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Structure and Ontogeny of Stomata in Some *Euphorbiaceae*

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Abstract

Structure and ontogeny of stomata in 53 species belonging to three tribes and seven sub-tribes of the *Euphorbiaceae* is presented. The lamina is either hypostomatic or amphistomatic. Cotyledons of *Ricinus communis* and bracts of *Euphorbia pycnostegia* and *Euphorbia rothiana* are amphistomatic. Stem of *Euphorbia antiquorum* is stomatic. The anticlinal epidermal walls are either straight, arched, sinuous or articulated, thin or evenly or unevenly thickened with or without pits. Small triangular intercellular spaces are present in the leaf epidermis of *Euphorbia heterophylla*. Cuticular striations radiating in any direction are also noticed. Sclerosed cells are recorded in the leaf epidermis of *Phyllanthus nivosus* var. *roseo-pictus*. The mature stomata noticed are: anomocytic, paracytic, diacytic, parallelocytic, anisocytic and with a single subsidiary cell. The ontogeny of anomocytic stomata is perigenous, stoma with a single subsidiary cell either peri- or mesogenous; paracytic meso-mesoperi- or perigenous; diacytic mesogenous; anisocytic mesoperi- or perigenous; while that of parallelocytic is meso-, or mesoperigenous. The confusion regarding the definition of 'anomocytic stomata' is also discussed. Abnormalities such as persistent stomatal cells, single guard cells, degeneration of gard cells, cytoplasmic connections, contiguous stomata, twin stomata, one and a half contiguous stomata, notching of guard cells and division of guard cells are seen. The stomatal types and their ontogeny in 53 species studied are charted in a tabular form. Both the stomatal types and their ontogeny show diversity even on

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the same surface of the leaf (*see* Table 2), which is a weak taxonomic criterion.

Zusammenfassung

Bau und Ontogenie der Spaltöffnungsapparate von 53 *Euphorbia*-Arten aus drei Triben und sieben Subtriben werden dargestellt. Auch dem Bau der Epidermiszellen wird Beachtung geschenkt. Zahlreiche Abnormitäten im Bau der Spaltöffnungsapparate werden beschrieben und in Zeichnungen dargestellt. Die Stomata-Typen und deren Ontogenie werden in Tabellenform übersichtlich zusammengefaßt; sie zeigen große Mannigfaltigkeit, erweisen sich aber von nur geringem taxonomischen Wert.

Introduction

The family *Euphorbiaceae* comprises about 300 genera and 5000 species, which are cosmopolitan in distribution except arctic. Several of these, e. g. *Manihot, Hevea, Croton, Ricinus* etc. are economically important (Willis 1966). According to Metcalfe & Chalk (1950) the mature stomata in the *Euphorbiaceae* are rubiaceous, cruciferous and ranunculaceous which are usually confined to lower surface, more rarely on both the surfaces of the lamina. Tognini (1897) reported paracytic stomata which are mesogenous in development in *Euphorbia variegata* and *Ricinus communis*. Sehgal & Paliwal (1974) recorded anomocytic, paracytic anisocytic, cyclocytic and stomata with a single subsidiary cell in the species of *Euphorbia*. The scanning electron microscopic study of the surface structure of about 37 species of *Euphorbia* L. was made by Ehler (1974). Rao & Raju (1975a, b) studied the development of stomata in *Micrococca mercurialis* and little known features in foliar epidermology respectively of some *Euphorbiaceae*. Surprisingly, in such a large family only a handful workers have studied the stomatal structure and ontogeny. Hence the present investigation has been undertaken to study the structure and ontogeny of stomata in 53 species.

Material and Methods

The material of 53 species of the *Euphorbiaceae* was collected from different parts of India. The names of the species studied, frequency of epidermal cells, stomata, stomatal index per mm^2 and size of guard cells and epidermal cells are given in Table I. Camera lucida drawings were made from the epidermal peels taken from young as well as mature organs of fresh and fixed (in FAA) materials, stained with Delafield's haematoxylin and mounted in glycerin. The ontogeny of stomatal types in different species is compiled in Table 2.

Table 1

Frequency of stomata (SF) and epidermal cells (EF), stomatal index (SI)/ mm², size of the guard and epidermal cells (L = length, B = breadth, μm) LL = lamina lower, LU = lamina upper

		Stomata		Guard Cells		Epidermal cells		
		SF	SI	L	B	EF		
Acalypha sp.	LL	240	33	23	5	480	62	39
	LU	64	12	26	9	480	61	43
A. ciliata Forsk.	LL	298	38	19	6	448	52	43
	LU	37	4	23	7	720	45	32
A. indica L.	LL	208	32	23	6	368	52	39
	LU	128	18	25	6	560	46	30
A. wilkesiana Muell.	LL	106	25	30	8	316	55	39
	LU	18	3	27	9	739	39	34
Antidesma ghaesembilla Gaertn.	LL	256	24	25	8	768	40	28
	LU	64	8	27	7	736	42	27
Baliospermum montanum (Willd.) Muell.-Arg.	LL	208	18	27	7	928	56	26
	LU	64	8	27	7	736	42	27
Bridelia hamiltonia Wall. ex Hook f.	LL	496	19	17	6	2064	25	18
B. squamosa (Muell.-Arg) Gehrm.	LL	504	23	17	5	1656	32	20
Chrozophora prostrata Dalz.	LL	336	28	25	8	592	63	24
C. rottleri (Geiss)	LU	192	25	30	8	576	46	30
Juss. ex Spr.	LL	368	28	28	8	928	59	30
	LU	160	15	25	7	864	43	28
Cicca acida (L) Merill.	LL	149	13	21	6	1021	36	25
Croton bonplandianum Baill.	LL	192	17	15	6	938	42	25
	LU	160	13	20	6	1091	42	28
C. oblongifolius Roxb.	LL	496	12	18	7	2788	19	13
	LU	176	6	19	7	2864	20	15
Dalechampia scandens L.	LL	400	33	19	6	800	36	23
	LU	78	6	20	6	1232	40	29
Emblica officianlis Gaertn.	LL	176	14	25	6	1056	49	37
Euphorbia acaulis Roxb.	LL	96	11	30	9	780	45	26
	LU	69	11	26	9	576	49	36
E. antiquorum L.	LL	112	12	40	24	850	40	30
	LU	96	11	40	24	800	42	35
E. geniculata Orteg.	LL	277	26	22	7	775	44	28
	LU	216	24	24	7	685	55	28
E. heterophylla L.	LL	128	21	29	9	480	54	42
	LU	96	14	27	8	528	51	36

		Stomata		Guard Cells		Epidermal cells		
		SF	SI	L	B	EF		
E. hirta L.	LL	192	28	28	6	480	41	34
	LU	96	13	20	5	656	55	35
E. hyperecifolia L.	LL	176	14	25	6	1056	49	37
	LU	96	13	20	5	656	55	35
E. microphylla HEYNE.	LL	252	22	17	6	900	42	28
	LU	96	13	20	5	656	55	35
E. milii CH.-DES-MOULINS	LL	128	9	23	6	1253	39	28
	LU	107	9	19	6	1055	39	26
E. neriifolia L.	LL	48	10	34	11	432	57	39
	LU	22	5	36	13	440	57	40
E. pulcherrima WILLD. ex KLOTZCH.	LL	512	21	18	6	1904	27	17
E. pycnostegia BOISS.	LL	256	17	17	6	1248	34	24
E. rothiana SPRENG.	LL	96	15	29	9	528	68	33
	LU	70	9	31	10	672	59	33
E. thymifolia L.	LL	240	27	18	6	922	44	30
	LU	224	12	15	5	960	30	23
E. tirucalli L.	LL	252	17	22	5	1188	30	20
	LU	72	5	22	5	1152	32	26
Glochidion hohenackeri BEDD.	LL	160	9	29	8	1504	34	20
Hevea brasiliensis MUELL.	LL	464	27	24	6	1280	31	17
	LU	72	4	25	8	1664	39	20
Homonoia riparia LOUR.	LL	368	20	20	6	1488	26	14
Jatropha curcas L.	LL	176	14	29	8	976	36	25
	LU	32	4	37	10	720	47	34
J. gossypifolia L.	LL	208	21	25	6	736	39	27
	LU	27	3	28	7	821	45	31
J. multifida L.	LL	272	9	23	8	2688	30	17
J. panduraefolia ANDR.	LL	288	27	26	7	760	45	26
J. podagrica HOOK.	LL	282	13	21	6	1840	30	21
	LU	17	2	29	7	896	41	39
Kirganelia reticulata (POIR.) BAILL.	LL	368	27	21	6	960	31	22
	LU	48	5	21	6	800	34	26
Macaranga roxburghii WIGHT	LL	480	15	17	6	2640	21	13
Mallotus phillippensis (LAMK.) MUEL.-ARG.	LL	496	17	13	6	2590	14	9
Manihot esculenta CRANZ.	LL	432	24	21	5	1296	37	24
Pedilanthus tithymaloides (L.) POIT.	LL	90	11	25	6	7	4116	31
	LU	35	4	22	6	7	5048	32

		Stomata		Guard Cells		Epidermal cells		
		SF	SI	L	B	EF		
Phyllanthus asperulatus HUTCH.	LL	378	40	8	3	584	20	11
	LU	208	7	3	5	571	18	10
P. maderaspatensis L.	LL	256	22	22	6	880	53	36
	LU	176	15	22	6	880	55	36
Phyllanthus nanus HOOK f.	LL	192	24	20	6	544	54	34
	LU	172	22	18	6	576	54	35
P. nivosus BULL var. *roseo -pictus* hort.	LL	128	8	21	5	1721	33	21
	LU	8	1	23	6	878	45	28
P. simplex RETZ.	LL	208	28	20	5	576	55	38
	LU	112	13	19	5	720	52	32
Putranjiva roxburghii WALL.	LL	572	26	19	8	1648	17	13
Ricinus communis L.	LL	136	25	32	10	413	60	40
	LU	96	15	31	10	538	60	30
Securinega virosa (ROXB. ex WILLD.) PAX & HOFFM.	LL	384	26	19	5	1088	33	25
Tragia cannabina L. f.	LL	450	32	18	5	1013	30	22
	LU	22	2	20	6	1062	35	28
T. mollurina PAX & HOFFM.	LL	96	12	27	8	544	60	34
	LU	8	2	28	8	368	58	36
Trewia polycarpa BENTH & HOOK.	LL	240	25	25	6	704	44	27

Table 2

Stomatal types and their ontogeny
(A = anomocytc, SS = stoma with a single subsidiary cell, P = paracytic, ANI = anisocytic, PAL = parallelocytic, D = diacytic; p = perigenous, m = mesogenous, mp = mesoperigenous)

Species	Types of stomata					
	A	SS	P	ANI	PAL	D
I. Tribe: *Euphorbieae:*						
Euphorbia acaulis	—	m	m, mp	—	m, mp	—
E. antiquorum	p	—	m	—	mp	—
E. geniculata	p	—	p	p	—	—
E. heterophylla	p	p	p	p	—	—
E. hirta	p	—	p	p	—	—
E. hypericifolia	p	—	p	p	—	—
E. microphylla	p	—	p	p	—	—
E. milii	—	—	m	—	—	—
E. neriifolia	—	—	m, mp	—	m	—
E. pulcherrima	p	p	p	—	—	—
E. pycnostegia	p	—	p	p	—	—

Species	Types of stomata					
	A	SS	P	ANI	PAL	D
E. rothiana	p	—	p	p	—	—
E. thymifolia	p	—	p	—	—	—
E. tirucalli	—	m	m	—	—	—
Pedilanthus tithymaloides	p	—	m, mp	—	—	—
II. Tribe *Phyllantheae:*						
Antidesma ghaesmbilla	p	—	m, mp	—	—	—
Bridelia hamiltonia	p	p, m	m, mp	—	—	—
B. squamosa	p	p, m	m, mp	—	—	—
Cicca acida	p	p, m	m, mp	—	—	—
Emblica officinalis	p	—	p	—	—	—
Glochidion hohenackeri	p	m	m	—	—	—
Kirganelia reticulata	p	—	p	—	—	—
Phyllanthus asperulatus	p	—	m, mp	mp	—	—
P. maderaspatensis	p	—	p	p	—	—
P. nanus	p	—	p	p	—	—
P. nivosus var. *roseo-pictus*	p	—	—	—	—	—
P. simplex	—	m	m	mp	—	—
Putranjiva roxburghii	p	—	—	—	—	—
Securinega virosa	p	—	p	—	—	—
III. Tribe *Crotoneae:*						
(i) Sub-tribe *Jatropheae:*						
Hevea brasiliensis	p	m	m, mp	—	—	—
Jatropha curcas	p	m	m, mp	—	—	—
J. gossypifolia	p	—	m	—	—	—
J. multifida	p	—	m	—	—	—
J. panduraefolia	—	—	m, mp	—	mp	—
J. podagrica	p	—	p	—	—	—
(ii) Sub-tribe *Eucrotoneae:*						
Croton bonplandianum	p	p, m	m, mp	—	—	—
C. oblongifolius	p	p, m	m, mp	—	—	—
(iii) Sub-tribe *Chrozophoreae:*						
Chrozophora prostrata	p	m	m	—	—	—
C. rottleri	p	—	m	—	—	—
(iv) Sub-tribe *Acalypheae:*						
Acalypha sp.	p	—	m, mp	—	mp	—
A. ciliata	p	—	m	—	—	—
A. indica	p	—	m	—	m	—
A. wilkesiana	—	—	m	—	m	m
Homonoia riparia	—	—	m	—	—	—
Macaranga roxburghii	p	—	—	—	—	—
Mallotus phillippensis	p	—	—	—	—	—
Ricinus communis	p	—	m	—	—	—
Trewia polycarpa	—	—	m	—	m	—

Species	Types of stomata					
	A	SS	P	ANI	PAL	D
(v) Sub-tribe *Gelonieae:*						
Baliospermum montanum	—	—	m	—	—	—
(vi) Sub-tribe: *Plukenetieae:*						
Dalechampia scandens	p	—	m	—	mp	—
Tragia cannabina	p	—	m, mp	—	—	—
T. mollurina	—	—	m	—	m	—
(vii) Sub-tribe: *Adrianeae:*						
Manihot esculenta	—	—	m	—	—	—

Observations

Mature epidermis: In addition to lamina of 53 species, bracts of *Euphorbia pycnostegia*, *E. rothiana*, cotyledons of *Ricinus communis*, and stem of *Euphorbia antiquorum* are studied for epidermis. The lamina is amphistomatic in all the species except *Bridelia hamiltonia*, *B. squamosa*, *Cicca acida*, *Emblica officinalis*, *Euphorbia pycnostegia*, *Glochidion hohenackeri*, *Homonoia riparia*, *Jatropha multifida*, *J. panduraefolia*, *Macaranga roxburghii*, *Mallotus phillippensis*, *Putranjiva roxburghii*, *Securenega virosa* and *Trewia polycarpa* where it is hypostomatic. The cotyledons of *Ricinus communis*, bracts of *Euphorbia pycnostegia* and *Euphorbia rothiana* are amphistomatic while the stem of *Euphorbia antiquorum* is stomatic. The epidermal cells are polygonal, isodiametric or variously elongated, often with papillose outgrowths in some species, with thin or thick, straight, arched, or sinuous or articulated anticlinal walls often with distinct pits (Figs. 2—5, 7, 8, 9, 11—19, 20—26, 28—31, 32—35, 37—46, 47—80, 82—91, 93—99, 101—110, 112—119, 121—137). The epidermal cell walls may be evenly or unevenly thickened. The epidermal cells are mostly compact without intercellular spaces, but in *Euphorbia heterophylla* small intercellular spaces are present (Figs. 38, 39). Cuticular striations radiating from hair bases as well as from guard cells or restricted to subsidiary cells (Figs. 21, 22, 103, 105, 107, 129) are noticed. In some cases, cuticular striations radiatıng in any direction occur all over the epidermis (Figs. 108, 113).

Sclerosed cells are present in the epidermis of *Phyllanthus nivosus* var. *roseo-pictus* (Figs. 88, 89, 145). Sclerosed cells originate from sclerose-initials. The sclerosed initial occur either solitary or in groups or in association of a stoma (Figs. 143—145). The sclerosed initial can be easily recognised by smaller size, dense staining and prominent nucleus. The sclerosed intitial increases in size, becomes highly vacuolated, secondary centripetal wall thickening also take place in the form of concentric layers. Sometimes a nucleus persists in the lumen (Fig. 145). Simple pits with narrow pit-canals seen over the walls which are indistinct.

Mature stomata: (i) Distribution and orientation: The stomata are uniformly distributed without any definite pattern of orientation all over the surface of lamina except the vein regions. Sometimes, they are arranged parallel to the longitudinal axes of the organs. In *Hevea brasiliensis* the stomata are present on either side of the veins especially near the midrib and are mostly parallel to the veins on the upper epidermis of lamina. Rarely stomata occur in groups.

(ii) Stomatal types: Mature stomata are either anomocytic, with a single subsidiary cell, paracytic, diacytic, anisocytic and parallelocytic. More than one type of stomata occur on the same surface of the lamina in majority of the species studied.

(iii) Structure: Anomocytic stomata are surrounded by 3—6 ordinary epidermal cells (Figs. 20, 25, 37, 38, 40, 42, 43, 53, 57, 58, 65, 88, 89, 93, 116, 118, 123, 131, 133, 136). Stomata with single subsidiary cell are flanked by a single parallel or oblique subsidiary cell (Figs. 15, 20, 23, 54, 56, 63, 90, 123, 127, 136). Paracytic stomata are flanked/surrounded by two parallel and lateral subsidiary cells which are either non-contiguous at both the poles or contiguous at one or both the poles (Figs. 2—5, 7—9, 11—15, 17, 18, 20, 21—25, 28—35, 39—41, 45—53, 55—59, 60—63, 65—67, 69—72, 74—79, 82—84, 85—87, 90—91, 96, 98, 99, 101, 103—107, 109, 110, 112, 114—116, 121—125, 127—129, 135—138). Diacytic stomata are surrounded by two subsidiary cells whose common walls are at right angles to the guard cells (Fig. 11). Anisocytic stomata are surrounded by three subsidiary cells of which one is distinctly smaller than the other two (Figs. 41, 42, 44, 51, 83—85, 90, 116, 121, 135). Parallelocytic stoma is surrounded by 3—4 parallel subsidiary cells (Figs. 2—5, 7—9, 11—14, 46, 48, 49, 71, 72, 78, 80, 105, 107, 137). In some cases the subsidiary cells undergo both transverse as well as longitudinal divisions (Figs. 7, 28, 29, 30, 46—48, 55, 62, 70, 77, 84, 105— marked by arrows). Wall thickening at the polar ends of guard cells is noticed (Fig. 140, marked by arrows).

(iv) Abnormal stomatal types: In addition to normal stomata several abnormalities such as persistent stomatal cells (Fig. 11), single guard cells (Figs. 1, 8, 11, 30, 32, 59, 98, 146), degeneration of one or both the guard cells of a stoma (Figs. 9, 30, 49, 55, 61, 73), contiguous stomata (Figs. 58, 82, 84, 88, 98, 133), twin stomata (Fig. 34), one and a half contiguous stomata (Fig. 122), notching of guard cells (Figs. 90, 98, 141, 142), division of guard cells (Fig. 97) and cytoplasmic connections (Figs. 32, 65, 76, 86) are noticed.

Ontogeny of stomata: The protoderm cells are polygona, isodia-l metric, uninucleate with uniform staining, mostly straight, rarely sinuous anticlinal walls. The stomatal meristemoid is cut off in a corner or on one side of a protoderm cell. A meristemoid can be easily distinguished by its smaller size, shape, prominent nucleus and dense staining properties (Figs.

1, 6, 36, 81, 92, 100, 111, 120, 139). The meristemoid undergoes further division/s to give rise to different types of stomata as follows:

(i) Anomocytic: Here, the meristemoid enlarges, divides by a straight wall to produce two equal guard cells without cutting off any subsidiary cells. A lenticular pore develops between the two guard cells (Figs. 1, 36, 81, 92, 120). Mature stoma is surrounded by ordinary epidermal cells.

(ii) Stoma with a single subsidiary cell: (a) Mesogenous: The meristemoid enlarges, divides by a slightly curved wall to form two unequal cells, the larger cell differentiates as a single subsidiary cell (s_1), while the smaller cell enlarges, divides by a straight wall parallel or oblique to the first to give rise to a pair of guard cells (Fig. 111). Mature stoma is flanked by a single mesogene subsidiary cell.

(b) Perigenous: The stomatal ontogeny conforms to that of anomocytic type except that a single perigene subsidiary cell is cut off from an adjacent epidermal cell. Sometimes, the cell which cuts off the meristemoid assumes the configuration of a subsidiary cell (Figs. 38, 120, 136).

(iii) Paracytic: (a) Mesogenous: The meristemoid undergoes two successive divisions parallel to each other by slightly curved walls to produce two outer cells and a central cell. The two outer cells form two subsidiary cells (s_1 and $_2$). The central cell functions as a guard mother cell, divides by a straight wall parallel to the subsidiary cells to produce two guard cells (Figs. 1, 6, 10, 111). Mature stoma is flanked/surrounded by two mesogene subsidiary cells which are either contiguous at both the poles or non-contiguous at one or both the poles depending upon the intersection or non-intersection of first two divisions.

(b) Mesoperigenous: Here there are two possibilities: (i) The meristemoid cuts off a single subsidiary cell (s_1) and then functions as a guard mother cell, divides to form a pair of guard cells while the other subsidiary cell (p_1) is cut off from an adjacent epidermal cell or (2) an adjacent epidermal cell assumes the shape of a subsidiary cell (Figs. 1, 27, 100, 111).

(c) Perigenous: The ontogeny of stomata is similar to that of anomocytic type. But, here, the two parallel and lateral subsidiary cells are cut off from adjacent epidermal cells (Fig. 65). Mature stoma is flanked by two perigene subsidiary cells (p_1 and p_2) (Figs. 39, 41, 43, 44, 45, 57, 116, 118, 120—122).

In some cases, a meristemoid is cut off between two protoderm cells (as in Figs. 36, 120). The meristemoid directly functions as a guard mother cell, divides to form a pair of guard cells. Here, the stoma at maturity looks like paracytic. Sometimes, the subsidiary cell/s of a paracytic stoma undergoes both transverse, oblique and longitudinal divisions (marked by arrows) so that some of the stomata look like anomocytic or anisocytic (Figs. 3, 7, 28—30, 46—48, 62, 75, 77). In *Euphorbia antiquorum* one of the subsidiary cells of a paracytic stoma regains meristematic activity which divides and give rise to an initial (Fig. 31). The initial may directly function as a guard mother cell (Fig. 31) or it cuts off a subsidiary cell and then functions as a guard mother cell, divides to produce a pair of guard cells. Here, a common subsidiary cell (cs) is present between the two stomata (Fig. 33). The guard cells may or may not degenerate.

(iv) Parallelocytic: (a) Mesogenous: The meristemoid cuts off 3—4 more or less c-shaped parallel subsidiary cells and then functions as a guard mother cell, divides by a straight wall parallel to earlier divisions to give rise to two guard cells. (Figs. 6, 10). Mature stoma is flanked by 3—4 mesogene subsidiary cells.

(b) Mesoperigenous: Here, the meristemoid cuts off two parallel subsidiary cells and then functions as a guard mother cell. The guard mother cell divides parallel to the first two divisions by straight wall to form a pair of guard cells. The cell which cuts off the meristemoid forms an encircling cell (ec) (Figs. 1, 6, 10, 111). Mature stoma is surrounded by two mesogene (s_1 and s_2) and a perigene (ec = encircling cell) subsidiary cells.

(v) Diacytic: Mesogenous: The ontogeny of this type conforms to that of mesogenous paracytic type up to triad stage in which the two subsidiary cells are contiguous at both the poles. Here, unlike paracytic stoma the middle guard mother cell divides at right angles to subsidiary cells to produce a pair of guard cells (Fig. 10). Mature stoma is surrounded by two mesogene subsidiary cells whose common walls are at right angles to the guard cells.

(vi) Anisocytic: (a) Mesoperigenous: The meristemoid cuts off one to two subsidiary cells and then functions as a guard mother cell which divides to produce a pair of guard cells. Here, the epidermal cell which cuts off the meristemoid and/or an adjacent epidermal cell assumes the shape of subsidiary cell/s. Mature stoma is surrounded by three unequal subsidiary cells, the later formed being the smallest (Figs. 84, 85, 90).

(b) Perigenous: Here, a triangular meristemoid is cut off in the corners of three epidermal cells (Figs. 36, 81, 92, 120). The stomatal development is anomocytic but, the mature stoma simulates with an anisocytic type.

Discussion

Metcalfe & Chalk (1950) reported that the stomata are rubiaceous in *Acalypheae*, *Dalechampieae*, *Euphorbieae* (in *Euphorbia* and *Mercurialis*), *Exocaria*, *Glochidion*, *Hippomanieae* (except in *Manihot*), *Phyllantheae* (except some *Euphyllantheae*), *Stillingia*; generally cruciferous in *Andrachne*, *Aporosa*, *Baccaurea* and *Richeria*. According to Dommel (cf. Metcalfe & Chalk 1950) rubiaceous and few ranunculaceous stomata occur in succulent species of *Euphorbia* from Madagaskar. SEHGAL & PALIWAL (1974) disagreed with the observations of DOMMEL and pointed out that several types of stomata occur in the succulent species. In succulent species of *Euphorbia* division of subsidiary cells is a common feature because of which anomocytic and paracytic stomata appear cyclocytic or anisocytic. But, cyclocytic stomata have not been observed during the course of present investigation. In the European species of *Euphorbia* METCALFE & CHALK (1950) recorded predominently ranunculaceous less sunken stomata with guard cells less cutinised than in tropical species. They also pointed out that in the *Euphyllantheae* sometimes, mixed cruciferous and rubiaceous stomata occur in a single leaf. The stomata are usually confined to lower surface of lamina (except *Crotoneae*), more rarely occuring on both the surfaces (METCALFE & CHALK 1950). HOLM (*cf.* METCALFE & CHALK, 1950) recorded presence of stomata on both surfaces of lamina of *Euphorbia corollata* and *Stillingia sylvatica* while REICHE (1923) reported their presence on both the surfaces in *Euphorbia radians*. SENANAYAKE & SAMARANAYAKE (1970) studied the intraspecific variation of stomatal density in *Hevea brasiliensis*. SEHGAL & PALIWAL (1974) who studied 150 species pointed out that in the *Euphorbia* complex the cell walls are ranging from straight to variously arched and undulated types, and stomata are anomocytic, paracytic, anisocytic, cyclocytic and with a single subsidiary cell. These authors have also given in a tabular form species-wise distribution of stomatal types, presence or absence of trichomes, stomatal frequency and index (SEHGAL & PALIWAL, 1974). The present observations regarding stomatal types, stomatal frequency and index do not agree with those of SEHGAL & PALIWAL (1974) (*see* Table I and II).

PALIWAL (1969) reported that the paracytic stomata are syndetocheilic in *Euphorbia pulcherrima*. Contrary to this SEHGAL & PALIWAL (1974) recorded only anomocytic stomata in the same species (see Table 2) (p. 147). In *Euphorbia pulcherrima* anomocytic, paracytic and stoma with a single subsidiary cell are observed. The paracytic stomata seems to have perigenous development. RAO & RAJU (1975a) recorded anomocytic paracytic, anisocytic and diacytic types of stomata in the lamina of *Micrococca mercurialis* and pointed out that all the types of stomata are mesogenous. During the course of present investigation stomatal types noticed in the lamina of 53 species are: anonocytic, paracytic, parallelocytic, diacytic, anisocytic and with a single subsidiary cell. The ontogeny of anomocytic stomata is always perigenous; diacytic mesogenous, parallelocytic mesogenous or mesoperigenous; paracytic mesogenous, mesoperigenous or perigenous, anisocytic mesoperigenous or perigenous and with a single subsidiary cell is mesogenous or perigenous. The differentiating stoma may simulate either with a paracytic or anisocytic one when a meristemoid-lenticular or triangular is cut off either on one side of the two parallel protoderm or in corners of three protoderm cells with the surrounding cells looking like subsidiaries respectively. Here, the ontogeny of stomata is infact like anomocytic.

RAJU, PATEL J. D. & SHAH J. J. (1975) reported the presence of uncommon wall thickening at polar ends of guard cells which may be restricted to the outer wall at polar regions or may also be extended to the common inner cell wall. Such thickenings are infact common and occur in many plants.

STRASBURGER (1866—67) reported that the subsidiary cells become meristematic and cut off a series of cells. PALIWAL (1967) noticed one or two but not serial divisions of the subsidiary cells in *Isatis tinctoria*. INAMDAR *et al.* (1974) observed that a subsidiary cell regains meristematic activity and cuts off a small meristemoid which gives rise to either anomocytic or paracytic stomata or arrested developments. In *Euphorbia antiquorum* we have noticed that a subsidiary cell of a paracytic stoma becomes meristematic and cuts off an initial which either directly functions as a guard mother cell to form an anomocytic stoma or cuts off a subsidiary cell and then functions as a guard mother cell. Here, a common subsidiary cell is present between the two stomata (*see* also RAMAYYA & RAJAGOPAL 1970).

During the course of present studies, abnormalities such as single guard cells, degeneration of guard cells, contiguous stomata, cytoplasmic connections between guard cells of nearby stomata and between guard cell of a stoma and an epidermal cell, notching of guard cells, division of guard cells, persistent stomatal cells and twin stomata have been noticed. INAMDAR *et al.* (1973) showed the difference between contiguous stomata and twin stomata and pointed out that twin stomata are abnormal since they are developed from the same meristemoid. INAMDAR & PATEL (1976) pointed out that eventhough contiguous stomata are regarded as an abnormality, whether they are actually abnormal or normal should be decided by studying their ontogeny. When they develop from two adjacent meristemoids or are formed as a result of readjustment, they should not be regarded as abnormal.

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References

EHLER N. 1974. Die Feinskulpturen madagassicher Euphorbien-Hochblätter und ihre taxonomische Wertigkeit. — *Feddes Repert.* **85**: 345—351.

INAMDAR J. A , BHATT D. C. & PATEL R. C. 1973. Normal and abnormal stomatal development in some *Begoniaceae* and *Gesneriaceae* — Acta Bot. Hung. **19**: 181—188.

INAMDAR J. A. GANGADHARA M. MANJIT SINGH S. & PATEL R. S. 1974. Epidermal studies in *Brassica juncea* LINN — Geobios **1**: 40—47.

INAMDAR J. A. & PATEL R. C. 1976. Ontogeny of normal and abnormal stomata in the seedlings of some *Solanaceae*: Phyton (Austria), **17**: 79—86.

METCALFE C. R. & CHALK L. 1950. Anatomy of Dicotyledons, Vol. 2. — Clarendon Press, Oxford

PALIWAL G. S. 1967. Ontogeny of stomata in some *Cruciferae*. — Can. J. Bot. **45**: 495—500.

— 1969. Stomata in certain Angiosperms: Their structure, ontogeny and systematic value. In "Recent Advances in the Anatomy of Tropical seed plants", p. 63—73; Hindustan Pub. Corp. India.

RAJU E. C. PATEL J. D. & SHAH J. J. 1975. An uncommon wall thickening of guard cells. — Ann. Bot. **39**: 125—127.

RAMAYYA N. & RAJAGOPAL T. 1970. Origin of 'common subsidiaries' of the stomata in the Angiosperms. — Curr. Sci. **39**: 363—366.

RAO P. N. & RAJU V. S. 1975a. Development and diversity of stomata in *Micrococca mercurialis* BENTH. — Curr. Sci. **44**: 594—596.

REICHE K. 1923. Entwicklung, Bau und Leben der *Euphorbia radians* BENTH, einer knollentragenden Art. — Flora, **116**: 259—69. (Not seen in original).

SEHGAL & PALIWAL G. S. 1974. Studies on the leaf anatomy of *Euphorbia* VII. General conclusions and systematic considerations — Phytomorphology, **24**: 141—151.

SENANAYAKE Y. D. A. & SAMARANAYAKE P. 1970. Intraspecific variation in *Hevea brasiliensis* MUELL. ARG. — Quart. J. Rubber Res. Inst. Ceylon. **46**: 61—68.

STRASBURGER E. 1866—1867. Ein Beitrag zur Entwicklungsgeschichte der Spaltöffnungen. — Jb. wiss. Bot., **5**: 297—342.

TOGNINI F. 1897 Contribuzione allo studio della organogenia comparata degli stomi. — Inst. Bot. Univ. Pavia, **4**: 1—42.

WILLIS J. C. 1966. A dictionary of flowering plants and ferns. — Cambridge.

Explanation to text figures:

Epidermal peels showing either developmental stages or mature stomata: Figs. 1—3: *Acalypha* sp. (1—2 lamina lower, 3 lamina upper); 4—5: *A. ciliata* (4 lamina lower, 5 lamina upper); 6—7: *A. indica* (lamina lower); 8—9: *A. indica* (8 lamina lower, 9 lamina upper); 10—12: *A. wilkesiana* (10—11 lamina lower, 12 lamina upper); 13—14: *Antidesma ghaesebilla*; 15—16: *Bridelia hamiltonia*;- 17—18: *B. squamosa*; 19: *Chrozophora prostrata*. (In figs. 13—19 the odd numbers refer to the lamina lower, the even numbers to the lamina upper respectively.) Figs. 1, 6, 10 ×880, figs. 2—5, 7, 8, 9, 11—19 ×360.

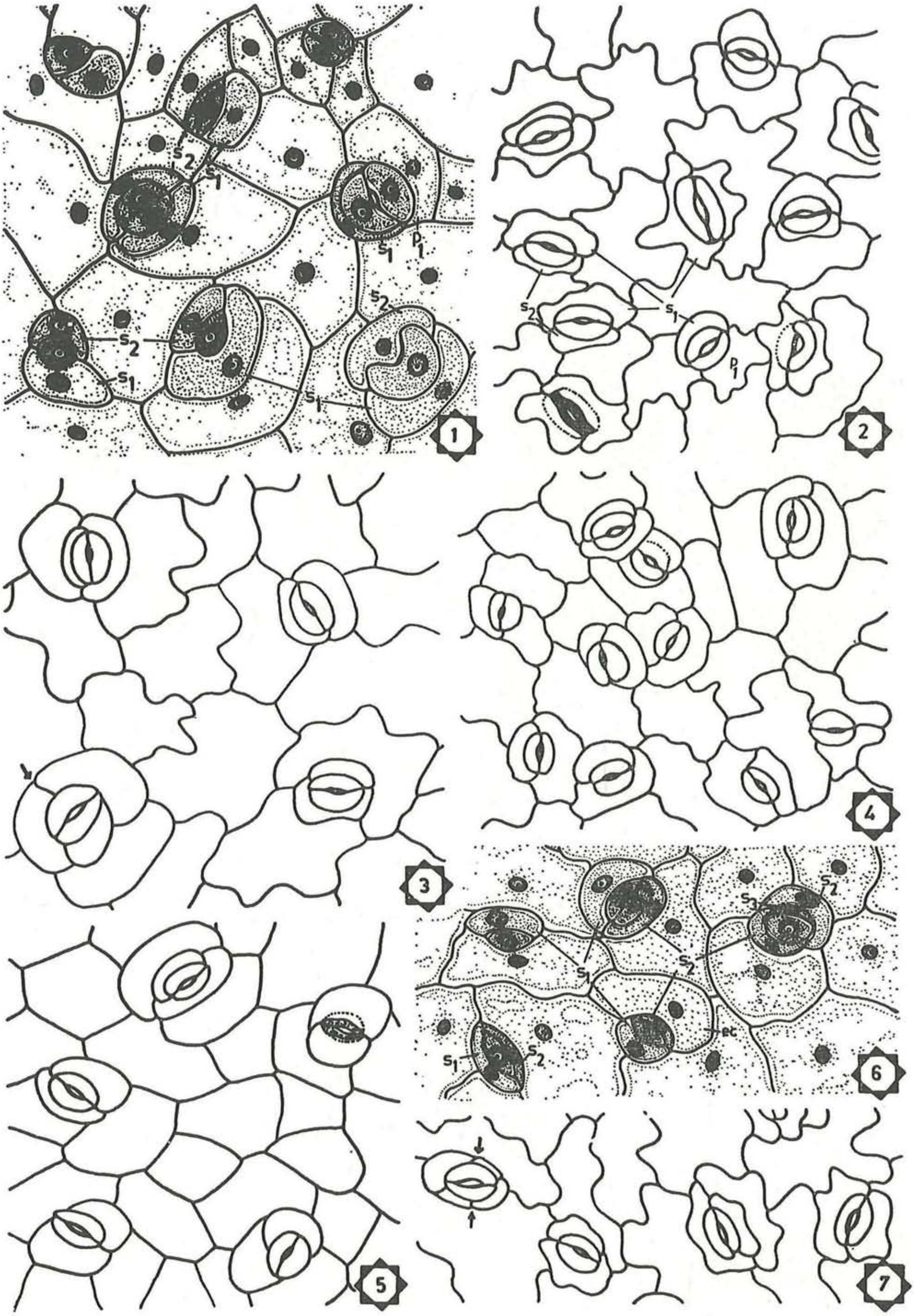
Figs. 20: *Chrozophora prostrata* (lamina upper); 21—22: *Croton bonplandianum*; 23—24: *C. oblongifolius*; 25—26: *Emblica officinalis*; 27—29: *Euphorbia acaulis* (27—28 lamina lower, 29 lamina upper); 30—31: *E. antiquorum* (lamina upper); 32—35: *E. antiquorum* (32—34 lamina upper, 35 stem); 36—39: *E. heterophylla* (36—37 lamina lower, 38—39 lamina upper); 40—41: *E. hirta* (40 lamina lower, 41 lamina upper); 42—43: *E. geniculata* (42 lamina lower, 43 lamina upper);

44—45: *E. microphylla* (44 lamina lower, 45 lamina upper); 46: *E. neriifolia* (46 lamina lower). Figs. 20—26, 28—29, 37—46 ×360, figs. 27, 30, 31, 32—36 ×880.

Figs. 47—48: *Euphorbia neriifolia*; 49—50: *E. milii*; 51—52: *E. hyperecifolia*; 53—54: *E. pulcherrima*; 55—56: *E. tircalli*; 57—58: *E. thymifolia*; 59—60: *Jatropha curcas*; 61—62: *J. gossypifolia*; 63—64: *J. multifida*; 65—66: *J. Podagrica*; 67—68: *Manihot esculenta*; 69—78: *Pedilanthus tithymaloides* (69—76 lamina lower ,77—78 lamina upper). (If not otherwise denoted, the odd numbers refer to the lamina lower, the even numbers to the lamina upper respectively.) ×360.

Figs. 79—80: *Cicca acida* (79 lamina lower, 80 lamina upper); 81—83: *Phyllanthus maderaspatensis* (81—82 lamina lower, 83 lamina upper); 84—85: *P. niruri* (84 lamina lower, 85 lamina upper); 86—87: *Kirganelia reticulata* (86 lamina lower, 87 lamina upper); 88—89: *Phyllanthus nivosus* var. *roseopictus* (88 lamina lower, 89 lamina upper); 90—91: *P. simplex* (90 lamina lower, 91 lamina upper); 92—94: *Putranjiva roxburghii* (92—93 lamina lower, 94 lamina upper); 95—99: *Ricinus communis* (95 lamina lower, 96 lamina upper, 97 cotyledon lower, 98 cotyledon lower, 99 cotyledon upper); 100—102: *Securenega virosa* (100—101 lamina lower, 102 lamina upper); 103—104: *Tragia cannabina*; 105—106: *T. mollurina*; 107—108: *Trewia polycarpa*; 109—110: *Dalechampia scandens*; 111—112: *Jatropha panduraaefolia* (111—112 lamina lower). (If not otherwise denoted, the odd numbers refer to the lamina lower, the even numbers to the lamina upper respectively.) Figs. 79, 80, 82—91, 93—96, 98, 99, 101—110, 112 ×360; 81, 92, 97, 100, 111 ×880.

Figs. 113: *Dalechampia scandens* (lamina upper); 114—115: *Chrozophora rottleri* (114 lamina lower, 115 lamina upper); 116—119: *Euphorbia pycnostegia* (116 bract lower, 117 bract upper, 118 lamina lower, 119 lamina upper); 120—124: *E. rothiana* (120—121 bract lower, 122 bract upper, 123 lamina lower, 124 lamina upper); 125—126: *Glochidion hohenackeri*; 127—128: *Hevea brasiliensis*; 129—130: *Homonoia riparia*; 131—132: *Macaranga roxburghii*; 133—134: *Mallotus phillippensis*; 135—136: *Phyllanthus nanus*; 137—138: *Baliospermum montanum*. Figs. 113—119, 121—124, 125—138 ×360; 120 ×880. (Abbreviations: p_1, p_2, p_3 = perigene subsidiary cells; s_1, s_2, s_3 = mesogene subsidiary cells; m = meristemoid; ec = encircling cell).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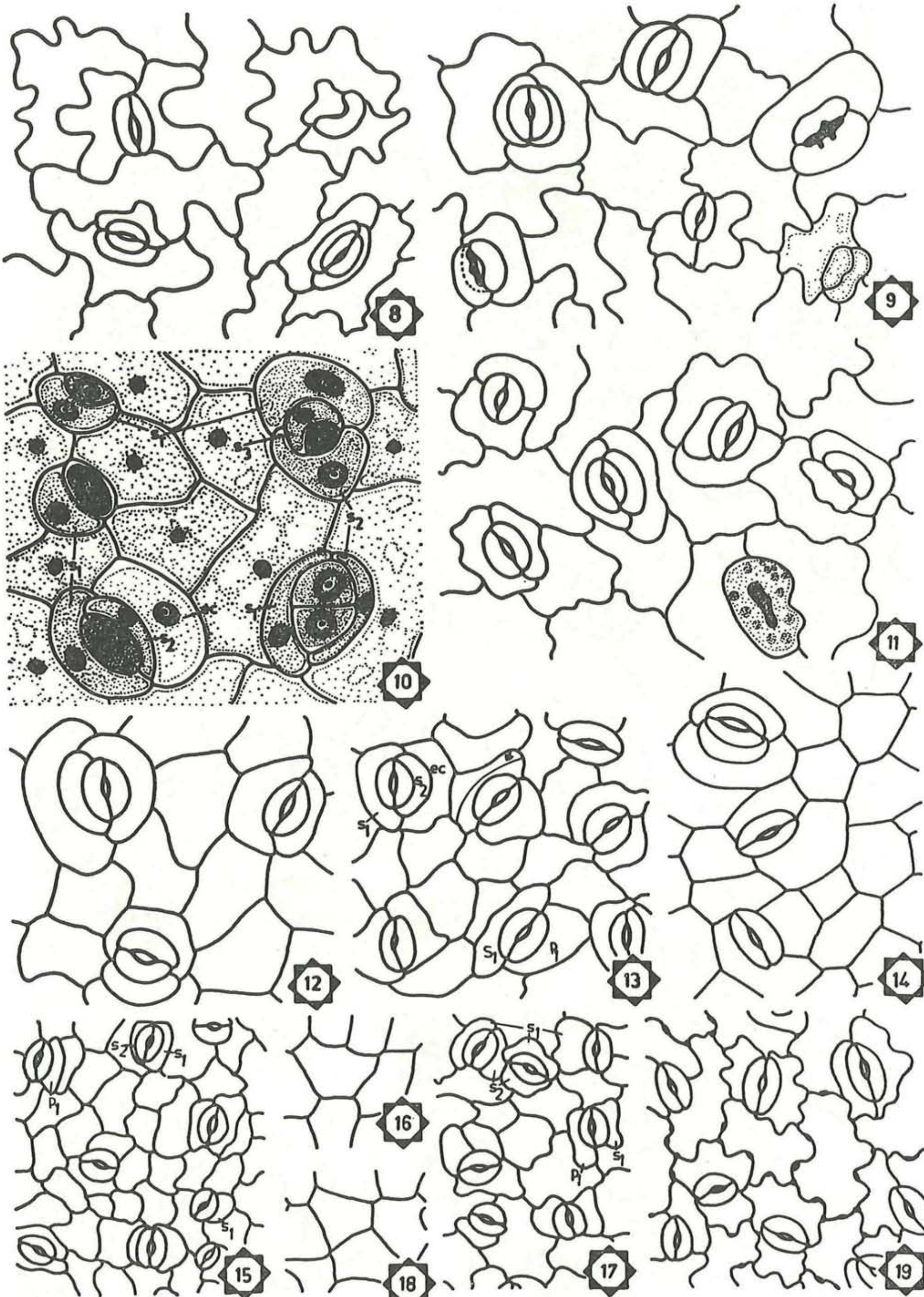
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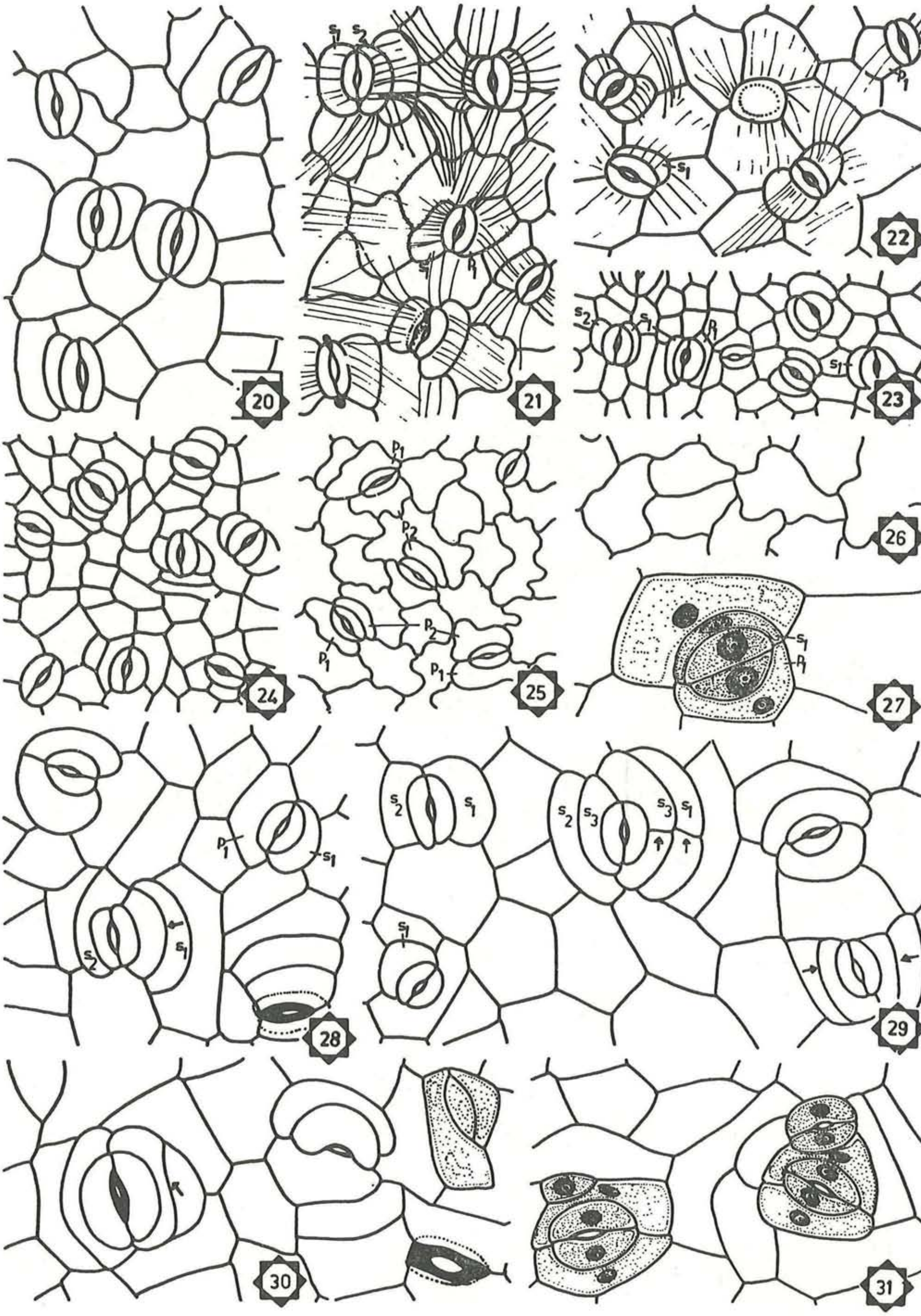
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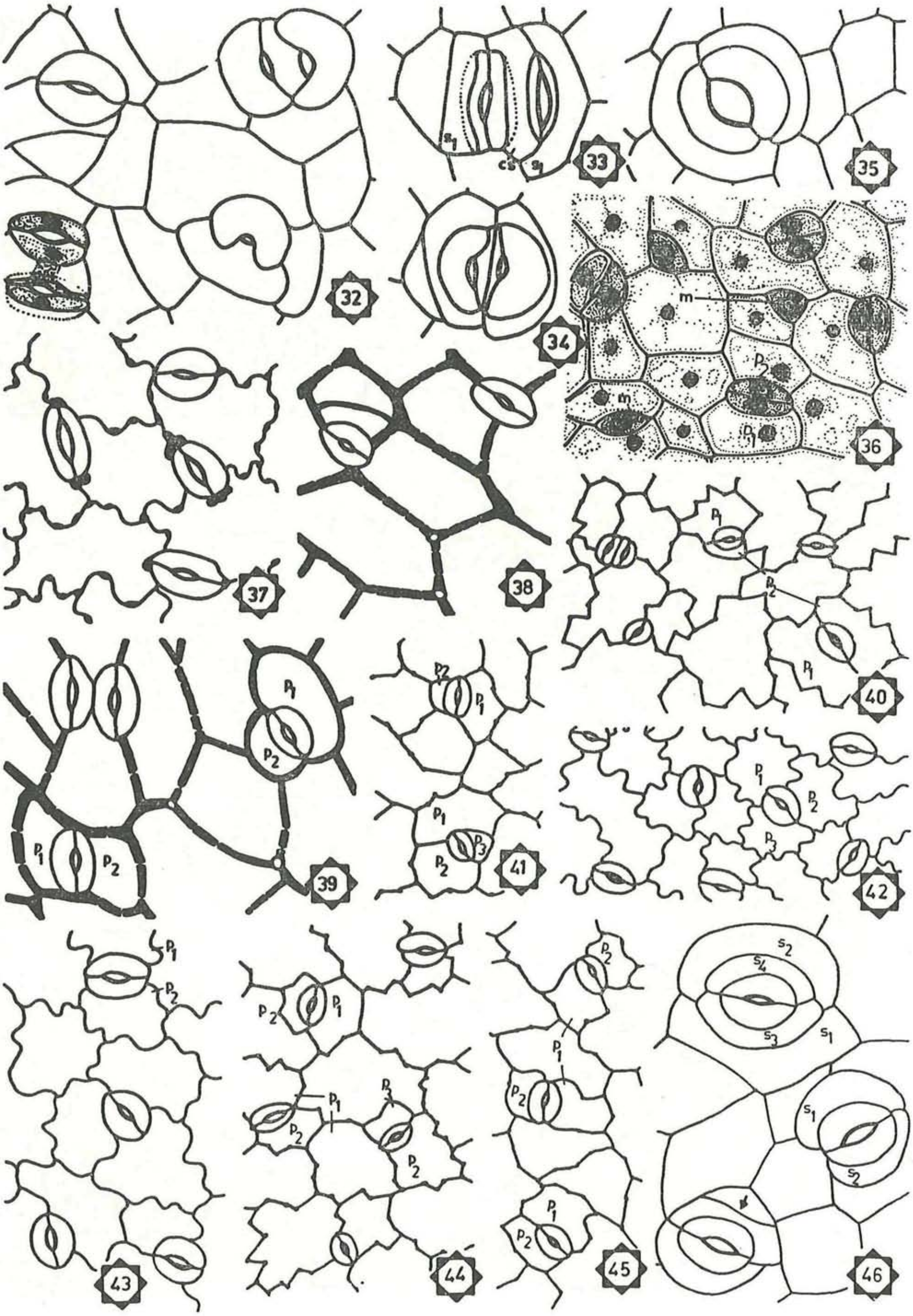

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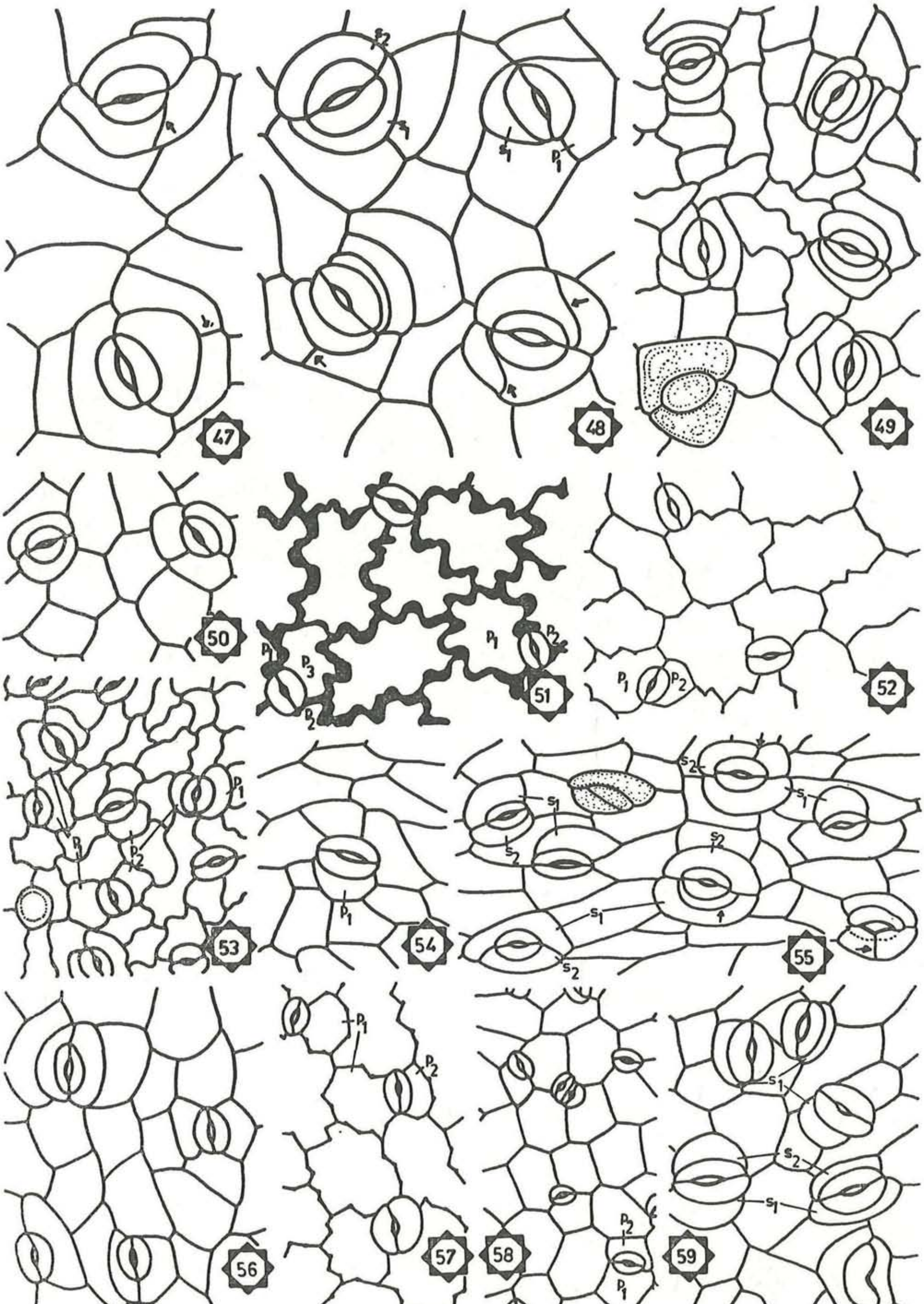
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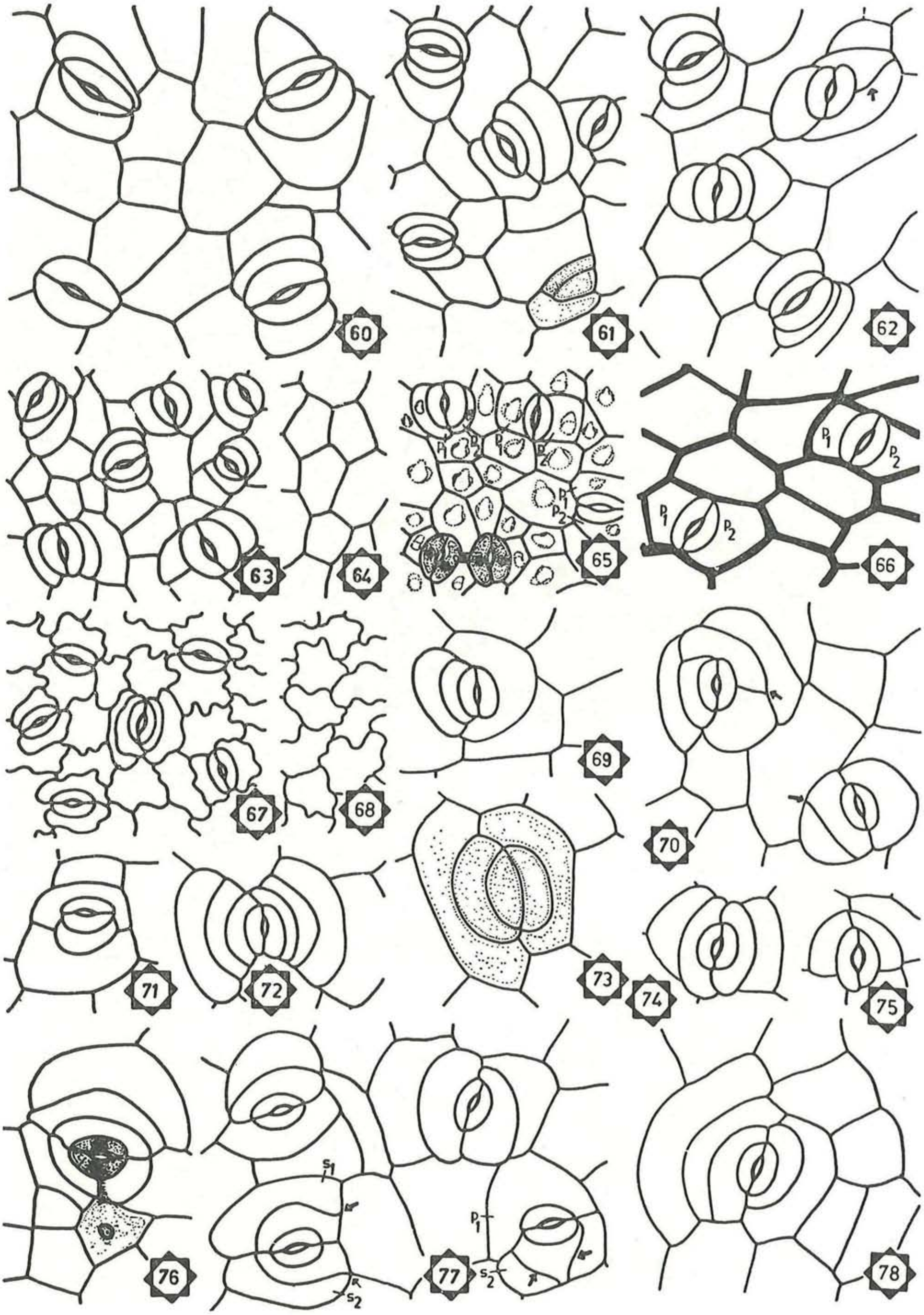
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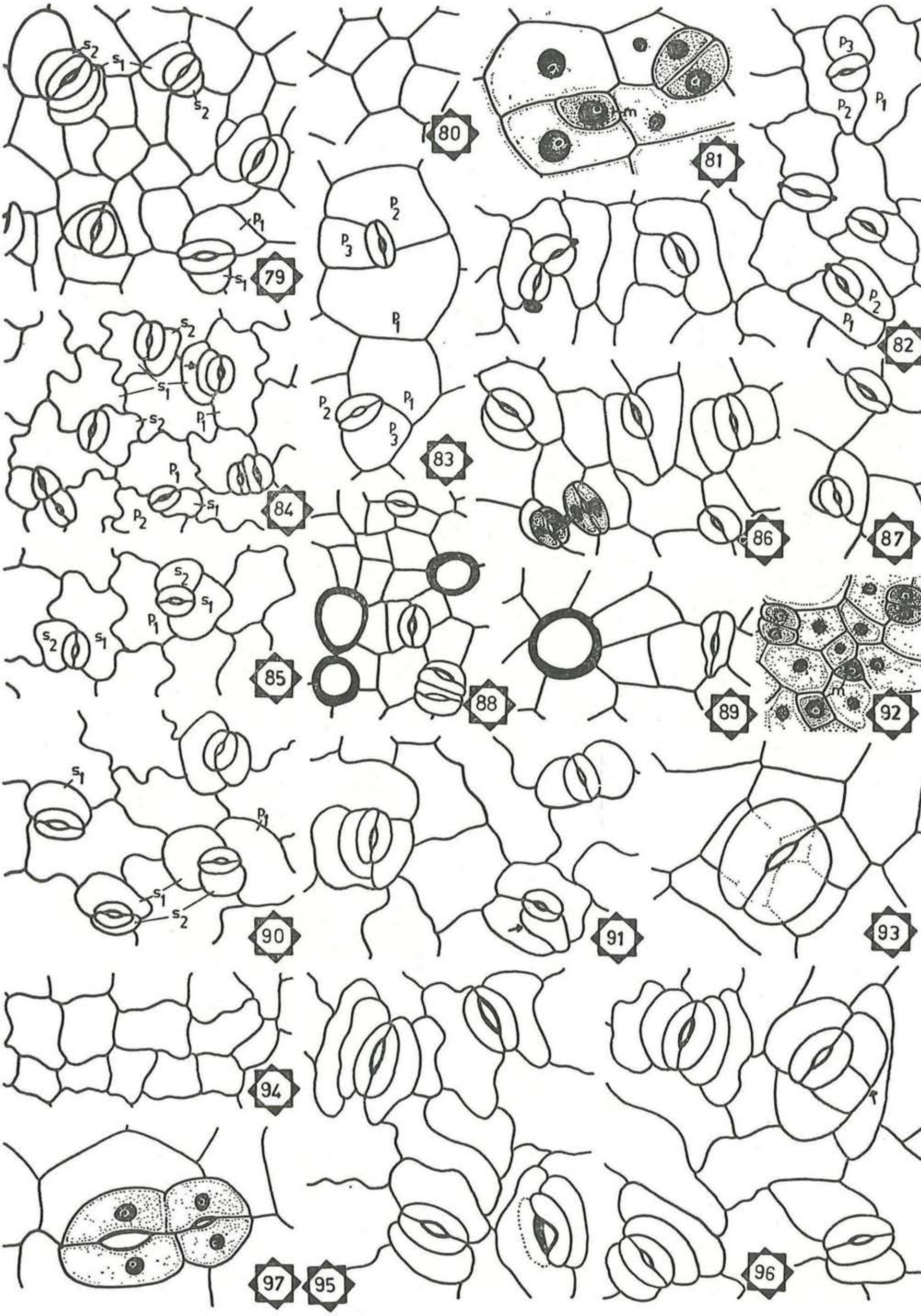
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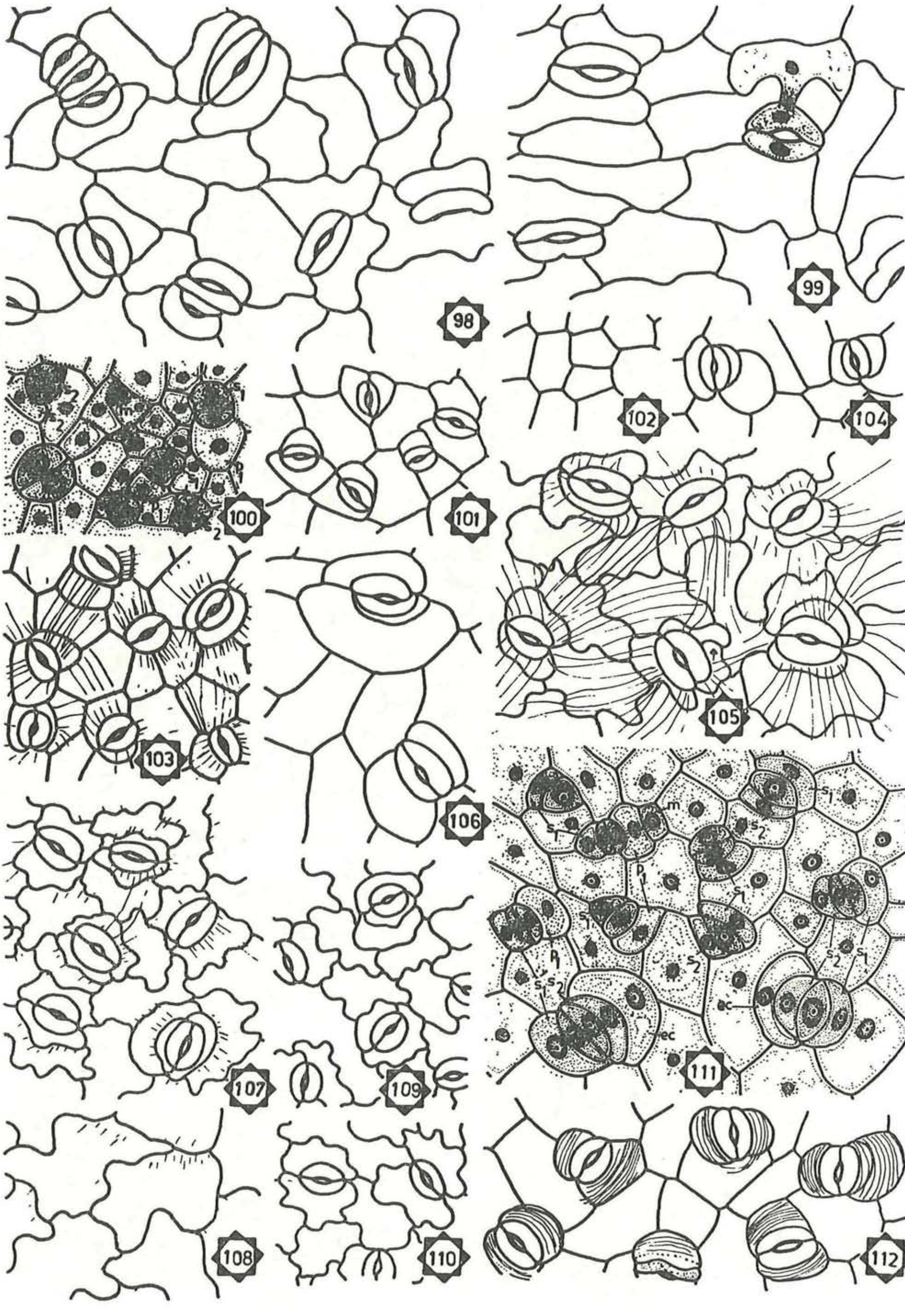
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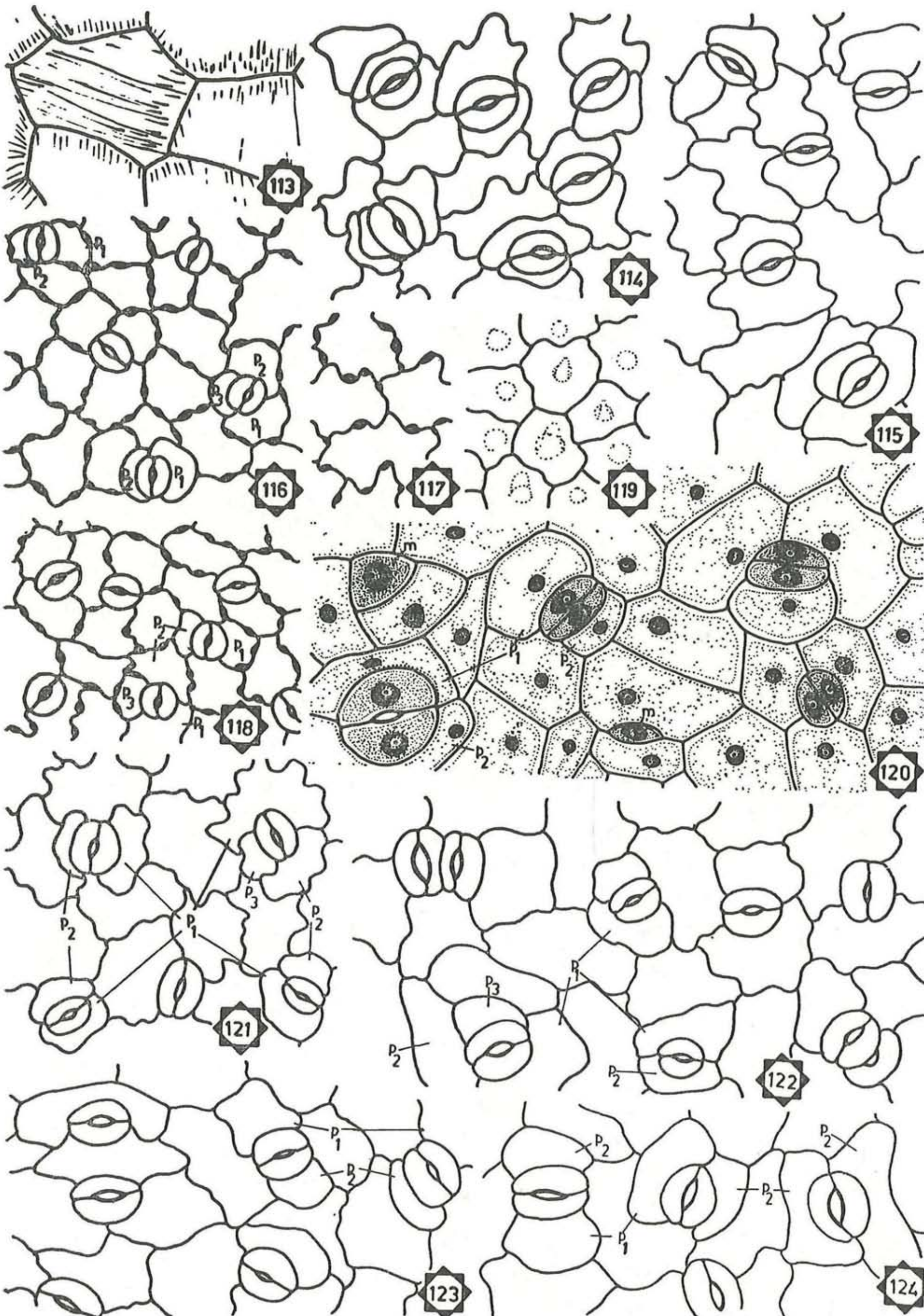
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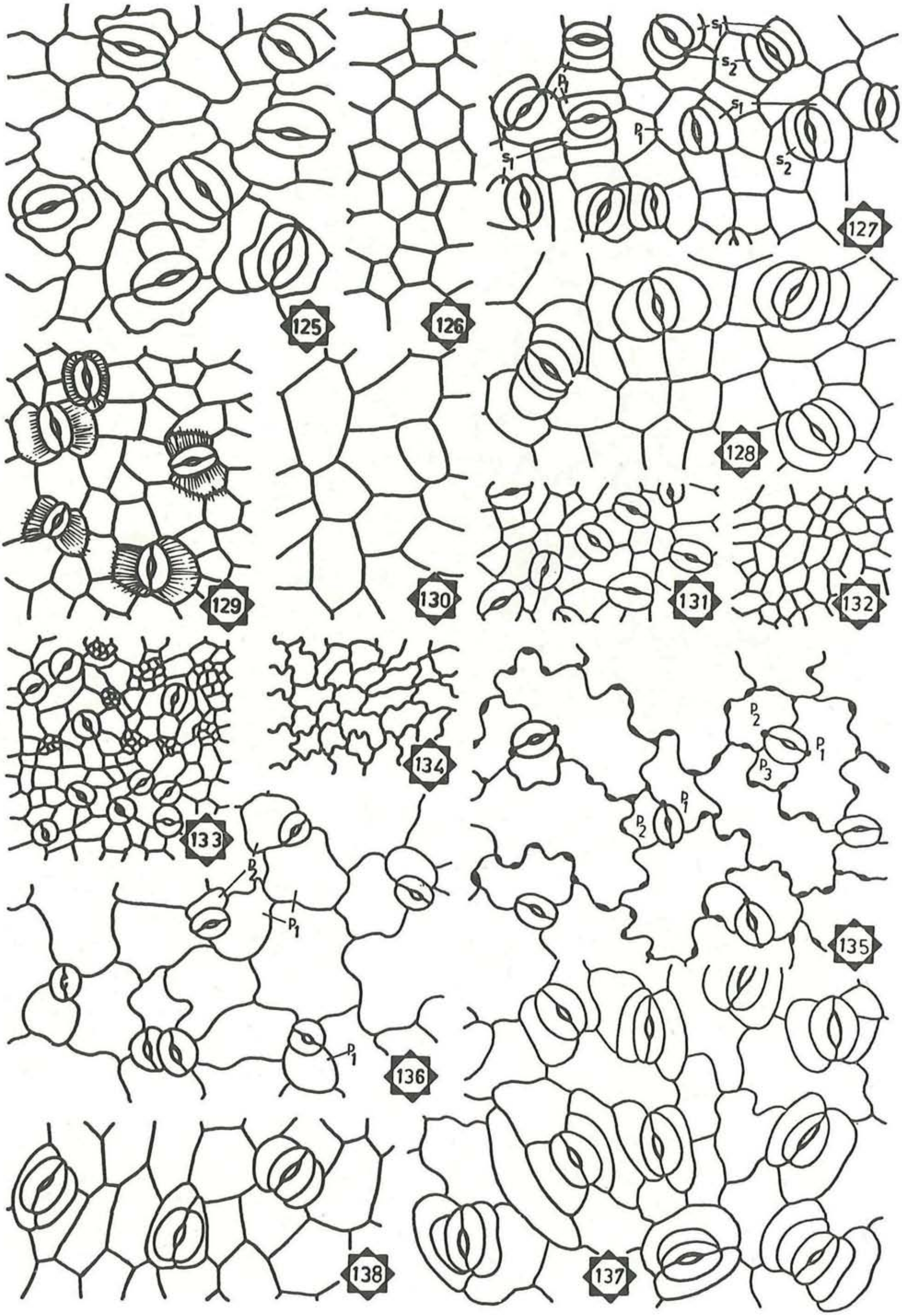
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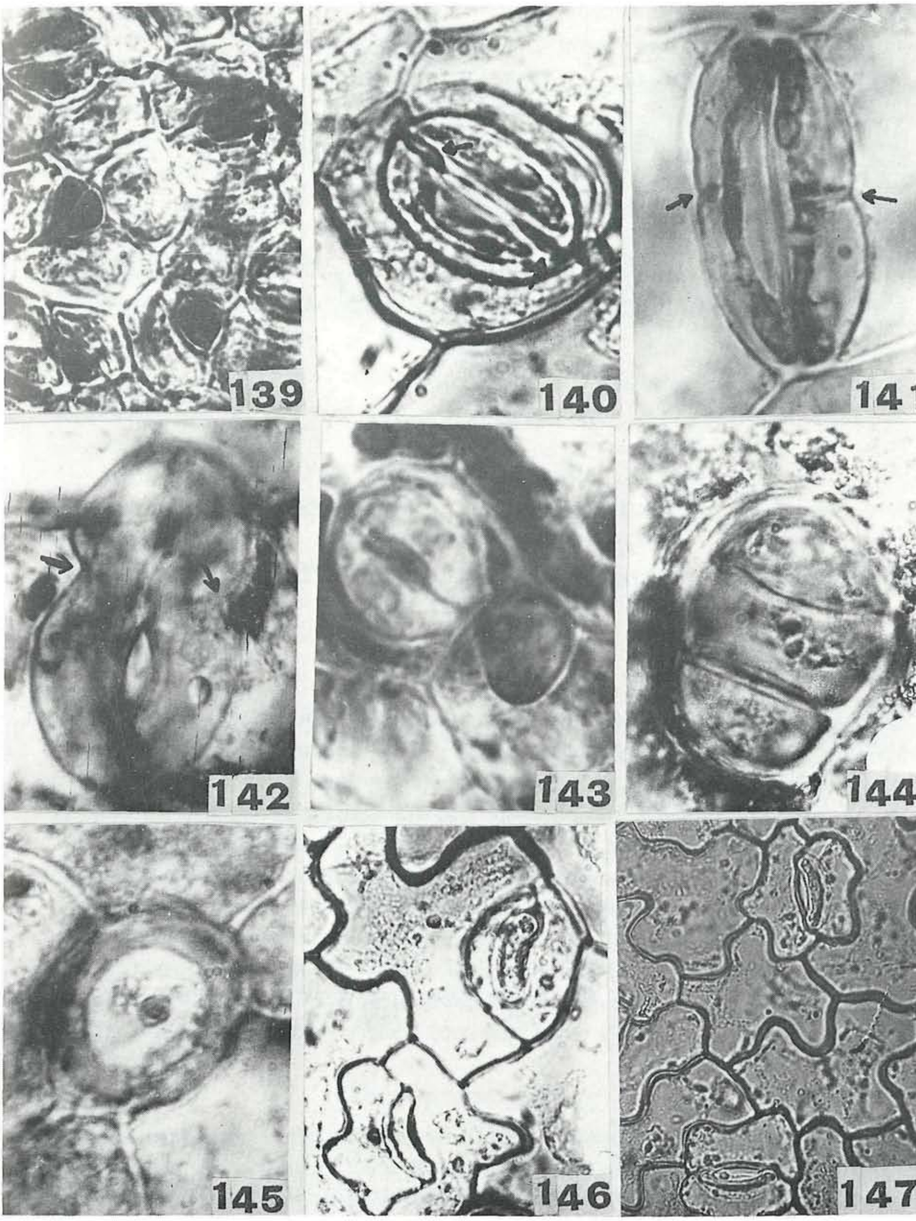

Figs. 139: *Euphorbia heterophylla*, Developmental stages; 140: *Acalypha* sp., Paracytic stoma; note polar thickenings (marked by arrows); 141—142: *Ricinus communis*, Notching of guard cells (marked by arrows); 143—145: *Phyllanthus nivosus* var. *roseo-pictus* (143. a sclerose cell initial in relationship with a stoma, 144. a group of sclerosed initials, 145. a scloresed cell); 146—147. *Acalypha indica* (146 single guard cells, 147 degeneration of guard cells). (Figs. 136, 146, 147 ×1800; 140—145 ×2200).