Classification, Evolution, and Phylogeny of the Families of Monocotyledons

Aaron Goldberg
Goldberg, Aaron. Classification, Evolution, and Phylogeny of the Families of Monocotyle-
dons. *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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Classification, Evolution, and Phylogeny of the Families of Monocotyledons

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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, Calochortiaceae, Geosiridaceae, Tecophilaceae, Cyanastraceae, Eriospermaceae, and Medeolaceae in Liliales; Asphodelaceae, Dasyypogonaceae, Aphyllanthaceae, Hyacinthaceae, Alliaceae, Hesperocallidaceae, Fumariaceae, Hemerocallidaceae, Phormiaceae, Blanfordiaceae, Doryanthaceae, and Ixioliriacese in Amaryllidales; Convallariaceae, Ruscaceae, Asparagaceae, Dracaenaceae, Nolinaceae, Herreriacese, Asteliaceae, and Hanguanaceae in Asparagales; Luzuriagaceae, Petermanniaceae, and Ripogonaceae in
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Smilacales; Trichopodaceae and Stenomeridaceae in Dioscoreales; Alstroemeriaceae in Alstroemeriaceae; Conostyliaceae, and Hypoxidaceae in Haemodorales; Heliconiaceae, and Costaceae in Zingiberales; Hydatellaceae in Hydatellales; Joinvilleaceae, Anarthriaceae, and Ecdieiocoleaceae 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; Luzuriaceae, Ruscaceae, Convallariaceae, Asparagaceae, Herreriacese, Hanguanaceae, Dracaenaceae, Asteliaceae, Nolinaceae, Dasygononaceae, Blandfordiaceae, Calceciaceae, Tecophilaeaceae, Ixioiaceae, Cyanastraceae, Phormiaceae, Doryanthaceae, Eriospervaceae, Asphodelaceae, Anthericaceae, Aphyllanthaceae, Histerocallidaceae, Funkiaceae, Hyacinthaceae, Alliaceae, and Hypoxidaceae in Asparagales; Colchiciaceae, Geosiridaceae, Alstroemeriales; Stenomeridaceae and Trichopodaceae in Dioscoreales; Hypoxidaceae and Apostasiaceae in Haemodorales; Heliconiaceae and Costaceae in Zingiberales; Hydatellaceae in Hydatellales; Joinvilleaceae, Ecdieiocoleaceae and Anarthriaceae in Poales; Melanthiaceae and Campynemaceae in Melanthiales; Thissiaceae in Burmanniales.

Hutchinson, 1973. Petrosaviaceae in Alismatales; Ruppiaceae in Potamogetonales; Cartonemateae in Commelinaceae; Tegophyllumaceae and Ruscaceae in Liliales; Alstroemeriaceae and Petermanniaceae in Alstroemeriaceae; Stenomeridaceae and Trichopodaceae in Dioscoreales; Hypoxidaceae and Apostasiaceae in Haemodorales; Thissiaceae in Burmanniales.


Stebbins, 1974. Limnocharitaceae in Alismatales; Ruppiaceae in Najadales; Petrosaviaceae in Triuridales; Heliconiaceae and Costaceae in Zingiberales; Tecophilaceae 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, Tecophilaceae, Cyanastraceae, Asparagaceae, Ruscaceae, Croomiaceae and Trichopodaceae in Liliales; Geosiridaceae in Iridales; Heliconiaceae and Costaceae in Zingiberales; Apostasiaceae in Orchidales; Cartonemataceae and Abolbodaceae in Commelinaceae; Anarthriaceae, Ecdieiocoleaceae, Joinvilleaceae and Hanguanaceae in Restionales; Hydatellaceae in Hydatellales; Anomochloaceae and Streptochaetaceae in Poales; Nypaceae in Aricares.

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


Emberger, 1960. Ruppiaceae in Potamogetonales; Phyltephasiaceae and Nypaceae in Palmales; Cyanastraceae, Geosiridaceae, and Petermanniaceae in Liliales; Thissiaceae 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. Staafleu 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 Physt (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
Table 2.—Evolutionary trends in the monocotyledons (reversibility: n = not; r = rarely; c = commonly).

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<th>Character</th>
<th>Primitive state</th>
<th>Derived state</th>
<th>Reversibility</th>
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<tr>
<td>climate of origin</td>
<td>warm temperate or subtropical</td>
<td>other</td>
<td>r</td>
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<tr>
<td>plant</td>
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<td>xerophyte</td>
<td>r</td>
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<td>perennial</td>
<td>hermaphroditic</td>
<td>r</td>
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<td>simple</td>
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<td>glandular</td>
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<td>absent</td>
<td>present</td>
<td>r</td>
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<td>r</td>
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<td>perforations plates</td>
<td>scalariform</td>
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<td>short, wide, round in cross-section</td>
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<td>opposite or whorled</td>
<td>r</td>
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<td>thin</td>
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<td>medium</td>
<td>thick and sclerophyllous</td>
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<td>closed</td>
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<td>green, white, or yellow</td>
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<td>perianth spur</td>
<td>homochlamydeous</td>
<td>heterochlamydeous</td>
<td>r</td>
</tr>
<tr>
<td>perianth parts</td>
<td>absent</td>
<td>present</td>
<td>r</td>
</tr>
<tr>
<td>corona</td>
<td>imbricate</td>
<td>valvate</td>
<td>n</td>
</tr>
<tr>
<td>perianth vasculature</td>
<td>absent</td>
<td>present</td>
<td>n</td>
</tr>
<tr>
<td>perianth parts, stamens, and carpels</td>
<td>indefinite in number</td>
<td>definite in number</td>
<td>r</td>
</tr>
<tr>
<td>perianth parts, stamens, and carpels</td>
<td>spirally arranged</td>
<td>whorled</td>
<td>n</td>
</tr>
<tr>
<td>stamens and carpels</td>
<td>separate</td>
<td>connate or adnate</td>
<td>n</td>
</tr>
<tr>
<td>stamens and carpels</td>
<td>pleiomerosial</td>
<td>isomerous</td>
<td>n</td>
</tr>
<tr>
<td>stamens and carpels</td>
<td>2 whorls</td>
<td>1 whorl</td>
<td>n</td>
</tr>
<tr>
<td>stamens and carpels</td>
<td>isomerous</td>
<td>oligomerous</td>
<td>n</td>
</tr>
<tr>
<td>staminodes</td>
<td>absent</td>
<td>present</td>
<td>r</td>
</tr>
<tr>
<td>staminodes</td>
<td>equal to pistil in length</td>
<td>shorter than pistil</td>
<td>r</td>
</tr>
<tr>
<td>staminodes</td>
<td>equal in length</td>
<td>anisogamous</td>
<td>r</td>
</tr>
<tr>
<td>staminodes</td>
<td>inserted on receptacle</td>
<td>adnate to perianth or epigynous</td>
<td>n</td>
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<tr>
<td>staminodes</td>
<td>present</td>
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Table 2.—Continued.

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<tr>
<th>Character</th>
<th>Primitive state</th>
<th>Derived state</th>
<th>Reversibility</th>
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<tr>
<td>anthers</td>
<td>separate</td>
<td>connate</td>
<td>r</td>
</tr>
<tr>
<td></td>
<td>adnate or basifixed</td>
<td>dorsifixed</td>
<td>r</td>
</tr>
<tr>
<td>oblong</td>
<td>about as long as wide</td>
<td>poricidal</td>
<td>n</td>
</tr>
<tr>
<td>dehiscence by slits</td>
<td>intorse</td>
<td>interor</td>
<td>r</td>
</tr>
<tr>
<td>extrorse or latorse</td>
<td>abundant</td>
<td>sparse or absent</td>
<td>n</td>
</tr>
<tr>
<td>connective</td>
<td>2 per anther</td>
<td>2 or 1 per anther</td>
<td>n</td>
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<tr>
<td>microsporangia</td>
<td>monosulcate</td>
<td>pored or nonaperturate</td>
<td>n</td>
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<tr>
<td>pollen grains</td>
<td>not sticky</td>
<td>sticky</td>
<td>r</td>
</tr>
<tr>
<td>cells in pollen grains at time of dispersal</td>
<td>free</td>
<td>in tetrads or pollinia</td>
<td>n</td>
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<tr>
<td>carpels</td>
<td>open</td>
<td>closed</td>
<td>n</td>
</tr>
<tr>
<td>ovary</td>
<td>number of locules correspond to number of carpels</td>
<td>unilocular in more than 1-carpellate pistil</td>
<td>r</td>
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<tr>
<td>style(s)</td>
<td>superior</td>
<td>semi-inferior to inferior</td>
<td>n</td>
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<tr>
<td>stigma(s)</td>
<td>separate</td>
<td>connate</td>
<td>n</td>
</tr>
<tr>
<td>placentas in more than 1-carpellate pistil</td>
<td>lobed</td>
<td>not lobed</td>
<td>n</td>
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<tr>
<td>ovules</td>
<td>axile</td>
<td>parietal</td>
<td>n</td>
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<tr>
<td>ovary</td>
<td>axile</td>
<td>apical or basal</td>
<td>n</td>
</tr>
<tr>
<td>stigma</td>
<td>not enlarged</td>
<td>enlarged and fleshy</td>
<td>r</td>
</tr>
<tr>
<td>ovules</td>
<td>few</td>
<td>= or 1 when carpels more than 1</td>
<td>r</td>
</tr>
<tr>
<td>fruit</td>
<td>crassinucellar</td>
<td>tenuinucellar</td>
<td>n</td>
</tr>
<tr>
<td>dehiscence of capsule</td>
<td>bitegmic</td>
<td>unitegmic or ategmic</td>
<td>n</td>
</tr>
<tr>
<td>seed</td>
<td>follicle</td>
<td>other types</td>
<td>n</td>
</tr>
<tr>
<td>embryo</td>
<td>ventricidal or septicid</td>
<td>loculicidal or by slits</td>
<td>n</td>
</tr>
<tr>
<td>endosperm</td>
<td>medium-sized</td>
<td>small</td>
<td>r</td>
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<tr>
<td></td>
<td>small</td>
<td>large</td>
<td>r</td>
</tr>
<tr>
<td></td>
<td>straight</td>
<td>curved</td>
<td>n</td>
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<tr>
<td></td>
<td>about as long as wide</td>
<td>much longer than wide</td>
<td>n</td>
</tr>
<tr>
<td></td>
<td>copious</td>
<td>scanty or absent</td>
<td>n</td>
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</tbody>
</table>

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...
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 aleurome. 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 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 scapoate 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; sepalis 3(2), green, rarely petaloid; petals 3(0), petaloid; stamens 6(3-10), free, or rarely connate, or some staminodal, the anthers basifixed or dorsifixed, introrse or extrorse; pollen 1-sulcate, forate or papillate; anthers basifixed or dorsifixed, extrorse; pollen 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 or laterally deciduous; ovules 2--8, basal or scattered over the wall of the pistils, bitigic, 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 tissues 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 2d,e).

Glabrous perennial herbs of wet habitats, rhizomatous, secreatory 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; infflorescence a scapoate, involucrate, cymose umbel; flowers bisexual, entomogamous, prostrate, some 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 connate ventrally, wet; ovules numerous, scattered over the wall of the ovary, bitigic, 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. marii 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.—HYDROCHAIUTACEAE: 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 Bailleon, Le Maout and Decaisne).

longitudinal and cross veins, and floating or emersed, entire, rarely toothed (Stratiotes), the stiomates mostly paracytic, often absent; often with prickie 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 4a,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 monocoeous, 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; Ø 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; Ψ flowers: pistils 1(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 nutlet; 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 monocoeous, 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 sub sessile, the style rarely elongate; ovary superior, 3-locular when the carpels are united, the ovules 1-2(2) 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.

Composition: 3 genera, ~20 species.

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

Chemistry: Cyanogenic; Scheuchzeriaceae tanniferous, Juncaginaceae not.

SCHUECHZERIACEAE (Figure 4c,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 stamates 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, papilllose; 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 5a,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 stamates tetracytic, intravaginal scales present; inflorescence scapose, an ebracteate spike; flowers small, anemophilous, protogynous, bisexual or the plant dioecious or monocoeous; perianth segments 6, biseriate, homochlamydeous; stamens 6, 3, (4), free, the anthers sub sessile, extrorse; pollen nonaperturate, 2- or 3- celled when shed; pistils 1(6), carpels 3-6, sometimes 3 aborted, the stigmas sessile or sub sessile, 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.

LILAECACEAE (Figure 5c,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 Ø above, bisexual in the middle and Ψ below; solitary Ø 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 sub sessile in the bisexual and upper Ø flowers, the style long, filiform, with a capitate, papilllose stigma in the basal axillary flowers; ovary superior, unilocular, uninovulate, the ovule basal,
Figure 4.—Triuridaceae: a, Sciaphila alboascens 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). Schuchzeriaceae: c, Schuchzeria palustris flower, stamen, a carpel, same laid open, plant in flower; d, fruit, seed (after Hutchinson).
FIGURE 5.—JUNCAEACEAE: 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. palustris* c.s. of fruit (after Baillon, Le Maout and Decaisne). LILACACEAE: c, *Lilaeae subulata* upper inflorescence, a flower, views of stamen and perianth (bract), 9 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 antipodal cells of the embryo sac degenerate during early embryogeny; endosperm formation Nuclear; fruit a compressed, longitudinally ribbed nuclet; 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, anepigynous 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 monocotilate 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 antipodal cells of the embryo sac persist into early embryogeny; endosperm formation Nuclear; fruit a nutrient, 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 7a–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, solitary or few in a row of bracts on each margin, at first enveloped by a leaf sheath, the plants monoecious or dioecious; perianth absent; \( \delta \) flowers consist of a single, sessile, dorsifixed, elongate anther; pollen filamentous, about 2500 \( \mu m \) long, 4-5 \( \mu m \) wide, 2-celled when shed; \( \varphi \) 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 Helobial; fruit a nutrient, achene or drupelet, the seed longitudinally ribbed, endosperm absent at maturity. Chromosomes: \( x = 8,10,13–15 \), especially 13,10.

**Composition**: 2 genera, ~100 species.

**Distribution**: Cosmopolitan, in fresh or somewhat brackish water.

### Zannichelliaceae (Figure 7d)

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,
SMITHSONIAN CONTRIBUTIONS TO BOTANY

Figure 6.—Aponogetonaceae: a, Aponogeton fenestratus 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. stenosiphys 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). ZANNICHILLIACEAE: 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, stamens 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 unonbate stigma, or 2–4-lobed and the stigmas filiform; ovary superior, unilocular with 1 basal, bitegmic, crassinucellar, or 2–4-lobed and the stigmas filiform; ovary superior, narial, glabrous herbs on rocks, with a short thick rhizome; xylem vesselless, the tracheary elements reduced; crystals absent; leaves linear, usually toothed, much branched; raphides and crystals absent; xylem vesselless, the tracheary elements reduced; leaves linear, anatropous ovule; the 3 antipodal cells 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 8a,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 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 8c).—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, stamens absent, intravaginal scales present; inflorescences spikes in axils of foliaceous bracts at the apex of a scape, the lower flowers bisexual, the upper generally δ; 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.

TYPHACEAE (Figure 9c,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 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 δ above the 9; 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, extrorse, the anthers large, sessile, extrorse; 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 antipodal cells 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 9a,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 δ above the 9; 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, extrorse, the anthers large, sessile, extrorse; 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 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.

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 antipodal cells sometimes multiplying to as many as 150 cells; endosperm formation Nuclear; fruit achenes or nutlets; embryo straight, elongate; endosperm copious.

Distribution: Cosmopolitan, Nearly cosmopolitan, most commonly in the Northern Hemisphere.
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 ulcer 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.
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) in 2 whorls, glaucous, rarely scarious, usually greenish or reddish brown, rarely white or yellowish; stamens 6(3), free, the anthers basifixed, rarely apically produced; pollen (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 10c).—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, oblong, 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 deciduous ventrally; ovary superior, 1-(3)-locular, the ovules axile-subbasal, 1-2 few per locule, anatropous; fruit a loculicidal capsule, the 3 seeds elongate, pointed at both ends; embryo axis 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 11a,b).—Small, tufted, annual or perennial herbs of wet habitats; raphides, crystals and silica bodies absent; sometimes with multilayered 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 stamates paracytic, somewhat similar to those in Poaceae; inflorescences scapose spikes or heads, or rarely
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. triticus flower, floral diagram of a flower, l.s. of a flower. Lamprocapnos grandis flower, l.s. of same; d, Restio tetraphyllus flower, a 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 11c,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 \( \varphi \) flower, free or rarely the inner ones basally connate, or different from the outer; \( \delta \) 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; \( \varphi \) 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 prickel-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 \( \frac{1}{2} \) 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; prickel-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, cauleine 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
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-
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 (Mictandra), 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 monoeocious or dioecious, anemophilous, usually consisting of spikelets; flowers (florets) small, usually bisexual, rarely the pistil 1, the carpels 2-3, styles 3-celled when shed, l-ulcerate; pistil 1, the carpels 2-3, styles 3(2), free or connate, the stigmas 2(1-3) generally plumose, sometimes only papillate, rarely ventral; florets below, spikelet@) usually subtended by the sheath and petiole, large to very large, pinnately formed or simple and scalariform, rarely vessels absent; 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.

ARECACEAE

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-enic acid (palmitoleic acid). Several produce waxes; very often tanniferous; various sorts of polyphehols 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 reductive, 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 monoeocious, 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, ovate 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,
**Figure 14.**—Poaceae: a, *Avena sativa* inflorescence, 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, *Zizania 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 nervosa* 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* gynoeceum and glumes, *Merosiachys 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-sulcate (-zonisulcate) 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.—Areceae: 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 goniata 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 rufia fruit and ♀ inflorescence, Arenga luangkai l.s. and c.s. of fruit; e, Triphirnax acanthocoma flower, calyx, petal, androecium, gynoeceum, l.s. of pistil (after Baillon, Le Maout and Decaisne, Martius).
Figure 17.—Arecales: 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 mariapa ♀ flower, petal with 2 stamens, Micrococos pulchra l.s. of ♂ flower, l.s. of ♀ flower, Astrocaryum weddelii ♀ 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, Atala a phalerata ♀ flower, pistil and staminodal cup, ♂ flower, stamens, stamen (enlarged) (after Le Maout and Decaisne, Baillon, Martius).
nectaries often present; ovules axile (subbasal to apical), 1 per ovary or locule, bithegmic, 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 sap-niferous; 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 monoeocious, the flowers

![Figure 18.—Arecales: *Elaeis melanococca* δ flower, sepal, petal, androecium, l.s. of same, androecium with all stamens but one removed, 2 views of anther, Ψ flower, pistil; *Phytelus macrocarpa* δ inflorescence, l.s. of Ψ inflorescence, pistil, l.s. of same, *Nypa fruticans* δ flower (3 connate stamens), c.s. of fruit (after Baillon, Martius).](image)

![Figure 19.—Cyclanthaceae: *Cyclanthus bipartitus* inflorescence before anthesis and at anthesis, l.s. of part of inflorescence, l.s. of 2 Ψ and 1 δ flower, upper part of leaf (greatly reduced); *Cyclanthus lomatophorum* inflorescence, *C. palmata* plant in flower, *C. laeva* spadix with fruits and δ flowers; *C. juniperus* δ flower, l.s. of same, *C. pulchra* δ flower from above, lateral view of same, l.s. of same; *C. funifera* Ψ flower, l.s. of same; *C. pulchra* c.s. of Ψ flower, c.s. of ovary, *C. palmata* group of fruits seen laterally and from above, *Carladudovia* l.s. of seed showing the minute embryo in abundant endosperm (after Baillon, Martius, Le Maout and Decaisne).](image)
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; \( \delta \) 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, basifixied or dorsifixied; pistillode absent; pollen 2-celled when shed, 1-sulcate or ulcereolate; \( \varphi \) 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, fleshy or horny, with oil, aleurone, hemicellulose, rarely starchy. 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, major veins parallel or more often palmate or pinnate, the minor ones reticulate, the major veins longitudinal and parallel or more often palmate or pinnate, the minor ones rhabdoid, 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 basified, 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 antipodal cells 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 Araceae 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, 21a).—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 Pista); 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; infflorescence 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 fied, the parts hypogynous, bisexual or usually unisexual, sometimes with a rudiment of the opposite sex, and the plants monoeocious, 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 basified rarely adnate, or the locules immersed in an

![Figure 20.—Araceae: a, Acorus calamus spadix (naturally not enclosed in spathe), flower, 1.s. of part of ovary showing the spadical ovules, fruit, Gymnostachya anceps flower from above, 1.s. of part of ovary showing the spadical ovules; b, Zantedeschia c.s. of left and upper part of ovary, Arum maculatum stamen, 1.s. of pistil, fruit, 1.s. of seed, embryo, spadix with the spadix removed showing 1 ovaries above the 9; c, Orontium aquaticum flower from above, stamen, 1.s. of pistil showing the single basal ovule, Calla palustris spadix and spathe, flower, 1.s. of same (the flower normally lacks a perianth); d, Anthurium scandens part of spadix, lateral view of flower, Pista stratiotes spadix opening showing the single pistil below and the androecium above, 1.s. of same, fruit adnate to the spadix, 1.s. of seed; e, Philodendron squamiferum 1.s. and c.s. of fruit, seed, 1.s. of same with exterior integument removed, Ambrosia 1.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, 1.s. and c.s. of same (after Baillon, Le Maout and Decaisne, Martinii).
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). Liliaceae: b, Lema minor in flower, inflorescence in bract, l.s. of pistil, fruit, L. paucicostata fruiting frond; c, L. valdiviana stamen, L. trisula seed, same with testa removed, l.s. of same, embryo, Spirodela polyrhiza 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)-sulcate, zonisulcate, 3(4)-porate, oligosulcate, polyporate or nonaperture, the type correlated with pollinator, rarely in tetads (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; anther of 2 separate sacs, 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: Panropical and subtropical, mostly on the forest floor or vines, few in the temperate zones.

Lemnaceae (Figure 21b,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 monocious rarely dioecious; perianth absent; ♂ flowers: stamens 1-2, filament present or the anthers sessile; ♂ flowers: stamens 1-2, filament present or the anthers sessile; ♂ 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.

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 scilladiенolides, some produce inulin and fructosans. Steroidal alkaloids also occur in Ranunculaceae. Siemona 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 Wurmbaooideae may warrant family status. A family Colchicaceae has been suggested; its outstanding chemical character is tropolone alkaloids, including colchicine. The Alliaceae lack the characteristic alkaloids of the Amaryllidaceae. Velloziaceae lack saponins, are often tanniferous, commonly produce resin or gum, are not cyanogenic. Some Xanthorrhoeaceae produce naphthaquinones.

Trilliaceae (Figure 21d,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, basified, 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, bithegmic, 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 22–24a).—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 racemes or spires, 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, basified, interorse; 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. Chromosomes: x = 13–16, especially 16.

Figure 22.—LILIACEAE: a, Tofieldia catylopta flower, 1.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, 1.s. and c.s. of seed, embryo, Zygadenus glaberimus 1.s. of flower; c, Aquillaria dioica 1.s. of ♀ flower, 1.s. of ♀ flower, Narcissium aestivum 1.s. of flower; d, inflorescence, dehisced fruit, 1.s. of seed showing the small embryo, part of tails cut off (greatly enlarged), Colchicum autumnum andruecum and perianth-limb laid open, stamen, apex of a style showing somewhat decurrent stigma, 1.s. of seed showing minute embryo in abundant endosperm, 1.s. of flower, e, ovary and base of styles, 1.s. of same, c.s. of ovary, dehisced fruit, c.s. of same, corn; f, seed and 1.s. of same, floral diagram, Maianthemum bifolium flower, 1.s. of same (after Baillon, Le Maout and Decaisne).
Composition: 4 genera, ~375 species.

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

Agavaceae (Figure 24d).—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-sulcate, provided with a thick reticulate or retiplate exine, usually single, rarely tetrad, 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 (Dasyliuron) 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 resinosus, 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 panicule, 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 whors, free or shortly connate, the inner whorl sometimes petaloid; stamens 6 in 2 whors, 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, zonosulculate or spiraperturate; pistil 1, carpels 3, the styles usually elongate, 3 or 1 and 3-lobed, stigmas 3, apical, sometimes capitulate; 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 New Guinea and 1 in New Caledonia.

Philesiaceae (Figure 26a).—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 Geionoplegium), 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 capitulate; ovary superior or rarely inferior.
(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.

STEMONACEAE (Figure 26b).—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 (Penastemona), sometimes 2–3 sheaths at the base of the stem, the stomates anomocytic; inflorescences axillary, the flowers solitary and pedicellate or few-flowered cincinni in racemes or subumbell; 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 (Penastemona); 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), basifixid or dorsifixid 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...
sessile; ovary superior, semi-inferior or inferior, unilocular, the ovules numerous to 2, basal, apical or parietal (Penastemon), 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 (Penastemon), 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 26c–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; \( \varphi \) 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, extorse 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)-sulcate, 2-celled when shed; \( \sigma \) 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 27a).—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 stamates anomocytic; inflorescence scapose, the flowers in a cymose umbel, often subtended by a combination of linear and broad bracts; flowers bisexual, actinomorphic; perianth homochlamydous, 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 somewhat 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, relied; 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 27b.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,
TACCACEAE: a. Tacca cristata inflorescence, flower, l.s. of same, T. leontopetalooides 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 epidermoides part of stem showing the persistent leaf bases and numerous adventitious roots (in c.s.) within them, V. caruncularis scape flower and parts of leaves, V. tenella part of perianth and stamens, V. hemisphaerica l.s. of flower, Barbacenia wandelli 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)-sulcate, 2-celled when shed; pistil 1, the carpels 3, style 1, often trimerophic, the stigma apical, punctiform or shortly 3- or 6-lobed; ovary superior, internal septal nectaries usually present (absent in Heteranthera), 3-local, the ovules numerous, axile or 1-local 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 27d,e, 28a). —Perennial herbs usually of dry habitats, with a unincised bulb, very rarely a rhizome; raphides 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 (ategmic in some species of Amaryllidaceae), as Platanthera, Heteranthera), copious, with cellulose or starch, enclosing the embryo. 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 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 (Barbaceniaopsis), actinomorphic; perianth segments 6 in 2 whors, petaloid, free or basally connate, sometimes with a small corona behind the anthers; stamens 6(4–8) in 6 bundles when more than 6, the filaments epignous (Talbotia) or adnate to the perianth, occasionally flattened, the anthers sometimes subsessile (Barbaceniaopsis), intorse, linear, basified or dorsifixed; pollen 1-sulcate or nonaperturate, sometimes in tetrad (Vellozia); pistil 1, the carpels 3, style 1, the stigma capitata or shortly 3-lobed; ovary with internal septal nectaries, inferior, 3-local, 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 length of the endosperm, 2.5–4.0 times longer than wide; endosperm copious, hard, with hemicellulose, protein, oil, and starch. Chromosomes: x = 50.

Composition: ~75 genera, ~1100 species.

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

VELLOZIACEAE (Figure 28b,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...
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, Baill.).
always actinomorphic, rarely weakly zygomorphic, bisexual or more rarely the plants polygamous or dioecious, entomogamous, ornithogamous, rarely anemogamous; perianth heterochlamydeous, but sometimes the sepal colors (Sedum, 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-sulcoide, 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 sepal 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 appressed 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, meaty, 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 Carionema), 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 polygamous-monocious, more rarely monocious, very rarely dioecious, 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, dehiscent longitudinally, or rarely by an apical pore; pollen 1-sulcate, rarely with additional apertures, 2-celled (3 in Floscopia 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 antipodal ephemeral but persistent in Tinania 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 embroyogea, 0.3 the length of the endosperm, 1.3–1.7 times longer than wide; endosperm copious, meaty, starchy. Chromosomes: x = 4–20, especially 6,8,9,12,14.

Composition: ~50 genera, ~700 species.

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 31a–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 Carionema), silica bodies sometimes present; xylem vessel perforation plates simple in all organs, rarely also scalariform, or vessels absent from the stem and leaves (Carionema); 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 stamens 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 (Carionema), sometimes within a protecting bract; flowers usually actinomorphic, sometimes zygomorphic, bisexual or rarely the plants polygamous-monocious, 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, dehiscent longitudinally, or rarely by an apical pore; pollen 1-sulcate, rarely with additional apertures, 2-celled (3 in Floscopia 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 antipodal ephemeral but persistent in Tinania 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 embroyogea, 0.3 the length of the endosperm, 1.3–1.7 times longer than wide; endosperm copious, meaty, starchy. Chromosomes: x = 4–20, especially 6,8,9,12,14.

Composition: ~50 genera, ~700 species.

Distribution: Primarily pantropical and subtropical, ex-
tending into the temperate zones, usually in mesic open or forest habitats.

**Mayacaceae** (Figure 31d–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; ovary 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 triolobed; 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 embroytage, 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:** Mainly pantropical and subtropical, mostly America, extending into temperate America and Africa.

**Rapateaceae** (Figure 32c,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, the 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, 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 zonisulcate; 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: x = 8,9,13,17.

**Composition:** 5 genera, ~250 species.

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

**Cdicomoaceae** (Figure 33).—Perennial, seldom annual herbs usually of wet habitats, emergent or rarely submerged, the stem short, rarely stoloniferous; raphides absent but...
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 poepigii flower, A. poepigii views of anther, A. poepigii pistil showing the stiglar appendages, c.s. of ovary, dehisced fruit (after Martius, Bail lon). RAPEACEAE: c, Schoenocephalium maritimum 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, Bail lon).
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, bietegmic, tenuinucellar, orthotropous; embryo sac antipodal cells ephem-eral; 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, ~1,150 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 Zingiberales, 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.
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, basified, rarely dorsifixed; pollen usually nonaperturate, sometimes forate or spiraperturate, 2–3-celled when shed; nectaries epigynous or sepall; pistil 1, the carpels 3(2), style 1, the stigma apical, 3-lobed, bilabiata 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 antipodal 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 34a,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 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, basified, 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; embryotega 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 34c,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, basified; pollen nonaperturate or aperture indistinctly porose-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; embryotega marginal or within the perisperm, 0.35–0.9 the length of the latter, 7.5 times wider than 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 35a).—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 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, Eleitaria cardamomum dehiscing fruit, Renealmia racemosa flower, labelium; 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, unilaterial, 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, arilate, their food reserve starchy; embryology unknown. Chromosomes: \( n = 9 \).

**Composition:** 1 genus, 2 species.

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

**ZINGIBERACEAE** (Figure 35b–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 both simple and scalariform in the root, vessels absent from the stem and leaves; leaves cauline or cauliform, 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 appressed and sometimes separating the locules, 2 or 4 petaloid staminodes usually present; pollen usually nonaperturate, forate or spiraperturate or \( \pm \) 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 capitulate 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, bithe­mic, crassin­cular, 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 \( \frac{2}{3} \) of South America; southern \( \frac{2}{3} \) of Africa, Madagascar, East Indies, northeastern Australia.

**CANNACEAE** (Figure 36a,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, bitemgic, crassin­cular, 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 36c,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 symposium 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. burchelliana 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, Haemodorus spicatum flower spread out, apex of stamen, c.s. of ovary, H. tereifolium l.s. of flower, fruit, Haemodorus 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, Anigozanthus flower, l.s. of same, seed, l.s. of same, stamen, floral diagram (after Baillon, Le Maout and Decaisne, Lindley). PHILYDRACEAE: c, Pritzella 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, bitemporal, crassinucellar, antapomorphic or anacampylotropous; embryo sac antipodal cells ephemeral or persisting at least until fertilization or multiplying secondarily; endosperm formation Nuclear; fruit a loculicidal capsule or berry, sometimes muricate (Trachyphrithyrium, Thymocarpus) or papillate (some Calathea), the seeds sometimes arillate; embryo curved or folded, 1.4–1.6 times longer than the perispem, 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)-sulcate, spiraperturate(oid)ate, non-aperturate, polygordiate, 2(-4)-porate, or 1(-3)-ulcerate, 2(-3)-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, bitemporal, 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.

PHILLYDRAEACE (Figure 37c).—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 perianth; stamens 3 or 6, sometimes 2-3 staminodes present, 1 plus 2, filaments 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 Pyrrhorrhiza, the filaments free from one another, adnate to the perianth; anthers elongate, basifixed or dorsifixed, intorse, 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, bitemporal, 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.
ovary superior, without sepal nectaries, 3-local and the ovules axile, or incompletely 3-local 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 37a, 38a–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 (*Oenostchys*); flowers bisexual, actinomorphic or zygomorphic; perianth petaloid, marcescent, free, 3, 6- or 9-seriate, free or connate, rarely with a spur or sac at the base (*Kentrostisiphon*); stamens 3, rarely one of them staminodal (*Dipilarrhena*), epigynous or adnate to the perianth, the filaments free or connate, anthers basifixed or dorsifixed, exstrose; pollen usually 1-sulcate, less often 2-sulcate, spiraperturate, 3-seriate, 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 sepal of the ovary; ovary inferior, very rarely superior (*Isophysis*), 3-local and the ovules axile or very rarely 1-local 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 (*Radiniphon*). 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 38d, e, 39a,b).—Saprophytic chlorophyll-less 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, Afrothisium*); perianth corolline, of 6(3) segments ciliate 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 ciliate in a ring or deflexed tube, the connective often broadened and apically produced, and the anther sacs separate, dehiscence latrotrous or intorose; pollen nonaperturate or with 1(3)–ulcerate, circular or slightly elongate apertures, 1-sulcate(2?), 2–3-celled when shed; pistil 1, the carpels 3, style 1, the stigmas 3, apical, usually enlarged, often capitulate, sometimes each bifid; ovary inferior, with septal or epigynous nectaries, 3- or 1-local; 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, dehiscence 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:** Panropical, mainly in rain forest, some in savanna or grassy fields, few in temperate regions.

**ORTHIDALES**

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, monococious 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 pollen; 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-local 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 39c).—Chlorophyllless 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 39d-41).—Perennial herbs (one species annual), rarely half-shrubs, obligately mycorrhizal (except some Anarthraeaceae), rarely saprophytic, rarely climbers (Vanilla), the stem mostly sympodial, sometimes monopodial, often thickened basally and with 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-veneined, the sheath nearly always closed, stomates paracytic, less often anomocytic, seldom tetracytic; inflorescence terminal or axillary, sometimes spactose, 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-sulcate, 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, tenuinuccellar, anatropous; embryo sac antipodals ephemeral and frequently not all 3 are produced; endosperm formation, when it occurs, Nuclear, and then only a 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, ~1500 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 achalermis inflorescence, flower, column, 1.s. of same (below) showing the entrance to the spur, pollinium, c.s. of ovary, H. arecbraeletae c.s. of ovary; c, Selenipedium palmifolium sepal, petal, labellum, S. isabelianum 3 views of column, 1.s. of same, S. palmifolium c.s. of ovary; d, Epidendrum schreiberi 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, pollinum of Stenorrhynchos speciosa, Epidendrum anther without the pollinia, pollinia (after Martin, Lindley, Le Maou and Decaisne).
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), Erythronium paterianus seed (greatly enlarged), Stenorrhynchos argentinus seed (greatly enlarged); c, Orchis dehisced fruit leaving in place the 3 median nerves of the carpels, Fendeszia acuta dehisced fruit, diagram of same; d, Angraecum dehisced fruit, diagram of same, Pleurothallis claude dehisced fruit, diagram of same; e, Epidendrum dehisced fruit, Coryanthes speciosa flower, Bipinnula polysyrta lateral sepal (after Martius, Le Maout and Decaisne, Lindley).
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