EPIDERMAL STRUCTURE AND ONTOGENY OF STOMATA IN *RAVENALA MADAGASCARIENSIS* J. F. GMEL.*

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Abstract

The paper describes the epidermal features of *Ravenala madagascariensis* J. F. Gmel. belonging to the family Strelitziaceae. Development of various types of stomata met in this taxon has also been discussed. Domatia and their development patterns have been studied in detail. Epidermal structures of Musaceae, Heliconiaceae and Strelitziaceae have been discussed. Efforts have been made to identify the taxa of these families on the basis of cuticular characters.

Introduction

Systematic position of the members of Musaceae has long been discussed by various workers Endlicher (1836-40), Richard (1931), Petersen (1889), Schumann (1900), Winkler (1930), Hutchinson (1934), Nakai (1948), and Lane (1955). Leaf morphology and anatomy has been discussed by Tomlinson (1959). Structure and development of stomata in Musaceae and related families have been studied by Tomlinson (1969, 1974), Paliwal (1969) and Stebbins and Khush (1961). Cuticular structures of *Ravenala*, a genus of the family Strelitziaceae has been discussed in the present investigation. Terminology used here is based on Fryns-Classens (1973) and Dilcher (1974).

Material and Methods

The material for the present investigation was obtained from the garden of Botany Department, Lucknow University, Lucknow. Fresh leaves of various stages were taken and fixed in a mixture of Chromic Acetic Acid. Cuticles were obtained by maceration of leaves in Schultze's fluid and stained in aqueous Safranin. For the development of stomata epidermal peels of fixed leaves were stained in Haidenhains Iron-Haematoxyline and mounted in Canada Balsam.

Observations

Leaves of *Ravenala madagascariensis* are large with long petiole and broad lamina. They are dorsiventral. Plant has a true sub-aerial stem which bears large two ranked leaves appearing fan-like. Plants possess water accumulating quality in the leaf bases. Important cuticular characters of the large leaves of this genus are discussed in the present investigation.

Epidermal Cells—Cell of adaxial surface are uniform, arranged in distinct files but they are short and irregular. Cells are highly variable rectangular, elongated or squarish and their walls are usually smooth (Text-Figs. 1, 4). Abaxial epidermis is differentiated into coastal and intercoastal regions. Coastal regions are narrow. Cells in this region are

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arranged in distinct files, generally elongated or rectangular and are 33x7 to 45x14 μm in size (Text-Figs. 2,5). Intercostal regions are fairly wide and consist of very irregular cells. Cells in this region are not arranged in distinct files and are 13x16 to 20x10 μm in size (Text-Figs. 2-3). Cell walls are usually cutinized and smooth.

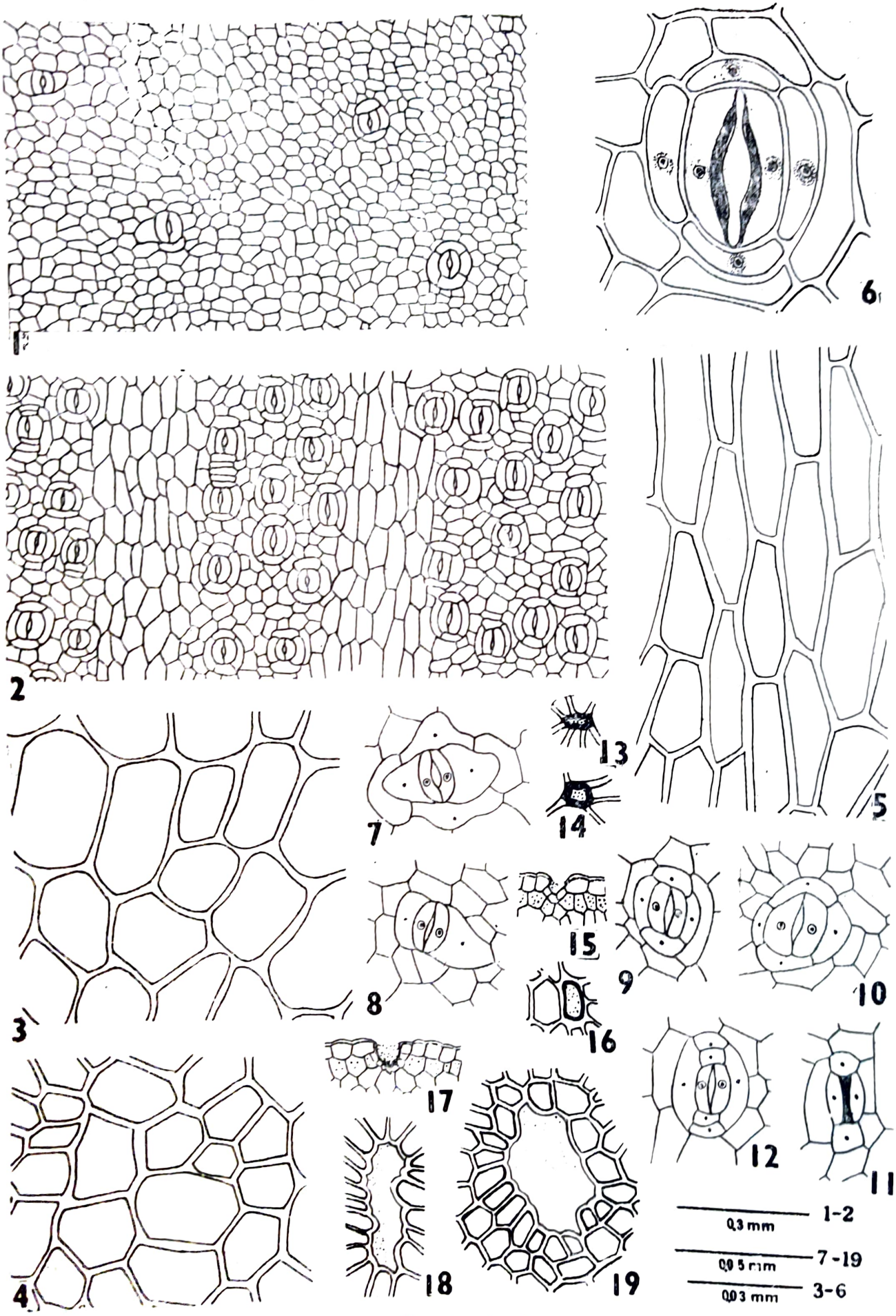
Stomata—They occur on both the surfaces of the leaf but are infrequent on the adaxial surface. Stomata are irregularly distributed on the adaxial surface and their frequency is low (Text-Fig. 1). On the abaxial surface, stomata are fairly large in number and confined to intercostal regions (Text-Fig. 2). They are not arranged in regular files but usually there are 2 to 5 rows of stomata in the intercostal regions.

Stomata occuring on the adaxial surface are tetracytic. It has been observed that either one or both the lateral subsidiary cells are greatly expanded (Text-Figs. 7-8). On the abaxial surface various types of stomata have been recorded but the frequency of tetracytic stomata is high. Stomatal frequency is 160 to 210/mm² and stomatal index is 15 or 16. Size of the stomata varies from 33x26 to 45x30 μm. Stomata recorded on the abaxial surface are: (i) Tetracytic: Stomata have a distinct vertical pore, pair of guard cells surrounded by four subsidiary cells; two terminal and two lateral. Terminal subsidiary cells are short and prominent. In some cases it has been noticed that the inner walls of guard cells have some thickenings (Text-Figs. 6, 9). (ii) Hexacytic: Guard cells of the stomata are surrounded by six subsidiary cells. There are either four lateral and two terminal subsidiary cells or four terminal and two lateral ones (Text-Figs. 12, 22); (iii) Paracytic: This type of stomata are rare but they have been observed at places. They have a pair of guard cells which are surrounded by two parallel subsidiary cells (Text-Fig. 24); (iv) Cyclocytic: They are few in number and occur towards the margins of the leaf. Guard cells of the stomatal apparatus are surrounded by a ring of subsidiary cells which are very distinct (Text-Figs. 10, 23); (v) Contiguous: They are commonly found on the abaxial surface. Two or more stomata are joined either laterally or terminally (Text-Figs. 20-21); (vi) Degenerated: They are recorded in the mature leaves at places. In a few stomata guard cells are completely degenerated leaving thickened vertical area. This structure is surrounded by four subsidiary cells, of which terminal subsidiaries are very distinct (Text-Fig. 11).

Domatia—They have been observed in the mature leaves. They are usually elongated, oval or sometimes irregular in shape and are surrounded by smaller cells (Text-Figs. 18-19). These structures are commonly found on the cuticular layers, but their development is little known. We have observed various stages of the development of domatia. At early stage an elongated or rectangular cell with slightly thickened walls has been recognised (Text-Figs. 13, 14). This cell further increases becoming larger and a small space is formed (Text-Figs. 16, 18-19). The cells surrounding this space are usually smaller than the remaining epidermal cells. As the leaf matures, this space increases to form various shapes of domatia on the cuticular layer. Developmental stages of domatia have been observed in 15 to 20 days old leaves. Many transverse sections of the leaf have been prepared to ascertain the nature of the domatia. It has been observed that at places there are distinct depressions. These depressions are the domatia having some contents in it (Text-Figs. 15-17).

Ontogeny of Stomata

Epidermal peels of 10 to 20 days old leaves show various stages of stomatal development. Numerous meristemoids have been observed scattered on the cutiles of the young leaves. Various developmental patterns of the stomata have been noted.



Text-figs. 1—19.

(i) *Di-perigenous*—Small meristemoid functions directly as a guard cell-mother cell and divides by an vertical wall to form two guards cells. The two subsidiary cells which are parallel to guard cells are formed from the neighbouring epidermal cells. Mature stomata, therefore, belong to paracytic type (Text-Figs. 25-27).

(ii) *Tetra-perigenous*—The meristemoid functions as guard cell-mother cell and divides vertically to form two guard cells. Surrounding the guard cells, adjacent epidermal cells, divide to form 4 subsidiary cells. Two large lateral subsidiaries are parallel while the two smaller ones are terminal and at right angle to stomatal complex (Text-Figs. 28-31).

(iii) *Hexa-perigenous*—The meristemoid directly functions as guard cell—mother cell and divides to form a pair of guard cells. Four subsidiary cells are formed by unequal divisions of four adjacent epidermal cells which surround the guard cells. Usually the two lateral subsidiary cells divide further by vertical walls to produce 4 lateral subsidiaries. Sometimes terminal subsidiary cells divide by transverse walls to form additional subsidiary cells. Thus, mature stomata have either 4 lateral and 2 terminal or 4 terminal or 2 lateral subsidiary cells (Text-Figs. 36-45).

(iv) *Cyclo-mesoperigenous*—The meristemoid divides to form two cells, the small cell further divides to form a pair of guard cells with intervening pore. The large cell which covers about half of the guard cells divides to form subsidiaries. Adjacent epidermal cells covering the remaining portion of the guard cells also divide transversely to produce subsidiary cells. Thus, mature stomata have a ring of subsidiary cells which surround the guard cells (Text-Figs. 32-35).

Discussion

Epidermal structures, distribution and type of stomata, their frequency and size, presence of domatia, trichomes their structures and frequency and the development of stomata in the genus *Ravenala* are important. Family Musaceae has seven genera, viz., *Musa*, *Ensete*, *Ravenala*, *Phenakospermum*, *Strelitzia*, *Heliconia* and *Orchidantha*. The status of the genus *Orchidantha* as agreed by Petersen (1889), Schumann (1900), Winkler (1930), Hutchinson (1934), Nakai (1948) and Lane (1955) is given to a monotypic family Lowiaceae. Remaining six genera are placed in three families, viz., Musaceae (*Musa* & *Ensete*), Heliconiaceae (*Heliconia*) and Strelitziaceae (*Strelitzia*, *Ravenala* & *Phenakospermum*).

Tomlinson (1959) has studied a few features of Musaceae. Members of Musaceae, Heliconiaceae, Strelitziaceae and Lowiaceae are related to one another in growth habit, vegetative and reproductive structures. We have tried to identify all the seven genera of above mentioned families on the basis of cuticular characters. Trichomes are comp-

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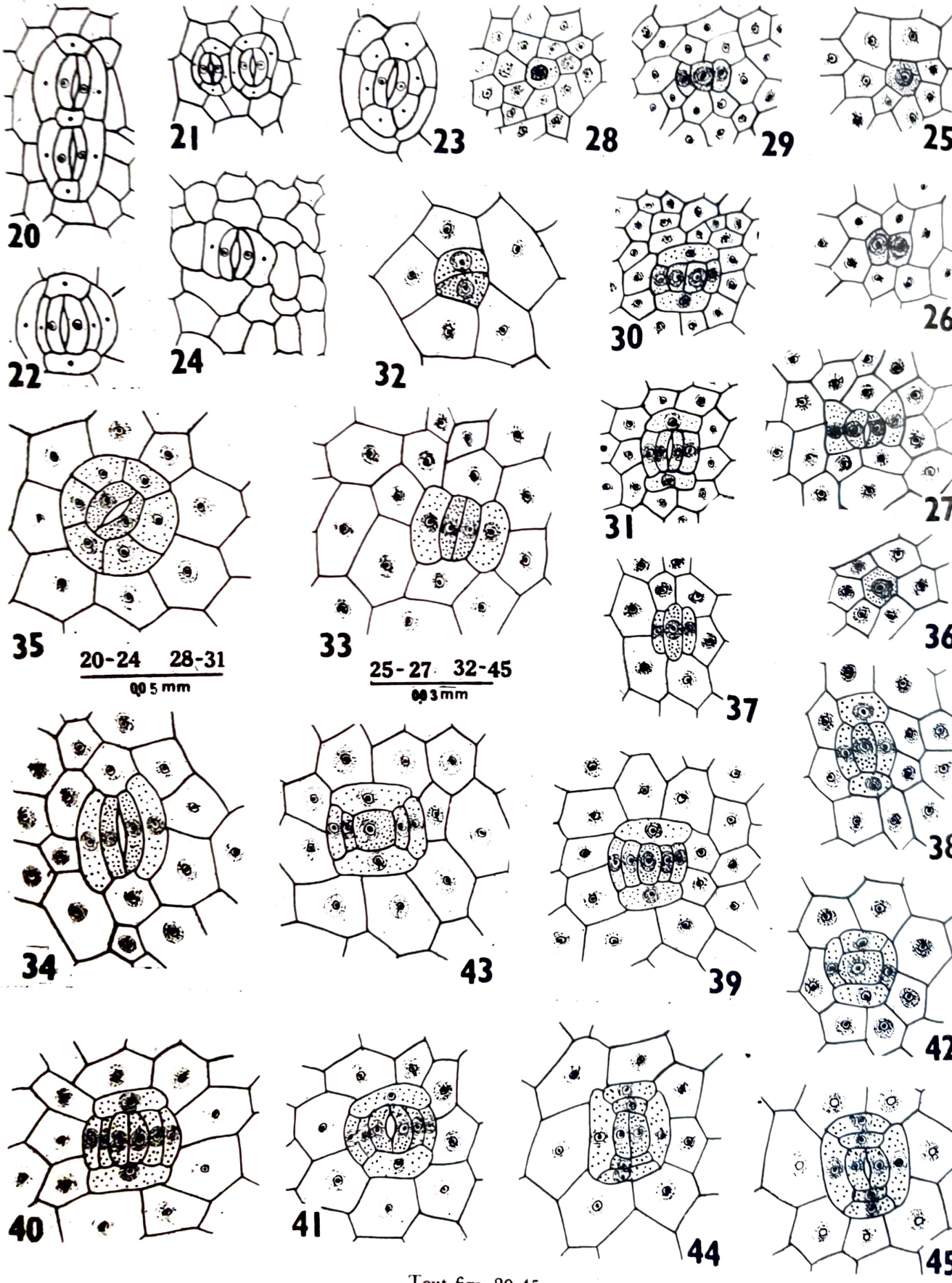
Text-figs. 1-19—1. Adaxial surface showing uniformly arranged cells and stomata.

2. Abaxial surface showing distinct costal and intercostal regions.
3. Cells of the intercostal region of abaxial surface.
4. Cells of the adaxial surface.
5. Cells of the costal region of adaxial surface.
6. Typical tetracytic stomata
7-8. Stomata of adaxial surface showing expanded lateral subsidiary cells.
9-12. Types of stomata. Fig. 9-Tetracytic. Fig. 10. Cycylocytic Fig. 11. degenerated and Fig. 12. Hexacytic.
13-14, 16. Developmental stages of domatia.
15, 17. T.S. of leaf showing depth and contents of domatial cavity.
18-19. Mature domatia.



Text-figs. 20-45.

letely lacking in all the families of this complex except in a species of *Heliconia*, *H. illustris* Sense & Mos., where they are uniseriate and confined to leaf sheath. Cuticle is thick in *Ravenala*, *Musa*, *Ensete* and *Strelitzia* while it is thin in *Orchidantha* and *Heliconia*. Epidermal cells are of various shapes, squarish, rectangular or elongated with usually smooth walls in all the genera except *Heliconia* where they are irregular and sinuate walls.

In *Musa*, *Ensete* and *Ravenala* adaxial cells are not in distinct files, uniformly distributed; in *Strelitzia* in distinct long files; in *Heliconia* cells in regular rows highly sinuate and in *Orchidantha* uniform with distinct files of long and short cells. Stomata are infrequent on the adaxial surface except in *Ensete* where they are equally distributed on both the surfaces. Stomata are numerous on the abaxial surface in the intercostal regions either in narrow rectangular or wide areas in all the genera except in *Orchidantha*, where there is no differentiation of costal and intercostal areas, therefore, they are uniformly distributed all over the surface. Guard cells are sunken only in *Ravenala* and *Strelitzia*. Terminal subsidiary cells are short and distinct in all the genera except in *Orchidantha*. In this genus terminal subsidiary cells are not differentiated from other epidermal cells.

The genus *Ravenala* can be distinguished by the presence of thick cuticle, uniform distribution of adaxial cells, sunken guard cells and varied types of stomata. Further, it has an important feature-domatia, which have not been recorded in other members of the family Strelitziaceae.

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Text-figs. 20-45—20-21. Contiguous stomata.

22-24. Different types of stomata. Fig. 22 Hexacyctic. Fig. 23 Cyclocytic and Fig. 24 Paracytic.

25-27. Developmental stages of Di-perigenous stomata. Fig. 25 stomatal menstemoid. Fig. 26-vertical division in the meristemoid. Fig. 27-mature paracytic stomata.

28-31. Developmental stages of Tetracytic stomata. Fig. 28-Protoderm cell. Fig. 29- a meristemoid and two lateral cells. Fig. 30- guard cell-mother cell and four subsididary cells. Fig. 31-mature tetracytic stomata.

32-35. Developmental stages of Cyclocytic stomata. Fig. 32- stomatal meristemoid showing division. Fig. 33-guard cell-mother cell (g.m.c.) and lateral cells, Fig. 34-showing two guard cells and two lateral cells. Fig. 35- mature cyclocytic stomata.

36-45. Developmental stages of Hexacytic stomata. Fig. 36-stomatal meristamoid. Fig. 37- central guard cell-mother cell and two lateral cells. Fig. 38-four subsidiary cells and a g.m.c. Fig. 39- two terminal and four lateral subsidiary cells surrounding g.m.c. Fig. 40- vertical division of g. m. c. surrounded by six subsidiary cells. Fig. 41-mature hexacytic stomata. Fig. 42- g.m.c. and four subsidiary dells. Fig. 43-g. m.c. and six subsidiary cells. Fig. 44—showing division in g.m.c. Fig. 45-mature hexacytic stomata.

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