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On the Types of Abnormal Stomata in Crassulaceae

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돌나물科(Crassulaceae)의 非正常 氣孔 類型에 關하여

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ABSTRACT

This study was carried out to investigate the types and frequency of abnormal stomata in Crassulaceae. We observed the surface of the leaves on twenty four species involved five varieties belonging to eight genera of Crassulaceae. Nineteen types of abnormal stomata were found in the families. Among them three types such as the single guard cell, the aborted stomata, and the single-aborted guard cell were highly observed from nineteen to twenty four species, and two types of the overlapped-thickening guard cells and the arrested stomata exhibited commonly from seven to thirteen species. The another types of them rarely occurred from one to five species. Most of abnormal stomata were found in *S. alboroseum*, *P. chinense* and *S. sarmentosum*, and a few types of them were observed in the other species. The three types of the ballooning guard cells, the cross cleaved stomata, and the fused pore stomata were first reported here in the seed plants. It was thought that the abnormal stomata were formed by the result of degeneration and abnormal development of normal stomata.

INTRODUCTION

All the vascular plants except for a few aquatic plants have stomata. Abnormal stomata have been reported in many vascular plants. Dehnel(1961) has tried to explain the development of abnormal stomata observed in the normal foliage of *Begonia aridicaulis*. The other workers have studied the developmental pathway of abnormal stomata in normal plants (Inamdar *et al.*, 1969; Inamdar, 1970) and mutants (Zeiger and Stebbins, 1972; Maynardo *et al.*, 1974). Nakagawa *et al.*(1980) reported the changes of stomatal structure on the fruit surface of grape berry. Abnormal stomata by hormone and chemicals (Kaufman *et al.*, 1967; Stebbins *et al.*, 1967; Fisher, 1970), and by gamma irradiation (Haber, 1962) have been reported.

In Crassulaceae, the stomatal development has been noted by many workers (Weiss, 1865; Strasburger, 1866; Yarbrough, 1934; Metcalfe and Chalk, 1950; Esau, 1965, 1977; Payne, 1970; Korn, 1972; Fryns-Claessens and Cotthem, 1973). However, the abnormal stomata having only the single guard cell, the cytoplasmic connection between a subsidiary cell and one guard cell, transverse division in one of the guard cells, and the arrested development in *Kalanchoe* have been reported by Inamdar and Patel (1970). This study was carried out to investigate and reorganize the type and frequency of abnormal stomata on both the upper and lower surface of normal leaves in Crassulaceae.

MATERIALS AND METHODS

The nineteen species and five varieties belonging to eight genera of Crassulaceae were used (Table 1). The plants were collected in the field at Chinju area. They were sand-cultured with Hoagland solution under the natural conditions for 1981～1983. The sampling laminae of the leaves were ensured by the paradermal hand section with razor blades. The epidermal peels were stained with safranin and eosin solution, and then mounted in the glycerine water solution on the slide glass. They were observed and microphotographed with the Olympus Universal Research Microscope of Vanox Model AD-1. The frequency of abnormal stomate was expressed by the number of the kinds of abnormal types found in each species.

RESULTS AND DISCUSSION

Types of normal and abnormal stomata. The comparative shape of normal and abnormal stomata was shown in Fig. 1 and 2. In the mature epidermis, the leaves of all the plants

Table 1. Material plants

Species	Species
Orostachys japonicus	*Sedum lineare* var. *albomarginatum*
O. malacophyllus	*S. mexicanum*
Sedum kamtschaticum	*S. adolphii*
S. ellacombianum	*S. robrodictum*
S. aizoon	*Bryophyllum crenatum*
S. aizoon var. *ramosum*	*Kalanchoe blossfeldiana*
S. aizoon var. *heterodontum*	*K. tomentosa*
S. aizoon var. *latifolium*	*Crassula arborescense*
S. aizoon var. *saxatile*	*Echeveria glauca*
S. alboroseum	*E. pulvinata*
S. bulbiferum	*Graptopetrarum paraguagense*
S. sarmentosum	*Penthorum chinense*

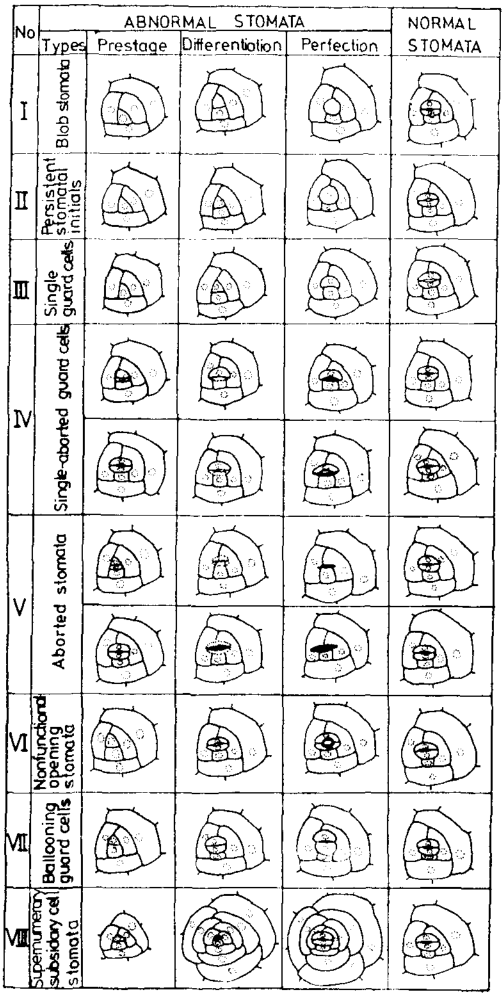

Fig. 1. Ontogeny of abnormal stomata in Crassulaceae. Prestage was expressed as the abnormal formation in stomata.

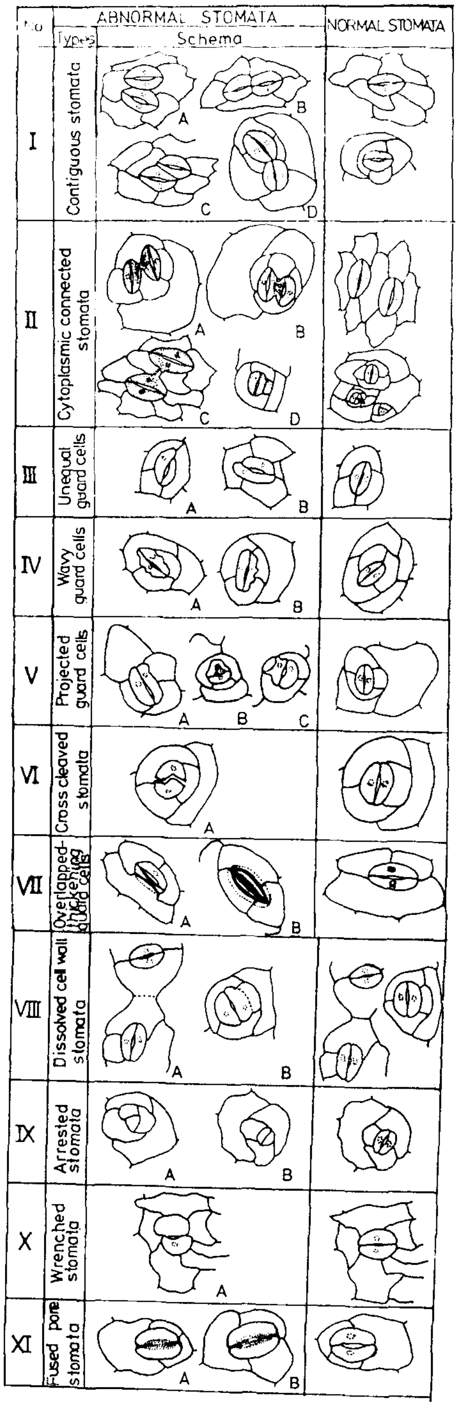

Fig. 2. Types of abnormal stomata in Crassulaceae. →

were amphistomatic. The epidermal cells were polygonal and elongated in vein area. The subsidiary cell walls were arched or sinuous. In the mature stomata, the great majority of stomata was helicocytic, sometimes allelocytic and anisocytic. In *P. chinense* the main type was anomocytic stoma.

The abnormal stomata occurred on both the upper and lower surface on the leaves. In the present study we observed nineteen kinds of abnormal types in stoma. They were summarized as follows; (a) blob stomata (Fig. 1-I), (b) persistent stomatal initials (Fig. 1-II), (c) single guard cell (Fig. 1-III), (d) single-aborted guard cell (Fig. 1-IV), (e) aborted stomata (Fig. 1-V), (f) nonfunctional-opening stomata (Fig. 1-VI). (g) ballooning guard cells (Fig. 1-VII), (h) supernumerary subsidiary cell stomata (Fig. 1-VIII), (i) contiguous stomata (Fig. 2-I), (j) cytoplasmic connected stomata (Fig. 2-II), (k) unequal guard cells (Fig. 2-III), (l) wavy guard cells (Fig. 2-IV), (m) projected guard cells (Fig. 2-V), (n) cross cleaved stomata (Fig. 2-VI), (o) overlapped-thickening guard cells (Fig. 2-VII), (p) dissolved cell wall stomata (Fig. 2-VIII), (q) arrested stomata (Fig. 2-IX), (r) wrenched stomata (Fig. 2-X), and (s) fused pore stomata (Fig. 2-XI).

Types of abnormal stomata. The types of abnormal stomata were observed as Fig. 1-2 and Plate 1-2. During the development of normal stomata, the meristemoid was cut off some protodermal cells. These cells could be easily distinguished from the adjacent epidermal cells. They were small in size, dense in staining properties, and had prominent nucleus. The meristemoid developed into a helix of four or more subsidiary cells surrounding the guard mother cell. The two guard cells were produced from the mother cell by an ultimate division and finally became helico-eumesogenous stoma. In case of ultimate division, after three times divisions of meristemoid, the aniso-eumesogenous stoma was produced. In *P. chinense* the meristemoid divided into two cells. One larger cell became a neighbouring cell, and the smaller cell differentiated into guard mother cell. This cell was divided into two guard cell, and then became the anomo-hemimesogenous stoma. Abnormal stomata in Crassulaceae have been reported only in *Kalanchoe* by Inamdar and Patel (1970). The abnormal stomata have already been known as four types such as the single guard cell, the cytoplasmic connection between a subsidiary cell and guard cell, the arrested development, and the transverse division of one of guard cells. In the present study all the types of abnormal stomata occurred in the Crassulaceae were discussed as follows.

(a) Blob stomata. The guard mother cell was aborted before the division into two guard cells, and then the nucleus and cytoplasm were degenerated as in the case of the report by Inamdar *et al.* (1969). This cell was shown as a blob at the center of three to six subsidiary cells (Pl. 1, Figs. 1, 2). After the degeneration of guard cells, the cytoplasmic degeneration of a few subsidiary cells surrounding cells in a stomatal complex was not reported until now, but first observed here in *C. arborescense* (Pl. 1, Fig. 3).

(b) Persistent stomatal initials. Dehnel (1961) has described that this type might either be isolated or occurred variably in close to normal stomata. In the present study, the guard mother cell differentiated without the final division into the formation of two guard cells, and then directly developed into the persistent stomatal initials (Pl. 1, Fig. 4).

(c) Single guard cell and (d) Single-aborted guard cell. Many workers (Dehnel, 1961; Pant and Kidwai, 1967; Inamdar, 1970; Inamdar and Chohan, 1969; Patel and Inamdar, 1971a) have described this type without regard to the developing process. Patel and Inamdar(1971b) have given two possibilities for the origin of the single guard cell. One was a meristemoid directly becoming one guard cell, the other was the degeneration of one of the two guard cells. They have reported two types of single guard cell with pore and without pore. Patel *et al.* (1972) suggested that the origin of single guard cell did not differentiate directly from a meristemoid in *Aganosma*. However, we observed two characteristics of stomatal ontogeny with regard to the developing process. (i) The guard mother cell differentiated directly into a single guard cell. This was various in shape and size, and the pore did not appear (Fig. 1-III, Pl. 1, Figs. 5, 6). (ii) After the equal division of two guard cells from a guard mother cell, one of young or mature guard cells degenerated (Fig. 1-IV, Pl. 1, Figs. 7-10). In other case one guard mother cell was unequally divided into both one small cell and one large cell. One large cell differentiated into a normal guard cell, and the small cell degenerated (Fig. 1-IV, Pl. 1, Figs. 7). As the result of the degeneration of one guard cell, only one guard cell was remained. The characteristics of the later became the single aborted guard cell with pore. The thickness of guard cell wall was developed unequally and the chloroplasts appeared. Therefore we separated the type of abnormal stomata into two kinds of the single guard cell and the single-aborted guard cell by the developing process.

(e) Aborted stomata. This type appeared in all the leaves of material plants. The number of this type was gradually increased during the aging of stomata. The guard cells were seemed to vary according to the intensity of their activity (Sawyer, 1932) and to lose their function during the aging of stomata like the report (Gambles and Dengler, 1974). Frequently mature guard cells and rarely young guard cells were vacuolated, lost their cytoplasm, developed into the thin back wall, and finally aborted as the remaining with a central thickening (Fig. 1-V, Pl. 1, Figs. 10, 11). The remaining of guard cells was observed in the several cases (Pl. 1, Figs. 11). These stomata might become nonfunctional, and it was seemed to be reduced transpiration like the report (Gambles and Dengler, 1974).

(f) Nonfunctional-opening stomata. The stomata on petals, stamens, filaments, carpels and seeds were reported to be almost nonfunctional (Esau, 1965; Fahn, 1974). Occasionally the stomata on seeds and fruits appeared as the opening shape (Rugenstein and Lersten, 1981). Jernstedt and Clark (1979) observed that the stomata of seed coat of inner fruit wall in *Eschachola* were always opening and plasmolizing state. In the present study the stoma was lost their opening and closing function, and remained always the opening state by the thickening of central abdomen walls of guard cells (Pl. 1, Figs. 13, 14). Therefore we called the stomata as the nonfunctional-opening stomata.

(g) Ballooning guard cells. Kaufman *et al.* (1967) reported on a substantial ballooning and expanding of guard cells in IAA-treated epidermis of *Avena sativa* internode. Zeiger and Hepler (1977) observed that the protoplast of onion guard cells was swollen at that time of the illuminating with blue light. In this study one guard mother cell was divided into two guard cells. The pore did not appear, and then these cells were the largest ballooned like opening stoma (Pl. 1, Figs. 15). This type was first observed here in *S. sarmentosum* and *S. alboroseum*.

(h) Supernumerary subsidiary cell stomata. Continuous divisions of meristemoid were induced to develop into stoma with supernumerary subsidiary cells. Common stomata have four to six subsidiary cells, but eleven number of subsidiary cells were observed in *S. bulbiferum* (Pl. 1, Figs. 16). The number of subsidiary cells increased due to spiral divisions of three subsidiary cells, like the report (Arora and Lamba, 1980).

(i) Contiguous stomata. Several workers (Korn, 1972; Esau, 1977; Marx and Sachs, 1977) have reported that the developing stomata inhibited the initiation of the neighbouring stomata. However, it was reported that the meristemoid had an inherent capacity to retain its meristematic activity (Paliwal, 1967; Inamdar *et al.*, 1969; Payne, 1970). After or during the developing stage of primary stoma, the secondary stoma was developed from the other subsidiary cells except for the inhibitory zone of three subsidiary cells directly surrounding the developing stoma in the present study. These two stomata developed into contiguous stomata due to the mutual readjustment of space between primary and secondary stomata, like the report (Pl. 2, Figs. 23, 24; Inamdar *et al.*, 1969; Inamdar and Chohan, 1969). In *P. chinense* the two derivatives of adjacent meristemoid were differentiated into two guard mother cells like the reports (Maheshwari and Vasil, 1961; Shah and Gopal, 1969a). These guard mother cells were divided into one line, and differentiated into the superimposed contiguous stomata (Pl. 1, Fig. 17; Pl. 2, Fig. 22). These cells existed side by side were differentiated into the juxtaposed contiguous stomata (Pl. 1, Fig. 19), and at any angle to each other (Pl. 1, Fig. 18, 20). They were also differentiated into various orientation of contiguous stomata, like the report (Patel and Inamdar, 1971a).

(j) Cytoplasmic connected stomata. Inamdar and Patel (1970) have reported on the cytoplasmic connection between a subsidiary cell and guard cell in *Kalanchoe*. Litz and Kimmins (1968) have reported that the cytoplasmic connection between the guard cell and adjacent cell served as pathway for the exchange of material in the guard cells without isolating physiologically from the other epidermal cells. The cytoplasmic connection was reported to serve as the transportation of materials by Gopal and Shah (1970). In the present study we observed the cytoplasmic strands of a bridge connected between the guard cells and the adjacent guard cells (Pl. 2, Figs. 25-28). This type was seemed to be closed up to each other due to mutual readjustment of space between primary and secondary stoma within the compound helico-eumesogenous stomatal complex. The bridge was not observed at an early stage of development of neighbouring stomata. The protuberances of the guard cells adjacent to the other stoma were extended and met each other. Finally the stomata became the contiguous type (Pl. 2, Figs. 28, 29). This type was largely observed in *S. mexicanum*, *O. japonicus*, and *P. chinense*.

(k) Unequal guard cells. This type has been reported by Inamdar (1969) and Siddiqui *et al.* (1976). During the ontogenic pathway, the guard mother cell was divided into unequal two cells. The larger cell was differentiated into a normal guard cell. If the smaller cell was not degenerated, the cell was differentiated into one abnormal smaller guard cell (Fig. 2-III, Pl. 2, Fig. 30).

(l) Wavy guard cells. This abnormal stoma has been only illustrated by Inamdar and Patel (1970) in *Kalanchoe*. Cause and ontogeny of the formation have been unknown. In the present study, after the guard mother cell was divided into two guard cells, the back wall of one or two guard cells was observed to develop into the wavy shape (Pl. 2, Fig. 31). However we did not find the cause and ontogenetic pathway of this guard cells.

(m) Projected guard cells. Farooqui (1979) has described that peg-like projections were extended into the cavity of the cells adjoining the stomata in *Fenaea myrtoides* and *Sarcocolla fucata*. The lateral walls of guard cell showed a small and spin-like outgrowth in some Cycads and *Phylloglossum*. In the present study a part of cytoplasm and wall in guard cell was projected into the cavity of the subsidiary cells during the maturation in *S. alboroseum* and *B. crenatum* (Pl. 2, Figs. 32, 33).

(n) Cross cleaved stomata. Stebbins *et al.* (1967) have reported that 2-mercaptoethanol treatment on the barley leaves interfered with the spindle formation and changed the orientation of the division of some guard cells. Kaufman *et al.* (1967) have reported that gibberellic acid caused the infrequent aberrant transverse divisions of guard mother cells of the developing stomata. In the present study the guard mother cell of the normal leaves without any treatment was divided into two guard cells by the transverse division changed with harelip-like shape having chloroplasts (Pl. 2, Fig. 31). The cross cleaved guard cells were observed firstly in *K. blossfeldiana* (Fig. 2-VI).

(o) Overlapped-thickening guard cells. The overlapped guard cells have been reported by the workers (Pant and Mehra, 1963; Inamdar, 1970). Raju *et al.* (1975) observed an uncommon wall thickening of guard cells. However the terminology used here has not been made as the type of abnormal stomata. We observed that some regions of guard cells were thickened and also overlapped by subsidiary cells or epidermal cells during the maturation (Pl. 2, Figs. 35-38) like Farooqui (1981). We used the terminology due to the thickening wall of guard cell and the overlapping.

(p) Dissolved cell wall stomata. Yamada and Nagasawa (1976) have reported dissolution and metamerism of epicuticular layer in stomata by fungal infection. We did not observe the dissolution of cell wall at an early stage of stomatal development. However, after the

Table 2. Frequency of abnormal stomata in Crassulaceae (+, occurrence)

Species	Types of abnormal stomata*																			
	BS	PSI	SGC	SAGC	ABS	NOS	BGC	SSCS	CS	CCNS	UGC	WGC	PGC	CCLS	OTGC	DCWS	ARS	WS	FPS	Total
O. japonicus			+	+	+					+							+			5
O. malacophyllus			+	+	+												+			4
S. kamtschaticum			+	+	+				+											4
S. ellacombianum	+		+	+	+															4
S. aizoon			+	+	+	+														4
S. aizoon var. *heterodontum*			+	+	+						+									4
S. aizoon var. *ramosum*			+	+	+															3
S. aizoon var. *latifolium*			+	+	+						+									4
S. aizoon var. *saxatile*			+	+	+															3
S. alboroseum		+	+	+	+	+	+		+		+	+	+		+	+	+		+	14
S. bulbiferum			+	+	+			+								+	+			6
S. sarmentosum	+	+	+	+	+	+	+								+		+			9
S. lineare var. *albomarginatum*	+	+	+	+	+										+		+			7
S. mexicanum			+	+	+					+					+		+			6
S. adolphii			+	+	+				+						+		+			6
S. robrodictum			+	+	+											+	+			5
B. crenatum			+	+	+								+							4
K. blossfeldiana				+	+							+		+			+			5
K. tomentosa				+	+															2
C. arborescense	+			+	+						+	+							+	6
E. glauca	+		+	+	+										+					5
E. pulvinata				+	+												+			3
G. paraguagense				+	+												+			3
P. chinense		+	+	+	+	+			+	+					+		+	+		10
Total frequency	5	4	19	24	24	4	2	1	4	3	4	3	2	1	7	3	13	1	2	126

* BS, blob stomata; PSI, persistent stomatal initials; SGC, single guard cell; SAGC, single-aborted guard cells; ABS, aborted stomata; NOS, nonfunctional-opening stomata; BGC, ballooning guard cells; SSCS, supernumerary subsidiary cell stomata; CS, contiguous stomata; CCNS, cytoplasmic connected stomata; UGC, unequal guard cells; WGC, wavy guard cells; PGC, projected guard cells; CCLS, cross cleaved stomata; OTGC, overlapped-thickening guard cells; DCWS, dissolved cell wall stomata; ARS, arrested stomata; WS, wrenched stomata, FPS, fused pore stomata.

maturation of stoma it was observed at the position between guard cells and subsidiary cells, or between two subsidiary cells (Pl. 2, Figs. 39, 40).

(q) Arrested stomata. Kaufman *et al.* (1967) reported that GA_3 treatment had its ability to arrest the cell division in the short cell which formed cork-silica cell pairs and stomata in internodes. Although the meristemoid at each stage of stomatal development was not treated with GA_3 in the present study, we observed that the initials in each stage were arrested by high vacuolation and the degeneration of nucleus (Pl. 2, Fig. 41) like Inamdar (1970).

(r) Wrenched stomata. This type has been reported in *Asparagas* by Gopal and Shah (1970). In the present study we observed the wrenching of two guard cells, but we did not find the ontogeny of the wrenched stomata. It was seemed to be the result of abnormal arrangement with an irregular fashion during the maturation (Pl. 2, Fig. 42).

(s) Fused pore stomata. This type could be fused with the pore between two guard cells after the maturation of guard cells (Fig. 2-XI, Pl. 2, Figs. 43, 44, 45). Each cell wall between two guard cells was closing to each other, dissolved, and then fused. After that pore was lost like Pl. 2, Fig. 45 and the left guard cell of Pl. 2, Figs. 43, 44. This type firstly reported here by the authors was observed in *S. alboroseum* and *C. arborescense.*

In the ontogeny of the abnormal stomata, Ahmad(1964) pointed out that the abnormal stomata in Solanaceae were formed as a result of the degeneration of normal stomata rather than through developmental abnormalities. Also several workers suggested that the abnormal stomata could be formed as a result of developmental abnormalities (Dehnel, 1961; Inamdar *et al.*, 1969; Inamdar, 1970). It was thought that the abnormal stomata could be formed as the results of the degeneration as well as the developmental abnormalities (Patel and Shah, 1971; Patel *et al.*, 1972).

Frequency of abnormal stomata. In the present study total nineteen types of abnormal stomata were found as shown in Table 2. Three types of them such as the single guard cell, the aborted stomata, and the single-aborted guard cell were observed as the highest frequency, occurring in nineteen to twenty four species. Two types of the overlapped-thickening guard cells and the arrested stomata exhibited the common frequency in seven to thirteen species. Another fourteen types of them showed the lowest occurring in one to five species among twenty four species. The other fourteen types except for the five types of SGC, CCNS, UGC, WGC, and ARS in Table 2 have never been found until now in the genera of Crassulaceae. Particularly the three types of the unrecognized abnormal stomata such as the ballooning guard cells, the cross cleaved stomata, and the fused pore stomata were firstly reported here in the seed plants.

In the stomatal morphology, the cause of abnormal stomata has been known as the various factors such as gene action (McClintock, 1951, 1956; Zeiger and Stebbins, 1972), extrinsic factors (Bünning, 1952; Gupta *et al.*, 1968), intrinsic factors (Dehnel, 1961), hormone and chemical action (Stebbins *et al.*, 1967; Kaufman *et al.*, 1967; Fisher, 1970), specific structure (Böcher, 1972; Gambles and Dengler, 1974), pathological origin (Gertz, 1919; Yamada and Nagasawa, 1976), polyploidy (Takahashi, 1960), and hybrid(Fukasawa, 1957).

摘 要

돌나무科(Crassulaceae)에 屬하는 植物 24種을 對象으로 非正常氣孔의 類型과 種間 出現頻度를 調査한 結果는 다음과 같다. 非正常氣孔의 類型은 helico-eumesogenous stomata와 anomo-hemimesoperigenous stomata에서 總 19個 類型이 觀察되었고 이들 중에서 single guard cell, single-aborted guard cell 및 aborted stomata의 3個 類型은 19∼24種에서 發見되어 가장 높은 頻度를 나타내었고 다른 14個 類型은 1∼5種에서만 發見되어 가장 낮은 頻度를 나타내었다. 種에 따른 非正常氣孔의 出現頻度는 總 19個 類型中 꿩의비름(*Sedum alboroseum*), 낙지다리(*Penthorum chinense*) 및 돌나물(*Sedum sarmentosum*)의 3種에서 9∼14個 類型이 發見되어 가장 높은 頻度를 나타내었으며, 餘他 種은 7個 類型以下의 낮은 頻度를 나타내었다. 非正常氣孔의 類型中 ballooning guard cell, cross cleaved stomata 및 fused pore stomata의 3個 類型은 지금까지 文獻上에서 發表되지 않았고 著者等에 依하여 最初로 發見되었다. 非正常氣孔은 正常氣孔의 退化의 結果이거나 非正常的 發生의 結果로 形成된다는 것을 觀察할 수 있었다.

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EXPLANATION OF PLATES

Plate 1.

Figs. 1-3. Blob stomata; aborted cytoplasm and nucleus of guard mother cell initial in *S. ellacombianum* (Fig. 1), aborted cytoplasm and nucleus of guard mother cell in *S. sarmentosum.* (Fig. 2) and aborted cytoplasm and nucleus of a pair of guard cell and a few subsidiary cells in *C. arborescense* (Fig. 3).

Fig. 4. Persistent stomatal initial and normal stoma in *S. sarmentosum.*

Figs. 5, 6. Single guard cell within helico-eumesoperigenous stoma, nucleous and chloroplasts appear in *S. aizoon* (Fig. 5) and *S. aizoon* var. *heterodontum* (Fig. 6).

Fig. 7. Single-aborted guard cells, aborted stoma and mature stoma in *P. chinense.* (the noted pore of the single-aborted guard cell is present and the aborted trace of young stoma is small).

Figs. 8, 9. Single-aborted guard cells; aborting guard cell and normal guard cell in *S. lineare* var *albomarginatum* (Fig. 8), and single-aborted guard cell in *E. glauca* (Fig. 9).

Fig. 10. Single-aborted guard cells and aborted stoma in *S. mexicanum.*

Figs. 11, 12. Aborted stomata in *B. crenatum* (Fig. 11) and *S. mexicanum* (noted development of thinner back walls and thickner inner walls (Fig. 12).

Figs. 13, 14. Nonfunctional-opening stomata in *S. sarmentosum* (noted inner wall of guard cells thickened, and pore is always opening).

Fig. 15. Ballooning guard cells in *S. sarmentosum.*

Fig. 16. Guard mother cell with supernumerary subsidiary cells in *S. bulbiferum.*

Figs. 17-21. Contiguous stomata in *P. chinense*: superimposed contigous stomata (Figs. 17, 22), at any angle to each other (Figs. 18, 20), juxtaposed contiguous stomata (Fig. 19).

Plate 2.

Fig. 21. Contiguous stomata in *P. chinese*:
developing stoma in neighbouring cells of primary developed stoma.

Figs. 23, 24. Contiguous stomata in *S. alboroseum.*

Figs. 25-29. Cytoplamic connected stomata; a portion of stomata showing protuberances touching each other in *P. chinense* (Fig. 25) and O. *Japonicus* (Fig. 29), protuberances from guard cell walls of nearby stomata connected by cytoplasmic strands in *P. chinense* (Fig. 26) and *S. mexicanum* (Fig. 27), protuberances extend and meet each other, and the two stomata contiguous in *S. mexicanum* (Fig. 28).

Fig. 30. Unequal guard cells in *C. arborescense.*

Fig. 31. Wavy guard cells in *C. arborescense.*

Figs. 32, 33. Projected guard cells in *S. alboroseum.*

Fig. 34. Cross cleaved stomata in *K. blossfeldiana.*

Figs. 35-38. Overlapped-thickening guard cells: a portion of guard cell overlapped by subsidiary cell, and guard cell walls thickened in *S. bulbiferum* (Fig. 35) and *E. glauca* (Figs. 36-38).

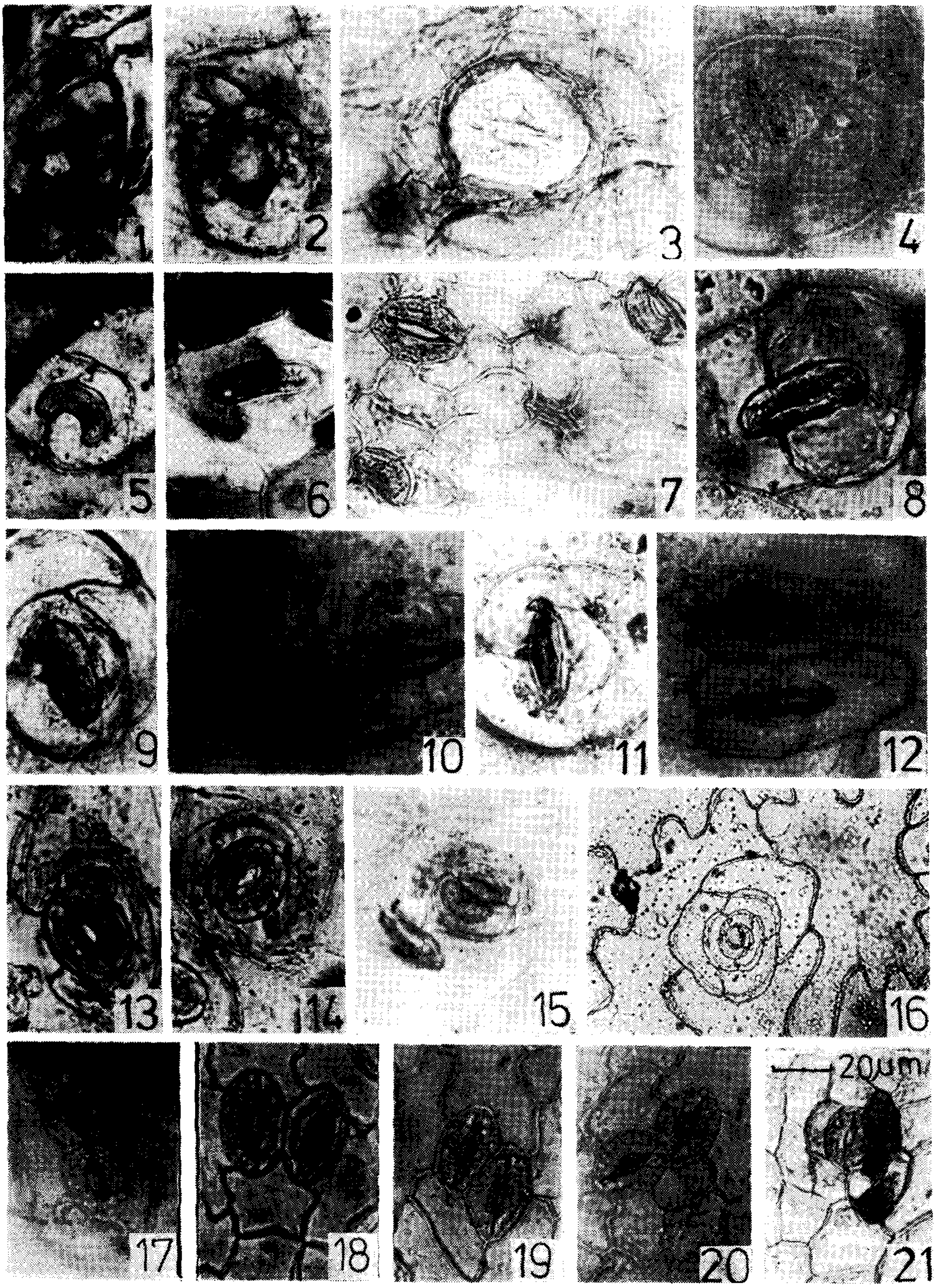
Figs. 39, 40. Dissolved cell wall stomata; subsidiary cell wall dissolved between the stoma and stoma in *S. bulbiferum* (Fig. 39), and cell wall dissolved between the guard cells and subsidiary cell in *S. alboroseum* (Fig. 40).

Fig. 41. Arrested stomata in *S. lineare* var. *albomarginatum*.

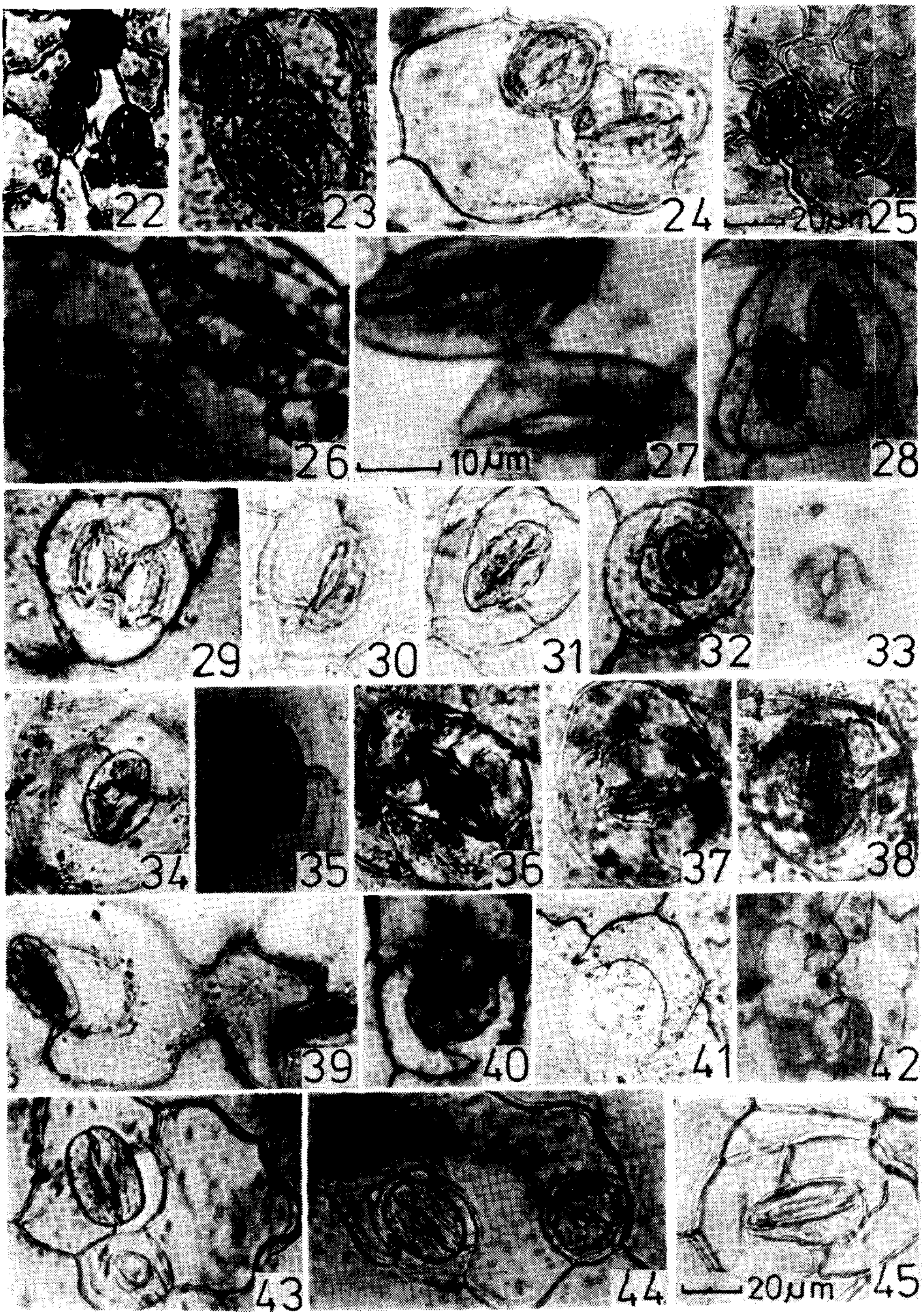
Fig. 42. Wrenched stomata showing abnormal arrengement of guard cells in *P. chinense*.

Figs. 43-45. Fused pore stomata in *S. alboroseum* (Figs. 43, 44) and *C. arborescense* (Fig. 45).

(**Plate 1**)



〔**Plate 2**〕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