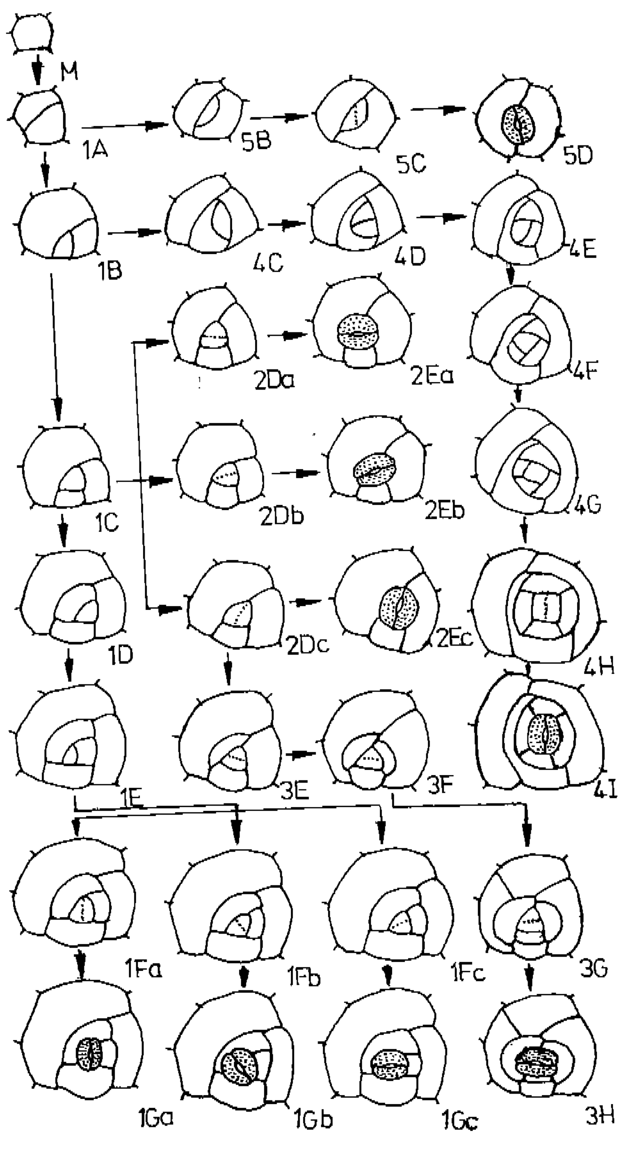
Species	Stomatal number/mm²		Stomatal size, μm			
			Upper		Lower	
	Upper	Lower	Length	Width	Length	Width
K. blossfeldiana	39.9	48.8	27.6	20.0	29.4	19.4
K. kewensis	34.4	42.8	49.3	30.0	50.0	30.9
K. tomentosa	43.4	48.3	37.3	27.3	37.9	29.4

lower surface in the leaf of *K. blossfeldiana*. The largest size of guard cell pairs was 50.0 x 30.9 μm on the lower surface in the leaf of *K. Kewensis*(Table 2).

Stomatal types. Mature stomatal complex in different organs of subsidiary cells(Figs. 8, 14, 15, 21-31). The number of subsidiary cells in the stomatal complex was mostly four to six in the epidermis of leaves, bracts, and sepals(Figs. 12, 27), but it was three to six in stems, peduncles, pedicels, petals, and ovaries(Figs. 21-25, 28-31). The last-formed subsidiary cells of stomatal complex in the leaves were mainly arranged parallel to the long axis of guard cells(Figs. 9, 14, 26). These cells in other organs were sometimes arranged at a right angle or at any angle to the long axis of guard cells(Figs. 14, 28-31).

The great majority of the mature stomata were helicocytic types without regard to all the parts of all the organs. These types were parahelicocytic(Figs. 21,23), anomohelicocytic(Figs. 8, 26), and diahelicocytic(Figs. 24, 25, 27) stomata with a helix of four to more subsidiary cells. Sometimes, anisocytic stomata surrounded with three subsidiary cells were observed to be three kinds of paranisocytic(Figs. 8,28), anomoanisocytic(Fig. 30), and dianisocytic(Figs. 29, 31) stomata. However, the subtype of helicocytic and anisocytic in each organ of *K. tomentosa* can be observed only to be parahelicocytic and paranisocytic stomata. The long axis of guard cells lay parallel, at any angle or at a right angle to the long axis of the last-formed subsidiary cell of helicocytic and anisocytic stomata. The varieties of these stomata with one to three subsidiaries developed by the secondary division of subsidiary cells were found(Figs. 7, 33, 34, 40).

A coaniso-tetracytic type with a girdle of three subsidiary cells directly surrounding two guard cells in a girdle of four subsidiary cells of tetracytic stoma(Fig. 36) and a tetracytic type with four subsidiary cells directly surrounding two guard cells in three subsidiaries of the intermediate stoma between allelocytic and anisocytic type were found in the leaves of *K. kewensis*(Fig. 43). In the sepal of *K. blossfeldfiana* we found intermediate stomata which appear to be intermediate between the paracytic and diacytic(Fig. 35), helicocytic and allelocytic(Fig. 36), and helicocytic and tetracytic(Fig. 37) types. A compound stoma between helicocytic and tetracytic type was observed. This stoma possessed a helix of seven subsidiaries including four subsidiary cells directly surrounding two guard cells(Fig. 38).



Figs. 1-5. Ontogeny pathway of stomata in various parts of each organ of *Kalanchoe*. *M: Stomatal merisemoid, 1-5: Ontogeny pathway of stomata. A-I: Sequence of stomatal development, a-c: Subtypes of stomatal types. Fig. 1. Ontogeny of the helicocytic types inducing parahelicocytic(1Ga), anomohelicocytic(1Gb), and diahlicocytic stomata(1Gc). Fig. 2. Ontogeny of the anisocytic types inducing paranisocytic(2Ea), anomoanisocytic(2Eb), and dianisocytic stomata(2Ec): Fig. 3. Ontogeny of the coaniso-tetracytic type. Fig. 4. Ontogeny of tetracytic type in the subsidiary cells of intermediate stoma between allelocytic type and anisocytic type. Fig. 5. Ontogeny of the intemediate type between anisocytic and paracytic type.

Abnormal stomata such as stomata with a subsidiary cell-like guard cell and without pore(Fig. 40) as well as nonfunctional-opening stomata(Fig. 41) were observed mostly in the petals and ovaries of *K. blossfeldiana* and *K. kewensis.*

Ontogeny of stomata. The ontogeny of stomata followed closely in all the parts of all the organs of each material. The developmental sequence of stomatal types was showed similarly in all the parts without regard to the organs of all the materials. The epidermis of any young organs was composed of uninucleate cells and polygonal, isodiametric or rectangular cells. These cells could act as the protodermal cells. The stomatal meristemoids were cut off from the protodermal cells of epidermis(Figs. 7-12). These cells could be easily distinguished from adjacent epidermal cells by their small size, prominent nucleus and vivid staining properties, and were scattered in a random fashion. Two guard cells and subsidiary cells originated from the same meristemiods. The ontogeny of all the stomata was eumesogenous or mesogenous type(Figs. 1-43).

The helicocytic type was commonly developed in all the organs without regard to all the parts of all the organs. The anisocytic type in most of the parts of each organ was sometimes observed. These two types were observed in all the material plants. The tetracytic type in three subsidiaries of the intermediate stoma of allelocytic type in three subsidiaries of the intermediate stoma of allelocytic and helicocytic types, and the coaniso-tetracytic types were rarely developed in the leaves of *K. kewensis.* Intermediate and compound types between two different types in the sepal of *K. blossfeldiana* were rarely developed. The ontogeny of various stomatal types from stomatal meristemoid was developed as follows.

(1) Helicocytic and anisocytic. The stomatal meristemoid was unequally divided into two cells. One large cell differentiated into the first subsidiary cell, while the other cell divided again. The new courved wall was placed at an interior angle of about 60° to the preceding one so that a helix of four or more subsidiaries was formed. At any stage of development, the last-formed and smallest cell might act as a guard mother cell and producec two guard cells by the ultimate division of parallel, at any angle or at a right angle to the last-formed subsidiary cell(Figs. 1Fa-c, 10-12). These became parahelicocytic(Figs. 1Ga, 23), anomohelicocytic(Figs. 1Gb, 8, 26), and diahelicocytic(Figs. 1Gc, 24, 26, 27).

In the case of ultimate division(Figs. 2Da-c), after three times division of stomatal meristemoid, three subtypes of anisocytic type were produced. They were observed to be the paranisocytic stomata(Figs. 2Ea, 8, 28), anomoanisocytic(Figs. 2Eb, 21, 30), and dianisocytic stomata(Figs. 2Ea, 8, 28), anomoanisocytic(Figs. 2Eb, 21, 30), and dianisocytic stomata(Figs. 2Ec, 29). The meristematic activity had retained for a long time. After the development of primary stoma, the secondary stoma very rarely developed from a corner of other subsidiary cells except for three subsidiaries directly surrounding two guard cells of the first-formed stoma(Fig. 8).

(2) Coaniso-tetracytic. The stomatal meristemoid was developed into anisocytc with three subsidiary cells by spiral division. After that three cells were added by the secondary division of three subsidiary cells. An outer girdle of three cells was developed into a new formed girdle of four cells by transverse division of the first-formed subsidiary cell. After division of guard mother cell, it differentiated into coaniso-tetracytic type(Figs. 3H, 42). Also, the other meristemoid was developed into tetracytic stoma with four subsidiaries directly surrounding two guard cells within three subsidiaries in the intermediate stoma between allelocytic and anisocytic type formed by spiral division(Figs. 42, 43).

(3) Intermediate and compound types between two different types. An Intermediate stoma between paracytic and diacytic might produce two guard cells by division of a guard mother cell at any angle to the long axis of the last-formed subsidiary cell of paracytic or diacytic stomata(Figs. 5D, 35). The ontogeny pathway of an intermediate stoma between allelocytic and helicocytic type(Fig. 36) and an intemediate stoma between tetracytic and helicocytic type(Fig. 37) and a compound stoma between helicocytic and tetracytic type(Fig. 38) was not in detail observed in this study.

DISCUSSION

The epidermal structure, the distribution of stomata, the mature stomata, the stamatal types, and the ontogeny of stomata in various parts of each organ of *Kalanchoe* were described. The shape of epidermal cells without regard to the parts of the organs differed in accordance with the external shape of the parts of the organs of all the materials.

The epidermal cells were polygonal or isodiametric cells in lamina and were rectangular or tetragonal in other organs. These cell walls were commonly thick and arched or sinuous in the laminas, petals, and ovaries. They were straight in stems, peticles, pedicels, and peduncles. The subsidiary cell walls were commonly thin as can be seen in other reports(Patel, 1978: Jeong and Sung, 1985b). The candelabrum-like, triradiate stellate hairs were tufted only on the aerial parts in all the organs of *K. tomentosa*. The cuticular striations of the cell of epidermis were found in petals of *K. blossfeldiana* as can be seen in the report(Inamdar and Patel, 1970). The square crystals of calcium oxalate on the epidermal cell in the petal of *K. blossfeldiana* have been unreported until now in other plants of Crassulaceae.

The number of stomata was the greatest on the epidermis of leaves among all the organs. The largest number of stomata was 48.8/mm^2 on the lower surface in the leaf of *K. blossfeldiana*. In the leaves, the number of stomata was recognized, but the stomatal number on two surfaces of leaves was not shown to be very different. In *S. ratiforium*, Weiss(1865) noticed that the succulents had relatively fewer stomata than thin-leaved dicotyledons with stomata on the lower surface. The other workers described that the succulents like Crassulaceae had low stomatal frequency(Meidner and Mansfild, 1968: Kluge and Ting, 1978; Jeong and Sung, 1985b). In these materials our results regarding the stomatal number agreed with their reports. The size of stomata was different in each species. The largest size was $50.0 \times 30.9\,\mu m$ on the lower surface of the leaves in *K. kewensis*(Table 2).

As early as 1866, the stomata in Crassulaceae have been described by Strasburger(1866). Mecalfe and Chalk(1950) introduced the terminology of anisocytic for the cruciferous type of Vesque(1889) on the basis of structure and orientation of the mature stomata. According to them, the stomata in Crassulaceae were surrounded with a girdle of three cells. Cronquest(1981) described that the stomata in Classulaceae were almost anisocytic. Other workers reported that the stomata in *Kalanchoe, Sedum,* and *Aeonium* were anisocytic stomata possessing usually three to six subsidiary cells directly surrounding two guard cells (Inamdar and Patel, 1970; Korn, 1972; Sach and Benouaiche, 1978). Payne(1970) classified them into two types. These were anisocytic type with a girdle of three subsidiary cells and helicocytic type with a helix of four to six subsidiary cells. In our observation, the type of mature stomata of *Kalanchoe* was helicocytic type of Payne(1970) or completely and incompetely amphicyclic anisocytic type of Inamdar and Patel(1970). Sometimes anisocytic type of other workers(Mecalfe and Chalk, 1950; Cotthem, 1970; Lleras, 1977) was obsevsed.

The stomatal ontogeny in Crassulaceae has been described by several workers(Yarbrough, 1934; Inamdar and Patel, 1970; Payne, 1970; Korn, 1972; Sach and Benouaiche, 1978). They reported that the stomata in the Crassulaceae were anisocytic type usually with three to six subsidiary cells formed by spiral division. Payne(1970) classified them into anisocytic mesogene with three mesogenous subsidiary cells and helicocytic mesogene with a helix of four or more mesogenous subsidiary cells. The authors(Jeong and Sung, 1985b; Jeong *et al.*, 1986) used the terminology of Stevens and Martin(1978) which derived from the combination of the types of mature stomata with the ontogeny of stomata in the study on the ontogenetic types of stomata in Crassulaceae, and reclassified anisocytic into aniso-eumesogenous and helicocytic into helico-eumesogenous type. The present results regarding the ontogenetic types and the ontogeny of stomata in all the parts of all the organs of *Kalanchoe* agreed with the heicocytic mesogene of Payne(1970) and helico-eumesogernous of Jeong and Sung(1958b) or Jeong *et al.*(1986) developed by spiral division of stomatal meristemoid. In 1979 Payne proposed the following basic classification schemes for embryophyte stomata based on the manner of production and division of the guard mother cell. They were the parameristic, diameristic, and anomomeristic patterns that the guard mother cell divided with a wall formed parallel, at a right angle or at any angle to the preceding wall. In recent Jeong and Sung(1985b), they subdivided helico-eumesogenous type into two subtypes of parahelico-eumesogenous and diahlico-eumesogenous stomata on the basis of the division angle of the guard mother cell to the long axis of the last-formed subsidiary cell. Also, Payne(1979) pointed out that all anomomeristic patterns were mesoperigenous usually with only a single mesogene cell, and that the anomomeristic pattern was unknown in mesogene. However, the authors observed that two guard cells were developed by an ultimate division at any angle to the long axis of the last-formed subsidiary cell of both helicocytic and anisocytic stomata. That was the anomomeristic patterns of Payne(1979) in mesogenous stomata category of Pant(1965) or in eumesogenous stomata category of Sevens and Martin(1979).

The anomomeristic pattern in mesogenous stomata cateory was known in the present study. The helicocytic type was subdivided into three subtypes on the basis of the division angle of the guard mother cell to the long axis of the last-formed subsidiary cell. These subtypes were parahelico-eumesogenous and diahclico-eumesogenous stomata of ontogenetic types as reported by Jeong and Sung(1958b), parahelicocytic and diahelicocytic of mature stomatal types, or a newly-found anomohelico-eumesogenous stoma as the ontogenetic types an anomohelicocytic stoma as the mature stomatal types. The anisocytic types was subdivided into three subtypes in the same way as the helicocytic type. They were a paranisocytic stoma of the mature stomatal type or a paraniso-eumesogenous stoma of the ontogenetic type reported as a cruciferous pattern of the parameristic-mesogenous group in a stomatal pattern of Payne(1979) and a dianisocytic and anomoanisocytic stoma as the mature stomatal types a dianiso-eumesogenous and anomoaniso-eumesogenous stoma as the ontogenetic types termed by authors.

Occurrence of the other type in the center of one stomatal type was only reported in Polypodiaceae(Patel *et al.*, 1975) and *Sedum*(Jeong and Sung, 1985b). A new stomatal type with an anisocytic stoma within a girdle of four subsidiary cells of the tetracytic type in the leaf of *K. kewensis* was firstly obeserved in the vascular plants. This type was termed the coaniso-tetracytic type by authors. Also, the tetracytic type in intermediate stoma between allelocytic and helicocytic type was developed in the leaf of *K. kewensis.* Intermediate types between paracytic and diacytic(Shah and Kothari, 1975), helicocytic and allelocytic(Payne, 1970), and helicocytic and tetracytic type were found in the sepal of *K. blossfeldiana*. A compound type of the helicocytic and tecracytic type was observed in the sepal of *K. blossfeldiana* as can be seen in the report(Jeong and Sung, 1985b).

Two guard cells and subsidiary cells of all the stomatal types originated from the same meristemoids. Therefore, the ontogeny of stomata was the mesogenous pattern of Pant(1965) or the eumesogenous pattern of Stevens and Martin(1978). The helicocytic, anisocytic, and coaniso-tetracytic types in this paper could be applied to the helico-eumesogenous, aniso-eumesogenous, and coaniso-tetra-eumesogenous types as the ontogenetic types.

Abnormal stomata such as nonfunctional opening stomata and stomata with a subsidiary cell like the guard cell and without a pore were found as can be seen in the reports of other workers(Jeong and Sung, 1985a).

Several reports existed on the ontogeny of foliage helicocytic and anisocytic stomata(Payne, 1970; Korn, 1972; Sach and Benouaiche, 1978; Jeong and Sung, 1985a,b; Jeong *et al.*, 1986; Jeong and Kim, 1986), but their development in various parts of each organ in Crassulaceae has been studied only by Inamdar and Patal(1970). There were two views regarding the ontogeny of stomata on the different organs within the same plant. As early as 1887 Tognini studied the ontogeny of stomata of 34 species of 29 dicotyledonous families. He surveyed the stomatal ontogeny in the different organs of a plant such as cotyledons, leaf, calyx, coralla, and fruit wall. According to his reports, "developmental modes were different from organ to organ within the same plant." Stebbins and Khush(1961) have investigated 192 species belonging to

49 monocotyledomous families. They have contradicted Tognini(1887) by saying that the "developmental modes are constant, even as to minute details, from organ to organ within the same plant".

According to Paliwall and Bhandari(1962) stomata on the outer integument of ovales, perianthlobes, and on the inner epidermis of pericarp in various Magnoliaceae followed the haplochelic development, where as in the leaves, they conform to the syndechoeilic type. Thus, these workers have supported Tognini's(1887) conclusions regarding these families. In the study on the development of stomata in vegetative and reproductive organs on *Bupleurum tenue* Gupta *et al*(1965) agreed with the findings of Stebbins and Khush(1961) since once again the ontogeny of most of the stomata in both vegetative and reproductive organs is of the syndetochelilic type. As to stomatal ontogeny from organ to organ within the same plant of *Kalanchoe* our observation supported the view of stebbins and Khush(1961). The ontogeny of stomata in various parts of all the organs was the eumesogenous type. But the mature stomatal complex in the different organs of the same plant showed variations in number and arrangement of subsidiary cells(Inamdar and Patel, 1970; Inamdar and Bhatt, 1972).

摘 要

*Kalanchoe*屬의 *K. blossfeldiana, K. kewensis, K. tomentosa*의 各器官 部位別 表皮構造와 氣孔의 類型 및 氣孔의 發生을 調査한 結果는 다음과 같다.

表皮細胞는 잎에서 多角形 또는 等直徑形이었고, 다른 기관들에서는 대부분 直四角形, 多角形 또는 伸張形이었다. *K. tomentosa*의 地上部 全部位에 양초형 三方射星狀毛가 총생하였고 *K. blossfeldiana*의 꽃잎 표피세포에서 角皮條紋과 옥살산칼슘의 結晶體가 發見되었다. 모든 기관의 각 부위에서 성숙한 氣孔의 대부분은 螺旋型이었다. 이 類型은 孔迅母細胞의 分裂角에 다라 平行螺旋型(parahelicocytic), 不規則螺旋型(anomohelicocytic) 및 直交螺旋型(diahlicocytic)의 3亞型으로 細分되었다. 전재료식물들의 각 기관의 전부위에서 螺旋型의 아형들은 대부분 平行螺旋型들이었다. 때론 不均等型이 대부분의 기관에서 발견되었고 이 유형도 나선형에서와 같은 基準에 의하여 平行不均等型(paranisocytic), 不規則不均等型(anomoanisocytic) 및 直交不均等型(dianisocytic)의 3亞型으로 細分되었다. 四副細胞型의 四副細胞로 된 떼 내에 不均等 氣孔을 갖인 새로운 유형이 管束植物에서는 最初로 *K. kewensis*의 잎에서 발견되었고, 四副細胞型內不均等型(coaniso-tetracytic)으로 命名되었다. 中位形成型(mesogenous)에서 氣孔母細胞의 不規則分裂型(anomomeristic)이 전재료식물들의 여러기관들에서 발견되었다. 氣孔의 發生樣式은 동일 식물체의 각기관의 모든 부위에서 일정했고, 氣孔은 모든 부위에서 몇개의 유사한 유형으로 관찰되었다. 전유형의 發生은 中位形成型 또는 全中位形成型(eumusogenous)이었고 發生學的 類型은 全中位形成螺旋型(helico-cumesogenous)이었다. 成熟한 氣孔은 器官에 따라 副細胞의 排列과 數에 變異가 있었다.

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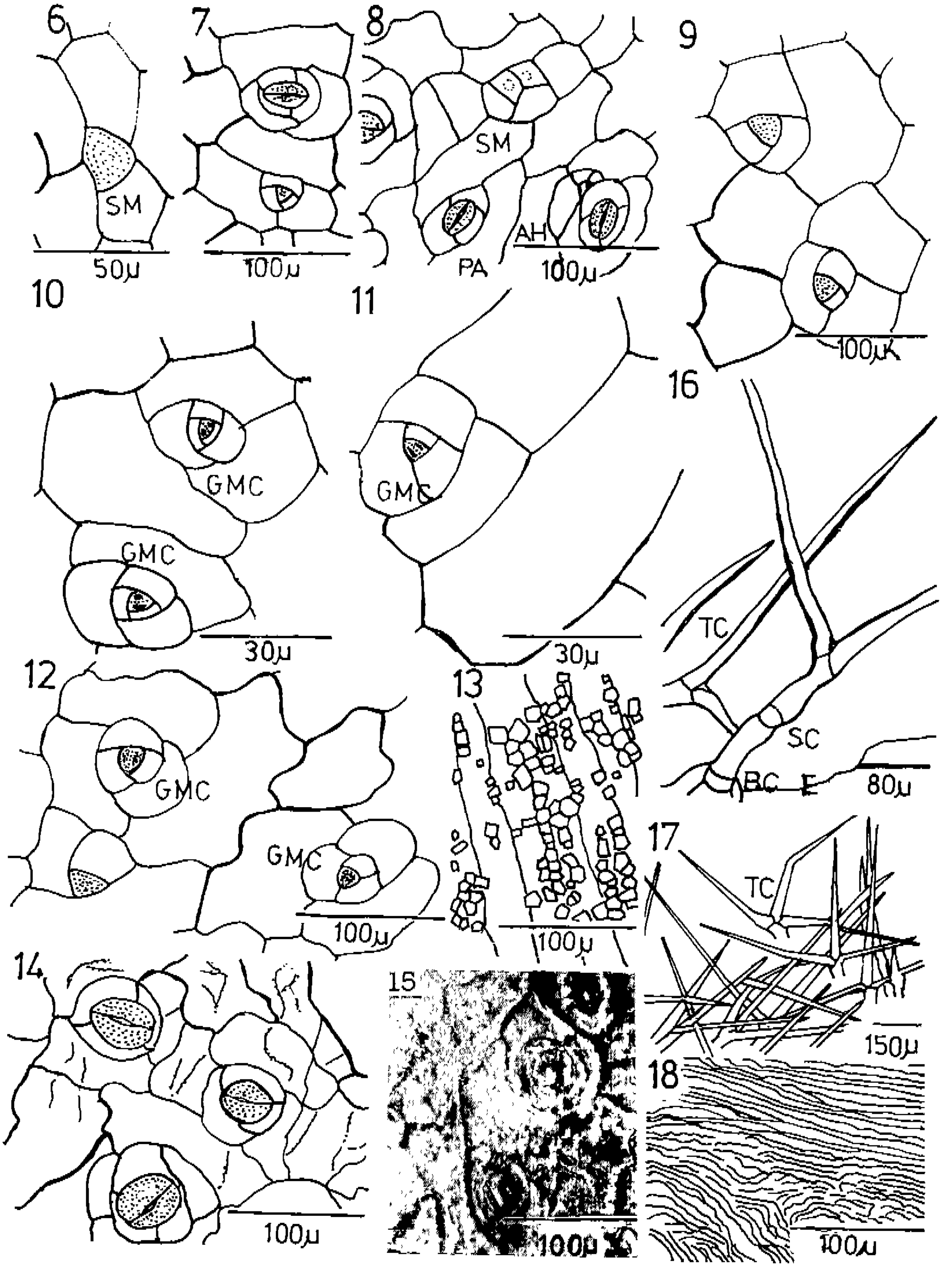
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(Received October 13, 1986)

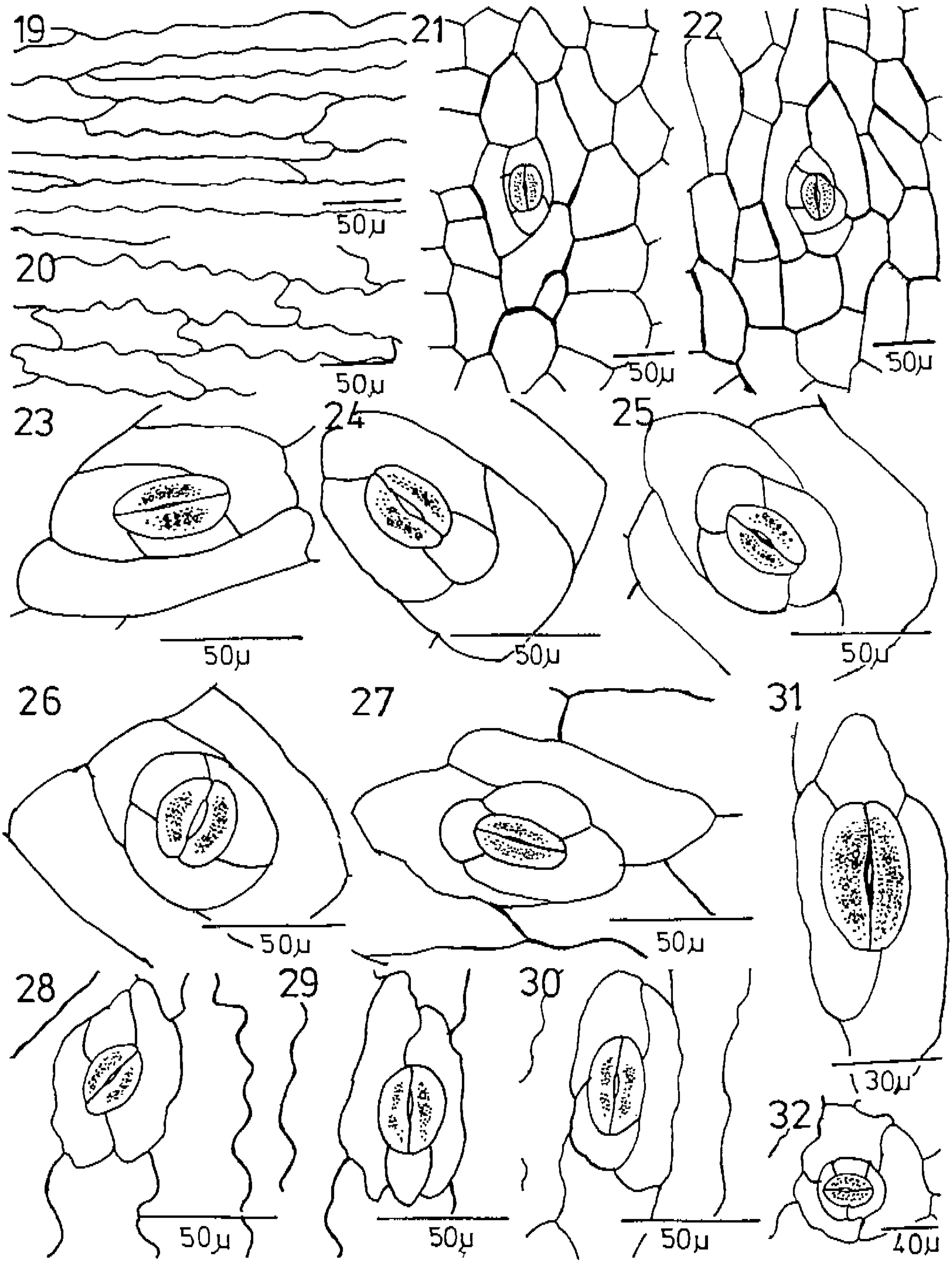
EXPLANTION OF FIGURES

Figs. 6-13. *K. blossfeldiana*(Fig. 6-12, leaf; Fig. 13, petal). Fig. 6. Stomatal meristemoid. Fig. 7. Early stage in ontogeny of helicocytic type(middle and lower) and varity of anisocytic type wih two subsidiaries formed by the secondary division of subsidiary cells. Fig. 8. Stomatal meristemoid (SM), anomohelicocytic(AH), and paranisocytic stoma(PA). Fig. 9. Developing and matured helicocytic type. Figs. 10-12. Developing palahelicocytic, dianisocytic, and anomohelicocytic stomata(noted the paralell, at right angle, and at any angle to the division of the guard mother cells: GMC) Fig. 13. Squere crystals of calcium oxalate.

Figs. 14-17. *K. tometosa*(Fig. 14-16, leaf; Fig. 17, stem). Fig. 16. Candelarum-like, biradiate hair with two terminal body cells(TC), four stalk cells(SC), one body cell(BC), and epidermal cells(E). Fig. 17. Candelarum-like, triradiate stellate hairs.

Figs. 18-41. *K. blossfeldiana*(Fig. 18, ovary; Fig. 20, 28-30, 41 petal; Fig. 21, peduncle; Fig. 22, pedicel; Fig. 23-25, 31 stem; Fig. 26, petiole; Fig. 27, bract; Fig. 32, leaf; Fig. 33-40. sepal). Fig. 18. Cuticular striation on epidermal cells. Figs. 19,20. Sinuous cell wall(noted long rectagular cells). Figs. 21,22. Pentagonal cells. Figs. 23-27. Parahelicocytic(Fig. 23), diahlicocytic(Fig. 24, 25, 27) and anomohelicocytic stoma(Fig. 26). Figs. 22-25. Paranisocytic(Fig. 28), dianisocytic(Fig. 29, 31), and diahlicocytic stoma(Fig. 30). Figs. 32-34. Varieties of helicocytic and anisocytic types with one and three subsidiaries formed by the secondary division of subsidiary cells. Fig. 35. Intemediate type between paracytic and diacytic type. Fig. 36. Intermediate type between allelocytic and helicocytic type. Fig. 37. Intemediate type between helicocytic and tetracytic type. Fig. 38. Compound type of helicocytic and tetracytic type. Figs. 39-41. Abnormal stomata(noted stoma with subsidiary cell like guard cell and without pore and nonfunctional-opening stoma).

Figs. 42-43. *K. kewensis*(leaf). Fig. 42. Coaniso-tetracytic type. Fig. 43. Tetracytic type in three subsidiary cells of the intermediate stoma between allelocytic and anisocytic type.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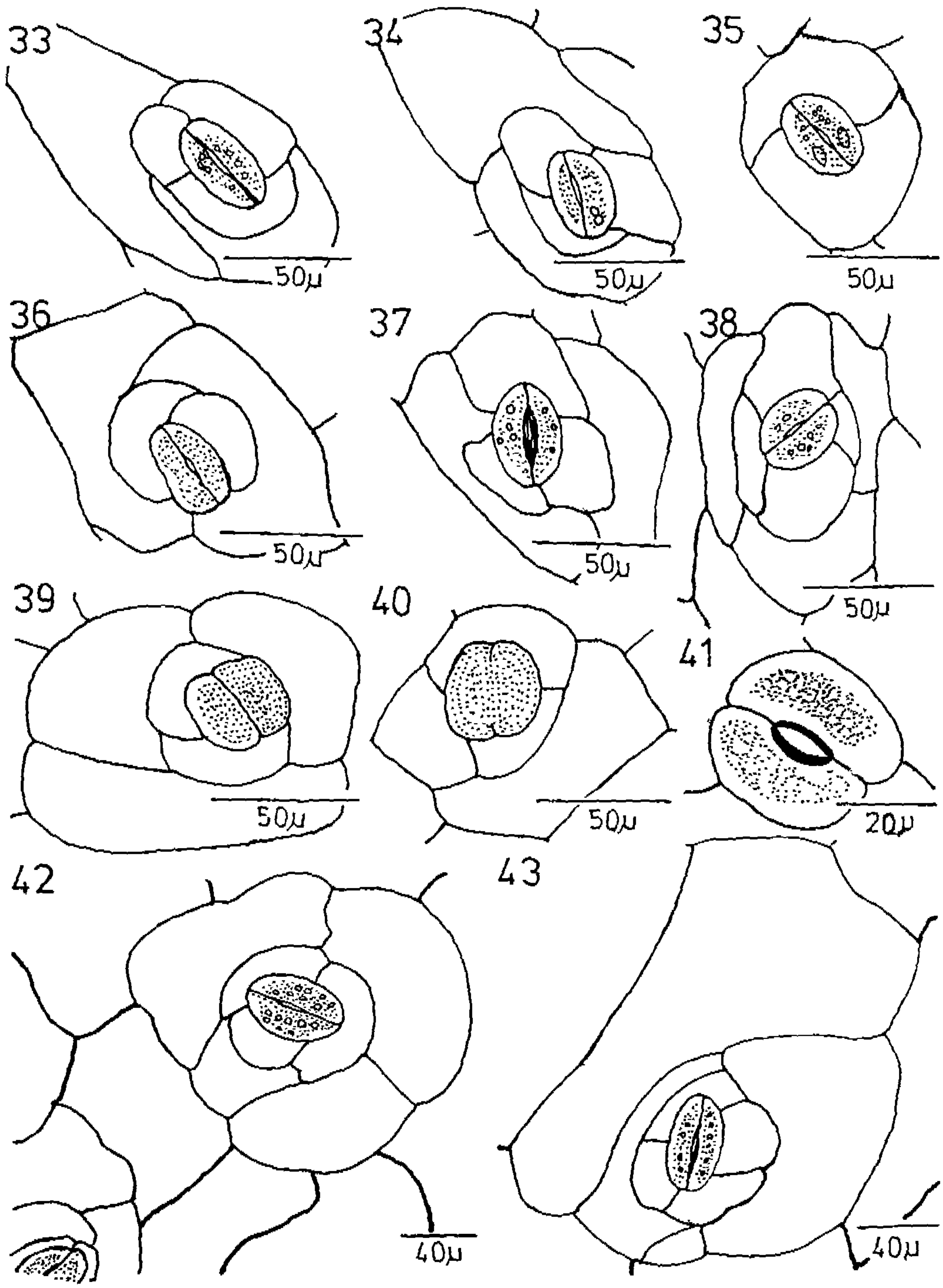
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