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Classification, Evolution, and Phylogeny of the Families of Monocotyledons

AARON GOLDBERG

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Aaron Goldberg

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ABSTRACT

Goldberg, Aaron. Classification, Evolution, and Phylogeny of the Families of Monocotyledons. *Smithsonian Contributions to Botany,* number 71, 74 pages, 41 figures, 2 tables, 1 diagram, 1989.—To some extent classification is subjective. Taxonomists differ in the relative importance they ascribe to particular characters and in the degree of difference between related taxa they deem sufficient to constitute family or ordinal rank. About 250 monocot family names have been published. Those who have attempted an overview of the system at the family level and above in the last quarter century recognize between 45 and 103 monocot families in 14 to 38 orders. I accept 57 families in 18 orders. In Table 1 I give my ordinal allocation of the families and that of 11 recent authors to indicate where there is agreement and where there are differences to be resolved. I have constructed a dendrogram to suggest relationships and degree of advancement of the orders.

I have written concise, uniform descriptions of all the families of monocots emphasizing those characters that show trends between families or occur in more than one family. Each family is illustrated by analytical drawings of the flower, fruit, seed, and usually inflorescence. Several species are usually used to show the range of major variation within families and trends toward related families.

Monocots and dicots have existed concurrently for most of their history, have been subjected to many of the same ecological pressures, and consequently show similar evolutionary trends. My approach to understanding evolutionary trends in characters is to relate them to the ecological factors that might be responsible for them by their selective action. The monocots probably originated under warm temperate or subtropical conditions favorable for growth. A major evolutionary trend in them has been the gradual development of characters and character states enabling them to cope with dry and hot or cold conditions and colonize generally unfavorable habitats.

A second major trend has been progressively greater specialization for insect pollination. The primitive monocots have flowers with numerous spirally arranged parts; those having flowers with few, opposite or whorled parts are derived.

The floral organs are homologous with leaves. Like leaves the parts were initially separate. The connate and adnate conditions are derived.

General character states are primitive; specialized states are derived. In attempting to determine which primitive states are most primitive I considered their occurrence among the families. The fewer the families with a particular primitive state, the more primitive the state. This is important in deciding whether a family is low or high on the family tree and the position within its particular order.

In accordance with the above rationale, I have constructed a table giving the primitive and derived states for about 85 characters. I also indicate the extent to which I consider the states reversible.

To determine a family's phylogeny, it must be compared with other families considered to be close to it. In general, the more characters and character states in common, particularly uncommon ones, the more likely are the subject families to be related. All parts of the plant and many characters should be considered. If a family has more than one state of a character, the state considered primitive for the particular family should be used in attempting to determine the extant family closest to its ancestor. A descendant has at least one more derived character or character state than its ancestor.

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Contents

Classification, Evolution, and Phylogeny of the Families of Monocotyledons

Aaron Goldberg

Introduction

To some extent classification is subjective. Taxonomists differ in the relative importance they ascribe to particular characters and in the degree of difference between related taxa they deem sufficient to constitute family or ordinal rank. About 250 monocot family names have been published. Those who have attempted an overview of the system at the family level and above in the last quarter century recognize between 45 and 103 monocot families in 14 to 38 orders. I accept 57 families and 18 orders.

In delimiting families and assigning them to orders I rely on many years of study in the National Herbarium and library of the Smithsonian Institution as well as examination of plants in the field and at botanical gardens in various parts of the world. I have examined numerous specimens in all families.

I have written concise, uniform descriptions of all the families of monocots, emphasizing those characters that show trends between families or occur in more than one family. Each family is illustrated by analytical drawings of the flower, fruit, seed and usually inflorescence. At present the only publications in English describing and illustrating all or almost all the monocot families in a single volume are Dahlgren et al. (1985) and Hutchinson (1973). Dahlgren et al. (1985) recognize twice as many families as I do. Hutchinson's concept of taxa is considerably narrower than mine. Also, I believe his Calyciferae and Corolliferae are not natural taxa.

The illustrations have been reproduced as economically as possible for the purpose of illustrating major features; no attempt has been made to represent the detail that would be expected in traditional taxonomic studies published in *Smithsonian Contributions to Botany*. Abbreviations used in the legends are as follows: l.s. = longitudinal section; c.s. = cross section.

Perusal of the references dealing with chemotaxonomy (Gibbs, 1974, and Hegnauer, 1962–1986) indicates how little is known for many of the families, so I did not consider chemical data under the family descriptions. However, under each order I have discussed those chemical data I consider most significant in understanding relationships of the families and occasionally genera.

In Table 1 I give my ordinal allocation of the families and that of 11 authors who have attempted an overview of the system in the last quarter century to indicate where there is agreement and where there are differences to be resolved. In my decisions I have also considered the opinions of 17 earlier generalists, starting with Bentham and Hooker (1862–1883), as well as those authors who have studied particular families.

Other families accepted by the above authors:

Cronquist, 1988. Limnocharitaceae in Alismatales; Ruppiaceae and Cymodoceaceae in Najadales; Petrosaviaceae in Triuridales; Acoraceae in Arales; Joinvilleaceae in Restionales; Hydatellaceae in Hydatellales; Heliconiaceae and Costaceae in Zingiberales; Cyanastraceae, Aloaceae and Hanguanaceae in Liliales; Geosiridaceae in Orchidales.

Takhtajan, 1987. Thalassiaceae and Halophilaceae in Hydrocharitales; Limnocharitaceae in Alismatales; Maundiaceae in Juncaginales; Ruppiaceae in Potamogetonales; Cymodoceaceae in Cymodoceales; Melanthiaceae, Calochortaceae, Geosiridaceae, Tecophilaeaceae, Cyanastraceae, Eriospermaceae, and Medeolaceae in Liliales; Asphodelaceae, Dasypogonaceae, Aphyllanthaceae, Hyacinthaceae, Alliaceae, Hesperocallidaceae, Funkiaceae, Hemerocallidaceae, Phormiaceae, Blanfordiaceae, Doryanthaceae, and Ixioliriaceae in Amaryllidales; Convallariaceae, Ruscaceae, Asparagaceae, Dracaenaceae, Nolinaceae, Herreriaceae, Asteliaceae, and Hanguanaceae in Asparagales; Luzuriagaceae, Petermanniaceae, and Ripogonaceae in

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TABLE 1.—Ordinal allocation of the monocotyledon families by recent authors.

Family	Goldberg	Cronquist 1988	Takhtajan 1987	Thorne 1983	Dahlgren et al. 1985	Hutchinson 1973
Pandan	Pandan	Pandan	Pandan	Pandan	Pandan	Pandan
Alismat	Alismat	Alismat	Alismat	Alismat	Alismat	Alismat
Butom	Alismat	Alismat	Butom	Alismat	Alismat	Butom
Hydrocharit	Alismat	Hydrocharit	Hydrocharit	Alismat	Alismat	Butom
Triurid	Triurid	Triurid	Triurid	Triurid	Triurid	Triurid
Scheuchzeri	Juncagin	Najad	Scheuchzeri	in Juncaginaceae	Najad	Alismat
Juncagin	Juncagin	Najad	Juncagin	Zoster Potamogetonineae	Najad	Juncagin
Lilae	Juncagin	in Juncaginaceae	Juncagin	in Juncaginaceae	in Juncaginaceae	Juncagin
Aponogeton	Najad	Najad	Aponogeton	Zoster Aponogetonineae	Alismat	Aponogeton
Zoster	Najad	Najad	Zoster	Zoster Zosterineae	Najad	Aponogeton
Potamogeton	Najad	Najad	Potamogeton	Zoster Potamogetonineae	Najad	Potamogeton
Zannichelli	Najad	Najad	Cymodoce	Zoster Potamogetonineae	Najad	Najad
Najad	Najad	Najad	Najad	Najad	Najad	Najad
Posidoni	Najad	Najad	Posidoni	Zoster Potamogetonineae	Najad	Juncagin
Junc	Junc	Junc	Junc	Commelin Juncineae	Cyper	Junc
Thurni	Junc	Junc	Junc	in Juncaceae	Cyper	Junc
Centrolepid	Junc	Restion	Restion Restionineae	Commelin Flagellariineae	Po	Junc
Restion	Junc	Restion	Restion Restionineae	Commelin Flagellariineae	Po	Junc
Flagellari	Junc (?)	Restion	Restion Flagellariineae	Commelin Flagellariineae	Po	Commelin
Spargani	Typh	Typh	Typh	in Typhaceae	Typh	Typh
Typh	Typh	Typh	Typh	Typh	Typh	Typh
Cyper	Cyper	Cyper	Cyper	Commelin Juncineae	Cyper	Cyper
Po	Po	Cyper	Po	Commelin Poineae	Po	Gramin
Arec	Arec	Arec	Arec	Arec	Arec	Palm
Cyclanth	Cyclanth	Cyclanth	Cyclanth	Cyclanth	Cyclanth	Cyclanth
Ar	Ar	Ar	Ar	Ar	Ar	Ar
Lemn	Ar	Ar	Ar	Ar	Ar	Ar
Trilli	Lili	in Liliaceae	Dioscore	in Liliaceae	Dioscore	Lili
Lili	Lili	Lili	Lili	Lili Liliineae	Lili	Lili
Smilac	Lili	Lili	Smilac	Lili Dioscoreineae	Dioscore	Lili

TABLE 1.—Continued.

Family	Melchior 1964	Stebbins 1974	Rouleau 1981	Young 1981	Benson 1979	Emberger 1960
Pandan	Pandan	Pandan	Pandan	Pandan	Pandan	Pandan
Alismat	Helobiae Alismatineae	Alismat	Alismat	Alismat	Alismat	Alismat
Butom	Helobiae Alismatineae	Alismat	Alismat	Alismat	Alismat	Alismat
Hydrocharit	Helobiae Hydrocharitineae	Hydrocharit	Hydrocharit	Alismat	Hydrocharit	Alismat
Triurid	Triurid	Triurid	Triurid	Triurid	Triurid	Triurid
Scheuchzeri	Helobiae Scheuchzeriineae	Najad	Najad	Zoster	---	Alismat
Juncagin	Helobiae Potamogetonineae	Najad	Najad	Zoster	Juncagin	Alismat
Lilae	in Juncaginaceae	---	Najad	in Juncaginaceae	Juncagin	Potamogeton
Aponogeton	Helobiae Potamogetonineae	Najad	Najad	Zoster	Naiad	Alismat
Zoster	in Potamogetonaceae	Najad	Najad	Zoster	Naiad	Potamogeton
Potamogeton	Helobiae Potamogetonineae	Najad	Najad	Zoster	---	Potamogeton
Zannichelli	Helobiae Potamogetonineae	Najad	Najad	Zoster	---	Potamogeton
Najad	Helobiae Potamogetonineae	Najad	Najad	Zoster	Naiad	Potamogeton
Posidoni	in Potamogetonaceae	---	Najad	Zoster	---	Potamogeton
Junc	Junc	Junc	Junc	Junc	Lili Juncineae	Junc
Thurni	Junc	Junc	Junc	in Juncaceae	Lili Juncineae	Junc
Centrolepid	Commelin Restionineae	Restion	Restion	Restion	Restion	Commelin
Restion	Commelin Restionineae	Restion	Restion	Restion	Restion	Commelin
Flagellari	Commelin Flagellariineae	Restion	Restion	Restion	Restion	Junc
Spargani	Pandan	Typh	Typh	in Typhaceae	Typh	Pandan
Typh	Pandan	Typh	Typh	Typh	Typh	Pandan
Cyper	Cyper	Cyper	Cyper	Cyper	Gramin	Cyper
Po	Gramin	Po	Po	Po	Gramin	Gramin
Arec	Principes	Arec	Arec	Arec	Palm	Palm
Cyclanth	Synanthae	Cyclanth	Cyclanth	Cyclanth	Ar	Cyclanth
Ar	Spathiflorae	Ar	Ar	Ar	Ar	Ar
Lemn	Spathiflorae	Ar	Ar	Ar	Ar	Ar
Trilli	in Liliaceae	---	Lili	---	---	in Liliaceae
Lili	Liliiflorae Liliineae	Lili	Lili	Lili	Lili Liliineae	Lili
Smilac	in Liliaceae	Lili	Lili	Lili	in Liliaceae	in Liliaceae

TABLE 1.—Continued.

Family	Goldberg	Cronquist 1988	Takhtajan 1987	Thorne 1983	Dahlgren et al. 1985	Hutchinson 1973
Agav	Lili	Lili	Amaryllid	in Liliaceae	Asparag	Agav
Xanthorrhoe	Lili	Lili	Amaryllid	in Liliaceae	Asparag	Agav
Philesi	Lili	in Smilacaceae	Smilac	Lili Dioscoreineae	Asparag	Alstroemeri
Stemon	Lili	Lili	Dioscore	Lili Dioscoreineae	Dioscore	Dioscore
Dioscore	Lili	Lili	Dioscore	Lili Dioscoreineae	Dioscore	Dioscore
Tacc	Lili	Lili	Tacc	Lili Dioscoreineae	Dioscore	Haemodor
Pontederi	Lili	Lili	Pontederi	Commelin Pontederiineae	Pontederi	Lili
Amaryllid	Lili	in Liliaceae	Amaryllid	in Liliaceae	Asparag	Amaryllid
Vellozi	Lili	Lili	Vellozi	Commelin Velloziineae	Vellozi	Haemodor
Bromeli	Bromeli	Bromeli	Bromeli	Commelin Bromeliineae	Bromeli	Bromeli
Commelin	Commelin	Commelin	Commelin Commelinineae	Commelin Commelinineae	Commelin	Commelin
Mayac	Commelin	Commelin	Commelin Commelinineae	Commelin Commelinineae	Commelin	Commelin
Xyrid	Commelin	Commelin	Commelin Xyridineae	Commelin Bromeliineae	Commelin	Xyrid
Rapate	Commelin	Commelin	Commelin Xyridineae	Commelin Bromeliineae	Commelin	Xyrid
Eriocaul	Commelin	Eriocaul	Commelin Eriocaulineae	Commelin Eriocaulineae	Commelin	Eriocaul
Mus	Zingiber	Zingiber	Zingiber	Zingiber Musineae	Zingiber	Zingiber
Strelitzi	Zingiber	Zingiber	Zingiber	Zingiber Musineae	Zingiber	Zingiber
Lowi	Zingiber	Zingiber	Zingiber	Zingiber Musineae	Zingiber	Zingiber
Zingiber	Zingiber	Zingiber	Zingiber	Zingiber Zingiberineae	Zingiber	Zingiber
Cann	Zingiber	Zingiber	Zingiber	Zingiber Zingiberineae	Zingiber	Zingiber
Marant	Zingiber	Zingiber	Zingiber	Zingiber Zingiberineae	Zingiber	Zingiber
Haemodor	Irid	Lili	Haemodor	Commelin Pontederiineae	Haemodor	Haemodor
Philydr	Irid	Lili	Philydr	Commelin Pontederiineae	Philydr	Haemodor
Irid	Irid	Lili	Lili	Lili Iridineae	Lili	Irid
Burmanni	Irid	Orchid	Burmanni	Lili Iridineae	Burmanni	Burmanni
Corsi	Orchid	Orchid	Burmanni	in Burmanniaceae	Burmanni	Burmanni
Orchid	Orchid	Orchid	Orchid	Lili Orchidineae	Lili	Orchid

TABLE 1.—Continued.

Family	Melchior 1964	Stebbins 1974	Rouleau 1981	Young 1981	Benson 1979	Emberger 1960
Agav	Liliiflorae Liliineae	Lili	Lili	Lili	in Liliaceae	in Amaryllidaceae
Xanthorrhoe	Liliiflorae Liliineae	Lili	Lili	Lili	---	in Liliaceae
Philesi	in Liliaceae	---	Lili	---	---	in Liliaceae
Stemon	Liliiflorae Liliineae	Lili	Lili	Dioscore	Lili Liliineae	Lili
Dioscore	Liliiflorae Liliineae	Lili	Lili	Dioscore	Lili Liliineae	Dioscore
Tacc	Liliiflorae Liliineae	Lili	Lili	Dioscore	Lili Liliineae	Dioscore
Pontederi	Liliiflorae Pontederiineae	Lili	Lili	Lili	Lili Liliineae	Pontederi
Amaryllid	Liliiflorae Liliineae	in Liliaceae	Lili	---	in Liliaceae	Lili
Vellozi	Liliiflorae Liliineae	Lili	Lili	Lili	Lili Liliineae	Lili
Bromeli	Bromeli	Bromeli	Bromeli	Bromeli	Lili Commelinineae	Bromeli
Commelin	Commelin Commelinineae	Commelin	Commelin	Commelin	Lili Commelinineae	Commelin
Mayac	Commelin Commelinineae	Commelin	Commelin	Commelin	Lili Commelinineae	Commelin
Xyrid	Commelin Commelinineae	Commelin	Commelin	Commelin	Lili Commelinineae	Commelin
Rapate	Commelin Commelinineae	Commelin	Commelin	Commelin	Lili Commelinineae	Junc
Eriocaul	Commelin Eriocaulineae	Eriocaul	Eriocaul	Eriocaul	Lili Commelinineae	Commelin
Mus	Scitamineae	Zingiber	Zingiber	Zingiber	Mus	Scitamin
Strelitzi	in Musaceae	Zingiber	Zingiber	Zingiber	in Musaceae	Scitamin
Lowi	Scitamineae	Zingiber	Zingiber	Zingiber	---	Scitamin
Zingiber	Scitamineae	Zingiber	Zingiber	Zingiber	Mus	Scitamin
Cann	Scitamineae	Zingiber	Zingiber	Zingiber	Mus	Scitamin
Marant	Scitamineae	Zingiber	Zingiber	Zingiber	Mus	Scitamin
Haemodor	Liliiflorae Liliineae	Lili	Lili	Lili	Lili Liliineae	Lili
Philydr	Liliiflorae Philydrineae	Lili	Lili	Lili	Lili Liliineae	Lili
Irid	Liliiflorae Iridineae	Lili	Irid	Lili	Lili Liliineae	Lili
Burmanni	Liliiflorae Burmanniineae	Orchid	Burmanni	Burmanni	Burmanni	Burmanni
Corsi	Liliiflorae Burmanniineae	Orchid	Burmanni	Burmanni	---	Burmanni
Orchid	Microspermae	Orchid	Orchid	Orchid	Orchid	Orchid

Smilacales; Trichopodaceae and Stenomeridaceae in Dioscoreales; Alstroemeriaceae in Alstroemeriales; Conostylidaceae, and Hypoxidaceae in Haemodorales; Heliconiaceae, and Costaceae in Zingiberales; Hydatellaceae in Hydatellales; Joinvilleaceae, Anarthriaceae, and Ecdeiocoleaceae in Restionales.

Thorne, 1983. Trichopodaceae in Liliales; Cymodoceaceae in Zosterales; Heliconiaceae and Costaceae in Zingiberales.

Dahlgren et al., 1985. Limnocharitaceae in Alismatales; Cymodoceaceae in Najadales; Trichopodaceae and Petermanniaceae in Dioscoreales; Luzuriagaceae, Ruscaceae, Convallariaceae, Asparagaceae, Herreriaceae, Hanguanaceae, Dracaenaceae, Asteliaceae, Nolinaceae, Dasypogonaceae, Blandfordiaceae, Calectasiaceae, Tecophilaeaceae, Ixioliriaceae, Cyanastraceae, Phormiaceae, Doryanthaceae, Eriospermaceae, Asphodelaceae, Anthericaceae, Aphyllanthaceae, Hemerocallidaceae, Funkiaceae, Hyacinthaceae, Alliaceae, and Hypoxidaceae in Asparagales; Colchicaceae, Geosiridaceae, Alstroemeriaceae, Calochortaceae, Uvulariaceae, Apostasiaceae and Cypripediaceae in Liliales; Heliconiaceae and Costaceae in Zingiberales; Hydatellaceae in Hydatellales; Joinvilleaceae, Ecdeiocoleaceae and Anarthriaceae in Poales; Melanthiaceae and Campynemaceae in Melanthiales; Thismiaceae in Burmanniales.

Hutchinson, 1973. Petrosaviaceae in Alismatales; Ruppiaceae in Potamogetonales; Cartonemataceae in Commelinales; Tecophilaeaceae and Ruscaceae in Liliales; Alstroemeriaceae and Petermanniaceae in Alstroemeriales; Stenomeridaceae and Trichopodaceae in Dioscoreales; Hypoxidaceae and Apostasiaceae in Haemodorales; Thismiaceae in Burmanniales.

Melchior, 1964. Cyanastraceae, Hypoxidaceae and Geosiridaceae in Liliiflorae.

Stebbins, 1974. Limnocharitaceae in Alismatales; Ruppiaceae in Najadales; Petrosaviaceae in Triuridales; Heliconiaceae and Costaceae in Zingiberales; Tecophilaeaceae and Cyanastraceae in Liliales; Geosiridaceae in Orchidales.

Rouleau, 1981. Limnocharitaceae in Alismatales; Elodeaceae in Hydrocharitales; Ruppiaceae and Cymodoceaceae in Najadales; Petrosaviaceae, Aphyllanthaceae, Alliaceae, Alstroemeriaceae, Hypoxidaceae, Petermanniaceae, Tecophilaeaceae, Cyanastraceae, Asparagaceae, Ruscaceae, Croomiaceae and Trichopodaceae in Liliales; Geosiridaceae in Iridales; Heliconiaceae and Costaceae in Zingiberales; Apostasiaceae in Orchidales; Cartonemataceae and Abolbodaceae in Commelinales; Anarthriaceae, Ecdeiocoleaceae, Joinvilleaceae and Hanguaniaceae in Restionales; Hydatellaceae in Hydatellales; Anomochloaceae and Streptochaetaceae in Poales; Nypaceae in Arecales.

Young, 1981. Cymodoceaceae in Zosterales; Cyanastraceae, Geosiridaceae, Aloeaceae and Hanguanaceae in Liliales; Joinvilleaceae, Ecdeiocoleaceae and Hydatellaceae in Restionales; Heliconiaceae and Costaceae in Zingiberales.

Benson, 1979. Cyanastraceae in Liliales.

Emberger, 1960. Ruppiaceae in Potamogetonales; Phytelephasiaceae and Nypaceae in Palmales; Cyanastraceae, Geosiridaceae and Petermanniaceae in Liliales; Thismiaceae in Burmanniales; Apostasiaceae in Orchidales.

The bibliography notes publications of several authors who have attempted to improve the system of classification of the monocots at the family level and above in the 19th and 20th centuries. It also mentions authors who have assembled the data dealing with particular characters for most families. Together, these publications contain references to the work of thousands of scientists who have made contributions in particular families. Stafleu and Cowan (1976–1988) and the Kew Record of Taxonomic Literature (Royal Botanic Gardens, Kew, 1974–1988) can also be consulted for relevant literature and Stapf (1929–1931) for illustrations.

Jackson (1928) and Lawrence (1951) can be used to determine the meaning of botanical terms. I use the term pistil to mean a separate female organ. It can consist of one or more carpels. The gynoecium may consist of one or more pistils.

Monocots have been extant nearly as long as dicots, have been subjected to many of the same ecological pressures, and consequently show similar evolutionary trends. Like the dicots, I believe the earliest monocots had wind pollinated unisexual flowers, monosulcate pollen, and lacked vessels. Stewart (1983) and Muller (1981) can be consulted for a summary of the contribution of paleobotany to our understanding of the evolution of the angiosperms.

My approach to understanding evolutionary trends in characters is to relate them to the ecological factors that might be responsible for them by their selective action. A major evolutionary trend has been from wind pollination to progressively better adaptation for insect pollination. Under favorable conditions where most families can survive and members of a species are often widely spaced, insect pollination is more proficient than wind pollination. Many plants developed colorful flowers or bracts, making the flowers easier for insects or other animals to find. Some flowers developed landing platforms for insects. Some became fragrant or malodorous indicating the presence of food to potential pollinators. Some produced nectar which may act as a substitute reward in place of reproductive organs. Access to the reward became more and more restricted, favoring insects with long sucking mouth parts and some flowers became specially adapted to the most proficient pollinators, the bees.

The primitive insect pollinated monocots often have large flowers with numerous spirally arranged parts. They gave rise to plants whose flowers have few, opposite or whorled parts. The proficiency of insects in pollination allows survival with fewer parts.

The monocots probably originated under warm temperate or subtropical conditions favorable for growth. Another major evolutionary trend in them has been the gradual development of characters and character states enabling them to cope with dry and hot or cold conditions, allowing them to colonize generally unfavorable habitats.

An entirely corolloid perianth was supplanted by one in which one series became an herbaceous calyx which provides

greater protection of the reproductive organs against unfavorable climatic conditions, as well as against some predators. Development of perigyny and epigyny also conserved moisture in the reproductive organs. The leaves evolved various conditions of the cuticle, epidermis and vasculature which enable them to resist moisture loss and prevent collapse. Also, in the xylem, tracheids were converted to vessels, scalariform perforation plates became simple and the vessels wider to facilitate rapid movement of water which is only periodically available under some unfavorable conditions.

The floral organs are homologous with leaves. Like leaves the parts were initially separate. The connate and adnate conditions are derived.

General character states are primitive; specialized states are derived. In attempting to determine which primitive states are most primitive I considered their occurrence among the families. The fewer the families showing a particular primitive state the more primitive the state. This is important in deciding whether a family is low or high on the family tree and the position within its particular order.

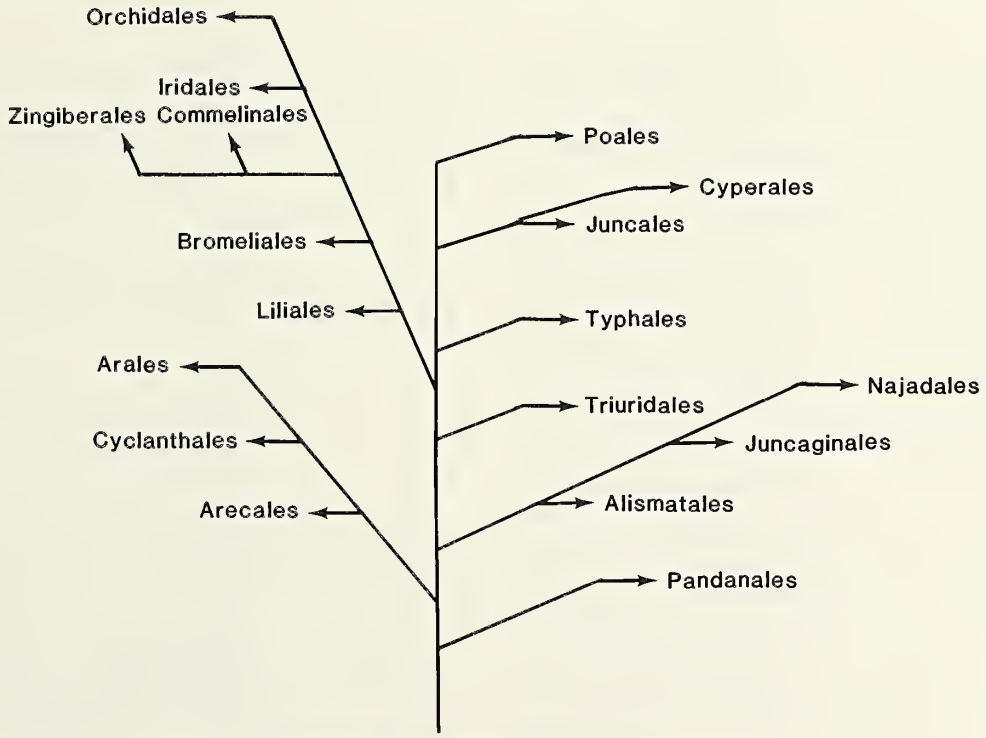
In accordance with the above rationale, I have constructed Table 2 giving the primitive and derived states for about 85 characters. I also indicate the extent to which I consider the states reversible. In general, character states which are most constant within families are least readily reversible. For example flower color is usually variable within families and commonly reversible, whereas connation of parts is much more constant within families and therefore difficult to reverse. The category "n" includes those character states which are practically irreversible.

To determine a family's phylogeny, it must be compared with other families considered to be close to it. In general, the more characters and character states in common, particularly uncommon ones, the more likely are the subject families to be related. All parts of the plant and many characters should be considered.

I agree with those who make a distinction between parallelism and convergence in attempting to determine relationships. The same character or character state may arise more than once in a single family or independently in related families. That is parallelism. If the same character or character state arises in unrelated families it is convergence. Unrelated taxa with one or more convergent characters or character states in common will differ from one another in most respects. I believe convergence is hardly ever prevalent enough to mask relationships.

If a family has more than one state of a character, the state considered primitive for the particular family should be used in attempting to determine the extant family closest to its ancestor. A descendant has at least one more derived character or character state than its ancestor. Collateral relatives differ from one another by having at least one different character from one another that is not in the main line of descent. Genera which are intermediate between families are particularly significant in a phylogenetic study. They are the knots that tie the families together.

I have constructed a dendrogram (below) suggesting relationships of the orders. In this treatise and in my



Suggested phylogenetic relationships of the orders of monocotyledons.

TABLE 2.—Evolutionary trends in the monocotyledons (reversibility: n = not; r = rarely; c = commonly).

Character	Primitive state	Derived state	Reversibility
climate of origin	warm temperate or subtropical	other	r
plant	mesophyte	xerophyte	r
	monoecious or dioecious	hermaphroditic	r
	perennial	annual	r
	autotrophic	saprophytic	n
indument	absent	present	r
	simple	glandular	r
spines	absent	present	r
tendrils	absent	present	r
latex	absent	present	r
xylem vessels	absent	present	n (r in some reduced aquatics ?)
perforations plates	scalariform	simple	n
xylem vessel and sieve tube elements	long, narrow, angular in cross-section	short, wide, round in cross-section	n
	end plate slanting	end plate transverse	n
	pores small	pores large	n
leaves	alternate	opposite or whorled	r
	in more than 2 ranks	distichous	r
	thin	thick and sclerophyllous	r
	medium	small relative to size of plant	r
leaf margin	entire	lobed or toothed	r
leaf venation	open	closed	n
	apparently parallel	obviously reticulate or pinnate	n
stomates	anomocytic	other	n
inflorescence	racemose	cymose	n
	raceme	corymb or spike	n
	spike or umbel	head	n
	open cyme	fascicle	n
flowers	in inflorescence	solitary	r?
	terminal	axillary	c
	unisexual	bisexual	c
	odorless	scented	r?
	green, white, or yellow	other colors	c
	actinomorphic	zygomorphic	n
pollinated by	wind	insects or birds	r
	various pollinators	particular pollinators	r
pollinators	Coleoptera	Hymenoptera, Diptera, or Lepidoptera	r
	short-tongued	long-tongued	n
involucre	absent	present	n
receptacle	convex	flat	n
	flat	concave	n
perianth	monochlamydeous	achlamydeous or dichlamydeous	r
	homoiochlamydeous	heterochlamydeous	r
perianth spur	absent	present	r
perianth parts	imbricate	valvate	n
corona	absent	present	n
perianth vasculature	evident	absent or obscure	n
perianth parts, stamens, and carpels	indefinite in number	definite in number	r
	spirally arranged	whorled	n
	separate	connate or adnate	n
stamens and carpels	pleiomerous	isomerous	n
	2 whorls	1 whorl	n
	isomerous	oligomerous	n
nectaries	absent	present	r
stamens	equal to pistil in length	shorter than pistil	r
	equal in length	anisostemonous	r
	inserted on receptacle	adnate to perianth or epigynous	n
staminodes	absent	present	r

TABLE 2.—Continued.

Character	Primitive state	Derived state	Reversibility
anthers	separate	connate	r
	adnate or basifixed	dorsifixed	r
	oblong	about as long as wide	r
	dehiscent by slits	poricidal	n
	extrorse or latrorse	introrse	r
connective	abundant	sparse or absent	n
microsporangia	4 per anther	2 or 1 per anther	n
pollen grains	monosulcate	pored or nonaperturate	n
	not sticky	sticky	r
	free	in tetrads or pollinia	n
cells in pollen grains at time of dispersal	2	3	n
carpels	open	closed	n
ovary	number of locules correspond to number of carpels	unilocular in more than 1-carpellate pistil	r
	superior	semi-inferior to inferior	n
style(s)	absent	present	r
	separate	connate	n
stigma(s)	decurrent along ventral surface of style	apical or style stigmatic all around	n
	lobed	not lobed	n
placentas in more than 1-carpellate pistil	axile	parietal	n
	axile	apical or basal	n
	not enlarged	enlarged and fleshy	r
ovules	few	∞ or 1 when carpels more than 1	r
	crassinucellar	tenuinucellar	n
	bitegmic	unitegmic or ategmic	n
fruit	follicle	other types	n
dehiscence of capsule	ventricidal or septicidal	loculicidal or by slits	n
seed	medium-sized	small or large	r
embryo	small	large	r
	straight	curved	n
	about as long as wide	much longer than wide	n
endosperm	copious	scanty or absent	n

comparable publication on the dicotyledons (Goldberg, 1986) I have laid the foundation for a third volume which will be an elaboration of my philosophy concerning the subjects of these treatises and its application by giving reasons for the composition and placement of each taxon. It will also contain a synoptical key to the taxa.

Some of my colleagues have reviewed all or part of the monocotyledon manuscript. I appreciate their suggestions for its improvement.

Ordinal and Family Descriptions

PANDANALES

The order is monotypic.

Chemistry: Does not indicate strong relationship with any other order; monoterpenes are present; saponins may be absent; cyanogenesis is rare if present.

PANDANACEAE (Figure 1).—Trees or shrubs, often branched, or perennial herbs, sometimes lianas, often with aerial or prop roots, usually coastal or in marshes, sometimes in forests; raphides present, silica absent; xylem vessel perforation plates scalariform in all organs (except vessels absent from the stem of *Sararanga*); leaves cauline or radical, spirally arranged along the stem, often clustered at the apex, rarely in 2 or 4 rows, simple, linear, sheathing, parallel-veined, leathery, the margins and midrib beneath spinulose, epidermal cells in longitudinal files, the stomates tetracytic, mostly on the lower surface; inflorescences terminal spadices with spathes or heads or panicle, or the flowers few, the bracts sometimes brightly colored; flowers minute, the plants dioecious, anemophilous or entomophilous, ornithogamous and chiropterogamous in *Freycinetia*; perianth absent or vestigial (in dispute), short and gamophyllous (*Sararanga*); ♂ flowers: stamens few to numerous, 9–~300, variable in number, spirally arranged on a short or long axis, or at the same level, the filaments free or connate, anthers basifixed, sometimes apiculate; pollen monoporate, 2-celled when shed; pistillode minute or absent; ♀ flowers: pistil 1 free or many connate in clusters, carpels 1–~80, the stigmas sessile or subsessile, free or connate, sometimes a canal leads to the ovary, the ovary superior, septal

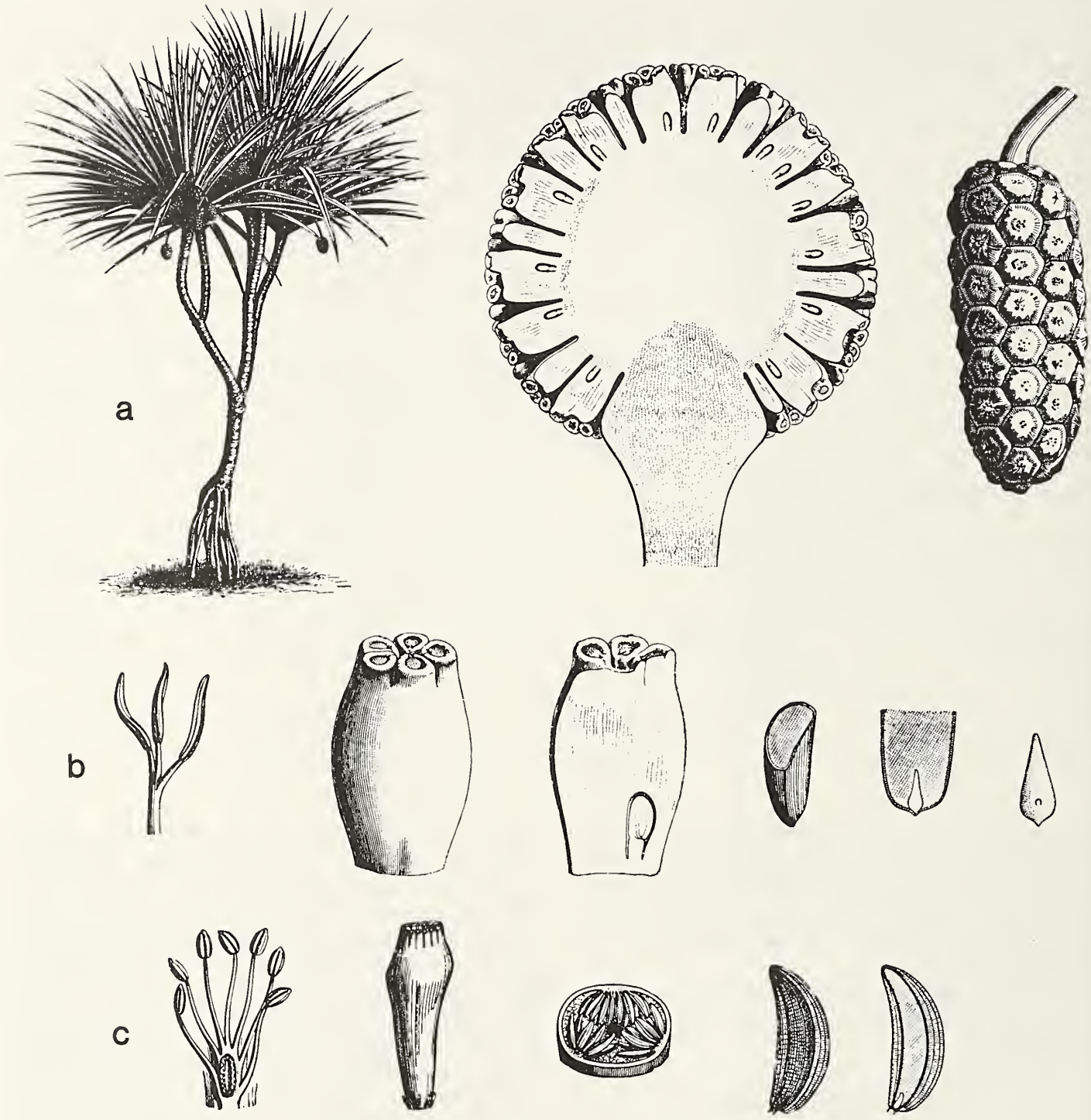


FIGURE 1.—PANDANACEAE: *a, Pandanus candelabrum* habit, l.s. of ♀ inflorescence, *P. utilis* fruiting spadix (reduced); *b, P. candelabrum* stamens, *P. utilis* ♀ flower, l.s. of same, c.s. and l.s. of seed, embryo; *c, Freycinetia banksii* l.s. of a group of stamens enclosing the abortive pistil, pistil and staminodes, *F. imbricata* c.s. of fruit, seed, l.s. of same (after Baillon, Le Maout and Decaisne).

nectaries reported but not confirmed, 1–many locular, the ovules 1 and sub-basal, or numerous and parietal, bitegmic, crassinucellar, anatropous, the embryo sac sometimes with increase in number of antipodals after fertilization, sometimes migration of nucellus nuclei into the embryo sac, endosperm formation Nuclear, later becoming cellular; staminodes absent or small, hypogynous or adnate to the ovary; fruits a syncarp or free, drupes or berries, the pericarp often with woody fibers,

the seeds 1–many, minute or medium-sized, sometimes with a little perisperm; embryo minute, basal, 0.1 the length of the endosperm, 2.5 times longer than wide; endosperm copious, fleshy, oily and with aleurone. Chromosomes: x = 27,30,31,32, especially 30.

Composition: 3 genera, ~500 species.

Distribution: Primarily tropical, mostly in coastal and marshy habitats; tropical West Africa, India, Malaya, East Indies, northern Australia, New Zealand.

ALISMATALES

Herbs of wet habitats, sometimes partly or entirely submerged, rooted in the substrate or free-floating, often rhizomatous or stoloniferous, in fresh water or marine; raphides rare or absent; xylem vesselless throughout, or xylem vessel perforation plates simple and scalariform in the root; leaves linear or differentiated into petiole and blade with longitudinal and transverse veins, radical, alternate, opposite or whorled; inflorescence scapose or axillary, racemes, panicle, or umbels, often cymose, or the flower solitary; flowers entomogamous, hydrogamous, or autogamous, rarely anemophilous, bisexual or the plants polygamous, monoecious or dioecious, the parts hypogynous, and the torus flat to globose, or epigynous; perianth segments usually 6, free; sepals 3(2), green, rarely petaloid; petals 3(0), petaloid; stamens 6(~40–1), free, or rarely connate, or some staminodal, the anthers basifixed or dorsifixed, introrse or extrorse; pollen 1-sulcate, forate or nonaperturate, sometimes connate in short threads or in tetrads, 3(2)-celled when shed; pistils to ~100 to 1, spirally arranged or whorled, carpels 3–6(2–15) when connate; ovary superior or inferior, unilocular, the placentas rarely meeting in the center, the ovules many to 2, often scattered over the ovary wall, sometimes basal, bitegmic, crassinucellar, rarely pseudocrassinucellar, anatropous or amphitropous, rarely orthotropous; embryo sac with 3–1 antipodal cells; endosperm formation Helobial; styles as many as the carpels, free or shortly connate, entire or 2–3-branched apically, the stigmas sometimes ventrally decurrent; fruit follicles, achenes or a berry; seeds often numerous, the embryo straight or curved, endosperm absent at maturity.

Distribution: Cosmopolitan.

Chemistry: Poorly known; cyanogenesis, tannin production, and mucilage are rare or absent; the unusual carbohydrate apiose is present in some members of some families, but it also occurs in some members of Potamogetonales and in the Lemnaceae; raffinose and stachyose have been reported from this order and Aponogetonaceae.

ALISMATACEAE (Figure 2*a–c*).—Perennial, rarely annual, herbs of wet habitats, erect or rarely with floating leaves or entirely submerged, rhizomatous, latex present, raphides in *Sagittaria*, crystals present; hairs generally absent, simple, unicellular or branched multicellular in a few members; xylem vessel perforation plates simple and scalariform in the root, vessels absent from the stem and leaves; leaves with an open sheathing petiole and blade, the latter strongly nerved, the venation longitudinal and transverse, the stomates paracytic and tetracytic, intravaginal scales present; inflorescence scapose, primary branches racemes or panicle, secondary branches often cymose, often whorls of pedicellate flowers, rarely the flowers subsolitary; flowers entomogamous or autogamous, bisexual or the plants polygamous, monoecious or rarely dioecious, the parts hypogynous, torus flat to globose, nectaries on the carpels, receptacular, or on the perigone (*Echinodorus*); sepals 3, green; petals 3(0), white or colored; stamens 6(3–~40), free, whorled or spirally arranged; anthers basifixed or dorsifixed, extrorse; pollen forate, 3-celled when shed; pistils to ~100, spirally arranged in a head, or 6(3) in a single whorl, sometimes basally connate or adnate to the floral axis, the style terminal or basal, the stigma ventrally decurrent; ovules 2–∞, basal or scattered over the wall of the pistils, bitegmic, weakly pseudocrassinucellar, anatropous, or amphitropous, the embryo sac with 1 antipodal cell, rarely 2–3; endosperm formation Helobial, in the large micropylar chamber many free nuclei are formed before the tissue becomes cellular; fruit achenes or follicles; seeds curved, with hippocrepiform embryo, endosperm absent at maturity. Chromosomes: x = 5–13, especially 7,11, large in at least some species.

Composition: ~15 genera, ~80 species.

Distribution: Cosmopolitan, but mostly America.

BUTOMACEAE (Figure 2*d,e*).—Glabrous perennial herbs of wet habitats, rhizomatous, secretory canals and raphides absent; xylem vessel perforation plates simple and scalariform in the root, vessels absent from the stem and leaves; leaves radical, linear, not differentiated into blade and petiole, the stomates mostly paracytic, intravaginal scales numerous; inflorescence a scapose, involucrate, cymose umbel; flowers bisexual, entomogamous, protandrous, the parts hypogynous; perianth segments 6, biseriate, free, petaloid, pink, persistent; stamens 9, the filaments elongate, the anthers basifixed, introrse; pollen monosulcate, 3-celled when shed; pistils 6, the lower lateral surfaces nectariferous, style elongate, the stigma slightly decurrent ventrally, wet; ovules numerous, scattered over the wall of the ovary, bitegmic, pseudocrassinucellar, anatropous; fruit follicles, the seeds numerous, minute, elongate, striate; embryo straight; endosperm absent. Chromosomes: x = 8,10,11,12,13,15, especially 13, small.

Composition: 1 genus, 1 species.

Distribution: Europe and temperate western Asia.

HYDROCHARITACEAE (Figure 3).—Freshwater and marine perennial, rarely annual, herbs, partly or entirely submerged, free-floating or rooted in the substrate, often stoloniferous; raphides and crystals absent; scalariform perforation plates in the roots of a few genera, the others vesselless throughout; leaves radical or alternate, opposite or whorled on an elongate stem, linear, ribbon- or strap-shaped or ensiform and submerged, or differentiated into blade and petiole, with

FIGURE 2.—ALISMATACEAE: *a, Hydrocleys commersonii* one of the pistils, same opened to show the parietal placentation, *H. martii* stamens, pistils, *Limnocharis plumieri* seed, l.s. of same, *H. commersonii* plant in flower; *b, Alisma plantago-aquatica* l.s. of flower, fruit, l.s. of same; *c, Damasonium stellatum* floral diagram, flower, l.s. of same, fruit (after Baillon, Lindley, Martius). BUTOMACEAE: *d, Butomus umbellatus* l.s. of flower, stamen, c.s. of same, pistils, inflorescence; *e,* dehisced fruit, seed, l.s. of same, floral diagram (after Le Maout and Decaisne, Baillon).

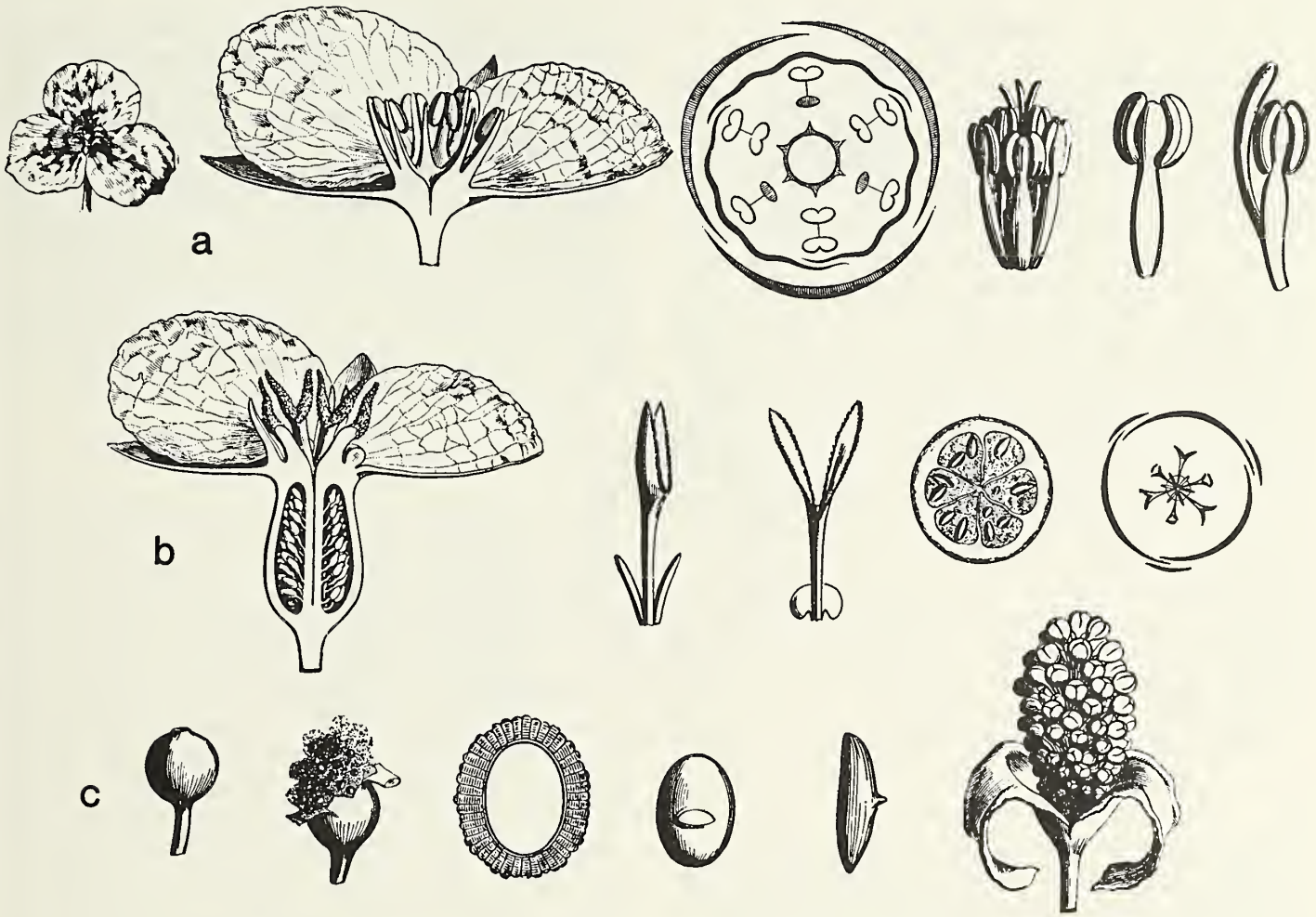


FIGURE 3.—HYDROCHARITACEAE: *a, Hydrocharis morsus-ranae* ♂ flower, l.s. of same, diagram of ♂ flower, androecium, outer stamen, inner stamen with appendage; *b,* l.s. of ♀ flower, style opposite the sepals, style opposite the petals, c.s. of ovary, floral diagram of ♀ flower; *c,* fruit, dehisced fruit, l.s. of seed, views of embryo, *Vallisneria spiralis* ♂ inflorescence (after Baillon, Le Maout and Decaisne).

longitudinal and cross veins, and floating or emersed, entire, rarely toothed (*Stratiotes*), the stomates mostly paracytic, often absent; often with prickle hairs, intravaginal scales present; inflorescence axillary, the ♂ usually a cymose umbel or cincinnus enclosed in a spathe, the ♀ usually solitary; flowers entomogamous or hydrogamous, sometimes with a nectariferous disk (*Hydrocharis*), rarely anemophilous (*Limnobium*), rarely bisexual, usually the plants dioecious, monoecious or polygamous, vestige of the opposite sex sometimes present; perianth rarely homochlamydeous, the sepals 3(2), free, green, valvate; petals 3(0), smaller or larger than the sepals, sometimes with a basal gland; stamens 12–1, free or sometimes connate, sometimes spirally arranged on an elongate receptacle, sometimes 3 staminodes present, the latter sometimes nectariferous (?); pollen 1-sulcate or nonaperturate, sometimes connate in short threads, occasionally in tetrads, 3(2)-celled when shed; pistil 1, the carpels 3–6(2–15), styles as many as the carpels, often bilobed, sometimes shortly connate at the base, the stigmas elongate, papillose; ovary inferior, unilocular, rarely the placentas meet in the center of the ovary, the ovules usually many, sometimes few, parietal, sometimes appearing to be scattered over the surface, bitegmic, crassinucellar, usually anatropous, rarely orthotropous; embryo sac antipodal cells 3, persisting into early embryogeny; endosperm formation Helobial, division free-nuclear in the micropylar chamber, later becoming cellular; fruit elongate or globose, a berry or dry, sometimes rupturing irregularly, rarely regularly; seeds usually numerous, the embryo large, straight, radicle thick, plumule usually evident, endosperm absent at maturity (scanty in *Ottelia*). Chromosomes: x = 6–12, especially 6–8,11.

Composition: 15 genera, ~90 species.

Distribution: Cosmopolitan, but mostly tropical and absent from the arctic region.

Triuridales

The order is monotypic.

Chemistry: Unknown.

TRIURIDACEAE (Figure 4*a,b*).— Saprophytic reddish, purplish or cream herbs, sometimes rhizomatous, with a few alternate scales, without chlorophyll; xylem vesselless, the tracheary elements reduced; inflorescence a terminal bracteate raceme or corymb; plants monoecious, dioecious or rarely polygamous; flowers very small, actinomorphic, the parts hypogynous; perianth segments 6(3–8) in one series, sometimes acuminate, with apical uniseriate hairs, corolline, valvate, sometimes basally connate; ♂ flowers: stamens 3 or 6(1–6), sometimes 3 of them staminodal, the filaments short, basally connate, or the anthers sessile; anthers extrorse, sometimes produced apically; pollen nonaperturate, 3-celled when shed; ♀ flowers: pistils ~15(6–50), the style terminal to basal, stigma decurrent or penicillate; ovule solitary, basal-axile, bitegmic, tenuinucellar, anatropous; embryo sac antipodal cells 3, ephemeral; endosperm formation Nuclear, the tissue later becoming cellular; fruits dehisce dorsally or nutlets; embryo undifferentiated, endosperm present, containing aleurone and fat (or starch ?). Chromosomes: x = 11,12,14.

Composition: 7 genera, ~80 species.

Distribution: Pantropical in rain forest; southern Africa.

Juncaginales

Marsh herbs, rhizomatous or tuberous; xylem vessel perforation plates scalariform in the root, vessels absent from the stem and leaves; leaves usually basal, linear, with an open sheath; inflorescence a scapose raceme or spike; flowers small, bisexual or the plant dioecious or monoecious, anemophilous; perianth segments 6(0), biseriate, homochlamydeous, greenish; stamens 6 (rarely more), 3, or 1, the filaments short, anthers extrorse, sometimes apiculate; pollen nonaperturate, sometimes in dyads, 2–3-celled when shed; pistil 1(6), carpels 3–6(1), the stigmas usually sessile or subsessile, the style rarely elongate; ovary superior, 3-locular when the carpels are united, the ovules 1–2(few) per carpel, basal, bitegmic, crassinucellar, anatropous; embryo sac antipodal cells ephemeral or undergo secondary multiplication; endosperm formation Helobial or Nuclear; fruit follicles, schizocarp, or nutlet; embryo straight, endosperm absent in mature seed.

Distribution: Cool temperate and cold Northern Hemisphere; southern tip of South America; southern Australia, New Zealand.

Chemistry: Cyanogenic; Scheuchzeriaceae tanniferous, Juncaginaceae not.

SCHEUCHZERIACEAE (Figure 4*c,d*).—Perennial marsh herbs with a jointed rhizome; raphides absent, some calcium oxalate crystals present; xylem vessel perforation plates scalariform in the root, vessels absent from the stem and leaves; leaves often basal, linear, petiole ligulate at junction with the blade, the stomates tetracytic; numerous long, uniseriate hairs in axils of leaves; inflorescence a terminal, bracteate, few-flowered raceme; flowers bisexual, small, anemogamous, protogynous; perianth segments 6, in 2 whorls, free, similar, yellowish-green; stamens 6 (rarely more), free, the filaments short; anthers linear, basifixed, apiculate, extrorse; pollen nonaperturate, in dyads, 3-celled when shed; pistil 1, carpels 3(–6), shortly ventrally connate at the base, the stigmas sessile, papillose; ovary superior, the ovules 2 (few) per carpel, basal, bitegmic, crassinucellar, anatropous; embryo sac antipodal nuclei 3, ephemeral; endosperm formation Helobial, at first nuclear, later becoming cellular in the micropylar chamber; fruit divaricate follicles; embryo straight, endosperm absent in mature seed. Chromosomes: n = 11.

Composition: 1 genus, 2 species.

Distribution: Cool temperate and cold Northern Hemisphere.

JUNCAGINACEAE (Figure 5*a,b*).—Perennial, seldom annual, glabrous marsh herbs, rarely plant submerged except for one or two floating leaves, rhizomatous or sometimes tuberous; raphides absent, calcium oxalate crystals sometimes present; xylem vessel perforation plates scalariform in the root, vessels absent from the stem and leaves; leaves radical, linear, sheathing basally, the stomates tetracytic, intravaginal scales present; inflorescence scapose, an ebracteate spike; flowers small, anemophilous, protogynous, bisexual or the plant dioecious or monoecious; perianth segments 6, biseriate, homochlamydeous; stamens 6, 3, (4), free, the anthers subsessile, extrorse; pollen nonaperturate, 2- or 3- celled when shed; pistils 1(6), carpels 3–6, sometimes 3 aborted, the stigmas sessile or subsessile, papillose or plumose; ovary superior, 3(4)-locular in compound ovary, the ovules 1 per locule, basal, bitegmic, crassinucellar, anatropous; the 3 embryo sac antipodal cells in *Triglochin* undergo secondary multiplication and persist into early embryogeny; endosperm formation Nuclear and small in amount; fruit a schizocarp or nutlet; embryo straight, endosperm absent in mature seed. Chromosomes: x = 6,8,9.

Composition: 3 genera, ~20 species.

Distribution: Cool temperate and cold regions of Northern Hemisphere; southern tip of South America; southern Australia, New Zealand.

LILAEACEAE (Figure 5*c,d*).—Aquatic or marsh annual, glabrous herbs with short rhizomes; xylem vessel perforation plates only in the roots; leaves basal, alternate, linear and terete, with an open sheath; inflorescence scapose, bracteate, dense spikes, either unisexual, or ♂ above, bisexual in the middle and ♀ below; solitary ♀ flowers also occur in the axils of the leaves; perianth absent; stamen 1, the filament short, anther extrorse, about as long as wide, the sacs separate basally, the connective slightly produced apically; pollen nonaperturate, 2-celled when shed; pistil 1, unicarpellate, the stigma subsessile in the bisexual and upper ♀ flowers, the style long, filiform, with a capitate, papillose stigma in the basal axillary flowers; ovary superior, unilocular, uniovulate, the ovule basal,

FIGURE 4.—TRIURIDACEAE: *a, Sciaphila albescens* plant in flower, ♂ flower, same with perianth removed, ♀ flower, a pistil; *b, Triuris brevistilis* fruit, same opened to show the solitary seed, l.s. of same showing the minute undifferentiated embryo in abundant endosperm (after Martius). SCHEUCHZERIACEAE: *c, Scheuchzeria palustris* flower, stamen, a carpel, same laid open, plant in flower; *d,* fruit, seed (after Hutchinson).

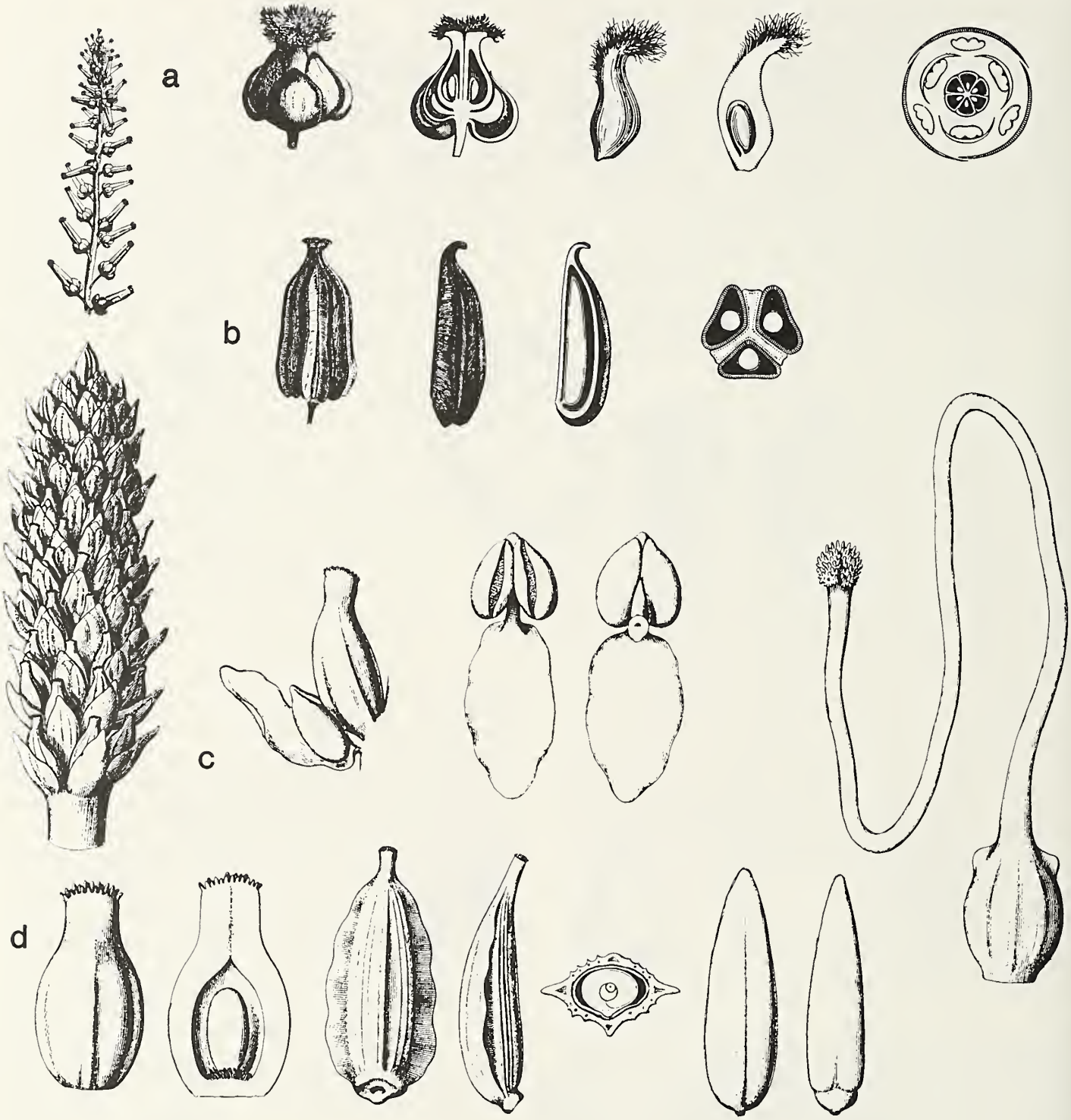


FIGURE 5.—JUNCAGINACEAE: *a, Triglochin maritimum* part of inflorescence, flower, l.s. of same, *T. laxiflorum* carpel, l.s. of same, *Triglochin* floral diagram; *b, T. maritimum* fruit, segment of same, l.s. of segment, *T. palustre* c.s. of fruit (after Baillon, Le Maout and Decaisne). LILAEACEAE: *c, Lilaea subulata* upper inflorescence, a flower, views of stamen and perianth (bract), ♀ flower from base of plant; *d,* pistil, l.s. of same, views of fruit, c.s. of same, views of embryo (after Martius).

bitegmic, crassinucellar, anatropous; the 3 antipodals of the embryo sac degenerate during early embryogeny; endosperm formation Nuclear; fruit a compressed, longitudinally ribbed nutlet; embryo straight, endosperm absent in mature seed. Chromosomes: n = 6.

Composition: 1 genus, 1 species.

Distribution: Western America from southern Canada to southern South America.

NAJADALES

Freshwater or marine rhizomatous or tuberous submerged or emergent herbs; xylem usually vesselless, sometimes scalariform perforation plates in the root; leaves distichous or basal, alternate or opposite, the blade linear to orbicular, the veins longitudinal, sometimes also transverse, the sheath open, stomates absent; inflorescence spikes, terminal or axillary, or flowers solitary or few in axillary cymes; flowers small or minute, bisexual or the plants monoecious or dioecious, the parts hypogynous, anemogamous or hydrogamous; perianth absent or of 3–4 scales; stamens 4–1(–12), the filament elongate or the anthers sessile, often extrorse, sometimes apically produced; pollen monocolpate or nonaperturate, globose or filiform, 2–3-celled when shed; pistils 3–4(1–9), the styles 1–4, elongate, or the stigmas sessile, sometimes decurrent ventrally; ovary unilocular, the ovules 1–8, basal, apical or ventral, bitegmic, crassinucellar or pseudocrassinucellar, anatropous, orthotropous or campylotropous; embryo sac antipodals ephemeral or undergoing secondary multiplication to form 4–5 cells; endosperm formation Helobial or Nuclear; fruit usually nutlets, achenes or drupelets, sometimes follicular; embryo straight or curved, endosperm absent in mature seed.

Distribution: Cosmopolitan.

Chemistry: No distinctive characters have been uncovered.

APONOGETONACEAE (Figure 6*a–c*).—Freshwater perennial herbs with tuberous rhizome; raphides absent, calcium oxalate crystals present; xylem vesselless; leaves radical, usually floating, sometimes submerged, long petiolate, the blade elliptic to linear, with some longitudinal and numerous transverse veins, the stomates paracytic, intravaginal scales present, otherwise glabrous; inflorescence a scapose ebracteate spike, sometimes branched; flowers small, bisexual or rarely the plants dioecious, the parts hypogynous; perianth parts 0–3, petaloid or bract-like, abaxial when 2; stamens 6–12, in 2–4 cycles, the filaments elongate, anthers small, extrorse; pollen monocolpate, 3-celled when shed; pistils 3–6, nectariferous, the style grading into the ovary, the stigmas somewhat decurrent ventrally; ovules 2–8, basal, bitegmic, the integuments free or ± connate, crassinucellar, anatropous; embryo sac with 3 antipodals which persist into early embryogeny; endosperm formation Helobial; fruit 3–6 follicles, the seeds with straight embryo, endosperm absent at maturity. Chromosomes: x = 8,12,13,24,26,38,46, especially 8.

Composition: 1 genus, ~25 species.

Distribution: Centered in tropical Africa and Madagascar; southern 2/3 of Africa; India, southeast Asia, few islands of the East Indies; northern Australia.

ZOSTERACEAE (Figure 6*d*).—Submerged marine perennial, glabrous herbs on rocks, with short creeping rhizome, sometimes tuberous, and erect branches; crystals absent; xylem vesselless, the tracheary elements reduced; leaves alternate, linear, sometimes minutely denticulate, the apex of the sheath with 2 lateral projections, stomates absent, intravaginal scales present; inflorescence on one side of a flattened spadix with a row of bracts on each margin, at first enveloped by a leaf sheath, the plants monoecious or dioecious; perianth absent; ♂ flowers consist of a single, sessile, dorsifixed, elongate anther; pollen filamentous, about 2500 µm long, 4 µm wide, 2-celled when shed; ♀ flowers consist of 1 pistil and a vestigial anther, the stigmas 2, large, flat; ovary unilocular with 1 pendulous, bitegmic, pseudocrassinucellar, orthotropous ovule; the 3 antipodal cells of the embryo sac persist into early embryogeny; endosperm formation Nuclear; fruit a nutlet, achene or drupelet, the seed longitudinally ribbed, endosperm absent at maturity. Chromosomes: x = 6,7,8,10.

Composition: 3 genera, 18 species.

Distribution: Mostly temperate, few tropical or arctic; North America; Eurasia; western and southern Australia, New Zealand; eastern Africa, Madagascar.

POTAMOGETONACEAE (Figure 7*a–c*).—Aquatic perennial, glabrous herbs with creeping rhizome and erect stems; xylem vessel perforation plates sometimes scalariform in the root, vessels absent from the stem and leaves; leaves distichous, alternate or opposite, immersed or floating, ribbon-like, linear, oblong, lanceolate, ovate or orbicular, entire or rarely serrulate, sometimes differentiated into blade and petiole, the stomates paracytic, intravaginal scales present; inflorescences axillary spikes; flowers small, bisexual, the parts hypogynous, anemogamous or hydrogamous; sepals 4, valvate, free, or 0 (*Ruppia*); petals 0; stamens 4, sessile, adnate to claw of sepal, or 2 (*Ruppia*), the anthers extrorse; pollen nonaperturate, round (*Potamogeton*) or tubular (*Ruppia*), 3-celled when shed; pistils 4(1, rarely more than 4, to 10 in *Ruppia*), the stigma sessile or subsessile, slightly decurrent ventrally, the ovule 1, bitegmic, crassinucellar, orthotropous or campylotropous; embryo sac antipodal cells 3, soon degenerate; endosperm formation Helobial, free-nuclear division occurs in the micropylar chamber, but later the tissue becomes cellular; fruit achenes, nutlets or drupelets; embryo curved, endosperm absent in mature seed. Chromosomes: x = 8,10,13–15, especially 13,10.

Composition: 2 genera, ~100 species.

Distribution: Cosmopolitan, in fresh or somewhat brackish water.

ZANNICHELLIACEAE (Figure 7*d*).—Submerged, slender, branching perennial glabrous herbs of fresh to salt water, with a creeping slender rhizome; raphides absent (?), crystals absent; xylem vesselless, the tracheary elements reduced; leaves linear,

FIGURE 6.—APONOGETONACEAE: *a, Aponogeton fenestralis* inflorescence and leaf, *A. distachyus* part of plant and inflorescence, part of inflorescence, *Aponogeton* flower; *b, A. bernierianus* flower, pistil laid open; *c, A. distachyus* l.s. of seed, germinating embryo (after Le Maout and Decaisne, Baillon). ZOSTERACEAE: *d, Zostera marina* anther, the same dehiscing, pistil, l.s. of same, fruit, l.s. of same, seed, embryo, inflorescence and part of spathe (after Baillon).

FIGURE 7.—POTAMOGETONACEAE: *a, Potamogeton crispus* flowering branch, flower, l.s. of same, *P. stenostachys* flower, views of stamen and perianth segment; *b,* gynoecium, l.s. of a pistil, fruit, l.s. and c.s. of same; *c, Ruppia maritima* inflorescences, anthers before and after dehiscence, pollen grain, pistil, l.s. of same, fruit, l.s. of same, embryo (after Martius, Baillon). ZANNICHELLIACEAE: *d, Zannichellia palustris* inflorescence, stamen and pollen grain, l.s. of pistil, fruitlets, l.s. of a fruitlet showing the folded embryo (after Martius).

alternate, opposite or whorled, sometimes minutely denticulate, with a short sheath and mostly ligulate, stomates absent, intravaginal scales filiform; plants monoecious or dioecious; flowers minute, solitary or few in cymes in the leaf axils; perianth of 3 free scales or cupular (*Zannichellia*) or absent; stamens 3–1, rarely connate, the filament elongate or the anthers sessile; anthers elongate, basifixed, the connective sometimes apically produced; pollen nonaperturate, globose (*Zannichellia*) or filiform (Cymodoceae) and 2000 μm by 10 μm, 2–3-celled when shed; pistils 3–4(1–9), the style 1, mostly elongate, with a capitate, peltate or umbonate stigma, or 2–4-lobed and the stigmas filiform; ovary superior, unilocular, the ovule solitary, apical, bitegmic, crassinucellar, anatropous; the 3 antipodals of the embryo sac may undergo secondary multiplication to form 4 or 5 cells; endosperm formation Helobial; fruits sessile or stipitate nutlets or achenes; embryo coiled, endosperm absent in mature seed. Chromosomes: x = 6–8.

Composition: ~6 genera, ~20 species.

Distribution: Cosmopolitan.

NAJADACEAE (Figure 8*a,b*).—Small annual, submerged, glabrous herbs of fresh or brackish water, the stem filiform, much branched; raphides and crystals absent; xylem vesselless, the tracheary elements reduced; leaves linear, usually toothed, with a short sheath, sub-opposite or verticillate; plants monoecious or rarely dioecious; flowers minute, 1–2 sessile in the axils of leaves at base of branches; ♂ flower consists of a single 4(–1)-locular sessile anther enclosed in a bilabiate close-fitting perianth and a spathe, the pedicel elongating prior to anther dehiscence; pollen ellipsoidal, nonaperturate, 3-celled when shed; ♀ flower naked or surrounded by a membranous perianth or spathe; pistil 1, the styles 3(2), stigmas 3(2), ventral, elongate; ovary unilocular with 1 basal, bitegmic, crassinucellar, anatropous ovule; the 3 antipodal cells of the embryo sac persist into early embryogeny; endosperm formation Nuclear, later becoming cellular throughout; fruit a nutlet, the seed smooth or sculptured; embryo straight, endosperm absent in mature seed. Chromosomes: x = 6,7, especially 6.

Composition: 1 genus, ~35 species.

Distribution: Cosmopolitan except the arctic region.

POSIDONIACEAE (Figure 8*c*).—Submerged marine, perennial, glabrous herbs on rocks, with a short thick rhizome; xylem vesselless, the tracheary elements reduced; crystals absent; leaves subbasal, alternate, liguliform, entire or serrulate, rounded at the apex, the sheath open and ligulate, the persistent fibrous leaf-bases cover the stem, stomates absent, intravaginal scales present; inflorescences spikes in axils of foliaceous bracts at the apex of a scape, the lower flowers bisexual, the upper generally ♂; perianth absent or of 3 caducous scales; stamens 3(4), hypogynous, the anthers large, sessile, extrorse, the anther sacs separated by connective which is also apically produced; pollen filiform; pistil 1, carpel 1, the stigma sessile, fimbriate; ovary superior, unilocular, the ovule 1(2), ventral; fruit a drupe; embryo straight; endosperm absent. Chromosomes: n = 10.

Composition: 1 genus, 3 species.

Distribution: Southern and western Australia; Mediterranean.

TYPHALES

Herbs of wet habitats, rhizomatous; raphides commonly present; xylem vessel perforation plates scalariform; leaves alternate, linear to strap-shaped, distichous; plants monoecious; inflorescences usually dense, scapose, the flowers numerous, small or minute, anemophilous; perianth absent or 3–6 sepaloid scales; stamens 2–6, the filaments free or connate, anthers elongate, basifixed; pollen 2–3-celled when shed, single or in tetrads, 1-ulcerate; pistil 1, carpels 1–2, the styles 1–2, stigmas decurrent ventrally; ovary superior, 1(2)-locular, ovule 1(2), bitegmic, crassinucellar, anatropous; embryo sac antipodals sometimes multiplying to as many as 150 cells; endosperm formation Nuclear; fruit achenes or nutlets; embryo straight, elongate; endosperm copious.

Distribution: Nearly cosmopolitan, most commonly in the Northern Hemisphere.

Chemistry: Tanniferous; sometimes cyanogenic; not saponiferous.

SPARGANIACEAE (Figure 9*a,b*).—Perennial herbs of wet habitats, rhizomatous; raphides and calcium oxalate crystals commonly present; xylem vessel perforation plates scalariform in root and stem and perhaps leaves; leaves linear, basally sheathing, distichous, usually emergent, sometimes floating, the stomates paracytic; plants monoecious, the inflorescences panicles or spikes of spherical heads, the ♂ above the ♀; flowers small, with 3–6 sepaloid scales, protogynous, anemophilous; stamens 3–6, the filaments free or partially connate, anthers oblong, basifixed, extrorse; pollen 3-celled when shed, ulcerate, the ulcus ± pore-like; pistil 1, carpels 1(2), very rarely 3, the style(s) elongate, stigma(s) 1(2), decurrent ventrally; ovary superior, 1(2)-locular, ovule 1 per locule, bitegmic, crassinucellar, anatropous; embryo sac antipodal cells undergo postfertilization multiplication, forming as many as 150 cells; endosperm formation Nuclear (Helobial ?); fruit a nutlet; embryo straight, 0.8–0.9 the length of the endosperm, 8–13 times longer than wide; endosperm copious, mealy, with starch, protein, and oil. Chromosomes: n = 15.

Composition: 1 genus, ~15 species.

Distribution: Throughout temperate and cold Northern Hemisphere; few in the East Indies, southern Australia, New Zealand.

TYPHACEAE (Figure 9*c,d*).—Perennial emergent herbs of wet habitats, aerial stems jointless, erect, with a thick rhizome; raphides and calcium oxalate crystals commonly present; xylem vessel perforation plates scalariform in root, stem and leaves; leaves alternate, distichous, strap-shaped, basally sheathing, the stomates paracytic; plants monoecious, the

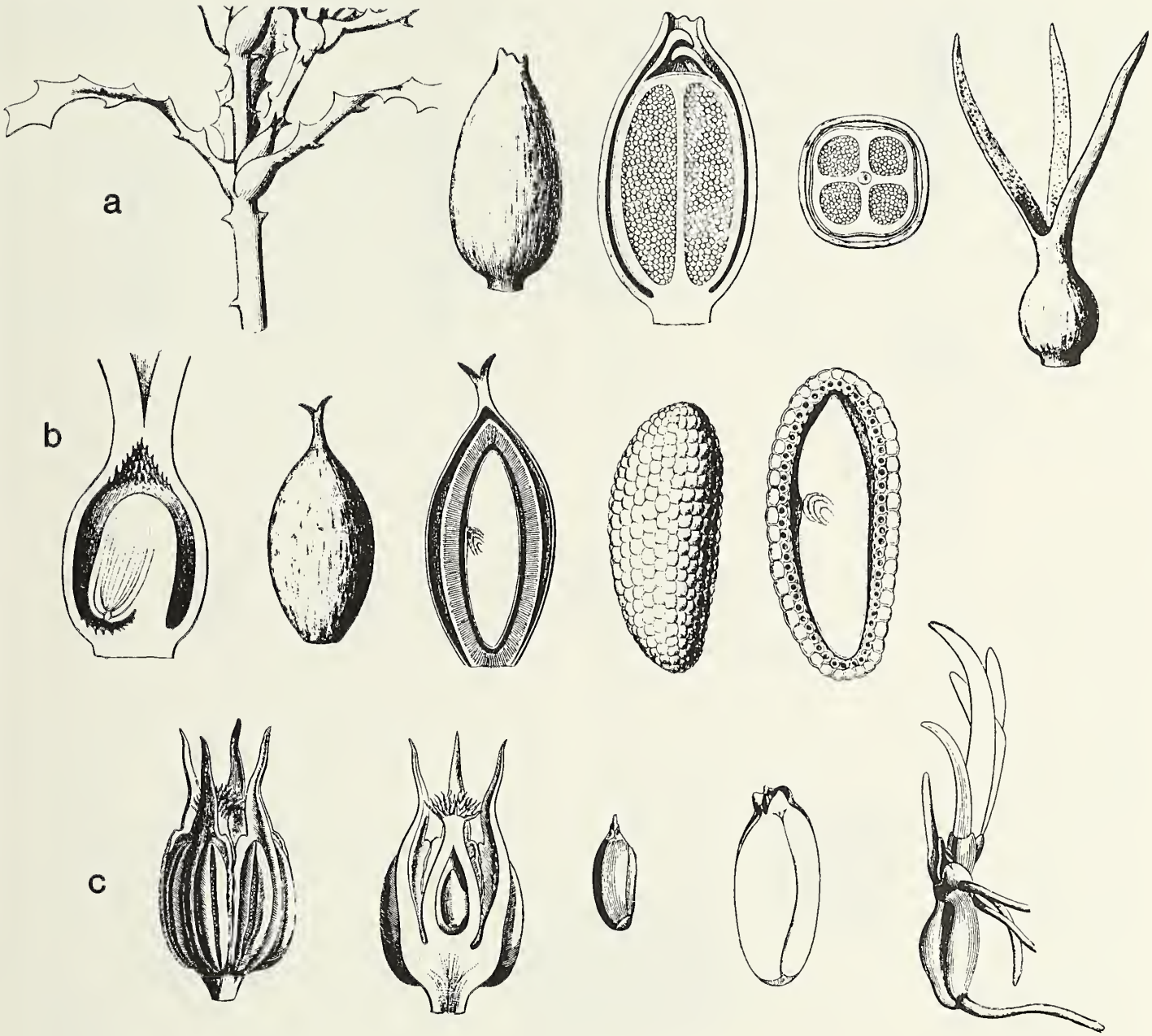


FIGURE 8.—NAJADACEAE: *a*, *Najas major* part of plant showing a flower in the axil of a leaf, ♂ flower, l.s. and c.s. of same showing the solitary stamen, ♀ flower; *b*, l.s. of ovary showing the solitary basal ovule, fruit, l.s. of same, *N. guadelupensis* seed, l.s. of same showing the straight embryo (after Martius). POSIDONIACEAE: *c*, *Posidonia oceanica* flower, l.s. of same, embryo, l.s. of same, plant soon after germination (after Baillon).

inflorescence a scapose, dense cylindrical spadix with numerous minute flowers, the ♂ above the ♀; flowers without a perianth, merely subtended by bristles, protandrous, anemophilous; stamens 2–5, the filaments free or connate, anthers linear, basifixed, the connective usually apically produced; pollen 2-celled when shed, single or in tetrads, ulcerate, the ulcus single, ± pore-like; pistil 1, stipitate, carpel 1, the style elongate, stigma decurrent ventrally; ovary superior, ovule 1, bitegmic, crassinucellar, anatropous; embryo sac antipodals degenerate soon after fertilization (Davis), or increase in number (Engler Syllabus); endosperm formation Nuclear; fruit achenes or nutlets with a tuft of long hairs (wind dispersed), the seed striate; embryo straight, 0.5–1.2 times the length of the endosperm, 6–9.7 times longer than wide; endosperm copious, mealy, with aleuron and oil. Chromosomes: x = 15.

Composition: 1 genus, ~10 species.


a
b
c
d

Distribution: Nearly cosmopolitan, but most widely distributed in the Northern Hemisphere.

JUNCALES

Herbs of wet to dry habitats, usually rhizomatous, the stem sometimes jointed, solid or the internodes hollow; raphides absent, silica rarely present; xylem vessel perforation plates usually scalariform and simple, sometimes only scalariform, vessels sometimes absent from the leaves; leaves alternate, sometimes distichous, often basal, usually elongate and narrow, sometimes reduced to a sheath, the latter usually open, sometimes ligulate; inflorescences usually terminal and compound; flowers small or minute, almost always anemophilous, bisexual or the plants dioecious or monoecious, the parts hypogynous; perianth segments 6–3(0), usually glumaceous, rarely scarious, free or rarely shortly connate; stamens 6 or 3(-1), the filaments elongate, anther basifixed or dorsifixed, sometimes apically produced; pollen 1-aperturate, ulceroid or sulcoid, sometimes shed in tetrads, 2–3-celled; pistil 1, carpels 3–1, the styles 3–1(0), usually long, the stigmas sometimes decurrent ventrally, sometimes plumose; ovary 3–1-locular, the ovules 1–many per locule, axile-basal or -apical, or parietal, bitegmic, crassinucellar or tenuinucellar, anatropous or orthotropous; embryo sac antipodal cells ephemeral or persistent into early embryogeny, sometimes multiplying to 15 cells; endosperm formation Helobial or Nuclear; fruit a loculicidal capsule or nutlet, the seeds small, 1 to many; embryo small, axile or lying against the endosperm; endosperm copious.

Distribution: Cosmopolitan.

Chemistry: Usually tanniferous, sometimes cyanogenic (not Restionaceae); usually not saponiferous; alkaloids absent; seed fats of some Juncaceae, Liliaceae and Philesiaceae contain eicosenoic acid.

JUNCACEAE (Figure 10*a,b*).—Perennial or seldom annual herbs often of moist habitats, rarely a shrub (*Prionium*), rhizomatous, usually glabrous but *Luzula* with long multicellular hairs; raphides, crystals and silica absent; xylem vessel perforation plates usually scalariform and simple in all organs or sometimes only scalariform in the stem and leaves; leaves filiform, flat or terete, mostly basal, alternate, often ligulate, the sheath usually open, rarely closed, rarely with a spinulose margin (*Prionium*); epidermal cells and stomates usually elongate longitudinally, stomates paracytic; inflorescence terminal and axillary cymes, panicles, corymbs or heads, sometimes solitary; flowers small, nectarless, almost always anemophilous, bisexual or rarely the plants dioecious, the parts hypogynous; perianth segments 6(3) in 2 whorls, glumaceous, rarely scarious, usually greenish or reddish brown, rarely white or yellowish; stamens 6(3), free, the anthers basifixed, rarely apically produced; pollen ulcer(oid)ate, shed in tetrads, each grain 3-celled; pistil 1, carpels 3, styles 1 or 3, short or long, stigmas 3, decurrent; ovary 1- or 3-locular, the ovules 3 to many, axile-basal or parietal, bitegmic, crassinucellar, anatropous; embryo sac 3 antipodal cells may persist into early embryogeny; endosperm formation Helobial, free-nuclear divisions in the micropylar chamber are followed by cell formation; fruit a loculicidal capsule, the seeds small, sometimes tailed, only *Voladeria* fruit 1-seeded (?Juncaceae); embryo axile, small, 0.2–0.3 the length of the endosperm, 1.3–2.0 times longer than wide; endosperm copious, starchy. Chromosomes: x = 3–36, especially 6,10; diffuse centromere in chromosomes of *Luzula*.

Composition: 9 genera, ~350 species.

Distribution: Cosmopolitan, chiefly cold temperate and montane, rare in tropical regions.

THURNIACEAE (Figure 10*c*).—Coarse rhizomatous glabrous herbs of wet habitats; raphides and calcium oxalate crystals absent, silica bodies present; xylem vessel perforation plates scalariform and simple in the root, scalariform in the stem and leaves; leaves basal, linear-acuminate, leathery, entire or with spinulose margins, keeled, the sheath short, open, the stomates paracytic, sometimes tetracytic; inflorescences dense globular heads, subtended by several leafy bracts, at the apex of a stout, 3–4-gonous or subterete scape; flowers small, bisexual, anemophilous; perianth of 6 free, (or shortly connate ?), similar, oblanceolate, membranous parts; stamens 6, the filaments long-exserted, adnate to the base of the perianth; anthers about 3 times longer than wide, basifixed; pollen united in tetrads, grains with an obscure roundish aperture; pistil 1, carpels 3, connate part of the style short, style arms 3, filiform, the stigmas decurrent ventrally; ovary superior, 1(3)-locular, the ovules axile-subbasal, 1–few per locule, anatropous; fruit a loculicidal capsule, the 3 seeds elongate, pointed at both ends; embryo axile in the endosperm, 0.3 the length of the endosperm, 7 times longer than wide; endosperm copious, mealy, starchy.

Composition: 1 genus, 3 species.

Distribution: Guayana, Venezuela, Amazon basin of Brazil, and rarely Colombia.

CENTROLEPIDACEAE (Figure 11*a,b*).—Small, tufted, annual or perennial herbs of wet habitats; raphides, crystals and silica bodies absent; sometimes with multicellular unbranched or branched filamentous hairs; xylem vessel perforation plates scalariform in all organs; leaves basal, more rarely imbricate along the stem, alternate, sometimes distichous, with a short open sheath; the stomates paracytic, somewhat similar to those in Poaceae; inflorescences scapose spikes or heads, or rarely

FIGURE 9.—SPARGANIACEAE: *a, Sparganium simplex* upper part of plant with 4 ♂ inflorescences above and 2 ♀ below, *S. ramosum* 1.s. of ♂ inflorescence, ♀ flower, 1.s. of same, *Sparganium* pistil with 2 styles; *b, Sparganium* 1.s. and c.s. of ovary, *S. natans* ♂ flower, c.s. of fruit with 4 bracts, seed, embryo (after Le Maout and Decaisne, Baillon). TYPHACEAE: *c, Typha latifolia* upper part of plant in flower (much reduced), *T. angustifolia* part of ♂ inflorescence, part of ♀ inflorescence, *Typha* ♂ flower, pollen in tetrads; *d,* 1.s. of ovary, diagram of ♀ flower, fruit, 1.s. of seed, embryo (after Le Maout and Decaisne, Baillon, Martius).

FIGURE 10.—JUNCACEAE: *a, Juncus bulbosus* plant in flower, l.s. of flower, floral diagram, *Juncus* one of the fruit valves showing the numerous seeds, seed, l.s. of same deprived of its cellular testa; *b, Luzula campestris* flower, l.s. of same, dehisced fruit, seed, l.s. of same (after Baillon, Le Maout and Decaisne). THURNIACEAE: *c, Thurnia sphaerocephala* part of plant showing globular inflorescence, *T. jenmanii* flower, l.s. of same, pistil, *T. sphaerocephala* seed, l.s. of same, l.s. of lower part of seed showing small embryo in abundant endosperm (after Hooker, Baillon, Pilger).

the flower solitary, mostly subtended by relatively large bracts; flowers minute, anemogamous, bisexual or the plants monoecious; perianth 0, the flower subtended by 1-3 bracteoles; stamens 1(2), the filaments filiform; anthers 1–2-locular, elongate, dorsifixed or basifixed; pollen 1-aperturate, sulcoid or ulceroid, 3-celled when shed; pistil 1, the carpels 1–3, styles 1 per carpel, free or connate, filiform, the stigmas ventrally decurrent; ovary superior, 1–3-locular; ovules 1 per locule or carpel, apical,

FIGURE 11.—CENTROLEPIDACEAE: *a, Centrolepis drummondii* plant in flower, inflorescence, pseudanthium, seed, l.s. of same showing the basal embryo; *b, Gaimardia australis* plant in flower, flower, l.s. of same, dehisced fruit, *Aphelia cyperoides* flower, l.s. of same (after Baillon). RESTIONACEAE: *c, Restio vaginatus* upper half of plant in flower, *R. triticeus* ♂ flower, floral diagram of ♀ flower, l.s. of ♀ flower, *Lamprocaulos grandis* ♀ flower, l.s. of same; *d, Restio tetraphyllus* ♂ flower, ♀ flower joined to its bract, l.s. of pistil, *Restio* dehisced fruit, seed, l.s. of same showing the basal embryo and abundant endosperm (after Le Maout and Decaisne, Baillon).

bitegmic, crassinucellar, anatropous, the antipodals of the embryo sac increased in number; endosperm development Nuclear; fruit a membranous loculicidal capsule, or rarely indehiscent; embryo small, marginal, lying against the endosperm, 0.25 the length of the endosperm, as long as wide; endosperm or perisperm copious, starchy, mealy. Chromosomes: x = 10–14.

Composition: 5 genera, ~30 species.

Distribution: Centered in southern Australia and New Zealand; Hainan, Indochina, East Indies; southern tip of South America.

RESTIONACEAE (Figure 11*c,d*).—Perennial herbs, usually xerophytic but sometimes in wet habitats, often covering large areas like grasses and sedges, tufted or with an elongate rhizome covered with scale-like sheaths, the stems often jointed, solid or the internodes hollow, quadrangular, flattened or terete; raphides absent, crystals generally absent, silica bodies present; xylem vessel perforation plates simple in the root, simple or scalariform or both in the stem, rarely simple and scalariform in the leaves, but vessels usually absent from the last; leaves usually reduced to a mostly open sheath, rarely with a linear blade, very rarely with a ligule, sometimes somewhat ensiform, distichous, rarely basal, the epidermis with long and short cells, stomates paracytic, similar to those in Poaceae, often sunken; hairs uncommon, unicellular or multicellular, simple or branched filaments or flattened, fan-shaped and closely appressed to the epidermis; inflorescences 1- to many-flowered spikelets arranged in spikes or panicles, rarely solitary or paired, sometimes differing between the sexes; flowers small, anemophilous, the parts hypogynous, very rarely bisexual (some *Phyllocomos, Lepyrodia hermaphrodita*), the plants usually dioecious or rarely monoecious; perianth 3–6 glumes, in 2(1) series, or rarely absent from the ♀ flower, free or rarely the inner ones basally connate, or different from the outer; ♂ flower: stamens 3 or 2(1), the filaments linear, free or rarely connate, the anthers oblong 1(2)-locular, dorsifixed, the sacs separate at base and apex, the connective often apically produced; pistillode present or absent; pollen 1-ulcerate, -ulceroidate or -sulcoidate, often graminoid, 2–3-celled when shed; ♀ flower: pistil 1, carpels 3–1, the styles 3–1(0 in *Chondropetalum*), free or connate, usually linear, sometimes plumose, the stigmas sometimes decurrent ventrally, rarely surrounded by a disk (*Hypodiscus*), 3 small staminodes present or absent; ovary 3–1-locular, the ovules 1 per locule, axile-apical, bitegmic, crassinucellar or tenuinucellar, orthotropous; the 3 antipodals of the embryo sac usually ephemeral, but in a few species secondary multiplication occurs and up to 15 cells are formed but degenerate soon after fertilization; endosperm formation Nuclear; fruit a loculicidal capsule or nutlet; embryo lenticular, lying against the endosperm, less than 0.1 the length of the endosperm, 4–5 times wider than long; endosperm copious, mealy, starchy. Chromosomes: x = 6–13, especially 6.

Composition: ~28 genera, ~350 species.

Distribution: Centered in South Africa and Australia; New Zealand; Madagascar, Malawi; Indochina, Malay peninsula; southwestern South America.

FLAGELLARIACEAE (Figure 12).—Erect herbs (*Joinvillea*), or somewhat woody climbers (*Flagellaria*) with a rhizome; stem internodes solid (*Flagellaria*) or hollow (*Joinvillea*); raphides absent; xylem vessel perforation plates simple and scalariform in the stem and leaves; leaves alternate, elongate, lanceolate or linear, entire, grass-like, distichous in at least *Flagellaria,* the apex ending in a cirrhose tip in the latter, with an elongate closed (*Flagellaria*) or open (*Joinvillea*) sheath, the epidermal cells often in longitudinal files, stomates paracytic, similar to those in Poaceae, silica present (*Joinvillea*) or absent (*Flagellaria*), secretory cells present (*Flagellaria*) or absent (*Joinvillea*), glabrous (*Flagellaria*) or with prickle-hairs or multicellular hairs (*Joinvillea*); inflorescence a terminal panicle or compound spike; flowers bisexual, small, apparently anemophilous; perianth of 6 parts, free or shortly connate, dry (*Joinvillea*) or somewhat corolloid (*Flagellaria*); stamens 6, rarely 1 aborts, hypogynous or adnate to the base of the perianth segments, the filaments free, elongate, the anthers rather small, oblong, sagittate at base, retuse at apex, basifixed or dorsifixed near base; pollen 1-ulcerate, the aperture ± circular, graminoid, 2-celled when shed; pistil 1, carpels 3, the styles 1, with 3 linear, shortly connate arms, or 3, ventrally stigmatic, plumose and papillate; ovary superior, 3-locular, the ovules 1 per locule, axile, orthotropous or anatropous; fruit a small drupe, the seeds 1–3, globose, embryotega present; embryo small, lenticular, lying against the endosperm, less than 0.1 the length of the endosperm, 8 times wider than long; endosperm copious, mealy, starchy. Chromosomes: *Joinvillea* x = 18; *Flagellaria* n = 19, 18?

Composition: 3 genera, 7 species.

Distribution: Tropical and subtropical; southern $^2/_3$ of Africa, Madagascar, southern India, Indochina, the East Indies, northeastern Australia.

CYPERALES

The order is monotypic.

Chemistry: Sometimes tanniferous; seldom cyanogenic or saponiferous; many silica rich; mucilage absent; rarely producing simple indole alkaloids and sometimes ethereal oils.

CYPERACEAE (Figure 13).—Perennial, or infrequently annual herbs or very rarely woody, usually of wet habitats, often tufted, sometimes rhizomatous or tuberous, stem solid or rarely hollow, often trigonous, rarely compressed, very rarely articulated; prickle-hairs ± ubiquitous, silica-bodies often present, raphides absent; xylem vessel perforation plates most often simple, also scalariform or both in roots, stems and leaves; leaves usually basal or subbasal, cauline ones usually 3-ranked rarely distichous (*Coleochloa*), linear, grass-like, rarely terete, rarely reduced to a sheath, the sheath closed, rarely open (*Coleochloa*), a ligule rarely present, the stomates

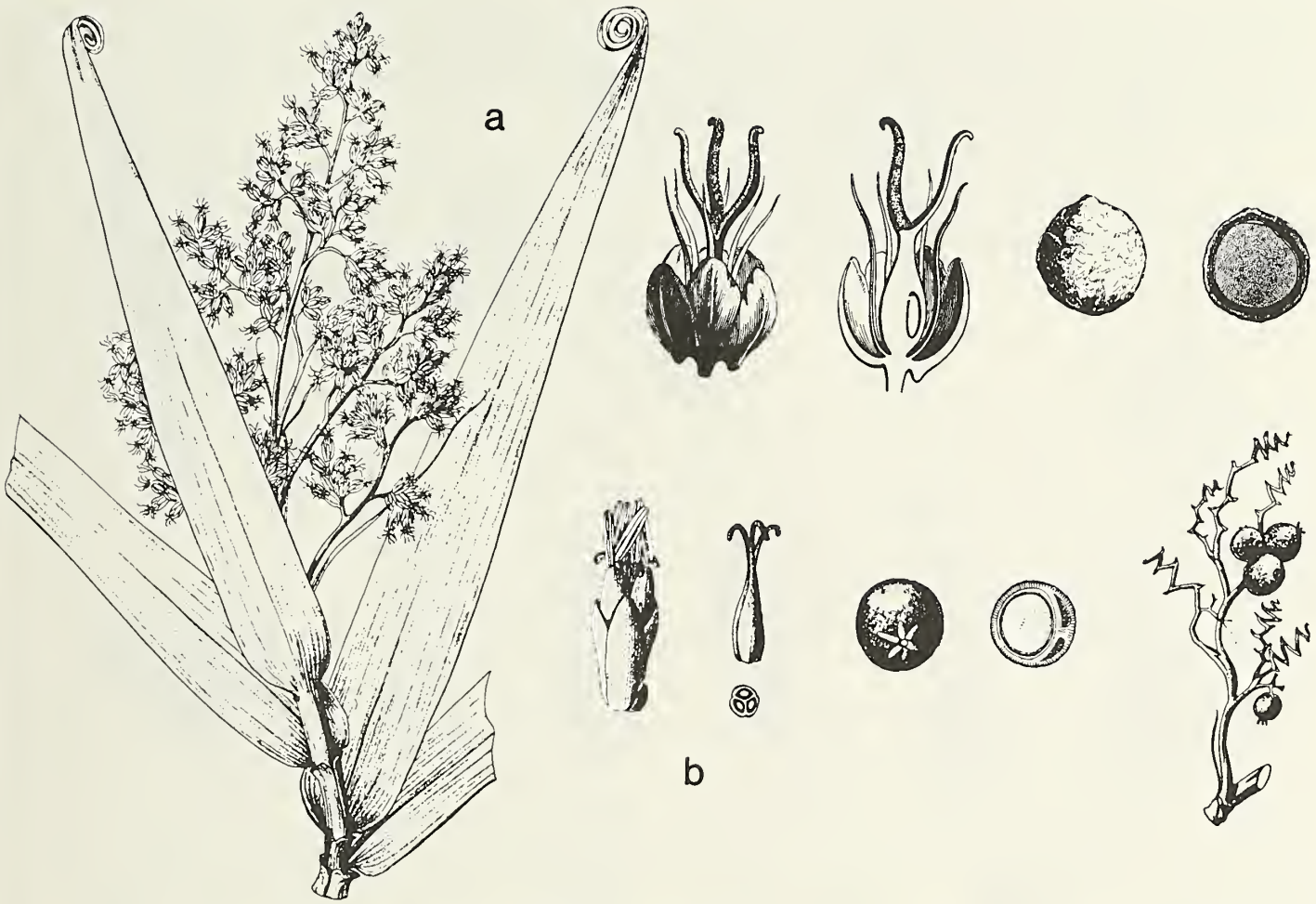


FIGURE 12.—FLAGELLARIACEAE: *a, Flagellaria indica* inflorescence and leaves showing the characteristic circinate apex, flower (the anthers fallen), l.s. of same, fruit, l.s. of same showing the minute embryo at the apex of abundant endosperm; *b,* flower, pistil and c.s. of same, fruit, l.s. of same with 2 aborted locules, part of infructescence (after Engler and Drude, Baillon).

paracytic or rarely tetracytic, usually in longitudinal rows, guard cells dumbbell-shaped; inflorescences simple or compound spikes, arranged in umbels or panicles, usually subtended by 1 or more leafy bracts; flowers small, each subtended by a glume, bisexual or the plants monoecious, very rarely dioecious, distichously or spirally arranged, rarely the ♀ spikelets reduced to 1 bract and 1 flower; anemophilous, or very rarely entomophilous (*Dichromena*); perianth absent, rarely scales, bristles or hairs in its place, very rarely subpetaloid; lodicules absent; stamens 3(1–22), hypogynous, the filaments free, anthers oblong or linear, basifixed, rarely apiculate; pollen 3-celled when shed, 1–4-aperturate, the apertures ulceroid, poroid or elongate; pistil 1, the carpels 3–2, style 1 with 2–3 branches, the stigmas papillate, usually decurrent; ovary superior, unilocular, uniovulate, the ovule basal, bitegmic, crassinucellar, anatropous; embryo sac antipodal cells ephemeral; endosperm formation Nuclear, the tissue later becoming cellular; fruit an achene, very rarely a drupe, often trigonous, sometimes lenticular; embryo axile, 0.2–0.5 the length of the endosperm, 1–1.5 times as long as wide; endosperm copious, starchy, oily, and with a protein layer, mealy or fleshy. Chromosomes: x = 3,5–45 or more; diffuse centromere in chromosomes of some species.

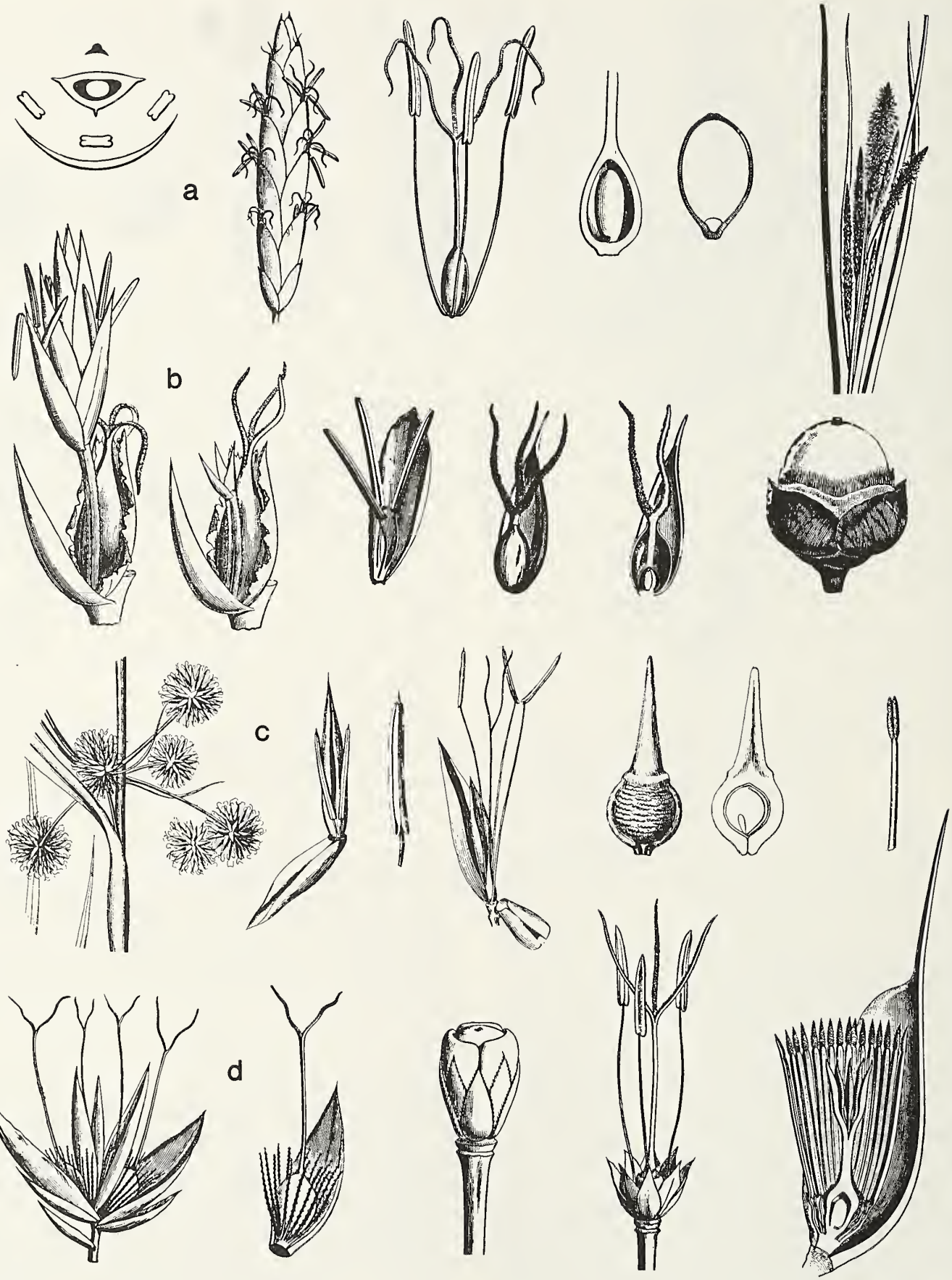
Composition: ~80 genera, ~3500 species.

Distribution: Cosmopolitan, centered in temperate regions.

POALES

The order is monotypic.

Chemistry: A variety of fructosans present; rarely tanniferous; occasionally cyanogenic; sometimes produce isoquinoline, simple indole or pyrrolizidine alkaloids; sometimes saponiferous; mucilage absent. There is very close similarity between the chemistries of Poaceae and Cyperaceae according to Hegnauer. Harborne points out the presence of the characteristic leaf flavonoids (glycoflavones, tricin) of the Poaceae in Cyperaceae; flavone, flavanols and leucoantho-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cyanins are fairly numerous in Poaceae and Arecaceae, but there is only one report of flavanol and no leucoanthocyanins from Araceae; coumarin and d-mannitol are present in Poaceae and Arecaceae.

POACEAE (Figures 14, 15).—Perennial or infrequently annual herbs, more rarely shrubs or trees, the stems terete, rarely flattened or angled, jointed, the nodes solid, often swollen, internodes usually hollow, rarely solid; silica present, raphides and calcium oxalate crystals absent; xylem vessel perforation plates simple, sometimes also less commonly scalariform, in roots, stem and leaves; leaves usually linear, occasionally broad, flat, rarely terete, ovate, elliptic, lanceolate or setaceous, alternate, distichous, very rarely spirally arranged (*Micraira*), the sheath usually open, rarely closed, a ligule usually present, sometimes a petiole between blade and sheath, the epidermis with long and short cells, stomates paracytic, in longitudinal rows, guard cells dumbbell-shaped; 2(1)-celled micro-hairs common, sometimes unicellular macro-hairs form an indument readily visible to the naked eye, hairs rarely uniseriate; inflorescences panicles, racemes, spikes or heads of spikelets; flowers (florets) small, usually bisexual, rarely the plants monoecious or dioecious, anemophilous, very rarely entomophilous, usually consisting of the reproductive organs enclosed in 2 bracts (lemma and palea), the floret(s) in a spikelet(s) usually subtended by 2 bracts (glumes), 2–3(0–many) hyaline scales (lodicules) internal to the lemma, sometimes the lemma, more rarely glumes, awned; florets 1–many per spikelet, distichous; perianth absent; stamens 3, 6(1–120), the filaments filiform or rarely short, free or rarely connate basally; anthers oblong, basifixed but the sacs usually partly separate basally and apically, rarely apiculate; pollen 3-celled when shed, 1-ulcerate; pistil 1, the carpels 2–3, styles 2(1,3), free or connate, the stigmas 2(1–3) generally plumose, sometimes only papillate, rarely ventral (*Chusquea gaudichaudii*); ovary superior, unilocular, uniovulate; ovule apical to basal, 2(1,0)-tegmic, usually pseudocrassinucellar, sometimes tenuinucellar, anatropous, hemitropous or campylotropous; secondary multiplication of the antipodal cells is characteristic and as many as 300 cells may be produced; endosperm formation Nuclear; fruit a caryopsis, rarely a drupe, nut, berry or utricle, sometimes hairy and wind dispersed; embryo with a relatively large haustorium (scutellum), basal to lateral, lying on the abaxial surface of the endosperm, 0.1–1.1 times the length of the endosperm, 3.3–8.0 times longer than wide; endosperm copious or rarely lacking in the mature seed (*Melocanna*), starchy, sometimes also oily, usually with a protein layer too. Chromosomes: x = 3–21, especially 7–10, monocentric.

Composition: ~600 genera, ~8000 species.

Distribution: Cosmopolitan and widespread, dominant in prairie, savanna and other open formations, less common in shady, wooded habitats, more common in dry than wet habitats.

FIGURE 13.—CYPERACEAE: *a, Cyperus longus* floral diagram, spikelet, flower, l.s. of ovary, l.s. of fruit showing small basal embryo and abundant endosperm, *C. stricta* inflorescences; *b, Schoenoxiphium rufum* spikelet with ♂ flowers above and ♀ flower below, spikelet reduced to the ♀ condition plus a glumigerous rhachilla, *Carex stricta* ♂ flower, ♀ flower, l.s. of same showing perigone enclosing ovary and style, *Scleria lucida* fruit; *c, Rhynchospora sparganioides* inflorescences, ♂ flower, anther, perfect flower, fruit, l.s. of same, *R. recurvata* stigma and upper part of style; *d, R. alba* part of inflorescence, ♀ flower, *Oreobolus pectinatus* fruit, flower, *Evandra aristata* l.s. of inflorescence (after Baillon, Martius).

ARECALES

The order is monotypic.

Chemistry: Noteworthy for their seed-fats. Lauric acid seems to be the most abundant fatty acid in seed-fats of most genera of palms. Lauric and myristic acids are also most abundant in the seed-fats of Lauraceae and Myristicaceae. Among other families Poaceae and Arecaceae have n-hexadec-9-enoic acid (palmitoleic acid). Several produce waxes; very often tanniferous; various sorts of polyphenols present; rarely producing pyridine alkaloids; occasionally saponiferous; seldom cyanogenic. See Poales for additional comparison with that order.

ARECACEAE (Figures 16–18).—Perennial trees, shrubs and climbers, sometimes rhizomatous, sometimes spiny; raphides and silica-bodies common; hairs sometimes absent, but often present particularly in the inflorescence and on young leaves, typically with a multicellular or unicellular base of sclerotic or cutinized cells and a distal uniseriate filamentous, or shield-like group of thin-walled cells, less commonly microscopic prickle-hairs; xylem vessel perforation plates scalariform or simple and scalariform, rarely vessels absent from the stem; leaf traces diverging toward center of stem before turning to exit in leaves; leaves alternate, clustered at the apex of the stem, scattered along the stem in climbing species, rarely radical, with a closed sheath and often a tubular ligule between the sheath and petiole, large to very large, pinnately or palmately divided or entire, folded in bud, induplicate or reduplicate, often prickly, the stomates tetracytic or hexacytic; inflorescence usually large, compound, rarely simple, spikes or a panicle, sometimes in dichasia, rarely heads, axillary or below the leaves, rarely terminal, subtended by one or more spathes; flowers entomophilous or anemophilous, usually bracteate, usually small, usually actinomorphic, the parts hypogynous, sometimes embedded in the spadix, bisexual or the plants monoecious, dioecious or polygamous; perianth usually in 2 whorls, rarely in a single whorl or the parts (to 10) spirally arranged, homochlamydeous or more rarely heterochlamydeous, often leathery, rarely glumaceous, usually green, sometimes white, tan or yellow to red; sepals 3(2), free or connate, imbricate or open in bud; petals 3(2), free or connate, valvate or imbricate; stamens usually 6, more rarely numerous or few (3–~400), the filaments free or connate, rarely adnate to the petals, the anthers as long as wide to linear,


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FIGURE 15.—POACEAE: *a, Zea mays* plant in flower, ♂ flower, part of ♂ inflorescence, ♀ inflorescence without the bracts, compound fruit, ♀ flower; *b, Tripsacum dactyloides* ♂ flower with palea, ♀ flower, l.s. of fruit, *T. angulatum* inflorescence; *c, Imperata brasiliensis* inflorescence, spikelet, essential organs (after Baillon, Martius).

FIGURE 14.—POACEAE: *a, Avena sativa* inflorescences, spikelet, flower with one glume removed, fruit, l.s. of same showing the basal lateral embryo, embryo, l.s. of same (below); *b, Oryza sativa* diagram of spikelet, spikelet, same with glumes removed, inflorescence, *Zizaniopsis microstachya* l.s. of part of leaf showing ligule at juncture of blade and sheath, *Digitaria lanuginosa* part of inflorescence, *Pariana intermedia* stamens; *c, Glyceria nervata* essential organs, *Bromus mollis* pistil, l.s. of same showing the solitary basal ovule, *Streptogyna crinata* stamen, pistil, floral diagram, base of plant showing distichous condition and open sheaths; *d, Bambusa bambos* part of inflorescence, spikelet, *Chusquea leptophylla* part of stem showing swollen joints and hollow internode, *Bambusa bambos* gynoecium and glumes, *Merostachys pluriflora* floral diagram, *Streptochaeta spicata* floral diagram (after Martius, Baillon).

dorsifixed or basifixed, the sacs sometimes separate at the base, and sometimes also apically, rarely separate from apex to base, spreading from a bifid connective and geniculate with the filament (species of *Geonoma*); pollen 2-celled when shed, usually monosulcate, trichotomo-sulcate, or 2-sulcate, 2-sulculate (-zonisulculate) in *Nypa*, usually smooth, sometimes echinate; sometimes an hypogynous disk present; pistils 1(3), the carpels 3(1–10), sometimes with the ventral suture open, the styles and stigmas usually 1–3, sometimes the styles absent, sometimes filiform with 4–10 very long stigmas (*Phytelephas*); ovary superior, 1–3(4–10)-locular, septal

FIGURE 16.—ARECACEAE: *a, Phoenix dactylifera* l.s. of ♂ flower, l.s. of ♀ flower, l.s. of fruit, seed, l.s. and c.s. of same showing the minute embryo in abundant endosperm, embryo enlarged, same with the cotyledon detached; *b, Cocos nucifera* l.s. of fruit showing the minute embryo in abundant endosperm, fruit with husk removed showing the 3 carpels, *Arenga gomutus* l.s. of ♂ flower; *c, Caryota urens* branch of inflorescence, *C. sobolifera* plant in flower, *C. urens* ♂ flower, ♀ flower in bud, same at anthesis, l.s. of same, *Areca catechu* fruit, l.s. of same; *d, Bactris balanophora* ♀ flower, l.s. of same, *Raphia ruffia* fruit and ♂ inflorescence, *Arenga langkab* l.s. and c.s. of fruit; *e, Trithrinax acanthocoma* flower, calyx, petal, androecium, gynoecium, l.s. of pistil (after Baillon, Le Maout and Decaisne, Martius).

FIGURE 17.—ARECACEAE: *a, Chamaerops humilis* part of inflorescence in spathe, ♀ flower, ♂ flower, diagram of ♂ and ♀ flowers; *b, Borassus flabellifer* l.s. of part of ♂ inflorescence, ♀ flower, part of ♂ inflorescence; *c, Maximiliana maripa* ♂ flower, petal with 2 stamens, *Microcoelum pulchra* l.s. of ♂ flower, l.s. of ♀ flower, *Astrocaryum weddellii* ♂ flower, petal with 2 stamens, fruit; *d, Allagoptera maritimum* androecium and a perianth segment, ♂ flower, *Calamus ciliaris* l.s. ♂ flower, ♀ flowers, l.s. of ♀ flower, pistil; *e, Geonoma rubescens* ♀ flower, pistil and staminode, staminode, pistil, *Attalea phalerata* ♀ flower, pistil and staminodal cup, ♂ flower, stamens, stamen (enlarged) (after Le Maout and Decaisne, Baillon, Martius).

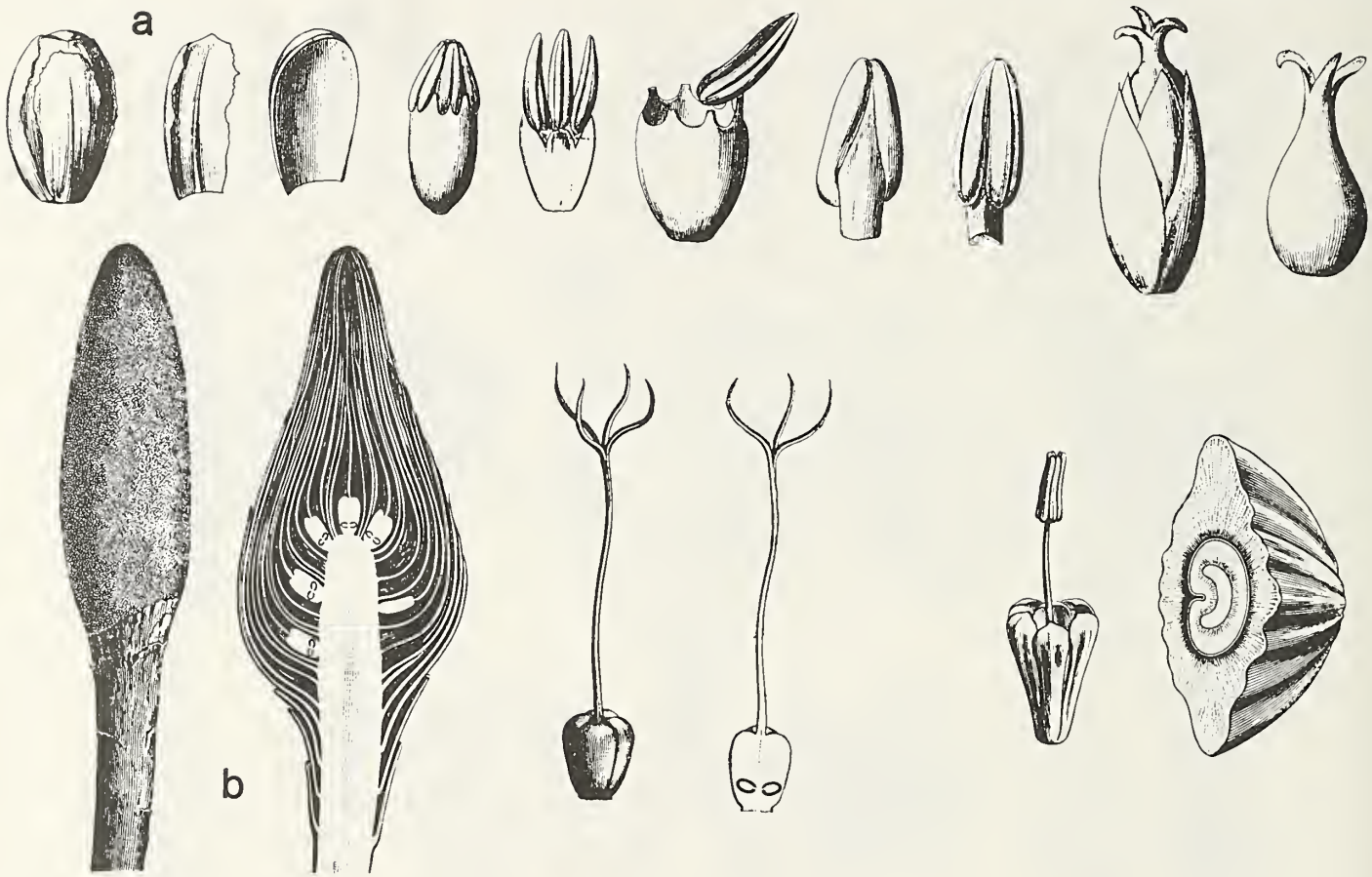


FIGURE 18.—ARECACEAE: *a, Elaeis melanococca* ♂ flower, sepal, petal, androecium, l.s. of same, androecium with all stamens but one removed, 2 views of anther, ♀ flower, pistil; *b, Phytelephas macrocarpa* ♂ inflorescence, l.s. of ♀ inflorescence, pistil, l.s. of same, *Nypa fruticans* ♂ flower (3 connate stamens), c.s. of fruit (after Baillon, Martius).

nectaries often present; ovules axile (subbasal to apical), 1 per ovary or locule, bitegmic, crassinucellar, anatropous, rarely semi-anatropous or orthotropous, embryo sac antipodal cells usually ephemeral, rarely persisting into embryogeny, endosperm formation Nuclear, later cellular; fruit a berry or drupe; seeds 1–6, large, the embryo minute, typically 0.2–0.5 the length of the endosperm, 1–3.5 times longer than wide, lateral or oblique, basal or above the middle; endosperm copious, often very hard, with cellulose, oil and aleuron, but starch absent. Chromosomes: x = (8–10),13–18,(19), especially 14,16,18.

Composition: ~220 genera, ~3000 species.

Distribution: Mainly pantropical, especially Asia and then America, extending into the warm temperate regions, in various habitats, including the understory of lowland rain forest, mangrove, deserts, but with accessible ground water, mountain thickets.

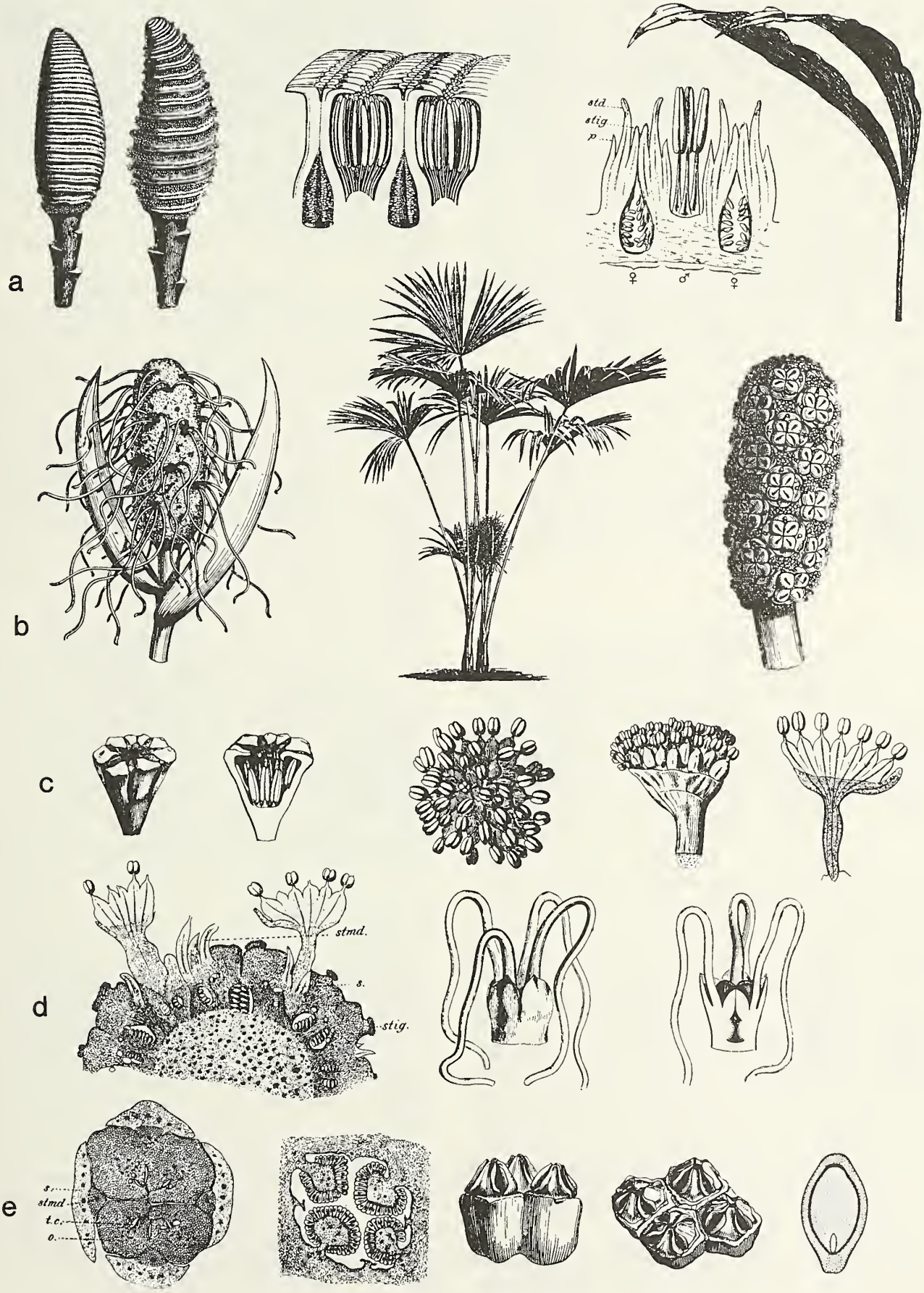
CYCLANTHALES

The order is monotypic.

Chemistry: Sometimes tanniferous; probably not saponiferous; mucilage present.

CYCLANTHACEAE (Figure 19).—Rhizomatous perennial herbs or shrubs, or lianas with aerial roots, rarely trees, rarely epiphytic; juice watery or milky; raphides commonly present, calcium oxalate crystals sometimes present, silica cells absent; xylem vessel perforation plates scalariform in the roots and leaves, vessels absent from the stem; leaves spirally arranged or distichous, large, sometimes fan-shaped, entire or bilobed apically, parallel veined, the petiole sheathing, the stomates tetracytic; inflorescence solitary, terminal or axillary, a spadix, sometimes screwlike, subtended by conspicuous green, white, yellow or red spathes; the plants monoecious, the flowers

FIGURE 19.—CYCLANTHACEAE: *a, Cyclanthus bipartitus* inflorescence before anthesis and at anthesis, l.s. of part of inflorescence, l.s. of 2 ♀ and 1 ♂ flower, upper part of leaf (greatly reduced); *b, Carludovica lancifolia* inflorescence, *C. palmata* plant in flower, *C. latifolia* spadix with fruits and ♂ flowers; *c, C. funifera* ♂ flower, l.s. of same, *C. plicata* ♂ flower from above, lateral view of same, l.s. of same; *d,* c.s. of spadix, *C. funifera* ♀ flower, l.s. of same; *e, C. plicata* c.s. of ♀ flower, c.s. of ovary, *C. palmata* group of fruits seen laterally and from above, *Carludovica* l.s. of seed showing the minute embryo in abundant endosperm (after Baillon, Martius, Le Maout and Decaisne).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small, spirally arranged, nectaries absent, the receptacle sometimes concave and the parts perigynous, more rarely epigynous, the female surrounded by 4 males, or the sexes in superposed whorls; pollinated by beetles; ♂ flowers: perianth in one whorl, cupular and several toothed or lobed, or rarely absent; stamens 6—~150, the filaments basally connate and sometimes adnate to the perianth, the anthers as long as wide or linear, basifixed or dorsifixed; pistillode absent; pollen 2-celled when shed, 1-sulcate or ulceroidate; ♀ flowers: free or connate; perianth absent or of 4 segments, free or basally connate, staminodes 4 and often filiform; pistil 1, the carpels 4(1,3), the style 1 or 0, stigmas 1, 2 or 4, often elongate and divergent; ovary unilocular, superior or often embedded in the spadix, the ovules numerous, bitegmic, crassinucellar, anatropous, parietal or apical; embryo sac antipodal cells 3; endosperm formation Helobial; fruit a syncarp or free berries; seeds numerous, small, sometimes with a sarcotesta, sometimes sculptured; embryo minute, basal, straight or curved, 0.1–0.2 the length of the endosperm, 2–4 times longer than wide; endosperm copious, fleshy or horny, with oil, aleurone, hemicellulose, rarely starch. Chromosomes: n = 9,15,16.

Composition: 11 genera, ~150 species.

Distribution: Mostly in moist forests; tropical America; West Indies.

Arales

Large herbs with a rhizome or corm to a minute thallus, rarely woody, sometimes climbers, often of wet habitats; raphides nearly universal (absent from *Acorus* and some Lemnaceae); xylem vessel perforation plates scalariform in the root, vessels absent in the minute plants; leaves simple to compound, radical or alternate, sometimes distichous, linear to nearly orbicular, the major veins longitudinal and parallel or more often palmate or pinnate, the minor ones reticulate, usually petiolate and with an open or closed sheath; inflorescence a spadix and spathe, bracteoles absent; flowers small, bisexual or the plants monoecious, rarely paradioecious; perianth homochlamydeous, the segments 0, 4, 6,(–9), free or connate; stamens 4, 6(1–8), free or connate, the anthers basifixed, rarely apically produced; pollen sulcate, porate, or nonaperturate, 2–3-celled when shed; pistil 1, the carpels 3(1–9), style 1, long or short, the stigma apical; ovary 3(1–9)-locular, superior or embedded in the spadix, the ovules 1–many, axile, basal, apical or parietal, bitegmic, crassinucellar, rarely tenuinucellar, anatropous or hemianatropous, rarely orthotropous; embryo sac antipodals ephemeral, rarely multiplying secondarily; endosperm formation ab initio Cellular; fruit usually a berry, sometimes a utricle; seed coat sometimes fleshy; embryo large or small, usually axile, endosperm copious to absent in the mature seed.

Distribution: Mostly pantropical and subtropical, few temperate.

Chemistry: Leucoanthocyanins, anthocyanins and flavonols present; mucilage fairly common, some have latex; many cyanogenic; amines common in the inflorescence, attracting carrion flies, also produced by Aristolochiaceae and Asclepiadaceae; some tannins and saponins common in Araceae but not Lemnaceae; the phenolic acids of Araceae and Lemnaceae are quite similar; alkaloids especially the indole group in Araceae but not Lemnaceae; the phenolic acids do not strongly support relation of Araceae and Pandanaceae. According to Gibbs the little we know of Cyclanthaceae is not against relation with Araceae and in general the chemistry of Arecaceae is in line with relation to the Arales. However there are differences. Gibbs has never found HCN in Araceae, but others have found it.

ARACEAE (Figures 20, 21*a*).—Perennial herbs, rarely woody, sometimes climbers with adventitious roots, or epiphytes, often of wet habitats, with a rhizome or corm, some with latex, very rarely aromatic (*Acorus*), raphides nearly universal (absent from *Acorus*), generally glabrous (uniseriate hairs in *Pistia*); xylem vessel perforation plates scalariform in the root, scalariform or vessels absent in the stem; leaves radical or alternate on elongate stems, sometimes distichous, simple, entire, divided, or compound, linear to nearly orbicular, the major veins parallel or more often palmate or pinnate, the minor ones sometimes evidently reticulate, usually petiolate and with an open or closed sheath, intravaginal scales rarely present, the stomates paracytic, tetracytic, or subsidiary cells more than four; inflorescence a scapose or axillary spadix, the flowers rarely few, subtended by and often enclosed in a sometimes colored spathe, individual floral bracts absent, very rarely vestigial bracteoles present (*Pothos*), the flowers sessile, very rarely pedicellate; flowers small, often fetid, the parts hypogynous, bisexual or usually unisexual, sometimes with a rudiment of the opposite sex, and the plants monoecious, males on the upper part of the spadix, often striking sterile flowers above or below the males, the females below, or rarely paradioecious, sometimes flowers absent from the apex of the spadix; perianth homochlamydeous, of 0, 4, 6,(–9) free or connate segments in 1 or 2 whorls, nectariferous in *Anthurium;* stamens 4, 6(1–8), free or connate, rarely completely so in synandria, the filaments often flattened, the anthers usually basifixed rarely adnate, or the locules immersed in an

FIGURE 20.—ARACEAE: *a, Acorus calamus* spadix (naturally not enclosed in spathe), flower, l.s. of part of ovary showing the apical ovules, fruit, *Gymnostachys anceps* flower from above, l.s. of pistil with a single apical ovule; *b, Zantedeschia* c.s. of lower and upper part of ovary, *Arum maculatum* stamen, l.s. of pistil, fruit, l.s. of seed, embryo, spadix with the spathe removed showing ♂ flowers above the ♀; *c, Orontium aquaticum* flower from above, stamen, l.s. of pistil showing the single basal ovule, *Calla palustris* spadix and spathe, flower, l.s. of same (the flower normally lacks a perianth); *d, Anthurium scandens* part of spadix, lateral view of flower, *Pistia stratiotes* spathe opened showing the single pistil below and the androecium above, l.s. of same, fruit adnate to the spathe, l.s. of seed; *e, Philodendron squamiferum* l.s. and c.s. of fruit, seed, l.s. of same with exterior integument removed, *Ambrosina* l.s. of inflorescence with pistil separated from androecium by a diaphragm, pistil and diaphragm from above, androecium; *f, Caladium striatipes* synandrium lateral view and from above, c.s. of same, pistil, l.s. and c.s. of same (after Baillon, Le Maout and Decaisne, Martius).

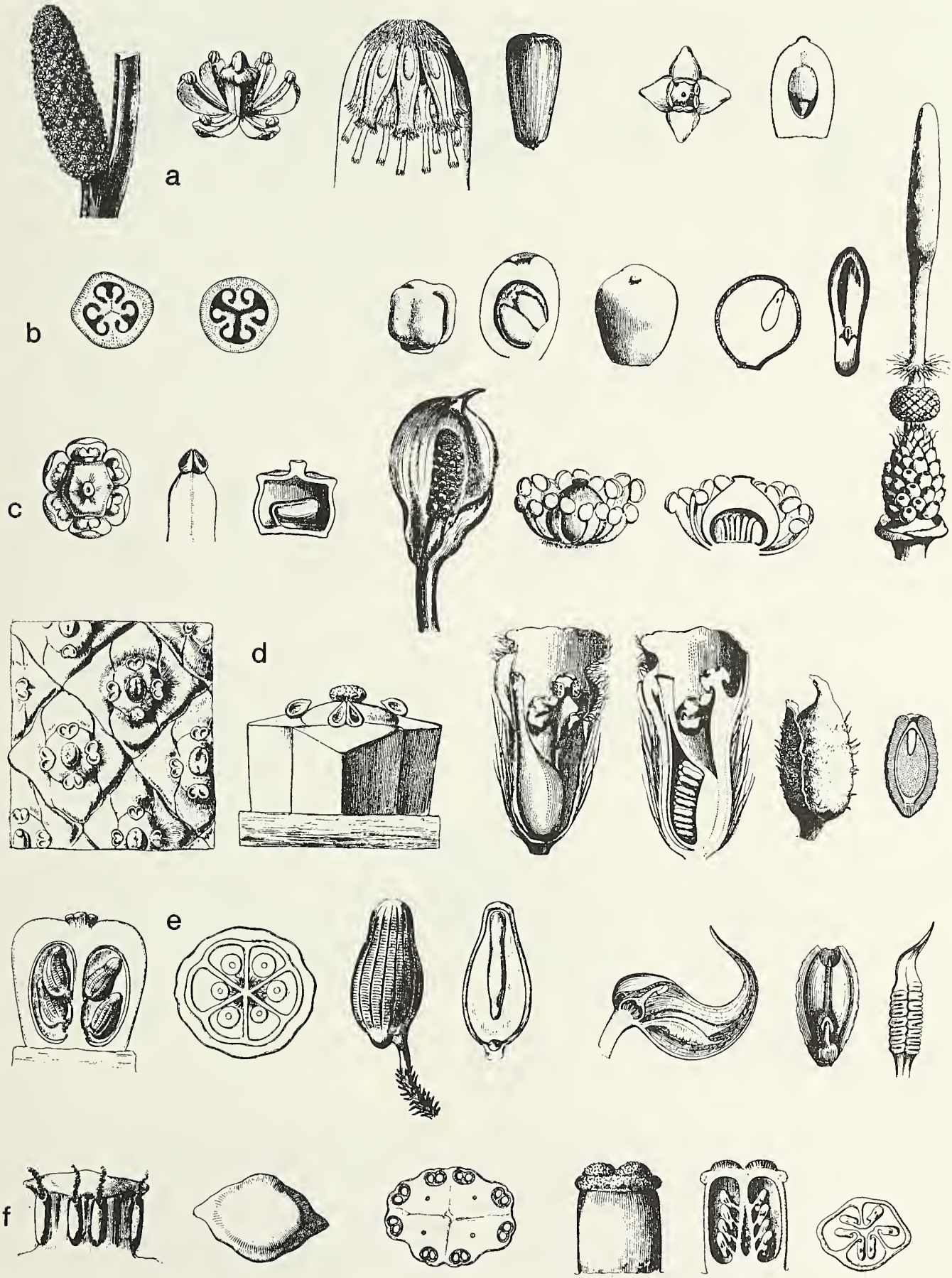
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FIGURE 21.—ARACEAE: *a, Arisarum vulgare* spadix showing ♂ flowers above and ♀ below, ♂ flower, l.s. of ♀ flower, *Amorphophallus konjac* group of ♂ flowers, l.s. of ♀ flower, *Symplocarpus* l.s. of seed (exalbuminous), *Cyrtosperma* l.s. of seed (after Baillon, Le Maout and Decaisne). LEMNACEAE: *b, Lemna minor* in flower, inflorescence in bract, l.s. of pistil, fruit, *L. paucicostata* fruiting frond; *c, L. valdiviana* stamen, *L. trisulca* seed, same with testa removed, l.s. of same, embryo, *Spirodela polyrrhiza* essential organs, stamen, fruiting frond (after Le Maout and Decaisne, Martius). TRILLIACEAE: *d, Paris quadrifolia* plant in flower, flower, l.s. of same, floral diagram; *e, P. polyphylla* c.s. of ovary, plant in flower, floral diagram, *Trillium erectum* floral diagram (after Baillon, Le Maout and Decaisne).

undifferentiated stamen, the connective rarely apically produced, dehiscence poricidal or longitudinal; pollen 1-sulcate, 3(2–4)-sulculate, zonisulculate, 3(4)-porate, oligoforate, polyforate or nonaperturate, the type correlated with pollinator, rarely in tetrads (*Xanthosoma*), 2–3-celled when shed; pistil 1, the carpels 3(1–9), the style long, short or absent, the stigma(s) apical, wet; ovary 3(1–9)-locular, superior or embedded in the spadix, the ovules 1–many, axile, basal, apical or parietal, bitegmic, crassinucellar, rarely tenuinucellar, anatropous or hemianatropous, rarely orthotropous; embryo sac antipodals usually 3 and ephemeral, rarely some secondary multiplication occurs; endosperm formation Cellular from the start; fruit a berry; seeds sometimes with a sarcotesta; embryo large or small (*Pistia*), usually axile in the endosperm, curved when the latter is absent, often 0.7–0.8 the length of the endosperm, 7–10 times longer than wide; endosperm copious, oily and sometimes also starchy, to absent in the mature seed, sometimes perisperm also present (*Acorus*). Chromosomes: x = 6?,7–9,11–17,21,22, especially 8,12–16.

Composition: ~110 genera, ~2500 species.

Distribution: Pantropical and subtropical, mostly on the forest floor or vines on trees, few in the temperate zones.

LEMNACEAE (Figure 21*b,c*).—Small or minute aquatic perennial herbs, a mere thallus, often rootless, the stomates anomocytic; raphides sometimes present; xylem vessels absent; inflorescence consists of 1 ♀ flower and 1–2 ♂ flowers on the surface of the thallus at its margin, sometimes with a small membranous spathe, the plants monoecious rarely dioecious; perianth absent; ♂ flowers: stamens 1–2, filament present or the anthers sessile; anther of 2 separate sacs, transversely or apically dehiscent; pollen 1-aperturate, ulceroid, 3-celled when shed; ♀ flowers: pistil 1, the carpel 1, style 1, short, the stigma apical; ovary superior, unilocular, the ovules 1–few, basal, bitegmic, crassinucellar, hemianatropous or anatropous; embryo sac antipodals usually ephemeral, rarely persisting to early endosperm formation; endosperm formation Cellular from the start; fruit a utricle, the seed with a fleshy outer seed coat; embryo axile, straight, 0.8 the length of the endosperm, 2.4 times longer than wide, endosperm scanty or absent in the mature seed, fleshy, with starch and other reserves. Chromosomes: x = 5,8,10,11, especially 10,11.

Composition: 6 genera, ~30 species.

Distribution: Cosmopolitan, except much of the arctic region, in quiet fresh water.

LILIALES

Usually herbs, less commonly shrubs, rarely trees, sometimes climbing, with rhizome, corm, bulb or tuber; raphides present in some Liliaceae, Agavaceae, Stemonaceae, Dioscoreaceae, Xanthorrhoeaceae, and Velloziaceae; xylem vessel perforation plates scalariform, simple or both, vessels sometimes absent from the stem or leaves; leaves linear to orbicular, basal or cauline, alternate or whorled, rarely opposite, the veins extending from the base to the apex, in the broader leaves transverse veins also evident; inflorescence a raceme, spike, umbel, panicle, thyrse, cyme, head, or the flower solitary; flowers usually conspicuous, bisexual, or less commonly the plants dioecious or polygamo-dioecious, actinomorphic, rarely zygomorphic, usually entomogamous; perianth segments usually 6, free or connate, corolline, rarely the outer whorl sepaloid; outer whorl 3(2–10) segments, inner 3(0–7) segments; stamens 6(1–~48, in bundles when many), hypogynous, epigynous or adnate to the perianth, the filaments free or connate, anthers basifixed or dorsifixed, rarely adnate, the connective sometimes apically produced; pollen usually 1-sulcate, sometimes 2-sulculate, trichotomosulcate, or 2-porate or nonaperturate, 2(3)-celled when shed; nectaries in the septa of the ovary or on the base of the perianth segments; pistil 1, the carpels 3(2–10), rarely nearly free, the styles 1(–10), the stigmas apical or ventrally decurrent; ovary superior, semi-inferior or inferior, 3(1–10)-locular, the ovules usually numerous, less commonly few to 1 per locule, axile, rarely parietal, basal or apical, 2(0–1)-tegmic, crassinucellar or tenuinucellar, anatropous, hemianatropous, campylotropous or orthotropous; embryo sac antipodals ephemeral or persistent into endosperm formation, rarely increased to 11; endosperm formation Helobial or Nuclear; fruit a loculicidal or septicidal, rarely ventricidal, capsule, less commonly a berry, rarely a samara, utricle or nutlet; seeds 1–many, various in size, shape and consistency, sometimes longitudinally ribbed; embryo small to large, straight or curved, axile; endosperm copious, hard or fleshy, very rarely floury.

Distribution: Cosmopolitan.

Chemistry: Steroidal saponins and sapogenes are characteristic of Liliaceae, Agavaceae and Dioscoreaceae. The order is not rich in alkaloids. The Liliaceae are notable for their steroidal alkaloids and tropolones, cardenolides and scilladienolides, some produce inulin and fructosans. Steroidal alkaloids also occur in Ranunculaceae. *Stemona* has a unique group of alkaloids. Amaryllidaceae has unique alkaloids which set it off from all other Liliales; however a few members of the Menispermaceae have one or two of the same alkaloids. Taccaceae has many alkaloids; dioscorin occurs in *Dioscorea*. The seed fats of Liliaceae, Xanthorrhoeaceae, Agavaceae and *Hypoxis* are rather similar. Gibbs knows of no chemical character that really distinguishes Dioscoreaceae from some, at least, of the other families of the order. No group of chemicals is unique to the Agavaceae; its chemistry is very like that of Liliaceae. According to Gibbs, chemistry does not favor segregating Smilacaceae from Liliaceae and the Wurmbaeoideae may warrant family status. A family Colchicaceae has been suggested; its outstanding chemical character is tropolone alkaloids, including colchicine. The Allieae lack the characteristic alkaloids of the Amaryllidaceae. Velloziaceae lack saponins, are often tanniferous, commonly produce resin or gum, are not cyanogenic. Some Xanthorrhoeaceae produce napthaquinones.

TRILLIACEAE (Figure 21*d,e*).—Herbs with simple erect stem, rhizomatous, raphides present; xylem vessel perforation plates

scalariform in the roots, vessels absent from the stem and leaves; leaves entire, whorled or opposite, usually fairly broad, with midrib and one major pair of longitudinal veins, the transverse veins between the midrib and longitudinal veins quite evident, the stem also with a few short basal leaf-sheaths, the young leaves sometimes floccose; inflorescence a terminal solitary flower or umbel; flowers bisexual, actinomorphic, the parts hypogynous; sepals 3–5(2–10), free, usually green, sometimes brownish, purplish or white; petals 3–5(0–7), free, usually colored, frequently differing in size and shape from the sepals; stamens 6(2–20), the filaments usually short, free, the anthers elongate, basifixed, connective usually produced apically and usually between the sacs; pollen 1-sulcate; pistil 1, the carpels 3(–10), the styles linear, 3(1–10), usually deeply lobed, the stigmas ventrally decurrent; ovary 3(–10)-locular, with septal nectaries, the ovules numerous, axile, bitegmic, crassinucellar, anatropous; embryo sac antipodal cells 3, usually ephemeral, occasionally persisting into early embryogeny; endosperm formation Helobial (sometimes Nuclear ?), division at first free-nuclear, later the tissue becomes cellular; fruit usually a berry, sometimes a fleshy loculicidal capsule; seeds several, globular, the embryo small, 0.1 the length of the endosperm, 1–2 times longer than wide; endosperm copious, hard or fleshy, starchy. Chromosomes: x = 5,7, especially 5.

Composition: 3 genera, ~50 species.

Distribution: Temperate North America and Eurasia.

LILIACEAE (Figures 22–24*a*).—Perennial or rarely annual herbs, or rarely somewhat woody, rarely climbing, with rhizome, corm, bulb or tuber; velamen present on roots of several genera; raphides present in some members; xylem vessel perforation plates scalariform, simple or both, vessels sometimes absent from the stem or leaves; leaves linear to orbicular, basal or cauline, alternate or whorled, rarely reduced to scales, the veins when conspicuous mostly extending from the base to the apex, in broader leaves cross veins also evident and sometimes the venation is pinnate (*Lilium* spp.), usually entire, rarely the margin prickly, the stomates mostly anomocytic, rarely paracytic (e.g., *Astelia*, *Hosta*), rarely with various kinds of hairs; inflorescences raceme or spike, rarely an umbel (*Allium*), subcapitate, cyme or solitary, rarely spathaceous (*Allium*), terminal, axillary or scapose; flowers actinomorphic, rarely slightly zygomorphic, usually bracteate, usually entomogamous, bisexual or rarely the plants polygamo-dioecious; perianth petaloid, the segments free or connate, 6(4,8,10 in *Antherolophus*) in 2 similar whorls, rarely basally saccate; stamens 6(3,4,8,9,12), hypogynous or adnate to the perianth, the filaments elongate, free or connate; rarely 3 staminodes present (*Erinna*); anthers basifixed or dorsifixed, dehiscing longitudinally, rarely poricidal, usually introrse or latrorse, more rarely extrorse; pollen 2(3)-celled when shed, usually 1-sulcate, sometimes 2-sulculate, trichotomosulcate, zonisulculate, 2-porate, 3-aperturate, irregularly aperturate or nonaperturate; nectaries in the septa of the ovary or on the base of the perianth segments, seldom absent; pistil 1, the carpels 3(2,4), rarely nearly free (*Tofieldia*, *Neodregea*, *Dipidax*),the style 1(3), stigmas 3, apical or decurrent ventrally; ovary 3(1,2,4)-locular, superior, rarely semi-inferior, the ovules many, rarely 1–few, axile, very rarely parietal (species of *Astelia*), bitegmic, crassinucellar or tenuinucellar, anatropous, hemianatropous or orthotropous; embryo sac antipodals 3, ephemeral or persistent into endosperm formation, rarely increased up to 11; endosperm formation Helobial, (Nuclear?); fruit a loculicidal or septicidal, rarely ventricidal capsule, more rarely a berry; seeds 1–many, the embryo axile in the endosperm, straight or curved, usually small, 0.1–2.0 the length of the endosperm, 1.6–16 times longer than wide; endosperm copious, fleshy or cartilaginous, never floury, with protein, oil, hemicellulose, rarely any starch. Chromosomes: x = 3–20,23,27, especially 6–8,12.

Composition: ~230 genera, ~3500 species.

Distribution: Cosmopolitan, except much of the arctic region, most abundant in temperate regions.

SMILACACEAE (Figure 24*b,c*).—Perennial herbs and shrubs, usually climbing, often with a large tuberous rhizome, the stem often with prickles; raphides generally present; xylem vessel perforation plates scalariform in the root, stem and leaves, vessels sometimes absent from the stem and leaves; leaves alternate, more rarely opposite, often leathery, usually fairly broad and petiolate, with a midrib and 1–2 pairs of arcuate veins from the base to the apex and conspicuous cross-veins, the petiole sometimes tendriliferous, the stomates anomocytic; inflorescences axillary umbels, racemes or spikes, rarely a terminal panicle; flowers small, actinomorphic, the parts hypogynous, rarely bisexual, the plants usually dioecious, staminodes present in ♀ flower but pistillode absent from ♂ flower; perianth segments usually 6, rarely the petals absent, usually greenish or yellowish, free or rarely connate; stamens 6(3,9), the filaments free or connate, adnate to base of perianth, the anthers about 3 times longer than wide, basifixed, introrse; pollen nonaperturate, 1-sulcate, 1-sulcoidate ?; pistil 1, the carpels 3, styles 3(–1), short, the stigma 3(–1)-lobed, decurrent ventrally; ovary 3(–1)-locular, the ovules 1–2 per locule, axile; fruit a berry, the embryo small, 0.2 the length of the endosperm, 3 times longer than wide; endosperm copious, hard, with hemicellulose, lipid, protein, and rarely some starch (*Ripogonum*). Chromosomes: x = 13–16, especially 16.

FIGURE 22.—LILIACEAE: *a, Tofieldia calyculata* flower, l.s. of same, apex of stamen, c.s. of ovary, seed (enlarged), floral diagram, *Veratrum* floral diagram; *b, Veratrum* apex of stamen, c.s. of ovary, l.s. and c.s. of seed, embryo, *Zygadenus glaberrimus* l.s. of flower; *c, Anguillaria dioica* l.s. of ♂ flower, l.s. of ♀ flower, *Narthecium ossifragum* l.s. of flower; *d,* inflorescence, dehisced fruit, l.s. of seed showing the small embryo, part of tails cut off (greatly enlarged), *Colchicum autumnale* androecium and perianth-limb laid open, stamen, apex of a style showing somewhat decurrent stigma, l.s. of seed showing minute embryo in abundant endosperm, l.s. of flower; *e,* ovary and base of styles, l.s. of same, c.s. of ovary, dehiscing fruit, c.s. of same, corm; *f,* seed and l.s. of same, floral diagram, *Maianthemum bifolia* flower, l.s. of same (after Baillon, Le Maout and Decaisne).


a
b
c
d
e
f

Composition: 4 genera, ~375 species.

Distribution: Mainly pantropical and subtropical, extending into temperate regions.

AGAVACEAE (Figure 24*d*).—Usually large perennial herbs, or shrubs or trees, rarely scandent, of dry habitats, usually rhizomatous, sometimes tuberous; raphides commonly present; xylem vessel perforation plates simple or scalariform in the roots, sometimes scalariform in the leaves, vessels absent from the stem and sometimes leaves; leaves elongate, crowded, often basal, sometimes spirally arranged along the stem, entire or toothed, usually thick, fibrous and leathery or fleshy, usually not sheathing, or the sheath open, the stomates usually anomocytic or tetracytic, sometimes paracytic (*Doryanthes*); inflorescence usually a large scapose panicle, thyrse, raceme or spike, rarely a head or the flower solitary; flowers usually bisexual, rarely the plants polygamo-dioecious or dioecious, actinomorphic or rarely slightly zygomorphic; perianth segments 6, corolline, free or connate; stamens 6, usually adnate to the corolla, more rarely epigynous or hypogynous, the filaments elongate, anthers oblong, usually dorsifixed, rarely basifixed (*Doryanthes*); pollen 1-sulcate or 2-sulculate, provided with a thick reticulate or retipilate sexine, usually single, rarely tetrads, 2-celled when shed; pistil 1, the carpels 3, style 1, usually elongate, slender, rarely short or absent, the stigma usually enlarged and shortly 3-lobed; ovary superior (e.g., *Yucca*) or inferior (e.g., *Agave*), septal nectaries usually present, 3-locular, the ovules numerous to 1 per locule, axile, or rarely unilocular (*Dasylirion*) with 3–6 basal ovules; ovules bitegmic, crassinucellar, anatropous; embryo sac antipodal cells rarely show secondary multiplication to 5 cells (*Doryanthes*); endosperm formation Helobial, perhaps sometimes incorrectly reported as Nuclear; fruit a loculicidal capsule or berry, the seeds many to one, usually compressed; embryo within the endosperm, 0.4 to as long as the endosperm, 5 times longer than wide; endosperm copious, fleshy, or hard, with hemicellulose, oil, protein, but no starch; perisperm present in *Yucca*. Chromosomes: x = 8,10,12,15–21,24,30, especially 19,30(5 large, 25 small).

Composition: ~20 genera, ~600 species.

Distribution: Pantropical and subtropical, extending into the temperate zones.

XANTHORRHOEACEAE (Figure 25).—Usually large xerophytic perennial herbs and shrubs, often with a thick, sometimes branched, woody stem, or rhizome, sometimes resinous, raphides commonly present; xylem vessel perforation plates simple or scalariform in the root, rarely scalariform in the leaves, vessels absent from the stem and usually leaves; leaves usually linear, sometimes liguliform, usually tufted, basal or apical, rarely scattered along the stem, alternate, not sheathing or with a short open sheath, sometimes with a prickly margin, the stomates anomocytic, less often paracytic; inflorescence a panicle, dense cylindrical spike, globular head, often scapose, or rarely the flowers solitary and axillary or terminal; flowers small or rarely large, bisexual or the plants dioecious; perianth mostly glumaceous rarely large and colored, the segments 6 in 2 whorls, free or shortly connate, the inner whorl sometimes petaloid; stamens 6 in 2 whorls, the inner attached to the base of the inner perianth segments, the outer free and hypogynous; anthers about as long as wide, 2-locular, basifixed or dorsifixed; pollen 1-sulcate, 2-sulculate, zonisulculate or spiraperturate; pistil 1, carpels 3, the styles usually elongate, 3 or 1 and 3-lobed, stigmas 3, apical, sometimes capitate; ovary superior, 3-locular, with 1–several axile ovules per locule, or 1-locular with 3 basal ovules; ovules bitegmic, crassinucellar, anatropous; embryo sac with 3 large antipodal cells; fruit a loculicidal capsule or rarely a nutlet; embryo straight, endosperm copious, hard, horny, with protein, oil, and hemicellulose. Chromosomes: x = 7–9,11,17,24, especially 11,8.

Composition: 8 genera, ~60 species.

Distribution: Endemic to Australia except for 3 species in New Guinea and 1 in New Caledonia.

PHILESIACEAE (Figure 26*a*).—Perennial shrubs, subshrubs, sometimes thin-stemmed climbers, rhizomatous; raphides sometimes present; xylem vessel perforation plates simple or scalariform or both in the roots, scalariform or vessels absent from the stem, vessels absent from, or perhaps plates rarely scalariform in the leaves; leaves alternate, sometimes distichous, usually petiolate, ovate or oblong with only the midrib conspicuous or often 1–2 pairs of arcuate lateral veins extending from the base to the apex or 4 pairs from the midrib to apex (*Petermannia*), reticulations between lateral veins mostly evident, rarely some leaves reduced to sheaths, the stomates anomocytic; inflorescences terminal or axillary (leaf-opposed in *Petermannia*), cyme, raceme, fascicle or the flower solitary; flowers bisexual, actinomorphic, often large, sometimes medium-sized, perianth nectaries present; perianth segments 6, corolline and similar or the inner much larger than the outer, free or rarely connate (*Behnia, Petermannia*); stamens 6, hypogynous or rarely adnate to the perianth, the filaments free or basally connate, anthers elongate, large, 3–6 times longer than wide, dorsifixed, introrse or latrorse (extrorse in *Petermannia*); pollen 1-sulcate, sometimes trichotomosulcate (both in *Geitonoplesium*), or nonaperturate (*Lapageria, Philesia*), spinulose in the latter 2 genera, 2-celled when shed; pistil 1, the carpels 3, style 1, elongate, the stigma terminal, shortly 3-lobed or capitate; ovary superior or rarely inferior

FIGURE 23.—LILIACEAE: *a, Polygonatum vulgare* plant in flower, flower, l.s. of same, *Aspidistra elatior* flower, l.s. of same, pistil, plant in flower; *b, Eriospermum parvifolium* flower, l.s. of same, dehisced fruit, l.s. of seed; *c, Aloe vera* l.s. of flower, *Asphodelus ramosus* locule of ovary with dorsal surface opened, l.s. of flower, *Peliosanthes teta* ruptured fruit showing the seeds, *P. campanulata* l.s. of flower, l.s. of seed; *d, Asparagus officinalis* l.s. of ♂ flower, l.s. of perfect flower, fruiting branch, l.s. of seed, *Tricyrtis* stigmas, floral diagram; *e, Ruscus* ♂ flower, ♀ flower, l.s. of ♀ flower, l.s. of fruit, *Allium cepa* seed, l.s. of same (after Baillon, Le Maout and Decaisne).


a
b
c
d
e


a
b
c
d

FIGURE 25.—XANTHORRHOEACEAE: *a, Xanthorrhoea hastilis* flower, l.s. of same, dehisced fruit, seed. *Lomandra longifolia* ♂ flower, l.s. of same; *b, Calectasia cyanea* part of plant in bloom, flower, l.s. of same, *Dasypogon bromeliifolius* inflorescence, flower, l.s. of same (after Baillon).

(*Petermannia*), 3- or 1-locular, the ovules usually numerous, sometimes few, axile or parietal, bitegmic, crassinucellar, campylotropous; embryo sac antipodals large; fruit a berry, sometimes large, rarely later becoming dry and dehiscent (*Eustrephus*), the seeds globose, embryo straight or slightly curved, 0.3 the length to as long as the endosperm; endosperm hard, with protein and oil. Chromosomes: x = 10, also n = 15,19.

Composition: 8 genera, 10 species.

Distribution: Peru to the southern tip of South America; eastern Australia, New Zealand, the East Indies to New Caledonia and Fiji; southeast Africa.

FIGURE 24.—LILIACEAE: *a, Danaë racemosus* flowering branch with cladodes and leaf scales, flower, l.s. of same, *Convallaria majalis* l.s. of flower, stamen inserted on base of corolla, pistil, inflorescence against part of leaf (after Baillon, Le Maout and Decaisne). SMILACACEAE: *b, Smilax brasiliensis* branchlet with tendrils and spines and inflorescence in bud, *S. mauritanica* flowering ♀ branch, *S. purpurata* l.s. of ♀ flower showing the decurrent stigmas; *c, S. herbacea* ♀ flower, *S. rotundifolia* fruit, *S. aspera* l.s. of seed, embryo, *S. brasiliensis* stamen, views of ♂ flower, *Smilax* ♂ floral diagram (after Baillon, Martius, Le Maout and Decaisne). AGAVACEAE: *d, Agave americana* flower, l.s. of same, plant in bloom (much reduced), *Yucca treculeana* l.s. of flower, l.s. and c.s. of a fruit, c.s. and l.s. of seed showing linear embryo in abundant endosperm (after Baillon, Sargent).

STEMONACEAE (Figure 26*b*).—Glabrous perennial herbs or rarely subshrub (*Stichoneuron*), erect or sometimes climbing, rhizomatous, or with tuberous roots; raphides sometimes present; xylem vessel perforation plates scalariform in the roots and sometimes in the stem, vessels absent from the leaves and sometimes stem; leaves alternate, opposite or in whorls of 3–5, often distichous, basal or along the stem or subapical, entire, petiolate, midrib and several pairs of lateral arcuate veins extending from the base of the blade to the apex or from the midrib toward the apex, with numerous fine straightish cross-veins between the arcuate veins, rarely with a short open sheath (*Pentastemona*), sometimes 2–3 sheaths at the base of the stem, the stomates anomocytic; inflorescences axillary, the flowers solitary and pedicellate or few-flowered cincinnae in racemes or subumbel; flowers bisexual, actinomorphic, small to moderate in size, nectaries absent (?); perianth petaloid, the segments free or connate, 4, 2-seriate or 5 in one whorl (*Pentastemona*); stamens 4 (5 in *Pentastemona*), the filaments short, free or connate (*Pentastemona*), or adnate to the very base of the perianth; anthers elongate or subglobose (*Pentastemona*), basifixed or dorsifixed or adnate and the anther sacs separate, the connective sometimes produced apically; pollen 1-sulcate, rarely nonaperturate (*Pentastemona*); pistil 1, the carpels 2 (3 in *Pentastemona*), style elongate or the stigma


a
b
c
d
e

sessile; ovary superior, semi-inferior or inferior, unilocular, the ovules numerous to 2, basal, apical or parietal (*Pentastemona*), bitegmic, crassinucellar, anatropous; embryo sac antipodal cells very ephemeral; endosperm formation Nuclear, the tissue later becoming cellular; fruit a capsule dehiscing by 2 valves, or indehiscent (*Pentastemona*), the seeds 1–many, broad-ellipsoid, longitudinally grooved or ribbed, with a basal, lobed aril, the funicle sometimes very long; embryo usually small, 0.1–0.7 the length of the endosperm, 1.5–7.0 times longer than wide; endosperm copious, fleshy or hard, starchy. Chromosomes: x = 7.

Composition: 4 genera, ~25 species.

Distribution: Southeastern Asia, the East Indies, northern Australia; southeastern United States.

DIOSCOREACEAE (Figure 26*c–e*).—Climbing perennial herbs or shrubs often with tuberous rhizomes, rarely spiny, glabrous, or hairs uni- or bicellular, stellate, or glandular; raphides present; xylem vessel perforation plates scalariform at least in the root and stem, vascular plexus in the nodes distinctive and consistent; leaves petiolate, alternate, rarely opposite and whorled, the blade usually broad, usually entire, sometimes palmately lobed or compound, often with a cordate base, the main veins extending from the base to the apex of the leaf and cross-veins quite evident, the stomates mostly anomocytic; inflorescences axillary cymes, spikes, racemes, panicles or heads, the plants dioecious; flowers small, inconspicuous, actinomorphic, entomophilous, perianth nectaries common; perianth segments 6 in 2 series, connate; ♂ flowers: stamens 6 or 3, sometimes 3 staminodes present, adnate to the base of the perianth, the filaments elongate, free or shortly connate, the anthers basifixed, extrorse or introrse, less than twice as long as wide, the sacs sometimes separate, the connective often apically produced, a pistillode sometimes present; pollen 1-sulcate or 2(3)-sulculate, 2-celled when shed; ♀ flowers: pistil 1, the carpels 3, styles 1 or 3, the stigmas 3, each sometimes 2-parted; ovary inferior, septal nectaries common, 3-locular, the ovules 2 or 4 per locule, axile, bitegmic, crassinucellar, anatropous; staminodes often present; embryo sac antipodal cells degenerate soon after fertilization; endosperm formation Nuclear, the tissue later becoming cellular; fruit usually a capsule, sometimes samara or berry, the seeds often winged; embryo small, 0.3 the length of the endosperm, as long as to 3 times longer than wide; endosperm copious, horny, with protein, oil, and hemicellulose. Chromosomes: x = 9,10,12,14,18, especially 10.

Composition: ~6 genera, ~600 species.

Distribution: Pantropical and subtropical, a few species extending into temperate regions.

TACCACEAE (Figure 27*a*).—Perennial herbs with creeping, sometimes tuberous rhizomes; raphides present; xylem vessel perforation plates scalariform in the root, vessels absent from the stem and leaves; leaves basal, large, broad, entire to deeply lobed, with a midrib and fairly numerous lateral veins extending from it, the petiole often long, the stomates anomocytic; inflorescence scapose, the flowers in a cymose umbel, often subtended by a combination of linear and broad bracts; flowers bisexual, actinomorphic; perianth homochlamydeous, the segments 6 in 2 series, connate, campanulate, petaloid, dark-colored (brownish); stamens 6, adnate to the perianth, the filaments very short, broad, concave, the anthers inflexed, about as long as wide, adnate or basifixed, anther sacs separated by connective, the connective shortly produced apically; pollen 1-sulcate, 2-celled when shed; pistil 1, the carpels 3, intercarpel nectaries sometimes present, the style 1, short, style arms broad, usually bilobed, relexed; ovary inferior, unilocular, the ovules numerous, parietal, bitegmic, crassinucellar, anatropous; embryo sac antipodal cells ephemeral; endosperm formation Nuclear, the tissue later becoming cellular; fruit a berry or rarely loculicidal capsule; seeds numerous, longitudinally ridged, the embryo minute, included in the endosperm, basal or lateral, less than 0.1 the length of the endosperm, twice as long as wide; endosperm copious, somewhat cartilaginous, with aleurone, lipid, but no starch and little or no hemicellulose. Chromosomes: x = 15.

Composition: 2 genera, ~30 species.

Distribution: Pantropical, centered in southeastern Asia, extending into Polynesia; limited to Amazon basin in America.

PONTEDERIACEAE (Figure 27*b,c*).—Freshwater perennial or rarely annual (*Hydrothrix*) herbs with a short or creeping rhizome, vertical stems short, rarely submerged (*Hydrothrix*); raphides present; xylem vessel perforation plates scalariform in the root, scalariform or vessels absent in the stem, vessels absent from the leaves; leaves mostly in a rosette, sometimes distichous, rarely spirally arranged along an elongate stem, the blade broad or narrow with primary veins extending from base to apex, petiole distinct, sheath mostly closed, intravaginal scales sometimes present, the stomates paracytic; inflorescence a raceme, panicle, thyrse or rarely the flower solitary; flowers bisexual, actinomorphic or zygomorphic; perianth petaloid, marcescent, the segments 6 (4 in *Scholleropsis*), biseriate, connate, rarely free (*Monochoria* species); stamens 6 or 3 (1 in *Hydrothrix*), mostly adnate to the perianth but free from one another, sometimes dissimilar and unequal in length, sometimes 1–2 staminodal; anthers oblong, rarely one larger than the others, basifixed or dorsifixed, dehiscence longitudinal,

FIGURE 26.—PHILESIACEAE: *a, Philesia buxifolia* flowering twig, *Lapageria rosea* flowering branch, l.s. of flower, anther, stigma, c.s. of ovary, floral diagram (after Lindley, Baillon, Le Maout and Decaisne). STEMONACEAE: *b, Stemona tuberosa* stamen, c.s. of same and c.s. of anther (above), flower, l.s. of same, *S. gloriosoides* flowering twig, dehisced fruit with pendent seeds on long funicles, seed, l.s. of same (after Baillon, Lindley). DIOSCOREACEAE: *c, Trichopus zeylanicus* flower, l.s. of same, views of stamen, style and stigmas, c.s. of ovary, fruit, seed, l.s. and c.s. of same; *d, Dioscorea batatas* part of ♂ plant in bloom, part of ♀ plant in flower and fruit, *D. adenocarpa* ♂ flower, l.s. of same, views of stamen; *e, Dioscorea* ♀ flower, *D. sativa* fruit, *D. adenocarpa* dehisced fruit, winged seed, *Tamus communis* ♀ flower, l.s. of same, fruits, *Rajania hastata* fruit (after Knuth, Baillon, Le Maout and Decaisne, Martius).

FIGURE 27.—TACCACEAE: *a, Tacca cristata* inflorescence, flower, l.s. of same, *T. leontopetaloides* fruit, seed, l.s. of same showing the minute embryo in abundant endosperm (after Baillon). PONTEDERIACEAE: *b, Pontederia cordata* flower, l.s. of same, flowering stem; *c, Eichhornia tricolor* part of inflorescence, views of fruit, same dehiscing, seed, *Monochoria vaginalis* seed, l.s. of same showing the long embryo in abundant endosperm (after Baillon, Martius). AMARYLLIDACEAE: *d, Hypoxis erecta* inflorescence and part of leaf, l.s. of bud, *H. decumbens* flower, views of stamen, *Hypoxis* c.s. of ovary, dehisced fruit, c.s. of same, seed, l.s. of same, embryo; *e, Alstroemeria monticola* perianth segments, *A. plantaginea* upper part of style and stigmas, apex of stamen, *A. versicolor* seed and l.s. of same showing the small embryo in abundant endosperm, *A. psittacina* l.s. of flower (after Le Maout and Decaisne, Martius, Baillon).

FIGURE 28.—AMARYLLIDACEAE: *a, Narcissus tazetta* dehisced fruit, seed, l.s. of same showing the minute embryo, l.s. of flower showing corona and stamens inserted on the perianth, pistil, *Hymenocallis calathina* l.s. of flower showing the staminodal corona (after Baillon). VELLOZIACEAE: *b, Vellozia epidendroides* part of stem showing the persistent leaf bases and numerous adventitious roots (in c.s.) within them, *V. caruncularis* scapose flower and parts of leaves, *V. tenella* part of perianth and stamens, *V. hemisphaerica* l.s. of flower, *Barbacenia vandellii* lateral view of stamen, *B. luzulifolia* flower opened out; *c, B. purpurea* flower, stamen, l.s. of flower, *Barbacenia* floral diagram, *B. gracilis* dehisced fruit, seed, l.s. of same showing the minute embryo in abundant endosperm, *B. amica* seed, l.s. of same (lower pair) (after Martius, Baillon).

rarely by pores; pollen elongate, 2(1,3)-sulculate, 2-celled when shed; pistil 1, the carpels 3, style 1, often trimorphic, the stigma apical, punctiform or shortly 3- or 6-lobed; ovary superior, internal septal nectaries usually present (absent in *Heteranthera*), 3-locular, the ovules numerous, axile or 1-locular and uniovulate, bitegmic, crassinucellar, anatropous; embryo sac antipodals ephemeral; endosperm formation Helobial, the tissue later becoming cellular; fruit a loculicidal capsule or utricle with one fertile cell; seeds small, longitudinally ribbed; embryo cylindrical, axile in the endosperm, as long as the endosperm, 5–7.8 times longer than wide; endosperm copious, floury, starchy and with an outer layer of aleurone. Chromosomes: x = 8,14,15,26, especially 8.

Composition: ~7 genera, ~30 species.

Distribution: Primarily pantropical, extending into temperate America, Asia and Africa.

AMARYLLIDACEAE (Figures 27*d,e*, 28*a*). —Perennial herbs usually of dry habitats, with a tunicated bulb, very rarely a rhizome; raphides usually present; xylem vessel perforation plates scalariform in the roots, vessels absent from the stem and leaves; leaves entire, often linear or lorate, basal, usually with inconspicuous veins, sometimes with a closed sheath, the stomates anomocytic, generally glabrous (except *Hypoxis*); inflorescence a scapose cymose umbel, rarely subcapitate, rarely a solitary flower, often enclosed in bud by 1 or more membranous bracts; flowers bisexual, actinomorphic rarely zygomorphic, usually showy; perianth 6 segments in 2 whorls, free above the ovary or connate, corolline, sometimes with nectaries, a corona sometimes present; stamens 6(3,–~20 in 1 species of *Gethyllis* and 6 bundles with about 8 anthers each in another), epigynous or adnate to the perianth, the filaments free or connate, long or short, the anthers elongate, dorsifixed or occasionally basifixed, introrse, dehiscence longitudinal, rarely by apical pores; pollen usually 1-sulcate or 2-sulculate, 2-celled when shed; pistil 1, the carpels 3, style slender, the stigmas apical, capitate or 3-lobed; ovary inferior, with septal nectaries, 3-locular, rarely 1-locular by abortion (*Calostemma*), the ovules mostly numerous, rarely 1–few per locule, axile or rarely parietal (*Leontochir*, *Empodium*), 1- or 2-tegmic (ategmic in *Crinum*), pseudocrassinucellar, anatropous or semi-anatropous; embryo sac antipodals often persist into early embryogeny; endosperm formation Helobial, the tissue later cellular, Nuclear reported but needs confirmation; fruit a loculicidal capsule or more rarely a berry; embryo 0.6 the length of the endosperm, 6 times longer than wide; endosperm copious, with cellulose or starch, also aleurone, and oil (?), enclosing the embryo. Chromosomes: x = 6–12,14,22–24, especially 7–9,11,12.

Composition: ~75 genera, ~1100 species.

Distribution: Pantropical and subtropical, extending into the temperate zones, especially of the Southern Hemisphere.

VELLOZIACEAE (Figure 28*b,c*).—Perennial herbs and sparsely branched shrubs, usually of dry habitats; raphides sometimes present; xylem vessel perforation plates simple in the root, scalariform or absent in the stem and leaves (*Talbotia*); leaves in a basal rosette or apical tufts, linear-acuminate, with midrib, sometimes with a saw-toothed margin, the sheath persistent, the stomates paracytic, rarely tetracytic; flowers usually solitary on each scape, pedicellate, terminal, bisexual, rarely functionally unisexual and the plants dioecious (*Barbaceniopsis*), actinomorphic; perianth segments 6 in 2 whorls, petaloid, free or basally connate, sometimes with a small corona behind the anthers; stamens 6(–~48) in 6 bundles when more than 6, the filaments epigynous (*Talbotia*) or adnate to the perianth, sometimes flattened, the anthers sometimes subsessile (*Barbaceniopsis*), introrse, linear, basifixed or dorsifixed; pollen 1-sulcate or nonaperturate, sometimes in tetrads (*Vellozia*); pistil 1, the carpels 3, style 1, the stigma capitate or shortly 3-lobed; ovary with internal septal nectaries, inferior, 3-locular, the ovules very numerous, axile on stalked placentas, bitegmic, pseudocrassinucellar, anatropous; fruit a loculicidal capsule, sometimes rupturing irregularly; seeds numerous, the embryo small, 0.2–0.3 the length of the endosperm, 2.5–4.0 times longer than wide; endosperm copious, hard, with hemicellulose, protein, oil, and starch. Chromosomes: n = 9,16 (Goldblatt in Raven), ~24,26.

Composition: 6 genera, ~270 species.

Distribution: Tropical South America (1 species in Panama) and Africa, Madagascar, southern Arabia.

BROMELIALES

The order is monotypic.

Chemistry: Steroid saponins sometimes present; tannin and mucilage common; alkaloids absent.

BROMELIACEAE (Figures 29, 30).—Perennial herbs or rarely woody plants often of dry habitats, and often epiphytic in moist habitats, sometimes rhizomatous or stoloniferous; hairs characteristically peltate shield-like scales with a uniseriate stalk, functioning to conserve and absorb water, rarely other types also present; raphides and silica present; xylem vessel perforation plates usually scalariform, sometimes simple in the roots, vessels sometimes absent from the stem and leaves; leaves mostly in a rosette, spirally arranged, rarely distichous, liguliform, without a midrib (except *Pitcairnia* spp.), entire or often with spiny teeth, the sheath open, the stomates tetracytic or sometimes hexacytic; inflorescence a terminal, rarely axillary, panicle, raceme, spike or head, rarely the flower solitary, often with brightly colored bracts; flowers almost

FIGURE 29.—BROMELIACEAE: *a, Navia acaulis* pistil, dehiscent fruit and calyx, seed, l.s. of same, *Brocchinia paniculata* c.s. of ovary, *Pitcairnia inermis* l.s. of pistil showing the semi-inferior ovary, *Dyckia encholirioides* l.s. of flower; *b,* sepal, petal, views of stamen, pistil, seed, l.s. of same, *Aechmea aquilega* indument scale greatly enlarged; *c, Vriesea gigantea* flower, l.s. of same, *V. platynema* seed greatly enlarged, *Tillandsia streptocarpa* inflorescence, parts of leaf, *Bromelia urbaniana* part of leaf; *d, Tillandsia spiculosa* stamen, l.s. of ovary, l.s. of seed showing the basal embryo, *Bromelia urbaniana* flower, sepal, petal and stamens, l.s. of ovary, apex of style arm showing the decurrent stigma, *Aechmea aquilega* l.s. of flower, the perianth and stamens removed (after Martius, Baillon).


a
b
c
d

FIGURE 30.—BROMELIACEAE: *a, Ananas comosus* multiple fruit, *Bromelia pinguin* fruit, *Billbergia speciosa* plant in flower, floral diagram, l.s. of flower; *b, B. nutans* c.s. of ovary, l.s. of seed showing the small embryo in abundant endosperm, *Portea petropolitana* lower part of petal with appendages, sepal, stamen, upper part of style with stigmas; *c, Streptocalyx longifolius* petal and stamen, l.s. of ovary, *Araeococcus parviflorus* calyx, *Acanthostachys strobilacea* flower, l.s. of same, fruit, seed, l.s. of same (after Martius, Baillon).

always actinomorphic, rarely weakly zygomorphic, bisexual or more rarely the plants polygamous or dioecious, entomogamous, ornithogamous, rarely anemogamous; perianth heterochlamydeous, but sometimes the sepals colored (*Sodiroa, Massangea*); sepals 3, free or basally connate; petals 3, free or connate, usually considerably larger than the sepals, sometimes with a pair of basal appendages; stamens 6, free or basally adnate to the petals, the filaments usually separate, sometimes basally connate, often long-exserted, the anthers linear, usually dorsifixed; pollen usually 1-sulcate or 1-sulcoidate, sometimes 2-polyaperturate, then the apertures slightly elongate, circular or irregular, 2-celled when shed, rarely in tetrads; pistil 1, the carpels 3, style 1, elongate, the stigmas 3, usually linear, sometimes spirally twisted around each other; ovary superior, semi-inferior or inferior, 3-locular, with internal septal nectaries, the ovules usually numerous, axile, bitegmic, crassinucellar, anatropous, rarely campylotropous; embryo sac with 3 small antipodal cells; endosperm formation Helobial, the tissue at first free-nuclear, later becoming cellular; fruit a septicidal, more rarely loculicidal, capsule, berry or syncarp; seeds usually numerous, small, sometimes appendaged or winged; embryo lateral to the endosperm or rarely embedded in it, 0.2–1.8 times the length of the endosperm, 2–10 times longer than wide; endosperm copious, mealy, starchy. Chromosomes: x = 8,9,17,25,27,28, especially 25,8.

Composition: ~50 genera, ~2000 species.

Distribution: Tropical and warm temperate America, except for one West African species.

Commelinales

Herbs, often of wet habitats, or mesophytic to somewhat xerophytic, sometimes succulent; raphides in Commelinaceae (except *Cartonema*), absent from the other families; xylem vessel perforation plates simple, scalariform or both, vessels sometimes absent from the leaves, very rarely from the stem; leaves spirally arranged or distichous, sometimes basal, usually elongate; flowers actinomorphic or zygomorphic, often ephemeral and marcescent, bisexual or rarely the plants polygamo-monoecious, more rarely monoecious, very rarely dioecious, the parts mostly hypogynous; perianth usually heterochlamydeous; sepals 3(2,0), green or hyaline, very rarely colored, rarely connate; petals 3(0), corolline, rarely scarious, rarely connate; stamens 6(4–1), sometimes 3(4) staminodes present, the filaments free or connate, very rarely epipetalous; anthers basifixed or dorsifixed, dehiscent longitudinally or by apical pores; pollen 1(2)-sulcate or nonaperturate or spiraperturate, 2–3-celled when shed; nectaries absent; pistil 1, the carpels 3(2), style 1, rarely appendaged, the stigma apical, usually unlobed, rarely trifid; ovary superior, 3(–1)-locular, the ovules 1–many per locule, axile or parietal, rarely basal, bitegmic, crassinucellar or tenuinucellar, orthotropous to anatropous; fruit a loculicidal capsule, rarely a berry; seeds often sculptured, the embryo small, lying against the endosperm; endosperm copious, mealy or floury, starchy.

Distribution: Primarily pantropical and subtropical, relatively few in temperate zones.

Chemistry: Sometimes saponiferous; sometimes tanniferous; phenolic acids, sinapic and ferulic acid common and sometimes abundant; mucilage in Commelinaceae at least. According to Gibbs, there is rather close agreement between the chemistries of Bromeliaceae and Commelinaceae at least.

COMMELINACEAE (Figure 31*a–c*).—Perennial or less commonly annual herbs, often succulent, erect to decumbent or rarely climbers, very rarely epiphytes, the stems usually articulated and the nodes swollen, sometimes tuberous, stoloniferous, rarely rhizomatous or bulbiferous; raphides present (not in *Cartonema*), silica bodies somtimes present; xylem vessel perforation plates simple in all organs, rarely also scalariform, or vessels absent from the stem and leaves (*Cartonema*); leaves spirally arranged or distichous along the stem, rarely in a rosette, often elongate, with a prominent midrib, more rarely the blade ovate to suborbicular, entire, the sheath closed, the stomates commonly tetra- or hexacytic, sometimes paracytic; sometimes a variety of hairs, e.g., 3-celled glandular microhairs much larger than those of grasses, and macrohairs present; inflorescences terminal or axillary, rarely leaf-opposed or basal, simple or compound cincinnus, thyrse, or fascicle, rarely 1-flowered, rarely spike-like (*Cartonema*), sometimes within a protecting bract; flowers usually actinomorphic, sometimes zygomorphic, bisexual or rarely the plants polygamo-monoecious, the parts mostly hypogynous; perianth heterochlamydeous, but sometimes the sepals are colored; sepals 3, free or rarely connate; petals 3, usually free, rarely connate, ephemeral and deliquescent; stamens 6(3–1), sometimes 2–4 converted to attractive staminodes, the filaments free or very rarely basally connate, very rarely basally epipetalous, sometimes bearded with brightly colored hairs; anthers usually less than twice as long as wide, rarely 1 larger than the others, basifixed, dorsifixed, or versatile, dehiscing longitudinally, or rarely by an apical pore; pollen 1-sulcate, rarely with additional apertures, 2-celled (3 in *Floscopa scandens*) when shed; nectaries absent; pistil 1, the carpels 3 (2 in a few genera), style 1, the stigma usually 1, acute or capitate, rarely trifid; ovary 3(2)-locular, the ovules few to 1, rarely many per locule, uniseriate or biseriate, axile, bitegmic, crassinucellar, rarely tenuinucellar, orthotropous, hemianatropous, (or anatropous ?); embryo sac antipodals ephemeral but persistent in *Tinantia erecta;* endosperm formation Nuclear, the tissue usually later becoming cellular; fruit a loculicidal capsule, rarely berry; seeds often sculptured, sometimes with an aril, rarely winged; embryo marginal, its position indicated by an embryotega, 0.3 the length of the endosperm, 1.3–1.7 times longer than wide; endosperm copious, mealy, starchy. Chromosomes: x = 4–20, especially 6,8,9,12,14.

Composition: ~50 genera, ~700 species.

Distribution: Primarily pantropical and subtropical, ex-


a
b
c
d
e
f

tending into the temperate zones, usually in mesic open or forest habitats.

MAYACACEAE (Figure 31*d–f*).—Herbs of freshwater and marshes, often submerged, the stems filiform, sometimes branched; raphides, calcium oxalate crystals and silica absent; xylem vessel perforation plates scalariform in root, stem and leaf; leaves numerous, linear, spirally arranged along the stem, apically minutely bidentate, not sheathing, the stomates paracytic, sometimes uniseriate hairs present in the leaf axils; inflorescence subumbellate or a solitary flower, at the apex of the stem, the pedicels long, the flowers subtended by a membranous bract; flowers bisexual, actinomorphic, the parts hypogynous, nectaries absent; sepals 3, free, green; petals 3, free, corolline, clawed; stamens 3, free, the anthers basifixed, 4-locular, dehiscing by an apical pore or short slit; pollen monosulcate; pistil 1, the carpels 3, style 1, the stigmas apical, 1 or shortly trilobed; ovary unilocular, the ovules several, parietal, orthotropous; fruit a loculicidal capsule, the seeds small, subglobose and reticulately sculptured, the embryo apical, lying against the endosperm, underlying an embryotega, 0.2–0.3 the length of the endosperm, 1.6 times wider than long to 1.3 times longer than wide; endosperm copious, mealy, starchy (?). Chromosomes: n = 8.

Composition: 1 genus, ~5 species.

Distribution: Tropical America, West Indies, southeastern United States; one species in Angola.

XYRIDACEAE (Figure 32*a,b*).—Perennial, less commonly annual herbs generally of wet habitats, with a short rhizome, rarely a bulb; raphides absent, but calcium oxalate crystals sometimes present; plant glabrous or with uniseriate mucus-secreting glandular hairs on inner surface of leaf sheath, rarely with branched hairs, rarely entirely pilose; xylem vessel perforation plates simple in the root, stem and leaves; leaves mostly basal, distichous or spirally arranged, linear, or sometimes terete or flattened, the sheath short, open, the stomates paracytic or anomocytic; inflorescence scapose, rarely terminal on a leafy stem (*Aratitiyopea*), head or dense spike, rarely loose (*Achlyphila*), rarely paniculate, or the flower solitary, the flowers subtended by imbricate, leathery, usually rigid bracts; flowers bisexual, ephemeral, nectaries absent; sepals 3 (sometimes 2 in *Abolboda*), all similar or two bractoid, the other membranous, usually free; petals 3, colored, actinomorphic or zygomorphic (*Orectanthe*), connate, sometimes only slightly so; stamens 3 fertile, and 3 staminodal or lacking (*Xyris lacera*), very rarely all fertile (*Xyris nigromucronata*), adnate to the perianth; anthers linear, extrorse or introrse, dehiscing longitudinally; pollen usually elongate, 1-sulcate, 2(3)-sulculate or nonaperturate, 2–3-celled when shed; pistil 1, the carpels 3, style 1, sometimes with 2–3 basal glandular appendages (*Abolboda, Orectanthe, Aratitiyopea*), the stigma apical, unlobed or 3-lobed; ovary superior, usually 1-locular and the ovules parietal, rarely 3-locular, sometimes imperfectly so, and the ovules axile (*Abolboda, Orectanthe, Aratitiyopea*); ovules usually numerous, sometimes few, bitegmic, tenuinucellar, orthotropous or anatropous (*Abolboda, Orectanthe*); embryo sac antipodals sometimes soon degenerate; endosperm formation Nuclear, the tissue later becoming cellular; fruit a loculicidal capsule, the seeds numerous, small, usually longitudinally striate; embryo small, lying against the endosperm, 0.2 the length of the endosperm (0.5 in *Abolboda, Orectanthe*), 0.5 as long as wide; endosperm copious, mealy, starchy and sometimes also oily. Chromosomes: x = 8,9,13,17.

Composition: 5 genera, ~250 species.

Distribution: Mainly pantropical and subtropical, mostly America, extending into temperate America and Africa.

RAPATEACEAE (Figure 32*c,d*).—Perennial herbs often of wet habitats, rarely epiphytic, often large, with a short, thick rhizome; raphides and calcium oxalate crystals absent; silica bodies present; xylem vessel perforation plates usually scalariform in root and stem, rarely simple in them and leaves, vessels usually absent from the leaves; leaves distichous, linear, ensiform, rarely terete, basal, equitant, the sheath short, open, stomates paracytic, anomocytic or tetracytic; uniseriate mucus-producing hairs present; inflorescence scapose, head or subumbellate, often subtended by 1–2 large sometimes white bracts and the individual flowers subtended by several sometimes colored bracteoles; flowers bisexual, actinomorphic, nectaries absent; sepals 3, hyaline, rigid, free or connate; petals 3, corolline, connate; stamens 6, sometimes adnate to the corolla, the filaments short or long, free or connate, the anthers linear, basifixed and sometimes apically produced, dehiscent by pore(s) or an apical cleft; pollen 1(2)-sulcate or zonisulculate; pistil 1, the carpels 3, style 1, the stigma apical, simple, often punctate; ovary superior, 3(1)-locular, sometimes incompletely so above, the ovules several to one per locule, axile or basal, anatropous; fruit a loculicidal capsule, the seed(s) sometimes longitudinally striate, rarely carunculate; embryo lying against the endosperm, small, 0.1 the length of the endosperm, 3 times wider than long; endosperm copious, mealy, starchy. Chromosomes: n = 11 (*Maschalocephalus*).

Composition: 16 genera, 80 species.

Distribution: Tropical South America, 1 genus extending into Panama; 1 genus in tropical West Africa.

ERIOCAULACEAE (Figure 33).—Perennial, seldom annual herbs usually of wet habitats, emergent or rarely submerged, the stem short, rarely stoloniferous; raphides absent but

FIGURE 31.—COMMELINACEAE: *a, Dichorisandra thyrsiflora* flower from front and behind, pistil and calyx, stamens and petals, essential organs, pistil, *D. tejucensis* stamens; *b,* leaf showing the closed sheath, *Commelina tuberosa* l.s. of flower, *Tradescantia virginica* l.s. of flower, dehisced fruit, embryo; *c, Commelina erecta* inflorescence, *C. diffusa* flower with petals removed, staminode, short stamen, long stamen, seed, l.s. of same showing the small embryo at margin of abundant endosperm, embryotega (after Martius, Baillon). MAYACACEAE: *d, Mayaca fluviatilis* flower, l,s. of same showing the parietal placentation, seed, l.s. of same showing small embryo in abundant endosperm; *e, Mayaca* floral diagram, *M. sellowiana* views of anther showing apical pore, c.s. of same; *f,* fruit, same dehiscing and dehisced, *M. longipes* apex of leaf (greatly enlarged), part of plant in flower and fruit (after Martius, Baillon).

FIGURE 32.—XYRIDACEAE: *a, Xyris laxifolia* inflorescence showing the numerous imbricate bracts, *X. indica* l.s. of flower, floral diagram showing different types of sepals, seed (greatly enlarged), l.s. of same showing the minute embryo in abundant endosperm; *b, X. laxifolia* sepals, style and stigmas, c.s. of ovary, fruit, one valve showing the numerous minute seeds, *Abolboda poeppigii* flower, *A. poarchon* views of anther, *A. poeppigii* pistil showing the stylar appendages, c.s. of ovary, dehisced fruit (after Martius, Baillon). RAPATEACEAE: *c, Schoenocephalium martianum* inflorescence, flower bud with bracts, part of flower showing the inner perianth parts and stamens and one external perianth part, c.s. of perianth, perianth parts and stamens, stamen, perianth part and base of filaments (enlarged), pistil; *d,* stigma, fruit, same dehisced, *Rapatea paludosa* flower, l.s. of same (after Martius, Baillon).

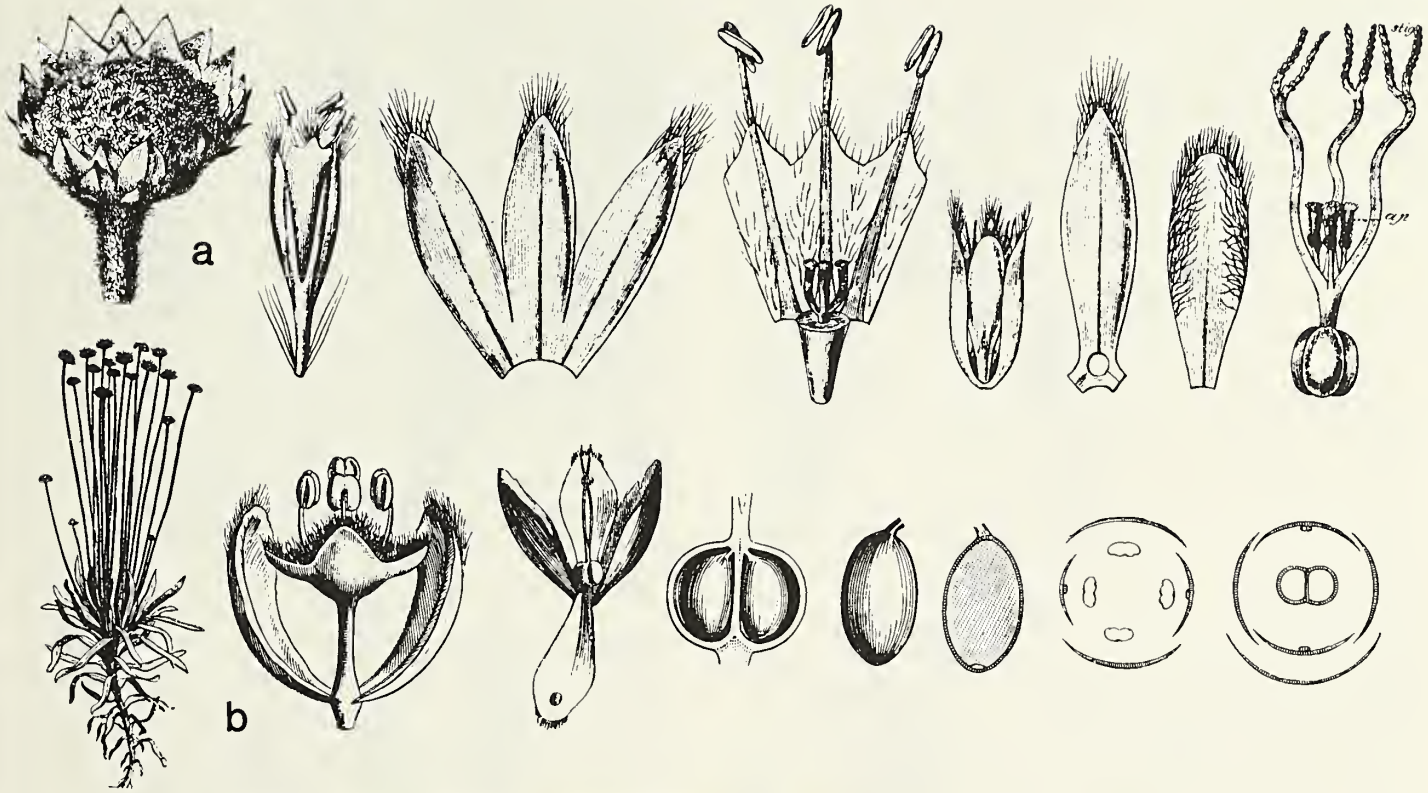

FIGURE 33.—ERIOCAULACEAE: *a, Paepalanthus lanato-albus* inflorescence, ♂ flower, calyx of ♂ flower, ♂ flower opened out, ♀ flower, sepal of ♀ flower, petal of ♀ flower, pistil showing the stylar appendages; *b, Eriocaulon caulescens* plant with many heads, *E. septangulare* ♂ flower, ♀ flower opened, l.s. of ovary, seed (enlarged), l.s. of same showing minute embryo in abundant endosperm, ♂ floral diagram, ♀ floral diagram (after Martius, Baillon, Le Maout and Decaisne).

calcium oxalate crystals present, silica very rarely present; xylem vessel perforation plates usually simple and scalariform in root, stem and leaves; leaves usually basal, sometimes clustered at the end of the stem or scattered along it, spirally arranged, rarely distichous, linear, rarely ensiform, the sheath short or absent, the stomates paracytic; hairs 3-celled, glandular, unequal-armed T-shaped, or filamentous uniseriate ones often forming dense axillary clusters; inflorescence often hairy scapose heads, subtended by an involucre which is sometimes white; flowers very small, numerous, actinomorphic or zygomorphic, unisexual, the plants monoecious, very rarely dioecious; nectaries absent; perianth scarious, often white, segments 4 or 6, in 2 whorls, outer segments free or connate, the inner free or connate, sometimes with an apical gland, inner segments and sometimes also outer rarely absent and replaced by hairs; stamens 4 or 6(1–3), the filaments free or rarely connate or adnate to the base of the perianth; anthers slightly longer than wide, the sacs separate at the base and apex, longitudinally dehiscent; pollen spiraperturate, 3-celled when shed; pistil 1, the carpels 2–3, style 1, often appendaged, 2–3-lobed, the lobes often bifid at the apex; ovary superior, 2–3-locular, the ovules 1 per locule, axile-subapical, bitegmic, tenuinucellar, orthotropous; embryo sac antipodal cells ephemeral; endosperm formation Nuclear or perhaps Helobial, the tissue later becoming cellular; fruit a thin-walled, loculicidal capsule; embryo lying against the endosperm, 0.2–0.4 the length of the endosperm, 0.5–0.8 as long as wide; endosperm copious, mealy or floury, starchy. Chromosomes: x = 8–10, especially 8.

Composition: 13 genera, ~1150 species.

Distribution: Mainly pantropical and subtropical, centered in South America, few temperate; eastern North America; Great Britain, Ireland; eastern Asia.

ZINGIBERALES

Usually large herbs, usually supported by rigid leaf sheaths rather than the stem, rarely small herbs or trees, rhizomatous or tuberous; raphides in Musaceae, Strelitziaceae and Lowiaceae, absent from Zingiberaceae, Cannaceae and Marantaceae; xylem vessel perforation plates simple or scalariform in the roots, rarely in the stem, vessels usually absent from the stem and leaves; leaves usually large, convolute in bud, spirally arranged, sometimes distichous or basal, the blade usually with a midrib and numerous lateral parallel veins extending from it, the petiole usually long, sheath usually open; inflorescence bracts often colored; flowers bisexual or the plants monoecious


a
b
c
d

or rarely polygamous, zygomorphic or irregular, entomogamous or ornithogamous; perianth segments 6 in 2 whorls, homochlamydeous or heterochlamydeous often differing in size, connate or free; stamens 5(6)–1, epigynous or adnate to the corolla, 1–4 often petaloid staminodes, the filaments long or short, anthers linear, basifixed, rarely dorsifixed; pollen usually nonaperturate, sometimes forate or spiraperturate, 2–3-celled when shed; nectaries epigynous or septal; pistil 1, the carpels 3(2), style 1, the stigma apical, 3-lobed, bilabiate or not divided; ovary inferior, 3(2,1)-locular, the ovules usually numerous, rarely few–1 per locule, axile, parietal or basal, bitegmic, crassinucellar, anatropous or semi-anatropous; embryo sac antipodals ephemeral, rarely persisting after fertilization or multiplying secondarily; fruit usually a loculicidal capsule or berry, rarely a schizocarp, the seeds often globose, sometimes arillate; embryo small to large, marginal or within perisperm; perisperm copious.

Distribution: Pantropical and subtropical, few extending into temperate regions.

Chemistry: Rich in phenolic acids; not alkaloid rich, sometimes producing indole alkaloids; sometimes tanniferous and producing flavonoids; mucilage sometimes present; sometimes aromatic. Characterization of individual families is difficult. Only Zingiberaceae stands out a little with very unusual flavonoids with no B-ring substitution, and a great variety of mono- and sesquiterpenoids.

MUSACEAE (Figure 34*a,b*).—Large rhizomatous glabrous perennial herbs; raphides and silica bodies present; xylem vessel perforation plates simple and scalariform in the root, vessels absent from the stem and leaves; leaves large, convolute in bud, spirally arranged, the blade entire, with a midrib and numerous parallel veins extending from it toward the margin, the sheath open, the stomates with several subsidiary cells only weakly differentiated from the other epidermal cells, guard cells symmetrical; inflorescence a raceme or spike of cymose clusters of flowers covered by colored bracts; flowers entomogamous and ornithogamous, zygomorphic or irregular, sometimes bisexual but usually the plants monoecious, ♂ flowers within the upper bracts, ♀ within the lower bracts; perianth segments 6 in 2 petaloid whorls, 5 connate, 1 free; stamens 5, sometimes a staminode also present, the filaments filiform, free of the perianth; anthers linear, basifixed, 2-locular; pollen nonaperturate; pistil 1, the carpels 3, style 1, elongate, the stigma 3-lobed, apical; ovary inferior, with septal nectaries, the nectar copious, 3-locular, the ovules axile, numerous, bitegmic, crassinucellar, anatropous; embryo sac antipodals ephemeral; endosperm formation Nuclear, the tissue later becoming cellular; fruit a berry, the seeds with an embryotega; embryo at the margin of the perisperm, 0.3 the length of the latter, twice as wide as long; perisperm copious, mealy, starchy, endosperm also present. Chromosomes: x = 9–11,16,17.

Composition: 2 genera, ~40 species.

Distribution: Tropical Africa, Madagascar; southeast Asia, the East Indies, Queensland.

STRELITZIACEAE (Figure 34*c,d*).—Perennial rhizomatous usually glabrous herbs or trees; raphides and silica bodies present; xylem vessel perforation plates scalariform and sometimes also simple in the roots, scalariform or vessels absent in the stem, vessels absent from the leaves; leaves distichous, large to very large, the blade with a midrib and numerous lateral parallel veins, the petiole long, with an open sheath, the stomates paracytic or with numerous subsidiary cells only weakly differentiated from the epidermal cells, guard cells symmetrical, some species with branched, uniseriate, candelabra-like hairs on the petiole and parts of the inflorescence (*Heliconia*); inflorescences cincinni, terminal or in the axil of cymbiform bracts, the latter sometimes colored (*Heliconia*); flowers large, zygomorphic, bisexual; perianth segments 6, often differing in size, shape and sometimes color, free or 5 connate and 1 free (*Heliconia*); stamens epigynous or adnate to base of perianth, 5(6), the sixth often a petaloid staminode; filaments linear, the anthers 2-celled, linear, basifixed; pollen nonaperturate or aperture indistinctly ± pore-like (*Heliconia*); pistil 1, the carpels 3, style 1, filiform, the stigmas 3, filiform or capitate; ovary inferior, with septal nectaries, 3-locular, the ovules many or 1 per locule (*Heliconia*), axile or basal (*Heliconia*), bitegmic, crassinucellar, anatropous; embryo sac antipodals soon degenerate; endosperm formation Nuclear; fruit a loculicidal capsule or schizocarp (*Heliconia*), the seeds globose, arillate or not arillate (*Heliconia*), with an embryotega; embryo marginal or within the perisperm, 0.35–0.9 the length of the perisperm, 1.4 times wider than long to 7.5 times longer than wide; perisperm copious, mealy and starchy. Chromosomes: x = 7–13, especially 11,12.

Composition: 4 genera, ~60 species.

Distribution: Moist tropical America; South Africa, Madagascar; New Guinea to Samoa.

LOWIACEAE (Figure 35*a*).—Perennial rhizomatous, glabrous herbs; raphides and silica cells present; xylem vessel perforation plates scalariform in the roots, vessels absent from the stem and leaves; leaves basal, distichous, fairly large, with a midrib and numerous parallel veins extending apically from it, also conspicuous transverse veins, the petiole long, sheath open, the stomates paracytic, guard cells asymmetrical; inflorescence directly from the rhizome, a few-flowered cyme, the bracts

FIGURE 34.—MUSACEAE: *a, Musa sinensis* inflorescence, young fruit and part of leaves (greatly reduced), *Ensete edule* flower, fruit, seed from below and c.s. of same showing the pit of the hilum; *b, Musa sapientum* floral diagram, flower, the free petal, *M. coccinea* flower, stamens and style, the free petal, stigma (after Le Maout and Decaisne, Martius). STRELITZIACEAE: *c, Ravenala (Phenakospermum) guyanensis* flower, seed with hairy aril, l.s. of same showing the moderate embryo, *Ravenala madagascariensis* seed, l.s. of same, *Heliconia formosa* l.s. of lower part of flower, *H. metallica* c.s. of base of flower, abortive stamen; *d, H. brasiliensis* part of inflorescence in flower and fruit, corolla opened out with lateral sepals, intermediate sepal, stamen, style, apex of style and stigma (after Martius, Le Maout and Decaisne).

FIGURE 35.—LOWIACEAE: *a, Orchidantha longiflora*, flower, stamen, *O. maxillarioides* interior tepals, stamens and style, l.s. of ovary, seed with aril (after Schumann). ZINGIBERACEAE: *b, Alpinia* flower, l.s. of same, c.s. of fruit, *Hedychium gardnerianum* floral diagram; *c,* flower, fruit, seed, l.s. of same, *Elettaria cardamomum* dehiscing fruit, *Renealmia racemosa* flower, labellum; *d,* l.s. and c.s. of ovary, fruit, views of seed, *Renealmia* arillate seed, l.s. of same showing the embryo enclosed by little endosperm (white) and much perisperm (stippled), c.s. of seed at level of embryo, embryo; *e, Kaempferia pandurata* inflorescence, the 3 inner perianth segments, anther enclosing the apex of the style between its lobes, style with 2 staminodes at its base, c.s. of ovary, *Costus spiralis* stamen and apex of style, *C. malortieanus* c.s. of anther, floral diagram (after Le Maout and Decaisne, Martius, Lindley).

colored but not very large; flowers large, zygomorphic, bisexual, malodorous; sepals 3, linear, connate basally into a slender tube; petals 3, the middle one large and colored, the laterals small; stamens 5, epigynous, unilateral, the filaments short, anthers 2-locular, linear, basifixed, the connective sometimes apically produced; pollen smooth, spheroidal, nonaperturate; pistil 1, the carpels 3, style fairly short, the stigmas 3, laciniate, wet; ovary inferior, the ovules numerous, axile, anatropous; fruit a loculicidal capsule, the seeds globose, arillate, their food reserve starchy; embryology unknown. Chromosomes: n = 9.

Composition: 1 genus, 2 species.

Distribution: Southern China, Hainan, Malay Peninsula, Borneo.

ZINGIBERACEAE (Figure 35*b–e*).—Perennial herbs with elongate or tuberous rhizomes, often aromatic; plants not often conspicuously pubescent, but micro-hairs common, usually unicellular, rarely forked or stellate or 2-celled, commonly thick and lignified, others uniseriate, long, thin-walled and ephemeral except for base; raphides absent but calcium oxalate crystals and silica cells present; xylem vessel perforation plates in the roots usually scalariform, sometimes also simple, rarely scalariform in the stem, vessels usually absent from the stem and leaves; leaves basal or cauline, distichous or spirally arranged (Costoideae), often large, often divided into blade, petiole and sheath, with a ligule between the latter two, the blade with a midrib and numerous fine parallel veins extending obliquely upward from it, the sheath open or closed (Costoideae), the stomates mostly tetracytic, sometimes paracytic or with more than 4 subsidiary cells, guard cells asymmetrical; inflorescence terminal, sometimes scapose, raceme, spike, head, cyme, or the flower solitary, the bracts often colored; flowers zygomorphic, bisexual or rarely the plants polygamous; sepals 3, calycine, connate; petals 3, connate, one usually larger than the others, colored and showy, sometimes pouched; stamen 1, adnate to the corolla, the filament long or short, sometimes petaloid, the anther adnate, rarely dorsifixed, elongate, 2-locular, sometimes spurred, the connective sometimes appendaged and sometimes separating the locules, 2 or 4 petaloid staminodes usually present; pollen usually nonaperturate, forate or spiraperturate or ± intermediate between both in Costoideae, 2-celled when shed; nectaries epigynous or septal (Costoideae); pistil 1, the carpels 3(2), style 1, the upper part usually enveloped by the anther, the stigma capitate or 2-lipped, or rayed, wet; ovary inferior, 3(2)-locular, the ovules numerous, axile, or 1-locular and the ovules parietal, or rarely basal and the ovules few, bitegmic, crassinucellar, anatropous or semi-anatropous; embryo sac antipodals ephemeral; endosperm formation Helobial, the tissue ultimately cellular; fruit usually a loculicidal capsule, sometimes a berry, the seeds often covered by an aril; embryo 0.8 to as long as the perisperm, 3.6–7.0 times longer than wide; endosperm small, hard or mealy, perisperm large, mealy or hard, starchy. Chromosomes: x = 7–14,16,17,21,26, especially 11,12.

Composition: 49 genera, ~1000 species.

Distribution: Centered in Indomalaysia; northern 2/3 of South America; southern 2/3 of Africa, Madagascar, East Indies, northeastern Australia.

CANNACEAE (Figure 36*a,b*).—Large perennial herbs, sometimes of wet habitats, glabrous, usually with tuberous rhizomes; raphides absent, but calcium oxalate crystals and silica cells present; xylem vessel perforation plates both simple and scalariform in the root, vessels absent from the stem and leaves; leaves cauline, spirally arranged, large, broad, the blade with a strong midrib and numerous lateral veins extending from it, the sheath open, ligule and pulvinus absent, the stomates with 2, 4, or more subsidiary cells, guard cells usually symmetrical; inflorescence terminal, composed of cincinni arranged in racemes or panicles; flowers bisexual, irregular, mostly large and showy; sepals 3, free, herbaceous; petals 3, one usually smaller than the others, basally connate; stamen 1, adnate to the corolla, the anther unilocular, adnate to one side of the petaloid filament; staminodes 3(1,4), petaloid, 2 shortly basally connate and adnate to the petals; pollen nonaperturate, 3-celled when shed; pistil 1, the carpels 3, style 1, petaloid, the stigma apical, linear; ovary inferior, with septal nectaries, 3-locular, the ovules numerous, axile, bitegmic, crassinucellar, anatropous; endosperm formation Nuclear (possibly Helobial), the tissue ultimately cellular; fruit a capsule, often warty, sometimes indehiscent; seeds round, the embryo straight, 0.8–0.9 the length of the perisperm, 2.4–4.3 times longer than wide; endosperm sparse, perisperm copious, very hard, starchy. Chromosomes: x = 9.

Composition: 1 genus, ~50 species.

Distribution: Southeastern United States, tropical and subtropical America, West Indies; according to some authors 1–3 species are indigenous to Africa and Asia.

MARANTACEAE (Figure 36*c,d*).—Perennial herbs, rarely shrubby, often with a tuberous rhizome, often of moist or swampy forests; raphides absent but calcium oxalate crystals and silica cells present; xylem vessel perforation plates simple or scalariform in the root and stem; leaves distichous along the stem or basal, differentiated into an asymmetrical blade, petiole, and open sheath, with a pulvinus at the apex of the petiole, with a distinct midrib and numerous lateral parallel veins, the stomates with 2, 4, or more subsidiary cells, guard cells asymmetrical; plants generally glabrous to the naked eye, the hairs usually unicellular, typically sunk in the epidermis; inflorescence terminal, sometimes scapose, sometimes on a separate shoot (*Thymocarpus,* some *Calathea*), sometimes a sympodium of racemes (*Thymocarpus*), cymose, spike- or panicle-like or capitate, the bracts sometimes colored; flowers bisexual, irregular; sepals 3, free; petals 3, unequal, connate; stamen 1, the anther unilocular, adnate to one side of the petaloid filament; staminodes 2–4, petaloid, adnate to the corolla, sometimes 2 connate; pollen nonaperturate; pistil 1, the carpels 3, two usually aborting, the style stout, curved, stigma apical; ovary inferior, with septal nectaries, 1(3)-locular,

FIGURE 36.—CANNACEAE: *a, Canna glauca* flower, *C. denudata* labellum, style and stamen, *C. coccinea* inflorescence on part of leaf, l.s. and c.s. of immature fruit; *b,* floral diagram, *C. flaccida* stamen (part petaloid), *C. indica* fruit, seed, l.s. of same (enlarged), embryo, *Canna* l.s. of embryo (after Martius, Le Maout and Decaisne, Lindley). MARANTACEAE: *c, Calathea villosa* flower, sepal, petal, stamen, c.s. and l.s. of ovary, *C. eichleri* stamen; staminode, stamen and style; corolla, calyx and ovary; *d, C. micans* views of seed, l.s. of same showing the curved embryo, *C. bachemiana* base of blade and enlarged apex of petiole, *Thalia dealbata* fruit, c.s. of same with only one fertile cell, floral diagram (after Martius, Le Maout and Decaisne, Lindley).

FIGURE 37.—HAEMODORACEAE: *a, Haemodorum spicatum* flower spread out, apex of stamen, c.s. of ovary, *H. teretifolium* l.s. of flower, fruit, *Haemodorum* seed, section of endosperm showing the small embryo in abundant endosperm, embryo; *b, Conostylis serratifolia* l.s. of flower, *Phlebocarya filifolia* l.s. of flower, *Anigosanthus* flower, l.s. of same, seed, l.s. of same, stamen, floral diagram (after Baillon, Le Maout and Decaisne, Lindley). PHILYDRACEAE: *c, Pritzelia pygmaea* plant in bloom, flower, floral diagram, *Philydrum lanuginosum* petals and stamen, dehisced fruit, seed, l.s. of same showing the moderate embryo in abundant endosperm (after Baillon). IRIDACEAE: *d, Iris germanica* habit showing the equitant, distichous leaves and rhizome, flower, l.s. of same showing parts of 4 perianth segments, one broadened entire style arm and another in l.s. with a stamen beneath it, flower with perianth and stamens removed, showing the style arms and ovary (after Le Maout and Decaisne).

the ovules 1 per locule, axile-basal, bitegmic, crassinucellar, anatropous or anacampylotropous; embryo sac antipodals ephemeral or persisting at least until fertilization or multiplying secondarily; endosperm formation Nuclear; fruit a loculicidal capsule or berry, sometimes muricate (*Trachyphrynium, Thymocarpus*) or papillose (some *Calathea*), the seeds sometimes arillate; embryo curved or folded, 1.4–1.6 times longer than the perisperm, 7.3–25 times longer than wide; perisperm copious, mealy, starchy. Chromosomes: x = 4,6,7,9,11–13, especially 9,12,13.

Composition: ~30 genera, ~350 species.

Distribution: Pantropical, centered in America, extending into temperate America.

Iridales

Herbs, very rarely low shrubs or saprophytic, with rhizomes, corms, tubers or stolons, rarely bulbs; xylem vessel perforation plates simple or scalariform in the roots, scalariform or vessels absent in the stem and leaves; leaves mostly basal, linear to ensiform, distichous, often equitant, the sheath short, open; flowers bisexual, actinomorphic or zygomorphic; perianth segments 6(3,4), petaloid, connate or free; stamens 3(6,1), epigynous or adnate to the perianth, the filaments free or connate, anthers basifixed or dorsifixed; pollen usually 1-sulcate, less often 2(3)-sulculate, spirapertur(oid)ate, non-aperturate, polyrugoidate, 2(–4)-porate, or 1(–3)-ulcerate, 2(–3)-celled when shed; pistil 1, the carpels 3, styles 1 or 3, the stigmas apical or decurrent ventrally; ovary usually inferior, less commonly semi-inferior or superior, 3(–1)-locular and the ovules axile or rarely 1-locular and the ovules parietal, usually numerous, rarely few or only 1 per locule, bitegmic, crassinucellar, rarely tenuinucellar, anatropous, rarely hemi-anatropous; embryo sac antipodal cells soon degenerate or sometimes persisting into early endosperm formation; endosperm formation Nuclear or Helobial; fruit a loculicidal capsule, very rarely dehiscing by slits or circumscissile, very rarely a berry, the seeds usually numerous; embryo enclosed in the endosperm, small to moderate in size; endosperm usually copious, rarely scant or absent, usually hard.

Distribution: Cosmopolitan, centered in the tropics, South Africa and Australia.

Chemistry: Often tanniferous; sometimes saponiferous; rarely cyanogenic; alkaloids absent; Iridaceae, Philydraceae and Burmanniaceae (except *Thismia*) lack raphides, Haemodoraceae usually has them. Iridaceae often produce mangiferin and sometimes naphthaquinones or anthraquinones. *Isophysis* is chemically in line with membership in Iridaceae. Haemodoraceae usually have a characteristic polyphenolic red pigment (phenalones) in the roots and rhizomes.

HAEMODORACEAE (Figure 37*a,b*).—Perennial herbs with tubers or short rhizomes, or sometimes stolons, stems and roots often with red sap; raphides usually present; xylem vessel perforation plates simple and scalariform in the roots, scalariform or vessels absent in the stem and leaves; leaves basal, linear to ensiform, distichous, equitant, the sheath short, open or closed, the stomates paracytic, or nearly anomocytic (*Lophiola*); inflorescence cymose, arranged in racemes or panicles, or subcapitate, often densely villous; flowers bisexual, actinomorphic or slightly zygomorphic; perianth segments 6, in 1 or 2 series, connate or free, often woolly; stamens 3 or 6, sometimes 2–3 staminodes present, 1 plus 2 staminodes in *Pyrrorhiza*, the filaments free from one another, adnate to the perianth; anthers elongate, basifixed or dorsifixed, introrse, dehiscing longitudinally; pollen 1-sulcate, 2(–4)-porate, 2-celled when shed; pistil 1, the carpels 3, style 1, elongate, the stigma apical, acute or capitate; ovary superior, semi-inferior or inferior, with septal nectaries, 3-locular or 1–2-locular by abortion, the ovules numerous to 1 per locule, axile, bitegmic, crassinucellar, hemianatropous to anatropous; embryo sac antipodals soon degenerate; endosperm formation Helobial, the tissue ultimately cellular; fruit a loculicidal capsule, rarely indehiscent (*Barberetta*); embryo 0.1 the length of the endosperm, as long as wide, rarely rather large; endosperm copious, fleshy, mostly starch, some protein, oil and hemicellulose. Chromosomes: x = 4–8,10,15, especially 6,8.

Composition: ~15 genera, ~75 species.

Distribution: Centered in eastern and western Australia; New Guinea; South Africa; tropical America, eastern United States.

PHILYDRACEAE (Figure 37*c*).—Perennial herbs of wet habitats, often floccose, the hairs uniseriate, sometimes glandular, sometimes with a short rhizome; raphides present (?), styloid crystals sometimes present; xylem vessel perforation plates scalariform in the roots, vessels absent from the stem and leaves; leaves basal with a short open sheath, distichous, equitant, linear or ensiform, the stomates paracytic or tetracytic; inflorescence a simple or compound spike, sometimes woolly; flowers bisexual, zygomorphic, covered by a bract in bud; perianth corolline, the segments 4, biseriate, the inner much smaller than the outer, free or basally connate, marcescent; stamen 1, free or adnate to the inner tepals, the filament elongate, flattened; anther straight, arcuate, or longitudinally coiled; pollen sometimes in tetrads, 2-celled when shed, 1-sulcate, rarely 3- or zonisulculate ?; pistil 1, the carpels 3, style 1, elongate, persistent, the stigma capitate, dry;

FIGURE 38.—IRIDACEAE: *a, Iris* dehisced fruit, l.s. of seed, floral diagram showing the stigmas opposite the stamens, *Belamcanda* floral diagram showing the stigmas alternate with the stamens, *Tigridia meleagris* essential organs, 3 stamens forming a column and 6 filiform style arms, lateral view and from above; *b, Sisyrinchium sellowianum* inflorescence, *Geosiris aphylla* 2 plants in flower, inflorescence, flower with 2 spathes, anther, essential organs, pistil; *c,* fruit, c.s. of same, branch of placenta with seeds, floral diagram (after Le Maout and Decaisne, Jonker, Martius). BURMANNIACEAE: *d, Burmannia bicolor* plant, flower, l.s. of same, *Apteria setacea* plant, flower laid open; *e, Burmannia selloviana* part of inflorescence, flower opened out, floral diagram, *Dictyostega* floral diagram (after Martius, Baillon, Le Maout and Decaisne).


a
b
c
d
e

ovary superior, without septal nectaries, 3-locular and the ovules axile, or incompletely 3-locular and the ovules parietal; ovules numerous, bitegmic, crassinucellar, anatropous; embryo sac antipodal cells degenerate soon after fertilization; endosperm formation Helobial, the tissue ultimately cellular; fruit mostly a loculicidal capsule, rarely indehiscent; seeds numerous, minute, sculptured, tailed at both ends; embryo straight, in the axis of the endosperm, 0.8 the length of the latter, 5.5 times longer than wide; endosperm moderate, starchy, sometimes also oil and protein present. Chromosomes: x = 8,17, especially 8.

Composition: 4 genera, 5 species.

Distribution: Eastern and southwestern Australia; southeastern China, Indochina, New Guinea.

IRIDACEAE (Figures 37*d*, 38*a–c*).—Perennial, rarely annual (*Sisyrinchium* spp.) herbs or very rarely low shrubs, with corms, rhizomes, tubers or rarely bulbs, very rarely a colorless saprophyte (*Geosiris*); raphides absent, but often calcium oxalate crystals present, rarely hairy; xylem vessel perforation plates simple or scalariform or both, but vessels frequently absent from the stem and leaves; leaves basal, often ensiform, or linear, equitant and distichous, very rarely scales (*Geosiris*); inflorescences terminal, cymose, arranged in spikes, racemes or panicles, or the flower solitary, the spathes very rarely colored (*Oenostachys*); flowers bisexual, actinomorphic or zygomorphic; perianth petaloid, marcescent, the segments 6, 2-seriate, free or connate, rarely with a spur or sac at the base (*Kentrosiphon*); stamens 3, rarely one of them staminodal (*Diplarrhena*), epigynous or adnate to the perianth, the filaments free or connate, anthers basifixed or dorsifixed, extrorse; pollen usually 1-sulcate, less often 2-sulculate, spirapertur(oid)ate, nonaperturate, or polyrugoidate, 2(3)-celled when shed; pistil 1, the carpels 3, styles 1 or 3, the stigmas 3, sometimes divided at the apex, apical or decurrent ventrally, sometimes the style branches petaloid; nectaries on the perianth, filaments or septa of the ovary; ovary inferior, very rarely superior (*Isophysis*), 3-locular and the ovules axile or very rarely 1-locular and the ovules parietal (*Hermodactylus*); ovules usually numerous, rarely few or one per locule, bitegmic, crassinucellar, anatropous; embryo sac antipodals sometimes persistent into early endosperm formation; endosperm formation Nuclear; fruit a loculicidal capsule; embryo enclosed in the endosperm, 0.4–0.7 the length of the endosperm, 4–7 times longer than wide; endosperm copious, hard, with hemicellulose, protein and oil, rarely also starch (*Radinosiphon*). Chromosomes: x = 3–19,22,24, especially 8–10,15.

Composition: ~60 genera, ~1500 species.

Distribution: Cosmopolitan, except the arctic, centered in South Africa and tropical America, to a lesser extent in eastern Mediterranean region.

BURMANNIACEAE (Figures 38*d,e*, 39*a,b*).—Saprophytic chlorophylless or green autotrophic annual or perennial herbs, sometimes with a creeping rhizome or small tuber; raphides sometimes present; xylem vessel perforation plates scalariform in the root, stem and leaves; leaves reduced to scales or linear or lanceolate, entire, sometimes equitant, basal or alternate all along the stem, the sheath short, open, the stomates mostly anomocytic, sometimes absent; inflorescence a terminal dichasial or monochasial cyme, or a solitary flower, sometimes with colored bracts; flowers bisexual, actinomorphic, or the corolla rarely zygomorphic (*Ophiomeris, Afrothismia*); perianth corolline, of 6(3) segments connate in a tube, sometimes winged, the outer often different in size or shape from the inner, sometimes appendiculate, sometimes persistent; stamens 3 or 6, usually adnate high, rarely low, on the perianth-tube, subsessile, sometimes connate in a ring or deflexed tube, the connective often broadened and apically produced, and the anther sacs separate, dehiscence latrorse or introrse; pollen nonaperturate or with 1(–3)-ulcerate, circular or slightly elongate apertures, 1-sulcate(?), 2–3-celled when shed; pistil 1, the carpels 3, style 1, the stigmas 3, apical, usually enlarged, often capitate, sometimes each bifid; ovary inferior, with septal or epigynous nectaries, 3- or 1-locular, the ovules very numerous, axile or parietal, bitegmic, tenuinucellar; embryo sac with 3 small antipodal cells; endosperm formation Helobial, the tissue cellular at time of zygote division; fruit usually a capsule, sometimes fleshy, sometimes winged, dehiscent by 3 longitudinal slits or by numerous transverse slits, or circumscissile, the seeds numerous, elongate, minute but larger than those of most orchids, the funicle often rather long; embryo arrested in 4–10-celled stage, further development occurring after the seeds are shed; endosperm scant or absent in the mature seeds. Chromosomes: x = 6,8,9.

Composition: ~17 genera, ~125 species.

Distribution: Pantropical, mainly in rain forest, some in savanna or grassy fields, few in temperate regions.

ORCHIDALES

Herbs, rarely saprophytic, often epiphytic or climbing in the tropics, sometimes with short rhizomes, tubers or swelling of the stem; raphides probably universal, silica cells sometimes present; xylem vessel perforation plates usually simple in the roots, sometimes also scalariform, vessels present or absent in the stem and leaves; leaves simple, entire, rarely plicate, often distichous, reduced to scales in saprophytes, the sheath nearly always closed; inflorescence racemose; flowers zygomorphic, bisexual or very rarely the plants polygamous, monoecious or dioecious; perianth segments 6 in 2 whorls, mostly petaloid, free or connate in each whorl, frequently one segment with a nectariferous spur; stamens 1 or 2, rarely 3 or 6, adnate to the style; pollen 1-sulcate, 2-sulculate(?), 3–4-poroid or nonaperturate, mostly in pollinia, 2-celled when shed; pistil 1, the carpels 3, the stigma short, apical or subapical; ovary inferior, unilocular, the ovules very numerous, parietal, very rarely 3-locular and the ovules axile, usually bitegmic, rarely unitegmic, tenuinucellar, anatropous; embryo sac antipodals

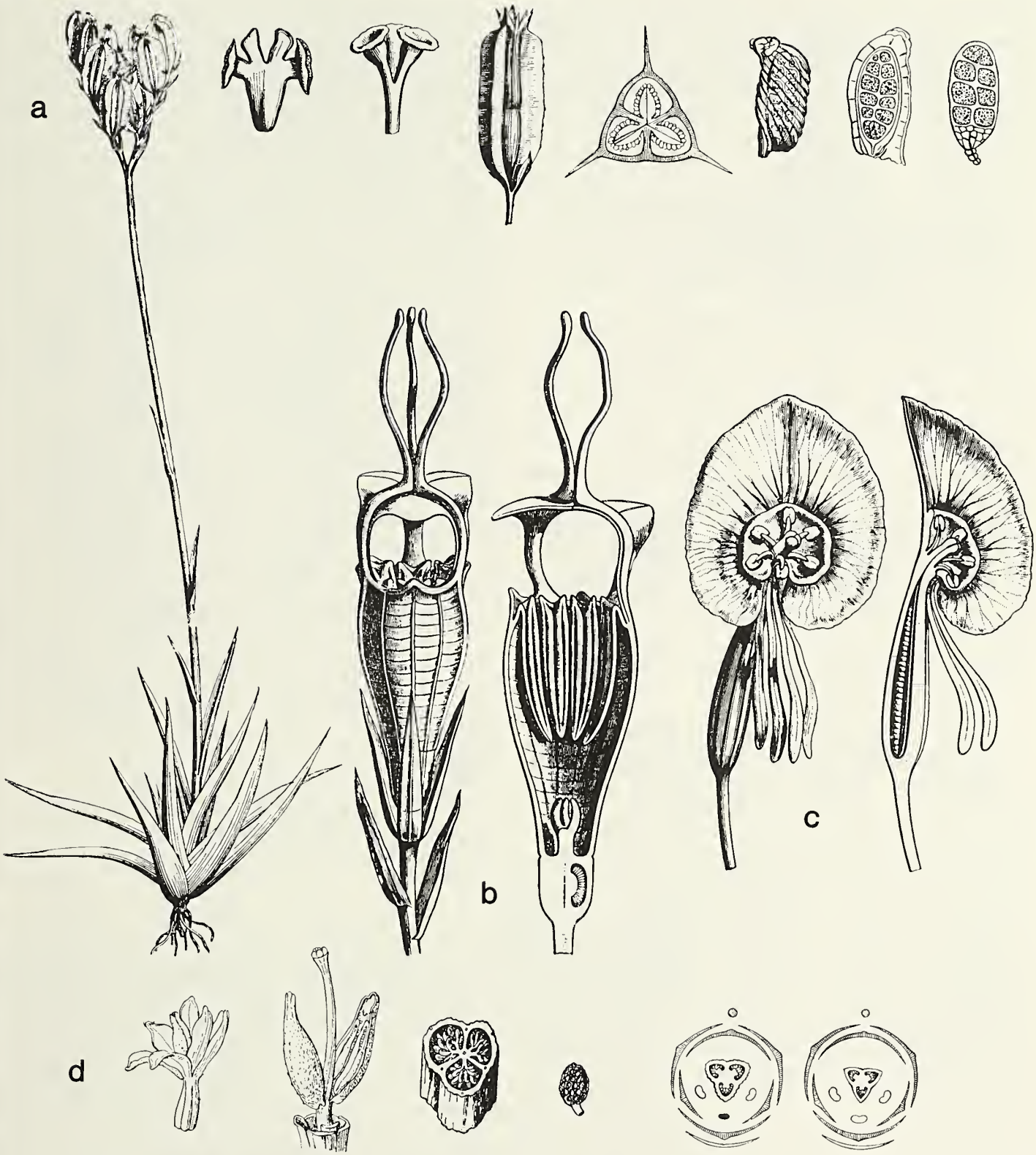

FIGURE 39.—BURMANNIACEAE: *a, Burmannia disticha* plant, dehiscing stamen, style and stigmas, fruit, c.s. of same, seed, l.s. of same, embryo at base of endosperm; *b, Geomitra clavigera* flower (greatly enlarged), l.s. of same (after Le Maout and Decaisne, Baillon). CORSIACEAE: *c, Corsia ornata* flower, l.s. of same (after Baillon). ORCHIDACEAE: *d, Apostasia odorata* flower, stamens and style, c.s. of ovary, seed, *Apostasia* floral diagram, *Neuwiedia* floral diagram (after Lindley, Le Maout and Decaisne).

ephemeral and frequently not all 3 produced; endosperm formation absent or Nuclear, the nuclei few; fruit a capsule mostly dehiscing by longitudinal slits, very rarely somewhat berried; seeds very numerous, minute, the embryo immature when the seeds are shed; endosperm absent, very rarely scanty in the mature seeds.

Distribution: Cosmopolitan, most diverse and abundant in the tropics.

Chemistry: Many have alkaloids, including alkaloid amines, a group of indole alkaloids peculiar to orchids, indolizidines, pyrrolidines and pyrrolizidines; saponins uncommon; not cyanogenic; no leucoanthocyanins; mucilage in many; occasionally tanniferous.

CORSIACEAE (Figure 39*c*).—Chlorophylless saprophytic perennial herbs with a short rhizome or small tubers; leaves reduced to scales alternate all along the stem; inflorescence a solitary terminal flower; flower bisexual or unisexual, zygomorphic; perianth parts 6, free, corolline, the median one of the outer series enlarged, usually with nectariferous tissue at its base, and enclosing 5 linear tepals; stamens 6, the filaments short, close to the style and adnate to it, or perhaps some epigynous, or adnate to the base of the large tepal; anthers as long as wide, subbasally dorsifixed, extrorse; pollen 1-sulcate, the sulcus not very distinct; pistil 1, the carpels 3, style short, the stigmas 3, short, not enlarged; ovary inferior, the ovules numerous, parietal; fruit a capsule dehiscing by 3 valves; seeds numerous, minute, elongate, with a long funicle, the testa obscurely longitudinally grooved; embryo undifferentiated; endosperm scanty. Chromosomes: x = 9.

Composition: 2 genera, ~10 species.

Distribution: Centered in New Guinea; Queensland, Solomon Islands; one species in Chile (*Arachnitis uniflora*).

ORCHIDACEAE (Figures 39*d*–41).—Perennial herbs (one species annual), rarely half-shrubs, obligately mycorrhizal (except some Arethuseae), rarely saprophytic, rarely climbers (*Vanilla*), the stem mostly sympodial, sometimes monopodial, often thickened basally and with aerial roots often with 2–many cell layers of velamen, rhizomes or roots often tuberous; plants usually appearing glabrous, but sometimes various kinds of hairs present in different species; raphides present, silica cells sometimes present; xylem vessel perforation plates usually simple in the roots, sometimes also scalariform, vessels present or absent in the stem and leaves; leaves simple, entire, rarely plicate, alternate, rarely opposite or whorled, often distichous, rarely deciduous in the dry season, or absent, often fleshy, reduced to scales in the saprophytes, various in shape, rarely reticulate-veined, the sheath nearly always closed, stomates paracytic, less often anomocytic, seldom tetracytic; inflorescence terminal or axillary, sometimes scapose, spikes, racemes or panicles or a solitary flower, rarely capitate; flowers zygomorphic, usually resupinate, rarely the corolla nearly actinomorphic (*Apostasia*), bisexual or very rarely the plants polygamous, monoecious or dioecious; perianth segments 6 in two whorls, usually petaloid, more rarely the outer whorl sepaloid; the segments often differ in size, shape and color, free or connate in each whorl, frequently a petal or sepal is prolonged into a nectariferous spur, sometimes extrafloral nectaries present; stamens 2 (the third sometimes a staminode covering the anthers), or 1 (sometimes with 2 staminodes), rarely 3 abaxial, 2 of the inner cycle and 1 of the outer (*Neuwiedia*), adnate to the style and the latter sometimes adnate to a petal; pollen 1-sulcate, 2-sulculate, 3–4-poroid or nonaperturate, in pollinia often elaborated by caudicles (formed from differentiated pollen grains) and viscidia or stipes (formed from part of the stigma or style), more rarely single, in tetrads or masses, the individual grains 2-celled when shed; pistil 1, the carpels 3, stigmas 3 fertile, or 2 and the third partially to completely transformed into a rostellum; ovary inferior, sometimes with nectaries in the wall between the carpels, unilocular, very rarely trilocular (*Apostasia, Neuwiedia, Selenipedium, Phragmipedium*), the ovules very numerous, minute, parietal or rarely axile, usually bitegmic, rarely unitegmic, tenuinucellar, anatropous; embryo sac antipodals ephemeral and frequently not all 3 are produced; endosperm formation, when it occurs, Nuclear, and then only few nuclei are produced; fruit a capsule, mostly opening by 3 or 6 longitudinal slits, rarely a berry (*Neuwiedia curtisii* and some *Vanilla*); seeds very numerous, minute, slightly larger and black in *Apostasia* and *Vanilla*, the embryo always immature when the seeds are shed; endosperm absent in the mature seed. Chromosomes: x = 6–16,18,20,21,24, especially 10,16,18,20,21.

Composition: ~700 genera, ~15000 species.

Distribution: Cosmopolitan, in almost all habitats, most diverse and abundant in the tropics where the majority are epiphytes in forests; almost all temperate and all arctic genera are terrestrial.

FIGURE 40.—ORCHIDACEAE: *a, Orchis* floral diagram, flower, same enlarged without ovary (ST = stigma, L = anther cell, P = pollinium, R = retinaculum), *Stanhopea oculata* flower; *b, Habenaria achalensis* inflorescence, flower, column, l.s. of same (below) showing the entrance to the spur, pollinium, c.s. of ovary, *H. arechavaletae* c.s. of ovary; *c, Selenipedium palmifolium* sepal, petal, labellum, *S. isabelianum* 3 views of column, l.s. of same, *S. palmifolium* c.s. of ovary; *d, Epistephium sclerophyllum* lateral sepal, petal, labellum and column, 2 views of column, ovary, *Stenorrhynchos argentinus* labellum, column (both in lateral view); *e,* pollinia of *Malaxis paludosa, Phaius tankervillii, Brassia maculata, Ophrys apifera, Orchis,* part of *Orchis* pollinium greatly enlarged, pollen of *Stenorrhynchos speciosus, Epidendrum* anther without the pollinia, pollinia (after Martius, Lindley, Le Maout and Decaisne).


a
L
P
R
ST
b
c
d
e

FIGURE 41.—ORCHIDACEAE: *a, Vanilla chamissonis* labellum, appendices of same, column, l.s. of same, c.s. of anther, *Vanilla* c.s. of fruit, dehisced fruit; *b,* column of *Arethusa, Stenorrhynchos, Brassia maculata, Orchis mascula, Ophrys apifera* c.s. of fruit, seed (enlarged), *Erythrodes peterianus* seed (greatly enlarged), *Stenorrhynchos argentinus* seed (greatly enlarged); *c, Orchis* dehisced fruit leaving in place the 3 median nerves of the carpels, *Fernandezia acuta* dehisced fruit, diagram of same; *d, Angraecum* dehisced fruit, diagram of same, *Pleurothallis clausa* dehisced fruit, diagram of same; *e, Epidendrum* dehisced fruit, *Coryanthes speciosa* flower, *Bipinnula polysyka* lateral sepal (after Martius, Le Maout and Decaisne, Lindley).

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