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STRUCTURE AND ONTOGENY OF STOMATA IN FERNS

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SUMMARY

On the basis of ontogeny and arrangement of the surrounding cells the stomata in ferns are classified into twenty-four types of which seven – plupolocytic, pseudocopolocytic, sepcopolocytic, pseudohemiparacytic, pluhemiparacytic, pluparacytic and codiacytic – are new. The ontogenetic interrelationships among different stomatal types are traced and the role of stomata in determining the taxonomic position of *Psilotum, Tmesipteris* and the *Ophioglossum* group of genera are discussed.

It is concluded that the mesogenous and mesoperigenous types of stomata are not distinct entities – one is the derived form of the other. The polocytic stoma which is mesoperigenous in origin is, however, not accepted as the direct descendant of the anomocytic (perigenous) type.

INTRODUCTION

One of the major events in the history of the evolution of plants was the origin of the first land plants. These organisms most probably arose from ancient green algae. During their transmigration from an aquatic habitat to life on land they acquired many a new adaptation for survival in the new environment. Among these were the formation of a waxy cuticle, of conducting tissue, and of stomata.

A stoma consists of a pore in most cases surrounded by two guard cells and only in two cases by a single cell (Lele & Walton, 1961; Sen, 1983). Although stomata are commonly associated with the leaves only, they may occur in the epidermis of any of the aerial parts of plants. Though there have been numerous detailed studies of fern stomata (Rauter, 1870; Prantl, 1881; Kondo & Toda, 1956, 1959; Maroti, 1958; Kondo, 1962; Pant, 1965; Mickel & Lersten, 1967; Pant & Khare, 1969; Thurston, 1969; Van Cotthem, 1970a, 1970b, 1973; Probst, 1971; Fryns-Claessens & Van Cotthem, 1973; Viane & Van Cotthem, 1977; Bir et al., 1980; Sen & Hennipman, 1981; Mehra & Soni, 1983; Sen & Bhunia, 1984; Sen, 1986), even then the structure and ontogeny of stomata of a large number of fern species still remain unexplored. Moreover, the ontogenetic interrelationships among many major types of stomata of the filicopsids have not been established beyond doubt. The contradictory reports about the pathways of development of stomata in many fern species are regrettable. A survey of relevant literature reveals that stomatal types have often been identified on the basis of their apparent structural properties in mature condition, ignoring the fact that stomata following different pathways during the course of their development may occasionally show apparently similar structure due to parallel evolution. These confusions, as also a comparative dearth of data on stomatal structure and ontogeny largely prompted this investigation. It is done in the hope that this will lead to a better appreciation of the stomata of this fascinating group of plants, especially their structure, ontogeny, and interrelationships.

MATERIALS AND METHODS

Pickled and dried specimens housed mainly at the Pteridology and Palaeobotany Laboratory of the University of Kalyani provided most of the material for a general survey of mature stomata and foliar epidermal cells. Spores of some species were obtained from the Botanic Gardens of Kew and Leiden. Gametophytes raised from these spores in the laboratory ultimately produced sporophytes. Fronds at various stages of development borne by these sporophytes also provided material, especially for ontogenetic studies. The provenance of material investigated is indicated in the Appendix.

Dried frond segments were boiled in water prior to fixing in FAPA (formalin, 5; acetic acid, 2.5; propionic acid, 2.5; 50% alcohol, 90). These were then macerated in equal volumes of 20% hydrogen peroxide and acetic acid at 58°C for 14 hours and stained in Sudan IV in 70% alcohol. Transparencies of dried frond segments were also prepared by soaking the pieces overnight in a solution of 2.5% NaOH. These were then rinsed in water and treated with 1% NaCl solution. After thorough rewashing these were treated for 30 minutes in 3 : 1 absolute ethanol : acetic acid, and finally stained in 1% acetocarmine.

Pieces of fresh lamina at different stages of development were treated according to the methods of Stebbins & Khush (1961). These were fixed in 3 : 1 absolute alcohol : acetic acid, heated for 1 minute at boiling point in a solution of acetocarmine diluted 1/2 strength with 50% acetic acid, and finally mounted whole in paraffin-bees wax mixture. Peels of epidermis stained with acetocarmine were also prepared. Occasionally, fixed material was stained with iron hematoxylin (Sass, 1958), but the time in hematoxylin and mordant was reduced from four hours to one and a half hour. The stained material was then dehydrated and mounted in clove oil.

The terminology used by Van Cotthem (1970a, 1970b, 1973), Sen & Hennipman (1981), and Sen (1986) to designate the stomatal types is adopted here after modifications. Seven new terms have been coined for new types here described for the first time, and a known type has been redesignated. Illustrations were made with the aid of a POM (India) drawing apparatus.

Permanent slides of stomata, and herbarium of specimens raised from spores for reference have been deposited at the Pteridology and Palaeobotany Laboratory, Kalyani University. For recording the data pertaining to stomata of different species the taxa have been arranged following the scheme of Crabbe, Jermy & Mickel (1975) only for practical purposes.

OBSERVATIONS

General properties of stomata

Stomata normally occur on all parts of the lamina except over the veins. But in thick laminas, they are found along the veins as well. Most of the fronds under investigation are hypostomatic, only a few amphistomatic. In amphistomatic taxa the stomata are, however, more numerous on the abaxial surface. Stomata vary in the level of their position in the epidermis. Some are flush with the epidermal cells, others are sunken below the surface.

Guard cells differ from other epidermal cells not only in their morphology but also in their anatomical properties. Chloroplasts occur in the epidermal cells of some fronds, but the presence of chloroplasts in practically all guard cells is a significant feature. Guard cell chloroplasts are smaller and less numerous than those in the mesophyll cells and are exceptionally rich in starch. The nucleus of the guard cells is more prominent than that of other epidermal cells.

The guard cells have unevenly thickened walls and a cutinous covering. The cutinous layer often forms ledges on the adaxial surface of the stomata. In very old fronds a small amount of lignin is also deposited on the walls close to the stomatal poles.

Ontogeny of stomata

The abaxial and adaxial epidermal layers of the lamina are formed by the marginal initials of the marginal meristems of the developing frond axis. These initials undergo anticlinal divisions and redivisions and act as protoderm cells. The protoderm cells initially are uncommitted cells. By processes of differentiation they become recognisably different from the cells which have produced them. Some of these cells become the precursors of epidermal cells, while others are transformed into meristemoids of stomata and trichomes. No protoderm cell can directly form a stoma or a trichome skipping the meristemoid stage of such an organ or appendage. Meristemoids of each of these kinds are distinct entities and each kind follows its specific pathway during the course of its development.

Stomatal meristemoids are uninucleate, isodiametric to polygonal, and have denser cytoplasm and a conspicuous nucleus. In many taxa contiguous protoderm cells are occasionally metamorphosed into stomatal meristemoids and form twin stomata. The occurrence of such stomata nullifies the view that stomatal meristemoids inhibit adjacent cells from developing also into stomatal initials (see Korn, 1972).

In the taxa studied, twenty-four different types of stomata are recognised on the basis of their ontogeny and the mode of orientation of the surrounding cells, especially the subsidiary cell or cells derived from the stomatal meristemoids.

1. Anomocytic type:

The stomatal meristemoid directly acts as the guard-cell mother cell (gcmc) and divides into two guard cells. None of the surrounding cells is, therefore, a derivative of the stomatal meristemoid (Fig. 1: 1–6).

At maturity surrounding cells are indistinguishable from other epidermal cells in size and aspect.

2. Polocytic type:

The stomatal meristemoid divides by a curved wall to form a subsidiary cell and gcmc. The subsidiary cell becomes U-shaped and encircles parts of the guard cells from the distal end; the cell(s) abutting on the distal parts of the guard cells originate independently of the stomatal meristemoid (Fig. 1: 7–12). The anticlinal wall of the subsidiary cell and that of the guard cells are linked together towards the distal end.

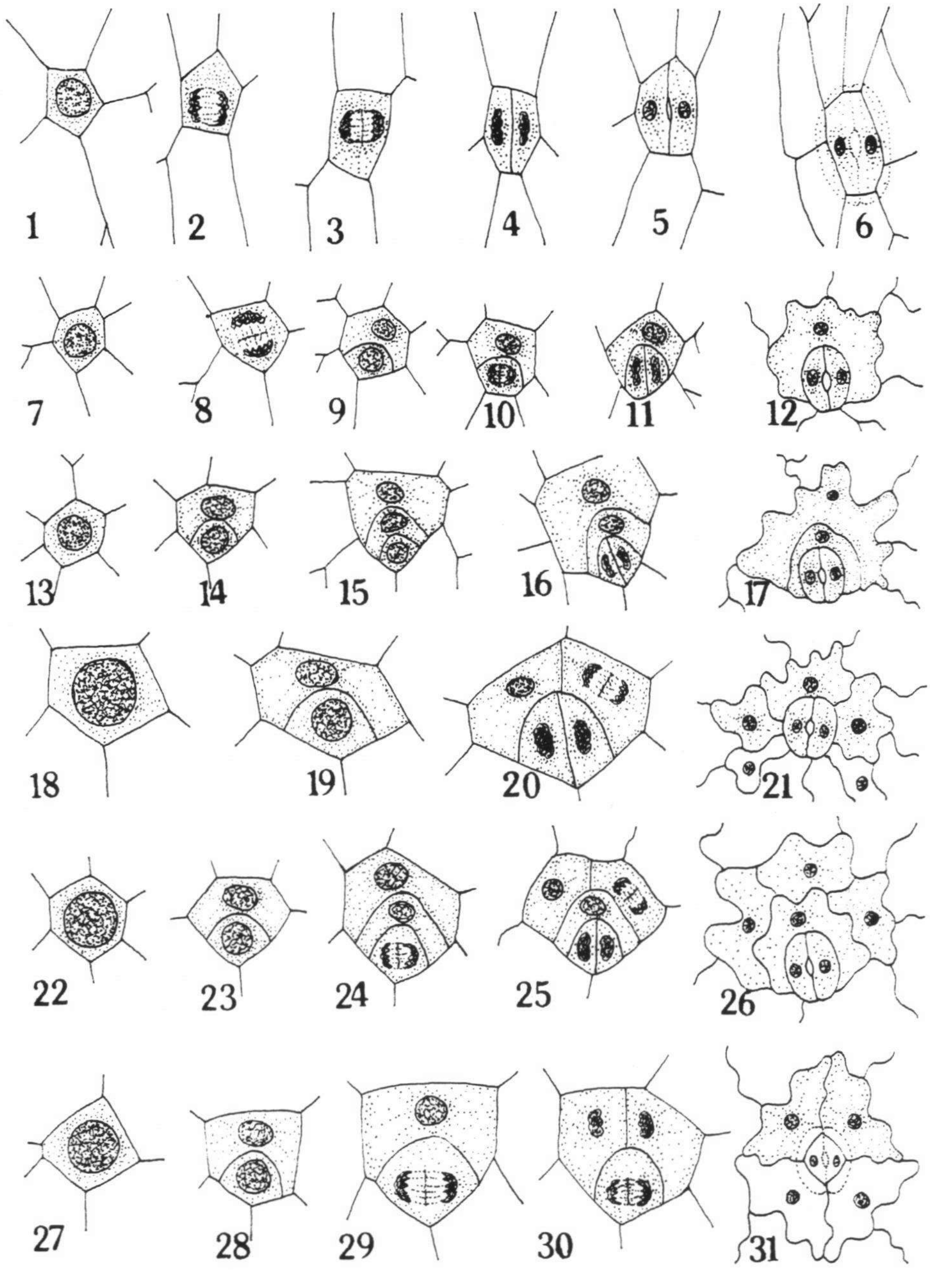

Fig. 1. Stages of development of anomo-, polo-, copolo-, seppolo-, pseudopolo-, and staurocytic types of stomata. — 1–6: *Botrychium daucifolium*, anomocytic stomata; 7–12: *Diplazium polypodioides*, polocytic stomata; 13–17: *Ibid.*, copolocytic stomata; 18–21: *Hypolepis punctata*, seppolocytic stomata; 22–26: *Pteris biaurita*, pseudopolocytic stomata; 27–31: *Davallodes hirsutum*, staurocytic stomata. — 1–5, 7–11, 13–16 & 22–25 × 275; 18–20 × 1020; 27–30 × 610; 6 & 21 × 240; 12, 17, 26 & 31 × 255.

3. Copolocytic type:

The stomatal meristemoid divides by two superimposed curved walls to form two subsidiary cells and the gcmc. It is a polocytic stoma with an additional U-shaped subsidiary cell encircling most of the stoma from the proximal end (Fig. 1: 13–17). The cell or cells abutting on the distal parts of the guard cells are not the derivatives of the meristemoid.

4. Seppolocytic type:

As in the polocytic type, the stomatal meristemoid divides to produce a subsidiary cell and gcmc. But instead of undergoing enlargement, the subsidiary cell divides by one or more anticlinal walls. The newly formed daughter cells surround the proximal parts of the stoma in such a way that they become almost indistinguishable in aspect from epidermal cells (Fig. 1: 18–21). In this type, also, the cell or cells abutting on the distal parts of the stoma are not the ontogenetic derivatives of the stomatal meristemoid.

5. Pseudopolocytic type:

As in the copolocytic type, the stomatal meristemoid forms two superimposed U-shaped subsidiary cells and gcmc. The only deviation from the copolocytic type is that soon after its differentiation, the first subsidiary cell undergoes one or more divisions by anticlinal walls. The daughter cells so formed after expansion very nearly resemble the neighbouring cells and the stomatal complex simulates the copolocytic stoma (Fig. 1: 22–26).

6. Plupolocytic type:

The stomatal meristemoid divides by three superimposed curved walls to form three subsidiary cells and gcmc. It is a copolocytic stoma with an additional U-shaped subsidiary cell encircling most of the stoma from the proximal end (Fig. 2: 1–6).

The cell or cells abutting on the distal parts of the guard cells are not derivatives of the meristemoid.

7. Pseudocopolytic type:

The sequence of divisions in a stomatal meristemoid forming pseudocopolocytic stoma is similar to that occurring in the meristemoids forming plupolocytic stomata up to the stage of forming three superimposed U-shaped subsidiary cells at the proximal parts of the gcmc. The distal subsidiary cell there divides by one or more anticlinal septa to produce two or more daughter cells which at maturity simulate the other epidermal cells (Fig. 2: 7–12), and the stoma so formed resembles a copolocytic stoma.

8. Sepcopolocytic type:

The stomatal meristemoid is at first divided by two curved walls into two subsidiary cells and gcmc. The gcmc by a wall at right angles to the previous plane of divisions form two guard cells. Following such divisions, both the developing subsidiary cells undergo one or more divisions by anticlinal walls. After the expansion of the newly formed daughter cells, the mature stoma very superficially simulates an anomocytic stoma (Fig. 2: 13–18).

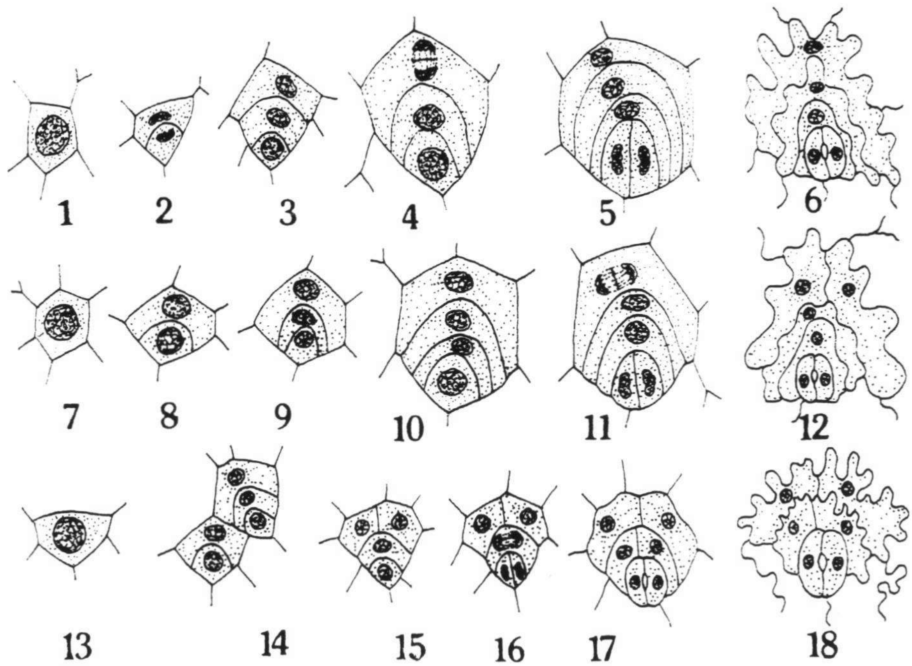

Fig. 2. Stages of development of plupolo-, pseudocopolo-, and sepcopolocytic types of stomata. — 1–6: *Pteris parviloba*, plupolocytic stomata; 7–12: *Ibid.*, pseudocopolocytic stomata; 13–18: *Cyrtomium falcatum*, sepcopolocytic stomata. — 1–5, 7–11 & 13–16 × 275; 6, 12 & 17 × 120; 18 × 350.

9. Hemiparacytic type:

The stomatal meristemoid divides to form a subsidiary cell and gcmc. Concomitantly with the enlargement of the subsidiary cell, there is a division of the gcmc. The metaphase spindle in the gcmc changes its polarity from transverse to longitudinal, and the gcmc is divided by a septum which is more or less parallel to the wall formed during the first division of the meristemoid. The distal side of the stoma is thus surrounded by one or more ordinary epidermal cells and the proximal side by the subsidiary cell (Fig. 3: 9–13).

10. Cohemiparacytic type:

This is a hemiparacytic stoma with an additional subsidiary cell. The stomatal meristemoid forms two superimposed subsidiary cells and gcmc. The nuclear spindle in the gcmc changes its polarity and therefore the wall separating the two guard cells lies more or less parallel to the wall by which the gcmc is separated from the subsidiary cell. The surrounding cells are of heterogeneous origin since only two superimposed cells extending along one side of the guard cells are ontogenetically related to the stomatal meristemoid (Fig. 3: 14–18).

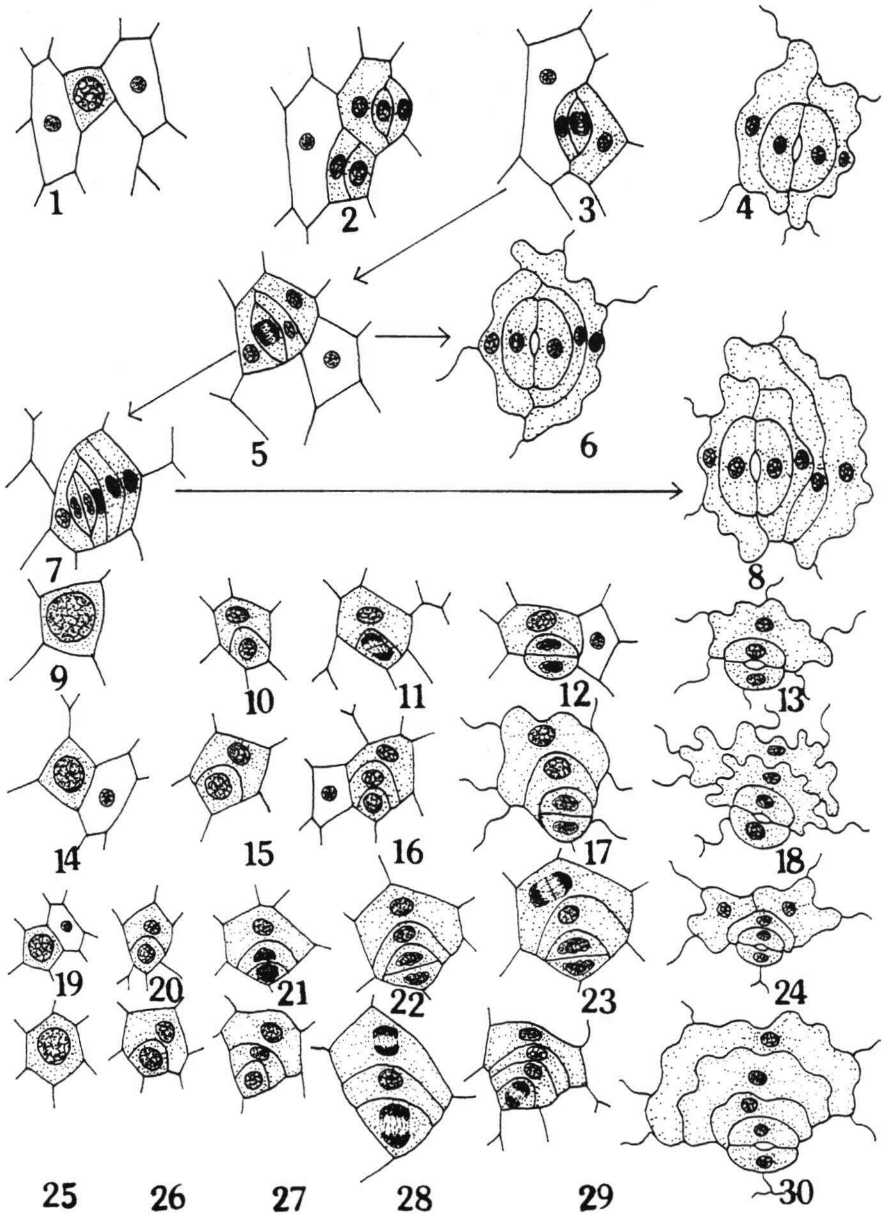

Fig. 3. Stages of development of para-, copara-, plupara-, hemipara-, cohemipara-, pseudohemipara-, and pluhemiparacytic types of stomata. — 1–4: *Cibotium glaucum*, paracytic stomata; 1–3, 5 & 6: *Ibid.*, coparacytic stomata; 1–3, 5, 7 & 8: *Ibid.*, pluparacytic stomata; 9–13: *Pseudophegopteris aurita*, hemiparacytic stomata; 14–18: *Ibid.*, cohemiparacytic stomata; 19–24: *P. hirtirachis*, pseudohemiparacytic stomata; 25–30: *Pteris biaurita*, pluhemiparacytic stomata. — 1–3, 5 & 7 × 360; 9 × 1020; 4, 6, 8, 10–12, 14, 16, 17, 21–23 & 25–29 × 275; 19 & 20 × 345; 13, 18 & 24 × 240; 30 × 255.

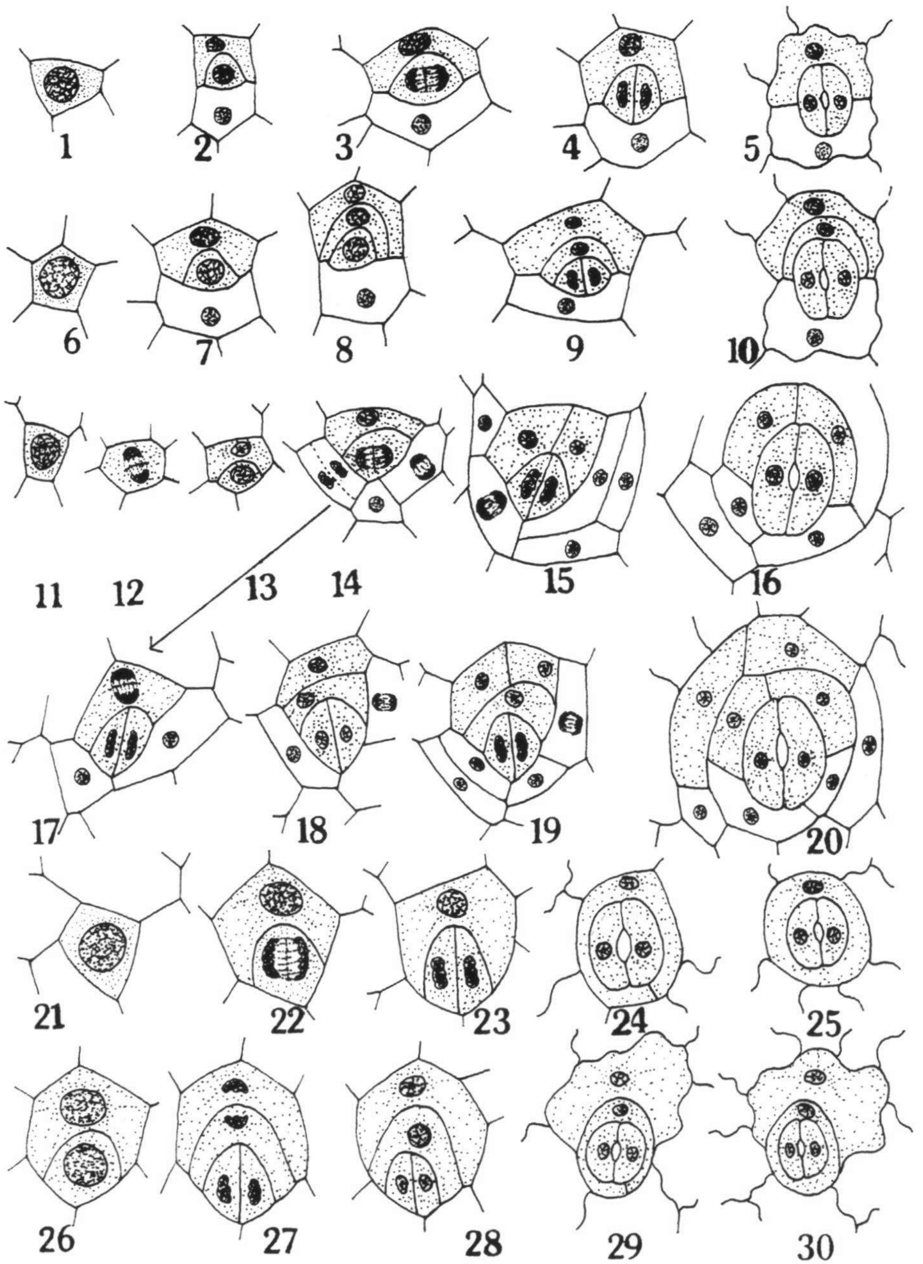

Fig. 4. Stages of development of dia-, codia-, cyclo-, cocylo-, desmo-, codesmo-, peri- and copericytic types of stomata. — 1–5: *Nephrolepis falcata*, diacytic; 6–10: *Ibid.*, codiacytic stomata; 11–16: *Angiopteris evecta*, cyclocytic stomata; 17–20: *Ibid.*, cocyclocytic stomata; 21–24: *Pyrrosia lanceolata*, desmocytic stomata; 25: *Ibid.*, pericytic stomata; 26–29: *Ibid.*, codesmocytic stomata; 30: *Ibid.*, copericytic stomata. — 1–4, 6–9, 11–23 & 26–28 × 275; 5, 10 & 24 × 255; 25, 29 & 30 × 240.

11. Pseudohemiparacytic type:
This is a cohemiparacytic stoma with its outer subsidiary cell divided by one or more anticlinal radial walls. Despite their distinctive nature the daughter cells of the outer subsidiary cell after expansion only very superficially resemble the other epidermal cell (Fig. 3: 19–24).

12. Pluhemiparacytic type:
This is a cohemiparacytic stoma with an additional subsidiary cell. The stomatal meristemoid forms three superimposed subsidiary cells and gcmc. The gcmc divides by an anticlinal wall which is more or less parallel to the walls separating the subsidiary cell from gcmc (Fig. 3: 25–30).

13. Paracytic type:
Meristemoids divide by a curved wall into a semilunar cell and a lenticular one. The semilunar cell enlarges to become one of the subsidiary cells. Instead of functioning directly as gcmc, the lenticular cell cuts off a lateral semilunar segment and a central cell by a curved wall. The second semilunar segment develops into a subsidiary cell and the central cell which now acts as gcmc forms two guard cells by a wall parallel to the long axis of the stoma. Both cells abutting on the guard cells are therefore the derivatives of the meristemoid (Fig. 3: 1–4).

14. Coparacytic type:
This is a paracytic stoma with an additional subsidiary cell on one or both sides of the guard cells. The pathway of development of this type of stoma is slightly different from that of the paracytic type. The stomatal meristemoid cuts off two segments at least at one of the sides, but more often on both sides, before differentiating the gcmc at the central region (Fig. 3: 1–3, 5 & 6).

15. Pluparacytic type:
This is a coparacytic stoma with an additional subsidiary cell at one or both lateral flanks of the guard cells. Before differentiating the gcmc, the stomatal meristemoid cuts off three lateral segments either on both the sides or at least on one (Fig. 3: 1–3, 5, 7 & 8).

16. Cyclocytic type:
The stomatal meristemoid forms a U-shaped subsidiary cell and gcmc. Soon after the differentiation of the gcmc two or more epidermal cells flanking the distal end of the meristemoid orient themselves in such a way that a circle is formed along with the subsidiary cell which in its turn may also undergo one or more divisions by vertical anticlinal walls (Fig. 4: 11–16).

17. Cocyclocytic type:
During the early stages of development the stomatal meristemoids follow the developmental pathway of copolocytic stomata. Soon after the formation of the two subsidiary cells and the gcmc, either both subsidiary cells, or only one of them, may undergo division by one or more radial anticlinal walls, thus increasing the number of encircling cells. The distal cells and the subsidiary cells orient themselves in a ring which is two-layered at least at the proximal part (Fig. 4: 17–20).

18. Desmocytic type:

The stomatal meristemoid follows the pathway of development of a polocytic stoma. A lenticular space soon appears in the intercellular material of the wall connecting the subsidiary cell and the guard cells. The lenticular space expands, bringing about the separation of the guard cells from the subsidiary cell, leaving links at two points and later at one point. Therefore, at maturity the guard cells become completely encircled by a subsidiary cell. The subsidiary cell and one of the guard cells or both remain connected in the distal region by one or two short anticlinal segments of cell wall (Fig. 4: 21–24).

19. Codesmocytic type:

This is a desmocytic stoma with an additional subsidiary cell. The stomatal meristemoid follows the same pathway of development as in a copolocytic stoma. Later a lenticular space separates the guard cells from the inner subsidiary cell; the anticlinal link between them is then maintained only by two or one short radial periclinal segment(s) of the cell walls (Fig. 4: 26–29).

20. Pericytic type:

This is a desmocytic stoma minus the radial link segment/segments of cell wall between the guard cell(s) and the subsidiary cell. Following the developmental pathway of a desmocytic stoma, it finally loses the radial connecting wall segments between the guard cell(s) and the subsidiary cell (Fig. 4: 25).

21. Copericytic type:

This is a codesmocytic stoma without the radial connecting link between the guard cell(s) and the inner subsidiary cell. Following the development of a copolocytic stoma, the radial anticlinal link between the guard cells and the inner subsidiary cell is gradually lost due to difference in the growth rate of the guard cells and the subsidiary cell (Fig. 4: 30).

22. Diacytic type:

The stomatal meristemoid divides by a curved wall to form a subsidiary cell and gcmc. During maturation the subsidiary cell on the proximal side and the cell abutting on the distal side of the stoma orient in such a way that their common walls meet the guard cells at their widest points almost at right angles. The distal cell incidently is not a derivative of the stomatal meristemoid (Fig. 4: 1–5).

23. Codiacytic type:

The sequence of cell divisions in the meristemoids forming this type of stomata is similar to that producing a diacytic stoma. The only difference is that in the codiacytic type the first two derivatives of the stomatal meristemoid form U-shaped subsidiary cells and the third cell acts as gcmc (Fig. 4: 6–10). This type is, therefore, a diacytic type with an additional subsidiary cell.

24. Staurocytic type:

The stomatal meristemoid divides into a subsidiary cell initial and gcmc. The subsidiary cell initial soon divides by a vertical anticlinal wall to form two subsidiary cells. The two subsidiary cells in the proximal position and the two adjacent cells in the distal position together constitute the surrounding cells of the guard cells. The four walls of the surrounding cells radiate into the shape of a cross (Fig. 1: 27–31).

The stomatal types occurring in different taxa are given in Table 1.

DISCUSSION

Among the twenty-four different types of stomata recognized in the plants under investigation, the anomocytic type appears to be the most simple, since in this type the stomatal meristemoid soon after its differentiation directly acts as guard-cell mother cell (gcmc). Incidentally, this type of stomatal organisation occurs only in the Ophioglossaceae (see Table 1). The occurrence of this type of stomata in the Marattiaceae, Osmundaceae, and Dicksoniaceae, as reported by Hildebrand (1866), Kondo & Toda (1959), Thurston (1969), and Mehra & Soni (1983), could not be confirmed in this study. It is signifcant that in none of the taxa belonging to the so-called Eusporangiatae (except of course the Ophioglossaceae), Protoleptosporangiatae, and Leptosporangiatae, anomocytic stomata occur in association with other stomatal types, even if only as freaks.

In the remaining twenty-three stomatal types the stomatal meristemoids cut off from one to as many as four primary segments before acting as gcmc. These segments form subsidiary cells either directly or after undergoing division or redivision by radial anticlinal walls.

Among these twenty-three types, the polocytic stomata are most widely distributed and occur in all fern families (except Ophioglossaceae) recognised by Crabbe, Jermy & Mickel (1975). Seppolocytic stomata (i.e., mesoperigenous anomocytic stomata of Sen & Hennipman, 1981, and Sen, 1986) have the second-widest distribution. Pseudohemiparacytic, pluhemiparacytic, desmocytic, codesmocytic, pericytic, copericytic, codiacytic and staurocytic stomata have a rather restricted distribution.

Not only is the occurrence of polocytic stomata universal in ferns (except in Ophioglossaceae), it is also the basic form from which practically all other stomatal types, especially the copolocytic, seppolocytic, pseudopolocytic, plupolocytic, pseudocopolocytic, sepcopolocytic, hemiparacytic, cohemiparacytic, pseudohemiparacytic, pluhemiparacytic, cyclocytic, cocyclocytic, desmocytic, codesmocytic, pericytic, copericytic, diacytic, codiacytic, and staurocytic types have ontogenetically been derived through certain elaboration or modification. Additional cell division(s), reorientation of the subsidiary cell(s) and other surrounding cells, disharmonious growth rate during the expansion of the subsidiary cell and gcmc, and reorientation of metaphase spindle in a developing polocytic stoma have all brought forth these more evolved forms. Figure 5 indicates the pathways of development of various types of *stomata,* and also the factors that bring about the development of different stomatal types. As already indicated in the paragraphs on the ontogeny of stomata, polocytic stomata and all their derivatives are mesoperigenous in origin (Figs. 1–4). The pericytic and copericytic types of stomata originate mesoperigenously only in the initial stage and technically remain mesoperigenous as long as the radial anticlinal wall links are not lost. After the detachment of the link walls, the stomata secondar-

Table 1. Distribution of stomatal types.

Explanation:

1 = anomocytic	9 = hemiparacytic	17 = cocyclocytic
2 = polocytic	10 = cohemiparacytic	18 = desmocytic
3 = copolocytic	11 = pseudohemiparacytic *	19 = codesmocytic
4 = seppolocytic	12 = pluhemiparacytic *	20 = pericytic
5 = pseudopolocytic	13 = paracytic	21 = copericytic
6 = plupolocytic *	14 = coparacytic	22 = diacytic
7 = pseudocopolocytic *	15 = pluparacytic *	23 = codiacytic *
8 = sepcopolocytic *	16 = cyclocytic	24 = staurocytic

* newly discovered

+ = stomatal type present
++ = stomatal type more abundant than the other associated type(s)
(+) = stomatal type infrequent

Ophioglossaceae
Botrychium daucifolium 1 +
lanuginosum 1 +
virginianum 1 +
Helminthostachys zeylanica 1 +
Ophioglossum bergianum 1 +
nudicaule 1 +
reticulatum 1 +
Marattiaceae
Angiopteris sp. 2 (+), 16 +, 17 (+)
evecta 2 +, 16 ++, 17 +
hypoleuca 2 (+), 16 +, 17 (+)
Marattia fraxinea 2 +, 16 ++, 17 (+)
Osmundaceae
Osmunda claytoniana 2 (+), 4 +
regalis 2 (+), 4 +
Todea barbara 2 (+), 4 +
Plagiogyriaceae
Plagiogyria glaucescens 2 +, 3 (+), 4 (+), 22 (+)
Schizaeaceae
Lygodium circinnatum 2 ++, 3 +, 4 (+)
microphyllum 2 +, 3 (+), 4 (+)
Anemia villosa 2 +, 3 (+), 4 (+), 18 (+), 19 (+), 20 (+), 21 (+)
Mohria caffrorum 2 ++, 3 (+), 4 +
Parkeriaceae
Ceratopteris thalictroides 2 ++, 3 +, 4 (+), 5 +, 9 (+)

Adiantaceae
Adiantoideae
Cheilanthes farinosa 2 +, 3 ++, 4 +, 5 (+)
Pellaea viridis 2 ++, 3 +, 4 +, 5 (+)
Doryopteris pedata 2 ++, 3 +, 4 +, 5 (+), 7 (+)
Trachypteris induta 2 ++, 3 (+), 4 +, 9 (+)
Pityrogramma calomelanos 2 ++, 3 +, 4 +, 9 (+)
Hemionites arifolia 2 ++, 3 +, 4 +
palmata 2 ++, 3 +, 4 +, 5 (+)
Taenitis blechnoides 2 +, 3 ++, 9 (+)
Coniogramme japonica 2 +, 3 ++, 5 (+)
Adiantum caudatum 2 ++, 3 (+), 4 +, 5 (+)
hispidulum 2 ++, 3 +, 4 (+), 5 (+), 9 (+)
philippense 2 ++, 3 (+), 4 +, 5 (+)
raddianum 2 +, 3 (+), 4 (+), 5 (+)
Vittarioideae
Antrophyum parvulum 2 ++, 3 +, 5 (+)
Vittaria elongata 2 ++, 3 +, 4 (+), 9 (+)
ensiformis 2 ++, 3 +, 4 +, 9 (+)
Pteridoideae
Pteris aff. *biaurita* 2 ++, 3 +, 4 (+), 5 (+), 9 (+), 10 (+)
biaurita 2 ++, 3 +, 4 +, 5 +, 6 (+), 9 (+), 10 (+), 12 (+)
catoptera 2 +, 3 ++, 4 +, 5 (+)

(Adiantaceae / Pteridoideae continued)

Pteris
dalhousiae 2 ++, 3 +, 4 +, 5 (+), 9 (+)
ensiformis 2 ++, 3 +, 4 +, 5 (+)
parviloba 2 +, 3 ++, 4 +, 5 (+), 6 (+), 7 (+), 9 (+)
semipinnata 2 ++, 3 +, 4 +, 5 (+), 9 (+), 10 (+)
vittata 2 ++, 3 +, 4 +, 5 (+), 9 (+), 10 (+)
Acrostichum aureum 2 +, 3 (+), 4 (+)
speciosum 2 ++, 3 +, 4 (+)

Gleicheniaceae
Gleichenia gigantea 2 ++, 3 (+), 4 +, 9 (+)
laevissima 2 ++, 3 (+), 4 +, 9 (+), 22 (+)
Dicranopteris linearis 2 ++, 3 +, 4 +, 9 (+), 13 (+)

Polypodiaceae
Drynarioideae
Drynaria quercifolia 2 ++, 3 +, 4 (+), 5 (+), 9 (+), 10 (+)
rigidula 2 +, 3 (+), 5 (+)
Photinopteris speciosa 2 +, 3 ++, 4 +, 5 (+)
Aglaomorpha meyeniana 2 ++, 3 +, 4 +, 5 +, 9 (+)
splendens 2 ++, 3 +, 4 (+), 5 (+), 9 (+)
Pseudodrynaria coronans 2 +, 3 ++, 4 (+), 5 +
Platycerioideae
Platycerium grande 2 ++, 3 +, 16 +, 17 +, 18 (+), 19 (+), 20 (+), 21 (+)
Pyrrosia heteractis 2 (+), 3 (+), 9 (+), 10 (+), 18 +, 19 +, 20 +, 21 ++
lanceolata 2 (+), 3 (+), 9 (+), 18 +, 19 +, 20 ++, 21 +
Drymoglossum piloselloides 2 +, 3 +, 18 +, 19 +, 20 +, 21 +
Microsorioideae
Microsorum musifolium 2 +, 3 ++, 4 (+), 5 +, 6 (+), 7 (+), 9 (+)
pteropus 2 +, 3 ++, 4 (+), 5 (+)
punctatum 2 ++, 3 +, 4 (+), 5 +, 9 (+)
sarawakense 2 ++, 3 +, 4 (+), 5 (+)
stigmosum 2 ++, 3 (+), 4 +, 5 (+), 8 (+), 16 +
Phymatosorus commutatus 2 +, 3 ++, 4 (+), 5 +, 9 (+), 10 (+)
lucidus 2 ++, 3 +, 4 (+), 5 +, 9 (+), 10 (+)

(Polypodiaceae / Microsorioideae continued)

Phymatosorus scolopendria 2 (+), 3 ++, 4 (+), 5 +, 9 (+), 10 (+)
Christiopteris tricuspis 2 ++, 3 +, 4 (+)
Crypsinus albido-squamatus 2 ++, 3 +, 4 (+), 5 (+)
Selliguea feei 2 ++, 3 +, 4 +, 5 (+), 8 (+)
Pleopeltoideae
Lepisorus nudus 2 +, 3 ++, 4 (+)
Polypodioideae
Niphidium crassifolium 2 +, 3 ++, 4 (+), 5 +
Campyloneurum angustifolium 2 ++, 3 +, 4 (+), 5 +
phyllitidis 2 (+), 3 +, 4 (+), 5 (+)
Phlebodium aureum 2 ++, 3 +, 4 (+)
Polypodium formosanum 2 ++, 3 +, 4 (+), 5 (+)
lepidopteris 2 ++, 3 (+), 4 +
Goniophlebium subauriculatum 2 ++, 3 +, 4 (+), 5 (+)

Grammitidaceae
Loxogramme lanceolata 2 ++, 3 (+), 4 +
subecostata 2 ++, 3 +, 4 +, 5 (+)

Metaxyaceae
Metaxya rostrata 2 (+), 3 (+), 9 +, 10 (+) 13 ++, 14 +, 15 (+)

Lophosoriaceae
Lophosoria quadripinnata 2 (+), 4 (+), 9 +, 13 ++, 14 +, 15 (+)

Cyatheaceae
Cnemidaria roraimensis 2 +, 3 ++, 4 (+), 5 (+), 9 (+)
Cyathea canaliculata 2 +, 3 ++, 5 (+), 9 (+)
latebrosa 2 ++, 3 +, 4 +, 5 (+), 9 (+), 10 (+)
Trichopteris oblonga 2 +, 3 +, 4 (+), 5 (+), 9 (+), 10 (+)
Nephelea tussacii 2 ++, 3 +, 4 (+), 5 (+), 9 (+)
Alsophila gigantea 2 ++, 3 +, 4 (+), 5 (+), 9 (+)
metteniana 2 +, 3 +, 4 (+), 5 +, 6 (+), 9 (+)
Sphaeropteris elmeri 2 ++, 3 +, 4 (+), 5 (+), 9 (+)
Dicksonia antarctica 2 ++, 3 ++, 4 +, 5 (+), 9 (+), 10 (+), 13 (+)
Cystodium sorbifolium 2 ++, 3 +, 4 (+), 5 (+), 9 (+)

(Table 1 continued)

Thyrsopteridaceae

Thyrsopteris elegans 2 ++, 3 (+), 4 +, 9 (+)
Culcita macrocarpa 2 ++, 3 (+), 4 +, 9 (+)
Cibotium glaucum 2 (+), 4 (+), 9 (+), 13 ++, 14 +, 15 (+)
hawaiiense 2 (+), 4 (+), 9 (+), 13 ++, 14 +, 15 (+)

Dennstaedtiaceae

Dennstaedtioideae

Dennstaedtia bipinnata 2 ++, 3 +, 4 +, 9 (+)
scabra 2 ++, 3 (+), 4 +, 9 (+)
tenera 2 ++, 3 +, 4 +, 9 (+)
Microlepia platyphylla 2 +, 3 +, 4 (+), 5 (+)
speluncae 2 ++, 3 +, 4 +, 5 (+)
strigosa 2 +, 3 +, 4 (+), 5 (+)
Hypolepis punctata 2 ++, 3 (+), 4 +, 5 (+)
Paesia luzonica 2 +, 3 (+), 4 (+)
Histiopteris incisa 2 ++, 3 +, 4 +, 5 (+)
Blotiella curroii 2 +, 3 ++, 4 +, 5 +, 10 (+)

Monachosoroideae

Monachosorum subdigitatum 2 ++, 3 +, 4 (+)

Lindsaeoideae

Lindsaea chienii 2 ++, 3 +, 5 (+), 9 (+)
ensifolia subsp. *coriacea* 2 +, 3 ++, 5 (+), 9 (+)
odorata var. *darjeelingensis* 2 ++, 3 +, 5 (+), 9 (+)
Tapeinidium pinnatum 2 ++, 3 +, 5 (+)

Thelypteridaceae

Thelypteris baramensis 2 +, 3 ++, 4 (+), 5 +
harveyi 2 ++, 3 +, 4 +, 5 +, 9 (+)
immersa 2 ++, 3 +, 4 (+), 5 (+)
uliginosa 2 ++, 3 +, 4 (+), 5 (+)
Pseudophegopteris aurita 2 ++, 3 +, 4 +, 5 (+), 9 (+), 10 (+)
hirtirachis 2 ++, 3 ++, 4 +, 5 +, 9 (+), 10 (+), 11 (+)
rectangularis 2 ++, 3 +, 4 +, 5 (+), 9 (+), 10 (+)
Cyclogramma auriculata 2 ++, 3 +, 4 (+), 9 (+), 10 (+)
Coryphopteris arthrotricha 2 ++, 3 +, 4 (+), 5 (+)
viscosa 2 ++, 3 +, 4 (+), 5 (+)
Macrothelypteris ornata 2 ++, 3 +, 4 (+), 9 (+)
torresiana 2 ++, 3 +, 4 (+), 9 (+)

(Thelypteridaceae continued)

Metathelypteris dayi 2 ++, 3 +, 4 (+), 5 (+)
flaccida 2 +, 3 ++, 4 (+), 5 (+)
Cyclosorus extensus 2 ++, 3 +, 4 +, 5 (+)
ferox 2 ++, 3 +, 4 (+), 5 (+)
gongylodes 2 ++, 3 +, 4 (+), 5 (+), 9 (+)
striatus 2 +, 3 +, 4 (+), 5 (+)
Pronephrium nudatum 2 ++, 3 +, 4 (+)
Mesophlebion crassifolium 2 ++, 3 +, 4 +, 5 (+), 11 (+)
Sphaerostephanos invisus 2 ++, 3 +, 4 (+), 9 (+), 10 (+)
unitus 2 ++, 3 +, 4 +, 9 (+), 10 (+)
penniger 2 ++, 3 +, 4 (+), 9 (+), 10 (+)
Ampelopteris prolifera 2 ++, 3 +, 4 +, 5 (+)
Pneumatopteris ecallosa 2 ++, 3 +, 4 (+), 5 (+), 9 (+)
truncata 2 ++, 3 +, 4 +, 5 +, 9 (+)
Pseudocyclosorus esquirolii 2 ++, 3 +, 4 (+), 5 (+)
repens 2 ++, 3 (+), 4 +, 5 (+)
tylodes 2 ++, 3 +, 4 +, 5 (+)
Christella appendiculata 2 ++, 3 (+), 4 +, 5 (+)
arida 2 ++, 3 +, 4 +, 5 (+)
dentata 2 ++, 3 (+), 4 +, 5 (+)
jaculosa 2 ++, 3 +, 4 (+), 5 (+)
molliuscula 2 ++, 3 +, 4 (+), 5 (+)
parasitica 2 ++, 3 +, 4 (+), 5 (+)

Aspleniaceae

Asplenioideae

Asplenium africanum 2 ++, 3 (+), 4 +
dalhousiae 2 ++, 3 (+), 4 +, 5 (+)
falcatum 2 ++, 3 (+), 4 +
formosum 2 ++, 3 +, 4 (+), 5 (+)
glaucophyllum 2 ++, 3 +, 4 +
hemitomum 2 ++, 3 (+), 4 +
lucidum 2 ++, 3 (+), 4 +, 5 (+)

Athyrioideae

Athyrium filix-femina 2 ++, 3 +, 4 +, 5 (+)
pectinatum 2 ++, 3 +, 4 (+)
Diplazium esculentum 2 ++, 3 +, 4 +
polypodioides 2 ++, 3 +, 4 +, 5 (+)
proliferum 2 ++, 3 ++, 4 +, 5 +, 6 (+)

Tectarioideae

Ctenitis ampla 2 +, 3 ++, 4 +, 5 +, 6 (+), 9 (+)

(Aspleniaceae / Tectarioideae continued)

(Ctenitis) eriocaulis 2 ++, 3 +, 4 (+)
Pleocnemia hemiteliiformis 2 ++, 3 +, 5 (+)
irregularis 2 ++, 3 +, 4 +, 5 +, 7 (+), 9 (+)
Pteridrys australis 2 +, 3 ++, 4 (+), 5 (+)
Tectaria fernandensis 2 ++, 3 +, 4 +, 5 +
incisa 2 +, 3 ++, 4 (+), 5 (+)
subtriphylla 2 ++, 3 +, 4 +, 5 (+), 6 (+), 7 (+)
Cyclopeltis sp. 2 ++, 3 +, 4 (+), 5 (+)
Didymochlaena truncatula 2 ++, 3 +, 4 +, 5 +, 9 (+)

Dryopteridoideae

Peranema cyatheoides 2 ++, 3 +, 5 (+)
Polystichum aculeatum 2 ++, 3 (+), 4 +, 5 (+)
anomalum 2 ++, 3 +, 4 (+), 5 (+), 9 (+)
varium 2 ++, 3 +, 5 +
Cyrtomium falcatum 2 ++, 3 +, 4 +, 5 +, 6 (+), 8 (+), 9 (+), 22 (+)
Arachniodes obtusissima 2 ++, 3 +, 4 (+), 9 (+)
Olfersia cervina 2 ++, 3 (+), 4 +, 5 (+)
Dryopteris filix-mas 2 ++, 3 +, 4 (+)

Lomariopsidoideae

Bolbitis crispatula 2 ++, 3 +, 4 +, 5 (+), 9 (+), 22 (+)
heteroclita 2 +, 3 ++, 4 +, 5 +, 9 (+)
semicordata 2 ++, 3 +, 4 (+), 5 +
singaporensis 2 ++, 3 +, 4 (+), 5 +, 8 (+)
Bolbitis sp. 2 +, 3 ++, 4 (+), 5 +
Teratophyllum ludens 2 +, 3 ++, 4 +, 5 (+)
Lomariopsis cochinchinensis 2 ++, 3 +, 4 (+), 5 +

Elaphoglossoideae

Elaphoglossum sp. 2 ++, 3 +, 4 (+), 5 +, 9 +

Davalliaceae

Davallioideae

Humata lanuginosa 2 ++, 3 +, 4 (+)
ophioglossa 2 ++, 3 +, 4 (+), 22 (+)
Trogostolon falcinellus 2 ++, 3 +, 4 +, 5 (+), 22 (+)
Scyphularia simplicifolia 2 ++, 3 ++, 4 +, 5 (+), 22 (+)
Parasorus undulatus 2 ++, 3 ++, 4 (+)

(Davalliaceae / Davallioideae continued)

Davallia denticulata 2 ++, 3 ++, 4 +, 5 +, 9 (+)
divaricata 2 ++, 3 ++, 4 +, 5 (+), 9 (+)
fijiensis 2 ++, 3 ++, 4 +, 5 (+), 9 +
Davallodes grammatosorum 2 ++, 3 ++, 4 +, 5 (+), 22 +
hirsutum 2 ++, 3 ++, 4 +, 5 +, 22 (+), 24 (+)
Araiostegia hymenophylloides 2 ++, 3 +, 4 (+), 5 (+)
Leucostegia immersa 2 ++, 3 ++, 4 +, 9 +
pallida 2 ++, 3 ++, 4 +, 5 +, 22 (+)
Gymnogrammitis dareiformis 2 ++, 3 +, 4 +, 5 (+), 9 (+)
Rumohra adiantiformis 2 ++, 3 +, 4 +, 5 (+), 9 (+)

Oleandroideae

Oleandra africana 2 +, 3 +, 24 (+)
articulata 2 +, 3 +, 24 (+)
neriiformis 2 ++, 3 +, 5 (+)
Arthropteris monocarpa 2 ++, 3 +
tenella 2 ++, 3 +, 5 (+)
Psammiosorus paucivenius 2 ++, 3 +
Nephrolepis acutifolia 2 +, 3 +, 5 (+), 16 (+), 17 (+)
cordifolia 2 ++, 3 ++, 16 +, 17 +
exaltata 2 +, 3 +, 5 (+), 16 (+), 17 (+), 22 (+), 23 (+)
falcata 2 ++, 3 +, 16 +, 17 (+), 22 (+), 23 (+)

Blechnaceae

Blechnum brasiliense 2 ++, 3 +, 4 (+), 9 (+)
orientale 2 ++, 3 +, 4 (+), 9 (+)
punctatum 2 ++, 3 +, 4 (+), 9 (+)
Sadleria pallida 2 +, 3 +, 4 (+)
Woodwardia radicans 2 ++, 3 +, 4 (+), 5 (+)
Stenochlaena palustris 2 ++, 3 +, 4 (+)
tenuifolia 2 ++, 3 +, 4 (+)

Marsileaceae

Marsilea drummondii 2 +, 3 (+), 4 +
minuta 2 ++, 3 (+), 4 +
Regnellidium diphyllum 2 +, 4 +

Salviniaceae

Salvinia cucullata 2 ++, 4 +, 9 (+), 13 (+)

Azollaceae

Azolla pinnata 2 +, 4 +, 9 (+)

Table 2. Distribution of stomatal types in different families and subfamilies (sensu Crabbe et al., 1975). * = Newly discovered.

Families / Subfamilies	anomocytic	polocytic	copolocytic	seppolocytic	pseudopolocytic	plupolocytic *	pseudocopolocytic *	sepcopolocytic *	hemiparacytic	cohemiparacytic	pseudohemiparacytic *	pluhemiparacytic *	paracytic	coparacytic	pluparacytic *	cyclocytic	cocyclocytic	desmocytic	codesmocytic	pericytic	copericytic	diacytic	codiacytic *	staurocytic
Ophioglossaceae	+																							
Marattiaceae		+														+	+							
Osmundaceae		+		+																				
Plagiogyriaceae		+	+	+																		+		
Schizaeaceae		+	+	+														+	+	+	+			
Parkeriaceae		+	+	+	+				+															
Adiantaceae																								
Adiantoideae		+	+	+	+		+		+															
Vittarioideae		+	+	+	+				+															
Pteridoideae		+	+	+	+	+	+		+	+		+												
Gleicheniaceae		+	+	+					+				+									+		
Polypodiaceae																								
Drynarioideae		+	+	+	+				+	+														
Platycerioideae		+	+						+	+						+	+	+	+	+	+			
Microsorioideae		+	+	+	+	+	+	+	+	+						+								
Pleopeltoideae		+	+	+																				
Polypodioideae		+	+	+	+																			
Grammitidaceae		+	+	+	+																			
Metaxyaceae		+	+						+	+			+	+	+									
Lophosoriaceae		+		+					+				+	+	+									
Cyatheaceae		+	+	+	+	+			+	+			+											
Thyrsopteridaceae		+	+	+					+				+	+	+									
Dennstaedtiaceae																								
Dennstaedtioideae		+	+	+	+				+	+														
Monachosoroideae		+	+	+																				
Lindsaeoideae		+	+		+				+															
Thelypteridaceae		+	+	+	+				+	+	+													
Aspleniaceae																								
Asplenioideae		+	+	+	+																			
Athyrioideae		+	+	+	+	+																		
Tectarioideae		+	+	+	+	+	+		+															
Dryopteridoideae		+	+	+	+	+		+	+													+		
Lomariopsidoideae		+	+	+	+			+	+													+		
Elaphoglossoideae		+	+	+	+				+															
Davalliaceae																								
Davallioideae		+	+	+	+	+			+													+		+
Oleandroideae		+	+		+											+	+					+	+	+
Blechnaceae		+	+	+	+				+															
Marsileaceae		+	+	+																				
Salviniaceae		+		+					+				+											
Azollaceae		+		+					+															

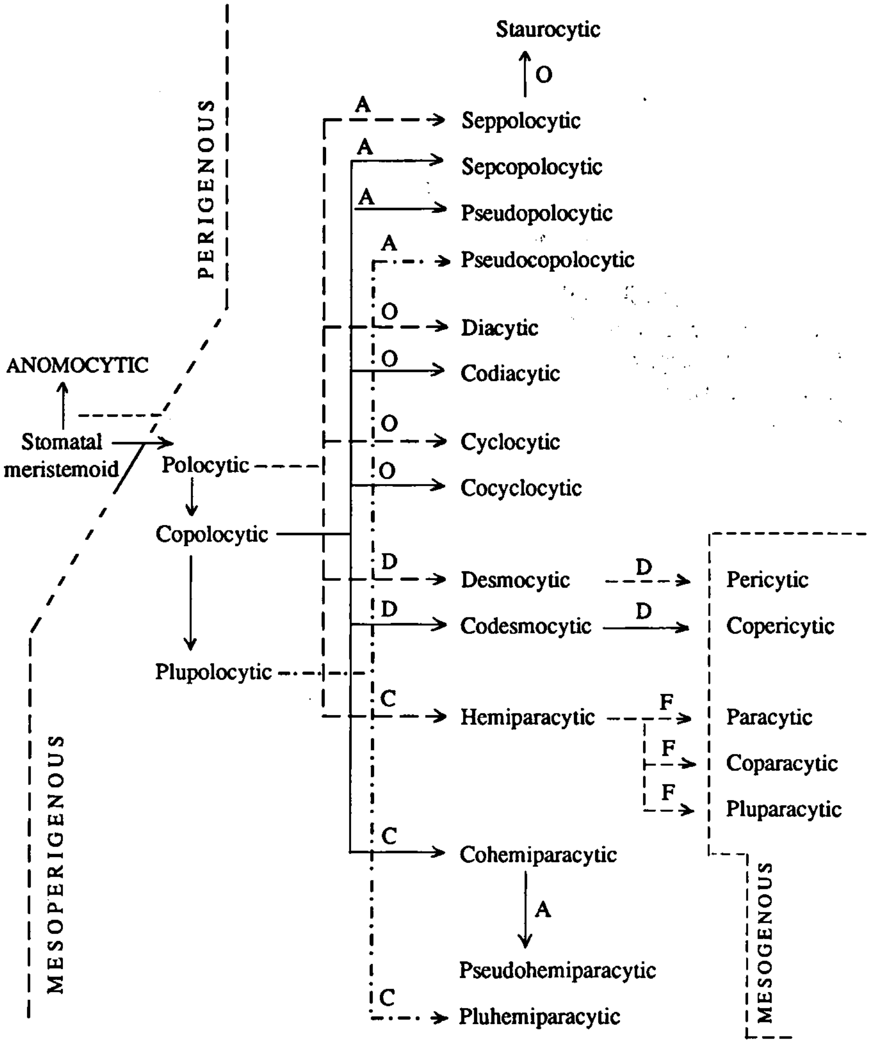

Fig. 5. Evolutionary trends in fern stomata and their ontogenetic interrelationships. — O = Orientation of subsidiary cell(s) and neighbouring cell(s). A = Additional segmentation in the subsidiary cell(s). D = Disharmonious growth of guard cells and subsidiary cell(s). C = Change in orientation of the metaphase spindle in gcmc. F = Formation of additional subsidiary cells on both sides.

ily become mesogenous. The present study thus confirms the observations of Sen & Hennipman (1981) that the polocytic and copolocytic stomata are the ontogenetic precursors of the pericytic and copericytic stomata, respectively. Pant (1965), Mickel & Lersten (1967), and Fryns-Claessens & Van Cotthem (1973) did not describe the origin of these types of stomata correctly, probably because the transitory stage between the polocytic/copolocytic and the pericytic/copericytic condition is extremely short-lived. Moreover, it is not at all possible to detect this stage unless one fixes the material at the right moment. Some of the developing hemiparacytic stomata, instead of developing into hemiparacytic forms, often initiate the development of a new category of stomata – the mesogenous type, that is, simply by changing over their cutting face. The initials destined to produce mesogenous stomata cut off subsidiary cells on both sides before differentiating gcmc and ultimately form paracytic, coparacytic, or pluparacytic stomata.

The occurrence of mesoperigenous and mesogenous types of stomata in the same frond in many taxa shows that the two forms do not represent two distinct entities. In fact, the mesogenous type is a derived form of the mesoperigenous type. It can be safely inferred that in ferns the mesogenous types of stomata have evolved on two distinct lines: one from the desmocytic stock, the other from the hemiparacytic one.

The polocytic type of stoma, however, should not be considered as the direct descendant of the anomocytic type, for the simple reason that these two stomatal types never occur in association, even accidently. It is now an established fact in ferns that two or more stomatal types having ontogenetic interrelationships among them often occur not only in the same taxon but also in the same lamina (see Table 1). In the light of this we can definitely conclude that the *Ophioglossum* group of genera characterised by anomocytic stomata, are not related to any other extant member of the Filicales where anomocytic stomata (in the sense of the present treatise) are conspicuously absent (Tables 1 & 2). Stomatal structure thus supports Sen's (Sen, 1967) view that the Ophioglossaceae should be placed in a distinct division, the Ophioglossophyta, and not in Filicophyta. Certainly the occurrence of collateral cauline bundles, collateral common stalk traces, non-circinately coiled leaves even in the embryonic condition, elliptic to circular bordered pits in the tracheids, and the lack of sclerotic cells in the stem and in the common stalk in the *Ophioglossum* group of genera, are not filicalean properties.

In a recent article Kato (1988) suggested that the Ophioglossaceae are living progymnosperms. He further presumed that among extant seed plants, the Ophioglossaceae are most clearly related to Cycadophyta. In the possession of oval circular bordered pits and in the development of eustelic vascular cylinder towards the distal end of the stem, the ophioglossoids indeed resemble the progymnosperms. Unfortunately nothing is known about the stomata of the progymnosperms. But unlike any of the progymnosperms, all ophioglossoids are non-arborescent, fleshy and devoid of any sclerenchyma. Moreover, the ophioglossoids differ not only from the progymnosperms but also from all other extant vascular cryptogams in the possession of anteroposteriorly divided phyllo-sporangiophore (i.e. 'aerial complex' of Bierhorst, 1971) associated with a fleshy, hairless storage root, as also in the development of tori in the pit membrane. So it appears that ophioglossoids are not living progymnosperms.

The extant cycads are similar to the ophioglossoids in the possession of perigenous stomata, upright simple rounded stems, eustelic vascular cylinder, cortical parenchyma and stipular outgrowths. Contrary to this, however, the cycads are characterised by circinately coiled leaves with a number of diploxylic traces originating from separate cauline strands, numerous stout tap roots often associated with apogeotropic roots from the bases of the stems, radially seriate secondary phloem, torusless pit membrane and mucilage ducts which all seem to exclude any affinity with the ophioglossaceous plants.

Taking stomatal features as a parameter of affinity, it is also very difficult to support Bierhorst's (Bierhorst, 1968, 1973) contention that *Psilotum* and *Tmesipteris*, which are characterised by having only perigenous anomocytic stomata (see Pant & Mehra, 1963; Pant & Khare, 1971), are at all ferns. Indeed the absence of megaphylly and the presence of plurilocular terminal sporangia in *Psilotum* and *Tmesipteris* strongly indicate their non-filicalean nature.

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APPENDIX

List of species studied. All material housed at the Pteridology and Palaeobotany Laboratory of the University of Kalyani, unless stated otherwise.

Ophioglossaceae — *Botrychium daucifolium* Wall. ex Hook. & Grev.: cult. Kew; U. Sen s.n.; *B. lanuginosum* Wall. ex Hook. & Grev.: B. De O2; *B. virginianum* (L.) Swartz: B. De SB1 – *Helminthostachys zeylanica* (L.) Hook.: U. Sen s.n. – *Ophioglossum bergianum* Schlecht.: U. Sen SA5; *O. nudicaule* L. f.: B. De B5; *O. reticulatum* L.: B. De M6.

Marattiaceae — *Angiopteris* sp.: U. Sen K63; *A. evecta* (Forst.) Hoffm.: B. De Dar9; *A. hypoleuca* De Vriese: U. Sen K68 – *Marattia fraxinea* Sm.: U. Sen K85.

Osmundaceae — *Osmunda claytoniana* L.: U. Sen S75; *O. regalis* L.: B. De P13 – *Todea barbara* (L.) Moore: U. Sen K47.

Plagiogyriaceae — *Plagiogyria glaucescens* Ching: B. De SB11.

Schizaeaceae — *Anemia villosa* Willd.: cult. Kew – *Lygodium circinnatum* (Burm.) Sw.: U. Sen K21; *L. microphyllum* Link: U. Sen K11 – *Mohria caffrorum* (L.) Desv.: U. Sen K114.

Parkeriaceae — *Ceratopteris thalictroides* (L.) Brongn.: B. De K197.

Adiantaceae — Adiantoideae: *Adiantum caudatum* L.: B. De Kln4; *A. hispidulum* Swartz: B. De Ta3; *A. philippense* L.: B. De B6; *A. raddianum* Presl: U. Sen K108 – *Cheilanthes farinosa* (Forssk.) Kaulf.: U. Sen K111 – *Coniogramme japonica* (Thunb.) Diels: U. Sen K50 – *Doryopteris pedata* (L.) Fée: U. Sen K65 – *Hemionitis arifolia* (Burm.) Moore: B. De Ke4; *H. palmata* L.: U. Sen K28 – *Pellaea viridis* (Forssk.) Prantl: U. Sen K125 – *Pityrogramma calomelanos* (L.) Link: U. Sen K106 – *Taenitis blechnoides* (Willd.) Sw.: B. De A2 – *Trachypteris* *induta* (Maxon) R. & A. Tryon: U. Sen K119 — Vitarioideae: *Antrophyum parvulum* Bl.: B. De A10 – *Vittaria elongata* Sw.: B. De A1; *V. ensiformis* Sw.: U. Sen K81 — Pteridoideae: *Acrostichum aureum* L.: B. De A4; *A. speciosum* Willd.: U. Sen K16 – *Pteris* aff. *biaurita* L.: U. Sen K8; *P. biaurita* L.: M. Mishra SMP6X; *P. catoptera* Kunze: U. Sen K39; *P. dalhousiae* Hook.: B. De Kln18; *P. ensiformis* Burm.: B. De H27; *P. parviloba* Christ: M. Mishra SMP8X; *P. semipinnata* L.: B. De Dar21; *P. vittata* L.: M. Mishra P15K.

Gleicheniaceae — *Dicranopteris linearis* (Burm. f.) Underw. var. *montana* Holttum: U. Sen K35 – *Gleichenia gigantea* Wall. ex Hook. (subg. *Diplopterygium*): U. & T. Sen s.n.; *G. laevissima* Christ: B. De SB10.

Polypodiaceae — Drynarioideae: *Aglaomorpha meyeniana* Schott: U. Sen K98; *A. splendens* (J. Sm.) Copel.: U. Sen K99 – *Drynaria quercifolia* (L.) Sm.: U. Sen K73; *D. rigidula* (Sw.) Bedd.: U. Sen K97 – *Photinopteris speciosa* Blume: U. Sen K61 – *Pseudodrynaria coronans* (Wall. ex Mett.) Ching: U. Sen K74 — Platycerioideae: *Drymoglossum piloselloides* (L.) Presl: B. De A3 – *Platycerium grande* (Fée) Kunze: U. Sen K84 – *Pyrrosia heteractis* (Mett. ex Kuhn) Ching: A. Bhattacharyya AB21; *P. lanceolata* (L.) Farwell: A. Bhattacharyya AB3 — Microsorioideae: *Christiopteris tricuspis* (Hook.) Christ: U. Sen K58 – *Crypsinus albido-squamatus* (Bl.) Copel.: U. Sen K28 – *Microsorum musifolium* (Bl.) Copel.: U. Sen K102; *M. pteropus* (Bl.) Copel.: U. Sen K22; *M. punctatum* (L.) Copel.: A. Bhattacharyya AB1; *M. sarawakense* (Baker) Holttum: U. Sen K90; *M. stigmosum* (Sw.) Ching: U. Sen K87 – *Phymatosorus commutatus* (Bl.) Pichi Sermolli: U. Sen K95; *P. lucidus* (Roxb.) Pichi Sermolli: U. Sen s.n.; *P. scolopendria* (N.L. Burm.) Pichi Sermolli: U. Sen s.n. – *Selliguea feei* Bory: U. Sen K79 — Pleoipeltoideae: *Lepisorus nudus* (Hook.) Ching: U. Sen K129 — Polypodioideae: *Campyloneurum angustifolium* (Sw.) Fée: U. Sen K86; *C. phyllitidis* (L.) Presl: U. Sen K127 – *Goniophlebium subauriculatum* (Bl.) Presl: U. Sen K33 – *Niphidium crassifolium* (L.) Lellinger: U. Sen K126 – *Phlebodium aureum* (L.) J. Smith: U. Sen K15 – *Polypodium formosanum* (Baker) Nakai: U. Sen K83; *P. lepidopteris* (Langsd. & Fisch.) Kunze: U. Sen K123.

Grammitidaceae — *Loxogramme lanceolata* (Sw.) Presl: A. Bhattacharyya 31; *L. subecostata* (Hook.) C. Chr.: U. Sen K120.

Metaxyaceae — *Metaxya rostrata* (H.B.K.) Presl: K.U. Kramer s.n.

Lophosoriaceae — *Lophosoria quadripinnata* (J.F. Gmelin) C. Chr.: cult. Kew.

Cyatheaceae — *Alsophila gigantea* (Wall.) Holttum: N.C. Das 149; *A. metteniana* Hance: AFS 67, 142 – *Cnemidaria roraimensis* (Domin) R. Tryon: cult. Kew – *Cyathea canaliculata* Willd.: s.n. (CAL); *C. latebrosa* (Wall.) Copel.: s.n. (CAL) – *Cystodium sorbifolium* (J.E. Smith) J. Smith: cult. Kew – *Dicksonia antarctica* Labill.: cult. Kew – *Nephelea tussacii* (Desv.) R. Tryon: H.H. Smith 1015 (CAL) – *Sphaeropteris elmeri* (Copel.) R. Tryon: CAL 10585 – *Trichopteris oblonga* (Kl.) R. Tryon: H.H. Smith 2224 (CAL).

Thyrsopteridaceae — *Cibotium glaucum* (Sm.) Hook. & Arnott: cult. Kew; B.P.S. s.n. – *C. hawaiiense* Nakai & Ogura: cult. Kew – *Culcita macrocarpa* Presl: cult. Kew – *Thyrsopteris elegans* Kunze: cult. Kew.

Dennstaedtiaceae — Dennstaedtioideae: *Blotiella curroii* (Hook.) R. Tryon: U. Sen K100 – *Dennstaedia bipinnata* (Cav.) Maxon: U. Sen K70; *D. scabra* (Wall.) Moore: U. Sen D75; *D. tenera* (Pr.) Mett.: U. Sen K1 – *Histiopteris incisa* (Thunb.) J. Sm.: U. Sen K131 – *Hypolepis punctata* (Thunb.) Mett.: U. Sen: K42 – *Microlepia platyphylla* (D. Don) J. Sm.: U. Sen K17; *M. speluncae* (L.) Moore: U. Sen K5; *M. strigosa* (Thunb.) Presl: G.B. Nair s.n. – *Paesia luzonica* Christ: G.B. Nair s.n. — Monachosoroideae: *Monachosorum subdigitatum* (Bl.) Kuhn: G.P. Nair s.n. — Lindsaeoideae: *Lindsaea chienii* Ching: B. De A9; *L. ensifolia* Sw. subsp. *coriacea* (Alderw.) Kramer: U. Sen K69; *L. odorata* Roxb. var. *darjeelingensis* Sen & Sen: T. Sen s.n. – *Tapeinidium pinnatum* (Cav.) C. Chr.: U. Sen K122.

Thelypteridaceae — *Ampelopteris prolifera* (Retz.) Copel.: B. De Kln84 – *Christella appendiculata* (Presl) Holttum: T. Sen s.n.; *C. arida* (D. Don) Holttum: B. De S84/1; *C. dentata* (Forssk.) Brownsey & Jermy: B. De H84/2; *C. jaculosa* (Chr.) Holttum: U. Sen K23; *C. molliuscula* (Kuhn) Holttum: Holttum s.n.; *C. parasitica* (L.) Lév.: T. Sen s.n. – *Coryphopteris arthrotricha* Holttum: Holttum s.n.; *C. viscosa* (Baker) Holttum: Holttum s.n. – *Cyclogramma auri-*

culata (J. Sm.) Ching: U. Sen T77. – *Cyclosorus*[1] *extensus* (Bl.) Ching: U. Sen K12; *C. ferox* (Bl.) Ching: Holttum s.n.; *C. gongylodes* (Schkuhr) Link: B. De Ke1; *C. striatus* (Schum.) Ching: U. Sen K25 – *Macrothelypteris ornata* (Wall. ex Bedd.) Ching: U. Sen L56; N.C. Das s.n.; *M. torresiana* (Gaud.) Ching: N.C. Das s.n. – *Mesophlebion crassifolium* (Bl.) Holttum: Holttum s.n. – *Metathelypteris dayi* (Bedd.) Holttum: Holttum s.n.; *M. flaccida* (Bl.) Ching: Holttum s.n.; U. Sen T76 – *Pneumatopteris ecallosa* (Holttum) Holttum: Holttum s.n.; *P. truncata* (Poir.) Holttum: U. Sen s.n. – *Pronephrium nudatum* (Roxb.) Holttum: U. Sen s.n. – *Pseudocyclosorus esquirolii* (C. Chr.) Ching: U. Sen L5; *P. repens* (Hope) Ching: Holttum s.n.; *P. tylodes* (Kunze) Ching: U. Sen L32 – *Pseudophegopteris aurita* (Hook.) Ching: U. Sen s.n.; B. De DarB14; *P. hirtirachis* (C. Chr.) Holttum: U. Sen L33; B. De DarJ; *P. rectangularis* (Zoll.) Holttum: B. De DarK – *Sphaerostephanos invisus* (Forst. f.) Holttum: Holttum s.n.; *S. penniger* (Hook.) Holttum: Holttum s.n.; *S. unitus* (L.) Holttum: B. De SB4 – *Thelypteris baramensis* (C. Chr.) Ching: Holttum s.n.; *T. harveyi* (Mett.) Proctor ex Iwats.: Holttum s.n.; *T. immersa* (Bl.) Ching: U. Sen K29; *T. uliginosa* (Kunze) Ching: U. Sen K38.

Aspleniaceae — Asplenioideae: *Asplenium africanum* Desv.: U. Sen K53; *A. dalhousiae* Hook.: B. De D6; *A. falcatum* Bedd.: B. De A15; *A. formosum* Willd.: B. De T2; *A. glaucophyllum* Alderw.: U. Sen K56; *A. hemitomum* Hieron.: U. Sen K7; *A. lucidum* Forst.: U. Sen K49 — Athyrioideae: *Athyrium filix-femina* (L.) Roth: B. De DarS; *A. pectinatum* (Wall.) Presl: B. De DarB3 – *Diplazium esculentum* (Retz.) Sw.: U. Sen K26; *D. polypodioides* Bl.: B. De SB6; *D. proliferum* (Lam.) Thouars: U. Sen K34 — Tectarioideae: *Ctenitis ampla* (Humb. & Bonpl. ex Willd.) Ching: U. Sen K32; *C. eriocaulis* (Fée) Alston: U. Sen K66 – *Cyclopeltis* sp.: U. Sen K118 – *Didymochlaena truncatula* (Sw.) J. Sm.: U. Sen K71 – *Pleocnemia hemitelliformis* (Racib.) Holttum: U. Sen K117; *P. irregularis* (Presl) Holttum: U. Sen K13 – *Pteridrys australis* Ching in C. Chr. & Ching: U. Sen K125 – *Tectaria fernandensis* (Baker) C. Chr.: U. Sen K62; *T. incisa* Cav.: U. Sen K27; *T. subtriphylla* (Hook. & Arn.) Copel.: U. Sen K64 — Dryopteridoideae: *Arachniodes obtusissima* (Mett.) Ching: B. De DarB21 – *Cyrtomium falcatum* (L. f.) Presl: B. De DarB32 – *Dryopteris filix-mas* (L.) Schott: U. Sen K104 – *Olfersia cervina* (L.) Kunze: U. Sen K124 – *Peranema cyatheoides* Don: B. De DarB19 – *Polystichum aculeatum* (L.) Schott: U. Sen K105; *P. anomalum* Bedd.: B. De SB2; *P. varium* (L.) Pr.: U. Sen K40 — Lomariopsidoideae: *Bolbitis crispatula* (Wall.) C. Chr.: B. De SB25; *B. heteroclita* (Pr.) Ching: U. Sen K88; *B. semicordata* (Moore) Ching: B. De Ca2; *B. singaporensis* Holttum: U. Sen K115; *B.* sp.: U. Sen K72 – *Lomariopsis cochinchinensis* Fée: U. Sen K9 – *Teratophyllum ludens* (Fée) Holttum: U. Sen K77 — Elaphoglossoideae: *Elaphoglossum* sp.: U. Sen K112.

Davalliaceae — Davallioideae: *Araiostegia hymenophylloides* (C. Chr.) Ching: Murata et al. T16067 (L); T. Sen T56 – *Davallia denticulata* (Burm.) Mett. ex Kuhn: B. De A8; *D. divaricata* Bl.: U. Sen K57; *D. fijiensis* Hook.: cult. Bot. Dept. Kalyani Univ. – *Davallodes grammatosorum* Copel.: Price s.n.; *D. hirsutum* (J. Smith) Copel.: Price 1478 under cult. Kew 207-71; Price 1178 (L); cult. Bot. Dept. Kalyani Univ. – *Gymnogrammitis dareiformis* (Hook.) Ching in Tardieu & C. Chr.: Smitinand & Sleumer 1074 (L); T. Sen S11 – *Humata lanuginosa* Alderw.: Bünnemeijer 3881 (BO); *H. ophioglossa* Cav.: Price 2759 (L); cult. Bot. Dept. Kalyani Univ. – *Leucostegia immersa* (Wall. ex Hook.) Presl var. *amplissima* Christ: Jermy 7358 under cult. Kew 637-69; Elmer 9900 (L); T. Sen D23; *L. pallida* (Mett. ex Kuhn) Copel.: M. Hotta 14393 (L); Price 1888 (L); Walker s.n. under cult. Kew 397-68.39702; cult. Bot. Dept. Kalyani Univ. – *Parasorus undulatus* Alderw.: Pleyte 363 (L); T. Sen T46 – *Rumohra adiantiformis* (G. Forst.) Ching: cult. Kew – *Scyphularia simplicifolia* Copel.: Hirano & Hotta 172 (L) – *Trogostolon falcinellus* (Presl) Copel.: Price & Hernaez 299 (L); Craig s.n. under cult. Kew 362-76 — Oleandroideae: *Arthropteris monocarpa* (Cordem.) C. Chr.: Pichi Sermolli 6763 (L); T. Sen T53; *A. tenella* (Forst. f.) J. Smith: Dockrill 268 (L); U. Sen K89 – *Nephrolepis acutifolia* (Desv.) Chr.: Surbeck 1035 (L); *N. cordifolia* (L.) Presl: T. Sen D19; T. Sen s.n. under cult. Kew; *N. exaltata* (L.) Schott: de Joncheere SEU39 (L); T. Sen A19; U. Sen K59; *N. falcata* (Cav.) C. Chr.:

1) Genus not recognised by Crabbe, Jermy & Mickel (1975).

Lee UL6 (L) – *Oleandra africana* Bonap.: U. Sen K24; *O. articulata* (Sw.) Presl: U. Sen K103; *O. neriiformis* Cav.: B. De Dar37 – *Psammiosorus paucivenius* C. Chr.: Last s.n. (BM).

Blechnaceae — *Blechnum brasiliense* Desv.: U. Sen K51; *B. orientale* L.: B. De Ca4; *B. punctulatum* Sw.: U. Sen K45 – *Sadleria pallida* (Hook. & Arn.) Hill: U. Sen K44 – *Stenochlaena palustris* (Burm.) Bedd.: B. De SO5; *S. tenuifolia* (Desv.) Moore: U. Sen K31 – *Woodwardia radicans* (L.) Sm.: U. Sen K43.

Marsileaceae — *Marsilea drummondii* A. Br.: U. Sen K91; *M. minuta* L.: B. De Kln21 – *Regnellidium diphyllum* Lindm.: U. Sen K92.

Salviniaceae — *Salvinia cucullata* Roxb.: B. De Kln22.

Azollaceae — *Azolla pinnata* R. Br.: cult. Bot. Dept. Kalyani Univ.