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The Families of the Monocotyledons

Structure, Evolution, and Taxonomy

In Cooperation with

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With 225 Figures

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Preface

In this book we present an integrated account of the monocotyledons. The classification is supported by an extensive character analysis and by evolutionary models constructed on the basis of this analysis. An assessment of the character states as either primitive or derived, in the monocotyledons as a whole and in their constituent groups, is presented. These parts of the book have their forerunners in *The Monocotyledons: a Comparative Study* (DAHLGREN and CLIFFORD, 1982) and in *Monocotyledon Evolution: Characters and Phylogenetic Estimation* (DAHLGREN and RASMUSSEN, 1983).

Thus the presentation gives great weight to evolutionary considerations. We have aimed at doing away with old heterogeneous families, and arranging the new, smaller and more homogeneous ones according to their presumed relationships. Most taxonomists may regard us as “splitters”. We believe, however, that a concept of Amaryllidaceae, for example, which includes Amaryllidaceae sensu stricto, Ixioliriaceae, Agavaceae pro parte, and, perhaps, Alstroemeriaceae, is of no help to the botanist seeking to recognize natural and comprehensible groups, and that it will prevent him from perceiving the evolutionary pathways which have led to the families and their genera. Again, it is certainly of no advantage to unite Liliaceae, as circumscribed here, with Alliaceae, Hyacinthaceae, Asphodelaceae, Hemerocallidaceae, Convallariaceae, Trilliaceae and other elements, if at the same time the Liliaceae are kept distinct from, for example, Alstroemeriaceae, Iridaceae or Philesiaceae.

Our classification has been based on an extensive body of evidence and the decisions taken are explained as fully as possible. It has been our intention to avoid the constraints of mere convention and to adopt an unbiased approach. Yet, in our concepts we have been greatly influenced by previous treatises, such as those by HUBER (1969) and HAMANN (1961), which were likewise based on extensive comparative studies.

The classification in most cases is sufficiently practical, we believe, for use in the herbarium and in the field, but convergent evolution has led to cases where it may be difficult to refer a genus to a particular family and where its position in that family is still uncertain. For some families supplementary studies are needed before we have a full understanding of their circumscriptions. All such cases are clearly indicated.

Because our orders and families are generally rather narrowly circumscribed the families are numerous, especially in Asparagales. Keys to the families of each order have therefore been provided. Further guidance can be obtained from the evolutionary models (“cladograms”) supplied.

One of the authors (R.D.) is involved with the preparation of the monocotyledon volume in the series *The Families and Genera of Flowering Plants* (Editor-in-chief: K. KUBITZKI, Cambridge University Press). We are keen to stress that the present work has been able to benefit little from the larger project, the information for which has been kept separate. In fact, only few family treatments were available when the manuscript of the present book was completed. However, great and often indispensable help has been given to us by some colleagues (see below), and the texts of some of the families are written wholly or mainly by specialists.

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Mr. BENT JOHNSEN, Copenhagen, made the original drawings for Figs. 46, 54, 59, 63, 64, 65, 66, 67A–I, 74, 77, 78, 81, 86, 88, 101, 108, 113, 114, 126 and 212. Many other illustrations, such as most of those for the orchids and the schematic and diagrammatic ones for Cyperaceae and Poaceae, have been redrawn by him. The illustration of *Alexgeorgia* (Fig. 213) has been placed at our disposal by Dr. J.P. JESSOP, Adelaide.

Most illustrations, however, have been taken from other sources. Many are from S. ROSS-CRAIG, *Drawings of British Plants*, for which paid copyright has kindly been granted by Bell & Hyman. M. CORREA has kindly permitted us to use many illustrations from *Flora Patagonica*. Further, Professor A. TAKHTAJAN has allowed us to use several illustrations from *Plant Life* Vol. 6; Dr. F.N. HEPPER several from *Flora of West Tropical Africa*, ed. 2, Vol. 3 (1); Dr. A. CRONQUIST several from *Intermountain Flora* Vol. 6; University of Washington Press several from *Vascular Plants of the Pacific Northwest* Vol. 1; Plenum Publishing Corporation some illustrations from *Evolutionary Biology* Vol. 16; Dr. A. EL-GADI some illustrations from *Flora of Libya*; and Dr. W. BURGER a plate from *Evolutionary Theory* Vol. 5. Illustrations come from many other works, all cited in the legends of the respective figures. We acknowledge gratefully our indebtedness to the persons, institutions and publishers responsible for all these publications.

The facilities available to us at the Botanical Museum, University of Copenhagen, where most of the work on the present book was carried out, were indispensable. The secretarial work has been carried out by Mrs. KIRSTEN HARDER and Mrs. LENE FUGMANN, and technical work by the Staff of the Museum. The generosity of the staff and colleagues in helping with this book is kindly acknowledged. We acknowledge similar help, though on a much smaller scale, from the University Botanic Garden, Cambridge, and the Botany Department of University of Queensland, St. Lucia, and their office staffs.

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Contents

Morphological Concepts	1
Underground Parts	1
The Aerial Stem	2
Anatomical Concepts (Leaf and Stem)	2
Leaves	3
The Inflorescence	5
The Flower	6
The Floral Axis	7
Numerical Conditions and Insertion of the Components of the Flower	7
The Perianth	7
The Androecium	8
The Anther Wall and Tapetum	8
The Pollen Grains and Their Dispersal	10
The Gynoecium	11
The Ovule	12
Embryo Sac Formation	14
Endosperm Formation	14
Embryo Formation	14
The Fruit	15
The Seed	16
The Embryo	16
Chemical Characters. By S.R. JENSEN and B.J. NIELSEN	17
Evolutionary Concepts, Classification	23
General Concepts	23
Divergent Evolution	25
Reduction	29
The Lemnaceae	30
The Zosteraceae	31
The Centrolepidaceae and Hydatellaceae	32
The Reproductive Structures in Cyperaceae Tribus Mapanieae	33
The Inflorescence and Flower in <i>Carex</i>	34
The Typhaceae and Sparganiaceae	35
The Genus <i>Cyclanthus</i> , Cyclanthaceae	35
Convergent Evolution	36
General	36
The Spadiciflorae	37
The Arales-Piperales	39
The Alismatales-Nymphaeales	42
Criteria for the Monocotyledons	44
Origin of the Monocotyledons	48
General Remarks	48
The Ranalean/Magnoliifloran Hypothesis	48
The Hypothesis of Monocotyledons as Ancestral Angiosperms	54

VIII Contents

Fossils	58
Distribution of Character Conditions	59
General	59
Vegetative Morphology	60
Vegetative Anatomy	62
Floral Morphology	65
Microsporangia, Pollen	67
Ovular Characters	70
Fruit and Seed Characters	71
Chromosomal Characters	73
Phytochemical Characters	74
Parasites	75
Ancestral and Derived Character States in Monocotyledons in General and in Various of the Major Groups	76
General	76
Vegetative Morphology	77
Vegetative Anatomy	79
Floral Morphology	80
Microsporangia, Pollen	83
Ovular Characters	84
Fruit and Seed Characters	86
Chromosomal Characters	88
Phytochemical Characters	89
Parasites	90
Evolution Within the Monocotyledons	91
The Hypothesis of Monocotyledons as Ancestral Angiosperms	91
The Ranalean/Magnoliifloran Hypothesis	91
The Liliiflorae	92
The Dioscoreales	92
The Asparagales	92
The Liliales (incl. Orchidales)	93
The Burmanniales	95
The Melanthiales	96
The Ariflorae-Triuridiflorae-Alismatiflorae Complexes	96
The Ariflorae	96
The Triuridiflorae	96
The Alismatiflorae	97
The Bromeliiflorae-Zingiberiflorae-Commeliniflorae Complexes	98
The Bromeliiflorae	101
The Zingiberiflorae	102
The Commeliniflorae	102
The Areciflorae-Cyclanthiflorae-Pandaniflorae Complexes	105
Taxonomy	106
General	106
Superorder Liliiflorae	107
Order Dioscoreales	110
Trichopodaceae Hutchinson (1934)	112
Dioscoreaceae R. Brown (1810)	115

Taccaceae Dumortier (1829)	118
Stemonaceae Engler in Engler & Prantl (1887)	121
Trilliaceae Lindley (1846)	123
Smilacaceae Ventenat (1799)	127
Petermanniaceae Hutchinson (1934)	128
Order Asparagales	129
Philesiaceae Dumortier (1829)	133
Luzuriagaceae J. Dostál (1857)	135
Convallariaceae P. Horaninow (1834)	137
Asparagaceae A.L. Jussieu (1789)	140
Ruscaceae Hutchinson (1934)	142
Herreriaceae S.L. Endlicher (1836)	143
Dracaenaceae R.A. Salisbury (1866)	144
Nolinaceae T. Nakai (1943)	146
Asteliaceae Dumortier (1829)	147
Hanguanaceae Airy Shaw (1965)	149
Dasypogonaceae Dumortier (1829)	151
Calectasiaceae S.L. Endlicher (1836)	154
Blandfordiaceae Dahlgren & Clifford, fam. nov.	155
Xanthorrhoeaceae Dumortier (1829)	156
Agavaceae S.L. Endlicher (1841)	157
Hypoxidaceae R. Brown (1814)	161
Tecophilaeaceae Leybold (1862)	164
Cyanastraceae Engler (1900)	167
Eriospermaceae S.L. Endlicher (1836)	168
Ixioliriaceae T. Nakai (1943)	170
Phormiaceae J.G. Agardh (1858)	172
Doryanthaceae Dahlgren & Clifford, fam. nov.	175
Hemerocallidaceae R. Brown (1810)	176
Asphodelaceae A.L. Jussieu (1789)	179
Anthericaceae J.G. Agardh (1858)	182
Aphyllanthaceae G.T. Burnett (1835)	186
Funkiaceae P. Horaninow (1834)	187
Hyacinthaceae Batsch (1802)	188
Alliaceae J.G. Agardh (1858)	193
Amaryllidaceae Jaume St. Hilaire (1805)	199
Order Melanthiales	207
Melanthiaceae Batsch (1802)	208
Campynemaceae Dumortier (1829)	213
Order Burmanniales	215
Burmanniaceae Blume (1827)	216
Thismiaceae J.G. Agardh (1858)	219
Corsiaceae Beccari (1878)	219
Order Liliales	220
Alstroemeriaceae Dumortier (1829)	224
Colchicaceae A.P. de Candolle in Lamarck & de Candolle (1805)	226
Uvulariaceae C.S. Kunth (1843)	229
Calochortaceae Dumortier (1829)	231
Liliaceae A.L. Jussieu (1789)	233
Geosiridaceae Jonker (1939)	238
Iridaceae A.L. Jussieu (1789)	238

Orchids. By F.N. RASMUSSEN	249
Apostasiaceae Lindley (1833)	253
Cypripediaceae Lindley (1833)	253
Orchidaceae A.L. Jussieu (1789)	255
Superorder Ariflorae	275
Order Arales. By N. JACOBSEN	278
Araceae A.L. Jussieu (1789)	278
Lemnaceae S.F. Gray (1821)	287
Superorder Triuridiflorae	290
Order Triuridales	291
Triuridaceae G. Gardner (1843)	291
Superorder Alismatiflorae	292
Order Alismatales	295
Aponogetonaceae J.G. Agardh (1858)	297
Butomaceae L.C. Richard (1815)	298
Limnocharitaceae Takhtajan ex Cronquist (1981)	299
Alismataceae Ventenat (1799)	301
Hydrocharitaceae A.L. Jussieu (1789)	303
Order Najadales	307
Scheuchzeriaceae Rudolphi (1830)	309
Juncaginaceae L.C. Richard (1808)	310
Potamogetonaceae Dumortier (1829)	312
Posidoniaceae Lotsy (1911)	315
Zosteraceae Dumortier (1829)	316
Zannichelliaceae Dumortier (1829)	318
Cymodoceaceae N. Taylor (1909)	320
Najadaceae A.L. Jussieu (1789)	322
Superorder Bromeliiflorae	323
Order Velloziales	326
Velloziaceae S.L. Endlicher (1841)	328
Order Bromeliales	329
Bromeliaceae A.L. Jussieu (1789)	330
Order Philydrales	333
Philydraceae Link (1821)	336
Order Haemodorales	336
Haemodoraceae R. Brown (1810)	338
Order Pontederiales	340
Pontederiaceae Kunth in Humboldt (1816)	344
Order Typhales	344
Sparganiaceae Rudolphi (1830)	346
Typhaceae A.L. Jussieu (1789)	349
Superorder Zingiberiflorae	350
Order Zingiberales	352
Lowiaceae Ridley (1924)	352
Musaceae A.L. Jussieu (1789)	353
Heliconiaceae T. Nakai (1941)	356

Strelitziaceae Hutchinson (1934)	358
Zingiberaceae Lindley (1835)	360
Costaceae T. Nakai (1941)	365
Cannaceae A.L. Jussieu (1789)	367
Marantaceae Petersen in Engler & Prantl (1888)	369
Superorder Commeliniflorae	374
Order Commelinales	378
Commelinaceae R. Brown (1810)	381
Mayacaceae Kunth (1842). By R.B. FADEN	387
Xyridaceae C.A. Agardh (1823)	388
Rapateaceae Dumortier (1829)	391
Eriocaulaceae Desvaux (1828)	395
Order Hydatellales	398
Hydatellaceae U. Hamann (1976)	400
Order Cyperales	401
Juncaceae A.L. Jussieu (1789)	403
Thurniaceae Engler (1907)	407
Cyperaceae A.L. Jussieu (1789)	407
Order Poales	419
Flagellariaceae Dumortier (1829)	422
Joinvilleaceae D.F. Cutler & Airy Shaw (1965)	425
Poaceae Barnhart (1895)	425
Ecdeiocoleaceae D.F. Cutler & Airy Shaw (1965)	453
Anarthriaceae D.F. Cutler & Airy Shaw (1965)	453
Restionaceae R. Brown (1810)	455
Centrolepidaceae S.L. Endlicher (1836)	458
Superorder Cyclanthiflorae	461
Order Cyclanthales	463
Cyclanthaceae Dumortier (1829)	463
Superorder Areciflorae. In Cooperation with K. JAKOBSEN	467
Order Arecales	471
Arecaceae C.H. Schultz-Schultzenstein (1832)	471
Superorder Pandaniflorae. In Cooperation with K. JAKOBSEN	480
Order Pandanales	482
Pandanaceae R. Brown (1810)	482
References	486
Index of Names	503

Les monopétales régulières constituent moins une famille qu'une grande nation dans laquelle on compte plusieurs familles bien distinctes; en sorte que pour les comprendre toutes sous une indication commune, il faut employer des caractères si généraux et si vagues que c'est paraître dire quelque chose en ne disant en effet presque rien du tout. Il vaut mieux se renfermer dans des bornes plus étroites, mais qu'on puisse assigner avec plus de précision.

J.-J. ROUSSEAU
Lettres sur la botanique. Lettre IV
19e Juin 1772.

The regular monopetals constitute less a family than a great nation in which one may recognize several quite distinct families; so that in order to describe them under a common heading, it is necessary to employ characters so general and so vague that the heading when it appears to say something is saying in effect almost nothing at all. It would be better to restrict oneself within narrower boundaries that can be delimited with greater precision.

Introduction

In this book we present an integrated account of the monocotyledons. We have attempted to decide whether the character states of the monocotyledons as a whole, and those of their constituent groups, are primitive or derived. On the basis of these considerations, and with the use of some justifiable general assumptions, we present some evolutionary models in accordance with DAHLGREN and RASMUSSEN (1983). In doing this we use the elementary terms currently employed by the school of cladistics. Many of the character states and their distributions are presented in greater detail by DAHLGREN and CLIFFORD (1982).

The major part of the book is taken up by our classification of the monocotyledons, which is synthetic in the sense that it uses data of many different kinds and evolutionary in the sense that the evolutionary model is given as much weight as possible. The classification is sufficiently practical, we believe, for use in the herbarium and in the field, though for the latter assistance from artificial diagnostic keys will be required as well. Our orders and families are generally rather narrow and the families, consequently, are numerous, especially in Asparagales. Keys to the families of each order have therefore been provided.

We believe that a concept of Amaryllidaceae, for example, which includes Amaryllidaceae sensu stricto, Ixioliriaceae, Agavaceae, pro parte, and, perhaps, Alstroemeriaceae, is of no help to the botanist seeking to recognise natural and comprehensible groups, and that it will prevent him from understanding the evolutionary pathways within and around the family. Again, it is certainly of no advantage to unite Liliaceae, as circumscribed here, with Asphodelaceae, Hypoxidaceae, Tecophilaeaceae, and Trilliaceae, if at the same time the Liliaceae are kept distinct from Orchidaceae, Alstroemeriaceae or Iridaceae.

It has been our intention to avoid the constraints of convention and to adopt an unbiased approach, using as wide a range of data as we could within the limitations of time (self-imposed), resources and competence.

Morphological Concepts

The following short explanations of terms refer to the monocotyledons only and are not meant to be general definitions. They apply primarily to the concepts used in the chapters on character states and their distributions and in the taxonomic section of the book.

Underground Parts

In monocotyledons the first root formed on the embryo, the radicle, is ephemeral and sometimes hardly distinguishable. The root system arises from the basal nodes of erect shoots or from any node in prostrate shoots. Roots produced by aerial shoots may be green and assimilatory (as are the roots of epiphytic orchids and aroids) or may form massive props, as in *Pandanus* and some palms.

Some of the cells of the root epidermis send out *root hairs*. These root-hair epidermal cells may resemble other epidermal cells of the root, but in some groups they are conspicuously shorter and are called *root-hair short cells* (Fig. 27).

The roots in some groups of monocotyledons are fusiform or tuber-like; these contain nutrients and function as *storage roots*.

The underground stem, when well-developed, may be a rhizome, corm or tuber. It is often elongate, and either horizontal or vertical, and then forms a *rhizome*; plants with a rhizome are described as *rhizomatous*. A short, compact underground stem filled with nutrients is a *corm*, which is synonymous with *rhizomatous tuber*. The corm axis generally extends over several internodes. It may be enclosed by a *tunic* of dry leaves or leaf bases which sometimes form a characteristically sculptured fibrous envelope; such tubers are called *tunicated corms* (Fig. 117B), and are particularly common in Iridaceae. Part of the underground stem may become inflated to form a globose storage organ and is then called a *tuber*. Frequently, as in many Dioscoreales and Arales, the tuber seems to be chiefly made up of the axis immediately below the cotyledon, the *hypocotyl*, and is then termed a *hypocotylar tuber*.

A *bulb* is defined as a short, often plate-like stem bearing a number of thick, fleshy leaves or leaf bases, which store water and nutrients; these are *bulb scales*. The bulb scales may vary from one to many, as in the Liliaceae s.str.

(*Pseudobulbs*, as found in many orchids, are dilated parts of the aerial stem that store water and nutrients. They are corms rather than bulbs.)

Velamen is a water-storing tissue in the outer layers of some roots. It has a parchment-like appearance and consists of one to several layers of non-living cells with thickened and lamellate cell walls. *Velamen* is particularly common in epiphytic orchids and aroids, but is also found in the roots of many other monocotyledons, in particular in the Liliiflorae (see BARTHOLOTT 1976a).

The Aerial Stem

Branching is *monopodial* when the shoot grows apically, the main shoot generally exceeding the lateral ones in length. It is *sympodial* when axillary branches successively take over the growth, as when the main shoot develops into an inflorescence or tendril, or dies off. A *sympodium* is a sequence of such lateral shoots which successively overtake their predecessors (Fig. 52A).

In most monocotyledons the aerial stem is herbaceous, i.e. soft, usually green, and withering within a limited time; in other groups it becomes strengthened with lignin fibres and may be provided with bark. In some groups it becomes conspicuously thick and long-lived, as in palms and pandans, neither of which, however, has secondary thickening. In other groups the stems are lignified but slender, and these plants are genuine shrubs; they are common among the berry-fruited Asparagales.

In only a few families does *secondary thickening* occur, and this is of a kind different from that found in dicotyledons, as explained on p. 45. Most of these plants have a thick woody trunk.

The stems in a great many groups are hairy (see below) but thorns and spines are rare, being found in *Smilacaceae* and *Petermanniaceae*. The stems are climbing (*scandent*) in both of these families as well as in *Dioscoreaceae* and some other groups.

Anatomical Concepts (Leaf and Stem)

The vascular tissue is mainly in the form of primary vascular strands that consist of *xylem* (with tracheids and/or vessels, see below), and *phloem*, which consists mainly of sieve tubes and their companion cells.

Although the vascular strands in monocotyledons initially arise in a single ring, secondary bundles soon develop so that the strands appear “*scattered*”. No cambium is formed between the phloem and xylem where it is present in most dicotyledons. Such an organization of vascular strands is called an *atactostele*, and the condition *atactostely*. It is contrasted with the condition of *eustely*, found in dicotyledons. There, a single ring of primary vascular strands is formed. Then a cambium develops within and between strands, producing xylem on the inside and phloem on the outside, so that a cylinder of secondary tissue is produced, an *eustele*. Where secondary tissue occurs in monocotyledons a meristematic tissue produces new sets of isolated vascular strands outside those first produced.

The *xylem* consists of *tracheids* or tracheids and vessels. The former are elongate living cells, the cavities of which are without direct contact with one another. *Vessels* begin as living cells which are produced in continuous rows; they die, and acquire direct connections by means of *perforations* in the end walls, the *perforation plates*. The end walls in narrow vessels are oblique and have a row of transverse, narrow, slit-like perforations, separated by “bars”, so-called *scalariform perforation*; but wider vessels, when present, have a less oblique, or even transverse, perforation plate with only a few perforations or one *simple*, circular *perforation*. Roots, rhizomes, aerial stems and leaves frequently differ in the type of xylem which they contain.

The sieve tubes of the phloem contain small *plastids* (leucoplasts). These may store starch and/or protein. The occurrence of protein [as compact bodies (*crystalloids*) or as an annular structure of thin filaments] and starch characterizes different groups of angiosperms. All monocotyledons have a number of triangular (*cuneate*) protein crystalloids in their plastids; a few also have starch and some have filaments. According to BEHNKE (1981), who has studied these structures, the monocotyledonous sieve tube plastids are of the PIIc Type (P = protein, II = type 2 according to BEHNKE, l. c., c = cuneate), with PIIcs and PIIcf representing

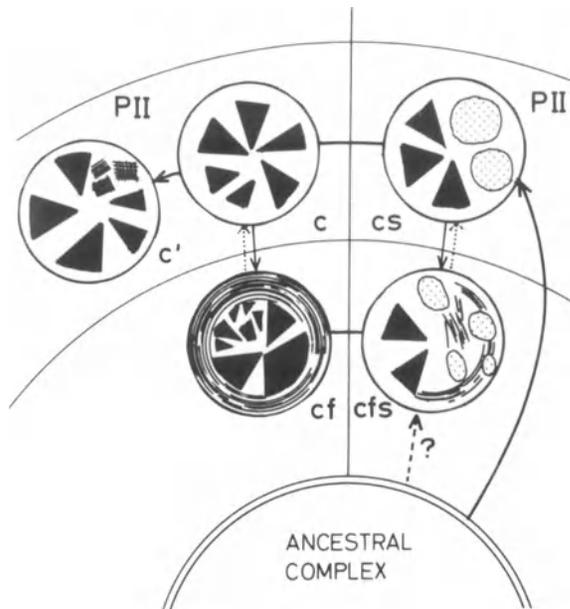


Fig. 1. Sieve tube plastids in monocotyledons and their presumed evolution, according to BEHNKE (1981 a). The forms with cuneate protein crystalloids are called *PIIc* (=cuneate). Protein filaments (*f*) are found in certain monocotyledons (*PIIcf*) and in some there are starch grains (*s*) as well as the protein crystalloids (*PIIcs*). Sometimes other protein crystalloids (*c'*) are found beside the normal cuneate ones.

forms with starch and filamentous protein respectively (Fig. 1).

Laticifers are tubes or rows of elongate cells, containing a fluid of a somewhat milky appearance, in the monocotyledons only rarely coloured (as in *Dilatris* of Haemodoraceae).

Crystals of calcium oxalate occur in monocotyledons rather frequently, most commonly as *raphides*, i.e. bundles of thin crystalline needles (Fig. 28), which are contained in cells filled with mucilage. These cells may be almost isodiametric, but sometimes are elongated ("sacs") or form narrow tubes ("*raphide vessels*"). In some groups oxalate occurs in the form of thicker solitary needles, so-called *styloids* (*pseudoraphides*), which occur in *suberized* (*cork*) cells. These are known in Pontederiaceae and Philydraceae, where raphides are rare, and in Nolinaceae, Phormiaceae and Agavaceae, where raphides are lacking.

Silica is deposited in several major groups of monocotyledons, either as numerous small granules (*silica sand*) or as larger bodies of various sizes and shapes. These shapes are described on p. 63. The silica bodies are often deposited in special short epidermal cells, *silica short cells*.

Stomata (sing. *stoma*) are epidermal structures composed of two *guard cells* embracing a pore

through which gas exchange takes place. The stomata may be surrounded by normal epidermal cells and are then *anomocytic*, but frequently they are surrounded by two or more cells differing in size and shape from other epidermal cells; these are called *subsidiary cells*. A stoma and its subsidiary cells make up the *stomatal complex*. When there are two subsidiary cells, one alongside each guard cell, as in many monocotyledons, the stoma is *paracytic*; when there are four or six subsidiary cells surrounding the guard cells the stoma is *tetracytic* or *hexacytic* respectively. As will be explained in the chapter on Distribution of Character Conditions the *ontogeny*, i.e. the individual development, of the stoma and the origin of the subsidiary cells is not always reflected in the appearance of the mature stomatal complex; a special terminology covering this situation is given in that chapter.

Trichomes are processes arising from the epidermis (hairs etc.). The hairs may be unicellular, i.e. comprise extensions of epidermal cells, but more often consist of a single row of cells. Sometimes, as in Bromeliaceae (Fig. 154I), the trichomes have a short row of cells at the base and are branched above to form a stellate (star-shaped) or peltate (shield-shaped) head. Some peltate hairs are of importance for water uptake. Multicellular hairs with a broad multicellular base occur on the leaf margins of *Luzula* (Juncaceae). *Microhairs* are small, generally bicellular thin-walled hairs found mainly in grasses (Fig. 193J–O). *Glandular hairs* are hairs where one or more cells, generally at the end of the hair, are enlarged and secretory.

Intravaginal squamules, here interpreted as trichomes, are non-vascularized multicellular processes situated in the leaf axils. They generally secrete mucilage, which is thought to protect the axils from micro-organisms (TOMLINSON 1982).

Epicuticular wax is wax secreted on the outer surface of the epidermis. It is frequently sculptured in different ways, typical of the main groups of monocotyledons (BARTHLOTT and FRÖHLICH 1983). See also the chapter on Distribution of Character Conditions.

Leaves

The arrangement of the leaves on the stem is called *phyllotaxy*. When three or more leaves are placed at the same level, they are said to be *whorled* (*verticillate*), when in pairs they are *opposite* and when solitary *alternate*. Where successive pairs of oppo-

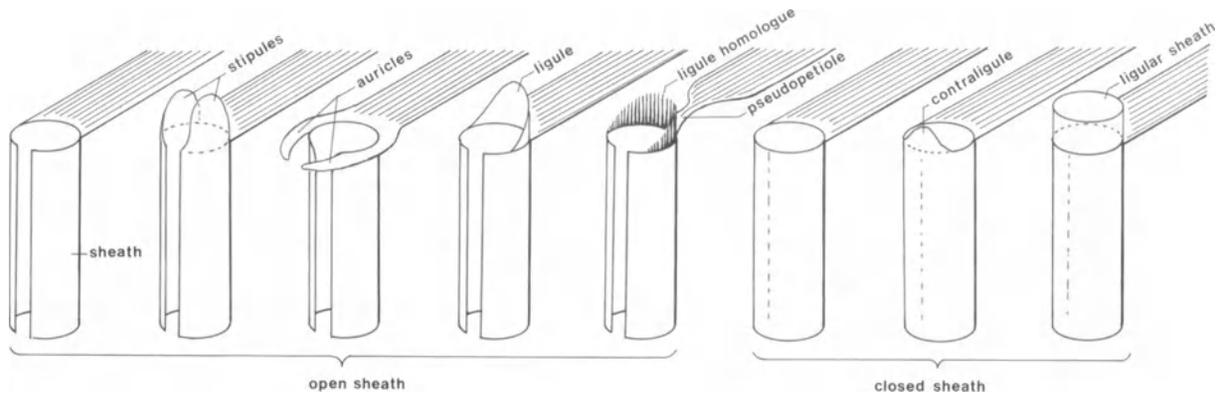
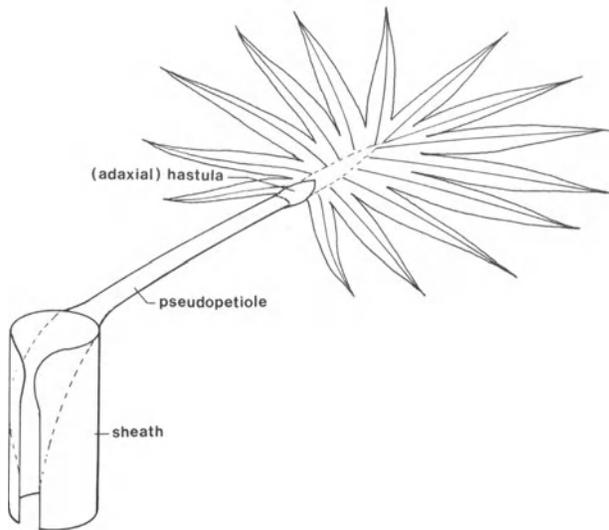


Fig. 2. Terms used for the bases of (chiefly grass) leaves (above) and for a palm leaf (below). (Orig. B. JOHNSEN)



site leaves are set at an angle of 90° to their predecessors the leaves are called *decussate*. The points of attachment of successive solitary (alternate) leaves form a spiral, the angle between successive leaves often being constant. When the angle is 180° , i.e. two leaves to a revolution, they are *distichous* (standing in two rows), and when it is 120° , i.e. three to a revolution, *tristichous* (standing in three rows).

The leaves of some monocotyledons, e.g. *Dioscorea*, are differentiated into a short *leaf base*, a distinct *petiole* and a *blade (lamina)*. However, the leaf base more often encloses the stem completely and forms a *sheath* of variable length which can be *open*, the two margins of the sheath being free, or *closed*, when the margins are fused with each other. Regardless of whether it is sheathing or not, the leaf base may be extended into *lateral lobes* or *stipules*. The base of a linear leaf, or leaf blade in the case of a leaf with a sheath, may be prolonged on either side of the stem as a lobe, the *auricle (ear)*. The stipules may be displaced into the leaf axil to form a *stipular sheath*, as in many

Potamogetonaceae. The homology of stipule-like structures is not in every case established, for example, hyaline extensions and stipular lobes (as in *Joinvillea* and *Juncus* species) which are always lateral on the leaf near its base. A *ligule* is a hyaline extension of the leaf sheath on the adaxial side of the leaf; it is typical of most grasses but is also known in Pontederiaceae. A *contraligule* is an extension of the leaf sheath on the side opposite the lamina. It occurs in the palms, grasses (Fig. 2) and sedges. The *hastula* found in palms is at the distal end of the pseudopetiole, but somewhat resembles the ligule of the grasses. (See Fig. 2.)

A true petiole is present only in certain groups of monocotyledons. In other groups the leaves are linear and there is no differentiation at all between petiole and lamina. Some regard such leaves as *phyllodial*, consisting of a flattened petiole only, but it may be more correct to interpret them as the result of a particular mode of development of the leaf meristem. However, even these leaves are frequently differentiated secondarily into a narrower proximal part, a *pseudo-petiole*, and a broader distal part. In certain bamboos and other grasses and in palms, the pseudo-petiole may be long and clearly delimited.

When the leaf is differentiated into a distinct petiole and lamina, as in some Dioscoreales and Arales, the lamina may be lobed or even *compound*. *Pseudo-compound* leaves are leaves which when initiated are simple, but which in the course of development split along the nerves to become "compound", as in many palms and Cyclanthales. In Musaceae and some other families, simple leaves may become torn so as to appear compound. The leaf margins in monocotyledons are typically entire, but in some, mostly succulent species they

are *serrate*, or beset with *spines* (*Aloë*, *Agave*, many genera of Bromeliaceae).

When distichous, the leaves, or their basal parts only, are sometimes strongly compressed from the sides and their adaxial surface (i.e. that facing the stem) merely forms a groove basally which acts as a sheath and is obliterated above. Such leaves are described as *ensiform* or *unifacial*, in contrast to the horizontally flat and *bifacial* normal leaves. They occur in several families, e.g. Iridaceae, Orchidaceae and Haemodoraceae.

In a few taxa the leaves are twisted through 180° at the base so that the morphologically abaxial side is adaxial; we refer to this condition as “*reversed leaf blades*” (it is sometimes called *resupinate*).

The terminology of the shape of the leaves follows general botanical practice.

Ptyxis is a term that refers to the folding or rolling of individual leaves in the bud stage. Types of ptyxis in monocotyledons are the *conduplicate*, *conduplicate-plicate*, *plicate*, *involute*, *supervolute*, and *explicative*. (Ptyxis is sometimes included in *vernation*, a term which covers the arrangement of parts in a bud with respect to each other).

Venation in monocotyledons is generally *acrodromous*, i.e. with longitudinal parallel or arched veins, converging at the apex, whereas the veins in many of the primitive dicotyledons are *camptodromous-brochidodromous*, with a midvein and, arising from it, lateral veins each of which is arched to meet the one arising next above it (see HICKEY and WOLFE 1975). In leaves with a broad blade a minor, reticulate, vein system is intercalated between the main veins.

Cataphylls are scale-like leaves similar to the sheath of a foliage leaf. They may be present at the base of the shoot and as the first leaves (scales) of lateral branches, especially those of the inflorescence.

The shoot may continue into an inflorescence, or the inflorescence may be distinctly separated from the vegetative part, especially where there is a *leaf rosette*, and the inflorescences are borne each on a leafless peduncle. A *peduncle* arising from a basal rosette is known as a *scape* and the plant (or inflorescence) is described as *scapose*, a condition found in Hyacinthaceae and Amaryllidaceae, for example.

The Inflorescence

Inflorescences are floriferous branch systems more or less distinctly delimited from the vegetative part of the plant. Inflorescences can be divided into *determinate* (closed), where the primary axis is terminated by a flower, and *indeterminate* (open), where the axis does not terminate in a flower.

Flowers of determinate inflorescences are normally actinomorphic, whereas indeterminate inflorescences can have either actinomorphic or zygomorphic (or even asymmetric) flowers (see below, Floral Symmetry).

Determinate inflorescences may be divided into panicles and cymes. In *panicles* there are lateral flowers, and branches terminated by flowers, at several levels below the terminal flower (as in *Tri-cyrtis*). Panicles may be many-flowered and complex or few-flowered. The panicle concept is also used for grasses, where the flowers are substituted by spikelets (which are indeterminate units). Panicles may be distally expanded and more or less flat-topped. Where the branches are very dense and the pedicels long this type may be *umbel-like*.

In *cymes*, lateral flowers are borne at only one level below the terminal flower, their stalks (pedicels) arising in the axils of prophylls (bracteoles) on the pedicel of the terminal flower. This process can be repeated indefinitely because every pedicel has its own prophyll(s). The number of flowers arising at the same level greatly affects the appearance of the inflorescence; in the cymes of monocotyledons there is generally only one, which makes the cyme a *monochasium*. As the prophyll subtending it is generally on that side of the pedicel which faces the preceding flower (the *adaxial* side) the cyme forms a zigzag and this is called a *rhipidium*. Where the prophyll and its axillary flower are not strictly adaxial the monochasium may resemble a *bostryx* (*helicoid cyme*). A bostryx in the strict sense results when each pedicel arises in the axil of a lateral prophyll (i.e. one set at right angles to the preceding one) and the direction of rotation is always the same. The umbel-like inflorescence of Alliaceae and Amaryllidaceae is probably derived, by condensation, from this type of cyme. Sometimes, each new flower emerges in the axil of an *abaxially* (opposite to adaxially) placed bracteole, resulting in a *drepanium*, a rare type of inflorescence (in some Juncaceae).

Indeterminate inflorescences may be divided into *thyrses*, where the pedicels of lateral flowers bear

new flowers in the axils of their bracteoles (these lateral components are thus lateral cymes), and *racemose inflorescences (botrya)* where this is not so. The latter are classified according to the length and thickness of the main axis and the length of the pedicels: *racemes* have a long inflorescence axis and long pedicels, *umbels* have a short inflorescence axis and long pedicels, *spikes* have a long, slender inflorescence axis and very short pedicels or none, *spadices* (sing. *spadix*) have a long fleshy inflorescence axis and very short pedicels or none and *capitula (heads)* have a short inflorescence axis, and very short pedicels or none.

The inflorescences of many monocotyledons are extremely complicated, and painstaking analyses may be necessary to reveal their true nature. Thus the superficially simple “spike” or “spadix” of *Typha* and the “head” of *Sparganium* have proved to be complex, branched inflorescences (D. MÜLLER-DOBLIES 1968 and U. MÜLLER-DOBLIES 1969, respectively). The asymmetric flowers of Marantaceae are aggregated into complex thyrses (ANDERSSON 1976, 1981), and the dense “fascicles” of *Bobartia*, Iridaceae, into complex panicles (DAHLGREN, unpublished).

The Flower

The flower is situated in the axil of a *subtending leaf or bract*. It consists of a *pedicel* (flower-stalk), which usually bears a *prophyll (bracteole)* on the adaxial side (i.e. the side opposite the subtending leaf and towards the parent axis). In the monocotyledons the prophyll is frequently two-ribbed, suggesting that it may have arisen by conrescence of two lateral prophylls (such as are present in most dicotyledons). Flower buds may also develop in the axil of the prophyll, as in cymose inflorescences. Rarely two or more prophylls are present on the pedicel.

The pedicel terminates in the *floral axis (receptacle)*, on which the *tepals (perianth)*, *stamens (androecium)* and *pistil(s) (gynoecium)* are inserted.

The flower is termed *complete* when perianth, stamens and pistil(s) are all present, *incomplete* if any of these parts are missing. It may be *bisexual (perfect, hermaphrodite)*, having both stamens and pistil(s), or *unisexual (imperfect)*, when it lacks either stamens or pistil(s). Species with unisexual flowers may be either *dioecious*, with *pistillate (female)* flowers and *staminate (male)* flowers on sep-

arate plants, or *monoecious*, with both kinds of flowers occurring on the same plant. *Sterile (neuter)* flowers lack both functional stamens and functional pistil(s); such flowers are often specialized for the attraction of pollinators.

In connection with the symmetry of the flower the concepts of the median and transverse planes are used. The *median plane* of a lateral flower is that falling through both the inflorescence axis and the pedicel and main axis of the flower. The *transverse plane* of a lateral flower is that cutting the floral axis at right angles to the median plane. Neither of these terms can be applied to a flower that is terminal on the inflorescence axis.

A flower is *actinomorphic (polysymmetric, radially symmetric, “regular”)* when three or more planes of symmetry (giving mirror images) can be placed through it. It is *bisymmetric* when two planes of symmetry can be placed through it, and *zygomorphic (monosymmetric)* when only one plane of symmetry can be placed through it. The zygomorphic flowers of monocotyledons always have a median plane of symmetry. The twisting of the pedicel or ovary through 180°, inverting the flower, is called *resupination*; it occurs in several groups and is prevalent in orchids. *Asymmetric (irregular)* flowers have no planes of symmetry at all (examples: Cannaceae, Marantaceae).

When describing a lateral flower, the lower side, which faces away from the inflorescence axis, is described as *abaxial*, and the upper, facing towards the inflorescence axis, as *adaxial*. These terms are also used to describe respectively the outer and inner sides of floral parts in relation to the floral axis (i.e. the centre of the flower).

Floral diagrams are constructed to illustrate and compare, in a uniform and schematic manner, the (transverse) plans of flowers. The floral components are placed in the diagram in such an order that the lowest and/or outermost parts are on the periphery and the uppermost/inner parts are in the centre (i.e. in the order bracteoles-tepals-stamens-pistils). It is usual to employ standard symbols for homologous parts. *Empirical floral diagrams* are those in which the components of the flower are shown in their position without any attempt at interpretation, whereas *theoretical floral diagrams* involve an interpretation, for instance they may indicate supposedly lost parts by crosses, and divisions and fusions by other suitable symbols.

The Floral Axis

The floral axis (receptacle) in monocotyledons (see above, The Flower) is generally not strongly developed. Thus a *floral disc*, i.e. a disc-shaped or annular process developed from the receptacle, is extremely rare, whereas in dicotyledons this structure is common and often functions as a nectary. In dicotyledons the receptacle is also frequently urceolate, but urceolate structures of monocotyledon flowers are mainly formed by the fused tepals (and stamens). See below under perigyny.

Numerical Conditions and Insertion of the Components of the Flower

A flower is described as *cyclic* when all the organs of the same type are in whorls (for *whorled*, see above, Leaves). This is the condition in perhaps all monocotyledons, whereas in many dicotyledons all or some of the floral parts are *spirally* set, the flowers being *acyclic* or *hemicyclic* respectively.

The number of whorls of floral parts (prophylls excluded) in the flower is indicated by the terms *pentacyclic* (with five whorls, which is a common and probably ancestral state in monocotyledons), *tetracyclic* (with four whorls; as when one whorl of stamens is lacking), *tricyclic* (with three whorls), etc.

A whorl of floral parts is classified according to its number of components (*merism*, *merous condition*). Thus nearly all monocotyledons are *trimerous* (parts in threes), but some are *dimerous* (parts in twos), or *tetramerous* (parts in fours).

According to the position of the tepals and stamens in relation to the ovary of the pistil (or the pistils), distinction is made between *hypogynous* flowers, where tepals and stamens arise from the floral axis “below the gynoecium”, and *epigynous* flowers, where these parts arise above the ovary, “on the gynoecium”, their basal parts being then fused with the pistil wall, taking part in the formation of the wall of the ovary and fruit. More rarely the flowers are *hemi-epigynous*, having the tepals and stamens inserted halfway up the ovary. *Perigynous* flowers, where there is a cup-shaped dilation of the receptacle, free from but surrounding the ovary or part of it, are common in some groups of dicotyledons but are strictly speaking not found in monocotyledons.

The Perianth

The *perianth* (*perigone*) represents the floral envelope and consists of *floral* (*perigonal*) *leaves* (*tepals*). In most monocotyledons the perianth consists of two whorls of tepals which are either similar or dissimilar. Even when dissimilar they are often not readily divisible into outer green *sepals*, and inner contrastingly coloured *petals*, though this is so in some groups (taxa of Alismatales, Bromeliales, Commelinales, etc.). When green and sepal-like the tepals are described as *sepaloid*, and when of a colour other than green (white or bright colours) as *petaloid*. In dicotyledons the sepals are often collectively termed the *calyx* and the petals the *corolla*, and this is also possible in monocotyledons showing this kind of differentiation, but we shall not follow this usage here.

When the tepals in the two whorls differ conspicuously the perianth is termed *heterochlamydeous*.

Flowers in which the tepals are fused are called *syntepalous*, and the condition *syntepaly*. Tepals are often fused to form relatively narrow *floral tubes*. The tepals may taper basally into a stalk and are then described as *clawed* (*unguiculate*), a rare condition in monocotyledons.

Some or all of the tepals may be provided basally with a nectary known as a *perigonal nectary*. The nectarial area is sometimes recessed to form a *pouch* or *spur* (Fig. 108H and N).

A median *labellum*, or lip petal, is present in some families. This is so in Orchidaceae, where it is the median, upper tepal of the inner whorl (though the flowers are usually resupinated), and in Zingiberaceae and Costaceae, where it consists of the two lower petaloid staminodes of the inner staminal whorl fused together. Though non-homologous, the labellum in each group has a similar function, namely as a landing place for pollen vectors.

When tepals are lacking the flowers are described as *atepalous* (*naked*) or, when the loss of the tepals is obvious, *apochlamydeous*.

The *paracorolla* (*corona*) is a structure derived from appendages of stamens or tepals as, for example, in Amaryllidaceae and Velloziaceae.

The Androecium

Androecium is the collective term for the stamens and stamen homologues (i.e. also staminodes, see below). By definition, stamens are the floral structures that carry *microsporangia* in which the *microspores* are formed and subsequently develop into *pollen grains*.

Diplostemonous flowers, where two whorls of stamens are present (*diplostemony*), are here considered to be the ancestral state in the monocotyledons. Flowers with only one whorl of stamens are *haplostemonous*, the condition, *haplostemony*, being assumed to have resulted from loss of either the outer or the inner staminal whorl.

Stamens are numerous in several groups of monocotyledons, presumably by secondary multiplication (“*dédoublément*”), and the androecium is then described as *multistaminate* or *pleiomerous*.

The stamens consist of a generally slender stalk, the *filament*, and an *anther*. The anther consists of the *connective*, which is the continuation of the filament, and two *thecae*, each of which consists of two *microsporangia* (*locules*, *pollen sacs*). Rarely, by reduction, the anthers have only one theca and are called *monothealous*, or have thecae that consist of only one microsporangium which are called *unisporangiate*.

In some monocotyledons, e.g. many Dioscoreales, the stamens are flat and somewhat leaf-like, and in some members of this order as well as many others, the microsporangia are attached below the apex, which is then often described as a *connective tip* or *appendage*. In these kinds of stamens the anthers are not clearly set off from the filament and may be described as “*undifferentiated*” (SCHAEPP 1931). Where the anther is attached at its base to the filament it is described as *basifixed* (*impeltate*). Basifixed anthers are called *sagittate* when the thecae are lobate and divergent from the connective at the base; otherwise they are *non-sagittate*. The anthers are described as *dorsifixed* (*peltate*) where the anther with its connective extends below its point of attachment, which is thus located somewhere along the mid-line of the anther. Peltate anthers can be divided into *epipeltate* when the part of the anther that is prolonged downwards beyond the attachment point of the filament faces *inwards*, and *hypopeltate* when this part faces outwards in relation to the centre of the flower. These two types have somewhat different distributions, the former being common in Liliales, the latter in Asparagales (HUBER 1969). (See Fig. 3.)

According to the position of the microsporangia in relation to the connective, the anthers can be divided into *introrse*, facing towards the centre of the flower, *extrorse*, facing away from the centre of the flower, and *latrorse*, facing laterally. Generally these are also the directions in which the microsporangia empty their pollen, which they do through longitudinal slits. In some groups, however, they dehisce by one, two or four apical pores and are then called *poricidal*; in these it is still possible to determine whether they are introrse or extrorse. When the anthers dehisce by longitudinal slits, the wall separating the two microsporangia of each theca has generally broken down beforehand, so that only a single line of splitting is required to open each theca.

In some monocotyledon flowers the filaments are laterally fused (connate) at the base to form a *staminal tube*. In male flowers of Araceae the stamens are often totally fused to form a *synandrium*; the fusion of the anthers is termed *synanthery*. Rarely, the filaments are fused with the style to form a *gynostemium* (*column*).

The terminology of the numerous specializations in the flowers of Orchidaceae appears under that family (pp. 255–259 and Figs. 119, 122, 124, 125, 126).

Staminodes are sterile homologues of stamens and may or may not have rudimentary anthers. Staminodes are considered to be derived (in the phylogenetic sense) from functional stamens, and stamens and staminodes together generally do not exceed six in any flower. When they are flat and brightly coloured, as in many Zingiberales, they are known as *petaloid staminodes* (Fig. 169 H).

The Anther Wall and Tapetum

The layers of the microsporangium wall can be classified according to the behaviour of the two parietal cell layers which line the microsporangial epidermis and invest the microsporangogenous tissue. There are four different types, named Basic, Dicotyledonous, Monocotyledonous and Reduced (DAVIS 1966).

The *Basic Type* is not known in monocotyledons and is rare in dicotyledons; it involves one periclinal division of each parietal layer to form four layers in all: an outer layer which becomes the endothecial layer with characteristic wall thickenings (see below), two middle layers and an inner layer which gives rise to the tapetum (see below).

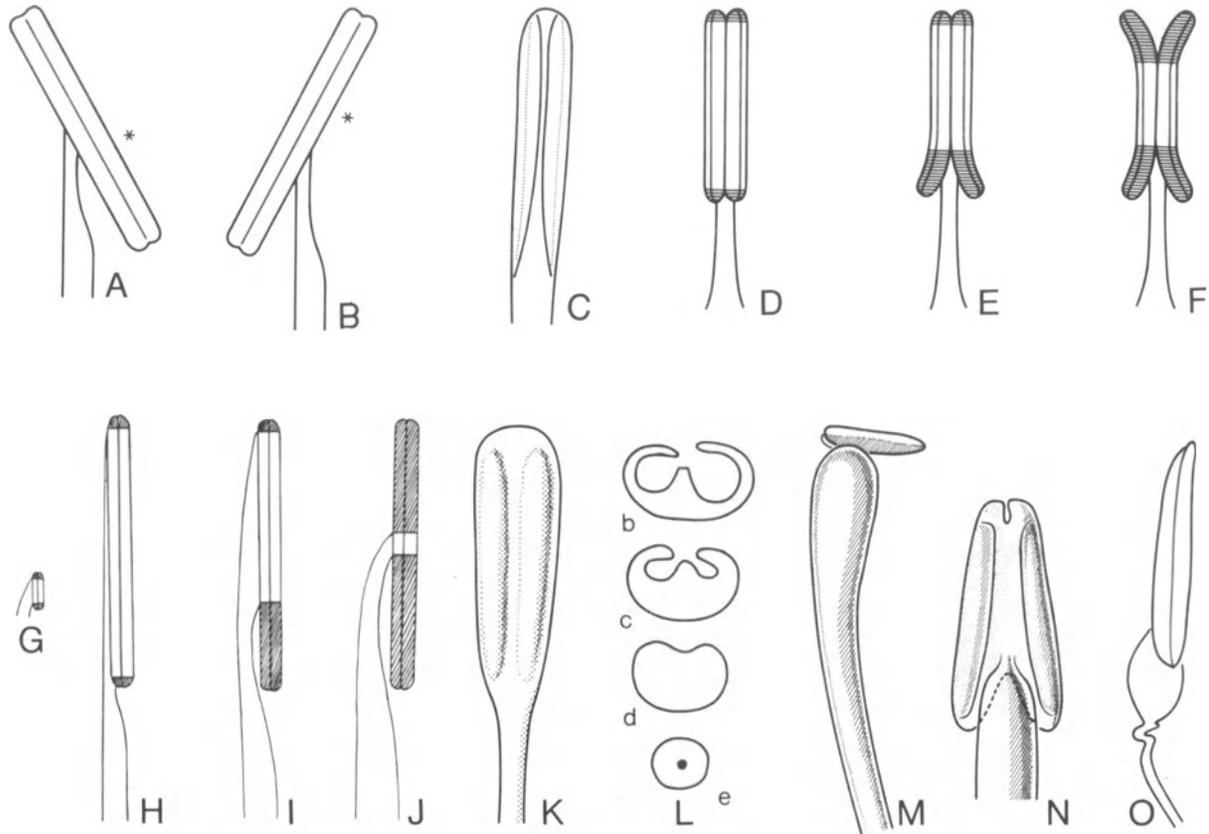


Fig. 3. Stamen characters. **A** and **B** comparison between hypopeltate (**A**) and epipeltate (**B**) anthers, the asterisk (*) representing the morphological upper side. **C** "Undifferentiated" anther. **D** Basifixed, impeltate, non-sagittate anther. **E** Basifixed, impeltate, sagittate anther. **F** Basifixed, impeltate, x-shaped anther. **G–J** Sequence to explain derivation of adnate (**H**), semiadnate (**I**) and dorsifixed (**J**) anther types from an initial (**G**). **K** "Undifferentiated" anther, exemplified by *Sparganium*. **L** Series of transverse sections through an undifferentiated anther, exemplified by *Smilax*. **M–N** Stamens of *Yucca filamentosa*, **M** fully developed in lateral view, **N** in juvenile stage, front view. **O** Anther of *Dianella caerulea*, with filament dilated below anther. (All after SCHAEPPPI 1939; from WEBERLING 1981)

In the *Dicotyledonous Type*, which is known among the monocotyledons only in *Tacca* (?), but is common in dicotyledons, the outer parietal layer divides as in the Basic Type, but the inner becomes the tapetal layer directly, so that there is only one middle layer. In the *Monocotyledonous Type*, which is by far the commonest in monocotyledons,

the *inner* parietal layer divides as in the Basic Type and the outer becomes the endothecium directly, so that again there is only one middle layer. In the *Reduced Type*, finally, neither parietal layer divides and there is no middle layer; the outer forms the endothecium directly and the inner the tapetum. This type is extremely rare in dicotyledons, and in monocotyledons is known only in *Najas* (Najadaceae) and in *Lemna* and *Wolffia* (Lemnaceae).

The *endothecium* is a layer in which the cells are provided with wall thickenings which play a part in the dehiscence of the microsporangial walls. The wall thickenings (DAHLGREN and CLIFFORD 1982) can be divided into two general types, the *Spiral* and the *Girdle* Types.

The *tapetal layer* (*tapetum*) is best developed when the microspores are in the tetrad stage. The tapetum then surrounds the spores and supplies them with nutrients. There are three types of tapetum (1) *secretory* or *glandular*, in which the tapetal cells remain in their initial position but lose their walls