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A PHYLOGENETIC CLASSIFICATION OF THE
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ABSTRACT

A synoptical key to the three orders Annonales, Berberidales, and Nymphaeales of the superorder Annoniflorae is presented with discussion as to why these orders, the core of the historical Ranales, are considered to be closely related to one another but divergent from the similarly primitive Hamamelidales of the Hamamelidiflorae, and why the names Annonales and Berberidales are preferred to the names Magnoliales and Ranunculales. For each of the three orders detailed synoptical keys to the 33 families and 30 subfamilies (21 additional to the typical subfamilies) recognized by the author are presented. Also the included families of each order are discussed with explanation of their accepted alignment, circumscription, and geography. Finally, an extensive bibliography is listed to those publications that represent the documentation for the author's interpretation of the Annoniflorae. Five new subfamilies are published by reference to their basonyms: Mollinedioideae of the Monimiaceae, Idiospermoideae of the Calycanthaceae, Peperomioidae of the Piperaceae, and Euryaloideae and Barclayoideae of the Nymphaeaceae.

INTRODUCTION

After more than 15 years of effort toward developing a phylogenetic classification of the Angiospermae, I presented in 1968 in *Aliso* a naked synopsis of my classification. I published that synopsis with considerable reluctance because a classification issued without thorough documentation and explanation is only of suggestive value. However, I had hoped shortly to complete a small volume containing considerable discussion of each order and a lengthy bibliography. Other activities intervened, but now I am rewriting and expanding considerably that manuscript and adding original drawings for at least one species for each order and suborder. I plan to prepare for each order detailed synoptical keys to the families and subfamilies currently recognized; present considerable discussion of each family explaining, where desirable, circumscription, geography, and reasons for the accepted alignment; and supply, by way of documentation, an extensive list of pertinent publications studied. Because the resulting large volume will require several years of preparation and editing before publication, I have decided to publish in various botanical journals at appropriate intervals my treatments of the various superorders or larger orders.

Piecemeal publication has certain advantages. I can expect much criticism, surely most of it constructive, from interested specialists who will want to know why I have so mistreated their favorite taxa. They will perhaps

be inspired to suggest for their special groups a more reasonable classification with appropriate exposition. Even my synopsis generated some very helpful suggestions. Such useful information from monographers will be most welcome, and will enable me in the final compilation to improve the classification, correct errors, remedy omissions, and expand discussion where the botanical audience seems to desire it. New discoveries and research and much expanded information about various angiospermous families since publication of the "Synopsis" (Thorne, 1968) have caused me to make a number of changes in my classification. The revised synopsis will, of course, be included in the book with the much requested phylogenetic "tree," which I prefer to present as a phylogenetic "shrub," or a bit facetiously, as a phylogenetic "hedge."

The principles or concepts that have guided me in the development of my classification of the Angiospermae have been published (Thorne, 1958, 1963) in outline form with some discussion and examples. They have also been touched upon in two recent papers on inclusion of the Apiaceae (Umbelliferae) in the Araliaceae (Thorne, 1973) and the artificiality of the once widely accepted "Amentiferae" (Thorne, 1974). I have greatly expanded and modified my statement of these principles in the manuscript for my text, but only one added principle needs mention here. Like most of the others, it is a generalization so much a part of our taxonomic philosophy that it never occurred to me before to enunciate it. Briefly, *the plasticity of angiospermous organs, tissues, and cells is so pervasive that the phylogenetic value of most of their characteristics is not determinable a priori*. This general plasticity, along with the prevalence of convergent evolution among the flowering plants, causes the phylogenist much pain and frustration but greatly adds to the challenge of his occupation. Each taxon requires careful study to ascertain which features are conservative and which are highly modified before we can decide which should receive the most weight in our search for the phyletic relationships of the taxon. Neither *a priori* nor equal weighting of characteristics is reasonable or feasible in phylogenetic studies.

SUPERORDER ANNONIFLORAE

SYNOPTICAL KEY TO ORDERS

1. Parenchymatous tissues mostly with spherical idioblasts (essential oil cells); mostly woody terrestrial plants with relatively unspecialized xylem (some taxa primitively lacking vessels); stomata commonly paracytic; pollen grains mostly anasulcate (distally aperturate) or phyletically closely derived types ANNONALES
- 1'. Parenchymatous tissues lacking spherical idioblasts; mostly herbaceous or soft-woody terrestrial plants with relatively specialized xylem or rhizomatous aquatic herbs; stomata commonly anomocytic; pollen grains various.
2. Plants mostly terrestrial herbs, soft-woody climbers or shrubs, or rarely trees; lacking cordate or peltate floating leaves; stomata mostly on the lower surface of leaves; cambium and relatively specialized vessels present; pollen grain never anasulcate but commonly tricolp(oroid)ate or phyletically closely derived types BERBERIDALES
- 2'. Plants all aquatic herbs, mostly rhizomatous; leaves mostly cordate to peltate, floating or emersed (or submersed and very thin or much dissected); stomata on

the upper surface of leaves; vascular bundles monocotyledonoid and mostly scattered, lacking cambium, and with vessels absent or tracheidlike; pollen grains mostly anasulcate or closely derived types (tricolpate only in *Nelumbo*) NYMPHAEALES

DISCUSSION OF ANNONIFLORAE

At the Tenth International Botanical Congress in Edinburgh I presented a realignment (Thorne, 1964) of the traditional Ranales in which I split this partly unnatural assemblage of plants retaining numerous primitive angiospermous characteristics into three superorders, Annoniflorae, Nymphaeiflorae, and Hamamelidiflorae. The last group really does not concern us here and needs but brief mention. Often treated in the Ranales, *Trochodendron* Sieb. & Zucc., *Tetracentron* Oliv., *Euptelea* Sieb. & Zucc., and *Cercidiphyllum* Sieb. & Zucc. (which form monogeneric families in my Trochodendrineae of the Hamamelidales, Hamamelidiflorae) are ancient relicts once widely distributed in the Northern Hemisphere but now restricted to the humid forests of eastern warm-temperate Asia. Like the Annoniflorae these living fossils retain many primitive features in their stem anatomy, both *Trochodendron* and *Tetracentron* being primitively vesselless, but their flowers, pollen, and other organs appear to be more specialized. Although trees like many Annonales, they lack the spherical idioblasts containing essential oils and the monosulcate or closely derived pollen grains characteristic of that order. Instead, they approach rather closely *Eucommia* Oliv., *Platanus* L., and the Hamamelidaceae in their stem anatomy, floral morphology, pollen, fruit, often winged seeds, leaf anatomy, embryology, past and present geography, and geological history. They are best treated as four suborders in the Hamamelidales. The Hamamelidiflorae presumably had distant common ancestry with the Annoniflorae but the two groups appear to have diverged rather widely from one another by late Cretaceous time. I will treat the Hamamelidiflorae in much more detail at a later date.

Further study of the Nymphaeales, especially of the serological data assembled by my former colleague J.-P. Simon (1970, 1971), has caused me to delete the superordinal name Nymphaeiflorae and to place the Nymphaeales with the Annonales and Berberidales in the Annoniflorae. Thus the traditional Ranales (*sensu lato*) are narrowed down to one superorder.

I have often been asked why I use the names Annonales and Berberidales instead of the currently more popular Magnoliales and Ranunculales. Although observation of priority is not required by the *International Code of Botanical Nomenclature* (Stafleu, 1972) for names above rank of family, I prefer to apply the principle of priority throughout my classification. Ordinal names ending in -ales and based upon a type genus and family were first used consistently by Lindley in 1833 in his *Nixus Plantarum* (as alliances); hence, I have chosen that work as the beginning of valid publication for ordinal names. Lindley's use of the name Annonales (as Anonales) in 1833 has nearly 100 years of priority over Hutchinson's first use of the name Magnoliales in 1926. Lindley in 1833 also recognized both Berberales and Ranales, but I have chosen the name Berberidales for the

taxon combining his two orders because of the ambiguous way that Ranales (correctly Ranunculales) has been used by most botanists subsequent to Lindley. The name Annoniflorae, based upon Annonales Lindley (1833), seemed more appropriate for the superordinal rank than one based on either the Berberidales Lindley (1833) or Nymphaeales Lindley (1845).

My use of the category superorder stems from my conviction that the angiosperms are better treated as a class, the Angiospermae, with the two subclasses, Dicotyledoneae and Monocotyledoneae, equivalent to the several classes of gymnosperms and of pteridophytes in the division of vascular plants, Tracheophyta. Those who follow Recommendation 16A of the *Code* (Stafleu, 1972) would presumably use the name Angiospermopsida, or better Annonopsida, for the angiosperm class and Dicotyledonidae or Annonidae and Monocotyledonidae or Liliidae for the two subclasses. I do not like the *Code's* recommended class and subclass endings because they deviate unnecessarily from the traditional endings and because -opsida has generally been used by morphologists as the suffix for subdivisional names. Fortunately, conformity to recommendations is not required by the *Code*. Proponents of the elevation of the Angiospermae and other classes of vascular plants to divisional rank include Bold (1956), Cronquist (1960), and Cronquist, Takhtajan, and Zimmermann (1966). Such taxonomic inflation seems to me to serve no useful purpose since the reasons for the elevation in rank are rather unconvincing. Debasement of categories and disintegration of taxa without solid, compelling evidence are pedagogically unsound.

The basis for treating the Annonales, Berberidales, and Nymphaeales as three closely related orders in one natural superorder Annoniflorae may not be so obvious as the reasons for distinguishing the three orders, as summarized by the synoptical key to orders above and as treated in the more detailed discussion of each order below. Their relationship and immediate common origin, however, are rather clearly indicated by their common possession of numerous primitive, ancestral angiospermous features, especially apocarpy, polymery, undifferentiated, styleless carpels, microsporophylls commonly unmodified into filament and anther, spiral arrangement of floral parts, radial symmetry, general absence of connation and adnation, prevailing bisexuality, often undifferentiated perianth, follicular fruit, and unspecialized ovules, seeds, and other embryological features. Other primitive characteristics are retained unevenly within the three orders. Monocotyledonlike pollen grains of the anasulcate type or closely derived types are within dicotyledons restricted to and prevalent within the Annonales and Nymphaeales. Vesselless wood, or xylem composed of primitive tracheidlike vessels, is characteristic of members of the same two orders. On the other hand, the woody or perennial herbaceous habit with much secondary growth from a cambium is absent from the Nymphaeales but typical of the Annonales and Berberidales. These latter two orders are also strongly linked by their chemistry for both of them are very rich in alkaloids of the phenylalanine type (Hegnauer, 1958). Simon's serological studies (1970, 1971) indicate a rather close relationship biochemically

for all three orders. Thus, despite their early and far-reaching divergence in habit and habitat, the treatment of these three orders together in one superorder is strongly supported by all available evidence.

ORDER ANNONALES Lindley 1833

SYNOPTICAL KEY TO FAMILIES AND SUBFAMILIES

1. Vesselless (and other xylem features also rather primitive); nodes trilacunar; leaves alternate, entire, evergreen, pinnately veined, and exstipulate; stomata paracytic, occluded with waxy deposits; flowers cymose, small, bisexual or unisexual, with floral parts mostly separate, spirally arranged, indefinite in number; perianth differentiated; stamens single veined, often relatively short microsporophylls with lateral to apical microsporangia; pollen grains in tetrahedral tetrads, each grain distally monoporate; carpels conduplicate, often stipitate with partly "unsealed," stigmatic margins; many anatropous ovules on submarginal placentae; seed with abundant endosperm and rudimentary embryo; chromosome numbers, $n = 13, 43$; trees and shrubs of southern hemisphere (WINTERINEAE) Winteraceae
- 1'. Vessels usually present; nodes and leaves various, but stomata not occluded; flowers, pollen, seeds, and habit various.
2. Pollen apparently 3- or 6-colpate; nodes unilacunar; cambiform "mucilage" cells in phloem; cuticle intruded between ends of guard cells; flowers with numerous, mostly separate, spirally arranged parts; chromosome numbers, $n = 13, 14$; small trees, shrubs, or lianas of eastern Asia and eastern North America (ILLCINEAE).
3. Plants small trees or shrubs with flowers bisexual; stamens numerous, free; carpels (20–11) in single whorl, each with vascularized, distally stigmatic style; fruit a follicetum of 1-seeded, spreading, ventrally dehiscent follicles; primary tissues in pseudosiphonostele; crystal-bearing sclerenchyma absent; petiole with single, arch-shaped vascular strand (*Illicium*) Illiciaceae
- 3'. Plants climbing shrubs or twining lianas with flowers unisexual; stamens numerous to few, variously aggregated, sometimes reduced to 5 in connate shield-shaped structure; carpels many, spirally arranged with stigmatic crests prolonged into nonvascularized style; gynoecea developing into 2- or 3-seeded berries on elongate and spicate or crowded and globose receptacle; primary tissues typically eustelic; crystal-bearing sclerenchyma present; petiole with 3 vascular traces (*Kadsura*, *Schisandra*) Schisandraceae
- 2'. Pollen not 3- or 6-colpate, usually anasulcate or various closely derived types; nodes various; cambiform "mucilage" cells usually absent from phloem; cuticle not intruded to same degree; flowers, chromosome numbers, and habit various.
4. Nodes trilacunar to multilacunar.
5. Flowers mostly with perianth, often well differentiated; if apetalous, sepals not petaloid; mostly trees, often large, and shrubs; flowers mostly solitary or in small clusters, bisexual, radially symmetrical, often beetle pollinated; stamens commonly laminar with median, embedded microsporangia to differentiated into filament and anther; carpels conduplicate with margins "unsealed" and stigmatic to carpels with margins sealed and with terminal, vascularized style; endosperm commonly ruminate (ANNONINEAE).
6. Flowers often conspicuous with perianth commonly petaloid and often trimerous; stamens and carpels mostly numerous, free, and spirally arranged on elongate or conical receptacle; staminodia absent; pollen grains monosulcate or variously modified therefrom; ovules several but often reduced to 2 or 1.
7. Leaves with large sheathing, early-deciduous stipules that leave an annular scar

at node; perianth not well differentiated; stamens, often laminar, rarely extrorse and never "peltate," and carpels on elongate receptacle; pollen grains anasulcate; fruit follicular, capsular, samaroid, or a fleshy syncarp; seeds not arillate, though often with sarcotesta; endosperm not ruminate; basic chromosome number, $x = 19$
 ----- Magnoliaceae

8. Fruit a conform follicetum, woody capsule, or fleshy syncarp, never samaroid; seed with sarcotesta, free from endocarp; leaves entire or sometimes basally auriculate ----- Magnolioideae
- 8'. Fruit a woody samara, indehiscent, deciduous; testa not fleshy, adherent to endocarp; leaves lobed with apex truncate or widely emarginate (*Liriodendron*)
 ----- Liriodendroideae
7. Leaves exstipulate; perianth well differentiated with 3 sepals in outer whorl and 6 petals in usually 2 inner whorls; stamens, extrorse and usually "peltate," and carpels on short, convex receptacle; pollen grains rarely anasulcate, usually catasulcate (proximally aperturate), inaperturate, or otherwise closely derived types; fruit rarely a follicle, never samaroid, usually baccate or a fleshy syncarp; seeds often arillate and endosperm usually ruminate; basic chromosome numbers, $x = 7, 8, 9$ (subfamilial division pending) ----- Annonaceae
- 6'. Flowers large or small but seldom conspicuous; perianth, if present, not markedly petaloid; stamens and carpels not on elongate or conical receptacle; staminodia present or absent; pollen grains anasulcate or 2- or 3-sulcate; ovules various.
9. Flowers calyptrate, or if perianth present and differentiated, not markedly 2- to 5-merous; stamens numerous, separate, and mostly laminar; staminodia present and often conspicuous; pollen grains anasulcate or 2- or 3-sulcate.
10. Leaves with brown peltate scales; large tree; perianth of single calyptrate sepal and 4 whorled petals; both outer- and innermost stamens staminodial; pollen grains anasulcate; microsporangia abaxial; carpels several, spirally arranged, largely closed, each with 1 or 2 pendulous ovules, concrescent at maturity; fruit a globose syncarp; endosperm oily, not ruminate; chromosome number, $n = 12$ (*Galbulimima*) ----- Himantandraceae
- 10'. Leaves glabrous, without peltate scales; trees or shrubs; perianth absent or differentiated; only innermost or outermost stamens staminodial; ovules several to numerous; fruit baccate or follicular; endosperm ruminate.
11. Plants shrubs or small trees; perianth absent and replaced by calyptrate bract; innermost stamens petaloid, staminodial, bearing food bodies and forming pseudoperianth; anthers with adaxial dehiscence; pollen grains 2- or 3-sulcate; carpels numerous, spirally arranged, syncarpous, in hollow receptacle, margins partially unsealed at anthesis and stigmatic; fruit an urceolate-turbinate berry; cotyledons 2; chromosome number, $n = 10$ (*Eupomatia*) ----- Eupomatiaceae
- 11'. Plant a tree; perianth present, not calyptrate, differentiated, in 4 or 5 series; only outermost stamens staminodial; anthers with abaxial dehiscence; pollen grains anasulcate; carpel solitary with unsealed, stigmatic margins (crests) and many submarginal ovules; fruit leathery, slipper shaped, follicular, but indehiscent; cotyledons 3 or 4; chromosome number, $n = 12$ (*Degeneria*) ----- Degeneriaceae
- 9'. Flowers not calyptrate, perianth present, 2- to 5-merous; stamens many to few, connate, not laminar; staminodia absent; pollen grains anasulcate.
12. Flowers unisexual, apetalous; filaments united in solid column with anthers free or laterally concrescent; carpel solitary with single basal ovule; fruit fleshy to subwoody, dehiscent; seeds arillate; endosperm usually ruminate, starchy; chromosome numbers, $n = 18, 21, 25$; rain-forest trees of all main tropical areas -----
 ----- Myristicaceae

- 12'. Flowers bisexual, petals usually present; stamens monadelphous with filaments connate around syncarpous, uniloculate ovary with 2 to 6 parietal placentae; ovules many to 2; fruit baccate, indehiscent; seeds not arillate; endosperm oily or fleshy (ruminate in *Cinnamodendron*); single chromosome number reported, $n = 13$; trees of tropical America, East Africa, and Madagascar Canellaceae
- 5'. Flowers usually naked or apetalous, if the latter, calyx typically gamosepalous and petaloid; mostly shrubs, lianas, or perennial, rhizomatous herbs, rarely trees; flowers bisexual or unisexual, radially or bilaterally symmetrical; stamens, carpels, and endosperm various; pollen grains mostly anasulcate or inaperturate; leaves commonly broad and cordate at base.
13. Perianth present, though usually apetalous; calyx gamosepalous, 3-lobed, often bilaterally symmetrical, petaloid, and bizarre in shape, color, and large size; flowers bisexual, solitary, clustered, or racemose; stamens 36-6, free or adnate to style forming gynostemium; pollen grains mostly inaperturate; ovary inferior, syncarpous, with 6 to 4 carpels and locules, each bearing many anatropous ovules on axile placentae (gynoeceum rarely apocarpous and hemisuperior); fruit a septicial capsule, often dehiscent basally like a parachute (rarely follicular); seeds with no perisperm but abundant endosperm, sometimes ruminate, and rudimentary embryo; basic chromosome numbers, $x = 7, 13$; shrubs, woody or herbaceous vines, and perennial herbs (ARISTOLOCHINEAE) Aristolochiaceae
- 13'. Perianth absent; flowers very small, bisexual or unisexual, bracteate, and crowded in spikes or racemes; stamens 10-1, with filaments usually distinct; pollen grains mostly anasulcate; gynoeceum of 5-2 carpels, apocarpous to mostly syncarpous with 1 locule; ovules orthotropous, many to few on parietal placentae, or 1 subbasally attached; fruit follicular, capsular, or drupaceous; seeds with abundant perisperm, scanty endosperm, and rudimentary embryo; shrubs, lianas, or perennial herbs, rarely trees or annuals; leaves mostly alternate or stipulate; basic chromosome numbers, $x = 11, 12$, or more (PIPERINEAE).
14. Flowers bisexual with ovules 10-1 in each of 5-3 carpels, which are spirally arranged, essentially apocarpous to syncarpous with axile or parietal placentation; stamens 8-3, hypogynous, or adnate to ovary and epigynous; grooved styles as many as carpels and distinct, conduplicate with 2 open, "unsealed," stigmatic crests; fruit warty and indehiscent, semisucculent follicle, or fleshy capsule dehiscing by apical valves; rhizomatous or stoloniferous perennials of wet habitats; leaves alternate; upper leaves or lowest bracts of inflorescence petaloid, white, with spike simulating *Anemone*-like flower; vascular bundles forming ring in stem; embryo-sac development of the normal *Polygonum*-type; basic chromosome numbers, $x = 11, 12$ Saururaceae
- 14'. Flowers bisexual or unisexual, minute, with 1 subbasal ovule in single locule of compound pistil of 5-2 fully connate carpels; bracts often shield shaped in the tight spikes; stamens 10-1; stigmas 5-1 or brushlike; fruit small drupe; trees, shrubs, lianas, or herbs of wet, tropical forests; leaves alternate, opposite, or verticillate; nodes often swollen; vascular bundles distinct in 2 or more circles; embryo-sac development tetrasporic, 8-16-nucleate (*Fritillaria* and *Peperomia*-types); basic chromosome numbers, $x = 11, 12, 13, 14$, or more Piperaceae
15. Plants mostly terrestrial subshrubs, shrubs, lianas, or rarely small trees; leaves mostly alternate, firm and coriaceous, stipulate, without multilayered epidermis; flowers bisexual or unisexual; stamens 10-2, pollen sacs separate, and pollen grains anacolpate; styles 5-2; ovules with 2 integuments; embryo sac 8-nucleate, *Fritillaria*-type; drupes with fleshy endocarp and endozoochorous dispersal Piperoideae
- 15'. Plants mostly epiphytic or rupicolous, less commonly terrestrial subshrubs, perennial herbs, or annuals; leaves alternate, opposite, or whorled, often quite succulent, exstipulate, with multilayered epidermis (with water-storing hypodermis); flowers

bisexual; stamens 2, pollen sacs confluent, and pollen grains acolpate; styles 1 (rarely 2), and often brushlike; ovules with 1 integument; embryo sac 16-nucleate, *Peperomia*-type; drupes with thin, mucilaginous pericarp, sometimes with barbed hairs, and epizoochorous dispersal *Peperomioideae*

- 4'. Nodes unilacunar (*LAURINEAE*).
16. Leaves alternate with undulate margins; xylem vesselless and other wood characteristics similarly primitive; spherical oil cells inconspicuous, if present; vascular strand from node single, broad, arc shaped; hippocrepiform (horseshoe shaped) sclereids present; flowers unisexual; bracteoles and tepals spirally arranged and little differentiated; stamens laminar with protuberant, subapical sporangia; pollen grains granular, acolpate or with single, irregularly unthickened, perhaps proximal area; carpels 5, free on convex apex of receptacle; sessile stigma oblique with 2 conspicuous feathery flanges, said to represent stigmatic crests of upper part of conduplicate carpel; ovule single, lateral, with micropyle directed down; fruit drupaceous, stipitate, pitted-reticulate when dry; chromosome number, $n = 13$; monotypic New Caledonian shrub (*Amborella*) *Amborellaceae*
- 16'. Leaves mostly opposite and entire; xylem with vessels present, though elements often tracheidlike and primitive; spherical secretory oil cells conspicuous and ubiquitous; vascular strands from node various; flowers, stamens, pollen, carpels, and fruit various.
17. Plants scandent shrubs, lianas, or small trees; vascular traces 2 at node; hippocrepiform sclereids absent; vessels and rays of primitive form; flowers bisexual or unisexual; bracts and tepals poorly differentiated; fruit baccate; endemics of southern Pacific area
18. Scandent shrubs or lianas; flowers bisexual; bracts decussate but tepals in compressed spiral; stamens numerous, laminar, with adaxial, median, protuberant microsporangia; pollen grains anasulcate; carpels 14-6, closed, with conduplicate, open style; ovules 13-8 in 2 series; chromosome numbers, $n = 22$, and perhaps 23; dispecific genus of NE Queensland (*Austrobaileya*) *Austrobaileaceae*
- 18'. Scandent shrubs or small trees; flowers bisexual or unisexual; bracts and tepals decussate, deciduous on convex receptacle; stamens differentiated into filament, anther, and slender latrorse or introrse sporangia that are not especially protuberant; pollen grains polyporate or with 2 irregular unthickened areas; carpels usually 1 with massive, coarsely dissected, sessile stigma and single pendulous ovule with micropyle directed up, chromosomes uncounted; digeneric, E Australia and New Guinea to Polynesia (*Piptocalyx*, *Trimenia*) *Trimeniaceae*
- 17'. Plants various in habit, mostly trees; vascular traces, vessels, rays, flowers, fruit various; families not restricted to S Pacific area.
19. Flowers greatly reduced, usually naked, rarely with ovary enveloped by adnate gamosepalous, 3-toothed calyx; single carpel with 1 orthotropous, pendulous ovule and mostly sessile stigma; stamens 3-1, often fleshy, adnate to ovary or in separate inflorescences; pollen anacolpate, polycolpate, or acolpate; fruit a drupe; small trees, shrubs, or suffrutescent herbs; leaves decussate, serrate, often connate and sheathing swollen nodes, with minute stipules; vessels absent or primitive and tracheidlike; basic chromosome number probably $x = 7$ or 8; pantropical except for mainland Africa and Australia *Chloranthaceae*
- 19'. Flowers not highly reduced but usually with normal perianth, many stamens, and/or many carpels; ovules anatropous; pollen, fruit, chromosome numbers various; trees or shrubs; leaves and xylem various.
20. Seeds with abundant endosperm and usually very small undifferentiated embryos.
21. Gynoecium apocarpous with many to 3 (rarely 1) carpels, hypogynous.

22. Plant a small shrub with alternate leaves and ochrealike stipules at swollen nodes; vascular strands 2 from nodes; xylem specialized: short vessel elements with simple perforation plates and alternate lateral-wall pitting, libriform fibers, diffuse to scanty paratracheal wood parenchyma, and few wide rays; sexuality variable but flowers often with whorl of 3 tepals, 2 whorls of 3 stamens, innermost sometimes staminodial, and whorl of 3 separate carpels, connate at base; stamens broad with extrorse microsporangia; pollen grains in permanent tetrads, each saccate grain with poorly defined anasulcate aperture; carpels with 8-6 marginal ovules; fruit follicular; chromosome number, $n = 20$; rare monotype of Juan Fernandez Islands (*Lactoris*) Lactoridaceae
- 22'. Plants trees, shrubs, or lianas with usually decussate, exstipulate, serrate leaves (rarely verticillate or anisophyllous); vascular strands 3-7 or single arc-shaped trace from node; xylem very primitive to somewhat specialized; flowers bisexual, transitional, or unisexual; receptacle flat to deeply concave, cupuliform, or urceolate; tepals variable in number (many to 4 or 0), size, shape, fusion, but basically decussate; stamens and carpels mostly many (rarely only 1) and separate; pollen grains anasulcate to dicolpate or acolpate; ovule single; fruit a cluster of drupelets or nutlets; chromosome numbers, $n = 19, 22, 39$; pantropical and south temperate Monimiaceae
23. Stamens dehiscing by vertical slits; pollen grains acolpate; ovule pendulous with micropyle directed up; leaves with 3 or more traces at node; hippocrepiform sclereids and fibers present in pericycle region of stems.
24. Stamens with associated pair of appendages (perhaps staminodial); pollen grains acolpate with semihelical bands or evenly distributed spinules; receptacle slightly concave to urceolate; vessel elements and wood parenchyma various; reported chromosome number, $n = 39$.
25. Receptacle slightly concave; flowers bisexual; pollen grains with semihelical bands; vessel elements long, angular, thin walled, with extensively overlapping, steeply inclined, scalariform-pitted end walls with many bars; wood parenchyma abundant; septate fibers absent; multiseriate vascular rays relatively narrow; endemic in Ceylon (*Hortonia*) Hortonioideae
- 25'. Receptacle campanulate to urceolate; flowers unisexual; pollen grains spinulose; vessel elements shorter, thicker walled, less angular, with less extensively overlapping, obtuse ends with simple perforation plate with mostly a single oval opening; wood parenchyma scanty; septate fibers present; multiseriate rays rather broad; one chromosome number reported, $n = 39$ (*Peumus*); digeneric and restricted to Chile (*Peumus*) and Mascarene Islands (*Monimia*) Monimioideae
- 24'. Stamens lacking associated pair of appendages; pollen grains acolpate but smaller and lacking semihelical bands or spinules, merely granular; receptacle flat to urceolate; vessel elements long, angular, thin walled, with extensively overlapping, steeply inclined, scalariform-pitted end walls with many bars; wood parenchyma scanty; septate fibers present; multiseriate rays relatively broad; chromosome numbers, $n = 19, 22$; pantropical Mollinedioideae
- 23'. Stamens dehiscing by valves (from base upwards); pollen grains anacolpate, dicolpate, or acolpate; ovule basal with micropyle directed down; leaves usually with arc-shaped trace at node; hippocrepiform sclereids present or absent; multiseriate rays relatively narrow; chromosome number, $n = 22$.
26. Flowers bisexual or transitional to unisexual; receptacle flat to deeply concave or urceolate; stamens with associated pair of appendages; pollen grains large, reticulate, 1- or 2-colpate; leaves opposite with stomata anomocytic; hippocrepiform sclereids present; wood parenchyma scanty or absent; restricted to New Guinea, Australasia, and temperate South America Atherospermatoideae

- 26'. Flowers unisexual; receptacle campanulate to urceolate; stamens lacking appendages; pollen grains granular, acolpate; leaves opposite, verticillate, or anisophyllous with stomata paracytic; hippocrepiform sclereids absent; wood parenchyma scanty or abundant; endemic in tropical America and West Africa Siparunoideae
- 21'. Gynoecium syncarpous, 2- or 3-carpellate, epigynous; tree with opposite, exstipulate leaves; flowers bisexual; tepals 10-5, adnate in spiral arrangement to ovary; stamens 15-10, free, spiral, some staminodial, with anthers opening introrsely by valves; inner stamens with paired glands at base of filament; pollen grains acolpate; inferior ovary 2- or 3-loculate, each loculus with 1 pendulous ovule with micropyle up; fruits drupaceous with large embryo in abundant endosperm; xylem with primitive features; vascular traces 2 from node; monotype endemic to central Chile (*Gomortega*) Gomortegaceae
- 20'. Seeds with endosperm wanting and embryo well developed.
27. Flowers perigynous, bisexual, solitary, with cup-shaped receptacle bearing on outside numerous, spirally imbricate, poorly differentiated tepals, outer bractlike, inner petaloid; stamens and staminodia (to inside) numerous, spiral on rim of hollowed receptacle, inflexed over opening; stamens with short, stout filament, extrorse anther, and prolonged connective, dehiscence by vertical slits; pollen grains dicolpate; carpels separate, sessile inside receptacle, each with 1 or 2 basal, ascending ovules; leaves opposite with paracytic stomata; fruits indehiscent, enclosed within much enlarged pseudocarp; cotyledons with strychninlike substance toxic to ruminants; 4 inverted vascular bundles in stem cortex; chromosome number, $n = 11$; trees or shrubs of NE Queensland, E Asia, W and E North America Calycanthaceae
28. Habit arboreal; leaf trace 1; stamens laminar with long, narrow, dorsal, extrorse microsporangia; gynoecium of 1 or 2 carpels with broad, fleshy, papillose, almost sessile stigma; cotyledons 4 or 3, massive, fleshy, subsessile, peltate in large seed 4-5 cm long; xylem diffuse-porous; vessel elements with multiple scalariform perforations; parenchyma abundant; rays high with mostly procumbent cells; vasicentric tracheids absent; endemic rain-forest monotype of NE Queensland (*Idiospermum*) Idiospermoideae
- 28'. Habit shrubby; leaf traces basically 2; stamens with laterally extrorse anthers; gynoecium with many (ca. 20) carpels, each with linear or filiform style; cotyledons 2, foliaceous, convolute in large achene; xylem semiring- or ring-porous; vessel elements with simple, oblique perforations; parenchyma scanty; rays low with few procumbent cells; vasicentric tracheids present; warm temperate forests of E Asia, California, and E North America (*Calycanthus*, *Chimonanthus*) Calycanthoideae
- 27'. Flowers hypogynous or epigynous, cyclic, bisexual or unisexual, basically cymose; perianth 5- to 2-merous; stamens in several whorls, dehiscing by flaplike valves; pollen grains mostly acolpate, spinulose; carpel solitary with single, apical, pendulous ovule; leaves mostly alternate; fruit and habit various; chromosome numbers, $n = 12, 15, 20$.
29. Flowers hypogynous (epigynous only in *Hypodaphnis*), usually small, bisexual, less commonly unisexual; tepals basically trimerous, usually in 2 whorls, free or outer gamosepalous; 4- or 2-locular stamens and staminodia typically in 4 whorls, at least 1 whorl having sessile or stalked, paired glands associated with each filament; usually 2 outer whorls of anthers dehiscing introrsely and inner third whorl extrorsely; fruits drupaceous or baccate, often subtended by cuplike calyx; trees or shrubs (except for the parasitic vines of *Cassytha*); leaves alternate, rarely opposite or verticillate, entire or rarely lobed; chromosome number, $n = 12$ Lauraceae
30. Plants trees or shrubs with normal green leaves, fully autotrophic Lauroidae

- 30'. Plants slender twiners with leaves absent or minute, scalelike; only partly autotrophic, parasitic by haustoria (*Cassytha*) Cassythoideae
- 29'. Flowers epigynous, bisexual or commonly unisexual; 5- to 3-merous; 10-3 tepals in 1 or 2 whorls; stamens equal to or fewer in number than outer whorl of tepals; anthers dehiscent laterally or introrsely by 2 valves; fruits dry, indehiscent, ribbed nuts, sometimes winged; trees, shrubs, or lianas; chromosome numbers, $n = 15, 20$ Hernandiaceae
31. Anthers dehiscent by valves opening upward; stamens fewer in number than single whorl of 8-4 tepals; floral glands none or fewer than stamens; stigma capitate and style not grooved; cotyledons leafy and convolute; leaves pubescent or tomentose, simple, entire or palmately lobed; fruit fusiform without or with terminal wings; vessel elements with relatively transverse end walls; cystoliths in leaves and axis; chromosome number, $n = 15$ (*Gyrocarpus*, *Sparattanthelium*) - Gyrocarpoideae
31. Anthers dehiscent longitudinally by laterally opening valves; stamens equal in number to outer of 2 whorls of tepals; floral glands in 1 or 2 whorls; stigma indented and style grooved on placental side; cotyledons fleshy, smooth, or ruminant; leaves largely glabrous, occasionally with sparse pubescence below on veins, simple, subcordate or subpeltate, or palmately compound; fruit globose and enclosed in fleshy cupule or 2 large bracts, or fusiform and laterally winged; vessel elements with relatively oblique end walls; cystoliths absent; chromosome number, $n = 20$ (*Hernandia*, *Illigera*) Hernandiaceae

DISCUSSION OF ANNONALES

The Annonales are a large, diverse aggregation of mostly relict families surviving in the moist, warm forests of the tropical and warm-temperate zones. They retain in common many more unspecialized, i.e., primitive and probably ancestral angiospermous, characteristics of stem, foliage, flowers, pollen, ovules, fruit, and seeds than any other angiospermous order, including the relatively unspecialized Berberidales, Nymphaeales, Hamamelidales, Rosales, and Liliales. Among these more primitive features, as currently accepted, and retained in varying degree by different members of the order, are: habit arboreal or shrubby; leaves simple, alternate, pinnate veined, entire, petiolate, glabrous, evergreen, exstipulate, with paracytic stomata, and often with two leaf traces from a single leaf gap; cambium initials very long and fusiform with overlapping ends; wood anatomy very unspecialized (vessels absent altogether or tracheidlike with vessel elements characterized by great length, small diameter, thin walls, angular cross-sectional appearance, very oblique end walls, scalariform perforation plates with numerous fine bars, scalariform intervascular pitting, diffuse and solitary vessel arrangement; tracheids medium to moderately long with conspicuous bordered pits; wood parenchyma diffuse; rays of primitive heterogeneous type with numerous uniseriades); flowers mostly bisexual, actinomorphic, with perianth parts often poorly differentiated, and floral parts generally indefinite in number, distinct from one another, and spirally arranged on a convex receptacle; stamens rather broad and unmodified into filament, anther, and connective; pollen grains anasulcate (distally mono-aperturate) or of closely derived types; carpels styleless with broad, involute or conduplicate lamina bearing an indefinite number of anatropous, marginal ovules, margins stigmatic over a large area or with stigmatic hairs abundant

Fig. 1. *Drimys winteri* J. R. & G. Forst., Winteraceae, Chile, representing the Winterineae.—a. Flowering branch with alternate, evergreen leaves and intercalary, cymose inflorescences of cream-colored flowers, $\times 0.4$.—b. Flower with much of perianth and some stamens removed and one carpel in longisection to show ovules, $\times 4.2$.—c. Stamens, with lateral microsporangia, $\times 7.7$.—d. Whorl of separate carpels, three in cross section to show ovule placement and vascular bundles, $\times 3.5$.—e. Microscopic section of carpel

on the free margins and internal surfaces; ovules crassinucellate with two integuments; embryo-sac development the normal monosporic *Polygonum*-type; and fruit follicular with numerous seeds, each with a rudimentary embryo embedded in abundant endosperm. No one family, of course, retains all these unspecialized characteristics; and each family display different trends toward specialization, fusion, amplification, or reduction. None of the families is, therefore, to be derived from any other annonalean family. All represent different surviving lineages from common but long-extinct protoannonalean stock.

Various families of other orders, especially the related Berberidales and Nymphaeales, retain many unspecialized features also. However, the members of the Annonales are distinguished from plants of these other orders definitively by the possession in their parenchymatous tissues of characteristic spherical secretory cells (Fig. 1e), containing essential, or "ethereal" oils or resinous contents. The evolutionary significance of these cells is not understood, but their presence is diagnostic for members of the order. Among dicotyledons only the Nymphaeales also have members with anasulcate or closely derived disulcate, polycolpoidate, or inaperturate pollen grains (Erdtman, 1952), and nymphaealean species lack the spherical essential oil cells.

The 23 families and perhaps 9,500 species of this diverse but natural assemblage have been divided into several orders by recent phylogenists such as Hutchinson (1964, 1973), Takhtajan (1969), and Smith (1972), mostly because of the several divergent evolutionary pathways followed by different groups of families. I believe that subdivision of the Annonales into several suborders serves the purpose of calling attention to these different evolutionary lines, while retaining them in one order indicates their close affinity and obviously close common ancestry.

SUBORDER WINTERINEAE

WINTERACEAE Lindley 1830.—Just as the Annonales share more primitive features than any other dicotyledonous order, so within this order the single family Winteraceae, comprising the suborder Winterineae, retains the largest number of primitive characteristics in the vegetative and reproductive structures of its members. The six currently accepted genera (*Bubbia* v. Tiegh., *Drimys* J. R. & G. Forst., *Bellium* v. Tiegh., *Pseudowintera* Dandy, *Tasmannia* R. Br., and *Zygogynum* Baill.) contain more than 100 species of small trees or shrubs found mostly in areas fringing

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wall to show especially spherical secretory (essential) oil cells in the parenchymatous tissues, $\times 26$.—f. Developing cluster of carpels in old flower, $\times 1.7$.—g. Carpel, $\times 2.4$.—h. Seed, $\times 7$.—i. Tracheids, ca. $10\ \mu$ in diam, from stem in radial view showing bordered pits.—j. Bordered pit between two tracheids.—k. Bordered pit, $2-3\ \mu$ in diam.—l. Cross section of xylem showing tracheids with bordered pits mostly limited to radial faces.—m. Permanent tetrahedral tetrads, ca. $50\ \mu$ in diam, of distally porate and distally reticulate pollen grains.

the Pacific Basin from Mexico south to Fuegia and the Juan Fernandez Islands (*Drimys* [Fig. 1]) and from New Zealand and Tasmania north to Borneo and the Philippines (the other genera), with one species ranging to southeastern Brazil and Guyana (Smith, 1943) and another to Madagascar (Capuron, 1963).

Among the most distinctive features of the Winteraceae are the entirely vesselless wood (Fig. 1 i-l), the stomata occluded by waxy deposits, and the pollen in permanent tetrahedral tetrads, each grain with a distal germination pore (Fig. 1m). Especially primitive, in addition to the vesselless xylem, are the long cambial initials and tracheids (Fig. 1i), heterogeneous rays; multiseriate (occasionally scalariform) bordered tracheary pitting (Fig. 1i); diffuse to tangentially banded wood parenchyma; mesogeneous paracytic stomatal apparatus (with one or more subsidiary cells parallel to the stoma) in the alternate, entire, pinnae-veined, exstipulate, evergreen leaves; intercalary (Fig. 1a) to subterminal cymose inflorescences; relatively small, bisexual, actinomorphic flowers (Fig. 1b) with variable number of mostly separate, spirally arranged parts; single-veined, relatively short microsporophylls with lateral to apical, protuberant microsporangia (Fig. 1c); carpels styleless megasporophylls with partly free margins bearing papillae and forming conspicuous double stigmatic crests; several anatropous ovules on marginal or submarginal placentae (Fig. 1b, d); and embryo rudimentary in abundant endosperm (Bailey, 1944; Bailey and Nast, 1943-1945; Nast, 1944; Smith, 1943a,b; Swamy, 1952; Vink, 1970).

The various genera of Winteraceae display many trends of morphological specialization leading to dwarfing of shrubs and leaves; simple, terminal flowers; calyptrate calices; few or no petals; functional unisexuality; differentiated and few stamens; reduced number of carpels (to one) with closure of the megasporophyll and restriction of the stigmatic crests to a subapical projection (Fig. 1b); and syncarpy.

SUBORDER ILLICIINEAE

ILLICIACEAE A. C. Smith 1947 and SCHISANDRACEAE Blume 1830—The two families of the Illiciineae, Illiciaceae and Schisandraceae, both basically southeastern Asiatic with meager representation in southeastern North America, are more closely related to the Winterineae than to any other group of Annonales. Besides the usual spherical secretory cells in the parenchymatous tissues, and the paracytic stomatal apparatus, *Illicium* L. (Fig. 2) especially resembles the Winteraceae in its small tree or shrubby habit, alternate, exstipulate, evergreen leaves (Fig. 2a), and primitive features of its wood. It does possess primitive vessels, but the vessel elements are tracheidlike: long, slender, thin-walled, angular with greatly overlapping end walls with numerous bars in the scalariform perforation plates, with intervacular pitting scalariform or transitional, and diffusely scattered throughout the xylem. The imperforate tracheary elements are thick-walled tracheids with conspicuous bordered pits. The xylem parenchyma is scanty diffuse and abaxial paratracheal, and the rays are multi-seriate. Although the flowers differ considerably from those of the Winter-

Fig. 2. *Illicium floridanum* Ellis, Illiciaceae, southeastern United States, representing the Illiciineae.—a. Fruiting branch bearing evergreen, alternate leaves and single follicetum of one-seeded ventrally-dehiscent follicles in whorl, $\times 0.4$.—b. Single flower consisting of undifferentiated perianth of many purplish red tepals, stamens similarly numerous and many-seriate, and single whorl of separate carpels, $\times 0.8$.—c. Floral axis with all parts removed except two carpels in longisection to show in each single, basally attached ovule, $\times 3$.—d. Developing young fruit, $\times 1.5$.—e. Stamens showing introrse dehiscence by longitudinal slits, $\times 1.7$.—f. Apparently syncolpoidate pollen grain, ca. 28μ .—g. Two glossy, flattened seeds in lateral view, $\times 2.7$, and one from hilum view, $\times 4$.

aceae, the free carpels (Fig. 2b,c) are basically conduplicate, with the stigmatic crests produced into a pseudostyle or a vascularized style stigmatic along all or much of its length or along the upper side (Bailey and Nast, 1948; Smith, 1947). In both *Illicium* and the Schisandraceae the chromosome numbers are $n = 14$ or 13 (Raven and Kyhos, 1965; Raven, 1974).

Nonetheless, the differences between the Winteraceae, Illiciaceae, and Schisandraceae suggest the segregation of the two groups into separate suborders. Among the more striking differences of the Illiciineae from the Winterineae are the xylem vessels, the unilacunar as opposed to trilacunar nodes, the pseudosiphonostelic arrangement of the primary vascular tissues in *Illicium*, the nonoccluded stomata with intercellular intrusions of the cuticle, apparently 3- or 6-colpate pollen grains released separately (Fig. 2f), reduced number of ovules in the carpels (Fig. 2a,c), and fundamental differences in the flowers and floral parts.

Although the lianous, unisexual-flowered, baccate-fruited species of Schisandraceae are considerably more specialized than members of the Illiciaceae, the two families are closely linked by their unilacunar nodes, elongated or cambiform "mucilage" cells in the phloem, similar stomata, cuticles, pollen, and chromosomes (Bailey and Nast, 1948; Wood, 1958). The Illiciaceae consist of the single genus *Illicium* (Fig. 2) with perhaps 37 species of evergreen-leaved shrubs or small trees in southeastern Asia from Japan south to India and Borneo and two to four species in the southeastern United States, Mexico, and the Greater Antilles. The Schisandraceae are monoecious or dioecious climbing shrubs or twining woody vines with coriaceous or often thinner, toothed leaves. The perhaps 47 species are divided nearly equally between the two genera *Schisandra* Michx. and *Kadsura* Juss., restricted to southeastern Asia from Japan and Korea to Ceylon and Java except for the single species, *Schisandra glabra* (Brickell) Rehder of the southeastern United States (North Carolina to eastern Louisiana and Arkansas).

SUBORDER ANNONINEAE

Forming the suborder Annonineae (Magnoliineae) is a closely related group of seven families: the relatively numerous Magnoliaceae, Annonaceae, and Myristicaceae; the smaller Canellaceae; and the monogeneric Degeneriaceae, Eupomatiaceae, and Himantandraceae. In addition to the usual spherical secretory oil cells and many primitive features of stem, foliage, flowers, and embryology, members of these families possess tri- to multilacunar nodes; stamens commonly laminar with marginal or median, embedded microsporangia to stamens well differentiated with narrow filaments and terminal anthers; pollen monosulcate to 2- or 3-sulcate, inaperturate, or other closely derived types; and carpels conduplicate with open, stigmatic margins (crests) to carpels variously specialized with closed margins and terminal styles, ovules reduced to two or one, and ovaries syncarpous with parietal placentation (Bailey, Nast, and Smith, 1943; Bailey and Smith, 1942; Bailey and Swamy, 1951; Canright, 1952-1960; Eames, 1961; Hotchkiss, 1958; Lemesle, 1936, 1938; Occhioni, 1948;

Periasamy and Swamy, 1956; Swamy, 1949; Swamy and Periasamy, 1964; Walker, 1971; Wilson, 1960, 1965; and Wilson and Maculans, 1967). Five of the families share ruminant endosperm.

Also in the Annonineae, five of the families show strikingly similar characteristics in the young stem: superficial origin of periderm, sclerified pith diaphragms, stratification of the secondary phloem into tiers of hard and soft bast, V-shaped rays in the phloem, cortical sclereids, and a eustelic vascular cylinder with each bundle capped by thick-walled fibers (Bailey, Nast, and Smith, 1943; Canright, 1955; Vander Wyk and Canright, 1956). Four of the families have crystalliferous parenchyma in the cortex and pith. All five families share many features in the mature wood as well, with similar vessel distribution, apotracheal banded wood parenchyma, and similarities in the rays. Of intermediate specialization in their wood are *Degeneria* and tropical genera of the Magnoliaceae; somewhat transitional are the Myristicaceae and temperate members of the Magnoliaceae; and relatively more specialized are the species of *Galbulimima* (Himantandraceae) and the Annonaceae (Vander Wyk and Canright, 1956). *Eupomatia* and the Canellaceae lack some of the above-listed features, especially the pith diaphragms of sclereids and stratification of the phloem. Furthermore, their wood is exceedingly primitive, with long, narrow vessel elements with long tapering end walls containing scalariform perforation plates with many (to 150) bars and with scalariform to opposite intervacular pitting; apotracheal diffuse to sparingly paratracheal wood parenchyma; and narrow, high, heterogeneous rays. In other features, however, of nodal anatomy, foliage, flowers, seeds, etc., *Eupomatia* displays its relatively close relationship to *Galbulimima* and *Degeneria* and the Canellaceae to the Annonaceae and Myristicaceae.

Because members of the Annonineae are relatively well known to north temperate botanists, their primitiveness as compared with that of species of the Winteraceae and Illiciaceae has perhaps been somewhat overplayed. Nevertheless, in comparison with most other families found in the north temperate zone, plants of the Annonineae are indeed well endowed with unspecialized characteristics. The phyllomelike stamens of *Degeneria*, *Galbulimima*, and some species of Magnoliaceae, with their embedded, median, elongate microsporangia have been considered by some morphologists as the most primitive among living angiosperms (Canright, 1952). Though the primitive stamens probably were relatively undifferentiated, much as those in some Winteraceae, the primitive microsporangia were probably marginal and protuberant. The laminar stamens with embedded microsporangia may well be a specialization protecting the pollen from the chewing mouthparts of beetles and other crawling insects much as closed carpels guard the ovules. The somewhat laminar type of placentation described for some of these taxa, like those in *Degeneria* and *Eupomatia*, may also be a modification from marginal placentation removing the ovules from too close proximity to the open, stigmatic margins of the apparently conduplicate carpels. Though retaining many very primitive features, members of the Annonineae also show considerable specialization beyond

that found in species of the Winteraceae and Illiciaceae, especially in their nodal and stem anatomy and in their flowers.

MAGNOLIACEAE A. L. Jussieu 1789.—The relatively well-known Magnoliaceae consist of 12 genera and 210 to 230 species (Dandy in Hutchinson, 1964). Although in the Tertiary they were widely distributed in the Northern Hemisphere, today all the genera are entirely or mostly restricted to eastern Asia from Japan and Manchuria to New Guinea and India, with three genera also represented in North America from Ontario and Wisconsin to Mexico, the West Indies, and South America south to Brazil and Ecuador. Members of the Magnoliaceae are easily recognized because of the usually conspicuous flowers with yellowish, white, or pink perianth, numerous stamens and carpels on an elongate receptacle, and the annular stipule scars at the nodes of twigs and branches. *Liriodendron tulipifera* L., with lobed and truncate leaves, and several species of *Magnolia* L., some with large leaves auriculate at the base, are among the dominant large trees of the mixed deciduous forest of eastern North America. Evergreen-leaved species of *Magnolia* south from the Atlantic coastal plain and *Talauma* Juss. south from Mexico and the Antilles are essentially subtropical and tropical trees of wet lowland or montane rain forests.

DEGENERIACEAE Bailey et Smith 1942, **HIMANTANDRACEAE** Diels 1917, and **EUPOMATIACEAE** Endlicher 1841.—Closely related to the Magnoliaceae are three monogeneric families restricted in range to the Australasian region. *Degeneria vitiensis* Bailey & A. C. Smith, a rain-forest tree of Fiji, shares many features with *Galbulimima belgraviana* (F. v. Muell.) F. v. Muell. (Himantandraceae), a similar large rain-forest tree of northeastern Queensland, New Guinea, and the Moluccas, with *Eupomatia laurina* R. Br., a small tree of coastal and montane wet sclerophyll and rain forests in eastern Australia from Victoria to Cape York Peninsula and in New Guinea, and with *E. bennettii* F. v. Muell., a shrub of rain forests in eastern New South Wales and Queensland. It is of considerable interest here that *Talauma* and *Elmerrillia* Dandy, two rather primitive genera of the Magnoliaceae, also have representatives in New Guinea. The chromosome numbers in these four families are $n = 19$ for all Magnoliaceae counted, $n = 12$ for *Degeneria vitiensis* and *Galbulimima belgraviana*, and $n = 10$ for both species of *Eupomatia* (Raven and Kyhos, 1965; Ehrendorfer, Krendl, Habeler, and Sauer, 1968; Sauer and Ehrendorfer, 1970; Raven, Kyhos, and Cave, 1971; and Raven, 1974).

ANNONACEAE A. L. Jussieu 1789.—The Annonaceae are a rather large family with perhaps 130 genera and 2,300 species (Walker, 1971). Except for the temperate American pawpaw genera *Asimina* Adans. (Fig. 3) and *Deeringothamnus* Small, the family is tropical with good representation in all four major sectors of the tropics. Unlike the preceding families, the Annonaceae seem to have their more primitive members not in Asia or Australasia but in tropical America and Africa (Walker, 1971, 1972), as with the closely related Myristicaceae and Canellaceae, possibly stemming from

Fig. 3. *Asimina triloba* (L.) Dunal., Annonaceae, eastern North America, representing the Annonineae.—a. Fruiting branch with deciduous, alternate leaves and two baccate fruits, one in longisection to show the several flattened seeds, $\times 0.4$.—b. Flower from above showing six purplish-brown petals in two whorls, the outer much larger, numerous stamens, and few distinct carpels, $\times 0.8$.—c. Vertical section of flower, less perianth, showing spiral arrangement of many stamens and few separate carpels, two in longisection to show many marginal ovules, $\times 1.5$.—d. Nodding flower bud showing whorl of three valvate sepals and outer whorl of three imbricated petals, $\times 2$.—e. Pubescent carpel, $\times 4$.—f. Cross section of carpel showing one ovule in each of two rows in ovary, $\times 6$.—g. Stamen with two pollen sacs dehiscing by longitudinal slits and overtopped by enlarged "peltate" connective, $\times 6$.—h. Tetragonal tetrad of heteropolar, bilateral, apparently catasulcate (proximally aperturate) pollen grains, each with longest axis ca. $100\ \mu$.—i. Seed, $\times 1$.—j. Seed in longisection to show ruminant endosperm, $\times 1$.

those Cretaceous times when Africa and South America were presumed to form West Gondwanaland. Of all living angiosperm families, at least, these seem to be the most likely survivors of such possible continental rifting and rafting. One genus, *Annona* L., is restricted to tropical America, including southern Florida, and tropical Africa, but this distribution, especially that of *A. glabra* L., very likely is a product of relatively recent long-distance dispersal by water currents.

The shrubs and small trees of the Annonaceae are rather easy to recognize from their often nodding, maroon, white, or yellowish flowers with trimerous perianth in three whorls (Fig. 3b,d); numerous, spirally arranged "peltate" stamens (Fig. 3c,g) and separate carpels (Fig. 3c,e); usually baccate (Fig. 3a) or syncarpous (rarely follicular) fruits; and seeds with ruminant endosperm (Fig. 3j). However, such specializations as unisexual flowers, reduced number of petals, few and whorled stamens, carpels reduced to one or fused into a compound, uniloculate pistil, and arillate or winged seeds can complicate recognition.

MYRISTICACEAE R. Brown 1810.—The Myristicaceae are a strictly tropical family best known for the once valuable spices nutmeg and mace from the seed and aril of *Myristica fragrans* Houtt., a native of the Moluccas, or Spice Islands. With about 15 genera and 250 species (Buchheim in Melchior, 1964) the majority of genera occur in Africa (5), Madagascar (1), and tropical America (5); whereas, the vast majority of species (213) belong to the four Asiatic genera that range from southern China to Australia, Polynesia, and Ceylon. In America *Compsonura* Warb. and *Virola* Aubl. range north to Mexico or the West Indies (Smith and Wodehouse, 1938). Members of the family can be recognized as rain-forest trees with small, apetalous, imperfect, cyclic flowers with synsepalous calyx, staminal column or single carpel with single basal ovule, and baccate to subwoody fruit usually dehiscent to show the single, usually ruminant seed with lacerate aril. The close similarity of the protein-accumulating sieve-tube plastids of Myristicaceae with those of the Annonaceae, Canellaceae, and Aristolochiaceae has been pointed out by Behnke (1971).

CANELLACEAE C. F. P. Martius 1832.—The six genera and 21 species (Occhioni, 1948; Wilson, 1960) of the small family Canellaceae are restricted to the tropical forests of America, eastern Africa (*Warburgia* Engl.), and Madagascar (*Cinnamosma* Baill.) (Thorne, 1973c). *Cinnamodendron* Engl., *Pleodendron* v. Tiegh., and *Canella* P. Br. occur in the West Indies, and *Canella winterana* (L.) Gaertn. reaches north to the Florida Keys and Cape Sable at the south end of the Florida peninsula. *Capsicodendron* Hoehne is endemic in southern Brazil. Despite the gynoecium of two to six syncarpous carpels forming a monoloculate ovary with two to six parietal placentae (as in two genera of Annonaceae), members of this family are readily placed in the Annonales by their spherical secretory oil cells, anacolpate pollen grains, and exceedingly primitive stem anatomy. The monodelphous stamens, embryology and occasional ruminant seeds, pollen grains, P-type sieve-tube plastids, wood anatomy, and other

Fig. 4. *Asarum caudatum* Lindl., Aristolochiaceae, western North America, representing the Aristolochiineae.—a. Flowering plant showing acaulescent, rhizomatous, herbaceous habit, basally attached, cordate leaves, and solitary, axillary flower, $\times 0.4$.—b. Flower with one of brownish-purple, petaloid sepals cut and bent back to show top of inferior ovary, twelve stamens, and six stigmas, $\times 1$.—c. Longisection through compound ovary showing numerous ovules on axile placentae in two of six locules, $\times 1.7$.—d. Cross section of pistil showing ovules attached in two rows to axis in each of six locules, $\times 1.5$.—e. Stamens dehiscent extrorsely by longitudinal slits and terminated by apiculate connective, $\times 5.6$.—f. Inaperturate, spherical, spinulose pollen grain, ca. $50\ \mu$ in diam.—g. Seeds from dorsal, ventral, and side views, and one in longisection to show large raphe and rudimentary embryo in abundant endosperm, $\times 4$.

features relate them rather closely to the Myristicaceae and less closely to the Annonaceae. In this closely allied group of three families the basic chromosome numbers are $x=7$, 8, 9 in the Annonaceae, $n=18$, 21, 25 in the Myristicaceae, and $n=13$ in the Canellaceae, the variety perhaps resulting from a combination of aneuploid increase and decrease with polyploidy from a base number of $x=7$ for the suborder, and probably for the whole order Annonales (Raven and Kyhos, 1965; Ehrendorfer, Krendl, Habeler, and Sauer, 1968; Raven, Kyhos, and Cave, 1971; Walker, 1972; and Raven, 1974).

SUBORDER ARISTOLOCHIINEAE

ARISTOLOCHIACEAE A. L. Jussieu 1789.—The Aristolochiaceae are a moderate-sized family of at least seven genera and perhaps 600 species (Melchior, 1964), widely distributed in the tropics and warm temperate areas, and consisting mostly of shrubs, lianas, or perennial herbs. *Aristolochia* L. and *Asarum* L. (Fig. 4) are represented in Europe and Asia and in both eastern and western North America, the latter as far north as Quebec. Because the largest and best-known genus *Aristolochia*, with up to 500 species, has often huge and bizarre flowers (Hoehne, 1942), always apetalous, with a highly specialized, gamosepalous, usually bilaterally symmetrical, petaloid calyx, stamens adnate to the style to form a gynostemium, inferior, syncarpous ovary, and lianous habit with expectedly specialized stem anatomy, the family has rarely been included in the Annonales (but see Wettstein, 1935). Often the family is treated as a separate order (Cronquist, 1968; Takhtajan, 1966, 1969) or allied with such improbable relatives as the parasitic Rafflesiaceae and Hydnoraceae and the tropical Nepenthaceae (Melchior, 1964; Hutchinson, 1973).

Nonetheless, the various well-known genera of the Aristolochiaceae retain enough primitive characteristics to serve quite adequately as clues to the annonalean relationships of the family. Throughout the family, and, for example, in the western American *Asarum caudatum* Lindl. (Fig. 4), one can observe such features as the spherical secretory oil cells; simple, entire, exstipulate, alternate leaves (Fig. 4a); trimerous bisexual flowers (Fig. 4b, c); stamens with prolonged connective (Fig. 4b, c, e); inaperturate pollen grains (Fig. 4f); and seeds with rudimentary embryo embedded in abundant endosperm (Fig. 4g). For those requiring more evidence, there is even a nonmissing link, *Saruma henryi* Oliv., a relict monotype from Hupeh, China, which offers definitive evidence. It is a perennial caulescent herb with radially symmetrical flowers (see drawing in Oliver, 1889; or Thorne, 1963), with three conspicuous, reniform, separate petals, as well as three green sepals, six essentially separate, semi-superior carpels, anasulcate pollen grains, and follicular fruit, along with the other primitive features listed above for all members of the family.

That food preferences of insect larvae indicate biochemical affinities of a family is shown vividly in the Aristolochiaceae by the swallowtail butterflies of the Papilioninae (Munroe, 1953). The larvae of members of the tribe Troidini feed primarily upon foliage of species of Aristolochiaceae.

The larvae of the other two tribes, Graphiini and Papilionini, feed mostly on Annonaceae, Canellaceae, Hernandiaceae, Lauraceae, Magnoliaceae, Monimiaceae, Piperaceae, and Winteraceae of the Annonales, as well as on the chemically related Rutaceae of the Rurales, and scattered members of other, unrelated families (Ehrlich and Raven, 1964). The competence of these pragmatic chemists is attested to by the publications of Hegnauer (1960b, 1964) and others, who have discussed the biochemical similarities of the family to the other Annonales. The basic chromosome number for the Aristolochiaceae seems to be $x = 7$, "with aneuploid reduction at either the diploid or tetraploid level to produce $x = 13$ " (Raven, 1974).

The closest living relatives of the Aristolochiaceae are probably the Annonaceae, as indicated by the trimerous flowers (Wagner, 1907), pollen grains (Samuelsson, 1914), embryology (Johri and Bhatnagar, 1955; Wyatt, 1955), ruminant endosperm (Periasamy, 1962; Maheswari and Kapil, 1966), serology (Mez, 1937), other chemistry (Hegnauer, 1960b, 1964), protein-accumulating sieve-tube plastids (Behnke, 1971), and chromosome base number. The extreme specialization in most members of the family, however, has gone so far, it seems desirable to treat the family as a separate suborder Aristolochiineae between the Annonineae and Laurineae.

SUBORDER LAURINEAE

Forming another apparently natural assemblage among the Annonales is the large group of ten families with unilacunar nodes, the nodal type considered as probably the most primitive among the flowering plants (Bailey, 1965; Fahn and Bailey, 1957). As with other suborders of the Annonales the members of the Laurineae show their relationship to one another as much by common trends of specialization in all their parts as by their rather sporadic retention of ancestral, primitive features. Aside from the nearly ubiquitous spherical secretory cells, some of the more primitive features retained by the Laurineae are: primitively vesselless xylem (only *Amborella* Baill. and *Sarcandra* Gardn.) and other commonly associated unspecialized xylem and phloem characteristics; bracteoles and tepals of the flowers often numerous, spirally arranged, and little differentiated; stamens and carpels similarly spirally arranged and little specialized; pollen grains anacolpate and numerous; ovules anatropous and developing into seeds with abundant endosperm and small undifferentiated embryo.

More striking similarities among the Laurineae are some relatively specialized conditions found in many of the families. Plants of most of the families have leaves that are opposite and exstipulate, exceptions being the rather primitive monotypes *Amborella trichopoda* Baill. and *Lactoris fernandeziana* Phil. and most species of the much more specialized Lauraceae and Hernandiaceae. Stamens with paired staminodial or glandular appendages and anthers opening by flaplike valves are unusual and often associated specializations commonly found in the Monimiaceae, Gomortegaceae, Lauraceae, and Hernandiaceae. Another common evolutionary tendency is the development of a cup-shaped floral receptacle, as found in various subfamilies of the Monimiaceae and Calycanthaceae. The

Calycanthaceae, Lauraceae, and Hernandiaceae have specialized seeds in which the cotyledons are so well developed before germination that the cotyledons have taken over food storage from the endosperm. *Gomortega keule* (Molina) Johnst. also has a well-developed embryo but retains much endosperm. Other evolutionary tendencies common in the suborder include the usual specializations of the stem tissues; modification of the basic two leaf traces to three or more or to a single arc-shaped trace; attainment of a definite number of parts in whorls in the flower; both connation and adnation in the flower leading to gamosepaly, syncarpy, and epigyny; specializations of the stamens and carpels; extreme reduction in the flowers, including loss of perianth, reduction of stamens, carpels, and ovules to one of each or even to the unisexual condition. The pollen grains have commonly evolved from the anasulcate to the acolpate, dicolpate, polycolpate, or even polyporate conditions. The basic follicle has mostly given way to the single-seeded, indehiscent berry, drupe, or nutlet. Finally, the arborescent habit has been replaced in several families by small shrubs, lianas, suffruticose herbs, and even, in *Cassytha* L., to slender, twining, parasitic vines.

AMBORELLACEAE Pichon 1948.—Showing the most remarkable assortment of retained ancestral and derived specialized features is the shrubby *Amborela trichopoda* of New Caledonia, the home of numerous other equally fascinating relicts. The wood is without vessels and the other stem features are very primitive, the nodes are unilacunar, and the leaves are alternate, exstipulate, glabrous, and evergreen. The vascular strand from the node, however, is a single arc-shaped leaf trace and the leaves have an undulate margin. The Winteraceae-like stamens are relatively undifferentiated, and the separate carpels, sealed below, retain conduplicate stigmatic crests above; yet the species is dioecious with no carpellodia in the male and only one or two staminodia in the female flowers. The pollen grains appear to be transitional from monoaperturate to acolpate; and the one-seeded, indehiscent fruit is stipitate, reticulate-pitted, and drupaceous (Bailey, 1957; Bailey and Swamy, 1948).

AUSTROBAILEYACEAE Croizat 1943.—With primitive vessels, otherwise unspecialized stem features, and two vascular strands from the nodes, the two species of *Austrobaileya* C. T. White of northeastern Queensland are scandent shrubs to high-climbing lianas with opposite leaves. Sparsely supplied with companion cells, the sieve tube elements were formerly believed to be exclusively sieve cells until studied by Carlquist (pers. commun.) and others. Its bisexual flowers with numerous, spirally arranged, undifferentiated tepals, laminar stamens, anasulcate pollen grains, carpels with unsealed, conduplicate styles, and relatively numerous marginal ovules, are considerably more primitive than those of any other members of the Laurineae (Croizat, 1940; Bailey and Swamy, 1949; Srivastava, 1970).

TRIMENIACEAE Gibbs 1917.—Also restricted to the southern Pacific area are the eight small trees or lianas of the two genera *Trimenia* Seem. of New Guinea to Polynesia and *Piptocalyx* Oliv. ex Benth. of New South

Wales and New Guinea. As with *Amborella* and *Austrobaileya*, the exclusion of these genera from the Monimiaceae seems fully justified. Though they possess primitive internal stem characteristics, nodal anatomy, and decussate leaves, the two genera of the Trimeniaceae differ from the Monimiaceae by the absence of hippocrepiform (horseshoe-shaped) sclereids, of any fusion in the floral parts, of any tendency toward a concave receptacle, and by the presence of mucilage cells (as in the Lauraceae), of intergrading, decussate bracteoles and tepals, and of the capitate, brushlike stigma (Money, Bailey, and Swamy, 1950; Rodenburg, 1971). In fact, these genera approach rather closely the Chloranthaceae in several significant characteristics: unilacunar, two-trace nodal anatomy; decussate, serrate leaves; mostly bisexual flowers; polyporate pollen; and single carpel with sessile stigma and single, pendulous ovule.

CHLORANTHACEAE R. Brown ex Lindley 1821.—The Chloranthaceae have such reduced flowers that they have been allied at times with the equally reduced Piperineae. However, their assignment to the Laurineae is necessitated by their nodal anatomy, their decussate, serrate leaves, abundance of endosperm in the seeds with total absence of perisperm (quite the opposite from the seeds of the Piperineae), the pollen grains, and very primitive xylem (without vessels in *Sarcandra*). The reduced, bisexual, mostly naked flowers with single pistil and one to three stamens, single orthotropous, pendulous ovule, drupaceous fruit, and sometimes herbaceous habit are convergences toward the Piperaceae through similar reduction. The single monolocate pistil of the Chloranthaceae is truly monocarpellate, whereas the solitary pistil of most of the Piperineae is five- to two-carpellate. The small trees, shrubs, and suffrutescent or perennial herbs of the Chloranthaceae are characteristic of the wet, warm temperate to tropical forests of Central and South America, eastern Asia from Japan south to Ceylon and Madagascar and east in the Pacific to New Zealand and Polynesia. There are about 70 species in the five genera, *Sarcandra* (3 species) and *Chloranthus* Sw. (15) of eastern Asia, *Ascarina* J. R. & G. Forst. (8) of Malesia to Polynesia, *Ascarinopsis* Humb. & Capuron (1) of Madagascar, and *Hedyosmum* Sw. (40) of tropical America and one in Hainan (Cordemoy, 1863; Thierry, 1912; Swamy and Bailey, 1950; Swamy, 1953a, b, c; Vijayaraghavan, 1964; and Endress, 1971).

LACTORIDACEAE Engler in Engler & Prantl 1888.—The monotype *Lactoris fernandeziana*, a relict and nearly extinct, rather succulent small shrub of Masatierra of the Juan Fernandez Islands, has with even less reason sometimes also been placed with the Piperineae. Presumably the much reduced size of the plant, the alternate, stipulate leaves from swollen nodes, and the small apetalous flowers have led to that treatment. However, the unilacunar nodes with two vascular strands; the relatively specialized xylem; the trimerous flowers usually with three tepals, six stamens in two whorls, and three separate carpels connate only at the base; pollen grains in permanent tetrads; carpels with six to eight marginal ovules; follicular fruit; and seeds with no perisperm, abundant endosperm, and undif-

ferentiated embryo (Carlquist, 1964), all argue against any close relationship with the Piperineae. These same characteristics, and others, do argue strongly, however, for inclusion of this species in the Laurineae, probably closest to the Chloranthaceae and Monimiaceae, which are rather more specialized in some reproductive features.

MONIMIACEAE A. L. Jussieu 1809.—The great diversity of the probably very old family Monimiaceae has invited many attempts at dissolution of the family, the latest efforts by Schodde (1969, 1970) and Smith (1972). In their very important treatment Money, Bailey, and Swamy (1950) removed from the family those taxa that were really extraneous there, as *Amborella*, *Austrobaileya*, and the Trimeniaceae. Although there are at least five, and probably several other, major evolutionary lines that have diverged from now extinct common ancestors, the rather large complex of retained primitive features, combined with common evolutionary tendencies, suggests to me parallel treatment of these diverse lineages as subfamilies in one variable family. The logical alternative treatment would be to erect five or more separate and obviously closely related families, an exercise in taxonomic inflation that would seem to serve no useful purpose. Among the features that tie the subfamilies together are the woody habit with decussate, exstipulate, often serrate leaves; hippocrepiform sclereids usually present in the pericycle region of the stem; receptacle usually slightly to deeply concave, cupuliform, or urceolate; basically decussate tepals; usually numerous and separate carpels and stamens; solitary anatropous ovule; and fruits indehiscent drupelets or nutlets. Common tendencies toward more specialized xylem; unisexual flowers; stamens with associated pairs of appendages and anthers opening by flaplike valves; and pollen grains acolpate, dicolpate, or other closely derived types from the anasulcate condition, are displayed in various of the subfamilies (Perkins, 1911; Garratt, 1934; Money, Bailey, and Swamy, 1950; Verdcourt, 1968; Sampson, 1969; and Schodde, 1969, 1970).

Because the subfamilies of the Monimiaceae are treated in some detail in the synoptical key to families and subfamilies of the Annonales above, they need little further consideration here. One or two comments, however, may be in order. A new subfamily Peumoioideae was published by Schodde (1970) for *Peumus boldus* Molina of Chile, formerly included in the Monimioideae. *Peumus* is indeed rather divergent from the rest of the Monimioideae, but so also in many of the same characteristics are the species of *Monimia* Thou. Because the two genera seem to belong together in a separate subfamily, that subfamily must be called the Monimioideae rather than the Peumoioideae because it contains the type genus of the family. The remaining genera that were formerly associated with the two genera must receive a new subfamily name, **Mollinedioideae** sta. nov. [based upon Mollinedieae J. R. Perkins, Bot. Jahrb. Syst. 25: 548. 1898]. *Glossocalyx* Benth., with three dioecious species in tropical West Africa, has primitive vessel elements, scanty parenchyma, septate fibers, anisophyllous leaves, and an oblique, cyathiform calyx. These features are certainly widely divergent from those in the American members of the

Siparunoideae. A thorough study of the subfamily probably would result in placing the African and American taxa in separate tribes if not separate subfamilies.

The Monimiaceae are a moderate-sized family of more than 30 genera and perhaps 350 species (Hutchinson, 1964). It is primarily a family of the tropics and the temperate regions of the Southern Hemisphere. It is especially well developed in the Asiatic, Malesian, and American tropics, in Australasia, and on the islands in the Indian Ocean, including Madagascar. Except for *Glossocalyx* and *Xymalos* Baill., the family is unrepresented in mainland Africa; and only *Peumus boldus* and *Laurelia aromatica* Juss. are found in temperate South America. The tropical American genera *Mollinedia* Ruiz & Pav. and *Siparuna* Aubl. range north into Mexico. Probably the most important members of the family from the phylogenetic point of view are the two species of the genus *Hortonia* Wight ex Arn. and subfamily Hortonioidae, endemic in Ceylon. Certainly they retain the largest constellation of primitive vegetative and reproductive features in the family. Smith has recently (1972) elevated the genus to family status.

GOMORTEGACEAE Reiche 1896.—Rather closely related to the Monimiaceae is *Gomortega keule*, the sole member of the Gomortegaceae, a small tree endemic to the area around Concepcion, Chile. It agrees with the former family in its primitive xylem features; unilacunar node; decussate, exstipulate leaves; undifferentiated tepals; separate, spirally arranged stamens with anthers opening by valves; inner stamens with paired glands; pendulous, anatropous ovules; and drupaceous fruits. On the other hand, it is amply distinct from the Monimiaceae in its syncarpous, two- or three-carpellate and -loculate, epigynous ovary with one ovule in each locule; the well-developed, large embryo; and the two leaf traces from the nodes (Reiche, 1896; Stern, 1955).

CALYCANTHACEAE Lindley 1819.—The Calycanthaceae are another small family, with eight species in the three genera *Calycanthus* L. (Fig. 5), *Chimonanthus* Lindl., and *Idiospermum* Blake. Except for the well-developed embryo, whose cotyledons in the seed take over the storage function from the endosperm, and the rather large, relatively conspicuous flowers (Fig. 5a, b, c), this group of species is very closely related to the Monimiaceae. Along with other characteristics more widespread in the Annonales and Laurineae, they share the arboreal or shrubby habit; opposite leaves (Fig. 5a); numerous, poorly differentiated tepals (Fig. 5a, b); cup-shaped receptacle with numerous separate stamens on the rim and separate, often 1-seeded carpels within (Fig. 5c); dicolpate pollen grains (Fig. 5g); and indehiscent fruits (Fig. 5f) (Schaeppi, 1953; Tiagi, 1963; Nicely, 1965; Blake, 1972).

Calycanthus australiensis Diels, a rain-forest tree of northeastern Queensland, has recently been rediscovered and redescribed as *Idiospermum australiense* (Diels) S. T. Blake (1972). Blake erected for it the new family Idiospermaceae. However, in view of the numerous features *Idiospermum*

Fig. 5. *Calycanthus occidentalis* H. & A., Calycanthaceae, California, representing the Laurineae.—a. Flowering twig with opposite, deciduous leaves and solitary, terminal reddish-brown flower, $\times 0.4$.—b. Flower with some of the strap-shaped tepals and stamens cut away, $\times 1$.—c. Longisection through flower showing numerous separate

shares with *Calycanthus* and *Chimonanthus*, as listed in the synoptical key above, this plant is better treated as representing a new subfamily **Idiospermoideae** stat. nov. [based upon Idiospermaceae S. T. Blake, Contr. Queensland Herb. 12: 3. 1972]. The differences between the two subfamilies generally are what one might expect between a large tree of the wet, tropical Queensland rain forest and shrubs of cooler, drier, more open deciduous forests and woodlands of the temperate United States and eastern Asia. Temperate shrubs typically have more specialized, often ring-porous xylem and deciduous leaves. On the other hand, tropical rain-forest trees tend to preserve more primitive, diffuse-porous xylem and evergreen leaves. Also to compete with other seedlings under heavily shaded, rain-forest conditions, large seeds with fleshy, massive cotyledons, sometimes three or four in number (cf. *Degeneria*), are common. In maturing such large-seeded fruits from individual carpels, a reduction in number of carpels in a flower is also predictable. However, the differences in habit, leaf traces, more primitive stamens, reduced number of carpels, sessile stigma, cotyledons, and xylem anatomy do seem to add up to subfamily status for *Idiospermum*. The flowers of the Calycanthaceae are known generally to be pollinated by beetles (Diels, 1916; Grant, 1950).

Taking a still different evolutionary pathway from their common ancestry with the Monimiaceae are the members of the large, mostly tropical family Lauraceae, and the much smaller, wholly tropical family Hernandiaceae. In both families there have evolved basically cymose, cyclic flowers with a definite number of perianth parts and sporophylls; several whorls of stamens with anthers dehiscing by valves; spinulose, acolpate pollen grains; a solitary carpel with single, apical, pendulous ovule; and single seed with a large embryo absorbing all the endosperm by maturity. Unlike members of the Monimiaceae, the species of these two families have retained primarily alternate leaves.

LAURACEAE A. L. Jussieu 1789.—The Lauraceae consist of 31 genera and between 2,000 and 2,500 species (Kostermans, 1957). They are primarily small to moderate-sized trees of the lowland to montane rain forests, though occasionally also among the canopy species. They are especially abundant in tropical America and southeastern Asia east to Malesia and eastern Australia and south to Madagascar. They are poorly represented in mainland Africa, and relatively few in species in temperate forests. Among the genera reaching temperate areas are *Lindera* Thunb., *Litsea* Lamk., *Persea* Boehm., and *Sassafras* Bercht. & Presl in eastern America and eastern Asia, and *Umbellularia* Nutt in western America. In the Canary and Madeira Islands off northwestern Africa in the relict laurel forests are *Apollonias*

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carpels enclosed in flask-shaped hollow of pubescent cup-shaped receptacle but with filiform styles exerted, and some of the numerous stamens inserted on receptacle, $\times 2$.—d. Stamens, each terminated by succulent food body on connective, $\times 11$.—e. Ovoid, conspicuously veined, indehiscent pseudocarp from accrescent receptacle, $\times 0.7$.—f. Velvety villous achene, $\times 1.5$.—g. Disulcate pollen grains, ca. 50 μ in diam.

Fig. 6. *Anemopsis californica* Hook., Saururaceae, western North America, representing the Piperineae.—a. Flowering perennial herb with one leafy stolon, mostly basal leaves, and two flowering stems terminated by *Anemone*-like conical spike subtended by involucre of white, often reddish-maculate bracts, each of the small flowers in spike also subtended by small, white bract, $\times 0.4$.—b. Individual flower dissected from rachis of spike to show absence of perianth, the six stamens, three styles, and inferior, compound ovary with many ovules on parietal placentae, $\times 6$.—c. Fruiting spike with persistent bracts, $\times 0.6$.—d. Cross section of ovary with ovules attached in two lines to each of the three parietal placentae, $\times 6$.—e. Stamen, $\times 12$.—f. Anasulcate pollen grain, ca. 13.5μ long.—g. Globose seed, containing copious perisperm and rudimentary embryo, $\times 24$.

Nees (also in India), *Laurus* L. (also in the Mediterranean region), *Ocotea* Aubl., and *Persea*. Reaching the south temperate areas are *Beilschmiedia* Nees, *Cryptocarya* R. Br., *Cassytha*, *Ocotea*, and *Persea*, the first three of which are also pantropical. Species of the tropical *Cassytha*, *Licaria* Aubl., and *Ocotea* (including *Nectandra* Rol. ex Rottb.) reach north into southern Florida. Separated from the rest of the Lauraceae, all trees or shrubs in the Lauroideae, are the species of *Cassytha*, which, because of their slender twining habit, scalelike leaves, and parasitic life style, are placed in the separate subfamily Cassythoideae (Allen, 1945; Kasapliligil, 1951; Sastri, 1952, 1962-1965; Stern, 1954; and Kostermans, 1957).

HERNANDIACEAE Blume 1826.—The tropical Hernandiaceae differ from the closely related Lauraceae mainly in their epigynous, commonly unisexual flowers, more frequently lianous habit, often palmately-lobed or -dissected leaves, and the dry, ribbed nuts, frequently winged. Although Shutts (1960) advocated the removal of *Gyrocarpus* Jacq. and *Sparattanthelium* Mart. as the Gyrocarpaceae from the Hernandiaceae with *Hernandia* L. and *Illigera* Bl., Kubitzki (1969) preferred to retain the two groups as subfamilies. The rather large number of significant characteristics possessed in common by the two groups, just as in the various subfamilies of Monimiaceae, force me to agree with Kubitzki, though earlier I had accepted the two groups as distinct families. The differences in the stamens, stigmas, cotyledons, vessel elements, and cystoliths do signify that the two subfamilies are well marked, and probably diverged from common ancestry long ago. *Hernandia*, *Gyrocarpus*, and *Sparattanthelium* all reach north into Mexico; and *Hernandia sonora* L. (*sensu lato*) and *Gyrocarpus americanus* Jacq., like *Cassytha filiformis* L. of the Lauraceae, are circumtropical, especially on sandy strands (Shutts, 1960; Kubitzki, 1969).

SUBORDER PIPERINEAE

Most phylogenists prefer to treat the Piperaceae and Saururaceae as a separate order Piperales, often including the quite distantly related Chloranthaceae and Lactoridaceae. However, the abundance of spherical secretory oil cells in the parenchymatous tissues, basically trimerous though naked flowers, mostly anasulcate pollen grains (Fig. 6f), crassinucellate, usually bitegumentary ovule, and rudimentary embryo in the seed all mark the Piperineae as merely highly specialized members of the Annonales with greatly reduced flowers and fruit. That the two families are closely related and do deserve separate status as a distinct suborder, however, are strongly indicated by the shared perisperm in the seeds, not found elsewhere in the Annonales, naked flowers with syncarpous pistil, orthotropous ovules, and commonly herbaceous habit (Fig. 6a).

SAURURACEAE E. Meyer 1827.—Members of the Saururaceae, though wholly herbaceous, mostly rhizomatous or stoloniferous perennials, are more primitive than species of the Piperaceae in their gynoecea, which range from nearly apocarpous to fully syncarpous with axile placentation and separate locules or parietal placentation in a single locule (Fig. 6b, d). They are

also more primitive in the numerous (Fig. 6b) to few ovules in each ovary; the separate, conduplicate styles (Fig. 6b); the follicular or capsular fruit (Fig. 6c); the ring of vascular tissue in the stem; and the normal (*Polygonum*) type of embryo-sac development. There are seven species of Saururaceae in five genera: *Saururus* L. of eastern North America and eastern Asia, *Anemopsis californica* Hook. (Fig. 6) of southwestern North America, and *Gymnotheca* Decaisne, *Circaeocarpus* C. Y. Wu, and *Houttuynia* Thunb., all of eastern Asia (Holm, 1926; Quibell, 1941; Steenis, 1948; Raju, 1961; Wood, 1971).

PIPERACEAE C. A. Agardh 1825.—Members of the much larger and more tropical family Piperaceae are more specialized in most respects than the species of Saururaceae. They vary in habit from small trees and shrubs to woody lianas, rhizomatous perennials, and even delicate annuals, often growing upon rocks or trees. The foliage is equally variable with leaves broad or narrow, pinnately or palmately veined, cordate or tapered at base, coriaceous or succulent, alternate, opposite, or whorled, and with or without stipules. The piperaceous stem usually has its vascular bundles distinct in two or more cycles with others often scattered inside the circles; however, the bundles are open and not closed like those of monocotyledons. The circumtropical *Peperomia* Ruiz & Pav., with perhaps 1,000 species, and three small associated West Indian genera are sometimes segregated as the separate family Peperomiaceae from the Piperaceae, with its huge circumtropical genus *Piper* L., with perhaps 2,000 species, and the small circumtropical *Pothomorphe* Miq. and the South American *Ottonia* Spreng. and *Trianaepiper* Trelease totalling about 100 more. The more diminutive, fleshy, and epiphytic peperomiads do seem to be distinctive enough in their leaves, flowers, pollen, and drupelets to merit subfamily status as **Peperomioideae** stat. nov. [based upon Peperomeae (as Peperomiceae) F. A. W. Miquel, Syst. Piperac. 45. 1843.]. Certainly nothing, however, would be gained by recognizing two such obviously closely related groups as distinct families (Trelease, 1930; Trelease and Yuncker, 1950; Yuncker, 1958; Melchior, 1964; Düll, 1973).

ORDER BERBERIDALES Lindley 1833

SYNOPTICAL KEY TO FAMILIES AND SUBFAMILIES

1. Gynoecium apocarpous, of many-1 separate carpels (rarely carpels connate into compound pistil); flowers, at least perianth, basically 3-merous; plants woody or herbaceous, mostly lianas, shrubs, perennial herbs, rarely trees or annual herbs; acrid, colored or white sap lacking; leaves various; sepals not markedly caducous; petals and stamens various; fruits usually follicles, berries, drupes, or achenes, rarely many-seeded capsules (BERBERIDINEAE).
2. Flowers usually unisexual, at least functionally; plants woody, mostly lianous; leaves simple, trifoliate, or compound with relatively large leaflets; mostly plants of the tropics or warm-temperate zone.
3. Leaves mostly compound; species mostly monoecious, less commonly dioecious; fruits follicular or baccate; seeds with small embryo and abundant endosperm.

4. Plants mostly monoecious, rarely dioecious or bisexual-flowered lianas, shrubs, or small trees; leaves palmately, rarely pinnately, compound, deciduous or evergreen; stamens usually 6 and often monadelphous; gynoecium of 15-3 carpels, each with many (-1) ovules on submarginal or lateral placentae; stigmas sessile, oblique; fruits fleshy follicles or baccate; cork arising superficially; pericycle fibers with simple pits; chromosome numbers, $n = 14, 15, 16$; 7 genera of eastern Asia and Chile Lardizabalaceae
- 4'. Plants dioecious high-climbing lianas; leaves 3-foliolate, deciduous; stamens 6 and free; gynoecium of numerous carpels, each with 1 pendulous ovule; styles subulate; fruits numerous, black, pruinose, stipitate, 1-seeded berries on enlarged torus; cork deep seated; pericycle a broad sclerosed, sinuous ring, fibers with circular-bordered pits; Chinese monotype (*Sargentodoxa*) Sargentodoxaceae
- 3'. Leaves mostly simple, entire or palmately lobed, evergreen or deciduous; species mostly dioecious; fruits drupaceous with bony endocarp characteristically curved and sculptured; seeds usually with large embryo, curved, folded, cochleate, or straight, endosperm present, scanty, sometimes ruminant; plants mostly lianas, some suffrutescent, scandent herbs, some shrubs or trees; petioles often swollen distally and/or basally; flowers mostly small, unisexual, hypogynous, 3-merous; stamens usually 6(4-3), free, monadelphous, or sessile on androphore; gynoecium 6-3(32-1) mostly separate carpels, often on gynophore; chromosome numbers, $n = 11, 12, 13$; pantropical, less common in temperate forests Menispermaceae
- 2'. Flowers usually bisexual; plants mostly herbs or shrubs, rarely lianas; leaves simple to compound, or commonly very much dissected; mostly plants of temperate or montane areas, rare in the lowland tropics.
5. Carpels solitary; stamens 18-4, mostly as many, or twice as many as and opposite petals; anthers mostly opening by flaplike valves, rarely by longitudinal slits; perianth usually with 6(9-4) petals in 2-3 series, sometimes gland- or nectary-bearing; fruits many-few(-1)-seeded, fleshy or dry, nonfollicular, indehiscent to irregularly ruptured or transversely loculicidal; perennial rhizomatous herbs or shrubs to small trees, often glabrous Berberidaceae
6. Plants woody; rachis of imparipinnate or trifoliolate leaves jointed or swollen at base of leaflets, or simple leaves articulated near base.
7. Shrubs with odd-pinnately decompound leaves; joints of pinnae or pinnules bulbous swollen at base; leaflets entire; flowers numerous in paniculiform inflorescences; sepals numerous, multiseriate on elongate receptacle, gradually merging with whitish petals; anthers dehiscing introrsely and longitudinally without apically hinged valves; fruit globose red berry; chromosome number, $n = 10$; monotype of Japan and China (*Nandina*) Nandinoideae
- 7'. Shrubs or small trees with leaves simple, usually fasciculate in axil of stout spine, trifoliolate, or pinnately compound; leaves and leaflets articulated near base, usually serrate to spiny-dentate; flowers many to few in racemose or subumbellate inflorescences; sepals and petals usually 6, cyclic, yellowish to orange; anthers dehiscing by 2 apically hinged valves; fruit oblong or oval berry; chromosome number, $n = 14$; widely distributed in temperate and montane areas (*Berberis*, *Mahonia*) Berberidoideae
- 6'. Plants herbaceous, rhizomatous perennials; leaves simple to decompound, not articulated; temperate Northern Hemisphere.
8. Leaves 2- or 3-foliolate to ternately compound (rarely unifoliate); flowers racemose or solitary; anthers dehiscing by 2 apically hinged valves; fruits follicular, obliquely or transversely loculicidal, nutlets, or early ruptured by seeds, which ripen naked, fleshy, and blue; basic chromosome numbers, $x = 6, 7, 8$ Epimedioidae

- 8'. Leaves simple, suborbicular and peltate, palmately veined and -lobed, or 2-cleft; flowers cymose or solitary; anthers dehiscing by 2 apically hinged valves or by longitudinal slits; fruits baccate; chromosome number, $n = 6$ (*Diphylleia*, *Podophyllum*) Podophylloideae
- 5'. Carpels and stamens mostly many, indefinite to few (rarely carpel solitary), separate (rarely connate), and spirally arranged; anthers dehiscing by longitudinal slits; perianth seldom with normal petals but often with petaloid nectaries (perhaps reduced and much-modified petals); fruits many-seeded follicles to 1-seeded achenes, less commonly berries or capsules; perennial rhizomatous or tuber-bearing herbs or annuals, some shrubs or vines Ranunculaceae
9. Outer integument longer than inner in ovule; flower single; tepals 4 or 3; petals and nectaries absent; stamens numerous; carpels numerous to 2 or 1; ovules numerous to 2 (1 maturing); carpel walls more or less fleshy in follicular fruits or head of small berries; rhizomatous herbs with palmately lobed, simple leaves; chromosome numbers, $n = 10, 13$; 2 genera of E Asia and E North America (*Glaucium*, *Hydrastis*) Hydrastidoideae
- 9'. Outer integument shorter than or equal to inner integument, or only 1 integument present; flowers numerous to few or 1; petals and/or petaloid nectaries present or absent; stamens mostly numerous, rarely few; carpels and ovules many to 1; carpel walls usually dry; fruits usually follicles or achenes, rarely berries or capsules; rhizomatous perennials, annuals, vines, or rarely shrubs; leaves various.
10. Leaves with reticulate venation; nodes trilacunar or multilacunar; flowers moderate in size, often conspicuous with mostly numerous, spirally arranged sporophylls; ovules anatropous; fruits mostly follicles or achenes, rarely berries or capsules; habit various, small shrubs or vines to rhizomatous perennials or delicate annuals.
11. Rhizomatous herbs or subshrubs with commonly ternately compound leaves, less commonly trifoliolate or pinnately compound; plants with small *Thalictrum*-type chromosomes; normal petals absent though tepals often petaloid; petaloid nectaries often present and tubular, in *Aquilegia* prolonged at base into hollow spur; fruits a cluster of follicles or achenes; chromosome numbers, $n = 7, 8, 9$ Thalictrioideae
- 11'. Rhizomatous herbs, subshrubs, vines, or annuals with leaves various, simple and entire to finely dissected; plants with large *Ranunculus*-type chromosomes; normal petals present or usually absent; tepals often petaloid; petaloid nectaries present or absent; fruits a cluster of follicles or achenes, rarely a capsule or many-seeded berry; chromosome numbers, $n = 6, 7, 8$ Ranunculoideae
- 10'. Leaves with open, dichotomous venation; nodes unilacunar with single or double leaf traces; flowers very small, reduced, and apetalous, solitary or clustered; tepals 7-2, stamens 21-1, carpels 9-1; ovules orthotropous, pendulous, solitary (or 2); fruits a small head of achenes with deflexed style or uncinata setae; rhizomatous perennial with solitary long-petiole leaf with suborbicular blade (*Kingdonia*) or delicate annual with simple leaves clustered rosulately at summit of slender stem (*Circaeaster*); cuneate leaves or leaf segments with dentate apical margins; chromosome number, $n = 15$ (*Circaeaster*); 2 genera of China and Himalayas Kingdonioideae
- 1'. Gynoecium syncarpous, of many-2 connate carpels, forming a compound ovary usually with 1 locule and parietal placentae; flowers basically 2- or 3-merous; perennial or annual, sometimes scandent, herbs, rarely shrubs or small trees, often glaucous and with acrid, colored, white, or colorless sap; leaves mostly pinnately lobed or -dissected, rarely palmately lobed or -dissected or entire; 2 or 3 sepals caducous; 2-seriate petals usually conspicuous; stamens many and indefinite, 6 and diadelphous, or 4 and separate; fruits mostly many-seeded capsules dehiscing by 2-many valves, nonvalvate and dehiscing through placentae, or indehiscent (*Papaverineae*) Papaveraceae

12. Flowers radially symmetrical; sepals 3 or 2, tightly enclosing buds until anthesis; outer petals neither saccate nor spurred (rarely absent); stamens usually many, indefinite in number; latex system mostly well developed with sap usually white or colored; ovules amphitropous (*Papaveraceae, sensu stricto*).
13. Hairs multicellular-multiseriate; seeds mostly lacking arils; perianth 3- or 2-merous; gynoecium 3-valved or dehiscent without formation of valves; median carpellary traces present or absent; pollen grains mostly 3-colpate or several-aperturate.
14. Fruits dehiscent through placentae without formation of valves; median carpellary traces present; stigmas discrete; perianth 3-merous; leaves narrow and entire, often opposite or whorled; vernal annuals of Pacific North America; chromosome numbers, $n = 6, 7, 8$ Platystemonoideae
- 14'. Fruits dehiscent by 3 or usually more valves basipetally; median carpellary traces usually absent and replaced often by pseudomedian traces; stigmas laterally confluent; perianth 2- or 3-merous; leaves mostly broad and toothed or much dissected (narrow and entire in *Canbya*); large suffrutescent herbs to tiny annuals; chromosome numbers, $n = 6, 7, 8, 10, 11, 19$ Papaveroideae
- 13'. Hairs multicellular-uniseriate, unicellular, or plants glabrous; seeds with or without arils; perianth 2-(rarely 3-)merous; gynoecium 2-valved (rarely 3-5-valved); median carpellary traces present; pollen grains 3-colpate, polycolpate, or polyporate.
15. Hairs multicellular-uniseriate; pollen grains 3-colpate or polyporate; seeds arillate; valvular dehiscence acropetal or basipetal; perianth 2-merous; rhizomatous perennials or arborescent plants of Northern Hemisphere; chromosome numbers, $n = 6, 7, 8, 9, 10$ Chelidonioideae
- 15'. Hairs unicellular or lacking; pollen grains polycolpate; seeds usually nonarillate; valvular dehiscence acropetal and usually violent; perianth 2-(rarely 3-) merous; perennial or annual herbs or arborescent plants of W North America; chromosome numbers, $n = 6, 7, 8$ Eschscholzioideae
- 12'. Flowers bilaterally symmetrical or slightly irregular; sepals 2, not enclosing buds to anthesis; 1 or 2 of outer petals more or less saccate or spurred basally, or 2 outer petals somewhat different from 2 inner petals; stamens 4 and free or 6 and diadelphous; latex system not well developed, watery, colorless sap contained in nonarticulated sacs; perennial or annual herbs, some scandent by petioles or tendrils ("Fumariaceae").
16. Outer petals not saccate nor spurred, but wider or less deeply partite than inner petals; stamens 4 and free.
17. Perennial, rhizomatous, scapose herb; leaves all radical, deeply pinnatifid, fernlike; petals entire, inner narrower than outer; ovules 2-4 basal; fruits siliculiform, dehiscent by 2 valves; chromosome number, $n = 9$; monotype of Japan (*Pteridophyllum*) Pteridophylloideae
- 17'. Perennial or annual, low herbs, branched from base; leaves, many radical, pinnately cut; petals not entire, outer trilobed, inner tripartite; ovules numerous on parietal placentae; fruits siliculiform, mostly breaking up into 1-seeded sections, or rarely a dehiscent 2-valved silique; chromosome number, $n = 8$; monogeneric in Eurasia (*Hypecoum*) Hypecoideae
- 16'. Outer petals saccate or spurred; inner petals connate apically over stigma; stamens 6 and diadelphous; perennial or annual herbs, some scandent, some from bulbs; leaves alternate, variously compound, or rarely simple; ovules many to 1 on parietal placentae; fruits slender, elongated or bladderly capsules, or 1-seeded nuts; chromosome numbers, $n = 7, 8$ Fumarioideae

DISCUSSION OF BERBERIDALES

The Berberidales (Ranunculales or Ranales *sensu stricto*) are a rather large order of mostly perennial herbs, shrubs, or lianas that appear to have close common origin with the more arborescent Annonales, particularly the Illiciineae. Unlike the Annonales, however, they lack the spherical secretory oil cells of parenchymatous tissues and the anasulcate or closely derived types of pollen grains so characteristic of that order. Their pollen grains are tricolpate or related types. Their stem anatomy, in line with their more specialized herbaceous or lianous habit of growth, is relatively specialized: primary stems with vascular bundles in a ring, in two or more rings, or scattered, and, especially in woody species, separated by very broad pith rays; vessel elements with simple perforation plates (or scalariform with few bars in the Lardizabalaceae and *Hydrastis* Ellis ex L.), alternate intervacular pitting, and medium to very short in length; parenchyma sparse and diffuse to paratracheal or absent; and fibrous tracheary elements with bordered, or more often, simple pits, sometimes septate and storied. Generally the berberidalean flower too has more specialized stamens and carpels than those characterizing members of the Annonales.

Despite their greater specialization in many features than most members of the Annonales, species of the Berberidales do retain many primitive features in their flowers, fruits, and seeds. The basically actinomorphic, bisexual flowers have separate parts many or indefinite in number, and arranged spirally or spirocyclically on a convex receptacle. The perianth, basically trimerous in several series, is frequently poorly differentiated. When "petals" are present, they usually appear to be petaloid nectaries. The apocarpous gynoecia usually mature into many- to several-seeded follicles or into clusters of few- or single-seeded berries, drupes, or achenes. Members of the Papaveraceae and *Nigella* L. of the Ranunculaceae, with syncarpous gynoecia, generally produce capsules. The usually anatropous ovules have a massive nucellus and two integuments and mature usually into seeds with a small embryo and abundant endosperm. In the Berberidaceae and *Sargentodoxa* Rehder & Wilson and those Menispermaceae with a definite number of stamens, the stamens are opposite the petals, which in turn are often opposite the sepals. Throughout the order there is a strong tendency toward compound leaves and often further to greatly dissected leaves, all usually alternate and exstipulate. Like their annonalean cousins plants of this order are heavily endowed with isoquinoline or phenylalanine alkaloids. The Menispermaceae, for example, share nine alkaloids with the Berberidaceae, six each with the Fumarioideae and Rutaceae, five each with the Ranunculaceae and Lauraceae, three with the Monimiaceae, two each with the Papaveraceae (*s. s.*), Magnoliaceae, Annonaceae, Buxaceae, and one with the Hernandiaceae and Aristolochiaceae (Willamin & Schubert, 1961; Ernst, 1964).

Some of the more outstanding evolutionary trends obvious in the Berberidales beyond those expressed characteristically in the specialized habit, stem anatomy, and foliage of member species, are displayed in the flowers, fruit, and seeds. There is a strong tendency toward unisexuality, particularly

well developed in the mostly monoecious Lardizabalaceae and dioecious *Sargentodoxa* and Menispermaceae. In *Thalictrum* L. of the Ranunculaceae unisexuality is part of the anemophilous syndrome. In most monoecious or dioecious species, however, the unisexual flowers generally retain vestiges of the missing sporophylls, as staminodia in the female and carpellodia in the male flowers. Apparently only one carpel is retained in the bisexual flowers of the Berberidaceae (but see Chapman, 1936; Eames, 1961; and Kaute, 1963) and species of *Actaea* L. and *Cimicifuga* Wernischek of the Ranunculaceae. Similar strong reduction is found sometimes in other floral parts. The carpellate flower of *Cissampelos* L. of the Menispermaceae is reduced to one sepal, one petal, and one carpel with no staminodium. In most of the apocarpous families, there is also a strong tendency toward reduction of the ovules in the carpels to one, frequently with the carpel maturing subsequently into a one-seeded berry, drupe, or achene.

Connation of the carpels into a syncarpous pistil, in the Ranunculaceae found only in the partly connate carpels of some *Helleborus* L. species and in *Nigella*, becomes a diagnostic family characteristic for the closely related Papaveraceae. The apocarpous ancestry of the poppies is, however, indicated by the internal and derived apocarpy of members of the Platystemonoideae (Ernst, 1967). Connation in the androecium is seen in members of the Lardizabalaceae and Menispermaceae.

Many stages in the differentiation of the perianth toward production of petals can be found among members of the Berberidales. The tepals may be sepaloid or petaloid, or the perianth may be differentiated into calyx and corolla (Papaveraceae). In many plants, especially in the Ranunculaceae, the petals seem to be modified, nectariferous staminodia (Honigblätter), often tubular in shape. In the Delphiniiinae of the Ranunculaceae and Fumarioideae of the Papaveraceae the flower is bilaterally symmetrical.

SUBORDER BERBERIDINEAE

LARDIZABALACEAE Decaisne 1839.—Despite their lianous habit and unisexual flowers, some species of the Lardizabalaceae seem to retain more primitive features than members of the other families. In some genera the stamens are broad, fleshy, and undifferentiated, with embedded extrorse sporangia, dehiscing longitudinally, and a massive connective with an elongated apex. At anthesis the separate carpels are open at the apex with a stigmatic crest, perhaps modified from a megasporophyll of the winteraceous type (Payne and Seago, 1968), and have ovules distributed submarginally or laterally on the ovary wall. Although usually functionally unisexual, the flowers generally retain vestiges of the nonfunctional sporophylls, and *Decaisnea* Hook. f. & Thom., an upright shrub or small tree, has bisexual flowers. The fruits, though often fleshy and somewhat baccate, are basically many-seeded follicles.

The Lardizabalaceae consist of perhaps 40 species in eight genera, six in eastern Asia (*Akebia* Decne., *Decaisnea*, *Holboellia* Wall., *Parvatia* Decne., *Sinofranchetia* (Diels) Hemsl., and *Stauntonia* Wall.) and two in central Chile (*Boquila* Decne. and *Lardizabala* Ruiz & Pav.), an extraor-

dinarily disjunct distribution (Thorne, 1973). The Asiatic distribution, ranging from Japan and Korea to the Himalayas, centers primarily in eastern and southern China, Indochina, Burma, Assam, and the Himalayan region. *Akebia quinata* (Houtt.) Decne., commonly cultivated in the United States, is apparently naturalized in North Carolina.

SARGENTODOXACEAE O. Stapf ex Hutchinson 1926.—The monotype *Sargentodoxa cuneata* Rehder & Wilson is a high-climbing liana in moist forests from western China to Laos and Tonkin. Stapf (1926), who established the family Sargentodoxaceae, described the species as looking like a plant resulting from the graft of the gynoeceium of *Schisandra* on a plant of the lardizabalaceous *Sinofranchetia*. This glabrous, dioecious climber has alternate, trifoliolate, deciduous leaves and small, racemose, trimerous, greenish-yellow, unisexual flowers with vestigial remnants of the nonfunctional sporophylls. Only the gynoeceium deviates from the trimerous condition, and it has numerous, one-ovulate carpels arranged spirally on an elongated receptacle. The solitary seeds with different shape, testa, and hilum readily differentiate the fruits of *Sargentodoxa* from those of *Schisandra*. Transitions from entire, simple leaves to trifoliolate leaves have been observed in the young shoots. In the phloem are large secretory cells with tanniferous contents similar to the tannin-mucilage receptacles found in certain Menispermaceae, Schisandraceae, and *Caulophyllum* of the Berberidaceae (Stapf, 1926).

MENISPERMACEAE A. L. Jussieu 1789.—Surely close to the preceding lianous taxa and to the more shrubby or herbaceous Berberidaceae are the perhaps 370 species of 80 genera of Menispermaceae. These plants, mostly dioecious woody vines but varying in habit from herbaceous twiners to moderate-sized trees, differ markedly from the Lardizabalaceae and from *Sargentodoxa* in having mostly simple, though sometimes lobed leaves with distally and/or basally swollen petioles; drupaceous fruits with bony, often curved and sculptured endocarp; and seeds with often curved, folded, or cochleate embryo in sometimes ruminant endosperm. Some taxa lack endosperm in the mature seed. Menisperms are readily distinguished from the Berberidaceae by their lianous habit, unisexual flowers, apocarpous gynoeceium, single ovule (rarely two) per carpel with micropyle directed up, and the drupaceous fruits. The menispermaceous alkaloids shared with other members of the Berberidales and Annonales are discussed above. Primarily circumtropical, the Menispermaceae are represented in the United States by five species in four genera (*Calycocarpum* Nutt. ex Gray, *Cissampelos*, *Cocculus* A. DC., and *Menispermum* L.). No species are known from the Pacific states or from Europe.

BERBERIDACEAE A. L. Jussieu 1789.—The Berberidaceae with about 14 genera containing perhaps 600 species are much better known to temperate botanists than are the preceding members of the order. Mostly shrubs (Fig. 7a) or rhizomatous herbs, they are essentially plants of temperate or montane forests, particularly numerous in eastern Asia and in eastern and western North America. Represented in the eastern United States are the woody

Fig. 7. *Mahonia nervosa* (Pursh) Nutt., Berberidaceae, Pacific North America, representing the Berberidineae.—a. Flowering stem of low, rhizomatous shrub with stem covered by persistent bud scales and bearing two alternate, pinnate, glossy, evergreen leaves and two erect racemes with buds, flowers, and young berries, $\times 0.4$.—b. Flower with six sepals in two series, six petals in two series, six stamens opposite the petals, and single carpel, $\times 4$.—c. Pendulous fruiting raceme bearing one-seeded blue berries with gray bloom, $\times 13$.—d. Stamen with anthers opening by two uplifting flaplike valves, $\times 13$.—e. Carpel with several largely basal ovules and broad, sessile stigma, $\times 9$.—f. Spiraperturate pollen grain, ca. $50\ \mu$ in diam.—g. Seeds, each containing a small embryo in abundant endosperm, $\times 4$.

genus *Berberis* L. (*B. canadensis* Mill.) and the herbaceous genera *Caulophyllum* Michx., *Diphylleia* Michx., *Jeffersonia* Bart., and *Podophyllum* L., all Tertiary relicts also represented in eastern Asia. In western North America are *Achlys* DC., *Berberis*, *Mahonia* Nutt. (Fig. 7), and *Van-*

couveria C. Morr. & Decne., only the last, a genus endemic to the Pacific Northwest, not also represented in northeastern Asia. Many botanists include *Mahonia* in *Berberis*. The two genera, or subgenera, are closely related but certainly as distinct from each other as many other widely accepted genera in western North America.

Members of the Berberidaceae are best defined by their bisexual, trimerous flowers with apparently single carpel (Fig. 7e) and definite number of stamens, some or all opposite the petals (Fig. 7b); anthers mostly opening by flaplike valves (Fig. 7d); and fleshy (Fig. 7c) or dry, nonfollicular, mostly indehiscent fruits. Some botanists, as Chapman (1936), Eames (1961), and Kaute (1963), have suggested that the apparently solitary carpel is pseudomonomerous, actually two or three fused carpels with one or two of them suppressed. Occasional biloculate carpels in *Berberis*, *Caulophyllum*, *Diphylleia*, *Nandina* Thunb., and *Epimedium* L. (Chapman, 1936) lend considerable weight to this suggestion but are offset by occasional specimens of *Podophyllum* with several pistils (Ernst, 1964). Teratological examples frequently can be more confusing than clarifying. The similarity of the abundant alkaloids of species of Berberidaceae to those in members of the Menispermaceae has been mentioned above. The characteristic yellow alkaloid berberine of the Berberidaceae and Menispermaceae is found also in the Ranunculaceae and Papaveraceae of this order, in the Annonaceae and Lauraceae of the related Annonales, and in the chemically similar Rutaceae (Rowson, 1958; Willaman and Schubert, 1961).

As is customary in larger angiospermous families with several evolutionary lines, a number of somewhat divergent genera or groups of genera have been split off from the Berberidaceae and treated as distinct families, as the Nandinaceae, Leonticaceae, and Podophyllaceae. Since these are generally retained close to the obviously related Berberidaceae (*s. s.*) anyway, they seem more logically treated as subfamilies within a broader Berberidaceae. *Glaucidium* Sieb. & Zucc. and *Hydrastis*, sometimes included in the Berberidaceae, fit better into the Ranunculaceae and are discussed below under that family.

RANUNCULACEAE A. L. Jussieu 1789.—Also largely temperate or montane in distribution are the Ranunculaceae, a large family of perhaps 40 to 50 genera and 1,800 to 2,000 species. Represented in the United States are about 20 genera and 300 species, the majority of the latter belonging to such large genera as *Ranunculus* L., *Delphinium* L., *Aquilegia* L., *Anemone* L., *Clematis* L., and *Thalictrum*. Although certainly closely related to the Berberidaceae, the members of the Ranunculaceae are somewhat more specialized in their habit of growth. Most are rhizomatous perennials, some are scandent or even woody vines, some annuals, and a few are shrubs. On the other hand, they are more primitive in their floral and fruit characteristics. Though the perianth usually lacks normal, conspicuous petals, the tepals are often petaloid, and frequently petaloid nectaries or honey-leaves are present. The stamens and carpels mostly are numerous, indefinite in number, separate, and spirally arranged on the often enlarged or elongated

receptacle. The carpels have many to few ovules or only one ovule, and they ripen into clusters of follicles or achenes, rarely into berries or capsules. The largely rhizomatous herbs agree rather closely in appearance with the similar herbs of the Berberidaceae and Papaveraceae both in habit and in the often alternate, exstipulate, compound, or much dissected leaves. With the Berberidaceae they share at least seven alkaloids, five with the Menispermaceae, and five with the Papaveraceae, including the Fumarioideae (Willaman and Schubert, 1961).

As with the Berberidaceae, various botanists have sought to elevate divergent taxa of the Ranunculaceae to family status, as the Hydrastidaceae, Kingdoniaceae, and Circaeasteraceae. All seem more logically retained in the Ranunculaceae as the Hydrastidoideae and the Kingdonioideae. Most divergent are *Kingdonia* and *Circaeaster* with their unilacunar nodes, freely terminating dichotomous leaf venation, apetalous, reduced flowers, orthotropous ovules, and distinctive chromosome number ($n = 15$). Both genera combine highly specialized with rather primitive characteristics. Foster (1959, 1961a,b, 1963; Foster and Arnott, 1960) has regarded the unilacunar node and open, dichotomous venation as representing the persistence of primitive features. It seems more likely that they are specializations associated with the moist, shaded habitats apparently preferred by these two species (Diels, 1932; Janchen, 1949).

Hydrastis and *Glaucidium*, sometimes placed with the Berberidaceae or as a distinct family, do have the berberidaceous rhizomatous habit of growth and *Glaucidium* frequently has only one carpel. However, their flowers have numerous stamens, many to two carpels or one carpel, no petals or nectaries, and their leaves are simple and palmately lobed. They are distinguishable from the other Ranunculaceae by the absence of nectaries, ovules with longer outer integument, rather fleshy fruit, and distinctive haploid chromosome numbers of $n = 10$ and 13. Their chemistry is very similar to that of the other Ranunculaceae (Hammond, 1955; Jensen, 1968) but they possess several alkaloids in common also with the Berberidaceae (Willaman and Schubert, 1961). They seem better treated as an intermediate group but close enough to the other ranunculads to warrant subfamily treatment in the Ranunculaceae (Kumazawa, 1938; Buchheim, 1964).

The long-standing division of the Ranunculaceae into the follicular-fruited Helleboroideae and achene-fruited Ranunculoideae has been shown to be artificial, for the achene in the ranunculoids is polyphyletic through reduction from the follicle in various helleboroid lineages. It seems better to combine the Helleboroideae, therefore, with the Ranunculoideae, and to recognize instead the division into the Thalicthroideae and Ranunculoideae suggested primarily on cytotaxonomic grounds by Langlet (1932) and Gregory (1941), and supported by phytochemical and embryological investigations by Hegnauer (1965), Jensen (1968), Vijayaraghavan and Marwah (1969), and Ruijgrok (1967). Whether the Ranunculoideae should be further subdivided as suggested by Ruijgrok (1967) into those taxa containing ranunculine and those not producing it can be decided only

after we have accumulated more data. At any rate, the name *Helleboroideae* could not be used because both *Ranunculus* and *Helleborus* produce ranunculine.

Paonia L. has been properly removed from the Ranunculaceae, and it is now generally considered to constitute a distinct family. I have placed it in the Theales under the Dilleniineae and will discuss it later with that group.

SUBORDER PAPAVERINEAE

PAPAVERACEAE A. L. Jussieu 1789.—The Papaveraceae (including the Fumariaceae) are another sizable family of mostly temperate perennial herbs. It contains perhaps 44 genera and 625 species, mostly of the Northern Hemisphere with especially strong representation in western North America and in Asia. Among the better known western American genera are *Argemone* L., *Corydalis* Ventenat, the woody tree poppy *Dendromecon* Benth., *Dicentra* Bernh., *Eschscholzia* Cham. in Nees, *Papaver* L., *Platystemon* Benth. (Fig. 8), and *Romneya* Harv. In tropical Mexico and farther south the most striking poppies are the arborescent species of *Bocconia* L. In eastern North America genera represented by native species are *Adlumia* Raf., *Argemone*, *Corydalis*, *Dicentra*, *Sanguinaria* L., and *Styliphorum* Nutt.

Traditionally the Papaveraceae have been included with the Capparaceae and Brassicaceae and their relatives in the Rhoeadales, presumably because of the syncarpous gynoecium with parietal placentation and the sometimes siliquiform capsule with valvate dehiscence and false dissepiment. That these features represent evolutionary convergence is indicated by the fundamentally different embryology (Lindley, 1836; Lebègue, 1952) and chemistry of the Papaveraceae and the Capparales. Like the other Berberidales, the species of Papaveraceae, including the Fumarioideae, are extremely rich in alkaloids, sharing at least six with the Menispermaceae and five with the Ranunculaceae (Rowson, 1958; Hegnauer, 1959, 1961, 1963, 1964, 1969a, b, 1971; Willaman and Schubert, 1961). The Capparales are relatively poor in alkaloids but rich in mustard oil glucosides, which are unknown from the Papaveraceae and other Berberidales (Buhr, 1936; Kjaer, 1963). Similarly, amyloid reserves in the pollen grains are lacking in the Capparales but present in the Papaveraceae and other Polycarpicae (Auger-Barreau, 1964). The apocarpous origins of the papaveraceous gynoecium are indicated by the internal vascular anatomy of *Meconella* Nutt. and the near-apocarp of the fruits of *Platystemon* (Fig. 8a, c, d) (Ernst, 1967). The trimery of the bisexual flowers (Fig. 8a, b) of the genera of the Platystemonoideae and some other papaveraceous genera as well as the often dissected leaves and rhizomatous herb growth habit of the poppies and fumitories are other berberidalean features.

If one accepts the basically berberidalean chemistry, growth habit, foliage, flowers, pollen (Fig. 8f), and seeds of the Papaveraceae, then the family is still distinct enough in its characteristics to warrant separate subordinal treatment in the order as the Papaverineae. Especially distinctive from the

Fig. 8. *Platystemon californicus* Benth., Papaveraceae, southwestern North America, representing the Papaverineae.—a. Villous annual with cream-colored flowers in various stages from bud, still bearing three deciduous sepals, to open flowers to almost mature fruits, $\times 0.4$.—b. Open flower with six petals, numerous spirally arranged stamens, and many separate stigmas, $\times 0.9$.—c. Cross section of syncarpous pistil with connate carpels arranged around large central chamber and each containing a row of ovules, two shown here, attached to parietal placentae, $\times 9$ (after Ernst, 1967).—d. Fruit of moniliform carpels here broken apart from one another and shattered into indehiscent, one-seeded segments, $\times 1.3$.—e. Stamen with expanded filament, $\times 4.9$.—f. Oblate spheroidal, tricolpate pollen grain, ca. 22μ in diam.

Berberidineae are the syncarpy and parietal placentation (Fig. 8c) of the gynoecium and the generally cyclic and dimerous perianth with the two or three sepals usually caducous and the two series of petals conspicuous, polypetalous, often wrinkled, fugaceous, and without nectaries (Fig. 8a, b). Also the usually numerous ovules are amphitropous or campylotropous

rather than anatropous, and the fruits are often capsules dehiscent by two to many valves.

The largest subfamily, Fumarioideae, represented in North America by the indigenous *Corydalis*, *Dicentra*, and *Adlumia*, and the introduced *Fumaria* L., is readily recognized by its bilaterally symmetrical flowers with one or both of the two outer petals saccate or spurred, the two inner petals connate over the stigma, and the six stamens diadelphous. The sap of the fumitories is watery and secretory cells or idioblasts in the stem replace the laticiferous elements found in the poppies. More American than European botanists have tended to recognize this group as a distinct family Fumariaceae, possibly because the two intermediate genera, *Hypecoum* L. and *Pteridophyllum* Sieb. & Zucc., are restricted to the Old World. To accept the Fumarioideae as a distinct family one would have to ignore the basic papaveraceous habit, foliage, stem anatomy, chemistry, cytology, and fruits of the fumitories and the two listed intermediate genera with their mildly bilaterally symmetrical corollas and four free stamens. The three groups are more logically treated as subfamilies coordinate with the four subfamilies recognized by Ernst (1962) for the poppies, the seven having diverged over a long period from now extinct common ancestors.

ORDER NYMPHAEALES Lindley 1845

SYNOPTICAL KEY TO FAMILIES AND SUBFAMILIES

1. Plants mostly rhizomatous perennials (*Euryale* annual) with floating or emerged leaf blades long-petiolate, alternate, leathery, orbicular to sagittate, with basal sinus or peltate, and/or submersed leaf blades opposite or whorled, petiolate, entire and filmy-thin or dichotomously divided into narrow segments; flowers bisexual, large or small but usually conspicuous, mostly long-pedunculate in leaf axils, with perianth; stamens and carpels various; pollen grains anasulcate or closely derived types or apparently tricolpate; pollination entomophilous or "hydrocleistogamous"; ovules anatropous, with two integuments; fruits and chromosome numbers various (Nymphaeaceae, *sensu lato*).
2. Aquatic, acaulescent perennials, large, from stout, horizontal rhizome bearing only long-petiolate, large, orbicular, centrally peltate and depressed, leathery, emerged or floating leaf blades; flowers large, pink, white, or yellowish, emerged on stout peduncles, with 4 involucre bracts (or sepals); 14-26 petaloid tepals, only 2-5 outermost persistent; stamens numerous (ca. 200) and spirally arranged; pollen apparently tricolpate; carpels 3-9, embedded separately in cavities in flat top of large, obconical, spongy receptacle, only stigmas protruding; each carpel with 1 or 2 pendulous ovules; fruits hard walled, ellipsoidal or globose acornlike nuts with 1 nonoperculate seed containing large embryo with 2 fleshy cotyledons and green plumule, but lacking endosperm and perisperm; chromosome number, $n = 8$ (*Nelumbo*) Nelumbonaceae
- 2'. Aquatic, acaulescent perennials or annuals from horizontal or erect rhizomes, or caulescent, with erect, slender stems; leaves and flowers various; pollen grains anasulcate or closely derived types; carpels not embedded in obconical receptacle; carpels many to few or 1, usually with many to rarely 1 ovule; fruits various; seeds operculate with small embryo in limited endosperm but abundant perisperm; chromosome number, $n = 12$ or more.
3. Plants caulescent with slender rhizomes and long, slender floating stems; floating leaf blades alternate, long-petiolate and elliptic- or linear-peltate; submersed leaves (*Cabomba* only) opposite or whorled, short-petiolate, and deeply 5-7-parted with

- each part dichotomously or trichotomously divided into many narrow segments; flowers small, with apparently cyclic (or low helical), distinct, hypogynous parts, 3(4-2) sepals, 3(4-2) petals, many (36-18)-6 or 3 stamens, 18-1 carpels, separate, each with small terminal stigma and 3 or 2 ovules borne laterally or dorsally; pollen grains anasulcate; fruits indehiscent, nutlike, with 3-1 pendulous seeds; chromosome numbers, $n = 12, 40, 52$ (*Brasenia*, *Cabomba*) Cabombaceae
- 3'. Plants acaulescent, with short, stout, erect or stout or thin, horizontal, branching, perennial or annual rhizomes; floating or emerged leaf blades alternate, long-petiolate, leathery with deep basal sinus or centrally peltate; submersed leaves alternate, simple, often cordate, thin or filmy; flowers mostly large with parts spirally arranged, hypogynous to epigynous; sepals 5 or 4 and petals numerous, some scalelike and nectariferous, often passing gradually into staminodia or stamens; stamens numerous; pollen grains rarely anasulcate to mostly 2-, 3-, 4-, or zoni-sulcate or inaperturate, sometimes released in tetrads; gynoecium of 35-5 carpels united along their sides or outer margins by adnation to receptacle, semiapocarpous to syncarpous, superior to inferior; stigmas radiate; ovules numerous and laminar; fruits spongy, irregularly dehiscent berries with many, sometimes arillate seeds; chromosome numbers, $n = 12, 14, 17, 18, 29$ Nymphaeaceae, s. s.
4. Plants perennial; leaves not peltate but with deep sinus; floating or emerged leaves leathery, submersed leaves cordate, thin, and delicate; flowers open, entomophilous; ovary hypogynous to semiepigynous with 35-5 carpels united to varying degrees; fruit not crowned with persistent calyx; basic chromosome numbers, $x = 14, 17$ (*Nuphar*, *Nymphaea*, and *Ondinea*) Nymphaeoidae
- 4'. Plants annual or short-lived perennial; leaves peltate or cordate-hastate, floating or submersed; flowers often not or scarcely open, then "hydro-cleistogamous"; ovary epigynous; fruit often crowned with persistent calyx and stigma.
5. Leaf blades floating, peltate, often huge, orbicular, strongly veined below and armed with prickles on petioles and lower surfaces; flowers without involucre; calyx 4-merous, with tube campanulate-urceolate, gynoecium not prolonged into cone, externally aculeate; fruits aculeate berries with nonsetose seeds; chromosome numbers, $n = 12, 29$ (*Euryale* and *Victoria*) Euryaloideae
- 5'. Leaf blades submersed, not peltate, without prickles, oblong-orbicular to linear-lanceolate, hastate to cordate from villous rhizome; flowers subtended by involucre of 5 oblong, sepeloid bracts; calyx tube elongate, 4-5-lobed and corolla gamopetalous, with many-8 lobes; gynoecium prolonged into connivent 10-rayed, stigmatic cone; fruits fleshy, globose, nonaculeate berries with numerous softly setose seeds; chromosome numbers, $n = 8, 17$ (*Barclaya*) Barclayoideae
- 1'. Plants submersed without roots or floating leaves, monoecious; leaves sessile, whorled with dichotomously dissected, linear to filiform, often serrulate segments; flowers unisexual, small, inconspicuous, sessile and solitary in leaf axils, lacking perianth but subtended by whorl of 8-12 basally connate bracts; stamens 10-20 in low spiral on low convex receptacle, with short filament and broad connective projecting beyond the 4-locular, extrorse anther; pollen grains large, spheroidal, inaperturate, nearly smooth, and thin walled; pollination hydrophilous; carpel single, elliptical with filiform, oblique style, stigma in lateral pocket, and single, pendulous, orthotropous ovule with 1 integument; fruits achenes topped by persistent style base and often with additional marginal or basal spines; seeds with large, straight embryo with fleshy cotyledons, well-developed plumule, and no endosperm nor perisperm; basic chromosome number probably $n = 12$ (*Ceratophyllum*) Ceratophyllaceae

DISCUSSION OF THE NYMPHAEALES

The members of the Nymphaeales show their common origin with other taxa of the Annoniflorae by their retention of various primitive features, including xylem without vessels or with primitive tracheidlike vessel ele-

ments (*Nelumbo* Adans.); bisexual, actinomorphic flowers with parts entirely separate, indefinite in number, and spirally arranged; perianth not at all or but poorly differentiated into sepals and petals; some stamens broad and undifferentiated into filament and anther; pollen grains anasulcate or closely derived therefrom; carpels separate to connate in varying degree; ovules relatively numerous, anatropous, bitegmic, and crassinucellate; and seeds with poorly developed embryo and abundant perisperm and some endosperm. In addition, they are well represented and ancient in the fossil record back into the early Cretaceous.

Unlike members of the Annonales, however, no species of the Nymphaeales has been found to contain spherical secretory cells in their parenchymatous tissues. And unlike the members of the Berberidales, only the two species of *Nelumbo* in the Nymphaeales have apparently attained the tricolpate stage of development in their pollen grains, the other members of the order having anasulcate or closely derived types of pollen grains. As in both the Annonales and Berberidales, plants of the Nymphaeales, with the exception of the completely submersed species of *Ceratophyllum* L., have been found to produce alkaloids (Willaman and Schubert, 1961).

From the fossil record one can readily deduce that the Nymphaeales are a group that early diverged from protoannonalean stock by entering freshwater habitats and quickly becoming adapted to an aquatic existence. The ten extant genera of the order have evolved along their own evolutionary pathways for many tens of millions of years. As a result this relatively small handful, perhaps 65 species, of survivors of an ancient group show an amazing diversity of characteristics, such a diversity that it prompted one botanist (Li, 1955) to divide the Nymphaeaceae *sensu lato* into five families distributed over three orders. Such disintegration of the group is not only unnecessary, it is quite misleading. Nonetheless, I do feel now after considerable study that the Nymphaeaceae *s. l.*, as treated in the synoptical key above, do consist of five recognizable groups. These groups have gaps among them of sufficient magnitude to warrant the acceptance of three distinct families, and three subfamilies within the Nymphaeaceae *sensu stricto*. Along with the Ceratophyllaceae, however, they retain enough characteristics in common to indicate their immediate common ancestry. In addition to the features listed above by which I place them in the Annoniflorae, the members of the Nymphaeales are linked by a number of characteristics that may not be convergent adaptations to their common aquatic habitat. Members of all three waterlily families, Nelumbonaceae, Cabombaceae, and Nymphaeaceae (here and subsequently used in the narrow sense), have retained the basic rhizomatous perennial herb habit of growth with very long petiolate, alternate, simple, floating or emersed, centrally peltate leaves with involute vernation. There are, of course, deviations from this pattern because *Euryale*, at least, is annual; *Cabomba* Aubl., caulescent like *Brasenia* Schreb. and *Ceratophyllum*, sometimes has only submersed, highly dissected, opposite or whorled leaves (also like *Ceratophyllum*); and most nymphaeaceous genera have nonpeltate floating pads with deep sinuses. These habital features, taken by themselves, cannot

be decisive for they are all found, to at least a limited extent, in some representatives of unrelated families that have become adapted to the same freshwater habitat. But to be added to them are the scattered vascular bundles lacking secondary growth, articulated laticiferous tubes or sacs, often polystelic rhizomes and stolons, root hairs arising from specialized cells, mucilage hairs, other hairs only uniseriate, and anomocytic stomata. Other anatomical features, like abundant intercellular air spaces, absence of cambium, and highly reduced sclerenchymatous and xylem tissues, are more likely ecological convergences, as perhaps also are such reproductive characteristics as laminar placentation in the carpels (also found in several aquatic monocotyledonous families), operculate seeds, and tardily dehiscent baccate or indehiscent fruits. Possibly nonconvergent are common tendencies toward cyclic and reduced number of floral parts, biseriate perianth, syncarpous, inferior ovary, or carpels and ovules few or even solitary, pollen grains modified from the anasulcate type, and large, well-developed embryos absorbing at maturity the endosperm and perisperm.

NELUMBONACEAE Dumortier 1829.—The Nelumbonaceae are represented by two species, *Nelumbo lutea* (Willd.) Pers., of eastern North America south through eastern Mexico and the Greater Antilles to Colombia and Guyana, and *N. nucifera* Gaertn., of China south through eastern Asia to Ceylon and Iran and through Malesia to northern Australia. The genus had a wider distribution in the Northern Hemisphere in Cretaceous and Tertiary times, apparently reaching northern Africa as well as Europe and western North America (Thorne, 1973). These large aquatics with large, orbicular, glaucous, concave, peltate leaf blades and large yellowish, white, or pink, solitary flowers usually borne well above the water surface on stout petioles and peduncles, differ quite markedly from the other water-lilies in their tricolpate pollen grains; much enlarged, spongy, obconical receptacles with embedded separate, acornlike, exceedingly long-lived nuts; nonoperculate seeds containing a large embryo with two large, fleshy cotyledons, green plumule, and neither endosperm nor perisperm; first foliage leaves peltate; primitive vessel elements; lack of mucilage hairs and laticifers; and a chromosome number of $n = 8$. Simon (1970, 1971) found *Nelumbo* to be serologically rather isolated from the other water-lilies, showing partial identity reactions with members of the Annonales and Berberidales as well as with other Nymphaeales.

CABOMBACEAE A. Richard 1828.—The Cabombaceae are represented by the monotype *Brasenia schreberi* Gmel. (Fig. 9), of nearly subcosmopolitan but sporadic distribution (lacking from Europe and South America), and seven species of *Cabomba*, of warm-temperate to tropical parts of the New World. Though less widely recognized as a distinct family (but see Lindley, 1836; Endlicher, 1839; Gray, 1848; Li, 1955; Snigirevskaya, 1955; Hutchinson, 1973; and Takhtajan, 1969), these plants seem to deserve separate family treatment on the basis of their distinctive slender rhizomes (Fig. 9a, g); caulescent, floating stems (Fig. 9a); much dissected, opposite, submersed leaves in *Cabomba*; small flowers with apparently cyclic, mostly

trimerous, biseriate perianth (Fig. 9b, c); 36–3 specialized stamens; strictly anasulcate pollen grains (Fig. 9h); 18–1 separate carpels containing three or two laterally or dorsally attached ovules (Fig. 9c); and indehiscent nutlets with three to one pendulous seeds (Fig. 9d,e). Though strictly apocarpous like *Nelumbo*, the species of *Brasenia* and *Cabomba* in many characteristics are closer to the Nymphaeaceae, which they resemble especially in pollen morphology (Fig. 9h), seeds (Fig. 9e), seedling ontogeny, mucilage hairs, and laticifers.

NYMPHAEACEAE R. A. Salisbury 1805.—The Nymphaeaceae are the largest family of waterlilies because of the large, subcosmopolitan genus *Nymphaea* L. with about 35 species bearing showy, white, yellow, blue, or red flowers. The other genera have few to only one species, and are: *Nuphar* J. E. Smith with one polymorphic yellow-flowered species of North America and Eurasia and a few other poorly known species of eastern Asia (Beal, 1956); *Victoria* Schomb. with huge, peltate, heavily ribbed, floating leaves of eastern lowland South America; *Euryale* and *Barclaya* Wall. of eastern and southeastern Asia; and the recently described *Ondinea* d. Hartog (1970) of northwestern Australia. These are acaulescent, rhizomatous, mostly perennial waterlilies with alternate, long-petiolate, thin or filmy, simple, cordate submersed leaves and leathery, peltate or deep-sinused floating or emersed leaves. They are readily distinguished from species of the Nelumbonaceae and Cabombaceae because of their usually large, showy flowers with numerous spirally arranged petals often passing gradually into staminodia and stamens, 35–5 variously united carpels tending strongly toward the perigynous or epigynous condition, numerous ovules distributed over the locule walls, radiate stigmas, and fruit a spongy irregularly dehiscent berry with numerous, often arillate seeds.

The six genera of this family are divisible into three well-marked groups, as demonstrated in the synoptical key above. However, the differences certainly are not great enough to warrant the family status awarded them by Li (1955).

The **Euryaliodeae** stat. nov. [based upon *Euryaleae* S. Endlicher, Gen. Pl. 899. 1839] consisting of *Euryale* and *Victoria*, differ from the Nymphaeoidae primarily in the very large peltate floating leaves, heavily armed

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Fig. 9. *Brasenia schreberi* Gmel., Cabombaceae, sporadically subcosmopolitan in fresh water, representing the Nymphaeales.—a. Flowering caulescent aquatic with floating, alternate, elliptic, centrally peltate leaves and emersed, small, purplish flowers on branches arising from slender rhizomes that root at nodes, $\times 0.3$.—b. Flower with six rather similar sepals and petals, 18–36 stamens, and six distinct carpels, $\times 1.3$.—c. Flower matured into essentially ripe fruits, $\times 1.3$.—Note that, as shown also in b and f, the submersed parts of the plant are covered by a thick layer of mucilaginous jelly.—d. Slenderly panduriform, two-seeded, indehiscent, nutlike fruit, $\times 2$.—e. Globose, operculate, grayish seed, $\times 3$.—f. Young submersed branch with buds, developing leaves, and stems all thickly covered with mucilaginous jelly, $\times 0.5$.—g. Node of rhizome from bottom mud producing branch, leaves, and numerous fibrous roots, $\times 1$.—h. Anasulcate pollen grains seen from different angles, ca. 58μ long.

on the lower surface and on the petiole with prickles; the completely inferior ovary with campanulate-urceolate floral tube; and the aculeate, baccate fruit. The **Barclayoideae** stat. nov. [based upon Barclayeae S. Endlicher, Gen. Pl. 900. 1839] consisting of the single genus *Barclaya*, also has a completely inferior ovary but the leaves are submersed, not floating, and oblong-orbicular to linear-lanceolate with hastate or cordate bases, neither orbicular nor peltate, and they are not armed with prickles. In addition, the elongate floral tube is subtended by an involucre of five sepaloid bracts; the gynoecium is prolonged into a connivent ten-rayed stigmatic cone; and the nonaculeate baccate fruit has numerous softly setose seeds. The chromosome numbers in all three subfamilies are varied. The diversity of the Nymphaeaceae does not seem extraordinary for such an ancient group of relicts.

CERATOPHYLLACEAE S. F. Gray 1821.—The Ceratophyllaceae, with perhaps six to ten species in the single genus *Ceratophyllum*, are probably the most ubiquitous submersed dicotyledons in cold temperate to tropical freshwater habitats. They require relatively warm water for fruit production, but *C. demersum* L. at least seems to reproduce and spread most rapidly by vegetative reproduction. They are beautifully adapted for their aquatic habitat with highly dissected leaves in whorls on slender stems completely lacking in roots, cuticle, stomata, and sclerenchymatous tissues. Specialization through reduction in the reproductive structures is also greatly advanced: flowers imperfect, naked, sessile, and minute with 20–10 four-loculate stamens or a single naked carpel with one suspended orthotropous ovule with only one integument. Pollination is hydrophilous by spherical, inaperturate, smooth, thin-exined pollen grains produced in great numbers. Species of *Ceratophyllum* resemble those of *Cabomba* most closely in their caulescent stems clothed with whorled leaves finely and dichotomously dissected and the single carpel (as in *Cabomba palaeformis* Fassett). Plants of *Cabomba* frequently lack the peltate floating leaves, and then are completely submersed like *Ceratophyllum* except for the flowers. In some other respects *Ceratophyllum* more closely approximates *Nelumbo*, especially in the monocarpellate, indehiscent, one-seeded fruit which has a large embryo with large, fleshy cotyledons, well-developed plumule, poorly developed or no radicle, and no endosperm nor perisperm. Other resemblances are the numerous extrorse stamens spirally arranged on a convex receptacle, prominent connective above the pollen sacs, and similar details of embryogeny.

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