The ligand molecule contains a thioamide moiety $\mathrm{H-\overset{|}{N}-\overset{|}{C}=S}$ or $\mathrm{\overset{|}{N}=\overset{|}{C}-SH}$ and hence gives rise to four characteristic 'thioamide bands' in the i.r. spectrum of the ligand. Because of redistribution of the electron cloud as a result of complex formation, one can expect systematic shifts in the positions of these thioamide bands in the i.r. spectra of the complexes as compared to those of the ligand (Table II).

Bonding of the metal with ligand through thiol sulphur would localise the double bond between N and C of the thioamide group. This would result in the blue shift of the band due to γ (CN) and red shift of the band due to γ (CS), disappearance of the band due to γ (S–H) and appearance of a new band due to γ (M–S) in the spectra of the metal complexes[11–13]. All these changes are observed (Table II).

Ag(I), Tl(I) and Cu(I) being soft acids show preference for bonding with sulphur — a soft base. Keeping this and their preferred geometries in view, linear polymeric structures are proposed for these complexes. Insolubility of these metal complxes in common non-coordinating solvents lends further support to the structures as proposed.

Metal ions like Zn(II), Cd(II) and Pb(II) have intermediate polarizabilities and so they can bond with 'a-class' bases like N or 'b-class' bases like S according as situation demands. Besides, they prefer to form tetrahedral complexes. Therefore they can bond with S of the thiolate group and co-ordinate with N of the benzylidene group of different ligand molecules simultaneously to form stable five membered chelates. This is in conformity with charge balance too. Hence monomeric complexes of these metals seem to be a distinct possibility. The solubility of the metal complexes in alcohol lends further support to the structures as proposed.

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1. Gadag, R. V. and Gajendragad, M. R., *Talanta*, 1978, **25**, 418.
2. — and —, *J. Indian Chem. Soc.*, 1978, **55**, 789.
3. — and —, *Indian J. Chem.*, 1978, **16A**, 703.
4. — and —, *Rev. Roum Chim.* (Communicated).
5. Dhaka, K. S., Mohan, J., Chadha, V. K. and Pujari, H. K., *Indian J. Chem.*, 1974, **12**, 288.
6. Vogel, A. I., *A Text Book of Quantitative Inorganic Analyses*, 2nd ed., Longmans, London, 1951.
7. Banerjea, D. and Singh, I. P., *Indian J. Chem.*, 1968, **6**, 34.
8. Pearson, R. G., *J. Am. Chem. Soc.*, 1963, **85**, 3533.
9. —, *Chem. Engg. News*, 1965, **43**, 90.
10. —, *Chem. Brit.*, 1967, **3**, 103.
11. Gajendragad, M. R. and Agarwala, U., *J. Inorg. Nucl. Chem.*, 1975, **37**, 2429.
12. — and —, *Aust. J. Chem.*, 1975, **28**, 763.
13. — and —, *Bull. Chem. Soc. Japan*, 1975, **48**, 1024.

ON THE OCCURRENCE OF ABNORMAL STOMATA IN PLANTS

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ABSTRACT

A number of different types of unusual and abnormal stomata are described along with examples of taxa in which they have been reported. As the abnormalities are more common in mature leaves it is suggested that they are due to an interaction of factors responsible for stomatal differentiation and leaf maturation and may belong to the last generation of meristemoids.

INTRODUCTION

ALTHOUGH extensive information is available on abnormalities of different plant organs, relatively little is known of similar occurrences in the stomata. However, from time to time there have been scanty reports or passing remarks of unusual or abnormal stomata in the literature. An exhaustive account of these is presented hereunder.

The term "stoma" (pl. stomata) is defined as a pore in the epidermis, bounded by two lenticular sister cells, called guard cells. The guard cells are normally elongated, their long axes being parallel to the pore. In *Azolla*, the guard cells are broader than long and the pore is directed at right angles to the polar axis. In *Hamelia patens*[8] a stoma with two

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pores has been reported (Fig. 1 A). The normal mature stomata of moss capsules[71] and *Azolla* are unusual in having a single ring-shaped cell around the pore, formed by the dissolution of the common wall between the two guard cells.

Subepidermal or internal stomata have been reported[41,45] in various plants, and in ericaceous and other unrelated fruits.[9,18] In etiolated shoots of *Opuntia blakeana*, 3 stomata were found developing under several layers of cork cells[11].

In hypostomatic leaves, stomata are usually uniformly dispersed throughout the lower epidermis but are less frequent or totally absent on the upper epidermis. In *Stangeria*[71], some Combretaceae[88,89] and *Bombax*[42], although the general surface of the upper epidermis is free of stomata, several rows of stomata are present adjacent to the midrib and at the base of major veins.

Most plants have scattered stomata placed singly and almost evenly between epidermal cells. In some plants (*eg*., Begoniaceae[16] and Cruciferae[64,46]) they are crowded in distinct groups (Fig. 1 B) but the individual members of a group are still separated by a few intervening epidermal cells.

Size of the stomata is more or less constant for a leaf, but in some plants, *e.g*., Myrtaceae, *Mangifera indica*, *Limonia acidissima*, *Plumeria rubra* and some Apocynaceae, Celastraceae and Convolvulaceae, abnormally large "giant stomata (Fig. 1C) are found intermixed with normal sized ones[98,14,85,93,94,25]. Leaves of *Prunus padus*[86] show stomatal polymorphism and they fall into three groups on the basis of differences in size. The size of stomata is also reported to decrease or increase considerably as a result of gall formation on leaves of *Rivea*[76].

In linear or strap-shaped leaves, especially those with parallel venation, the stomata tend to be orientated parallel to the longitudinal axis of the leaf. However, in the leaves of Cycadeoidales, stems and scale leaves of *Casuarina*[73], leaves of some species of *Portulaca*[77] and some others[87], they are transversely oriented, with their pores at right angles to the long axis of the organ.

The convex side of the guard cells is usually almost semicircular but in some species of *Selaginella*, *Salvinia* and *Azolla*, etc., it is irregular or three or four sided (Fig. 1 D). In *Penaea myrtoides* and *Sarcocolla fucata* (Fig. 1 E) peg-like projections extend into the cavities of the cells adjoining the stomata[48]. The lateral walls of guard cells in some Cycads[71,72] and *Phylloglossum*[61] show small, spine-like outgrowths.

In *Escallonia discolor* and *E. resinosa*, the accessory cells which form a ring around the guard cells are prominently horned and the circle of horns overlaps the guard cells[90].

Stomata are either flush with the general surface of the leaf or sunken to various degrees below overlapping epidermal cells. Sometimes they may be placed in specialized pits. In some Celastraceae[62], *Platanus kerrii*[6] and others, the surrounding cells of the stomata creep under the guard cells, which are, therefore, slightly raised (Fig. 1 F). On the revolute leaf margins of *Escallonia polifolia*, the stomata present on the incurving portions of the lamina are raised above the leaf surface at various angles[90] probably due to mechanical stress or drying.

Gertz[19–21] was perhaps one of the earliest authors to report a number of aberrant stomata in leaves of *Avena*, *Cucurbita*, *Luffa*, *Phaseolus* and *Secale*. His observations were, however, on plants grown under controlled conditions of moisture, temperature and light.

According to Ahmad[3] and Kannabiran[37], stomatal abnormalities are usually absent or very rare in young and developing leaves, but their frequency increases as the leaf matures. My own observations confirm this statement. In *Clerodendrum phlomidis*[37] abnormal stomata are reportedly as frequent as normal stomata on the lower epidermis.

Types of Abnormal Stomata

Abnormal stomata may be classified into the following groups, although intermediate and intergrading types are also present.

1. *Contiguous stomata*

These have been reported from a large number of plants. They are usually developed from two or more stomatal meristemoids lying adjacent to each other.

Shah and Gopal[81,82] have described their formation by a method which they have termed as budding (Fig. 1 G–I). According to these authors, in *Lathyrus sativus*, one of the guard cells gives out a protuberance towards one or both ends. The nucleus of the guard cell divides and one of the daughter nuclei moves into the bud. The bud gets cut off from the guard cell and behaves as an independent stomatal initial forming a stoma which is contiguous to the parent stoma. This peculiar method of contiguous stomata formation has not been described elsewhere.

In *Asparagus*[22], often the guard cells of the nearby stomata show protuberances which extend and meet each other and the two stomata become contiguous.

Neubauer and Apandi[50] were successful in inducing the formation of contiguous stomata in seeds of *Bauhinia* by irradiation and Jain and Mukherjee[36] by treatment with Morphactin. Raman and Devadas[76] have reported formation of contiguous stomata in *Rivea*, due to the formation of galls by *Asphondylia riveae*.

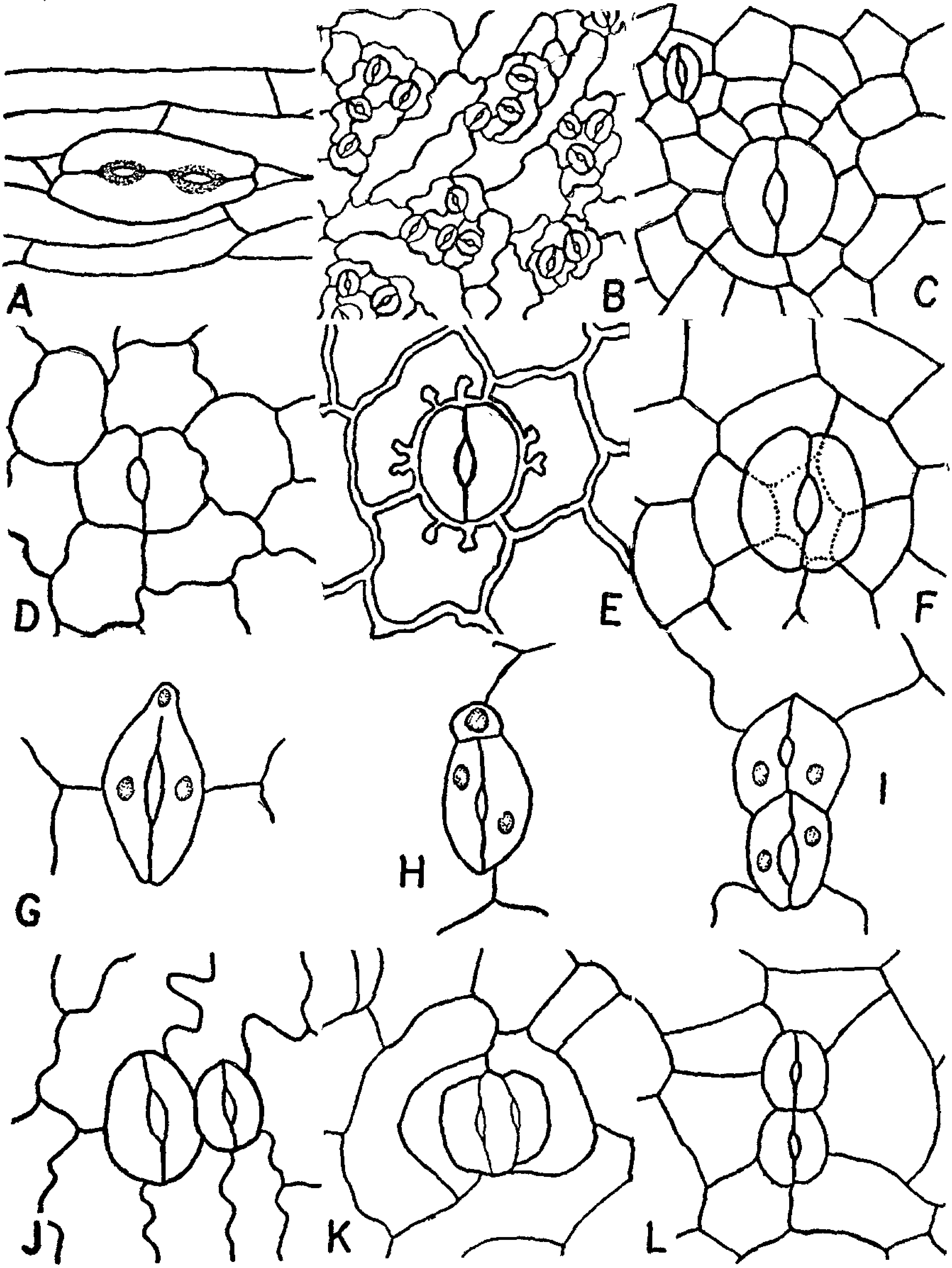

FIG. 1. Unusual and abnormal stomata in plants (diagrammatic). A, Stoma with two pores; B, Stomata arranged in groups; C, Giant stoma—compare with normal sized stoma of the same leaf; D, Guard cells with irregular convex sides; E, Stoma showing peg-like projections extending into cavities of adjacent cells; F, Stoma with raised guard cells and subsidiary cells lying below them; G, H, I, Stages in the development of contiguous stomata by budding; J, Side to side contiguous stomata; K, Three-celled stomatal twins with two pores and three guard cells; L, Pole to pole contiguous stomata.

Zimmermann and Schwegler[99] have reported the occurrence of as many as seven contiguous stomata in *Pulsatilla albana* and Abbott[1] has also recorded a remarkable aggregation of numerous contiguous stomata in *Annularia stellata*. A similar aggregation of upto 6 stomata was reportedly formed due to treatment with Niagara (Ethyl hydrogen I- Propyl Phosphonate)[51]. Stomatal contiguity may be of the following types:

(*a*) *Side to side* (lateral contiguity; Juxtaposed stomata).

When two or more adjacent stomata touch each other on the sides (Fig. 1 J). Examples*: *Gnetum*[47,49] *Phyla nodiflora*[60], *Selaginella helferi*[68], Ranunculaceae[69], Piperaceae[56], Araceae[63], *Elaeodendron glaucum*[62], Magnoliaceae[57], *Scoevola frutescens*[78], Gentianaceae[65], *Equisetum ramosissimum*[66], Caryophyllaceae[26], Nyctaginaceae[27], Fabaceae[81], *Crotalaria*[82], Verbenaceae[29], *Ophioglossum* sp.[58], Amaryllidaceae[84], *Tmesipteris tannensis*[59], *Polygonum glabrum*[39], *Argemone*[41], *Laurus abchasica*[17], *Micrococca mercurialis*[79], *Amaranthus*[98] and Bignoniaceae[34].

In *Michelia fuscata*[57], besides laterally contiguous stomata with a total of four guard cells, there are also a few three-celled twins where a central common guard cell intervenes between two pores and two guard cells (Fig. 1 K). A similar stoma is figured in *Lycopersicon esculentum* after treatment with morphactin[36].

(*b*) *Pole to pole* (Polar contiguity; Superimposed stomata)

Where the contiguous stomata touch each other at the polar ends (Fig. 1 L). These are less frequent than laterally contiguous stomata.

Examples:

Isoetes panchananii[68], Ranunculaceae[69], *Zamioculcas*[63], *Canscora decussata*[67], *Ophioglossum nudicaule*[58], Papilionaceae[81,82], pedicel epidermis of *Crinum bulbispermum*[84], *Cratoxylem*[7], spikes of *Ophioglossum* sp.[30], *Tmesipteris tannensis*[59], *Argemone*[41], *Amaranthus*[98].

(*c*) *Intermediate types*

In some cases an intermediate type of contiguity also exists, the polar end of a stoma being contiguous with the side of another stoma (Fig. 2 A). These, though not pointed out as such by the authors, have been represented in drawings or photographs in the following: *Ephedra*[69], *Mussaenda, frondosa*[70], *Crotalaria*[83], *Ophioglossum gramineum*[58], Araliaceae[32], *Asparagus*[22], *Polygonum glabrum*[19], *Micrococca mercurialis*[79] and Bignoniaceae[34].

Sometimes the two contiguous stomata may neither be wholly parallel nor precisely at right angles, but at various other angles to each other, *e.g.*, *Gnetum*[49], *Amaranthus*[98], Bignoniaceae[34] and others.

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* Examples are given in chronological order throughout,

2. *Stomata connected by cytoplasmic strands*

Gopal and Shah[22] have reported the presence of peculiar cytoplasmic strands between guard cells of nearby stomata in four species of *Asparagus* (Fig. 2 B). Upto four stomata may thus be connected by such cytoplasmic strands. According to these authors, the strands are extensions of cytoplasm of the guard cells through pits present in their walls. Similar connections have also been reported in *Amarylis*, *Crinum asiaticum* and *Pancratium* by Shah and Gopal[84] but in these cases the authors are not sure whether they are cytoplasmic or not. Rao and Raju[79] and Yunus *et al.*[98] have also reported cytoplasmic connections between adjacent stomata in 3 species of Euphorbiaceae and *Amaranthus* respectively and between guard cells and adjacent epidermal cells in *Euphorbia milli*.

3. *Stomata with unequal guard cells*

In *Asparagus*, Gopal and Shah[22] have figured a stoma with one guard cell larger on one side of the pore and the other extending towards the opposite side (Fig. 2 C). Stomata with one guard cell smaller than the other (Fig. 2 D) have been reported in some Araceae[63].

4. *Stomata where one or both the guard cells are like subsidiary cells* (Fig. 2 E)

Examples can be seem in leaf epidermises of Cucurbitaceae, Convolvulaceae and Piperaceae[54–56].

5. *Stomata with single guard cells*

Stomata with single guard cells are formed (i) due to the failure of the guard ell mother cell to divide further and its direct conversion into a single guard cell. In such cases there is usually no pore formation (Fig. 2 F);

(ii) due to the degeneration of one of the guard cells. Such stomata have a pore and also show degenerated remnants of the lost guard cell (Fig. 2 G).

Stomata with single guard cell have been reported in *Begonia aridicaulis*[16], Solanaceae[3], *Phyla nodiflora*[60], other Verbenaceae[28], Convolvulaceae[54], Cucurbitaceae[55], Piperaceae[56], Araceae[63], Cruciferae[67], Oleaceae[25], Nyctaginaceae[26], Caryophyllaceae[27], Malvaceae and Bombacaceae[31], Araliaceae[32], Polygonales and Centrospermae[28], some Eusporangiate ferns[78], *Ophioglossum* sp.,[30] *Kalanchoe* sp.[33], *Clerodendrum*[37], *Micrococca mercurialis*[79], *Amaranthus*[98] and Bignoniaceae[34].

Kropfitsch[44] found that by treating leaves with ultraviolet radiation, stomata with single guard cells could be induced to form. Similarly Paliwal *et al.*[51] were successful in inducing such stomata by treatment with Niagara. According to Ahmad[3] in *Brunfelsia americana* and *Withania somnifera* "they are often as frequent as normal stomata".

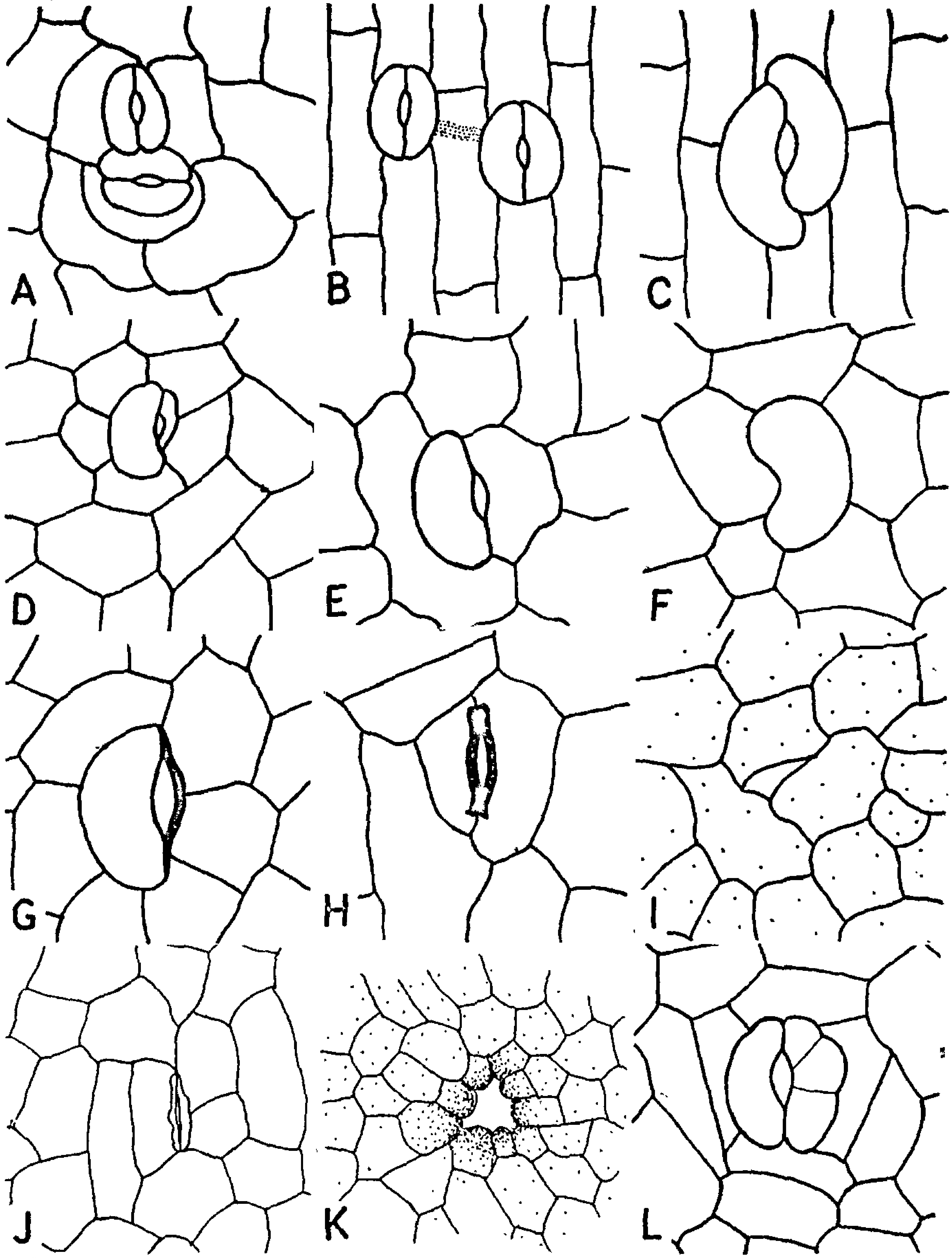

FIG. 2. Unusual and abnormal stomata in plants (diagrammatic). A, Contiguous stomata where the pole of one is contiguous with the side of the other; B, Stomata connected by cytoplasmic strands; C, Stoma with one guard cell larger on one side and the other extending towards the other side; D, Stoma with one guard cell smaller than the other; E, Stoma with one guard cell like subsidary cell; F, Stoma with a single guard cell and no pore G, Stoma with a single guard cell and pore; H, Pore with degenerated remnants of guard cells; I, Pore between ordinary epidermal cells; J, Degenerated stoma; K, Degenerated stoma with the pore surrounded by thick-walled epidermal cells; L, Stoma with one guard cell divided into three.

6. *Stomata without guard cells*

These may be formed by the degeneration of both the guard cells (Fig. 2 H) or by the formation of a pore between two or more ordinary epidermal cells (Fig. 2 I). In the later case, the pores are not stomata in the strict sense. Pores without the accompanying guard cells have been reported in Solanaceae[9], Rubiaceae[70], Piperaceae[36], Araceae[63], Magnoliaceae[57], Cruciferae[64], Oleaceae[24,27], Nyctaginaceae[35], *Tmesipteris*[30], *Thunbergia alata* and *T. fragrans*[5].

7. *Degenerated stomata*

Stomata in various stages of degeneration and showing shrivelled guard cells (Fig. 2 J) have been reported in Cucurbitaceae[55], Rubiaceae[70], Araceae[63], Apocynaceae[39], subfamily Nelsonioideae of Acanthaceae[4], *Thunbergia*[5], *Clerodendrum*[37], Celastraceae and Convolvulaceae[35], *Micrococca mercurialis*[80], *Casuarina*[73], and *Gnetum* sp.[49].

According to Pant and Kidwai[63], in some Araceae, even the surrounding cells become disorganised and the mesophyll cells become exposed. The epidermal cells bounding these wide openings become somewhat thickened (Fig. 2 K).

According to Gupta *et al.*[23], in *Nelumbo nucifera* the young leaves show well organized stomata on both surfaces. However, at a later stage, almost all the stomata of the lower surface degenerate. The guard cells show irregularly thickened walls, disintegrated nuclei and highly vacuolated cytoplasm which lead to the degeneration and finally the complete disappearance of the stomata.

Degeneration of guard cells, following treatment by external factors such as radiation[50] and by wounding of mature leaves[15] has also been reported.

8. *Occluded stomata*

Fischer[18] has described the frequent occlusion of the stomatal pores by outgrowths from the guard cells and from cells of the subjacent tissue, in fruits of a number of species.

In the Pandanaceae, Tomlinson[91] reported stomata which stain intensively with safranin. Such stomata become occluded by resinous or tanniferous material which plugs the stomatal pores. Subsequently the guard cells die and their back walls collapse against the front walls. The substomatal, hypodermal cells put out tylose-like structures which fill up the substomatal chamber. Later these protuberances may become thick-walled and lignified. This, according to the author seems to be an antitranspiration device.

9. *Stomata with divided guard cells*

These are reported in *Carya aquatica*, *Cucurbita pepo* and *Populus pyramidiqles*[21] and in *Alocasia*[63]. In *Alocasia*, such stomata have one normal guard cell while the other, seems to have been partitioned into three (Fig. 2 L). Sometimes the pore is surrounded by 3 cells formed by the division of one of the guard cells (Fig. 3 A).

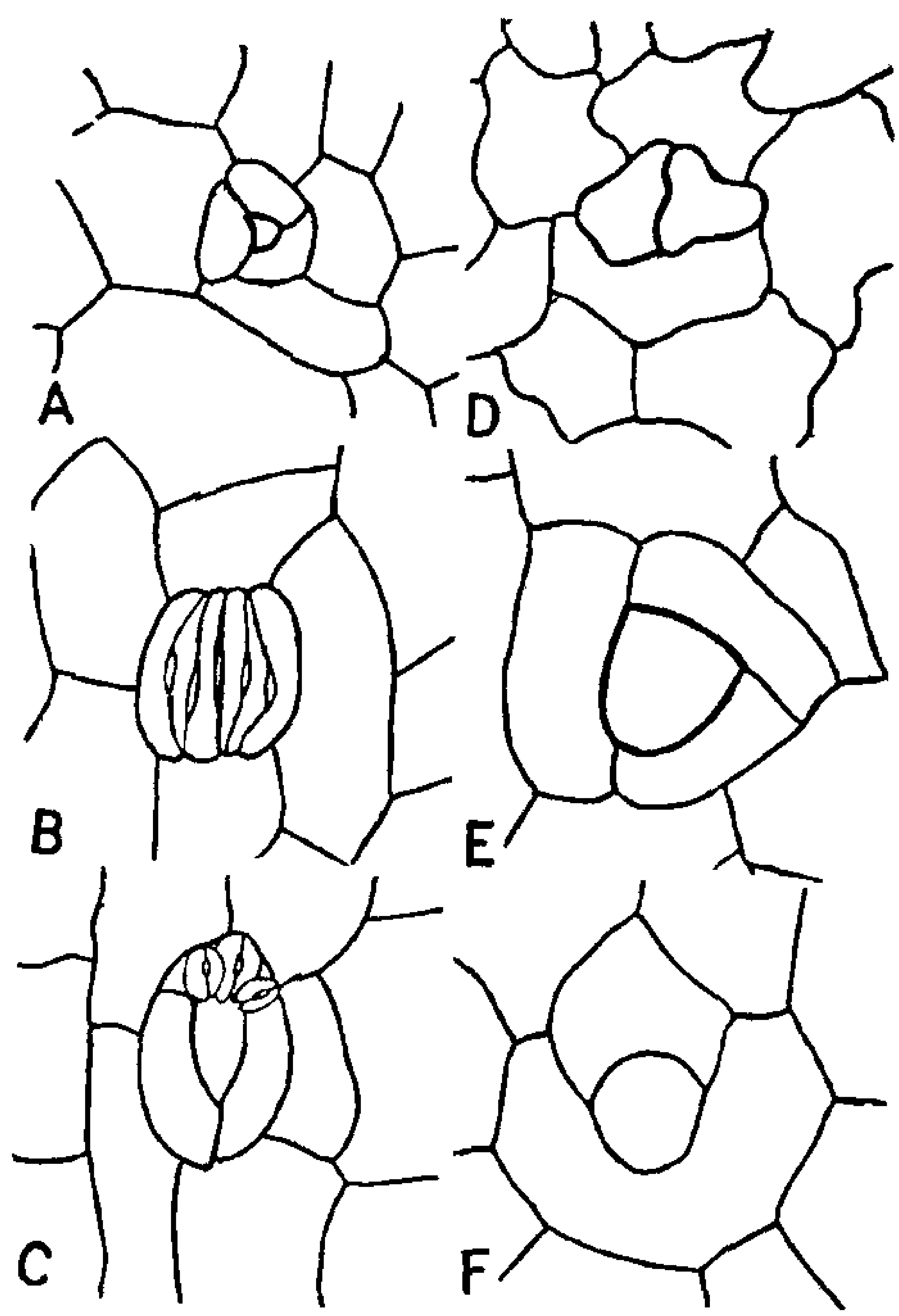

FIG. 3. Unusual and abnormal stomata in plants (diagramatic). A. Pore surrounded by three cells formed by division of guard cells. B. Subdivisionl of guard cells by longitudinal walls, each forming a pore. C. Subdivision of guard cells in different directions, some segments forming miniature stomata D, E, F. Arrested stomata showing anomocytic, anisocytic and diacytic arrangements of subsidiary cells.

In the stomata, borne by the connective of *Momordica charantia* (Cucurbitaceae), a number of bizarre structures are seen. The abnormality is due to an unusual proliferation of the guard cells and their irregular arrangements[78]. The guard cells subdivide several times, in longitudinal (Fig. 3 B) and other directions to give rise to a cluster of guard cells usually with pores between them. In the extreme formations of this type, the guard cells become irrecongnisable. The guard cells may sometimes proliferate into small sized stomata through their subdivision across the guard cells and give rise to miniature stomata (Fig. 3 C). Formation of miniature stomata is also recorded in the lower leaf epidermis of *Scaevola frutescens*[78].

10. *Arrested stomata*

Gertz[19–21] was probably the first to notice "persistent stomatal initials" in various plants, particularly those associated with galls of fungal and insect etiology.

Subsequently, they were reported from a large number of plants. Weber[96], Tonzig and Ott-Candela[92], Weisenbock[97], Kropfitsch[43,44], and Neubauer and Apandi[50] were successful in inducing such cells by various experimental proceedures and Paliwal *et al.*[51] by treatment with Niagara. Kenda and Weber[40] reported their presence in green leaf-like corolla members of *Verbascum blattaria* and Brat and Weber[10] observed them on the petals of *Nymphaea zanzibariensis.* Dehnel[16] reported them from leaves of *Begonia aridicaulis* and described such a structure as "essentially a circular cell with chloroplasts and a wall of uniform thickness". Because of the shape and arrangement of the three cells adjacent to the persistent stomatal initial, he suggested that it may have developed from a normal stomatal initial after it had formed subsidiary cells, the final division of the guard cell mother cell into the two guard cells being eliminated. Ahmed[2,3] has reported their presence in *Cestrum.* Pant and Kidwai[63] have also recorded them in *Phyla nodiflora* and have named them "arrested stomata". They have suggested that "the arrested structures are possibly laggards in the last generation of the meristemoid whose development was prematurely cut short by the maturation of the leaf".

In support of their view that such groups of cells are indeed "arrested stomata", Pant and Kidwai[63] have brought forth evidence to which additional support can now be extended:—

(i) The arrangement of the cells in the group resembles various developing stages of stomata.

(ii) The reported presence of chloroplasts (otherwise normally present only in the guard cells of the epidermis) in such epidermal cells of *Begonia aridicaulis*[16], *Cestrum purpurascens*[2], *Rhaphidiophora calophyllum*[63] and *Ophioglossum* sp.[30] confirms that even when the guard cell mother cell fails to divide and forms the two guard cells, it retains the potentiality of forming chloroplasts. As chloroplasts in arrested stomata are not reported in other cases, the present author feels that even this capability is lost in most of the other plants.

(iii) The cells in these groups are otherwise like ordinary epidermal cells.

(iv) The groups are found in the epidermis of mature leaves which do not show any developing stages of stomata.

Pant[52,53] has reviewed their presence in a number of living as well as fossil plants and has pointed out that these groups of cells form important or "indelible" clues to the mode of stomatal development as they simulate various developmental stages of stomata (Fig. 3 D–F). Their presence has been reported in widely diverse taxa like Convolvulaceae[54], Curcurbitaceae[55], Piperaceae[56], Magnoliaceae[57], Celastraceae[62] Araceae[63], Cruciferae[64], Caryophyllaceae[65], Gentianaceae[66], Polygonales and Centrospermae[29], *Ophioglossum* sp.[30], *Asparagus*[22], Papavaraceae[11] and *Micrococca mercurialis*[80].

Discussion

It is clear that unusual or abnormal stomata are formed in a large number of plants — pteridophytes, gymnosperms, monocotyledons and dicotyledons. Phylogenetically, they may be of no significance but morphologically they are important and should be noted and recorded by workers undertaking epidermal studies. Occurrence of abnormal stomata further emphasizes the need to determine the full range of stomatal variations in plants chosen for experimental purposes.

As pointed out by Ahmad[2,3], Kannabiran[37] and also from my own studies, the striking feature of stomatal abnormalities is that they are almost absent or very rare on young leaves and are found only on mature leaves. As is well known, most plants with wide leaves show stomatal development of the mixed type and successive generations of stomatal meristemoids are formed between older ones in consecutive waves. It is likely that the last generation forms such abnormalities because the differentiation is (p. 481), "cut short in infancy by the over-powering tide of leaf maturation" (Pant[53] —on arrested stomata). Again, the factors responsible for their proper differentiation, *e.g.*, enzymes, growth substances, etc., may be withdrawn or replaced by factors favouring leaf maturation. The interaction of these two sets of opposing factors and the urgency on the part of the initials to complete their differentiation may be responsible for producing such abnormalities like arrested stomata ("persistent stomatal initials" of Dehnel[16]) and stomata with single guard cells (without pores).

According to Bunning[12,13] each developing stoma is surrounded by an inhibitory zone, which inhibits other cells within a certain range from turning into meristemoids and giving rise to new stomata. With the onset of leaf maturation, the opposing causes may be removed, resulting in the formation of contiguous stomata.

Stomata showing shrivelled or degenerated remains of one or both guard cells may be formed secondarily due to the degeneration of the guard cells, with the stoma being represented by either only the pore or, the pore with a single guard cell.

According to Rao and Ramayya[78] stomatal abnormalities in general may arise (p. 357) "due to a momentary disturbance in the factors controlling the normal stomatal development". If such were the case, abnormalities should be equally frequent in younger leaves as the disturbances could occur at any moment in time and not necessarily on the verge of the maturation of the leaf. In my view, therefore, in reticulate-veined, dorsiventral leaves, abnormal stomata are normally produced by the last generation of meristemoids. However, the view of Rao and Ramayya[28] may still hold good in cases where abnormal stomata are produced as a result of exposure to injury, chemicals, pathogens, radiation, etc., or where they are present on young organs also.

The frequent presence of abnormal stomata on reproductive organs of flowers, on submerged leaves or on the lower surface of floating leaves shows that they replace normal stomata, as the latter are in any case not required by such organs. This supports the idea of Porsch[75] that stomata when once acquired become hereditarily associated with the plant organ, irrespective of their utility. When present on such organs, stomata are frequently modified (larger guard cells and permanently open pores) to adopt to functions other than transpiration, *e.g.*, as hydathodes or as outlets for secretions of nectaries and glands.

The formation of stomata with a single guard cell, degenerated guard cells or occluded pores seem to be an antitranspiration device.

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1. Abbott, M. L., *Bull. Am. Palaeont.* 1958, **38**, 298.
2. Ahmad, K. J., *J. Indian bot. Sac.*, 1964, **43**, 165.
3. —, *Sci. and Cult.*, 1964, **30**, 349.
4. —, *Bot. J. Linn. Soc.*, 1974, **68**, 73.
5. —, *Ibid.*, 1974, **69**, 53.
6. Baas, P., *Ibid.*, 1969, **62**, 413.
7. —, *Blumea*, 1970, **18**, 370.
8. Bahadur, B., Rajagopal, T. and Ramayya, N., *Bot. J. Linn. Soc.*, 1971, **64**, 295.
9. Bergmann, H. F., *Bull. Torrey Bot. Cl.*, 1920, **47**, 213.
10. Brat, L. and Weber, F., *Phyton*, 1951, **3**, 22.
11. Brown, J. G., *Bot. Gaz.*, 1920, **70**, 295.
12. Bunning, E., *Surv. of biol. Progr.* (Ed. Avery, G. S.), 1952, **2**, 105.
13. Bünning, E., *The growth of Leaves*, (Ed. Milthorpe, F. L.), London, 1956, p. 18.
14. Chandran, V., Kapoor, S. L., Sharma, P. C. and Kapoor, L. D., *Bull. bot. Surv. India*, 1969, **11**, 286.
15. Dehnel, G. S., *Bot. Gaz.*, 1960, **112**, 124.
16. —, *Amer. J. Bot.*, 1961, **48**, 129.
17. Ferguson, D. K., *Bot. J. Linn. Soc.*, 1974, **68**, 51.
18. Fischer, M., *Bot. Zentrolbt*, 1929, **49**, 231.
19. Gertz, O., *Acta Univ. Lund.*, 1919, **15**, 3.
20. —, *Ber. dtsch. bot. Ges.*, 1919, **37**, 237.
21. —, *Ibid.*, 1919, **37**, 329.
22. Gopal, B. V. and Shah, G. L., *Amer. J. Bot.*, 1970, **57**, 665.
23. Gupta, S. C., Paliwal, G. S. and Ahuja, R., *Ibid.*, 1968, **55**, 295.
24. Inamdar, J. A., *Curr. Sci.*, 1967, **36**, 443.
25. —, *Flora*, 1968, **158**, 159.
26. —, *Aust. J. Bot.*, 1968, **16**, 445.
27. —, *Proc. Indian Acad. Sci.*, 1968, **67B**, 157.
28. —, *Ann. Bot.*, 1969, **33**, 541.
29. —, *Ibid.*, 1969, **33**, 55.
30. —, *Ibid.*, 1970, **34**, 975.
31. — and Chohan, A. J., *Ibid.*, 1969, **33**, 865.
32. —, Gopal, B. V. and Chohan, A. J., *Ibid.*, 1969, **33**, 67.
33. — and Patel, R. C., *Ibid.*, 1970, **34**, 965.
34. Jain, D. K., *J. Indian bot. Soc.*, 1978, **57**, 161.
35. — and Singh, V., *Curr. Sci.*, 1975, **44**, 170.
36. — and Mukherjee, D., *Ibid.*, 1978, **47**, 811.
37. Kannabiran, B., *Ibid.*, 1974, **43**, 321.
38. Kapoor, S. L., Sharma, P. C., Chandra, V. and Kapoor, L. D., *Bull. bot. Surv. India*, 1969, **11**, 372.
39. —, — and Kapoor, L. D., *Ibid.*, 1971, **13**, 244.
40. Kenda, G. and Weber, F., *Öst. Bot. Z.*, 1950, **27**, 503.
41. Kidwai, P., *Ann. Bot.*, 1972, **36**, 1011.
42. —, *Bot. Jour. Linn. Soc.*, 1974, **68**, 227.
43. Kropfitsch, M., *Protoplasma*, 1951, **40**, 256.
44. —, *Ibid.*, 1951, **40**, 266.
45. Kuster, E., *Pathologische Pflanzenantomie*, 1925, Jena.
46. Landre, P. P., *Ann. des. Sci. Nat.* (*Botanique*), 1972, **13**, 247.

47. Maheshwari, P. and Vasil, V., *Ann. Bot.*, 1961, **25**, 313.
48. Metcalfe, C. R. and Chalk, L., *Anatomy of the Dicotyledons*, Vols. I and II, Clarendon Press, Oxford, 1950, LXIV + 1500 pp.
49. Nautiyal, D. D., Singh, S. and Pant, D. D., *Phytomorphology*, 1976, **26**, 282.
50. Neubauer, H. F. and Apandi, A., *Protoplasma*, 1958, **50**, 290.
51. Paliwal, N., Paliwal, G. S. and Barma, B., *Curr. Sci.*, 1974, **43**, 662.
52. Pant, D. D., *Naturwiss.*, 1965, **16**, 481.
53. —, *Curr. Sci.*, 1965, **34**, 588.
54. — and Banerjee, R., *Senck. biol.*, 1965, **46**, 155.
55. — and —, *J. Indian bot. Soc.*, 1965, **44**, 191.
56. Pant, D. D. and Banerjee, R., *J. Linn. Soc. (Bot.)*, 1965, **59**, 223.
57. — and Gupta, K. L., *Ibid.*, 1966, **59**, 265.
58. — and Khare, P. K., *Ann. Bot.*, 1969, **33**, 795.
59. — and —, *Ibid.*, 1971, **35**, 151.
60. — and Kidwai, P., *Curr. Sci.*, 1964, **33**, 653.
61. — and —, *Proc. nat. Inst. Sci. India*, 1965, **31**, 54.
62. — and —, *New Phytol.*, 1966, **65**, 288.
63. — and —, *Senck. biol.*, 1966, **47**, 309.
64. — and —, *Ann. Bot.*, 1967, **31**, 513.
65. — and —, *Jour. Linn. Soc. Bot.*, 1968, **60**, 309.
66. — and —, *Ann. Bot.*, 1968, **32**, 601.
67. — and —, *Bot. J. Linn. Soc.*, 1969, **68**, 71.
68. — and Mehra, B., *New Phytol.*, 1964, **63**, 91.
69. — and —, *Proc. nat. Inst. Sc. India*, 1964, **30**, 92.
70. — and —, *Phytomorphology*, 1965, **15**, 300.
71. — and Nautiyal, D. D., *Curr. Sci.*, 1963, **32**, 280.
72. — and —, *Senck. biol.*, 1963, **44**, 257.
73. —, — and Singh, S., *Ann. Bot.*, 1975, **39**, 1117.
74. Paton, J. A., *Trans. Brit. Bryol. Soc.*, 1957, **3**, 228.
75. Porsch, O., *Lichte der Phylogenie*, Jena, 1905, p. 1.
76. Raman, A. and Devadas, C., *Curr. Sci.*, 1976, **45**, 672.
77. Ramayya, N. and Rajagopal, T., *Bot. Jour. Linn. Soc.*, 1974, **68**, 81.
78. Rao, B. R. and Ramayya, N., *Curr. Sci.*, 1967, **36**, 357.
79. Rao, P. N. and Raju, V. S., *Ibid.*, 1975, **44**, 750.
80. — and —, *Ibid.*, 1975, **44**, 594.
81. Shah, G. L. and Gopal, B. V., *Aust. J. Bot.*, 1969, **17**, 81.
82. — and —, *Can. J. Bot.*, 1969, **47**, 387.
83. — and —, *Ann. Bot.*, 1969, **33**, 553.
84. — and —, *Ibid.*, 1970, **34**, 737.
85. Sitholey, R. V. and Pandey, Y. N., *Ibid.*, 1971, **35**, 641.
86. Singh, V. and Jain, D. K., *Curr. Sci.*, 1975, **44**, 63.
87. Smith, C. E., *Ann. Bot.*, 1935, **49**, 451.
88. Stace, C. A., *Jour. Linn. Soc. (Bot.)*, 1965, **59**, 229.
89. —, *Bull. Brit. Mus. (N.H.)*, 1965, **4**, 1.
90. Stern, W. L., *Bot. J. Linn. Soc.*, 1974, **68**, 1.
91. Tomlinson, P. B., *Pacific Sci.*, 1965, **19**, 38.
92. Tonzig, S. and Ott-Candela, A., *Nuovo Gior. Bot. Ital. (N.S.)*, 1946, **53**, 535.
93. Trivedi, B. S. and Upadhyay, N., *Curr. Sci.*, 1973, **42**, 401.
94. — and —, *Ibid.*, 1974, **43**, 28.
95. Vochting, H., *Untersuchungen sur Experimentelion Anatomie und Patholgie der Pflanzen*, Korpars Tubingen, H. Lanpp., 1909.
96. Weber, F., *Protoplasma*, 1943, **37**, 556.
97. Weissenbock, K., *Phyton*, 1949, **1**, 282.
98. Yunus, M., Rastogi, K., Ahmad, K. J. and Pal, M., *Flora*, 1978, **167**, 141.
99. Zimmermann, W. and Schwegler, H. B., *Flora*, 1962, **152**, 315.

(References 9, 18, 19, 42, 75 and 92—original not seen.)