

## Epidermal Structure and Stomatal Types in Vegetative and Reproductive Organs of Three Species of *Bryophyllum*

Jeong, Woo-Gyu and Chung Suk Kim

(Department of Biology, Gyeongsang National University, Chinju)

*Bryophyllum* 3種의 營養器官과 生殖器官에서 表皮構造와 氣孔類型

鄭宇珪·金鼎錫

(慶尙大學校 自然科學大學 生物學科)

### ABSTRACT

The epidermal structure and stomatal types in vegetative and reproductive organs of three species of *Bryophyllum* (*B. crenatum*, *B. diagremontian*, *B. tubiflorum*) were described. The epidermal cells were polygonal, isodiametric, and rectangular in the leaves and stems, and elongated cells in the stamens, styles, and ovaries. These cells were commonly thick, and arched or sinuous in the leaves, epiphyllous buds, petals and ovaries. They were straight in the stems, petioles, pedicels, and peduncles. In both vegetative and reproductive organs, the subsidiary cell walls were commonly thin and mostly arched in all the organs. The great majority of the mature stomata in all the organs were heliocytic type with a helix of four to six subsidiary cells. The mature stomata varied from organ to organ with regard to the number and arrangement of subsidiary cells. The ontogenetic type of stomata in all the organs was mostly helico-eumesogenous type. This type was subdivided into three subtypes such as parahelico-eumesogenous, anomohelico-eumesogenous, and diahelico-eumesogenous stomata on the basis of the division angle of the guard mother cell. Sometimes, the aniso-eumesogenous type was found in various organs. This type was subdivided into three subtypes such as paraniso-cumesogenous, anomoaniso-cumesogenous, and dianiso-cumesogenous stomata. The tetra-eumesogenous and duplotetra-eumesogenous types were rarely found; the former in the leaf of *B. crenatum* and the latter in the leaf of *B. diagremontiana*. Anomomeristic patterns in the mesogenous category of stomatal types was observed in a few organs of all the materials. A new stomatal type with tetra-eumesogenous stoma within a girdle of three subsidiary cells of aniso-eumesogenous in the leaf of *B. diagremontiana* was firstly observed in the vascular plants. This stoma was termed the cotetra-aniso-eumesogenous type. Anormal stomata such as aborted stomata, single guard cells, stoma with a constricted part in the middle of large guard cells, and arrested stomata were found in the various organs of all the materials.

## INTRODUCTION

Vesque(1889) proposed a terminology for the four common stomatal types in the leaves of dicots based upon representative families (taxa) which he believed to be constant: ranunculacée, crucifère, rubiacée and labiace or caryophyllée. Meebold and Chalk(1950) discussed the difficulties of the terminology proposed by Vesque(1889). They developed a second terminology which was widely used for anomocytic(ranunculaceous) anisocytic(cruciferous), paracytic(rubiaceous) and diacytic(caryophyllaceous). They found the fifth stomatal type and named it actinocytic type. Pant(1965) and Payne(1979) reclassified the embryophyte stomata on the basis of stomatal ontogeny. Other workers classified mature stomata on the basis of their morphological feature into fifteen(Cotthem, 1970) or seventeen types (Lleras, 1977). Other workers discussed(Dilcher, 1974) and invented a new terminology which derived from the combination of the type of mature stomata with the ontogeny types of stomata to which most of the authors of recent publications on stomatal ontogeny were referred(Fryns-Claessens and Van Cotthem, 1973; Stevens and Martin, 1978).

In Crassulaceae, as early as 1866 Strasburger reported the stomatal development in the leaves of *Sedum spurius*. Vesque(1889) coined a terminology named cruciferous on the basis of the stomatal development in Cruciferae. Meebold and Chalk(1950) introduced the terminology of anisocytic for the cruciferous stomata on the basis of structure and orientation of the mature stomata in *Crassula muscosa*, *S. spurium*, and many other plants. They described that the stomata in members of the Crassulaceae were nearly always surrounded by a girdle of three subsidiary cells. Several workers reported stomatal ontogeny in *Kalanchoe*, *Sedum* and *Aeonium* that the stomata were the anisocytic types usually possessing three to six subsidiary cells(Inamdar and Patel, 1970; Korn, 1972; Sachs and Benouaiche, 1978). The subsidiary cells were formed by spirial series of cell division, the last part 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; a helicocytic type with a helix of four or more subsidiaries and an anisocytic type with three subsidiaries. In recent, Jeong and Sung(1985b) used the terminology of Stevens and Martin(1978) derived from the combination of the types of mature stomata with those of stomatal ontogeny. They classified helicocytic into helico-cumescogenous and anisocytic into aniso-cumescogenous. The above studies except that of Inamdar and Patel(1970) were reported only on the leaves of Crassulaceae.

The present study was carried out to make a comparative study of the epidermal structure, the distribution of stomata, the mature stomata, and the ontogenetic types and ontogeny of stomata in vegetative and reproductive organs of three species of *Bryophyllum*.

## MATERIALS AND METHODS

Three species of *Bryophyllum crenatum*, *B. diagremontiana* and *B. tubiflorum* were chosen out of plants grown as ornaments in the greenhouse of Gyeongsang National University campus. They were sand-cultured with Hoagland solution under natural conditions for five months from March to July, 1983. The investigated organs were leaves, petioles, stems, peduncles, pedicels, bracts, sepals, petals, epiphyllous buds, ovaries, stamens, and styles. The epidermal peels of young and mature organs were taken from their fresh organs by paradermal hand section. These peels were stained with 0.5 % safranin solution and mounted in the glycerine water on slide glass. Their epidermal structure, mature stomata, and ontogenetic types and ontogeny of stomata were observed and microphotographed with Olympus Universal Research Microscope of Vanox Mod. AD-1. The photographs were then copied onto the tracing paper. The size and number of stomata per square millimeter on the leaves and epiphyllous buds were measured. The terminology used here was according to Lleras(1977) as well as Stevens and Martin(1978).

## RESULTS

**Epidermal structure.** Epidermal structure in vegetative and reproductive organs was not shown to be very different. However, the shape of epidermal cells differed in external shape of constituent organ composing both the organs. Without regard to vegetative and reproductive organs, they were wider and shorter in a relatively wide or thick organs such as the leaf and stem but narrower and longer in a relatively slender organs such as pedicels, stamens, and styles. The leaves, bracts, and sepals were amphistomatic. The epidermal cells were polygonal or isodiametric in the leaves, epiphyllous buds, bracts, and sepals(Figs. 1,2,5,8,13,17,18,22,27) They were rectangular, tetragonal or elongated cells in the other organs(Figs. 6,9,10,20,24-26,32). These cell walls were thick and arched or sinuous in the leaves, epiphyllous buds, bracts and sepals. The nature of sinuous was more pronounced in the leaves of *B. crenatum*(Figs. 17-19,21,22) and epiphyllous bud of all the material plants. The walls in the stems, petioles, peduncles and pedicels were straight(Figs. 6,9,10,20,24-26,32) and arranged commonly parallel to the long axis of these organs (Table 1). The subsidiary cell walls were thin and mostly arched in both vegetative and reproductive organs. The size of subsidiary cells was smaller than that of epidermal cells(Figs. 6,10,20,24-26,34).

**Distribution of stomata.** On the leaves, bracts, epiphyllous buds, and sepals, the stomata were unevenly distributed in the epidermis and oriented into various directions. On the stems, petioles, peduncles, pedicels, and ovaries, the stomata were generally uniformly distributed in the epidermis and oriented in the direction of the long axis of these organs(Figs. 9,25). The number of stomata was greater on the epidermis in the leaves,

**Table 1.** Epidermal structure and stomatal types in vegetative and reproductive organs of *Bryophyllum*

PO:Polygonal; Is:Isodiametric; RE:Rectangular; HEX:Hexagonal; PE:Pentagonal; TG:Tetragonal; LR:Long Retangular; AR:Arched; ST:Straight; SI:Sinuous; MS:More Sinuous; DS:Deeply Sinuous; VD:Various Direction; CP:Common Parallel; HE:Helico-eumesogenous; CTAE:Cotetra-aniso-eumesogenous; DE:Duplotetra-eumesogenous; AE:Aniso-eumesogenous; TE:Tetraeumesogenous; Rarely; So:Sometimes; No:Nonobserved

Species	Organe	Epidermal cells		Subsidiary cell walls	Stomata	
		Shape	walls		Arrangement	Types
<i>B. diagremontiana</i>	Leaf	PO or IS	AR, ST or SI	AR	VD	HE Ra CTA DE
	Bract	PO or RE	AR or ST	AR	VD	HE Ra DE
	Petiole	RE or HEX	ST	AR	CP	HE
	Stem	RE or HEX	ST	AR	CP	HE So AE
	Peduncle	RE or HEX	ST	BR AR	CP	HE So AE
	Pedicele	RE or TG	ST	AR	CP	HE
	Sepal	RE or IS	AR or SI	AR	VD	HE
	Petal	LR	MS or SI	AR	CP	HE So AE
	Ovary	LR	MS or SI	AR	CP	HE So AE
	Stamen	LR	ST	NO	NO	
	Style	LR	ST or SI	NO	NO	
	Epiphyllous bud	PO IS or EL	DS	AR or SI	VD	HE
<i>B. crenatum</i>	Leaf	PO or IS	DS	AR or SI	VD	HE Ra TE, AE
	Bract	PO or IS	DS	AR or SI	VD	HE Ra AE
	Petiole	RE or TG	ST	AR	CP	HE
	Stem	RE or TG	ST	AR	CP	HE
	Peduncle	RE or TG	ST	AR	CP	HE Ra AE
	Pedicele	RE or TG	ST	AR	CP	HE
	Sepal	RE or IS	DS	AR or SI	VD	HE
	Petal	LR or RE	MS or SI	AR	CP	HE So AE
	Ovary	LR	MS or SI	AR	CP	HE Ra AE
	Stamen	LR	ST	NO	NO	
	Style	LR	ST	NO	NO	
	Epiphyllous bud	PO IS or EL	DS	AR or SI	VD	HE
<i>B. tubiflorum</i>	Leaf	PO or IS	SI	AR or SI	VD	HE
	Bract	TE or RE	SI	AR or SI	VD	HE Ra AE
	Petiole	TE or RE	ST	AR	CP	HE Ra AE
	Stem	PO or TG	ST	AR	CP	HE
	Peduncle	TS or RE	ST	AR	CP	HE
	Pedicele	RE	ST	AR	CP	HE
	Sepal	RE	MS or SI	AR or SI	VD	HE So AE
	Petal	LR	MS or SI	AR	CP	HE

(Table 1. Continued)

Ovary	LR	MS or SI	AR	CP	HE
Stamen	LR	ST	NO	NO	
Style	LR	ST or SI	NO	NO	
Epiphyllous bud	PO IS or EL	DS	AQ or SI	VD	HE
			AR		

bracts, epiphyllous buds, and sepals than that of stomata on the epidermis in other organs. The number of stomata in the leaves and epiphyllous buds was smaller than that of thin-leaved dicots with stomata only on the lower surface. The greatest number of stomata was 29.9/mm<sup>2</sup> in the epidermis of the leaves of *B. diagremontiana*. The stomatal number on the two surfaces in the leaves of this species was shown to be very different. However, the stomatal number on the two surfaces of the two organs was not shown to be different in *B. crenatum* and *B. tubiflorum*. The largest size of stomata was 34.4×24.6 μm on the lower surface in the leaves of *B. crenatum* (Table 2).

**Table 2.** Distribution and size of stomata on the upper and lower surfaces of the leaves and epiphyllous buds in *Bryophyllum*

Species	Organs	Stomatal number/mm <sup>2</sup>		Stomatal size, μm			
		Upper	Lower	Upper		Lower	
				Length	Width	Length	Width
<i>B. diagremontiana</i>	Leaf	19.8	29.9	30.3	19.4	32.0	18.3
	Epiphyllous bud	17.7	19.8	29.3	20.0	25.9	17.6
<i>B. crenatum</i>	Leaf	29.0	28.3	34.4	19.8	34.4	24.6
	Epiphyllous bud	27.6	20.9	28.1	17.1	28.0	18.7
<i>B. tubiflorum</i>	Leaf	22.7	20.2	30.1	20.1	30.6	23.4
	Epiphyllous bud	13.5	17.6	27.4	25.1	28.9	19.1

**Mature stomata.** Mature stomatal complex in different organs of the same plant showed some variation in the number and arrangement of subsidiary cells(Figs. 1,8,9,13-29). The number of subsidiary cells in the stomatal complex was mainly four to six subsidiary cells in the epidermis of the leaves, bracts, epiphyllous buds, and sepals, but it was three to six subsidiary cells in the stems, peduncles, pedicels, petals, and ovaries(Figs. 1,8,9,11-34). The last-formed subsidiary cells of stomatal complex in the leaves were mainly arranged parallel to the long axis of guard cells(Figs. 1,8,16,19,22,30) These cells in other organs were sometimes arranged at right angle or at any angle to the long axis of guard cells(Figs. 9,24,25).

The great majority of the stomata in all the organs were heliocytic types such as parrahelicocytic(Figs. 18,21,22,30), anomohelicocytic(Figs. 21,27,28,31), and diahelicocytic-

tic(Fig. 25) stomata with a helix of four or more subsidiary cells. Sometimes, anisocytic stomata surrounded by three subsidiary cells in leaves and stems of vegetative organs and in the petals, sepals, and ovaries of reproductive organs were observed to be three kinds of paranisocytic(Figs. 20,23,32), anomoanisocytic(Figs. 9,17), and dianisocytic(Fig. 24) stomata. The long axis of guard cells of these stomata lay parallel to, at any angle to or at right angle to 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. 8,11,12,14,18,26,29). The duplotetracytic stomata in the leaves of *B. diagremoniana*(Fig. 7) and tetracytic stomata in the leaves of *B. crenatum*(Fig. 17) were observed.

Abnormal stomata such as aborted stomata(Figs. 15,23), a single guard cell(Fig.16), a stoma with a constricted part in the middle of large guard cells(Fig. 33), and arrested stomata(Fig.34) were found in all the organs of all the materials.

**Ontogenetic types and ontogeny of stomata.** The ontogeny of stomata followed closely in all constituent organs composing vegetative and reproductive organs. The developmental sequence of each stomatal type showed similar in both the organs without regard to vegetative and reproductive organs. The epidermis of any young organs was composed of uninucleate 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 the epidermis(Figs. 1-5,8). These meristemoids could be easily distinguished from adjacent epidermal cells by their small size, prominent nucleus and vividly staining properties, and were scattered in a random fashion(Figs. 1-5,8).

The helico-eumesogenous types developed commonly in all the organs of constituent organs composing vegetative and reproductive organs of all the material plants. Sometimes, the aniso-eumesogenous types developed mainly in the peduncles, stems, bracts, and ovaries. The tetra-eumesogenous type and duplotetra-eumesogenous type rarely developed; the former in the leaf of *B. crenatum* and the latter in the leaf of *B. diagremoniana*. The cotetra-aniso-eumesogenous type rarely developed in the leaf of *B. diagremoniana*. The secondary stoma in the subsidiary cell of stoma developed only in the leaf of *B. crenatum*.

The ontogeny of various stomatal types from stomatal meristemoids was observed as follows without regard to vegetative and reproductive organs in all the material plants.

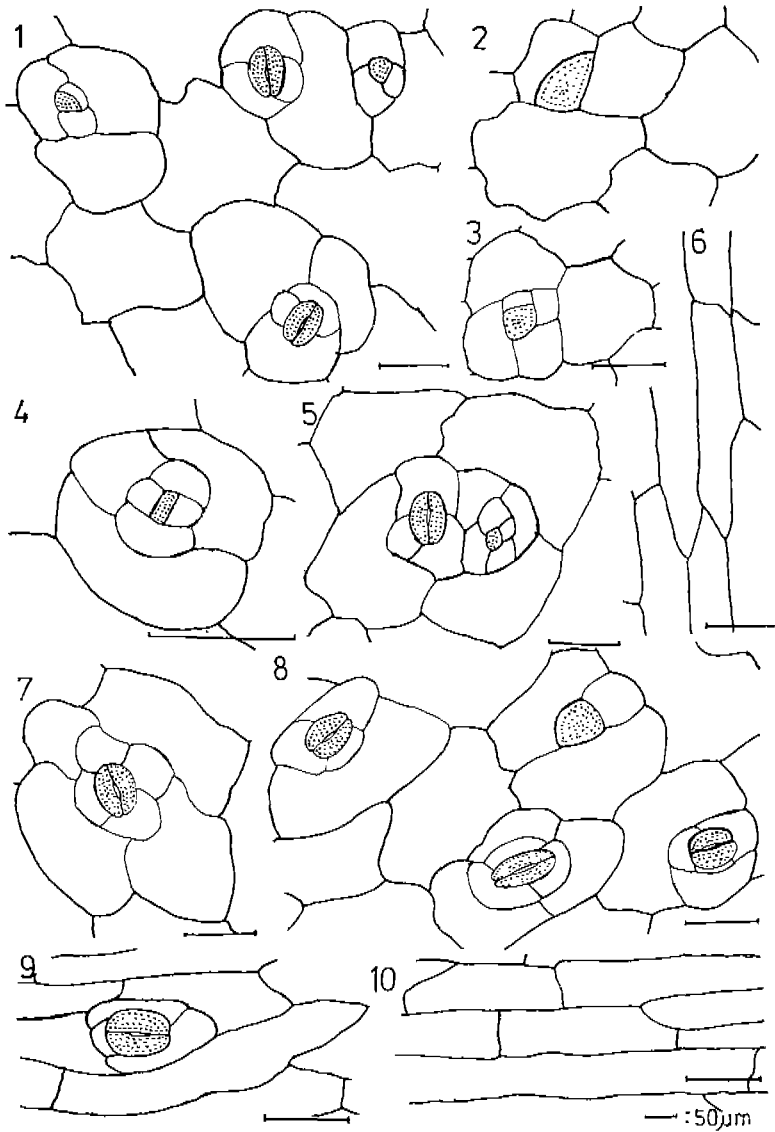
(1) **Helico-eumesogenous and aniso-eumesogenous type.** The stomatal meristemoid was unequally divided into two cells. One large cell differentiated into the first subsidiary cell, while the other cell divided again. The new curved wall was placed at an interior angle of about 60° to the preceding one so that a helix of four or more subsidiaries was formed(Figs. 1,21,22,28). At any stage of development, the last-formed and the smallest cell might act as a guard mother cell and produced two guard cells by an ultimate division parallel, at any angle or at right angle, to the last-formed subsidiary cell. These became

parahelico-eumesogenous stomata(Figs. 1,8,22,30), anomohelico-eumesogenous stomata(Figs. 27,28,31), and diahelico-eumesogenous stomata(Figs. 8,25). If the ultimate division happened after three times division of stomatal meristemoid, three subtypes of aniso-eumesogenous type by division of the guard mother cell were produced. They were observed to be the paraniso-eumesogenous stomata(Figs. 20,23,32), anomoaniso-eumesogenous stomata(Figs. 9,17), and dianiso-eumesogenous stomata(Fig. 24). The meristematic activity was retaining for a long time. After the development of the primary stoma, the secondday stoma developed from a corner or a side of other subsidiary cells except for three subsidiaries directly surrounding two guard cells of the first-formed stoma(Figs. 21,22). The varieties of helico-eumesogenous and aniso-eumesogenous stoma with one to three subsidiaries formed by the secondary division of the subsidiary cells directly surrounding two guard cells of these stomata were developed (Figs. 8,11-14,18,26,29).

(2) **Duplotetra-eumesogenous and tetra-eumesogenous type.** The stomatal meristemoid was divided into two unequal cells by a curved wall at a corner of meristemoid cell. In subsequent division the new curved walls were placed at an interior angle of about  $90^\circ$  to the preceding one so that a spiral of eight mesogenous subsidiary cells was formed. Every four subsidiary cells in this helix completely surrounded the guard cells or the preceding four cells in the spiral. At any stage of this development, the last-formed cell may act as a guard mother cell and produces the two guard cells by an ultimate division. This became duplotetra-eumesogenous stoma(Figs.3,5,7). If the guard mother cell was generated after the four divisions of stomatal meristemoid in this development, a tetra-eumesogenous stoma with four mesogenous subsidiaries was produced(Fig. 17).

(3) **Cotetra-aniso-eumesogenous type.** The stomatal meristemoid was divided into unequal cells. In subsequent division the curved wall was placed at an interior angle of about  $60^\circ$  to the preceding cell. After that, three subsidiary cells were produced. And the new curved walls were placed at an interior angle of about  $90^\circ$  to the preceding cell. Finally four subsidiary cells directly surrounding the guard cells in a girdle of three subsidiary cells were formed(Figs. 4,35).

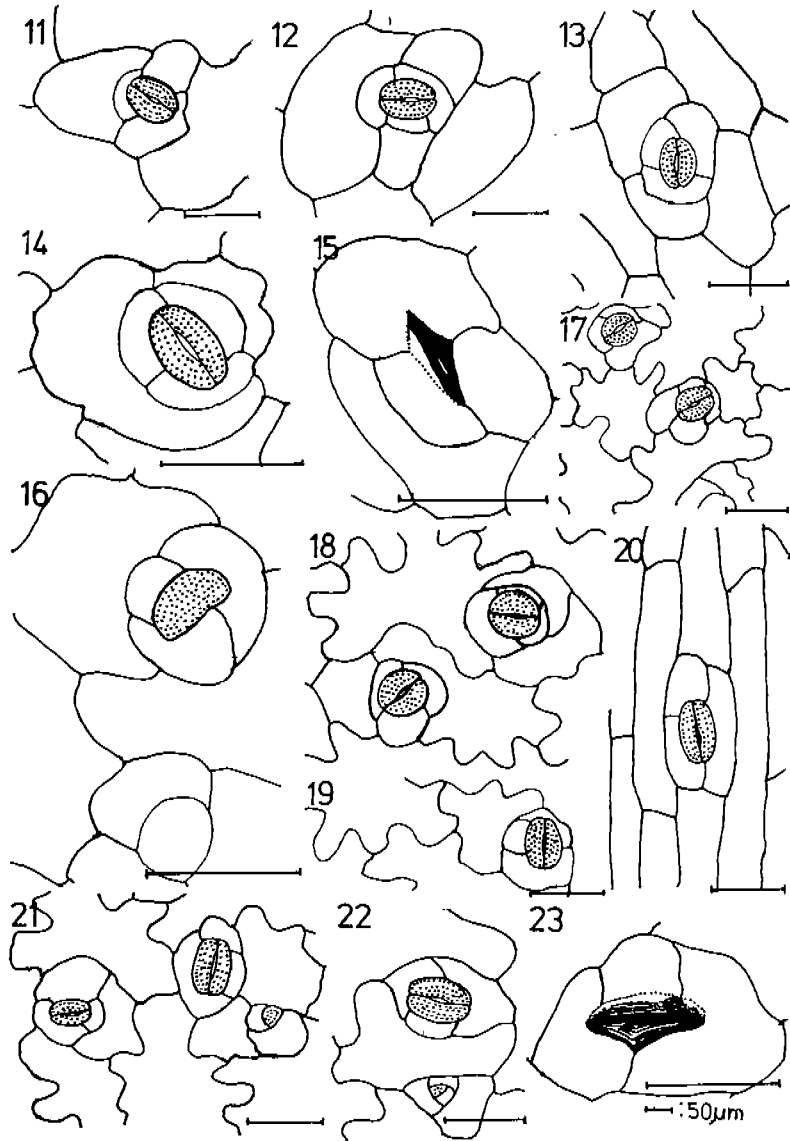
(4) **Abnormal stomata.** The guard cells of mature stomata lost their cytoplasm, developed into the thin back wall, and were left finally a central thickening cell. They became the aborted stomata(Figs. 15,23). After a guard mother cell with three or more subsidiary cells differentiated, this cell directly developed into a single guard cell(Fig. 16). The guard mother cell was divided into two cells, which may be developed into stomata with a constricted part in the middle of guard cells and one pore(Fig. 33). A initial cell of each stage during the development of stomata was formed into the arrested stomata by high vacuolation of cytoplasm and degeneration of nucleus(Fig. 34).



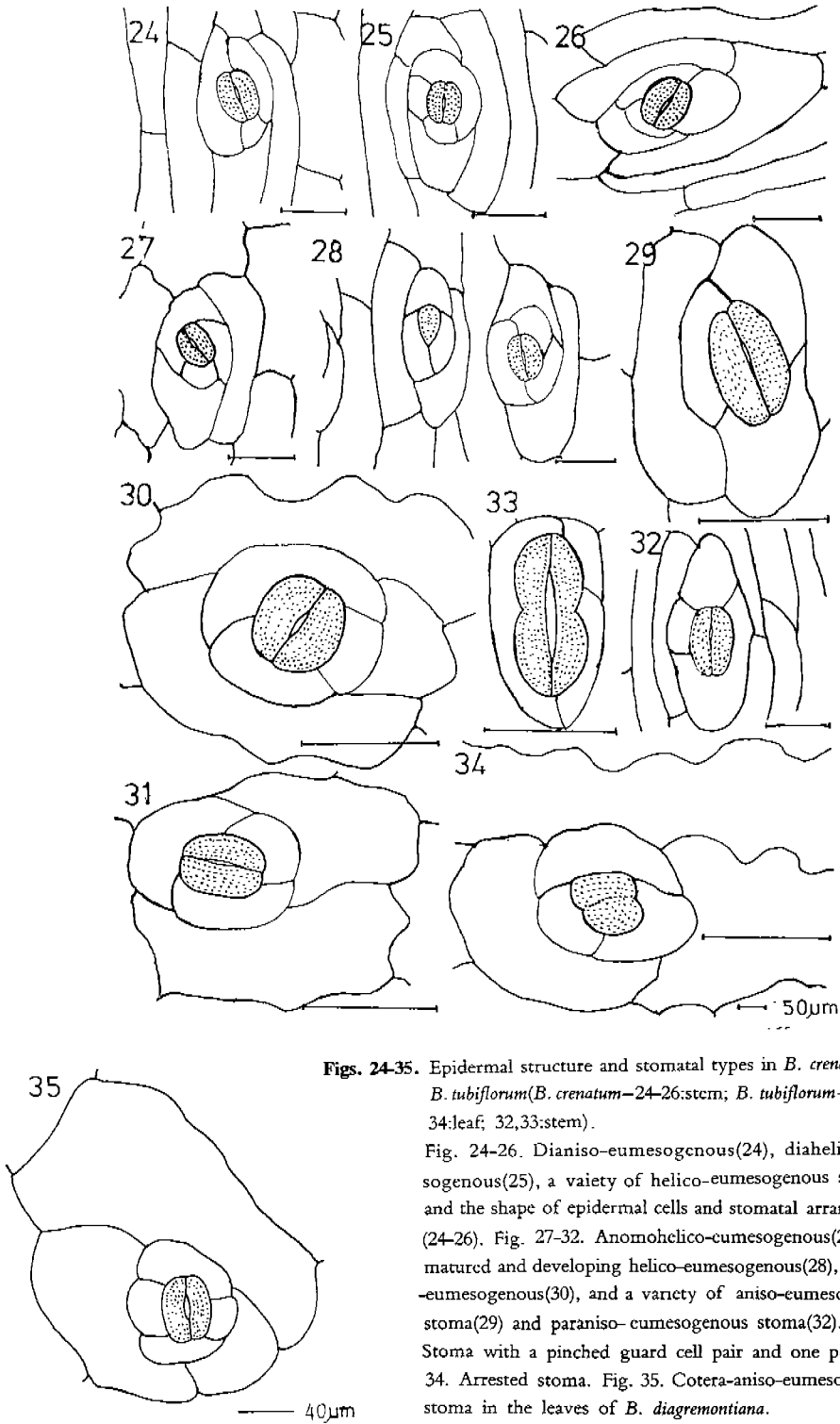
**Figs. 1-10.** Epidermal structure, stomatal type, and stomatal ontogeny in *B. diagraemontiana*(1-5, 7: leaf; 6: pedicel; 8: bract; 9: stem; 10: petiole).

Fig. 1. Matured and developing stomata of helico-eumesogenous types (noted parahelico-eumesogenous stomata). Fig. 2. The first division of the stomatal meristemoid and epidermal cells. Fig. 3. Developing duplotetra-eumesogenous stoma. Fig. 4. Developing cotetra-aniso-eumesogenous stoma. Fig. 5. Developing duplotera-eumesogenous stoma and matured helico-eumesogenous stoma. Fig. 6. Rectangular cells of epidermmis. Fig. 7. Duplotetra-eumesogenous stoma. Fig. 8. Parahelico-eumesogenous(left and right), variety of aniso-eumesogenous stoma with the secondary formed three subsidiaies developed by the secondary division of three subsidiary cells of aniso-eumesogenous stoma(middle-lower), and developing stoma(middle-upper). Fig. 9. Anomoaniso-eumesogenous stoma and epideremal cells. Fig. 10. Arrangement of rectangular epidermal cells.





**Figs. 11-23.** Epidermal structure and stomatal types in *B. diagremontiana* and *B. crenatum*(*B. diagremontiana*-11,12:petal; 13,15:sepal; 14:ovary; 16:leaf; *B. crenatum*-17-19, 21-23:leaf; 20:petiole).  
 Figs. 11,12,14: The varieties of aniso-eumesogenous(11,14) and helico-eumesogenous stomata(12).  
 Fig. 13. Anomohelico-eumesogenous stoma. Fig. 15. Aborted stoma. Fig. 16. Single guard cell.  
 Fig. 17. Anomanoisogenic(upper), tetra-eumesogenous stoma(lower), and deeply sinuous epidermal cell walls. Fig. 18. Parahelico-eumesogenous variety of anomanoisogenic stoma(lower), and sinuous subsidiary cell walls. Fig. 19. Parahelico-eumesogenous stoma. Fig. 20. Paranoisogenic stoma. Figs. 21,22. Developing stoma within a subsidiary cell of a helico-eumesogenous stoma (21,22) and stomatal arrangement(22). Fig. 23. Aborting guard cells in normal stoma.



**Figs. 24-35.** Epidermal structure and stomatal types in *B. crenatum* and *B. tubiflorum* (*B. crenatum*—24-26; stem; *B. tubiflorum*—27-31, 34; leaf; 32, 33; stem).

Fig. 24-26. Dianiso-eumesogenous(24), diahelico-eumesogenous(25), a variety of helico-eumesogenous stoma(26) and the shape of epidermal cells and stomatal arrangement (24-26). Fig. 27-32. Anomohelico-cumesogenous(27, 31), matured and developing helico-eumesogenous(28), parahelico-eumesogenous(30), and a variety of aniso-eumesogenous stoma(29) and paraniso-cumesogenous stoma(32). Fig. 33. Stoma with a pinched guard cell pair and one pore. Fig. 34. Arrested stoma. Fig. 35. Cotera-aniso-eumesogenous stoma in the leaves of *B. diagemontiana*.

## DISCUSSION

The epidermal structure, the distribution of stomata, the mature stomata, and the ontogenetic types of stomata in vegetative and reproductive organs of three species of *Bryophyllum* were described in this paper.

The epidermal structure in vegetative and reproductive organs was not shown to be very different. However, the shape of epidermal cells differed in external shape of constituent organs composing both the organs. The epidermal cells were polygonal or isodiametric cells in the leaves, bracts, sepals, and epiphyllous buds and rectangular cells in other organs. These cell walls were thick and arched or sinuous in the leaves, bracts, sepals, epiphyllous buds, petals, and ovaries. The cell walls in the stems, petioles, pedicels and peduncles were thick and straight. The subsidiary cell walls were thin and mostly arched as in other reports (Patel, 1978; Jeong and Sung, 1985b).

The number of stomata was the greatest on the epidermis of leaves among all the organs. The stomatal number in the leaves and epiphyllous buds was counted in each species. Weiss (1865) noticed that the succulents had relatively fewer stomata than thin-leaved dicotyledons with stomata only on one lower surface. Other workers described that the succulents like Crassulaceae had low stomatal frequency (Meidner and Mansfield 1968; Kluge and Ting, 1978; Jeong and Sung, 1985b). In these material plants our results agreed with the reports (Weiss, 1865; Meidner and Mansfield; Kluge and Ting, 1978; Jeong and Sung, 1985b). The difference of stomatal number in both surfaces of the leaves and epiphyllous buds in each species was relatively less than that of stomata number in the both surfaces in the leaves of thin-leaved dicotyledons.

Mecalfé and Chalk (1950) introduced the terminology 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 by a girdle of three cells. Cronquist (1981) described that the stomata in Crassulaceae were almost anisocytic. Other workers reported on the mature stomata types and ontogeny of stomata that stomata in *Bryophyllum*, *Kalanchoe*, *Sedum*, and *Aenium* were anisocytic stomata usually possessing three to six subsidiary cells. These cells were formed by a spiral series of cell division, the last part of which produced two guard cells (Yarbrough, 1936; Inamdar and Patel, 1970; Korn, 1972; Sachs and Benouaiche, 1978). Payne (1970) classified them into two types. They were anisocytic types with a girdle of three subsidiary cells, and helicocytic types with a helix of four or more subsidiary cells. Jeong and Sung (1985b) used the terminology of Stevens and Martin (1978) in their study on the types of normal and abnormal stomata of Crassulaceae. They reclassified anisocytic into anisocumesogenous, and helicocytic type into helicocumesogenous type. The present observations regarding the type and ontogeny of stomata agreed with the report of Payne (1970), and Jeong and Sung (1985b). In this paper, the helicocytic (Payne, 1970), anisocytic (Mecalfé

and Chalk, 1950; Payne, 1970), tetracytic(Cotthem, 1970), and duplotetracytic(Jeong and Sung, 1985b) as the types of mature stomata could be applied to the helico-eumesogenous, aniso-eumesogenous, and tetra-eumesogenous of Stevens and Martin(1978) and duplotetra-eumesogenous type of Jeong and Sung(1985b) in the stomatal ontogenetic types.

In 1979, Payne proposed the following basic classification scheme for embryophyte stomata based on the manner of production and division of the guard mother cell. They were parameristic, diameristic and anomomeristic patterns into which the guard mother cell divided with a wall fomed parallel, at right angle and at any angle to the preceding wall, respectively. In recent Jeong and Sung(1985b) subdivided helico-eumesogenous type into two subtypes such as parahelico-eumesogenous and diahelico-eumesogenous stomata on the basis of the division angle of the guard mother cell to the long axis of the last-fomed subsidiary cell. Also, Payne(1979) pointed out that all anomomerristic patterns were mesoperigenous stamata usually with only a single mesogene cell, and that the anomomeristic patterns were unknown in mesogene. However, the authors observed that two guard cells were produced by an ultimate division at any angle to the long axis of the last-formed susidiary cell of both helico-eumesogenous and aniso-eumesogenous stomata. These were anomomeristic patterns of Payne(1979) and mesogenous stomata category of Pant(1965). The anomomeristic patterns in mesogenous stomata category were known in present study. The helico-eumesogenous type was subdivided into three subtypes on the basis of the last-formed subsidiary cell. These subtypes were parahelico-eumesogenous and diahelico-eumesogenous stomata as reported by Jeong and Sung(1985b), and newly-found anomohelico-eumesogenous stomata. The aniso-eumesogenous type was subdivided into three subtypes in the same way as the helico-eumesogenous type. They were paraniso-eumesogenous stomata reported as a cruciferous pattern of the parameristic-mesogenous group in stomatal pattern of Payne(1979), and newly named dianiso-eumesogenous and anomoaniso-eumesogenous stomata classified into subtypes.

The duplotetra-eumesogenous type was firstly reported in *Sedum* by Jeong and sung(1985b). The difference between this type and the cyclocytic type of Cotthem(1970) or cyclo-mesogenous type of Fryns-Claessens and Van Cotthem(1973), was that a helix of eight mesogenous subsidiary cells doubly surrounding two guard cells was produced by the spiral division of stomatal meristemoid.

Occurrence of another type in the center of one stomatal type was reported in Polypodiaceae(Patel *et al.*, 1975) and *Sedum*(Jeong and Sung, 1985b). The stomatal type with four subsidiary cells directly surrounding two guard cells within a girdle of three subsidiary cells of aniso-eumesogenous in the leaves of *B. diagremontiana* was firstly found in the vasular plants. Therefore, the authors named this a cotetra-aniso-eumesogenous type.

Several reports existed on the ontogeny of foliage helico-eumesogenous and aniso-eumesogenous stomata(Payne, 1970; Korn, 1972; Jeong and Sung, 1985a,b) but their

development in vegetative and reproductive organs in Crassalaceae has been studied only by Inamdar and Patel(1970). There were two views regarding the ontogeny of stomata on different organs within the same plant. According to Tognini(1897), 'developmental modes are different from organ to organ within the same plant'. According to Stebbins and Khush(1961), 'developmental modes are constant even to the minutest details from organ to organ of the same plant.' As regards stomatal ontogeny from organ to organ within the same plant our observations support the view of Stebbins and Khush(1961), but the mature stomatal complex in different organs of the same plant showed variations in number, form, and arrangement of subsidiary cells(Inamdar and Patel, 1970; Inamdar and Bhatt, 1972).

In abnormal stomata, Ahmad(1964) pointed out that the abnormal stomatal cells in the Solanaceae were formed as a result of degeneration of normal stomatal cells rather than through developmental abnormalities. Inamdar *et al.*(1969) reported that abnormal stomatal cells were formed as a result of developmental anomalies. The present observations regarding the development of abnormal stomata agreed with both those of Ahmad(1964) and Inamdar *et al.*(1969) as reported by Jeong and Sung(1985a).

## 摘 要

*Bryophyllum*屬이 속하는 3種(*B. crenatum*, *B. diagremontian*, *B. tubiflorum*)의 營養器官과 生殖器官에서 顯微鏡 觀察에 의한 表皮構造와 氣孔의 類型을 記述하였다. 表皮細胞는 營養器官에서 多角形, 等徑形 또는 直四角形이나 生殖器官의 수술, 앞술 및 씨방에서는 伸長形細胞들이 共通의이었다. 이들의 細胞壁은 共通的으로 肥厚되었고, 잎, 잎의 재생아, 꽃잎 및 씨방에서는 아치형이거나 波狀形이었으며, 줄기, 葉병, 花경 및 소화경에서는 直線形이었다. 副細胞壁은 共通的으로 얇고, 대부분이 아치형이었다. 全器官에서 成熟한 氣孔의 대부분은 4~6개의 副細胞를 가진 螺旋型 氣孔이었다. 각 器官에서 成熟한 氣孔은 副細胞의 數와 排列에 差異를 나타내었다. 氣孔의 發生學的 類型은 全器官에서 全中位形成 螺旋型(helico-eumesogenous)이 共通的이었다. 이 類型은 孔邊母細胞의 分裂角을 基準으로 全中位形成平行螺旋型(parahelico-eumesogenous), 全中位形成直交螺旋型(diahelico-eumesogenous) 및 全中位形成不規則螺旋型(anomohelico-eumesogenous)의 3亞型으로 細分되었다. 때때로 全中位形成不均等型(aniso-eumesogenous) 氣孔이 發見되었고 이 類型도 전자와 같은 기준에 따라 全中位形成平行不均等型(paraniso-eumesogenous), 全中位形成直交不均等型(dianiso-eumesogenous) 및 全中位形成不規則不均等型(anomoaniso-eumesogenous)의 3亞型으로 細分되었다. 全中位形成四副細胞型(tetra-cumcsogenous)이 *B. crenatum*의 잎에서, 全中位形成重四副細胞型(duplotetra-cumcsogenous)이 *B. diagremontiana*의 잎에서 더물게 觀察되었다. 中位形成型(mesogenous)에서 不規則分裂型(anomomeristic)이 몇개의 器官에서 觀察되었다. 全中位形成不均等型的 세 부세포로 된 때 내에 全中位形成四副細胞型을 가진 새로운 類型이 *B. diagremontiana*의 잎에서 管束植物에서 最初로 관찰되었고 全中位形成不均等型內四副細胞型(cotetra-aniso-eumesogenous)으로 命名되었다. 退化된 氣孔, 한 개의 公변세포만 가진 氣孔, 큰 公변세포의 중앙부가 狹窄된 氣孔 및 發生이 靜止된 氣孔 등의 非正常 氣孔들이 全器官에서 發見되었다.

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