THE BOTANICAL REVIEW

VOL. 46 JULY–SEPTEMBER, 1980 NO. 3

OUTLINE OF THE CLASSIFICATION OF FLOWERING PLANTS (MAGNOLIOPHYTA)[1]

ARMEN L. TAKHTAJAN
Komarov Botanical Institute
Leningrad

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[1] Reprints of this article may be obtained from: CLASSIFICATION 46(3); Publications Office; The New York Botanical Garden; Bronx, NY, 10458, USA. PRICE (Includes postage and handling fee): **US orders**: US $8.75. **Non-US orders**: $9.50 (Payment on US currency drawn on a US bank. Thank-you.).

The Botanical Review 46: 225–359, July–September, 1980. 225

I. INTRODUCTION

Already Charles Darwin explicitly set down the basic principles of evolutionary systematics: "I believe," says Darwin (1859: 420) in his great book on the origin of species,

> that the *arrangement* of the groups within each class, in due subordination and relation to the other groups, must be strictly genealogical in order to be natural; but that the *amount* of difference in the several branches of groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders.

Later, in his book on the descent of man Darwin (1874) wrote that the system

> must be, as far as possible, genealogical in arrangement,—that is the co-descendants of the same form must be kept together in one group, apart from the co-descendants of any other form; but if the parent-forms are related, so will be their descendants, and the two grouped together will form a larger group.

Thus Darwin equated "affinity" with evolutionary relationship, "natural" with "genealogical," systematic groups with genealogical units, and considered the system of hierarchical relationships to be the result of evolution; hence he erected a new paradigm.

In spite of many objections raised at different times against the Darwinian evolutionary approach to classification, it is becoming more and more evident that it is evolutionary or phylogenetic classification which is really synthetic and acquires all the explanatory, heuristic, and predictive value (see Mayr, 1969, 1976) and can therefore serve as the best reference system.

The main objection against phylogenetic systematics is the belief that without a complete fossil record phylogenetic study is impossible. But there is a misunderstanding in this assertion of the opponents of evolutionary classification. When an evolutionary systematist says that a system is phylogenetic, he means that the hierarchical system of taxa is so arranged as to represent both the sequence of repeated branching ("cladogenesis") and the degree and the character of evolutionary modifications of branches ("the degrees of modification" or "the amount of difference," as Darwin says) and their "grades." Some authors, mainly zoologists, have even developed a special method of deducing the branching sequence and designing a "cladogram" (a "branching diagram," Darwin, 1859), based on the study of contemporary organisms (see, for example, Gisin, 1967). As all the history of the post-Darwinian biology witnesses, both zoologists and botanists are quite able to reach certain conclusions on phyletic relationships and on branching sequence of systematic groups based only on the comparative study of living organisms. In the sixth chapter of his "Origin of Man" Darwin (1871, 1874) on the example of genealogy of man and hominoids gave an excellent model of the analysis of phyletic relationships, based on the investigation of living organisms only. "As we have no record of the lines of descent," says Darwin (1874: 229) "the pedigree can be discovered only by observing the degrees of resemblance between beings which are to be classed." Though Darwin knew nothing of *Homo erectus* nor of *Australopithecus* and *Ramapithecus,* the general features of the scenario that he drew on the relationships and evolution have been confirmed by contemporary palaeoanthropological studies.

Any phylogeny based on the study of geochronological sequences of extinct forms, e.g. phylogeny of ammonites, horses, or some branches of lycopodiophytes, equisetophytes, and gymnosperms, differs essentially from phylogeny based on living organisms only. In the first there is a possibility to reveal lineages in a time dimension and to construct a geochronological phyletic dendrogram (phylogram). The plausibility of such a time-scale diagram depends on the completeness of fossil remains and the reliability of their interpretation. But even when there are enough palaeontological data, they can be interpreted and ranked quite differently and lead to the construction of very different phylogenetic systems. As a matter of fact the palaeosystematist comes across many more difficulties in interpretation of phyletic relationships than the neosystematist who studies the phylogeny of contemporary forms.

For many taxa a fossil record is almost or quite lacking. For the flowering plants there are numerous fossils, but mainly leaves, wood and isolated remains of fruits, seeds, pollen grains, and only rarely flowers. Such material, though very important for the geological history of angiosperm flora and vegetation, as well as for a study of evolution of leaves, pollen grains, etc., has almost no significance for the phyletic interpretation of taxa. Therefore phyletic relationships within the flowering plants and their branching diagram can be deduced only from the comparative study of living forms. But in studying living flowering plants we can speak of a degree of their mutual two-dimensional "horizontal" relationships and by means of logical reasoning deduce their "vertical" relationships (the sequence and character of branching in a vertical dimension). It is one of the typical examples of application of hypothetico-deductive method, which was so successively used by Darwin (see Ghiselin, 1969; Mayr, 1976). Though such a model is not geochronological, it nevertheless is "as far as possible" phylogenetic. Therefore, following Darwin we have all reason to speak of genealogy or phylogeny (after E. Haeckel's "Generelle Morphologie der Organismen" was published in 1866 he used both terms). Some authors (e.g. Gisin, 1967) prefer the term cladogeny to the term phylogeny, considering it less committal. But phylogeny is somewhat more than just the sequence of branchings (see especially Mayr, 1969, 1976). The phylogenetic scenario also includes the amount of evolutionary modification following the branching, and general trends of evolution.

We shall give some well-known examples showing the possibility of phyletic analysis, based on the study of living families. The families Berberidaceae and Ranunculaceae are no doubt closely related, as well as the families Amaranthaceae and Chenopodiaceae. In both cases we can speak of the common ancestry of the two families, that is on the basis of the horizontal relationships we reach a conclusion on their phyletic branching pattern (vertical relationships). As regards the Berberidaceae and Ranunculaceae we would not find their nearest ancestor among the living taxa, even notwithstanding the fact that the family Lardizabalaceae is more primitive in many characters than the Berberidaceae and Ranunculaceae. It is even possible to state that in the phyletic dendrogram of the order Ranunculales none of the families could take the initial position, all of them corresponding to the final points of branchings. According to all available data the situation in the order Caryophyllales is quite different. Many botanists, beginning with Pax (1889), consider the family Phytolaccaceae as a probable common ancestor of all the other families of the order Caryophyllales. Of course, they do not mean any particular living representatives of the Phytolaccaceae, but the family in general, moreover the family in its vertical section including the less specialized hypothetical extinct forms. Systematists are no less sure of the origin of the Brassicaceae from the Capparaceae, or the Apiaceae from the Araliaceae, or of the origin of the Lemnaceae from the Araceae. Nevertheless, linear filiation between living taxa on the family level does not occur very often, and is quite rare on the generic level. As regards the level of species it is rather an exception and we know just a few species, which at least with a slight confidence we could derive directly from another living species. On the contrary, the higher the rank of the taxa, the more likely is the origin from related living taxa, though not from their living members, but rather from their ancient and primitive extinct representatives. Thus, it is highly probable that the Laurales originated directly from the Magnoliales, the Papaverales from the Ranunculales, the Theales from the Dilleniales, the Capparales from the Violales, and the Poales from the Restionales, etc. It should be noted that if a systematist speaks of the Papaverales arising from the Ranunculales, he means that if the extinct ancestor of the Papaverales were ever discovered, it would have been included into the order Ranunculales. This explanation neutralizes some of the arguments, which have been put against the phylogeny of living organisms.

Phylogeny of living organisms would confront insuperable obstacles, if the organisms were all at the same level of evolutionary development. But in reality, as already Lamarck and Darwin knew, they are on quite different levels of development, from the most primitive to the highest one. Due to the survival of many archaic and primitive forms, the modern organic world consists of the taxa of very different geological age and of very different evolutionary grade. Some authors, including Rensch (1959: 300) explain such survival of primitive forms by the fact that

> At all times there have been the habitats suited not to higher types, but exclusively to primitive, simple, structural types, and it is because of the existence of such habitats

> that protozoans, lower worms, primitive insects, and similar groups could evade extinction, not being forced to enter into competition with higher animals.

Another explanation is offered by A. N. Sewertzoff (1931), who thinks that the paradoxical fact of the simultaneous existence and biological flourishing of living forms, which belong to such various geological epochs, can be understood only if we accept that evolution can proceed not only by way of "aromorphosis," but by other ways as well, particularly by way of "idioadaptation." Probably idioadaptative evolution, during which the general level of its organization remains unchanged (not being increased), is the most common reason for the survival of ancient primitive forms; but in the plant world at least, the subordinate position of the primitive forms in the ecosystem is also significant. The most primitive living flowering plants are rarely dominants and usually occupy more modest niches, in the undergrowth of the tropical forests, in the mountain mossy forests, etc. Many of them, e.g. *Degeneria* and most genera of the family Winteraceae, are typical phylogenetic relicts.

At the end of the past century and especially during the first quarter of the XX century much was done in the development of the evolutionary macrosystem of the flowering plants. One of the most outstanding and remarkable figures was Hans Hallier (1905, 1908, 1912), who probably has done more than anyone else in this field. He was constructing a synthetic system based on all available data, including data of comparative phytochemistry. Hallier (1905: 152) reached the conviction, that to construct a really natural system

> systematic botany should be founded on a much broader and more universal base than at present, comprehending not only the morphology of reproductive organs, but also all the other branches of botany, such as comparative morphology of the vegetative organs; comparative anatomy, ontogeny and embryology; phytochemistry, physiology and ecology; structure of pollen and seed coat; relations to climate, seasons and to the surrounding organic world; plant geography, palaeophytology, etc.

But in those times botanists knew very little of the inner structure of plants, the development of embryology and comparative anatomy was poor, palynology was just at its birth, there was no electron microscope, and chemosystematics actually did not exist. Later the situation changed markedly. Our knowledge of the plant world was enlarged, and modern botany was enriched by new methods and ideas. First of all, botanical collections were greatly enlarged—herbaria, botanical gardens, wood and pollen collections, and also collections of pickled flowers and other parts of plants. The tropical flora of our planet has been much better studied, resulting in the discovery of some new archaic genera and even families, including the famous *Degeneria,* which is of paramount importance for both phylogenetic systematics and evolutionary morphology.

Studies in the comparative embryology, palynology, comparative anatomy of floral and vegetative organs (especially the conductive system and the stomatal apparatus) gained a wide scope. The last decades were marked with the studies of ultrastructure of different parts of a plant, armed with the electron microscope. There is accumulated the most interesting material on the ultrastructure of pollen grains and of the sieve-element plastids, which is successfully used for evolutionary systematics. Systematists continue using the data of comparative phytochemistry and modern advanced methods of comparative serology. Together with the employment of the secondary products of metabolism (secondary metabolites) such as alkaloids, flavonoids, betalains, glucosides, terpenes, iridoid compounds etc., the study of such high-molecular-weight compounds as nucleic acids and proteins has gained special significance. There have been successfully applied such methods as DNA hybridization, the comparison of amino acid sequences of proteins, immunoelectrophoresis and others, which are still being improved. As a result, the factual material which is at the disposal of a contemporary systematist, cannot be compared with that, accessible only two decades ago. This avalanche-like growth of information complicates the work of a systematist and makes him face some intricate operational problems.

One of the most important questions, causing great difficulties, is the comparison and the evaluation of frequently conflicting information derived from such different sources. In many cases there are discrepancies or even contradictions in the conclusions reached by different authors on the basis of different characters or different groups of characters. Quite instructive in this respect is the 1969 paper of the four authors (Erdtman et al., 1969) on the systematic position of the Australian genus *Emblingia,* forming a separate family Emblingiaceae (the order Sapindales). The authors of this joint work, who had studied different parts and organs of the plant, reached four quite different conclusions on its systematic position. This example, as many others, proves that a satisfactory decision can be reached only after the appropriate taxonomic and phyletic weighting of the characters, which is a competence of a systematist.

The problem of the weighting of characters has recently been the subject of intensive discussion; moreover, the supporters of the so called phenetic method, giving equal importance to all the characters, logically deny weighting. For a systematist, characters have different information content and many of them, if not most, are merely ''noise'' (Mayr, 1969: 208). Besides, the same characters could have different weight in various related taxa. It is also well-known that weighting can be only a posteriori, that is, based on experience. It is determined by the trial and error method, based on the personal experience of a systematist as well as on the experience of his predecessors and colleagues. Weighting is a specific taxonomic problem, which can be solved only by the systematist himself. The higher the rank of a taxon, the more important weighting becomes (Mayr, 1969: 211).

The problem of weighting would not be so difficult if all the characters of an organism evolved harmoniously, at an equal rate, and occupied the same level of the evolutionary development. But as is well-known, the rates of evolution of different organs and parts of an organism are different, often drastically different. "Either trend of evolution may be accelerated or retarded in relation to the other," says Bailey (1956). This phenomenon of unequal rate of evolution of different features within one lineage is known under various names, including "chevauchement des spécialisations" (Dollo, 1893) and "mosaic evolution" (De Beer, 1954). But it is useful to distinguish between the very process of mosaic evolution and the result (the product) of this process—the different evolutionary stages or grades of different characters of the given taxon. Therefore this difference in the grades I named "heterobathmy" (Greek bathmos—step, grade) (see Takhtajan, 1959, 1966).

Because of heterobathmy, an organism may present a mosaic combination of characters of quite different evolutionary levels. Thus, for example, the genera *Trochodendron, Tetracentron* and *Sarcandra,* with their primitive, vesselless wood have rather specialized flowers, whereas in the genus *Magnolia,* which possesses a comparatively much more primitive type of flower, the wood is already rather advanced and frequently even has vessels with simple perforation plates. Heterobathmy may be expressed even within the flower, within the wood, or in their elements, for example, in the vessel members.

The concept of heterobathmy is naturally of the greatest importance for phylogenetic construction. Thus, taking two taxa, differing from each other by a pair of characters A and B, suppose, that in one of them the first of the two characters is primitive and the second one is comparatively advanced, whereas in the other one the situation is the opposite. In such a case of "crossing of specializations" the phyletic interrelationship between two given taxa is conceivable only through a third taxon (real or hypothetical), in which both of these two characters are on the primitive level of evolution. That is why Dollo, already long ago emphasized the importance of the "crossing of specializations" when establishing cladistic relationships of reçent organisms. Later, many other authors came to the same conclusion.

The more strongly heterobathmy is expressed, the more contradictory is the taxonomic information provided by different sets of characters and the more difficult it is to pass from the evolutionary series of separate characters to the phyletic sequences of the organisms themselves. Thus in the overwhelming majority of cases, especially in the more primitive taxa of the flowering plants, where heterobathmy is most clearly expressed (as, for example, in the Magnoliaceae and Winteraceae), we cannot establish phyletic relationships and construct phyletic lineages using only floral characters. It is all the more impossible to construct phyletic lineages on the basis of the characters of vegetative organs only, as, for example, on the basis of wood anatomy. In such cases instead of phyletic lineages we usually obtain only a comparative-morphological series of forms arranged according to evolutionary trends of certain characters. Such series of forms illustrate the gradual evolutionary changes of these or other structures, but they do not express the phyletic interrelationships between organisms. The greater the number of properly chosen high weight characters used for phylogenetic constructions, the closer we shall approach phyletic interrelationships. On the basis of the study of evolution of an adequate number of independent non-correlated characters belonging to a sufficient number of different high weight character complexes, we can establish the basic trends of the evolution of a taxon, discover those of its members which are the nearest to the phylogenetically initial forms and which are derivative, and deduce the cladistic relationships among orders and families of the flowering plants. But in doing this we must always reckon with the phenomenon of heterobathmy.

The more heterobathmic the taxon, the more complete and allround must be its study. Only the application of various methods can reveal those "critical characters" and "critical tendencies" (Wernham, 1913: 136), which are reliable phyletic markers. Correct weighting of the characters and their evolutionary tendencies gains special significance in such cases. It depends on the experience of a systematist and his erudition.

In many different lines of the evolution of the flowering plants there takes place a simplification of various structures, which is accompanied by the loss of characters. In regressive development of the organ the entire structure could disappear, which is an irretrievable loss of taxonomic and phyletic information. Simplification and loss of information is typical for many aquatic plants and especially for parasites. A considerable loss of information is also characteristic for specialized anemophilous flowers. Therefore for a long time some families with the simplified anemophilous unisexual and apetalous flowers had been united into a completely unnatural grade group: "Monochlamydeae." At present this artifical group is disbanded and its members find their more or less sound place in a phylogenetic system. Reduction of flowers for a long time had hampered the establishment of the systematic position of such families as Chloranthaceae, Callitrichaceae, and Hippuridaceae, and only now it became more or less evident that the Chloranthaceae belong to the Laurales, whereas the Callitrichaceae stand near the Lamiaceae and Verbenaceae, and Hippuridaceae s.str. are most likely related to the Scrophulariaceae and Plantaginaceae.

During the last three decades, by the joint efforts of a limited number of botanists of various countries, great progress in constructing the macrosystem of flowering plants has been achieved. As a result modern systems have much more in common than the systems constructed for example in the first quarter of the XX century. Such questions as monophyly of the flowering plants, relationships of the classes of monocotyledons and dicotyledons, the primitiveness of the Magnoliales and related orders, the secondary nature of the anemophilous families with reduced unisexual flowers and many other more particular questions, do not cause any major disagreement any longer among the authors of modern systems. A famous Polish science-fiction writer S. Lem said in his "Solaris": "Every science always has a corresponding pseudoscience—its savage refraction in the intellects of a certain type." Fortunately, there does not exist a "paraphylogeny," though we know many precarious and groundless ideas, contradicting elementary logic of scientific research. But they are insignificant and cannot influence a general impression of a considerable progress of phylogenetic studies, and quite substantial achievements in this field. And the matter is not just in the continually increasing amount of factual material. The facts themselves are just a raw material for the science, and the improvement of understanding is not less important than the enrichment of the data bank. But phylogenetic systematics has been enriched not only with the factual material, but with the theory, the conceptual apparatus. Nevertheless, in very many cases we are limited by lack of data and there is still quite a number of the taxa of obscure affinities, even among the families and the orders. In spite of the great success of systematic and evolutionary botany, only comparatively few groups of the flowering plants have been studied thoroughly enough to draw reliable phylogenetic conclusions from the available data. Future studies will of course bring many important changes in modern systems of classification of the flowering plants, but there is every reason to believe that the basic principles and the fundamental results will not undergo any drastic changes.

The system of classification outlined here has a rather long history. In 1942 in my paper on the structural types of gynoecium and placentation I published a very preliminary phyletic diagram of the angiosperm orders (mentioned by Gundersen, 1950: 54). The actual system of classification was published only twelve years later as an appendix to my semi-popular book on the origin of angiosperms (1954, English translation published in

1958). I was especially inspired by Hallier's attempts to create a synthetic evolutionary classification of flowering plants based on Darwinian philosophy.

The Hallier system, which has been better known in Europe than in the New World, was more synthetic and displayed much deeper insight into morphological evolution and phylogeny of the flowering plants than any other contemporary classification, including the Bessey system. Some of Hallier's works, such as "Über *Juliania*" (1908) and "L'origine et le systême phyletique des Angiosperms" (1912) have not lost interest till now and still deserve to be consulted. "It is a classification," says Lawrence (1951: 133), "that must be consulted for the ideas expressed, and frequently one finds situations indicative of possible or probable relationship that others overlooked."

Another stimulating work was "A review of the system of plants" (in Russian with French summary) by Professor C. Gobi of Petrograd University (1916). In some respects the Gobi system, which is still almost unknown in the West, was a considerable advance and had some noticeable advantages over the contemporary systems of classification. For example, Gobi derives the monocotyledons, as well as the Ranales, Aristolochiales and Hamamelidales directly from the Polycarpicae s.str. (which he equates with the Magnoliales), and derives the Proteales from Rosiflorae.

As regards the Bessey system, I found it more interesting for its basic philosophy than for the arrangements of the orders and families. The Besseyan system, even in its final form (1915), was essentially a revised arrangement of the Bentham and Hooker system (1862–1883), with a more drastic rearrangement of the monocotyledons and the distribution of the "Monochlamydeae" among the other orders.

Of course I could not pass over the Hutchinson system, which was based on many of the principles adopted earlier by Hallier, Bessey and Gobi. But Hutchinson's system rests mainly upon gross morphological data and has some important weaknesses, among which the basic one is his division of the dicotyledons into two main groups, Lignosae and Herbaceae, which leads to the wide separation of some obviously closely related families. I could not accept this subdivision, as well as the derivation of the monocotyledons from the ranunculaceous ancestors, Salicales from the rosalean stock, Cactales from the Passiflorales, Piperales from the Berberidales, Gentianales and Lythrales from the Caryophyllales, Primulales from the Gentianales, Liliales from the Butomales, Palmales from the "Agavales," Graminales from the Juncales, etc. But in the Hutchinson system there are also some positive elements, the most important of which is the derivation of the Myricales, Leitneriales, Fagales, Juglandales, Casuarinales, Balanopales, and Urticales from the

Hamamelidales (a point of view expressed in 1903a and 1905 by Hallier, though later he changed his opinion).

In my system published in 1954 I considered the order Magnoliales s.l. as the most primitive and archaic group which gave rise to all the other major branches of the angiosperms. As regards the monocotyledons I concluded that they could have originated only from a primitive apocarpous herbaceous dicotyledonous ancestor which was vesselless and had monocolpate pollen grains, and denied any possibility of their taking rise from the Ranunculaceae, Berberidaceae, Lardizabalaceae and related families. The only vesselless herbaceous dicotyledons with monocolpate pollen and apocarpous gynoecium are Nymphaeales s.str. (without Nelumbonaceae). However the order Nymphaeales is too specialized to be accepted as the possible ancestor of the monocotyledons. But there is every reason to assume their common ancestry, and in my phyletic diagram the Nymphaeales and the monocotyledons are shown as two sister branches diverging from a hypothetical common ancestor evolved from the Magnoliales. As regard to "Amentiferae," following Hallier's earlier works and the Hutchinson system, as well as new comparative-morphological data, I considered the order Hamamelidales s.l. (including the Cercidiphyllaceae, Eupteleaceae, Daphniphyllaceae, Buxaceae and Simmondsiaceae) as an intermediate group between the Magnoliales s.l. and the orders Casuarinales, Fagales, Betulales, Balanopales, Myricales, Rhoipteleales, Juglandales and Leitneriales. Following Hallier and Gobi I excluded Salicales from the "Amentiferae" and derived them from the Cistales (Violales), particularly from the Flacourtiaceae-Idesiinae. From the Cistales I derived also Capparales, Cucurbitales and Tamaricales. The orders Ericales, Primulales and Diospyrales (Ebenales) I derived from the Theales, the orders Papaverales, Sarraceniales and Caryophyllales from the Ranales (Ranunculales), and Polygonales and Plumbaginales from the Caryophyllales. The Graminales (Poales) I derived from the Commelinales s.l., while the Cyperales derived from the Juncales. The orders are grouped into superorders, for which the traditional names Polycarpicae, Centrospermae, Rosiflorae, Amentiferae, Myrtiflorae, Disciflorae, Umbelliflorae, Cistiflorae, Columniferae, Heteromerae, Tubiflorae, Campanulatae, Helobiae, Spadiciflorae, Liliiflorae, Enantioblastae and Glumiflorae are used.

The system published in 1954 has later gone through a series of modifications and elaborations, but the nucleus of the system and the basic features of the branching pattern of phyletic diagram remained essentially the same.

In a new, amplified version of my general system of the angiosperm classification published in 1959 I introduced some important modifications, incuding the subdivision of the Magnoliales s.l. into Magnoliales s.str., Laurales, Illiciales and Trochodendrales, the subdivision of the Nymphaeales s.l. into Nymphaeales s.str. and Nelumbonales, and the subdivision of the Theales s.l. into Dilleniales and Theales s.str., the subdivision of the Rosales s.l., a considerable rearrangement of the monocotyledonous orders and families, etc.

In a new elaborated version of the system, published in 1966, I gave a more detailed rationale for the delimitation and arrangement of families and orders than was done in 1959. The main innovation was the subdivision of both classes of the magnoliophytes into a series of subclasses—Magnoliidae, Hamamelididae, Caryophyllidae, Dilleniidae, etc. The subclasses were first proposed in 1964 and "validated" in 1966. According to Cronquist (1968: 128), this grouping of the flowering plants into subclasses "reflects some ideas of relationship which have been developed over the years by a number of phylogenists, and in my opinion it is a major advance in the conceptual scheme." The grouping into subclasses proved to be useful from a didactic point of view, and it has been introduced into some American and German textbooks, including the last two revised editions of Strasburger's classical "Lehrbuch der Botanik" (1971, 1978). I have retained the rank of superorder as a supplementary rank intercalated between subclass and order, which in my opinion is useful both from the phylogenetic and didactic points of view. But in 1964 I proposed to change the traditional -florae ending, which had been used by various authors both for orders and superorders, into an ending -anae and derived all the superordinal names (as well as all the other names of taxa above the rank of genus) from generic names. The grouping of closely related orders into superorders with -anae endings has been accepted by Ehrendorfer (1971, 1978) in Strasburger's Lehrbuch and by Dahlgren (1975, 1977) in the earler version of his system. Dahlgren added a number of new superorders, some of which (Rafflesianae, Nymphaeanae, Plumbaginanae, Gentiananae, Zingiberanae and Aranae) I consider advantageous and quite acceptable. Recently (1980) he has returned to the traditional -florae ending, but as he himself points out, a disadvantage with the ending -florae is that it cannot be used for superorders of lower divisions.

After 1966 the system of classification has been gradually undergoing some modifications (e.g. Takhtajan, 1969, 1973). Recently I have prepared a new revision of the system based on the accumulated data and my own observations, as well as on discussions and consultations with my colleagues. I have introduced some modifications in the arrangement of the magnoliopsids, but the liliopsids have undergone more significant changes, especially in the delimitation and arrangement of the families of the superorder Lilianae. All these changes are summarized in this outline of the general system of classification.

Since evolutionary morphology in its broader sense (including palynology, embryology, etc.) is fundamental for the general system of phylogenetic classification, I find it useful to preface the outline with a concise summary of the subject.

II. MAIN TRENDS OF EVOLUTION IN FLOWERING PLANTS

THE CRITERIA USED IN EVALUATING THE RELATIVE DEGREE OF THEIR ADVANCEMENT.

Growth habit.—The most primitive angiosperms are woody plants, and the herbaceous growth habit is always secondary (Jeffrey, 1899, 1917; Hallier, 1901, 1905, 1912; Sinnott and Bailey, 1914, and many subsequent authors including Eames. 1961, and Stebbins, 1974). The evolution of flowering plants most probably begins with small, relatively weakly branched woody forms. According to Hallier (1912) the early angiosperms were small trees with a weak crown of relatively few thick branches, like the fossil bennettitaceous genus *Wielandiella* or some living cycads. Stebbins (1974), on the other hand, visualizes the earliest angiosperms as low-growing shrubby plants, having a continuous ring of secondary vascular tissue, and no single well-developed trunk. Amongst the living primitive flowering plants there are both trees (the majority) and shrubs (*Eupomatia laurina,* for example, is a shrubby plant with several trunks). At the present state of our knowledge it is difficult to say whether the earliest magnoliophytes were small trees or shrubs. The only thing we can say is that they were small woody plants, which occupied only a modest and insignificant position in the Early Cretaceous vegetation. Big stately trees of tropical rain forest are derived, having originated from primitive, small, woody angiosperms. Trees with numerous slender branches evolved from sparingly branched trees. Deciduous woody plants evolved from evergreen ones.

The evolutionary trend from woody plants to herbs is not irreversible. In some phyletically distant taxa of flowering plants the reverse process of the transformation of herbaceous plants into arborescent plants took place, for example, in Ranunculaceae, Berberidaceae, Papaveraceae, Phytolaccaceae, Nyctaginaceae, Chenopodiaceae, Polygonaceae, Cucurbitaceae, Campanulaceae-Lobelioideae, Asteraceae, and many liliopsids (including Agavaceae, Dracaenaceae, Philesiaceae, Smilacaceae, Poaceae-Bambusoideae, Arecaceae, Pandanaceae). But usually these secondary arborescent plants, especially arborescent liliopsids, strikingly differ from the primary woody plants. As Stebbins (1974: 150) aptly remarks, "Palms and bamboos are as different from primitive preangiospermous shrubs and trees as whales and seals are from fishes."

Leaves and leaf arrangement.—The leaves of primitive living flowering plants are mostly simple, entire, pinnately nerved, coriaceous and glabrous. This indicates that the simple entire leaf with pinnate venation is primitive (Parkin, 1953; Takhtajan, 1959, 1964; Eames, 1961; Cronquist, 1968; Hickey, 1971; Stebbins, 1974), and it is very likely that the leaves of the earliest angiosperms were more or less similar. But this is not certain—they may have been of a still more primitive type. In Stebbins's (1974: 331) opinion, "The leaves of the original angiosperms are believed to have been elliptical, obovate, or spatulate in outline, and tapered at the base to an indistinct petiole."

Simple, pinnately-nerved leaves are ancestral to pinnately-lobed, pinnatifid, and pinnatisect leaves with pinnate venation. Both pinnatisect and palmatisect leaves gave rise to compound leaves—pinnately compound in one case and palmately compound in the other. These trends in leaf evolution are reversible. Such reversal is well documented in some instances, such as the genera *Berberis* and *Citrus*.

The most primitive type of venation is pinnate venation with brochidodromous secondaries, especially leaves which are characterized by the general irregularity of their venation, expressed in such features as the highly irregular size and shape of areas between secondary veins, the irregularly ramifying courses and poor differentiation of the tertiary and higher vein orders (Hickey, 1971; Hickey and Doyle, 1972; Doyle and Hickey, 1976). Among the living flowering plants this primitive type occurs in some members of Magnoliales, especially in Winteraceae, Himantandraceae and Canellaceae. All other types of pinnate venation are derived.

Palmate (actinodromous) venation evolved from pinnate venation, and in its turn gave rise to various types of campylodromous and acrodromous venation. The most advanced type is parallel (parallelodromous), which is characteristic for the majority of liliopsids and for some magnoliopsids. But parallel venation is not a climax type, and in some taxa of liliopsids, such as the Smilacaceae, Dioscoreaceae and Stemonaceae, it gave rise to reticulate venation with free vein-endings.

Among the various types of leaf vernation (ptyxis) the most primitive is conduplicate vernation with lamina folded once adaxially along midrib (Takhtajan, 1948), which is characteristic for some primitive taxa including Magnoliales.

In the evolution of leaf arrangement (phyllotaxy), the most primitive is alternate arrangement. Both the opposite and verticillate types are derived from the alternate arrangement. But as Cronquist (1968) points out, the origin of opposite leaves from alternate leaves is not immutable and is subject to reversal. In his opinion, among the family Asteraceae it is perfectly clear that opposite leaves are primitive and alternate leaves are advanced. As regards verticillate leaves, they are probably less reversible.

Stomatal apparatus.—At the present stage of our knowledge it is possible to make only some very broad generalizations regarding the trends of stomatal evolution. The general trend is probably from the mesogenous to perigenous ontogenetic type and from stomata with subsidiary cells[2] to stomata lacking subsidiary cells. In dicotyledons evolution most probably started with mesogenous, paracytic stomata (Takhtajan, 1966, 1969; Baranova, 1972), which correspond to the mesoparacytic type of Pant (1965) or to the para-mesogenous and para-mesoperigenous types of Fryns-Claessens and Van Cotthem (1973). In Winteraceae, Degeneriaceae, Eupomatiaceae, Himantandraceae and in the majority of Magnoliaceae stomata are mesoparacytic (para-mesogenous or para-mesoperigenous). All other types, including the perigenous anomocytic type, are derived.

This general trend from a para-mesogenous and para-mesoperigenous stomatal apparatus to a perigenous type is reversible, and in monocotyledons the direction is opposite. The monocotyledons, both primitive and advanced, are characterized by a perigenous stomatal apparatus (Pant, 1965; Paliwal, 1969). Until now there is found only one exception in Orchidaceae-Neottioideae, which have mesoperigenous stomata (N. H. Williams, 1975, 1979). The other two exceptions (*Dioscorea* and *Strelitzia*), mentioned by Fryns-Claessens and Van Cotthem (1973), are not substantiated (Blunden et al., 1971, and Tomlinson in C. Williams, 1975). Tomlinson (1974) concluded that the liliaceous type of stomata (without subsidiary cells) is probably the unspecialized ancestral condition for monocotyledons, and recently N. H. Williams (1979) has convincingly shown, that in Orchidaceae the presence of subsidiary cells is an advanced condition. Thus in all likelihood in monocotyledons the most primitive type of stomatal apparatus is the perigenous, anomocytic type (aperigenous in terminology of Paliwal, 1969, and Fryns-Claessens and Van Cotthem, 1973). It is the more so, as in the Nymphaeales, the closest dicotyledonous relatives of monocotyledons, the stomatal apparatus is also aperigenous. Therefore in liliopsids paracytic stomata, as well as all other types with subsidiary cells, are probably of secondary origin.

Nodal structure.—It is generally agreed that in gymnosperms the unilacunar node structure is more primitive, and the multilacunar nodes of cycads and *Gnetum* are derived. But the evolutionary trend in nodal

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[2] According to Stevens and Martin (1978), subsidiary cells can be defined morphologically as those cells associated with the guard cells and which are morphologically distinct from other epidermal cells and which have been derived from either stomatal or subsidiary meristemoids.

structure of angiosperms is much more debatable. In addition to unilacunar and multilacunar nodal types in flowering plants there is a third type, the trilacunar, unknown in gymnosperms. The presence of three different types of nodal structures complicates the situation and makes more difficult the ascertainment of the evolutionary trends in angiosperms.

At different times and by different authors each of these three types has been accepted as the most primitive and basic nodal structure in angiosperms. The study of all the available data accumulated in literature brings me to the conclusion, that Sinnott's (1914) theory of the primitiveness of the trilacunar type, based on the extensive reconnaissance of 164 families of dicotyledons, is nearest to the truth. It also much better corresponds to the widely accepted theory of the primitiveness of the magnolialian stock. The presence of trilacunar nodes in such an archaic family as the Winteraceae, as well as in Himantandraceae, Annonaceae, Canellaceae, Myristicaceae, Tetracentraceae, Cercidiphyllaceae, and in the orders Ranunculales, Hamamelidales, Caryophyllales, Dilleniales and Violales is very suggestive. But some members of the Magnoliales are penta- or multilacunar. Such an extremely primitive genus as *Degeneria* has pentalacunar nodes (Swamy, 1949; Benzing, 1967) and in the genus *Eupomatia,* which in its vegetative anatomy is one of the most primitive among the vessel-bearing angiosperms, the nodes are multilacunar (Eames, 1961; Benzing, 1967). The nodal structure of the Magnoliaceae is usually also multilacunar (6–17 gaps), except in the relatively primitive genus *Michelia,* which is tri-pentalacunar (see Ozenda, 1949). This distribution of tri-, penta- and multilacunar types most probably indicates that tri- and pentalacunar nodes are more primitive and multilacunar nodes are derived. But it is much more difficult to decide which of these two types, trilacunar and pentalacunar, is the basic one. In my opinion it is quite possible that the earliest angiosperms were tri-pentalacunar, like the living genus *Michelia.*

The unilacunar nodal structure, which Sinnott (1914) considered as having arisen by reduction from the trilacunar, is according to Marsden and Bailey (1955) the most primitive and basic nodal type in all seed plants, including angiosperms. They considered the primitive node to be the unilacunar type with two discrete leaf traces. This new concept of nodal evolution was based on the fact that the unilacunar node with two distinct traces is characteristic not only for some ferns and gymnosperms (as was well-known earlier), but also occurs in certain dicots (Laurales, certain Verbenaceae, Lamiaceae and Solanaceae). Also it is repeatedly found in the cotyledonary node of various flowering plants. Bailey (1956) concluded that we could no longer think of the unilacunar node of dicotyledons as having arisen by reduction from the trilacunar; in his opinion, "during early stages of the evolution and diversification of the dicotyledons, or of their ancestors, certain of the plants developed trilacunar nodes, whereas others retained the primitive unilacunar structure." Canright (1955), Eames (1961), Fahn (1974) and several other anatomists have even more strongly favored the primitiveness of the unilacunar node with two traces, which they consider the basic type in the evolution of angiosperm nodal structure. But there are also objections. Thus Benzing (1967) has pointed out that the occurrence of plants with two-trace unilacunar nodal structure proposed as primitive by Marsden and Bailey (1955) is limited to a few families characterized by derived decussate phyllotaxy and many specialized floral characters. He also correctly points out that the anatomy of cotyledonary nodes does not necessarily reflect ancestral conditions in the mature stem. "The unique seedling morphology and decussate insertion of the cotyledons make this unlikely," says Benzing. He comes to the conclusion that either the unilacunar node with one trace or the trilacunar node with three traces is more likely to be primitive in the angiosperms than the unilacunar node with two traces. Bierhorst (1971) is also very skeptical about the theory of primitiveness of two-trace unilacunar type and says that "the issue is far from settled."

In my opinion neither of the two types of unilacunar nodes is primitive and basic in flowering plants. The unilacunar nodal structure is characteristic mostly for the advanced taxa. In the Magnolianae the unilacunar node is present only in orders Laurales and Illiciales, which are considerably more advanced than the Magnoliales. The only unilacunar members of the whole subclass Hamamelididae are *Euptelea, Barbeya* and *Casuarina.* On the other hand it is significant that the unilacunar node is characteristic for such advanced orders as Ericales, Ebenales, Primulales, Myrtales, Polygalales, Gentianales, Polemoniales, Scrophulariales, Lamiales and Campanulales. Among the gamopetalous dicotyledons only Plantaginaceae and Asteraceae are exceptions. In some orders, such as Celastrales and Santalales, it is possible to follow the transition from the trilacunar to the unilacunar type, which occurs along with general specialization of the vegetative organs. It is particularly well shown in the family Icacinaceae (see Bailey and Howard, 1941). One may see the same evolutionary trend in the series Dilleniales-Theales or Violales-Tamaricales. All these facts lead to the conclusion that the unilacunar type of nodal structure is secondary in flowering plants, having originated from the basic tri-pentalacunar type.

Wood anatomy.—One of the most reliable and well documented evolutionary trends thus far revealed among the flowering plants is the derivation of vessel members (elements) from tracheids with scalariform bordered pits. And what is more, "this particular phylogenetic sequence clearly is a unidirectional and irreversible one, and cannot be read in reverse" (Bailey, 1956: 271). Vessels evolved entirely independently in diverse lines of evolution of angiosperms. They originated independently not only in dicotyledons and monocotyledons, but even independently in some major taxa of these two classes. But in all the cases the evolution of vessels was unidirectional and irreversible from vessel members with scalariform perforations to vessel members with simple perforations. With this main trend in the evolution of vessels are more or less correlated (but not always synchronized) other trends in specialization of vessel members (see any modern textbook of plant anatomy).

Extensive comparative anatomical studies have revealed trends in evolution of xylem fibers (from tracheids, through fiber-tracheids, to libriform fibers), in radial and axial parenchyma, sieve tubes, plastids in sieve elements, and other structures. All these trends are important as criteria which one can use in evaluating the relative degree of specialization of the conducting system.

Inflorescences.—Among living flowering plants solitary flowers, both terminal and axillary, probably represent the surviving members of reduced inflorescences (Eames, 1961; Stebbins, 1974). In the Winteraceae, for example, the solitary terminal flower of *Zygogynum* represents "the end of a reduction series" (Bailey and Nast, 1945a).

The various forms of inflorescence are divided into two major categories—cymose, determinate or "closed" and racemose, indeterminate or "open." The boundary between these two basic groups is not sharp and there are many intermediate and combined forms. Nevertheless for phylogenetic purposes this traditional classification is much more suitable than Troll's (1928) typological classification which is based on Aristotelian logic and the tenets of methodological essentialism rooted in Plato's idealistic philosophy.

Of two basic groups of inflorescences, the cymose inflorescence is more primitive and the racemose inflorescence is derived (Parkin, 1914). The most primitive form of cymose inflorescence is probably a simple, few-flowered terminal leafy cyme (Takhtajan, 1948, 1959, 1964; Stebbins, 1974). Such a leafy cyme one can see for example in *Paeonia delavayi* or in some primitive ranunculaceous genera. In various evolutionary lines the primitive leafy cyme has given rise to more specialized forms.

By means of repeated branching the simple cyme gives rise to compound cymes—pleiochasium, compound dichasium, and cymose panicle. In some evolutionary lines the compound cymes undergo drastic transformations and give rise to very specialized types such as the capitate inflorescences of some species of *Cornus,* of Dipsacaceae and of certain Valerianaceae and Rubiaceae and especially the inflorescences of Urticaceae, Moraceae, Betulaceae, Fagaceae and Leitneriaceae.

In some genera and even families, for example in Caryophyllaceae, the compound monochasium results by the suppression of one of the two branches of each ramification of the compound cyme.

From the compound cyme evolved the raceme, which is the most primitive form of the racemose inflorescence. The transitions from pleiochasium to raceme may be observed in the genera *Aconitum* and *Thalictrum* or in the Papaveraceae-Fumarioideae and in the Campanulaceae (Parkin, 1914; Takhtajan, 1948). The simple raceme gives rise to the compound raceme, the spike, and the umbel. The umbel in its turn gives rise to a still more specialized form of racemose inflorescence—the capitulum s.str. or calathidium. It characterizes certain Apiaceae, as *Eryngium* and *Sanicula*. The ancestry of the capitulum in the Calyceraceae and Asteraceae is more debatable, and no opinion is offered here.

GENERAL FLORAL STRUCTURE

The most primitive and archaic flowers, like those of *Degeneria* and Winteraceae, are of moderate size with a moderately elongated receptacle. Stebbins (1974) concluded that the original angiosperms had flowers of moderate size, which is in harmony with the hypothesis that they were small woody plants inhabiting pioneer habitats that were exposed to seasonal drought. "Under these ecological conditions, rapid development of flowers and seeds would have had an adaptive advantage and would be most easily acquired by reduction in size of the reproductive shoots" (Stebbins, 1974: 219). It is also in harmony with my hypothesis of the neotenous origin of flowering plants, according to which they arose under environmental stress, probably as a result of adaptation to moderate seasonal drought on rocky, mountain slopes in an area with monsoon climate (Takhtajan, 1976)[3]. Under such conditions flowers of moderate (or even less than moderate) size would be better adapted than the large flowers postulated by Hallier (1912) and Parkin (1914).

Large flowers, like those of some Magnoliaceae and Nymphaeaceae, and especially very large flowers (*Rafflesia arnoldii*) are of secondary origin and evolved in response to selection pressure for different methods of pollination. Small and especially very small flowers are also derived and their origin is usually correlated either with the specialization of inflorescences or with the reduction of the whole plant.

The most primitive flowers have a more or less indefinite and variable number (but not necessarily a large number) of separate parts arranged spirally upon a moderately elongated floral axis. The progressive shortening of the floral axis brings floral parts closer together and gives rise

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[3] On the role of seasonal drought in monsoon climate see Takhtajan, 1957, 1969; Axelrod, 1970; Stebbins, 1974.

to the gradual transition from spiral to cyclic arrangement and to the fixation of the number of parts. At its earlier evolutionary stages this progressive shortening is reversible, and in some relatively primitive taxa, such as Magnoliaceae (especially *Magnolia pterocarpa*), *Schisandra* or *Myosurus*, the elongated receptacle is of secondary origin. Another result of shortening of the floral axis is a gradual fusion of floral parts—their connation and adnation.

Partial or overall reduction of the flower occurs in many evolutionary lines.

Although in the original flowering plants there probably was no corolla yet (Hallier, 1912) and the perianth consisted entirely of modified bracts (sepals), in modern angiosperms the presence of petals is a primitive condition and their absence is derived. Petals are a later evolutionary acquisition. It is almost generally agreed that they are of dual origin—in some groups, such as Magnoliales, Illiciales, and Paeoniales, they are of bract origin, whereas in many other groups, including Nymphaeales, Ranunculales, Papaverales, Caryophyllales and Alismatales, they are modified stamens. To designate these two types of petals Kozo-Poljanski (1922) aptly coined the terms "bracteopetals" and "andropetals."

Among the living angiosperms there are probably no primary apetalous plants. Flowers with vestigial petals, with petals transformed into glands, or devoid of petals are secondary, derived from flowers with normally developed and functioning petals.

Androecium.—Comparative studies of the stamens of flowering plants leads to the conclusion that within living angiosperms the most primitive type of stamen is a broad, laminar, three-veined organ not differentiated into filament and connective, and produced beyond the microsporangia; it develops four slender elongated microsporangia embedded in its abaxial or adaxial surface between the lateral veins and the midvein (see especially Bailey and Smith, 1942; Ozenda, 1949, 1952; Canright, 1952; Moseley, 1958; Eames, 1961; Foster and Gifford, 1974). Canright (1952) regards the stamen of *Degeneria*, as "the closest of all *known* types to a primitive angiosperm stamen." It is important to note, however, that in *Degeneria, Galbulimima, Lactoris,* Annonaceae, *Belliolum* (Winteraceae) and *Liriodendron* the microsporangia occupy the abaxial surface (and therefore the stamens are extrorse), whereas in the Magnoliaceae (except *Liriodendron*), Austrobaileyaceae and Nymphaeaceae they are situated on the adaxial surface (the stamens being introrse). In my opinion both the abaxial and adaxial position have been derived from a common ancestral type, which could only have been the marginal. Thus we must come to the logically inescapable conclusion that in the ancestors of living Magnoliales the microsporangia were marginally situated on the microsporophylls (Takhtajan, 1948, 1959, 1964, 1969). Were the original microsporophylls of angiosperms flattened organs, entire or pinnate, or were they branched three-dimensional structures? In my opinion the stamens of the earliest angiosperms or of their immediate ancestor were leaflike pinnate microsporophylls with marginally situated microsporangia, which in their turn originated from the branched and three-dimensional structures of the more remote ancestors.

Many authors, among them Ozenda (1952), Canright (1952), Moseley (1958), Eames (1961) and Cronquist (1968) consider that the immersion of the microsporangia in the tissue of the stamen is a primitive feature. In *Degeneria* and *Galbulimima* the microsporangia are deeply sunk in the tissue of the stamen, as they are in the Magnoliaceae (except *Liriodendron*) and *Victoria amazonica*. This immersion of the microsporangia is probably a result of the neotenous origins of stamens and the flower as a whole (Takhtajan, 1976).

All the accumulated evidence indicates that the stamen is not a surviving solitary branch of the ancestral compound organ, but an individual organ which is homologous to an entire microsporophyll. As regards the stamen fascicles and the branched system like that of *Ricinus*, these are of secondary origin and are not homologous to the ancestral compound microsporangiate organ (see Eames, 1961). I do not agree with Stebbins (1974), according to whom individual stamens could be interpreted as being homologous to stamen bundles in other families, which have, during evolution, been reduced to single stamens.

Pollen grains.—Comparative study of the pollen morphology (systematic palynology) leads to the conclusion that in terms of taxonomic-phylogenetic usefulness, pollen aperture type and the internal structure of exine are the most important characters. Therefore both the morphology of apertures and the internal structure of sporoderm have recently received much attention from palynologists, palaeobotanists and systematists.

As long ago as 1912 Hallier concluded that the most primitive type of pollen grain is characterized "par une seul pore germinal," by which he apparently meant aperture and not a pore in the strict sense of the word. Later it was shown that the most primitive angiosperm pollen grain is a type with one distal germinal furrow (distal colpus or "sulcus") in the sporoderm (Wodehouse, 1936; Bailey and Nast, 1943; Takhtajan, 1948, 1959, 1964; Eames, 1961; Cronquist, 1968; Doyle, 1969; Muller, 1970; Sporne, 1972; Agababian, 1973; Stebbins, 1974; Walker, 1974b, 1976a, 1976b; Walker and Doyle, 1975; Straka, 1975; Meyer, 1977). Such monocolpate ("unisulcate") pollen grains still have a continuous aperture membrane devoid of special openings (ora) in the exine for the emergence of the pollen tube.

The distal furrow has given rise to a few other types of distal apertures.

In some taxa, there are two parallel, morphologically distal furrows instead of one (dicolpate or "bisulcate" pollen grains) or even three parallel furrows. In some other taxa, including both dicotyledons and monocotyledons, the distal colpus has been transformed into a peculiar three-armed (very rarely four-armed) distal aperture (trichotomocolpate pollen grains). In some primitive angiosperms, including *Eupomatia* and Nymphaeaceae, the distal aperture has changed its polar position and forms one more or less continuous subequatorial or equatorial ring-like or band-like, encircling aperture, or several apertures parallel to each other (zonacolpate or "zonasulculate" pollen grains). Intermediate stages in the evolution of the zonacolpate type may be observed in the pollen of *Nymphaea* (Walker, 1974b). More frequently, as a result of complete reduction of the aperture, monocolpate grains give rise to inaperturate ones. In the inaperturate type the whole exine, which is thin, is a kind of global aperture. But the main trend in distal aperture evolution is the transformation of the distal colpus into a distal pore, which is characteristic for many monocotyledons. In monocotyledons monocolpate pollen grains have also given rise to two-polyporate pollen grains, like those in the Alismatales. In some dicotyledons (Chloranthaceae) monocolpate pollen grains give rise to polycolpate pollen, but the main trend of evolution of sporoderm apertures in dicotyledons is from monocolpate to tricolpate and from tricolpate to tricolporate. According to Straka (1963, 1975) and Wilson (1964) the trichotomocolpate aperture, characteristic of some of the pollen of members of the Winteraceae and Canellaceae, represents an intermediate stage between the monocolpate and tricolpate condition. But nobody has seen any intermediate stage between the trichotomocolpate and tricolpate types, and as Cronquist (1968) has pointed out, several families of monocotyledons including the palms, have trichotomous furrows in the pollen of some species, but here this has not led to the typical tricolpate grains so commonly seen in the dicotyledons.

According to Walker (1974b; Walker and Doyle, 1975), the tricolpate aperture, as well as distally dicolpate ("disulculate"), polycolpate and forate apertures are derived de novo from inaperturate pollen grains. I agree that all these apertures types originated de novo, but I can not accept their derivation from the inaperturate type. Typical inaperturate pollen grains have a specialized sporoderm with a more or less reduced, thin exine and a usually thick intine. Functions of the aperture are transferred to the whole of the exine which is transformed into a global aperture. The inaperturate sporoderm is a climax type which hardly can give rise to any type of aperturate pollen grain.

In my opinion the tricolpate condition arose not as a result of the gradual transformation of the monocolpate aperture, but rather as a result of evolutionary deviation of the earlier stages of sporoderm development from their previous course (Takhtajan, 1948, 1959, 1964). It originated de novo from monocolpate pollen grains. The sporoderm of monocolpate pollen is less specialized than that of the inaperturate type and therefore is more liable to radical changes in the number and position of apertures. In some cases (in the Canellaceae, for example) polycolpate pollen grains have also evolved the same way.

Tricolpate pollen grains have given rise independently in a number of major taxa of flowering plants to polycolpate pollen, as well as to polyrugate, triporate and polyporate (including pantoporate) types.

The next grade of tricolpate and tricolpate-derived pollen is the origin of composite apertures—tricolporate, polycolporate, tripororate, polypororate (including panpororate). The highest stage of the evolution of the pollen grains in dicotyledons is tri-multiaperturate pollen with composite apertures.

From the taxonomic-phylogenetic point of view, the study of the evolutionary trends and grades of the internal structure of exine, and of the sporoderm in general, is also a very important source of information. Recent comparative studies of the internal structure of the exine led to the conclusion that the most primitive pollen grains, including those of *Degeneria* and *Eupomatia,* are characterized by columellaless exine structure (Walker and Skvarla, 1975; Walker, 1976b; Takhtajan and Meyer, 1976; Meyer, 1977). The most primitive columellaless exine, like that of *Degeneria* (see Dahl and Rowley, 1965, and Takhtajan and Meyer, 1976) is structurally amorphous and essentially homogenous. From homogenous, structureless exine, pollen grains with granular exine evolved; these are found in both the Magnoliaceae and Annonaceae. According to Walker and Skvarla (1975), the granular layer seems to lead to a more or less unstabilized stage characterized by development of what appear to be incipient columellae. "The culmination of this trend in exine structure is apparently reached with the evolution of well-developed columellae, either by enlargement and stabilization of intraexinal cavities resulting in a well-defined columellate layer, or by fusion of granules to form a basal exine layer and well-marked columellae" (Walker and Skvarla, 1975: 446). Like various kinds of tri-multiaperturate sporoderm, the columellate exine evolved independently a number of times, even within, for example, different subfamilies of the Annonaceae (Walker and Skvarla, 1975). The most primitive type of columellate pollen is tectate (columellae are internal, being covered by a roof-like tectum), which at an early stage of its evolution is imperforate. From such relatively primitive tectate-imperforate pollen grains an evolutionary trend runs to tectate-perforate to semitectate and more rarely to intectate pollen (Walker, 1974b, 1976b; Walker and Doyle, 1975).

The most primitive pollen grains with structureless exine are devoid or almost devoid of external sculpturing. They are more or less psilate, sometimes with foveolae (pits). In more advanced pollen grains external sculpturing of various types is more or less well developed. The type of the sculpturing is frequently very useful for taxonomy at the generic and especially at the specific level.

Carpels, gynoecium and placentation.—The most primitive carpels are unsealed, conduplicate and more or less stipitate structures (resembling young petiolate leaves lying still in the adaxially folded state inside the bud), containing a relatively large number of ovules (Bailey and Swamy, 1951; Eames, 1961, and many others). Such primitive conduplicate carpels are especially characteristic of such archaic genera as *Tasmannia* and *Degeneria* (Bailey and Nast, 1943; Bailey and Swamy, 1951) and to a lesser degree of some other primitive taxa including some primitive monocotyledons. This harmonizes with my hypothesis (Takhtajan, 1948, 1959, 1964) that the emergence of the angiosperm carpel occurred due to the hereditary fixation of the early stage of ontogeny of the ancestral gymnosperm megasporophyll when it was still in an unexpanded (conduplicate) stage. The carpel and the flower as a whole had a neotenic origin.

A very important characteristic of the most primitive carpels is the absence of styles, the stigmas being decurrent along the margins of the carpels (Hallier, 1901, 1912; Takhtajan, 1948; Parkin, 1955; Eames, 1961). Such stigmatic margins (approximated but not fused at the time of pollination) are the prototypes of the stigma. As Kozo-Poljanski (1922: 121) first pointed out in his commentary on Hallier's codex of characters of the primitive angiosperms, "the stigma developed from the sutures." In the course of evolution the primitive decurrent stigma was transformed into a more localized subapical and then apical stigma. As the stigma is localized in the upper part of the carpel, the latter is usually elongated into a style (stylode), which raises the stigma above the fertile portion of the carpel. During earlier evolutionary stages of the development of the style it is conspicuously conduplicate (Bailey and Swamy, 1951).

The most primitive taxa of the flowering plants are characterized by an apocarpous gynoecium. But already in the most primitive families a tendency is observed towards a greater or lesser union of carpels, which leads to the formation of the coenocarpous gynoecium. As a result, forms with more or less coenocarpous gynoecia appear even in such families as Winteraceae, Magnoliaceae, Annonaceae etc. The overwhelming majority of the magnoliophytes has one or another type of coenocarpous gynoecium. I distinguish three main types of coenocarpous gynoecium: syncarpous (in the narrow sense of the term), paracarpous, and lysicarpous (Takhtajan, 1942, 1948, 1959, 1964). A syncarpous gynoecium sensu stricto emerged independently in many lines of evolution from an apocarpous gynoecium by lateral concrescence of closely connivent carpels. The syncarpous gynoecium usually originates from a more advanced cyclic apocarpous gynoecium. The most primitive forms of syncarpous gynoecium still have free upper portions of the fertile regions of the carpels. With specialization of the syncarpous gynoecium the concrescence extends also to the individual styles, which finally coalesce completely into one compound style with one apical compound stigma. The union of carpels leads also to anatomical changes: with close fusion of carpel margins, the epidermal layers on the surface of contact are lost and the two ventral bundles form a single bundle (Eames, 1931).

The paracarpous gynoecium evolved in many lines of dicotyledons as well as in certain groups of monocotyledons. Usually the paracarpous gynoecium denotes a unilocular gynoecium, consisting of several carpels and having parietal or free-central placentation. But I prefer to limit the concept of paracarpous gynoecium to only the form of unilocular coenocarpous gynoecium that has a parietal arrangement of ovules (Takhtajan, 1942, 1948, 1959). A paracarpous gynoecium is characterized by unfolded individual carpels. Their margins are disconnected, while the connection of the borders of the adjoining carpels is maintained.

The paracarpous gynoecium is already found among Magnoliales where it is present in *Takhtajania* (Winteraceae), *Isolona* and *Monodora* (Annonaceae) and the whole family Canellaceae. In these cases, as in many others, including Saururaceae, Cactaceae, Alismatales etc., the paracarpous gynoecium evolved directly from the apocarpous one. The possibility of such an origin of the paracarpous gynoecium is based not only on the existence of apocarpous gynoecia with open conduplicate carpels, but also on the well known fact that the carpels in an apocarpous gynoecium begin development as open structures. If a whorl of such open carpels remained so and became coherent, as is presumed by Parkin (1955: 55), the paracarpous gynoecium originated directly from the apocarpous one (see also Cronquist, 1968: 101).

In many other cases, e.g. in the genus *Hypericum* and within the superorder Lilianae, the paracarpous gynoecium arises from the primitive type of syncarpous gynoecium in which the margins of individual carpels are not fused yet. As a result of unfolding of these unsealed carpels the syncarpous gynoecium gives rise to the paracarpous one.

In many cases the placentae in the paracarpous gynoecium grow thick, expand and intrude inside the ovarian cavity where they meet and often coalesce, forming false septa and pseudoaxile placentation, as for example in the family Campanulaceae. Puri (1952) is quite right in inclining to the conviction, that the multilocular character of this type, i.e. which appeared due to the concrescence of the placentae and not the carpellary margins, is more common than was earlier thought. In many cases, e.g. in the family Campanulaceae, the intruded placentae meet in the center of the ovary and coalesce among themselves; as a result the ovary is subdivided into loculi or rather chambers (pseudoloculi). Thus a typical unilocular paracarpous gynoecium gives rise to the multilocular paracarpous one.

In several lines of evolution of dicotyledons, for example in Primulales, the syncarpous gynoecium gave rise to a special type of gynoecium with a unilocular ovary which I named lysicarpous (Takhtajan, 1942, 1948, 1959). Like the paracarpous gynoecium, the lysicarpous type is also unilocular but it originates in a completely different manner and is characterized by free-central ("columnar") placentation instead of parietal. The unilocular ovary of the lysicarpous gynoecium is due to the disappearance of the septa of the multilocular ovary, which takes place either during ontogeny, as in Portulacaceae, or during evolution, as in Primulaceae. In this context, the carpellary sutures themselves remain entire and the ovules continue to be perched on them as earlier (for literature see Puri, 1952). Thus the sutural portion of the carpels together with the placentae is transformed into a column freely rising at the center of the locule and not reaching the top of the ovary.

Specialization of the coenocarpous gynoecium as well as that of the apocarpous is usually (but not always) accompanied by greater or lesser reduction in the number of carpels and in most cases also by reduction in the number of ovules. An extreme form of reduction in the number of carpels in the coenocarpus gynoecium is the so-called pseudomonomerous gynoecium (Eckardt, 1937, 1938), where only one of the carpels is fertile. The sterile carpels (or carpel, if the gynoecium is dimerous) in the pseudomonomerous gynoecium attain often such a degree of reduction that their presence can be detected only through an anatomical study of the vascular system and ontogeny. The pseudomonomerous gynoecium is characteristic for such taxa as Eucommiales, Urticales, Casuarinales, a majority of Thymelaeaceae, Gunneraceae, Garryaceae, Valerianaceae, etc.

The main directions of evolution of the gynoecium determine the main trends of evolution of placentation.

The types of placentation in the flowering plants may be classified as follows (see Takhtajan, 1942, 1948, 1959, 1964):

A. Laminar (superficial) placentation.
   1. Laminar-lateral placentation. The ovules occupy the side portions of the adaxial surface of the carpel between the median and the lateral veins. Examples: *Tasmannia, Degeneria.*
   2. Laminar-diffuse placentation. The ovules are scattered over almost the entire adaxial surface of the carpel. Examples: *Exospermum,* Nymphaeaceae, Butomaceae, Limnocharitaceae.

   3. Laminar-dorsal placentation. The ovules are attached pseudomedially, occupying the back of the carpel. Examples: *Nelumbo, Ceratophyllum,* Cabombaceae.

B. Sutural (submarginal) placentation.

   4. Axile placentation. The ovules are attached along the sutures of the closed carpel i.e. in the corner formed by the ventral area of the carpel in an apocarpous or syncarpous gynoecium. Examples: Ranunculaceae, Dilleniaceae, Rosaceae, Liliaceae.
   5. Parietal placentation. The ovules are situated along the sutures in a paracarpous gynoecium or on the intrusive placentae which in their turn are attached to the sutures. Examples: Violales, Capparales, Juncales.
   6. Free-central or columnar placentation. The ovules are situated along the central column of the lysicarpous gynoecium. Examples: Portulacaceae, Myrsinaceae, Primulaceae.

The most primitive type of placentation is laminar-lateral (Takhtajan, 1942, 1948, 1959, 1964; Stebbins, 1974). It characterizes such archaic genera as *Degeneria* and *Tasmannia* and certain species of the genus *Bubbia*. The ovules of these plants are rather far away from carpellary margins and are arranged in the space between the median and lateral veins. Such an arrangement of ovules is most probably an initial one in the evolution of angiosperm placentation. Both the laminar-diffuse and the laminar-dorsal types of placentation are derived from the laminar-lateral (Takhtajan, 1942, 1964).

In the course of evolution laminar placentation evolved into sutural. This is the most widespread type of placentation in flowering plants and it is found already in a majority of taxa with an apocarpous gynoecium, as Magnoliaceae, Annonaceae, Ranunculaceae etc. But the largest variety of forms of sutural placentation can be found in coenocarpous gynoecia. Two basic types of sutural placentation are the axile and the parietal types. Their origin and evolution is correlated with the origin and evolution of syncarpous and paracarpous gynoecia.

Lastly, free-central or columnar placentation is characteristic for the lysicarpous gynoecium.

Ovules.—The ovule is a solitary megasporangium surrounded by a protective cover—the integument. In the most primitive Palaeozoic seeds the integument was segmented (as in *Lagenostoma*), lobed (as in *Archaeosperma, Eurystoma,* and *Physostoma*) or even consisted of more or less separate elongated structures (as in *Genomosperma*) (completely separate in *G. kidstonii* and partially fused around the very base of the megasporangium in *G. latens*—see Long, 1960). These and other facts suggest that the integument evolved from a distal truss of separate structures (sterilized telomes) which once immediately subtended and surrounded the megasporangium, later became fused together, and eventually more or less fused with the megasporangium, which became almost completely enclosed by the integument (except the terminal micropyle) (see Walton, 1953; Zimmermann, 1959; Andrews, 1961, 1963; Camp and Hubbard, 1963; Long, 1966; Pettit, 1970). This telomic theory of the origin of the ovule is a modernized version of Margaret Benson's (1904) "synangial hypothesis."

The morphological interpretation of the integument in the magnoliophytes is complicated by the fact that many dicotyledons and a majority of monocotyledons are bitegmic, that is have two integuments. In all probability the outer integument of the angiosperm ovule emerged from the cupule of the ancient gymnospermous ancestor. The cupule is known to have emerged first in the Lyginopteridaceae, but it is not found in these primitive gymnosperms only. In a modified form it was preserved both in several later gymnosperms and in angiosperms. Already Mary Stopes (1905) considered the outer layer of the seed of Cycadaceae or the sarcotesta as a structure homologous to the "outer integument" (i.e. cupule) of *Lagenostoma*. This homology of the "outer integument" and the cupule is still more clearly visible in the Medullosaceae (Takhtajan, 1950; Walton, 1953). The cupule gave rise not only to the outer layer of the ovular envelope in a number of gymnosperms but also to the outer integument of the angiosperms. The cupular origin of the outer integument of the angiosperm ovule was suggested by Gaussen (1946), Takhtajan (1950, 1959, 1964), Walton (1953), and Stebbins (1974).

It is generally accepted that unitegmic ovules arose from the bitegmic ones in various lines of angiosperm evolution. As the "single" integument of the sympetalous dicotyledons is usually as massive or even more massive as compared to the "double," a suggestion was made (Coulter and Chamberlain, 1903), that the single envelope has a dual character and resulted from the complete fusion of two integuments at the earliest stages of the differentiation of the integumentary primordia. Presumably in most cases the unitegmic ovule resulted from the congenital fusion of both the envelopes, but in certain taxa it was formed due to the abortion of the inner or the outer integument. In some families, like the Piperaceae, Ranunculaceae, Ericaceae, Salicaceae, Rosaceae, Fabaceae and others, even quite close genera are often distinguished by the number of integuments. This shows that the unitegmic condition arose from the bitegmic independently and heterochronously in different evolutionary branches of the flowering plants.

In some taxa the ovular envelope disappears completely, and as the result the megasporangium is naked. This is quite typical in the order Santalales, where in many genera and even entire families ovules are ategmic, the integuments completely lacking. In the Balanophorales this process of reduction goes even further and more or less involves the megasporangium wall.

It is also generally accepted that crassinucellate ovules are more primitive and tenuinucellate ovules evolved from crassinucellate by reduction of the megasporangial wall. Thus the most primitive ovules of the flowering plants are bitegmic and crassinucellate and the most advanced ones are unitegmic and tenuinucellate. But these two types of angiosperm ovules are not always strictly exclusive of each other and there are intermediate types—bitegmic-tenuinucellate (e.g. Theaceae and Primulaceae) and unitegmic-crassinucellate (e.g. Cornaceae and Araliaceae) (see Philipson, 1974, 1977).

There is also a definite evolutionary trend in the form and orientation of the ovule. Although many botanists have taken the orthotropous ovule to be a more primitive type in flowering plants, there is every reason to believe that in flowering plants the orthotropous type, as well as campylotropous and amphitropous ones, arose from the anatropous ovule (Netolizky, 1926; Takhtajan, 1959; Eames, 1961; Cronquist, 1968; Corner, 1976).

Pollination.—Long ago the idea was expressed that in angiosperm evolution, entomophily preceded anemophily (Henslow, 1888; Bessey, 1897; Robertson, 1904, and others). The initial agents of cross pollination were undoubtedly animals, insects in the beginning and later small birds, bats and some other animals as well. The original pollinators were most probably beetles (Diels, 1916; Faegri and van der Pijl, 1979). The original attractant in insect pollination was the pollen (Darwin, 1876; Faegri and van der Pijl, 1979). But the necessity for pollen economy leads to a course of evolution in which the flower starts producing a cheaper foodstuff, nectar, as its alternative. For the production of nectar special structures are formed as nectaries. They originated independently in the most diverse lines of angiosperm evolution and on a most widely varying morphological basis. With the emergence of nectaries the plant gets an opportunity for producing pollen in more limited quantities and using it only for transport to other flowers. But the less the pollen production, the more effective should be the utilization of both the pollen and the pollinators. This inevitably leads to the perfection of pollination mechanisms.

In some evolutionary lines of flowering plants a transition takes place from entomophily to anemophily and more rarely to hydrophily. Anemophily arose from entomophily in completely different lines of evolution of both dicotyledons and monocotyledons. As Cronquist (1968: 97) says

> Wind-pollination and insect-pollination are not necessarily mutually exclusive. The change from one to the other can take place gradually, without any sudden jumps,

> especially if the adaptation to insect-pollination is generalized and does not involve complex or unusual structure associated with a particular kind of pollinator.

In all the known cases of anemophily the more primitive entomophilous relatives of anemophilous forms have relatively "generalized" entomophilous flowers. The evolutionary trend from entomophily to anemophily is reversible and in a number of cases there is a return to entomophily in groups earlier adapted to wind pollination (e.g. *Ficus, Castanea*). Again the secondary entomophily evolves from the less specialized types of anemophily.

Self-pollination emerged only as a secondary phenomenon, and it is a sort of blind alley for the further evolution "and rarely if ever contributes to major evolutionary trends" (Stebbins, 1974). Morphological and phylogenetic analysis indicates that self-pollinating taxa emerged in all cases from cross-pollinating ancestors.

The evolution of pollination was of exceptionally great importance in angiosperm evolution. It had a decisive role in the evolution of flowers and inflorescences and determined many important directions in the evolution of flowering plants.

Gametophytes and fertilization.—In the course of evolution both the male and female gametophytes of flowering plants reached a very high degree of simplification and specialization. Gametogenesis occurs in them at such an early stage of an extremely abbreviated ontogeny of the gametophyte that gametangia cannot even be formed, and the gametes are formed without them. Moreover, the development of the gametes themselves is also cut short, and they became extremely simplified. Due to a sharp abbreviation and acceleration of their ontogeny, the gametophytes of angiosperms completely lost their gametangia. As I have suggested in my previous works (beginning with 1948) these drastic changes in the gametophyte structure and development resulted from neoteny and subsequent specialization (see Takhtajan, 1976).

The entire male gametophyte of the flowering plants consists only of two cells—a small generative cell and a large tube cell ("vegetative" cell). It has neither the prothallial cells, nor the stalk cell ("dislocator" according to terminology of Goebel, 1933) and the true spermatogenous cell ("body cell"). The function of the spermatogenous cells has been transferred to the generative cell, which divides to form two nonmotile male gametes, and the function of the stalk cell became unnecessary. Thus the angiosperm male gametophyte reached the climax of simplification and miniaturization, which precluded any further major structural changes.

In the majority of flowering plants, including the primitive taxa, the pollen is released from the anther in the two-celled stage in the development of the gametophyte. But in many other flowering plants, including some advanced taxa, the generative cells divide before the pollen grain is shed and the male gametophyte is therefore three-celled. The two-celled condition is primitive and the three-celled type is derived and originated independently in many lines of angiosperm evolution (see Brewbaker, 1967; Cronquist, 1968; Stebbins, 1974).

The female gametophyte of the flowering plants resembles the early stages of the female gametophytes of archegoniate gymnosperms, possessing a peripheral layer of free nuclei arranged around a large central vacuole. It is therefore quite possible that the nonarchegoniate angiosperm gametophyte originated by way of progressive acceleration of gametogenesis and retardation of all other developmental processes (see Coulter, 1914; Takhtajan, 1976). Even the angiosperm egg is not the former egg of the archegonium but one of the very first cells of the gametophyte which is transformed into a female gamete (see Gerasimova-Navashina, 1958).

The female gametophyte is considerably less simplified than the male gametophyte and therefore is more liable to evolutionary modifications. But the evolutionary modifications of the female gametophyte take place within the bounds of some limits. The different types of female gametophytes are distinguished mainly on the basis of the number of megaspores or megaspore nuclei that participate in their formation, on the number of mitotic divisions during gametogenesis, and on the number and arrangement of the cells and free nuclei present in the mature gametophyte (see Johri, 1963; Romanov, 1971). It is generally agreed that the monosporic eight-nucleate female gametophyte of the *Polygonum* type, which characterizes the majority of angiosperms, is the basic and the most primitive type. All other types of the development and organization of the female gametophyte are derived. The tetrasporic types of female gametophyte are considered as the most specialized.

In a vast majority of cases the pollen tube penetrates into the female gametophyte through the micropyle (porogamy). Porogamy is the basic and primitive condition. Aporogamy (mesogamy and chalazogamy) is derived.

As it is well known, syngamy in flowering plants is accompanied by triple fusion of one of the two male gametes with the two polar nuclei. Triple fusion, which is one of the most characteristic features of the flowering plants, originated as a result of neotenic simplification of the female gametophyte. It triggers the formation of an entirely new structure, the triploid endosperm, which compensates for the extreme scarcity of nutrient materials in the simplified and miniaturized female gametophyte.

Seeds.—The seeds of primitive flowering plants are of medium-size, 5–

10 mm long (Corner, 1976). Both small and large seeds are derived. The more primitive seeds are characterized by abundant endosperm and a minute and undifferentiated embryo (Pritzel, 1898; Hallier, 1912; Martin, 1946; Eames, 1961, and many others). In advanced seeds, on the contrary, the embryo is large and well differentiated, and the endosperm is more or less reduced or even wanting. Here we observe something analogous to what happens in the animal world where the embryo in the mother's body attains greater development in the higher forms (Nägeli, 1884; Hallier, 1902, 1912).

The period of dormancy is very weakly expressed or even absent in seeds of some tropical angiosperms. Since there is a long-continuing after-ripening development in some primitive families, absence of dormancy is considered by Eames (1961) as a survival of primitive condition. Dormancy, on the contrary, is considered as an advanced stage in the evolution of the seed.

It is almost universally accepted that the monocotyledonous embryo arose from the dicotyledonous embryo.

The basic primitive type of seed-coat is one with "multiplicative" integuments (Corner, 1976), exarillate (Eames, 1961), and probably with well developed pinkish or reddish sarcotesta (Zazhurilo, 1940; Takhtajan, 1948, 1959; van der Pijl, 1955, 1969), like those of *Degeneria* and *Magnolia*. The presence of a sarcotesta in some primitive families suggests that endozoochory (possibly at first saurochory and later ornithochory) was probably characteristic of the earliest angiosperms (Zazhurilo, 1940; Takhtajan, 1948; van der Pijl, 1969).

Considering the seed-coat structure of *Degeneria* and *Magnolia* as the initial one for the primitive flowering plants, the derivation of all other types can be easily imagined as a result of reconstructions connected with a transition towards some other non-endozoochorous mode of dissemination. This transition determined the development of the outer layer of sclerenchyma and the reduction of parenchyma, which have become superfluous.

In many lines of angiosperm evolution a gradual simplification of the seed-coat is observed. The maximum simplification of the spermaderm is attained in those cases where the seed adjoins closely or is fused with the pericarp. The role of the protection of the embryo as well as the function of dissemination passes over to the pericarp and so the seed-coat is strongly reduced. In some cases the reduction of the seed-coat goes very far. At times only the outer epidermis is retained in the mature seed.

During the evolution of zoochory, starting from the primitive endosaurochory and ending in the most highly specialized forms of myrmecochory, various types of the succulent nutritive tissue of the outer portion of the seed-coat play a big role. At first presumably the sarcotesta served as the bait for attracting arboreal reptiles and later birds. The aril is a more specialized type of nutritive tissue than sarcotesta. In some cases the aril possibly results from a decrease in the area of sarcotesta and its localization in a definite (usually basal) part of the seed (see van der Pijl, 1955, 1969). But in the vast majority of cases arils arise as new structures on very different parts of the ovule and independently in many unrelated taxa. I therefore agree with Eames (1961) that it seems unlikely to consider the arillate seed as a primitive angiosperm character (but see Corner, 1976).

Fruits.—The most primitive and basic fruit type is a fruit consisting of many-seeded distinct follicles (Hallier, 1901, 1912; Harvey-Gibson, 1909; Bessey, 1915; Gobi, 1921, and many others). Such a fruit, developing from a multicarpellate apocarpous gynoecium, was called "multifolliculus" (follicetum) by Gobi. The multifolliculus gave rise to unifolliculus by reduction in the number of carpels (e.g. *Degeneria, Consolida*).

From follicular fruits arose many other types of apocarpous fruits, which in their turn gave rise to numerous coenocarpous fruit types.

III. DIVISION MAGNOLIOPHYTA OR ANGIOSPERMAE

Class Magnoliopsida or Dicotyledones

Subclass A. Magnoliidae

Superorder I. Magnolianae

Order 1. Magnoliales (Annonales).

Retains many more archaic and primitive features in both vegetative and reproductive structures of its members than any other order of flowering plants. But the order is extremely heterobathmic, and these primitive features are always found in association with more advanced ones. No one family combines all the primitive features, and no one of them can be selected as the most primitive: each family is specialized in its own way. Therefore, as in most other cases, no linear sequence of these families can reflect their phylogenetic relationships.

Suborder Winterineae (Winterales).

1. Winteraceae. Stands somewhat apart from all other members of the order (segregated in its own order Winterales by Němejc, 1956, and Smith, 1971). Subfamilies Winteroideae and Takhtajanioideae.

Suborder Magnoliineae.

2. Degeneriaceae (*Degeneria*). Probably related to Winteraceae and more or less similar in degree of primitiveness.
3. Eupomatiaceae (*Eupomatia*). Vessels of the most primitive type

("only the vesselless genera have more primitive wood"—Eames, 1961) and pollen grains with very primitive sporoderm (Takhtajan and Meyer, 1976), and carpels spirally arranged and slightly open, with decurrent stigma, but congenitally united (as those of *Zygogynum* in Winteraceae).

4. Himantandraceae (*Galbulimima*). Related to both Degeneriaceae and Eupomatiaceae but less primitive.

5. Magnoliaceae. Related to Degeneriaceae, but in general more advanced. Subfamilies Magnolioideae and Liriodendroideae.

Suborder Annonineae (Annonales).

6. Annonaceae. Related to Magnoliaceae, but more advanced. Subfamilies Annonoideae and Monodoroideae.

7. Canellaceae. Closely related to Annonaceae. Both the androecium and gynoecium resemble the most advanced members of Annonaceae.

8. Myristicaceae. Closely related to Annonaceae and Canellaceae. The sieve-element plastids of all of these three families are very similar (Behnke, 1971c, 1971d, 1972, 1975).

Order 2. Illiciales.

Evidently derived from Magnoliales, most probably from the same stock as the Winteraceae.

1. Illiciaceae (*Illicium*).
2. Schisandraceae.

Order 3. Laurales.

Near to Magnoliales, but more advanced. Evidently derived from some ancient vesselless member of Magnoliales.

Suborder Monimineae.

1. Austrobaileyaceae (*Austrobaileya*).

2. Amborellaceae (*Amborella*). Related to Austrobaileyaceae, and to Trimeniaceae and Monimiaceae.

3. Trimeniaceae. Related to Amborellaceae.

4. Monimiaceae. Closely related to Trimeniaceae. Subfamilies Hortonioideae, Monimioideae, Mollinedioideae, Atherospermatoideae, Siparunoideae (see Thorne, 1974).

5. Gomortegaceae (*Gomortega*). Closely related to Monimiaceae, especially to Atherospermatoideae.

6. Calycanthaceae (incl. Idiospermaceae?). Very closely related to Monimiaceae. Subfamilies Idiospermoideae and Calycanthoideae.

Suborder Chloranthineae (Chloranthales).

7. Chloranthaceae. Evidently nearest to Austrobaileyaceae and Trimeniaceae. Xylem is very primitive (vesselless in *Sarcandra*), and seeds

with minute embryo and copious endosperm, but flowers extremely specialized. Pollen grains are both 1-colpate and 4–8-colpate.

Suborder Lactoridineae (Lactoridales).

8. Lactoridaceae (*Lactoris*). The monotypic genus *Lactoris* occupies a rather isolated position within the order. Apparently stands nearest to Chloranthaceae, with which it probably had a common origin.

Suborder Laurineae.

9. Lauraceae. Nearest to the primitive members of Monimiaceae, especially to the genus *Hortonia*. Subfamilies Lauroideae and Cassythoideae.

10. Hernandiaceae. Closely related to Lauraceae, especially through the genus *Gyrocarpus* (Endress, 1972). Subfamilies Gyrocarpoideae and Hernandioideae.

Order 4. Piperales.

Stand nearest to Laurales and probably had a common origin with Chloranthaceae and Lactoridaceae.

1. Saururaceae.
2. Piperaceae. Subfamilies Piperoideae and Peperomioideae.

Order 5. Aristolochiales.

Evidently derived directly from Magnoliales, most probably from the common ancestor of Annonaceae and Myristicaceae. Sieve-element plastids of *Aristolochia* closely resemble those of *Annona,* both containing a prominent protein inclusion body that often tends to build up a crystalline arrangement. Additional starch grains—always present in *Aristolochia* plastids—are rare in *Annona,* but are a constant part of *Myristica* sieve-element plastids (Behnke, 1971b).

1. Aristolochiaceae. Subfamilies Asaroideae and Aristolochioideae.

Superorder II. Rafflesianae

Order 6. Rafflesiales.

Probably derived from the same annonaceous stock as Aristolochiales.

1. Hydnoraceae (*Hydnora* and *Prosopanche*).
2. Rafflesiaceae. Subfamilies Mitrastemonoideae, Cytinoideae, Rafflesioideae, Apodanthoideae. The subfamily Apodanthoideae probably deserves a family rank (Apodanthaceae, Van Tieghem).

Superorder III. Nymphaeanae

Order 7. Nymphaeales.

Probably derived from some ancient vesselless stock of the order Magnoliales.

Suborder Nymphaeineae.
1. Cabombaceae (*Brasenia* and *Cabomba*).
2. Nymphaeaceae (incl. Barclayaceae—see Schneider, 1978). Subfamilies Nymphaeoideae, Barclayoideae, Euryaloideae.

Suborder Ceratophyllineae.
3. Ceratophyllaceae (*Ceratophyllum*). Evidently related to Cabombaceae and probably had a common origin with them.

Order 8. Nelumbonales.

Usually placed in Nymphaeales or even in the family Nymphaeaceae, but differ in many important features.
1. Nelumbonaceae (*Nelumbo*).

Subclass B. Ranunculidae

Superorder IV. Ranunculanae

Order 9. Ranunculales (Berberidales).

Evidently related to Illiciales and have a common origin with them. The most primitive families of the order exhibit definite links with Illiciales.

1. Lardizabalaceae. The most primitive family within this order. "There is a close likeness between the seeds of *Akebia* and *Illicium*" (Corner, 1976: 28).
2. Sargentodoxaceae (*Sargentodoxa*). Stands near to Lardizabalaceae. The structure of the gynoecium somewhat resembles that of the Schisandraceae.
3. Menispermaceae. Stand near to Lardizabalaceae and had a common ancestry with them.
4. Berberidaceae. Have a common origin with Menispermaceae. *Nandina* serologically very near to the Berberidaceae, especially to *Berberis* and *Mahonia* (Jensen, 1974), but differs in many respects: joints of pinnae or pinnules of odd-pinnately leaves bulbous, swollen at base, sepals numerous, spirally arranged on an elongate receptacle, six petals in two series which morphologically are equivalent to sepals (i.e. the differentiated perianth of *Nandina* is completely of bract nature—Hiepko,

1965b), no nectaries, endotegmic seeds (Corner, 1976), and $n = 10$. There are also some differences in wood anatomy: vessel elements always spirally thickened, intervascular pitting opposite, scanty and diffuse wood parenchyma, rays of primitive heterogenous type with short wings, and fibers with bordered pits (Shen, 1954; Takhtajan, 1966). Subfamilies Podophylloideae (*Podophyllum* and *Diphylleia*), Epimedioideae, Nandinoideae (*Nandina*), Berberidoideae (*Mahonia* and *Berberis*).

5. Ranunculaceae (incl. Helleboraceae). Stands near to Berberidaceae. Subfamilies Hydrastidoideae, Thalictroideae, Ranunculoideae, Kingdonioideae.

6. Glaucidiaceae (*Glaucidium*). The monotypic genus *Glaucidium* is usually placed in the family Ranunculaceae but differs markedly from Ranunculaceae by some important characters (see Tamura, 1963, 1972; Takhtajan, 1966).

7. Circaeasteraceae (*Circaeaster*). Near to Ranunculaceae, but differing by persistent cotyledons, rosulately-crowded leaves at the summit of elongated hypocotyl, vascular system of the stem, morphology of inflorescence and flower, cellular formation of endosperm, and tenuinucellate ovule.

Order 10. Papaverales.

Very near to Ranunculales, especially to Glaucidiaceae and Ranunculaceae-Hydrastidoideae, and likewise to Berberidaceae-Podophylloideae.

1. Papaveraceae (incl. Fumariaceae). Traditionally Papaveraceae are subdivided into three subfamilies—Hypecoideae, Papaveroideae and Fumarioideae (see Engler's Syllabus, 1964). The subfamily Fumarioideae is frequently accepted as a distinct family. Nakai (1943) proposed three new unigeneric families—Pteridophyllaceae, Hypecoaceae and Chelidoniaceae, and later A. C. Smith (1971) added two more—Eschscholziaceae and Platystemonaceae. According to Smith we have seven distinct families, whereas Thorne (1974a, 1976) treats them as subfamilies. At present a comprehensive concept of the family Papaveraceae seems preferable (see also Ilyina, 1976). Subfamilies Platystemonoideae, Papaveroideae, Chelidonioideae, Eschscholzioideae, Pteridophylloideae, Hypecoideae, Fumarioideae.

Order 11. Sarraceniales.

A very specialized order, which has nevertheless some primitive features that place it near to Ranunculales and Papaverales. Had a common origin with the Papaverales from the ranunculaleous stock.

1. Sarraceniaceae.

Subclass C. Hamamelididae

Superorder V. Hamamelidanae

Order 12. Trochodendrales.

In many respects Trochodendrales occupy, as it were, an intermediate position between Magnoliales and Hamamelidales, but in the totality of their characters they stand nearer to the latter.

1. Trochodendraceae (*Trochodendron*).
2. Tetracentraceae (*Tetracentron*).

Order 13. Cercidiphyllales.

An isolated unigeneric order which probably shares a common origin with Trochodendrales.

1. Cercidiphyllaceae (*Cercidiphyllum*).

Order 14. Eupteleales.

The morphological peculiarities of this unigeneric order indicate its marked systematic isolation.

1. Eupteleaceae (*Euptelea*).

Order 15. Didymelales.

The Malagsy genus *Didymeles* had usually been placed near Leitneriaceae (Baillon, 1877; Leandri, 1937; Engler's Syllabus, 1964), less often with Hamamelidaceae (Hallier, 1912, with some hesitation, Stebbins, 1974), Euphorbiaceae (Novák, 1961; Thorne, 1968, 1976) and other families. Notwithstanding some similarity in pollen grain morphology (as noted by Erdtman, 1952), *Didymeles* stands very remote from Euphorbiaceae (monocarpellate gynoecium!) and has much more in common with Leitneriaceae (including the naked male flower, apetalous female flower, similar position of epitropous ovule, and drupaceous fruit). But the genus *Didymeles* is sharply distinct from *Leitneria* in its racemose inflorescence, in the unique type of pollen grains (tricolpate with 2-orate colpi—Erdtman, 1952; Straka, 1967), in its monocarpellate gynoecium, in connate filaments, in the structure of the ovule, in the very peculiar encyclocytic stomata with 4–7 or 7–10 subsidiary cells (Takhtajan, 1966), in the absence of secretory canals in the leaves and pith, and the wood anatomy (vessel elements with scalariform perforation plates with 6–25 thin bars; end walls with well expressed tails with numerous bordered pits; intervascular pitting opposite to alternate, in wider vessel elements mainly alternate). Wood parenchyma lacking. Rays of primitive heterogenous type with long or rarely short wings. Fibers with small, but distinctly bordered pits (Takhtajan, 1966). The genus *Didymeles* is related to Hamamelidales, but the stomata, pollen grains and ovules are different, the gynoecium is monocarpellate, and the leaves are exstipulate. Moreover, the seed-coat anatomy of *Didymeles* is sharply distinct from that of the Hamamelidales and related orders (Melikian, 1973).

1. Didymelaceae (*Didymeles*).

Order 16. Hamamelidales.

This order in many ways serves as a connecting link between Trochodendrales on the one hand and the "amentiferous" orders Casuarinales, Urticales, Fagales, etc., on the other. The order Hamamelidales is evidently derived from an immediate ancestor of Trochodendrales.

Suborder Hamamelidineae.

1. Hamamelidaceae (incl. Altingiaceae). Subfamilies Disanthoideae, Hamamelidoideae, Rhodoleioideae. Exbucklandioideae, Chunioideae, Liquidambaroideae.

2. Platanaceae (*Platanus*). Stands near to Hamamelidaceae (especially to the subfamily Liquidambaroideae). Most probably arose from a common ancestor.

3. Myrothamnaceae (*Myrothamnus*). Related to Hamamelidaceae and "closely resembles the genus *Distylium* in general floral appearance" (Endress, 1977; see also Jäger-Zurn, 1966).

4. Daphniphyllaceae (*Daphniphyllum*). Usually placed in the order Euphorbiales or even included in the family Euphorbiaceae (Bentham in Bentham and Hooker, 1880; Wettstein, 1935; Rendle, 1938; Gundersen, 1950), but some authors associate them with Hamamelidaceae (Hutchinson, 1926, 1959, 1969; Croizat, 1940; Takhtajan, 1954) or even include in Hamamelidaceae (Hallier, 1904, 1905, 1908, 1912). From Euphorbiaceae they differ in the absence of stipules, wood anatomy (Metcalfe and Chalk, 1950), stamens with three vascular traces and protruded connective, pollen grain morphology (Bhatnagar and Garg, 1977), paracarpous gynoecium, cellular formation of endosperm, absence of obturator and hypostase, and especially in a minute embryo. According to Corner (1976) "Seed-structure forbids alliance of this small family with Euphorbiaceae, there is no tegmic differentiation such as happens even in drupaceous Euphorbiaceae." At the same time he emphasizes the similarity of seed anatomy of Daphniphyllaceae and Buxaceae and notes the resemblance of ovary, ovule and fruit of *Daphniphyllum,* with those of *Sarcoccoca* (Buxaceae). The totality of evidence (including wood anatomy—see Janssonius, 1950) indicate that Daphniphyllaceae have closer affinity with Hamamelidaceae rather than with Euphorbiaceae. Morphology does not

support the inclusion of Daphniphyllaceae in "Pittosporales" as suggested by Thorne (1968, 1977).

Suborder Buxineae.

5. Buxaceae (incl. Pachysandraceae and Stylocerataceae). Systematic position is still open to question. Usually they are placed in the order Euphorbiales and in the past some botanists even included in the family Euphorbiaceae (Endlicher, 1841; Bentham in Bentham and Hooker, 1880). Many botanists place Buxaceae in Celastrales (Baillon, 1887; Bessey, 1915; Gobi, 1916; Pulle, 1952; Dang-Van-Liem, 1962; Scholz in Engler's Syllabus, 1964; Soó, 1967; Dahlgren, 1975, 1977). On embryological grounds Dang-Van-Liem (1962) concluded that Buxaceae show affinities to Celastraceae. Some authors associate Buxaceae with Hamamelidaceae (Hutchinson, 1926, 1959, 1969; Tippo, 1938; Takhtajan, 1954; Croizat, 1960; Melikian, 1973) or even include in this family (Hallier, 1903a, 1905, 1908, 1912). Though the Buxaceae share with Euphorbiaceae some important characters (including characters of floral morphology, morphology of pollen grains, usually carunculate seeds and petiolar anatomy), they differ in the dorsal, not ventral raphe, in cellular endosperm of some genera (*Buxus* and *Pachysandra*), in the development of integuments (Wunderlich, 1967), in the absence of obturator and also in the loculicidal dehiscence in the members with capsular fruit. In many important characters Buxaceae resemble Hamamelidaceae and related families. "The Buxaceae are hamamelidaceous by their floral morphology in the very first place" (Croizat, 1960) and "the exo-mesotestal structure of the Buxaceae agrees with the disposition of the family in the Hamamelidales away from the exotegmic Euphorbiaceae" (Corner, 1976). Though it seems that the totality of evidence shows the hamamelidaceous affinity rather than euphorbiaceous or celastraceous, the affinity of the family is not fully clear. Subfamilies Buxoideae and Styloceratoideae.

6. Simmondsiaceae (*Simmondsia*). Contains monotypic North American genus *Simmondisia,* usually included in Buxaceae. But it differs from Buxaceae in biochemistry (Brown, 1976), in much more specialized anatomy of vegetative organs (Metcalfe and Chalk, 1950), in dioecious and anemophilous flowers lacking any traces of nectaries, in 3–4-porate sporoderm with different ectexine sculpture (Chang Tsin-tan, 1964), in deciduous styles, in the structure of integuments (Wunderlich, 1967), large exalbuminous seeds with thick and fleshy cotyledons with abundant liquid waxes (Vaughan, 1970), and in basic number of chromosomes ($x = 13$, see Raven, 1975). At the same time it shares some common features with the Buxaceae both in floral morphology and seed-coat anatomy ("its seed structure is Buxaceous"—Corner, 1976). Besides according to M. A. Baranova (personal communication) stomata of *Simmondsia* are of lat-

erocytic type or intermediate between laterocytic and anomocytic, and very much resemble those of the buxaceous genus *Styloceras*.

Order 17. Eucommiales.

Evidently related to Urticales and had a common origin with them from the Hamamelidales.

1. Eucommiaceae (*Eucommia*).

Order 18. Urticales.

Connected with Hamamelidales and perhaps derived directly from them.

Suborder Ulmineae.

1. Ulmaceae (incl. Celtidaceae). Comparatively the most primitive member of the order. Subfamilies Ulmoideae and Celtidoideae.

Suborder Urticineae.

2. Moraceae.
3. Cannabaceae (*Cannabis* and *Humulus*). Related to Moraceae, but rather isolated within Urticales (Berg, 1978).
4. Cecropiaceae (Berg, 1978). A somewhat intermediate family between Moraceae and Urticaceae.
5. Urticaceae. The most advanced member of the order. Subfamilies Urticoideae and Conocephaloideae.

Order 19. Barbeyales.

This order is evidently related to Urticales and had a common origin with them, but differs markedly in unilacunar nodes (Dickison and Sweitzer, 1970) and apocarpous gynoecium, as well as in very oblique sieve plates (Dickison and Sweitzer, 1970), pollen morphology (Kuprianova, 1965; Dickison and Sweitzer, 1970), and seed anatomy (Melikian, 1973).

1. Barbeyaceae (*Barbeya*).

Order 20. Casuarinales.

Exhibits many features in common with Hamamelidales and Fagales and to a lesser degree with Urticales and Myricales. Stands close to Betulaceae both in pollen grains (Erdtman, 1952; Kuprianova, 1965) and flower morphology (Eames, 1961). Already Bessey (1915) derived Casuarinaceae from Hamamelidaceae, which is corroborated by the totality of morphological and anatomical data (Moseley, 1948) including seed anatomy (Melikian, 1973). Both Casuarinales and Fagales had probably a common origin from Hamamelidales.

1. Casuarinaceae (*Casuarina*).

Order 21. Fagales (incl. Betulales).

In all probability derived directly from Hamamelidales.

Suborder Fagineae.

1. Fagaceae (incl. Nothofagaceae). Subfamilies Fagoideae, Castaneoideae, Quercoideae.

Suborder Betulineae.

2. Betulaceae (incl. Carpinaceae and Corylaceae which is also supported by serological data—see Brunner and Fairbrothers, 1979). Subfamilies Betuloideae and Coryloideae.

Order 22. Balanopales.

Probably derived directly from Hamamelidales. It is a very isolated order consisting of one unigeneric family Balanopaceae, which some authors put in Fagales. But from Fagales the genus *Balanops* differs in many respects, including basal apotropous ovules, an obturator-like enlargement of the funicle, a thin layer of endosperm around the large embryo, and drupaceous fruit (as well as seed anatomy—Melikian, 1973). According to Hallier (1908) Balanopaceae "gehoren zu der Hamamelidaceen neben *Daphniphyllum, Trochodendron* und *Rhodoleia.*" Thorne (1968, 1977) places Balanopaceae near Daphniphyllaceae in his order Pittosporales.

1. Balanopaceae (*Balanops*).

Order 23. Leitneriales.

This unigeneric order is evidently also one of the anemophilous derivations of Hamamelidales.

1. Leitneriaceae (*Leitneria*).

Superorder VI. Juglandanae

Order 24. Myricales.

Has much in common on the one hand with Casuarinales and Betulaceae, and on the other with Juglandales.

1. Myricaceae.

Order 25. Juglandales.

Has much in common with Myricales (including serological similarities between Juglandaceae and Myricaceae—Chupov and Cutjavina, 1978; Petersen and Fairbrothers, 1979) and also with Fagales and evidently had a common origin with these orders from the hamamelidalean ancestor. Especially many common features with Myricaceae in the structure of flower, pollen grains, ovules, fruit, basic chromosome number and chemistry.

1. Rhoipteleaceae. In many respects this unigeneric family approaches closely to the hypothetical intermediate between the Hamamelidaceae and Juglandaceae.
2. Juglandaceae. Subfamilies Juglandoideae and Platycaryoideae.

Subclass D. Caryophyllidae

Superorder VII. Caryophyllanae

Order 26. Caryophyllales.

In all probability had a common origin with the Ranunculales. The Phytolaccaceae in particular is linked with both the Ranunculales (especially with the Menispermaceae and Lardizabalaceae) and with the Illiciales. But the Caryophyllales specific P-type sieve-element plastid with the ring-shaped bundle of filaments is unique among the seed plants investigated (Behnke and Turner, 1971; Behnke, 1975, 1976a).

Suborder Phytolaccineae.

1. Phytolaccaceae (incl. Agdestidaceae, Barbeuiaceae, Gisekiaceae and Petiveriaceae and excluding *Rhabdodendron*). The most primitive and generalized family of the order. Subfamilies Phytolaccoideae, Gisekioideae, Rivinoideae, Agdestidoideae, Microteoideae, Barbeuioideae.
2. Achatocarpaceae. Closely related to Phytolaccaceae. Though the pollen morphology does not in Nowicke's opinion (1975) support a close tie, the two genera (*Achatocarpus* and *Phaulothamnus*) that comprise the family do have the P-type plastids with globular crystalloids (Behnke, 1976a).
3. Nyctaginaceae. An advanced family derived directly from Phytolaccaceae.
4. Aizoaceae (incl. Mesembryanthemaceae, ? Sesuviaceae, and Tetragoniaceae). Closely related to Phytolaccaceae, but somewhat more advanced. According to Hofmann (1973) *Tetragonia* and *Mesembryanthemum* s.l. are linked with the other Aizoaceae through *Galenia* and *Plinthus* or *Aizoon* respectively and should not be separated from the

Aizoaceae. Subfamilies Aizoideae, Mesembryanthemoideae, Tetragonioideae.

5. Cactaceae. Closely related to Aizoaceae and Phytolaccaceae and most probably derived from the phytolaccaceous stock. Subfamilies Pereskioideae, Opuntioideae, Cactoideae.

6. Portulacaceae (incl. Montiaceae). Near to Aizoaceae and Cactaceae and had a common origin from Phytolaccaceae. Subfamilies Portulacoideae and Montioideae.

7. Hectorellaceae. Very near to Portulacaceae.

8. Basellaceae. Very near to Portulacaceae.

9. Didiereaceae. Have a common origin with Cactaceae, Portulacaceae and Nyctaginaceae and stand closest to the first two.

10. Stegnospermataceae (*Stegnosperma*). Related to Phytolaccaceae but differ in the ultrastructure of sieve-element plastids (Behnke, 1975, 1976a) and flower morphology (Hofmann, 1973).

Suborder Caryophyllinae.

11. Molluginaceae (excluding *Gisekia*, which contains betalains—Mabry et al., 1976). Related to the Phytolaccaceae, Aizoaceae and Stegnospermataceae. Connected with Phytolaccaceae, especially with *Gisekia*.

12. Caryophyllaceae (incl. Illecebraceae and *Geocarpon*). Closely related to Molluginaceae and have a common origin with them from the phytolaccaceous stock. Caryophyllaceae can be distinguished from the other families of the order by their sieve-element plastids with polygonal crystalloid (Behnke, 1975, 1976a). Subfamilies Paronychioideae, Alsinoideae, Caryophylloideae.

Suborder Chenopodiineae.

13. Amaranthaceae. Related to Phytolaccaceae and probably derived from them. Subfamilies Amaranthoideae and Gomphrenoideae.

14. Chenopodiaceae (incl. Dysphaniaceae, Salicorniaceae, and Salsolaceae). Stand very close to Amaranthaceae with which they have a common origin. Subfamilies Chenopodioideae and Salsoloideae.

Order 27. Polygonales.

Related to Caryophyllales, especially to Portulacaceae and Basellaceae, but do not contain the proteinaceous inclusions in their sieve-element plastids (sieve-element plastids are of S-type—Behnke, 1972, 1975, 1976a, 1977a) and seeds are without perisperm and with copious mealy endosperm surrounding the curved or straight embryo. Probably derived from the same stock as the Caryophyllales.

1. Polygonaceae. Subfamilies Eriogonoideae, Polygonoideae, Coccoloboideae.

Superorder VIII. Plumbaginanae

Order 28. Plumbaginales.

Related to Caryophyllales, but sieve-element plastids are of S-type (Behnke, 1972, 1975, 1976a, 1977a) corolla is gamopetalous, embryo is straight, and seeds without perisperm and usually with endosperm. Probably derived from the same stock as the Caryophyllales and Polygonales. Friedrich (1956) suggested that Plumbaginaceae are related to Nyctaginaceae. Both the Plumbaginales and Polygonales are mycologically linked with the Caryophyllales (see Savile, 1979).

1. Plumbaginaceae (incl. Limoniaceae). Subfamilies Plumbaginoideae and Staticoideae.

Subclass E. Dilleniidae

Superorder IX. Dillenianae

Order 29. Dilleniales.

A connecting link between Magnoliidae (especially Magnoliales and Illiciales) on the one hand, and Theales and Violales on the other.

1. Dilleniaceae. Subfamilies Tetraceroideae and Dillenioideae.
2. Crossosomataceae. Near to Dilleniaceae but more advanced.

Order 30. Paeoniales.

Near to Dilleniales, but distinguished by the structure of thick-walled fleshy carpels, broad stigmas, the presence of a peculiar, prominently lobed, fleshy nectariferous disc surrounding the gynoecium, ovules with a massive outer integument which are borne on placental projections, the structure of seed-coat, and extremely peculiar type of embryogeny with the coenocytic proembryo stage (see Yakovlev and Yoffe, 1957, 1965; Cave et al., 1961; Mathiessen, 1962; Walters, 1962).

1. Paeoniaceae (*Paeonia*).

Order 31. Theales.

Near to Dilleniales and evidently derived from early Dilleniaceae. Nearest to Dilleniaceae is Ochnaceae, which is the most primitive family in the order.

1. Ochnaceae (incl. Lophiraceae ?). Combines primitive and advanced characters, but in general perhaps the most primitive family in the order.
2. Sauvagesiaceae (incl. Luxemburgiaceae) (see Corner, 1976: 249). Near to Ochnaceae.
3. Strasburgeriaceae (*Strasburgeria*). Near to Ochnaceae.

4. Diegodendraceae (*Diegodendron*). Probably near to Ochnaceae (see Capuron, 1963, 1965; Hutchinson, 1973; Straka and Albers, 1978).

5. Ancistrocladaceae (*Ancistrocladus*). Affinities obscure.

6. Dioncophyllaceae. Probably related to Ancistrocladaceae.

7. Theaceae (incl. Sladeniaceae and Ternstroemiaceae). Related to Ochnaceae and shares with them a common origin from Dilleniales. Subfamilies Theoideae and Ternstroemioideae.

8. Oncothecaceae (*Oncotheca*). Near to Theaceae, especially to the subfamily Ternstroemioideae (see Takhtajan, 1966; Baas, 1975; Carpenter and Dickison, 1976; Shilkina, 1977).

9. Pentaphylacaceae (*Pentaphylax*). Very near to Theaceae, especially to the genus *Eurya*.

10. Tetrameristaceae (*Tetramerista*). Closely related to Theaceae.

11. Caryocaraceae. Near to Theaceae and connected with them through Tetrameristaceae.

12. Asteropeiaceae (*Asteropeia*). Related to Theaceae.

13. Marcgraviaceae. Near to Theaceae.

14. Pelliceriaceae (*Pelliceria*). Related to Theaceae and Marcgraviaceae.

15. Quiinaceae. Related to Ochnaceae, especially to the tribes Ochneae and Elvasieae (see Gottwald and Parameswaran, 1967).

16. Medusagynaceae (*Medusagyne*). Systematic position is not wholly clear. Possibly have a thealean affinity.

17. Bonnetiaceae. In some respect an intermediate group between Theaceae and related families and Clusiaceae, but nearer to Clusiaceae (see Kubitzki et al., 1978).

18. Clusiaceae or Guttiferae (incl. Hypericaceae). Closely related to Bonnetiaceae and had a common origin from the theaceous stock. The most primitive subfamily is Kielmeyeroideae, which is nearest to Bonnetiaceae. Subfamilies Kielmeyeroideae, Calophylloideae, Clusioideae, Moronoboideae, Lorostemonoideae, Hypericoideae.

19. Elatinaceae. Related to Clusiaceae-Hypericoideae (see Takhtajan, 1959; Corner, 1976).

Order 32. Violales.

Very near to Theales and Malvales, and share with them a common ancestry in the dillenialean stock.

Suborder Violineae.

1. Flacourtiaceae (incl. Erythrospermaceae, Homaliaceae, ? Lacistemataceae, Neumanniaceae, Prockiaceae, and Samydaceae). Closely related to Dilleniaceae, especially through the most primitive tribes Berberidopsideae and Oncobeae. There are also many similarities with

Ochnaceae (Theales) and Tiliaceae (Malvales). Probably originated from the early Dilleniaceae. The family is rather heterogeneous and as Miller (1975) says "is composed of homogeneous tribes loosely united into a family." Occupies a basal position in Violales.

2. Passifloraceae (incl. Paropsiaceae and excl. *Physena*). Derived from Flacourtiaceae through the tribe Paropsieae and so close to them that it is difficult to draw a clear taxonomic boundary between these two families. The family Passifloraceae or its immediate ancestor was the basal stock from which Turneraceae, Malesherbiaceae, Caricaceae, Achariaceae and Cucurbitaceae arose.

3. Stachyuraceae (*Stachyurus*). Closely related to Flacourtiaceae, especially to the tribe Scolopieae, but seeds without the fibrous exotegmen (Corner, 1976).

4. Violaceae (incl. Leoniaceae). Closely related to Flacourtiaceae and is linked to them through the primitive tribe Rinoreae, especially the genus *Rinorea*. Subfamilies Violoideae and Leonioideae.

5. Bixaceae (incl. Cochlospermaceae ?). Related to Flacourtiaceae, especially to the tribe Oncobeae. Pollen of Bixaceae lies within the range of Flacourtiaceae (Keating, 1973). Subfamilies Bixoideae and Cochlospermoideae.

6. Cistaceae. Related to Bixaceae and shares with them a common origin from Flacourtiaceae.

7. Peridiscaceae. Related to Flacourtiaceae, especially to its primitive taxa, such as *Erythrospermum*.

8. Scyphostegiaceae (*Scyphostegia*). Probably derived from Flacourtiaceae (see Metcalfe, 1956; Van Heel, 1967).

9. Dipentodontaceae. Affinities obscure. Despite a free-basal placenta which is unknown in Violales this family probably related to Flacourtiaceae as suggested by T. A. Sprague (see Metcalfe and Chalk, 1950: 126). Pollen-grains are flacourtiacean (Lobreau, 1969).

10. Turneraceae. Very near to Passifloraceae.

11. Malesherbiaceae (*Malesherbia*). Close to Turneraceae, differ in valvate petals, persistent calyx, and in absence of aril.

12. Achariaceae. Closely related to Passifloraceae, from which they differ mainly in the absence of stipules and in their sympetalous, campanulate corolla. The climbing herbaceous genus *Ceratosicyos* in habit is similar to that of some Cucurbitaceae.

13. Caricaceae. Related to Passifloraceae, but much more advanced.

Suborder Cucurbitineae.

14. Cucurbitaceae. Related to Passifloraceae and derived from some of their primitive members. They also resemble Caricaceae and Achariaceae. Subfamilies Cucurbitoideae and Zononicideae.

Order 33. **Begoniales** (Datiscales).

Near to Violales, especially to the Flacourtiaceae, and derived from them.

1. Datiscaceae (incl. Tetramelaceae—see Davidson, 1973, 1976). Tribes Datisceae (*Datisca*) and Tetrameleae.

2. Begoniaceae. Near to Datiscaceae in fruit and ovule, and especially in seed and pollen morphology, as well as in asymmetrical leaves. Embryologically Begoniaceae are also close to Datiscaceae (Crété, 1952).

Order 34. Capparales.

Derived from primitive representatives of Violales, most likely from Flacourtiaceae (probably from the tribe Oncobeae).

Suborder Capparineae.

1. Capparaceae (incl. Cleomaceae, Koeberliniaceae, Pentadiplandraceae and *Oceanopapaver* and excluding *Emblingia* and *Physena*). Related to the tribe Oncobeae of Flacourtiaceae. Subfamilies Capparoideae, Pentadiplandroideae, Calyptrothecoideae, Cleomoideae, Podandrogynoideae, Dipterygioideae, Buhsioideae.

2. Tovariaceae (*Tovaria*). Closely related to Capparaceae-Cleomoideae and probably originated from a common ancestor.

3. Brassicaceae or Cruciferae. Derived from Capparaceae-Cleomoideae and linked to them through the tribe Stanleyeae.

Suborder Resedineae.

4. Resedaceae. Probably related to and derived from Capparaceae. Many similarities with Capparaceae-Cleomoideae and Brassicaceae, but also many peculiarities.

Suborder Moringineae.

5. Moringaceae (*Moringa*). Probably related to Capparaceae. Share many common features with Capparaceae, including palynology (Erdtman, 1952), embryology (Narayana, 1970) and the presence of myrosin cells, but differ serologically (Kolbe, 1978) and in the seed-coat anatomy (Corner, 1976).

Order 35. Tamaricales.

Derived from Violales (most probably from Flacourtiaceae) and highly advanced.

Suborder Tamaricineae.

1. Frankeniaceae.

2. Tamaricaceae. Closely related to Frankeniaceae and share a common ancestry.

Suborder Fouquierineae.

3. Fouquieriaceae. Position not fully clear (see Dahlgren et al., 1976; Thorne, 1977), but probably related to Tamaricaceae (sieve-element plastids of *Fouquieria* (incl. *Idria*) are of the S-type and similar to those of Tamaricaceae and Frankeniaceae—see Behnke, 1976b).

Order 36. Salicales.

Derived from the Flacourtiaceae, most likely from ancestors closely related to present-day Idesiinae (Hallier, 1908, 1911, 1912; Gobi, 1916; Cronquist, 1957; Gzyrian, 1952, 1955; Takhtajan, 1959, 1966, 1969; Miller, 1975). According to Miller (1975) it is possible to construct a reduction series from *Idesia* and *Itoa* to *Populus* and *Salix.* A rust genus *Melampsora,* which is very common on *Populus* and *Salix,* also parasitizes *Idesia* (Holm, 1969).

1. Salicaceae.

Superorder X. Ericanae

Order 37. Ericales.

Related to Theales, and especially to Dilleniales, with which it is closely linked through the family Actinidiaceae.

1. Actinidiaceae (without *Sladenia,* but including Saurauiaceae—see Dickison, 1972a). The most primitive family within the order which has many similarities with the Dilleniales. Subfamilies Actinidioideae, Saurauioideae, Clematoclethroideae.

2. Clethraceae (*Clethra*). Stands near to Actinidiaceae, but has also much in common with Theaceae (especially with *Eurya*).

3. Ericaceae (incl. Monotropaceae, Pyrolaceae, and Vacciniaceae). Close to Clethraceae. The family is rather diversified and is subdivided into six natural subfamilies: Rhododendroideae (incl. Epigaeoideae), Ericoideae, Vaccinioideae (incl. Arbutoideae), Pyroloideae, Monotropoideae, and Wittsteinioideae (Stevens, 1971). The last subfamily, which is rather isolated within the family, is included by some authors in Epacridaceae. Pyroloideae and Monotropoideae are considered as separate families by many authors, but they are not separable from the rest of the Ericaceae by clear cut differences and represent the final stages in the evolution toward the increasing dependance on a fungal symbiont (see Henderson, 1919; Copeland, 1941, 1947; Veillet-Bartoszewska, 1960; Terekhin, 1962; Stevens, 1971).

4. Empetraceae. Close to Ericaceae, especially to Rhododendroideae.

5. Epacridaceae (incl. Prionotaceae). Stands very near to Ericaceae, especially to Ericoideae. The genus *Sprengelia* is one of the most primitive within the family and more closely related to Ericaceae (Paterson, 1961). Subfamilies Epacridoideae and Richeoideae.

6. Diapensiaceae. Related to Ericaceae and Epacridaceae, but neither terminal nor chalazal haustoria are developed (Yamazaki, 1966).

7. Cyrillaceae. Evidently close relatives of Ericaceae and probably derived from them or their immediate ancestor. Embryological data indicate that the Cyrillaceae show close correspondence with Ericaceae (Vijayaraghavan, 1970). Pollen grains resemble those of Ericaceae and especially Clethraceae.

8. Grubbiaceae. Most probably related to Ericaceae and derived from their most primitive members.

Order 38. Ebenales.

Probably share a common origin with Ericales from the Dillenialean stock.

Suborder Styracineae.

1. Styracaceae (without *Afrostyrax*—see Baas, 1972). The most primitive family of the order which is especially close to Theales.

2. Symplocaceae. Closely related to Styracaceae and have also many characters in common with Theaceae. Probably share a common origin with Styracaceae from the theaceous ancestor.

3. Lissocarpaceae (*Lissocarpus*). Closely related to Styracaceae.

Suborder Ebenineae.

4. Ebenaceae. Near Styracaceae and share a common origin.

5. Sapotaceae (incl. Sarcospermataceae). Stand close to Ebenaceae. Subfamilies Sideroxyloideae, Madhucoideae, Sarcospermatoideae.

Order 39. Primulales.

Stands close to both Ericales and Ebenales. A serological correspondence between Primulales and Ericales is very clear, but less clear between Primulales and Ebenales (Frohne and John, 1978).

1. Myrsinaceae. Subfamilies Myrsinoideae, Maesoideae, Aegiceratoideae.

2. Theophrastaceae. Near Myrsinaceae.

3. Primulaceae (incl. Coridaceae). Very close to Myrsinaceae (separation almost artificial) and Theophrastaceae and had a common origin with them. Subfamilies Primuloideae and Coridoideae.

Superorder XI. Malvanae

Order 40. Malvales.

Derived from early Violales. Exhibits many features in common with Flacourtiaceae, especially with the tribe Scolopieae sensu amplo (including Hutchinson's Prockieae and Banareae), as well as with the primitive members of Theales (especially with the Ochnaceae). Both the vegetative anatomy and palynology support the derivation of the order Malvales from Flacourtiaceae through the intermediate tribe Scolopieae (Keating, 1973; Miller, 1975). Such derivation is also supported by chemotaxonomic evidence (see Alston and Turner, 1963). In fact the tribe Scolopieae is closely allied to both Flacourtiaceae and Elaeocarpaceae-Tiliaceae and occupies almost an intermediate position between two orders. It is therefore very difficult to draw a clear-cut boundary between Flacourtiaceae and the primitive members of Malvales.

1. Elaeocarpaceae. The most primitive family of the order, showing closer affinity with the tribe Scolopieae of Flacourtiaceae than any other family of Malvales.
2. Tiliaceae (incl. *Pakaraimaea* ?—see Kostermans, 1978). Very close to Elaeocarpaceae. Subfamilies Brownlowioideae, Tetralicoideae, Tilioideae, Neotessmannioideae.
3. Sterculiaceae (incl. Byttneriaceae and probably the genus *Maxwellia*—see Robyns et al., 1977). Closely related to Tiliaceae and evidently derived from the same stock.
4. Huaceae. Contains two African genera *Hua* and *Afrostyrax,* which are clearly related to each other (Chevalier, 1947; Baas, 1972). Near to Sterculiaceae.
5. Scytopetalaceae. Related to Elaeocarpaceae and Tiliaceae. In many embryological features *Scytopetalum* resembles Elaeocarpaceae, Tiliaceae and Bombacaceae (Vijayaraghavan and Dhar, 1976).
6. Dipterocarpaceae. Near to Tiliaceae. Hallier (1912) placed Dipterocarpaceae (without *Monotes,* which has marked affinities with Elaeocarpaceae and Tiliaceae) in the Columnifères (i.e., Malvales). According to Bancroft (1933, 1935) the African and Madagascan subfamily Monotoideae is a connecting link between Dipterocarpaceae and tropical Asiatic members of Tiliaceae. There are definite similarities between Dipterocarpaceae and Tiliaceae including the presence of a tillioid exine structure in both families (Maury et al., 1975). It is interesting to note that *Marquesia excelsa* was originally described as *Schoutenia*—a Malesian genus of Tiliaceae, and a recently described Neotropical genus *Pakaraimaea* (Maguire et al., 1977), which was originally included in Dipterocarpaceae, is considered by Kostermans (1978) as a representative of Tiliaceae closely related to *Schoutenia.* Monotoideae differ from Dip-

terocarpoideae by their colporate pollen grains with four-layered exine, but the difference is not so clear cut and the endemic Ceylonese genus *Stemonoporus* forms a link between two subfamilies (Maury et al., 1975). There are also differences in calyx and fruit morphology, but the genus *Marquesia* (Monotoideae) with a valvate calyx and five-winged fruit forms the connecting link (Maury et al., 1975). Subfamilies Dipterocarpoideae and Monotoideae.

7. Sarcolaenaceae (incl. Chlaenaceae, Rhodolaenaceae and Schizolaenaceae). Related to Tiliaceae and Dipterocarpaceae. Dehay (1957) emphasizes the similarity of the petiolar vascular anatomy to that of Tiliaceae. There are also many similarities in pollen morphology (Carlquist, 1964).

8. Sphaerosepalaceae (=Rhopalocarpaceae). Definitely belong to Malvales (Boureau, 1958; Capuron, 1962; Huard, 1965; Keating, 1968, 1970; Baas, 1972) and probably nearest to Scytopetalaceae and Sarcolaenaceae.

9. Bombacaceae. Closely related to Sterculiaceae. The closest to Sterculiaceae are the most primitive tribes with simple pinnately nerved leaves (Hutchinson, 1967).

10. Malvaceae. Very closely related to Bombacaceae and the two families practically merge. The most advanced family of Malvales.

Order 41. Euphorbiales.

The primitive members of Euphorbiales show obvious links with Malvales, in particular with the family Sterculiaceae. Evidently the gynoecium was originally typically paracarpous in Euphorbiales (as in Malvales) and became multilocular as a result of fusion of intrusive parietal placentae in the center of the ovary (secondary syncarpy—see Takhtajan, 1966). On the other hand Euphorbiales have much in common with the primitive members of Violales, especially with Flacourtiaceae. Therefore Hallier (1912) placed Euphorbiaceae immediately after Flacourtiaceae. According to him the Euphorbiaceae arose from Flacourtiaceae "près des Pangiées et Idesiées." One may presume that Euphorbiales may have arisen from some ancient group intermediate between Flacourtiaceae and Malvales (Takhtajan, 1959, 1966).

1. Euphorbiaceae (incl. Androstachydaceae, Bischofiaceae, Hymenocardiaceae, Peraceae, Picrodendraceae, Stilaginaceae, Uapacaceae). A very large and highly diverse family which is clearly related to both Sterculiaceae and Flacourtiaceae. *Picrodendron* is probably best placed in Euphorbiaceae-Oldfieldioideae (Webster, 1975; Hayden, 1977). Subfamilies Phyllanthoideae, Oldfieldioideae, Acalyphoideae, Crotonoideae, Euphorbioideae.

2. Pandaceae. Very near to Euphorbiaceae (see Forman, 1966; Takhtajan, 1966; Webster, 1967).

3. Dichapetalaceae (Chailletiaceae). Near to Euphorbiaceae, especially to the subfamily Phyllanthoideae (Wettstein, 1935; Takhtajan, 1966).

4. Aextoxicaceae (*Aextoxicon*). Probably related to Euphorbiaceae. Bentham (in Bentham and Hooker, 1880) included the genus *Aextoxicon* in Euphorbiaceae-Phyllantheae. Pollen grains more or less similar to those in *Aextoxicon* are encountered in Euphorbiaceae (Erdtman, 1952). *Aextoxicon* was excluded from Euphorbiaceae mainly on the basis of apotropous ovules and seeds with ruminate endosperm and orbiculate-cordate cotyledons.

Order 42. Thymelaeales.

Has much in common with Euphorbiaceae and also with Malvales, but closer to the former. Has a common origin with them from flacourtiaceous stock.

1. Thymelaeaceae (incl. Aquilariaceae and Gonystylaceae). According to Heinig (1951) floral morphology of Thymelaeaceae "suggests a derivation of the family from some polymerous parietalean family such, perhaps, as the Flacourtiaceae." The subfamily Gonystyloideae, as well as the genera *Lethedon, Solmsia, Octolepis* and *Trilepisium* occupy a somewhat isolated position within the family. Subfamilies Gonystyloideae, Aquilarioideae, Gilgiodaphnoideae, Thymelaeoideae.

Subclass F. Rosidae

Superorder XII. Rosanae

Order 43. Saxifragales.

Related to Dilleniales and evidently had a common origin with them. A basic group for many other orders.

Suborder Cunoniineae.

1. Brunelliaceae (*Brunellia*). Flowers apetalous, but the gynoecium is apocarpous with a primitive decurrent sutural stigma (Cuatrecasas, 1970). Ovules epitropous.

2. Cunoniaceae (incl. Baueraceae). Closely related to Brunelliaceae. Ovules usually apotropous, but epitropous in *Acsmithia* and *Spiraeanthemum*. The gynoecia of these two genera are also unlike other members of the family (Dickison, 1975). Dickison is of the opinion that they might best be removed from Cunoniaceae. Hideux and Ferguson (1976) concluded that palynologically *Bauera* should be included in Cunoniaceae in the group with *Geissois*. Subfamilies Cunonioideae and Baueroideae.

3. Davidsoniaceae (*Davidsonia*). Closely related to Cunoniaceae. Although the floral anatomy of Davidsoniaceae generally resembles members of Cunoniaceae, ovules epitropous and seeds without endosperm.

4. Eucryphiaceae (*Eucryphia*). Closely related to Cunoniaceae (see Bausch, 1938; Metcalfe and Chalk, 1950; Takhtajan, 1966, and especially Dickison, 1978). Planchon (1854) and Hallier (1903a, 1908, 1912) included *Eucryphia* in Cunoniaceae. Hideux and Ferguson (1976) concluded that palynologically *Eucryphia* (together with *Bauera*) should be included in Cunoniaceae in the group with *Geissois*.

Suborder Pittosporineae.

5. Escalloniaceae (incl. Brexiaceae, Dulongiaceae, or Phyllonomaceae, Iteaceae, Tetracarpaeaceae, Tribelaceae and *Corokia* and excl. *Pottingeria*). The genus *Corokia* has a definite escalloniaceous affinity and is close to *Argophyllum* (see Hallier, 1908; Engler, 1930; Agababian, 1961; Eyde, 1966; Patel, 1973; and Ferguson and Hideux, 1980). *Ixerba* occupies a somewhat intermediate position between *Brexia* and Cuttsieae (incl. Agrophylleae). *Phyllonoma* has some common features in seed structure with *Ribes* (Krach, 1977). The genera *Itea* and *Choristylis* differ from the other members of the family in pollen morphology (Agababian, 1964; Hideux and Ferguson, 1976), ovule structure, chromosome numbers. *Itea* contains allitor (Plouvier, 1965). *Tetracarpaea* is the only escalloniaceous genus with apocarpous gynoecium and tetramerous flowers. *Tribeles* differs in pollen morphology (Hideux and Ferguson, 1976). Both *Tetracarpaea* and *Tribeles* have no disc, which is characteristic for the majority of genera. Probably at least some of these isolated genera deserve a family status, but for the final decision of this taxonomic problem a comparative-morphological and chemical study of the whole family Escalloniaceae s.l. is necessary. Subfamilies Escallonioideae, Corokioideae, Tetracarpaeoideae, Iteoideae, Brexioideae, Dulongioideae (Phyllonomoideae).

6. Hydrangeaceae (incl. Kirengeshomaceae ?, Philadelphaceae, and *Pottingeria*—see Lobreau, 1969, and Hideux and Ferguson, 1976). Related to Escalloniaceae and had a common origin with them, but differing by usually opposite leaves and cellular endosperm. Palynologically the genera *Platycrater, Broussaisia* and *Dichroa* are transitional between Escalloniaceae and Hydrangeaceae (Hideux and Ferguson, 1976). Agababian (1961) concluded that palynologically Hydrangeaceae are linked with Montiniaceae through *Hydrangea anomala*. Subfamilies Philadelphoideae, Kirengeshomoideae, Hydrangeoideae.

7. Montiniaceae. Near to Escalloniaceae and Hydrangeaceae, but much more advanced: perforation plates always simple, flowers unisexual, etc. Pollen grains of *Grevea* and *Montinia* have many similarities with those

of Escalloniaceae (Hideux and Ferguson, 1976). *Montinia* contains the iridoid montinioside, structurally related to a compound found in *Deutzia* (Hydrangeaceae), as well as in *Viburnum* and members of Valerianaceae (Dahlgren et al., 1977).

8. Columelliaceae (*Columellia*). Hallier (1912) included the genus *Columellia* in Saxifragaceae-Philadelpheae, Cronquist (1968) put the family Columelliaceae (separated already by D. Don in 1828) near Pittosporaceae and Grossulariaceae s.l., and Stern et al. (1969) conclude, that "perhaps the nearest relatives are in the Escalloniaceae." Columelliaceae differ from Escalloniaceae in sympetalous and slightly zygomorphic flowers, in two stamens with broad connective and one twisted pollen sac.

9. Roridulaceae (*Roridula*). Systematic position is not very clear. Most probably related to the Escalloniaceae and Hydrangeaceae. Has notably primitive wood features (Carlquist, 1976a), much more primitive than those in the Pittosporaceae.

10. Pittosporaceae. Related to Escalloniaceae, but perforations simple, secretory canals are present in the pericycle of the stem, roots and leaves, parenchyma vasicentric, flowers usually more or less sympetalous, ovules unitegmic and tenuinucellate (in Escalloniaceae they are sometimes bitegmic and crassinucellate).

11. Byblidaceae (*Biblis*). Related to Pittosporaceae (Domin, 1922) and probably had a common origin with them, but the endosperm formation is cellular and very well developed primary and secondary haustoria are present (Vani-Hardev, 1972). Flowers of *Byblis,* especially those of *B. gigantea,* strikingly resemble flowers of the Australian pittosporaceous genus *Cheiranthera* (Planchon, 1848; Diels, 1930).

12. Bruniaceae. Probably related to Escalloniaceae and Pittosporaceae, but ovule with a long micropyle and pollen morphology different (Erdtman, 1952). Petals of *Lonchostoma* united at the base into a short tube.

13. Alseuosmiaceae. Probably related to Escalloniaceae, differing mainly by their sympetalous flowers.

14. Pterostemonaceae (*Pterostemon*). Probably related to Hydrangeaceae, differing mainly by the alternate leaves with very small, deciduous stipules and the absence of endosperm from the seeds. The toothed (denticulated) stamens of *Pterostemon* are also met with in some Hydrangeaceae (i.e. *Fendlera* and *Deutzia* spp.—see Hutchinson, 1969).

Suborder Saxifragineae.

15. Saxifragaceae (incl. Astilbaceae, Peltiphyllaceae and ? Penthoraceae). Probably had a common origin with Escalloniaceae and Hydrangeaceae, but ovule usually bitegmic (except *Peltiphyllum*) and crassinucellate. The most primitive genus is *Astilbe* (apocarpous gynoecium). The genus *Penthorum* occupies a somewhat intermediate position between

Saxifragaceae and Crassulaceae (Berger, 1930; Mauritzon, 1933a; Agababian, 1961; Hideux and Ferguson, 1976). *Peltiphyllum* is rather isolated within the family (Lébeque, 1952; Krach, 1977). Subfamilies Penthoroideae, Astilboideae, Saxifragoideae, Peltiphylloideae.

16. Crassulaceae. Very near to Saxifragaceae, especially to the monogeneric subfamily Penthoroideae, and had a common origin. In some respects, including embryological characters (Subramanyam, 1962), Crassulaceae are even more primitive than Saxifragaceae. Subfamilies Sedoideae, Sempervivoideae, Echeverioideae, Cotyledonoideae, Kalanchoideae, Crassuloideae.

17. Cephalotaceae. Probably closely related to Crassulaceae, but pollen grains have more similarities with Escalloniaceae (Hideux and Ferguson, 1976).

18. Grossulariaceae (=Ribesiaceae; incl. Rousseaceae ?). Closely related to Saxifragaceae. Floral anatomy resembles Saxifragaceae s.str. (Bensel and Palser, 1975) and "the seed-structure is similar to that of Crassulaceae and Saxifragaceae but the aril, the sarcotesta and the firm endotesta suggest a more primitive state" (Corner, 1976). The genus *Roussea* "has close palynological affinities with *Ribes* with its polyporate aperture type and complete tectum" (Hideux and Ferguson, 1976). As regards the genus *Ribes*, it shows "a very wide range of pollen types some of which are transitional to Escalloniaceae" (Hideux and Ferguson, 1976).

19. Vahliaceae (*Bistella*). Related to the Saxifragaceae, but ovules tenuinucellate, micropyle formed only by the inner integument, embryogeny of the Caryophyllad type, ovary with two to three large placentae hanging from the apex of the locule. Besides the seeds do not show any traces of the raphe when ripe (Krach, 1977).

20. Eremosynaceae (*Eremosyne*). Related to the Saxifragaceae, but with only one sub-basal axile ascending ovule per locule and loculicidal capsule. Pollen morphology is also different (Agababian, 1961).

21. Greyiaceae (*Greyia*). Probably related to Saxifragaceae and Grossulariaceae. Leaf-shape, venation, resinous glands, petiole, etc. resemble *Ribes*, e.g. *R. pentlandii* (Airy Shaw, 1973), but palynologically closer to Francoaceae (Hideux and Ferguson, 1976).

22. Francoaceae (*Francoa* and *Tetilla*). Related to Saxifragaceae, but flowers usually tetramerous and stigmas commissural. These are also notable differences in pollen morphology (Agababian, 1961).

23. Parnassiaceae (incl. Lepuropetalaceae ?). Related to Saxifragaceae, but ovule tenuinucellate, endosperm formation nuclear, stigmas commissural, and seeds with scanty endosperm. Subfamilies Parnassioideae and Lepuropetaloideae.

24. Droseraceae. Related to Parnassiaceae and had a common origin with them.

25. Gunneraceae (*Gunnera*). Possibly belong to the order Saxifragales (Huber, 1963), but relationships obscure. Much more information is necessary before a correct assignment can be made.

Order 44. Rosales.

Linked to Dilleniales and to the primitive families of Saxifragales through the Rosaceae-Spiraeoideae and had a common origin with Saxifragales. In general more advanced than Saxifragales (seeds without endosperm or rarely with scanty endosperm, perforation plates mostly simple, etc.), but ovules crassinucellate. Endosperm formation is always nuclear.

1. Rosaceae (incl. Amygdalaceae, Malaceae, and Spiraeaceae). Subfamilies Spiraeoideae, Rosoideae, Maloideae, Prunoideae.
2. Chrysobalanaceae (excl. *Stylobasium*). Closely related to Rosaceae, especially to the subfamily Spiraeoideae.
3. Neuradaceae. Closely related to Rosaceae, especially to the subfamily Rosoideae, but more more advanced.

Order 45. Fabales.

Closely related to Saxifragales, especially to the suborder Cunoniineae, and derived from the saxifragalean stock.

1. Fabaceae or Leguminosae (incl. Caesalpiniaceae and Mimosaceae). Subfamilies Mimosoideae, Caesalpinioideae, Faboideae.

Order 46. Connarales.

Has much in common with Saxifragales, Rosales and Fabales (see Dickison, 1971, 1972b, 1973) and probably has a common ancestry with Fabales from the saxifragalean stock.

1. Connaraceae. Subfamilies Jollydoroideae and Connaroideae.

Order 47. Podostemales.

Related to and derived from Saxifragales, most probably from the Crassulaceae-like ancestor (see Mauritzon, 1933b, 1939; Maheshwari, 1945; Subramanyam, 1962; Kapil, 1970). Maheshwari (1945: 31) concludes, that it is "almost certain that the Podostemaceae are much reduced derivatives of the Crassulaceae" (among the Crassulaceae *Crassula aquatica* "has a mode of life somewhat similar to Podostemaceae"—Subramanyam, 1962).

1. Podostemaceae. Subfamilies Tristichoideae and Podostemoideae.

Order 48. Nepenthales.

Probably related to Saxifragales, especially to Droseraceae.

1. Nepenthaceae (*Nepenthes*).

Superorder XIII. Myrtanae

Order 49. Myrtales.

Evidently derived from Saxifragales-Cunoniineae.

Suborder Myrtineae.

1. Crypteroniaceae. Although shows some connections with Cunoniaceae, the totality of floral morphological, palynological and anatomical evidence support inclusion in Myrtales (see Muller, 1975; Vliet and Baas, 1975).

2. Lythraceae. Closely related to Crypteroniaceae.

3. Sonneratiaceae. Closely related to Crypteroniaceae and Lythraceae.

4. Punicaceae (*Punica*). Closely related to Lythraceae.

5. Melastomataceae (incl. Memecylaceae). Related to Crypteroniaceae and Lythraceae. Subfamilies Melastomatoideae, Astronioideae, Memecyloideae.

6. Oliniaceae (*Olinia*). Related to Crypteroniaceae and Melastomataceae.

7. Penaeaceae. Close to Oliniaceae.

8. Myrtaceae (incl. Heteropyxidaceae and ? Psiloxylaceae). Related to Lythraceae, Punicaceae and Melastomataceae. Subfamilies Leptospermoideae and Myrtoideae.

9. Combretaceae. Related to Lythraceae. Subfamilies Strephanematoideae and Combretoideae.

10. Onagraceae. Somewhat isolated within the order. Probably related to Lythraceae. The closest to Lythraceae is the genus *Ludwigia* (incl. *Jussiaea*).

11. Trapaceae. Related to Onagraceae, especially to the genus *Ludwigia*.

Suborder Haloragineae.

12. Haloragaceae (incl. Myriophyllaceae and excl. Gunneraceae and Hippuridaceae). Probably related to Onagraceae.

Suborder Rhizophorineae.

13. Rhizophoraceae (incl. Anisophylleaceae, Legnotidaceae and Polygonanthaceae—see Pires and Rodrigues, 1971, and Vliet, 1976). Probably related to Lythraceae and possibly to Combretaceae, but differ from the all other families of the order Myrtales except Lecythidaceae in the lack of vestured pits and internal phloem (Vliet, 1976).

Suborder Lecythidineae.

14. Lecythidaceae (incl. Asteranthaceae, Barringtoniaceae, Foetidiaceae, and Napoleonaceae). Isolated within the order. Probably related to Lythraceae. Subfamilies Planchonioideae, Lecythidoideae, Napoleonoideae.

Superorder XIV. Rutanae

Order 50. Rutales.

Evidently derived from the immediate ancestor of Saxifragales-Cunoniineae.

Suborder Rutaneae.

1. Rutaceae (incl. Flindersiaceae: *Flindersia* and *Chloroxylon*—see Price, 1952; Ritchie et al., 1963; Hartley, 1969, and Pennington and Styles, 1975, and *Tetradiclis*—see Fenzl, 1841; Hallier, 1908, 1912, and Takhtajan, 1966). Subfamilies Rutoideae, Dictylomatoideae, Flindersioideae, Spathelioideae, Toddalioideae, Aurantioideae.

2. Rhabdodendraceae. Probably very near to Rutaceae (see Puff and Weber, 1976), but sieve-element plastids are of P-type (Behnke, 1976b), whereas in all the investigated Rutaceae they are of S-type.

3. Cneoraceae. Very near to Rutaceae.

4. Simaroubaceae (incl. Surianiaceae—see Rock, 1972). Very near to Rutaceae and ? Irvingiaceae—see Corner, 1976, who concluded, that there is undoubted resemblance in seed-structure of *Irvingia* with Simaroubaceae and Balanitaceae. Subfamilies Simaroubioideae, Irvingioideae, Picramnioideae, Alvaradoideae, Surianoideae.

5. Zygophyllaceae (incl. Peganaceae and excl. *Tetradiclis*). Related to Rutaceae and Simaroubaceae.

6. Nitrariaceae (*Nitraria*). Related to Rutaceae and Zygophyllaceae.

7. Balanitaceae (*Balanites*). Related to Simaroubaceae and Zygophyllaceae.

8. Meliaceae (incl. Aitoniaceae: *Nymania* and excl. *Cedrelopsis* and *Ptaeroxylon*—see Pennington and Styles, 1975). Near to Rutaceae. *Flindersia* and *Chloroxylon* occupy a somewhat intermediate position between Rutaceae and Meliaceae. Subfamilies Cedreloideae, Swietenioideae, Melioideae.

9. Kirkiaceae (*Kirkia*). Near to Meliaceae.

10. Ptaeroxylaceae (*Ptaeroxylon* and *Cedrelopsis*). Near to Kirkiaceae.

11. Burseraceae. Very close to Simaroubaceae.

12. Anacardiaceae (incl. *Blepharocarya* and Pistaciaceae). Closely related to Burseraceae, Rutaceae, Simaroubaceae, and Meliaceae.

13. Julianiaceae. Very near to Anacardiaceae.

14. Podoaceae (Dobineaceae). Near to Anacardiaceae.

Suborder Coriariineae.

15. Coriariaceae (*Coriaria*). Probably related to Rutaceae.

Order 51. Sapindales (Acerales).

Near to Rutales and descended from a common ancestor.

1. Staphyleaceae. According to Hallier (1908) "Die Staphyleaceen sind verwandt mit den Cunoniaceen." According to Linden (1960) the affinity of Staphyleaceae with the Cunoniaceae seems to be without much doubt and is shown by the fact that species of *Turpinia* have twice been wrongly described as members of the Cunoniaceae.

2. Sapindaceae. Related to Staphyleaceae. Subfamilies Dodonaeoideae and Sapindoideae.

3. Aceraceae. Very closely related to Sapindaceae, especially to the tribe Harpullieae (see Radlkofer, 1890, 1931–1934; Muller and Leenhouts, 1976).

4. Hippocastanaceae (*Aesculus* and *Billia*). Very closely related to Sapindaceae, especially to the tribe Harpullieae (see Radlkofer, 1890, 1931–1934; Muller and Leenhouts, 1976). Both Aceraceae and Hippocastanaceae could with nearly the same right be added to Sapindaceae as two more tribes (Muller and Leenhouts, 1976).

5. Stylobasiaceae (*Stylobasium*). Near to Sapindaceae (see Prance, 1965, and Carlquist, 1978).

6. Gyrostemonaceae. Close to Sapindaceae-Dodonaeoideae and especially to Stylobasiaceae (see Thorne, 1976, 1977, and Carlquist, 1978).

7. Bataceae (*Batis*). Related to Gyrostemonaceae and shares a common sapindalean affinity (see Thorne, 1977, Carlquist, 1978).

8. Emblingiaceae (*Emblingia*). Probably allied to Sapindaceae (see Leins in Erdtman et al., 1969).

9. Bretschneideraceae (*Bretschneidera*). Near to Sapindaceae and Hippocastanaceae.

10. Melianthaceae. Near to Sapindaceae.

11. Akaniaceae (*Akania*). Related to Sapindaceae.

12. Sabiaceae (incl. Meliosmaceae). Probably related to Sapindaceae. Subfamilies Meliosmoideae and Sabioideae.

13. Physenaceae fam. nov. (Name based on and including only *Physena* Noronha ex Thouars, Gen. Nov. Madag. 6. 1806.) Affinities very obscure. Perhaps related to Sapindaceae (see Capuron, 1968).

Order 52. Geraniales.

Linked with Rutales, especially with the family Rutaceae.

Suborder Linineae.

1. Linaceae (incl. Ctenolophonaceae—see Narayana and Digamber Rao, 1971; Hugoniaceae, and Ixonanthaceae). The subfamily Hugonioi-

deae (especially the genus *Indorouchera*) is the most primitive member of the order Geraniales. Subfamilies Linoideae, Ctenolophonoideae, Ixonanthoideae.

2. Houmiriaceae ("Humiriaceae"). Closely related to Linaceae.
3. Erythroxylaceae (incl. Nectaropetalaceae). Closely related to Linaceae and Houmiriaceae.

Suborder Geraniineae.

4. Oxalidaceae (incl. Averrhoaceae, Hypseocharitaceae and Lepidobotryaceae). Related to Linaceae, but the micropyle formed by both integuments. Probably had a common ancestry with Linaceae. Subfamilies Averrhoideae, Oxalidoideae, Lepidobotryoideae, Hypseocharitoideae.
5. Geraniaceae (incl. Biebersteiniaceae, Dirachmaceae, Ledocarpaceae, and Vivianiaceae). Related to and had a common origin with Oxalidaceae, but ovule crassinucellate. Subfamilies Geranioideae, Dirachmoideae, Biebersteinioideae, Vivianoideae, Ledocarpoideae.

Suborder Balsamininеae.

6. Balsaminaceae. Related to Geraniaceae, but ovule tenuinucellate and endosperm cellular, with the formation of terminal haustoria.
7. Tropaeolaceae. Related to Geraniaceae (but ovule tenuinucellate) and to Balsaminaceae (but endosperm nuclear). From both Geraniaceae and Balsaminaceae the family Tropaeolaceae differs by the formation of aggressive suspensor haustorium which penetrates the seed coat and the pericarp, and by the presence of myrosin.

Suborder Limnanthineae.

8. Limnanthaceae. Probably related to Geraniaceae, Balsaminaceae and Tropaeolaceae. Ovule unitegmic.

Order 53. Polygalales.

Very closely linked with Geraniales, especially through the family Malpighiaceae, which with almost equal reason might be included in either of these two orders.

1. Malpighiaceae. Subfamilies Gaudichaudioideae and Malpighioideae.
2. Trigoniaceae. Closely related to Malpighiaceae through the West-Malesian genus *Trigoniastrum*.
3. Vochysiaceae. Closely related to Trigoniaceae.
4. Polygalaceae (incl. Diclidantheraceae and Xanthophyllaceae). Related to Malpighiaceae, Vochysiaceae and Trigoniaceae. Subfamilies Xanthophylloideae, Polygaloideae, Moutabeaoideae (incl. *Diclidanthera*).
5. Krameriaceae (*Krameria*). Near to Polygalaceae.
6. Tremandraceae. Affinities much disputed. Possibly related to Polygalaceae (Hallier, 1908, 1912). According to Carlquist (1977a) wood anat-

omy tends to support a pittosporaceous affinity, but pollen grains of *Tremandra* are more or less similar to those of *Thryallis* (*Calphimia*) (Malpighiaceae) (Erdtman, 1952).

Superorder XV. Aralianae

Order 54. Cornales.

Evidently derived from Saxifragales–Pittosporineae. The most primitive members of the order show clear affinity with Escalloniaceae and Hydrangeaceae. Palynological studies show that there are no well defined barriers between these two orders but different degrees of overlapping seem to occur between some genera of both groups (see Ferguson and Hideux, 1980).

1. Davidiaceae (*Davidia*) ("*Davidia* is the nearest thing to the common ancestor of *Cornus* and *Nyssa*"—Eyde, 1967).

2. Nyssaceae (*Camptotheca* and *Nyssa*). Closely related to Davidiaceae.

3. Alangiaceae (*Alangium*, incl. *Metteniusa* ?). Probably related to Nyssaceae, but see Eyde, 1968, who concluded that the prevailing opinion that Alangiaceae belong to the Cornales is not well supported by anatomical characters of the flower. According to Eyde (1968) the similarity in alkaloid content (Hegnauer, 1965, 1966) and certain details of floral structure suggest that the closest allies of Alangiaceae may be found in the Rubiaceae.

4. Cornaceae (incl. Curtisiaceae, and ? Mastixiaceae and excl. *Corokia* and *Kaliphora*). *Curtisia* and especially *Mastixia* morphologically are rather isolated within the family. Subfamilies Cornoideae, Curtisioideae, Mastixioideae.

5. Aucubaceae (*Aucuba*). The genus *Aucuba* is usually included in the Cornaceae, but from all the other cornaceous genera it markedly differs by its conspicuously oblique stigma, by its very short embryo at the apex of the endosperm, and as Eramian (1971) and Ferguson (1977) and Ferguson and Hideux (1980) have shown, by its very distinct intectate pollen grains. *Aucuba* has $x = 8$ and thus stands out sharply on its basic chromosome number (see Raven, 1975).

6. Garryaceae (*Garrya*). Related to Cornaceae. Pollen morphology is nearest to *Aucuba* (Eramian, 1971). Besides *Aucuba* and *Garrya* have the decarboxylated iridoid aucubin and no tannins (Bate-Smith et al., 1975). *Garrya* and *Aucuba* have been grafted.

7. Melanophyllaceae (Takhtajan, 1970) (*Melanophylla* and ? *Kaliphora*). Probably related to Cornaceae but differs in free and subulate styles, glandular hairs with spherical heads, etc. According to Ferguson (1977) "*Melanophylla* and *Kaliphora* although easily sepa-

rable on pollen characters are relatively closely related palynologically and have totally closely distinct pollen grains from other Cornaceae, apart from perhaps a small similarity with *Griselinia*." Needs special morphological, cytological and biochemical study.

8. Griseliniaceae (Takhtajan, 1970; Airy Shaw, 1973) (*Griselinia*). The genus *Griselinia* is very isolated within the order, both morphologically (Philipson, 1967), palynologically (Ferguson and Hideux, 1980), cytologically (Raven, 1975), and serologically (Brunner and Fairbrothers, 1978). According to Philipson (1967, 1977) and Rodriguez (1971) *Griselinia* is a type in which features of Cornaceae, Araliaceae and Escalloniaceae were blended (see also Ferguson and Hideux, 1980). $x = 9$.

9. Toricelliaceae (*Toricellia*). Related to Cornaceae but differs in many respects (thick branches and broad *Sambucus*-like pith, palmatilobed leaves, presence of multicellular glandular hairs, simple perforation plates, characteristic lax pendulous thyrses, funicle thickened to form an obturator, pollen morphology, etc.). Intermediate between Cornaceae and Araliaceae. Dahlgren (1975, 1977) included his family in Araliales. This most interesting family needs special study.

10. Helwingiaceae (*Helwingia*). Related to Cornaceae, but differs in many respects (including pollen morphology—see Ferguson and Hideux, 1980, and the absence of iridoids) and approaches to Araliaceae. Eyde (1966, 1967) and Rodriguez (1971) suggest returning *Helwingia* to Araliaceae, where Bentham and Hooker had it. Hutchinson (1959, 1967, 1969) retained it in Araliaceae. *Helwingia* differs from Araliaceae mainly in complete lack of secretory canals. $x = 19$ (Raven, 1975).

Order 55. Araliales (Apiales).

Very closely linked with Cornales, especially with Toricelliaceae, Helwingiaceae and some cornaceous genera (especially *Mastixia*). It is difficult or even impossible to draw a distinct clear cut morphological boundary between these two orders. However, according to Bate-Smith et al. (1975), the chemical relationships of Cornales and Araliales is remote and in the latter almost all species have essential oil and resins in schizogenous cavities, especially those of falcarinone type, contain oleanene and ursene types of steroidal sapogenins and generally posesses high amounts of petroselenic acid in their seed fats. But chemical differences between these two orders are also by no means clear cut and the necessity of subdivision of the order into two separate orders is still open.

1. Araliaceae.

2. Apiaceae or Umbelliferae (incl. Hydrocotylaceae). Very closely related to Araliaceae and included in Araliaceae by Baillon (1880), Calestani (1905), Hallier (1905, 1912) and Thorne (1968, 1973). According to Thorne (1973, 1976) the phylogenetic gap between the Araliaceae and the Api-

aceae is at most only of subfamily width. Subfamilies Hydrocotyloideae, Saniculoideae, Apioideae.

Superorder XVI. Celastranae

Order 56. Celastrales.

Evidently derived from the saxifragalean stock, most probably from the common ancestor of such families as Escalloniaceae and Hydrangeaceae. According to Hallier (1908) "Die Aquifoliaceen sind reducierte Brexieen" and "die Celastraceen verwandt mit den Aquifoliaceen und Brexieen." Plouvier (1965) reported that in *Brexia* (Escalloniaceae) occurs dulcitor which is characteristic for Celastraceae. See also Perrier de la Bâthie (1942).

Suborder Icacinineae.

1. Icacinaceae (incl. Phytocrenaceae).
2. Sphenostemonaceae (*Sphenostemon*). Close to Icacinaceae (Baas, 1975).
3. Aquifoliaceae. Related to Icacinaceae.
4. Phellinaceae (*Phelline*). Related to Aquifoliaceae, but differ in many respects (see Takhtajan, 1966; Baas, 1975).
5. Paracryphiaceae (*Paracryphia*). Possibly related to Sphenostemonaceae (see Dickison and Baas, 1977).
6. Cardiopterygaceae (*Peripterygium*). Probably related to Icacinaceae. The articulated laticiferous tubes of *Peripterygium* (*Cardiopteris*) similar to those which are found in the tribe Couleae of the Olacaceae (Metcalfe and Chalk, 1950: 375), but pollen grains similar to those of some Icacinaceae (*Cassinopsis tinifolia*—see Lobreau, 1969).
7. Medusandraceae (*Medusandra*). Relationships not fully clear. Probably related to Icacinaceae.

Suborder Celastrineae.

8. Celastraceae (incl. Chingithamnaceae, Hippocrateaceae, and ? the genus *Pottingeria*—see Airy Shaw et al., 1973). Subfamilies Celastroideae, Tripterygioideae, Cassinoideae, Campylostemonoideae, Hippocrateoideae. Subfamilies Campylostemonoideae, Cassinoideae and Tripterygioideae are rather isolated within the family.
9. Stackhousiaceae. Closely related to Celastraceae.
10. Siphonodontaceae (Capusiaceae) (*Siphonodon*). Close to Celastraceae, but pollen grains "have not been encountered in Celastraceae proper" (Erdtman, 1952) and resemble those of some Icacinaceae of the *Apodytes*-type (Lobreau, 1969).
11. Goupiaceae (*Goupia*). Near to Celastraceae.
12. Geissolomataceae (*Geissoloma*). Probably related to Celastraceae

(Baillon, 1877; Takhtajan, 1966; Cronquist, 1968), but pollen morphology different (of the Euphorbiaceae type according to Lobreau, 1969). See also Dahlgren and Rao (1969) and Carlquist (1975).

13. Salvadoraceae. Systematic position much disputed. Possibly related to Celastraceae (see Maheshwari, 1972).

14. Corynocarpaceae (*Corynocarpus*). Relationships obscure. Usually placed in Celastrales, but pollen grains bilateral and two-aperturate and according to Erdtman (1952) have some characters in common with the grains in Crypteroniaceae, Cunoniaceae, Eucryphiaceae and *Bauera*. Lobreau (1969) concluded, that "Pollen rappelant celui de certaines Saxifragaceae (type *Itea*), mais apertures de type different."

15. Lophopyxidaceae (*Lophopyxis*). Relationships obscure. By its author Hooker f. (1887), by Pax (1896) and by Hallier (1912) *Lophopyxis* was included in Euphorbiaceae, but Engler (1893) placed it in Icacinaceae and Hutchinson (1959, 1969) and Scholz (in Engler's Syllabus, 1964) in Celastraceae. Pfeiffer (1951) segregated this genus as a distinct family Lophopyxidaceae, but the affinity is still uncertain. Dahl (1955) stated that the range of pollen forms within Euphorbiaceae could include those of *Lophopyxis*. According to Lobreau (1969) "Pollen rappelant celui des Tiliaceae: de type non Célastrale."

Order 57. Santalales.

The most primitive members of the order (especially Olacaceae) are very near to the primitive families of Celastrales (especially to Icacinaceae). However, the order Santalales does not appear to be a direct descendent of Celastrales, but rather shares a common origin with them.

Suborder Santalineae.

1. Olacaceae (incl. Aptandraceae, ? Erythropalaceae, Octoknemaceae, and Schoepfiaceae). Subfamilies Schoepfioideae and Olacoideae.

2. Opiliaceae. Closely related to Olacaceae.

3. Santalaceae (incl. Antholobaceae, Arjonaceae, Exocarpaceae, and Osyridaceae). Closely related to and derived from Olacaceae (Hallier, 1912; Pilger, 1935; Fagerlind, 1948; Agarwal, 1963; Kuijt, 1968, 1969).

4. Misodendraceae ("Myzodendraceae") (*Misodendrum*). Near to Santalaceae, especially to the South American genera *Arjona* and *Quinchamalium* (Skottsberg, 1935) and probably derived from them (Hallier, 1912).

Suborder Loranthineae.

5. Loranthaceae (incl. Elytranthaceae, Lepidariaceae, Nuytsiaceae, Psittacanthaceae, Treubaniaceae, and Treubellaceae). Probably derived directly from Olacaceae (Hallier, 1912), possibly from a *Chaunochiton*-like ancestor (Kuijt, 1968, 1969).

6. Viscaceae (incl. Arceuthobiaceae, Bifariaceae, Dendrophthoaceae, ? Eremopelidaceae and Ginalloaceae). Near to Loranthaceae and probably had a common origin with Loranthaceae. Kuijt (1968) resurrected Van Tieghem's Eremolepidaceae to accommodate *Eremolepis, Antidaphne* and *Eubrachion.* In his opinion Viscaceae s.str. derived from Santalaceae plants similar to *Phacellaria,* whereas Eremolepidaceae may have *Opilia*-like ancestor.

Order 58. Balanophorales.

Probably near to and derived from Santalales, but the affinity is not fully clear.

1. Cynomoriaceae (*Cynomorium*). The most primitive member of the order: flowers polygamous, ovule with thick integument.

2. Balanophoraceae (incl. Hachetteaceae, Helosidaceae, Langsdorffiaceae, Lophophytaceae, and Sarcophytaceae). Probably related to Cynomoriaceae and had a common origin, but more advanced: flowers unisexual, ovule without an integument. The genus *Mystropetalon,* which is taxonomically very isolated within the family, is the most primitive member of Balanophoraceae and probably the nearest to *Cynomorium* (see Kuijt, 1969). Subfamilies Mystropetaloideae, Dactylanthoideae, Sarcophytoideae, Helosidoideae, Lophophytoideae, Balanophoroideae.

Order 59. Rhamnales.

Near to Celastrales, from which they are chiefly distinguished by the antepetalous stamens (stamens are opposite to the petals). Both Rhamnales and Celastrales evidently had a common origin from a diplostemonous saxifragalean stock.

1. Rhamnaceae. Contain S-type sieve-element plastids.

2. Vitaceae. Related to Rhamnaceae, but contain P-type sieve-element plastids.

3. Leeaceae. Closely related to Vitaceae. Contain P-type sieve-element plastids.

Order 60. Elaeagnales.

Shows many similarities with Rhamnales including seed-anatomy ("The seed-structure is typically Rhamnaceous"—Corner, 1976), and uredinological data (see Holm, 1979, and Savile, 1979), but gynoecium is evidently unicarpellate, which forbids the direct derivation from Rhamnales. Both these orders together with the whole superorder Celastranae evidently derived from an apocarpous multicarpellate saxifragalean ancestor.

1. Elaeagnaceae.

Superorder XVII. Proteanae

Order 61. Proteales.

According to Gobi (1916) Proteales derived from "Rosiflorae." Several other authors including Johnson and Briggs (1975) also accept some affinity with Rosales s.l. Most probably Proteales derived from some saxifragalean ancestor which was near to modern Cunoniineae.

1. Proteaceae. Subfamilies Persoonioideae, Proteoideae, Sphalmioideae, Carnarvonioideae, Grevilleoideae.

Subclass G. Asteridae

Superorder XVIII. Gentiananae

Order 62. Gentianales.

Related to Cornales (both morphological and chemical data) and evidently had a common origin with them from Saxifragales-Pittosporineae.

1. Loganiaceae (incl. Antoniaceae, ? Desfontainiaceae, ? Plocospermataceae, Potaliaceae, Spigeliaceae, and Strychnaceae). A very heterogenous family and at least some of its members most probably deserve a family rank, especially *Desfontainia* and *Plocosperma*. Subfamilies Desfontainioideae, Potalioideae, Loganioideae, Antonioideae, Spigelioideae, Strichnoideae, Plocospermatoideae.

2. Rubiaceae (incl. Cinchonaceae, Galiaceae, Henriqueziaceae, and Naucleaceae). Closely related to Loganiaceae, especially to the genus *Mitreola* (see Tiagi and Kshetrapal, 1972, and Thorne, 1976), and had a common origin with them from the saxifragalean stock. It is interesting to note that *Escallonia* contains asperuloside (Plouvier, 1965), a heteroside of relatively limited distribution which occurs commonly only in Rubiaceae. Subfamilies Cinchonoideae, Guettardioideae, Ixoroideae, Rubioideae, Henriquesioideae.

3. Theligonaceae (*Theligonum*). Very closely related to Rubiaceae especially to the subfamily Rubioideae, and perhaps does not deserve family status (see Wunderlich, 1971, Kooiman, 1971, and Thorne, 1976).

4. Apocynaceae. Closely related to Loganiaceae, especially to the genus *Plocosperma* (Takhtajan, 1966; Thorne, 1976). Subfamilies Plumerioideae, Cerberoideae, Apocynoideae.

5. Asclepiadaceae (incl. Periplocaceae). Very close to Apocynaceae and have with some justification been included by Hallier (1905, 1912), Thorne (1968, 1976) and Stebbins (1974) in Apocynaceae. Subfamilies Periplocoideae, Secamonoideae, Asclepiadoideae.

6. Gentianaceae. Related to and probably derived from Loganaceae (incl. ? Saccifoliaceae Maguire and Pires, 1978).

7. Menyanthaceae. Probably related to Gentianaceae and agree with them in chemical characters (Hegnauer, 1969), but differ in some important anatomical characters (see Lindsey, 1938, and Metcalfe and Chalk, 1950) and in having cellular endosperm (Vijayaraghan and Padmanabhan, 1969).

8. Dialypetalanthaceae (*Dialypetalanthus*). Affinities obscure. Probably related to Loganiaceae and Rubiaceae.

Order 63. Oleales.

Relationships much disputed. Most probably related to Gentianales (see Wagenitz, 1977). Data from double diffusion reactions as well as immumoelectrophoresis, reveal strong affinities of the Oleales with the Gentianales and Scrophulariales (Piechura and Fairbrothers, 1979). Uredinological data are also in favor of placing Oleaceae close to the Gentianales (Holm, 1979).

1. Oleaceae (incl. Fraxinaceae, Jasminaceae, and Nyctanthaceae). Subfamilies Jasminoideae and Oleoideae.

Order 64. Dipsacales.

Related to Gentianales (especially to Loganiaceae and Rubiaceae) and to Cornales and had a common origin with them. In Wagenitz's opinion (1977) Dipsacales are nearer to Scrophulariales than to Gentianales.

1. Caprifoliaceae (incl. Carlemanniaceae, ? Sambucaceae and ? Viburnaceae). The family is probably a heterogenous one (see Sax and Kribs, 1930; Wilkinson, 1949; Hillebrand and Fairbrothers, 1970; Fukuoka, 1972). *Sambucus,* which is very isolated within the family, exhibited about as much serological correspondence with *Cornus* as with any tested member of Caprifoliaceae (Hillebrand and Fairbrothers, 1970). Subfamilies Caprifolioideae, Carlemannioideae, Viburnoideae, Sambucoideae.

2. Adoxaceae (*Adoxa*). Closely related to Caprifoliaceae, especially to the genus *Sambucus* (Eichler, 1875; Hallier, 1908, 1912) "*Adoxa* n'est à vrai dire qu'un *Sambucus* réduit" (Hallier, 1912).

3. Valerianaceae. Near to Caprifoliaceae, especially to the tribe Linnaeeae (Wilkinson, 1949). The nearest to Caprifoliaceae, particularly to *Abelia,* is *Nardostachys,* which is the most primitive member of Valerianaceae (Wilkinson, 1949).

4. Morinaceae (*Morina*) (a distinct family—see Vijayaraghavan and Sarveshwari, 1968; Kamelina, 1976, 1977). Near to Caprifoliaceae (Kamelina, 1977).

5. Dipsacaceae (incl. *Triplostegia,* which provides an obvious link to Valerianaceae—see Burtt, 1977).

Order 65. Loasales.

Affinities obscure. A combination of unitegmic tenuinucellate ovule, cellular endosperm, development of terminal haustoria (García, 1962) and occurrence of loganin (Kooiman, 1974; Jensen et al., 1975) makes Loasaceae quite at home within Asteridae (Wagenitz, 1977). Chemistry indicates affinity with Dipsacales in particular (Dahlgren, 1979b). Perhaps the best solution is to put in a separate order placed after Dipsacales and before Polemoniales. Dahlgren (1977b, 1980) creates even a superorder Loasiflorae which he places between his Corniflorae and Gentianiflorae.

1. Loasaceae (*Mentzelia* is very isolated within the family and Leins and Winhard [1973] proposed to exclude it from Loasaceae).

Superorder XIX. Lamianae

Order 66. Polemoniales (incl. Boraginales and Convolvulales).

Near to Gentianales and probably derived from the immediate ancestor of Loganiaceae and allied families.

Suborder Convolvulineae.

1. Convolvulaceae (incl. Dichondraceae and Humbertiaceae). The only family within the order which has intraxylary phloem. It also differs from all other members of the order by the special development of the three outer cell-layers of the integument (Corner, 1976). Subfamilies Humbertioideae, Dichondroideae, Convolvuloideae.

2. Cuscutaceae (*Cuscuta*). Close to Convolvulaceae, but aphyllous and parasitic, with imbricate corolla, with a whorl of scales on the inside of the corolla-tube below the stamens, more copious endosperm, undifferentiated filiform embryo, which is completely without cotyledons, and the absence of intraxylary phloem (which most probably is the result of great reduction of vascular system—see Metcalfe and Chalk, 1950). Tiagi (1951) and Johri and Tiagi (1952) compared the embryological features of *Cuscuta* with those of Convolvulaceae and supported the separation of the family Cuscutaceae.

Suborder Polemoniineae.

3. Polemoniaceae (incl. Cobaeaceae). Related to Convolvulaceae and probably had a common origin with them from the gentianialean stock. Subfamilies Cobaeoideae and Polemonioideae.

Suborder Boraginineae.

4. Hydrophyllaceae (incl. Hydroleaceae and excl. *Ellisiophyllum*). In some respects occupy an intermediate position between Polemoniaceae and Boraginaceae.

5. Boraginaceae (incl. Cordiaceae, Ehretiaceae, Heliotropiaceae and

Wellstediaceae). Closely related to Hydrophyllaceae. Subfamilies Cordioideae, Ehretioideae, Heliotropoideae, Boraginoideae, Wellstedioideae.

6. Lennoaceae. Related to Hydrophyllaceae and Boraginaceae (Hallier, 1912, 1923; Suessenguth, 1927; Copeland, 1935; Maheshwari, 1945, 1950; Avetisian, 1952; Erdtman, 1952; Drugg, 1962).

7. Hoplestigmataceae (*Hoplestigma*). Hallier (1911, 1912) included *Hoplestigma* in the Boraginaceae, but from Boraginaceae it differs by many (11–14) petals, by 20–35 stamens free from the corolla, and by some other features. Related to Boraginaceae-Ehretioideae. According to Erdtman (1952) pollen grains more or less similar to those of Hoplestigmataceae occur in Boraginaceae (*Ehretia*).

Order 67. Lamiales.

Closely related to Polemoniales, especially to Boraginaceae-Ehretioideae, and probably derived from them.

1. Verbenaceae (incl. Avicenniaceae—see Padmanabhan, 1960, 1964, 1970; Chloanthaceae, Dicrastylidaceae, Phrymaceae—see Hallier, 1901, Wernham, 1913, Whipple, 1972; Stilbaceae, Symphoremataceae, and *Lithophytum*—see D'Arcy and Keating, 1973). Subfamilies Viticoideae. Chloanthoideae, Verbenoideae, Lythophytoideae, Rhymatoideae, Nyctanthoideae, Caryopteridoideae, Stilboideae, Symphorematoideae, Avicennioideae.

2. Lamiaceae, or Labiatae (incl. Tetrachondraceae ?). Very near to Verbenaceae. The taxonomic boundary between these two families is not clear-cut. Subfamilies Prostantheroideae, Ajugoideae, Scutellarioideae, Lamioideae, Saturejoideae, Ocimoideae, Catopherioideae, Tetrachondroideae.

3. Callitrichaceae (*Callitriche*). Probably related to Lamiaceae and Verbenaceae (see Jörgensen, 1925; Schürhoff, 1926; Maheshwari, 1950).

Order 68. Scrophulariales (incl. Bignoniales, Hydrostachyales, and Solanales).

Very near to Polemoniales (especially to Convolvulaceae) with which they share a nearer common ancestor.

Suborder Solanineae.

1. Solanaceae (incl. Goetzeaceae, Nolanaceae and Salpiglossidaceae and excl. *Lithophytum*). Related to Convolvulaceae and probably had a common origin with them from the loganiaceous stock. Intraxylary phloem is present, but whereas in Convolvulaceae it arises in the stem above the level of the hypocotyl, in Solanaceae (incl. Nolanaceae) the

intraxylary phloem rises in the hypocotyl (see Mirande, 1922). Endosperm formation cellular, nuclear or helobial and embryogeny conforms to the Solanad-type (in Convolvulaceae endosperm formation is nuclear and embryogeny conforms to the Caryophyllad type). As Corner (1976) points out, "there is certainly no indication that the solanaceous seed is connected with the more complicated construction of Convolvulaceae." On the other hand in seed-structure of *Solanum* and *Lycopersicon* there is a great resemblance with the seed coat of *Strychnos* (Loganiaceae) (Corner, 1976). The small subfamily Nolanoideae (*Alona* and *Nolana*) is characterized by pentamerous gynoecium and by a dry fruit consisting of 1–8-seeded mericarps, but among the Solanoideae *Nicandra* has 3–5-merous gynoecium and in some members of Solaneae there are expressed different stages of the sclerification of pericarp (see Johnston, 1936). Serologically *Schizanthus* is very isolated within the family (see Hawkes and Tucker, 1968, and Tucker, 1969). Subfamilies Nolanoideae and Solanoideae.

2. Duckeodendraceae (*Duckeodendron*). Probably related to Solanaceae.

Suborder Scrophulariineae.

3. Buddlejaceae. Show many similarities with Loganiaceae in external morphology and embryology, but differing in the absence of true stipules (only "auriculae") and of intraxylary phloem, in the glandular, stellate or lepidote indumentum, and chemically. In general rather nearer to Schrophulariaceae than to Loganiaceae (Wagenitz, 1959, 1977; Takhtajan, 1966; Punt and Leenhouts, 1967). As Punt and Leenhouts (1967) point out, "Palynology reveals a close relationship to the Scrophulariaceae and hardly any to the Loganiaceae." Besides, "In Buddlejaceae, *Buddleja* has been reported to contain Group I iridoids typical to Scrophulariales but not of Gentianales" (Jensen et al., 1975).

4. Retziaceae (*Retzia*). Possibly related to Buddlejaceae and Scrophulariaceae. Hallier (1903, 1908, 1912) placed *Retzia* in Scrophulariaceae near *Ixianthes* and *Bowkeria* (but see Dahlgren et al., 1979).

5. Scrophulariaceae (incl. Ellisiophyllaceae, Globulariaceae—see Hallier, 1903b, 1905, 1908, 1912, Thorne, 1968, 1976, Savile, 1979; Halleriaceae, Selaginaceae—see Wettstein, 1891, and Burtt, 1977; Trapellaceae—see Hallier, 1912; and *Oftia*—see Dahlgren and Rao, 1971). Close to Buddlejaceae. The close affinity between these two families is supported both by morphology (including embryology) and chemistry. There are also some similarities with Solanaceae, especially with the tribes Cestreae and Salpiglossideae. *Ellisiophyllum*, though rather isolated within the family, does not deserve the family rank. As Burtt (1977) points out, the evidence

shows a close relationship between Selagineae and Manuleae and the difference between Manuleae and Selagineae is no greater than that between Manuleae and the neighboring tribes in Scrophulariaceae, and is much less than that between, say, Manuleae and Rhinantheae. Therefore he rightly concluded, that Selaginaceae cannot be retained as a separate family. The same is true about Trapellaceae and Globulariaceae. Already Hallier (1912) came to the conclusion that *Trapella* is probably related to Gratioleae and included it in Scrophulariaceae. Pollen grains more or less similar to those in *Trapella* occur in such scrophulariaceous genera, as *Gratiola, Stemodia,* etc. (Erdtman, 1952) and embryologically *Trapella* is close to *Sutera* (*Chaenostoma*) (Singh, 1970). Subfamilies Scrophularioideae (incl. *Trapella*), Rhinanthoideae, Globularioideae, Selaginoideae.

6. Bignoniaceae (incl. *Paulownia* and *Wightia*—see Hallier, 1903a, 1905; Campbell, 1930; Westfall, 1949; Maheshwari, 1961; Takhtajan, 1966; Thorne, 1976, and possibly also *Brandisia*). Very near to Scrophulariaceae, especially to Scrophularieae (Cheloneae) and probably had a common origin with them.

7. Pedaliaceae. Near to Bignoniaceae and Scrophulariaceae.

8. Martyniaceae. Closely related to Bignoniaceae and Pedaliaceae.

9. Orobanchaceae. Very near to Scrophulariaceae. An advanced group which "represents the final stage of the parasitic tendency exhibited in Rhinanthoideae" (Wernham, 1912). Probably derived from Scrophulariaceae-Rhinanthoideae through forms like *Striga orobanchoides* (Tiagi, 1956, 1963, 1970). Hallier (1903b, 1905, 1908, 1912) and Thorne (1976) included them in Scrophulariaceae s.l.

10. Gesneriaceae. Very near to Scrophulariaceae, especially to the tribe Scrophularieae. "A highly advanced, and presumably recent, family" (Burtt, 1977). Subfamilies Cyrtandroideae and Gesnerioideae.

11. Plantaginaceae. Near to and derived from Scrophulariaceae. Hallier (1903a, 1903b, 1905, 1908, 1912) included them in Scrophulariaceae s.l. and placed near Selagineae and Manuleae (Hallier, 1903b, 1912).

12. Lentibulariaceae. Near to and derived from Scrophulariaceae. Hallier (1903a, 1903b, 1905, 1908, 1912) included Lentibularieae in Scrophulariaceae s.l. deriving them from Gratioleae (Hallier, 1903b, 1912; see also Casper, 1963).

13. Myoporaceae (excl. *Oftia*—Hallier, 1905, 1912). Related to Scrophulariaceae and probably had a common origin with them.

14. Acanthaceae (incl. Mendonciaceae ? and Thunbergiaceae). Near to Scrophulariaceae, especially to the tribe Scrophularieae, and probably derived from them (Hallier, 1901, 1912). Subfamilies Nelsonioideae, Thunbergioideae, Mendoncioideae, Acanthoideae, Ruellioideae.

15. Hydrostachyaceae (*Hydrostachys*). Probably derived from Scrophulariaceae (see Jäger-Zurn, 1965; Rauh and Jäger-Zurn, 1966; Takhtajan, 1966; Cronquist, 1968) and possibly had a common origin with Plantaginaceae.

Suborder Hippurineae.

16. Hippuridaceae (*Hippuris*). Relationships are not fully clear. Recent studies suggest inclusion in Scrophulariales, perhaps near Scrophulariaceae, or Plantaginaceae (see Wagenitz, 1975, 1977; Hegnauer, 1966; Dahlgren, 1975).

Superorder XX. Asteranae

Order 69. Campanulales (incl. Goodeniales).

Evidently shares a common origin with Gentianales from a saxifragalean stock. "It is not a very big jump from Saxifragaceae to Campanulaceae, and it is from the stock of the former family that I believe them to have been derived," says Hutchinson (1969). But it is more probable that the common ancestor of Campanulales and Gentianales was nearer to Saxifragales-Pittosporineae rather than to Saxifragales-Saxifragineae. It is interesting to note that a monotypic campanulaceous genus *Berenice* (Reunion), which was formerly included in Saxifragaceae-Escallonioideae or Escalloniaceae, has been transferred to Campanulaceae (see Erdtman and Metcalfe, 1963; Badré et al., 1975; Hideux and Ferguson, 1976). The genus *Berenice* combines some features of both Escalloniaceae and Campanulaceae, but stands much nearer to the latter. From the phylogenetic point of view the Sino-Himalayan genus *Cyananthus* is also of great interest: it is the only campanulalean genus with a completely superior ovary, and besides has also a rather primitive type of pollen grains (like those of *Codonopsis, Leptocodon* and *Ostrowskia*—see Avetisian, 1967, 1973). There are also some exomorphic and palynological similarities between Campanulales and Polemoniales-Boraginineae, including terminal scorpioid cyme of *Pentaphragma,* resembling an inflorescence of many Boraginaceae and Hydrophyllaceae. But Campanulales are only remotely related to Polemoniales and the similarities most probably due to parallel evolution.

Suborder Campanulineae.

1. Campanulaceae (incl. Cyananthaceae, Cyphiaceae, Lobeliaceae, Pentaphragmataceae, Sphenocleaceae). An Asiatic genus *Pentaphragma* (South China, Indochina, Malesia) is somewhat isolated within the family, but in spite of its peculiarities is correctly placed in Campanula-

ceae (Hutchinson, 1959, 1969; see also Kapil and Vijayaraghavan, 1965; Avetisian, 1967; Subramanyam, 1970a). A somewhat aberrant genus *Sphenoclea* is equally correctly placed in Campanulaceae (see Hutchinson, 1959, 1969; Thorne, 1976). Subfamilies Campanuloideae, Cyphioideae, Lobelioideae, Pentaphragmatoideae, and Sphenocleoideae.

2. Stylidiaceae (Candolleaceae). Related to Campanulaceae, differing chiefly in the presence of iridoid compounds, glandular hairs with multicellular stalks, absence of laticiferous canals, reduced number of stamens (only two) which are completely fused with their filaments to the style to form a gynostemium and extrorse anthers. Pollen grains are usually 3–5-colpate and resemble those of primitive members of Campanulaceae-Campanuloideae (Erdtman, 1952) and are even somewhat more primitive (Avetisian, 1973). According to Crété (1951) the haustoria in the Stylidiaceae arise from endospermal cells by the same sequence of divisions as in *Codonopsis* in Campanulaceae. The embryological similarities between Stylidiaceae and the other families of Campanulales (especially Campanulaceae-Lobelioideae) has been also shown by Rosén (1935, 1949), Subramanyam (1950a, 1950b, 1951, 1953, 1970b), and Philipson and Philipson (1973).

3. Donatiaceae (*Donatia*). Very closely related to Stylidiaceae (see Milbread, 1908; Carolin, 1960; Philipson and Philipson, 1973), but differ, *inter alia,* in stamens adnate only to style bases and not forming a gynostemium and in 3–4-colporoidate pollen grains which are slightly similar to those of some Campanulaceae-Cyphioideae (Erdtman, 1952; Bronckers and Stainer, 1972; Avetisian, 1973). According to Philipson and Philipson (1973), embryologically *Donatia* is very far from Saxifragaceae and is so similar to *Forstera* and other members of Stylidiaceae, that the position of this genus in Campanulales, close to Stylidiaceae, is confirmed.

Suborder Goodeniineae.

4. Goodeniaceae (incl. Brunoniaceae—see Carolin, 1959, 1960, 1978; Duigan, 1961, and Skvarla et al., 1977). Related to Campanulaceae-Lobelioideae, differing in the presence of secoiridoids, absence of laticiferous canals, presence of sclerenchymatous idioblasts and the glandular hairs with multicellular stalks, in the orientation of flowers, presence of the characteristic indusiate pollen-collecting cup that subtends the stigmas, in more specialized colporate pollen grains (Erdtman, 1952; Avetisian, 1973), and in the absence of endosperm haustoria. Probably derived from the lobelioid stock. Subfamilies Goodenioideae, Dampieroideae, Brunonioideae.

Order 70. Calycerales.

Related to Campanulales, differing mainly by the pendulous ovule and achene-like fruits crowned by the persistent calyx lobes. In having a pendulous ovule and in presence of iridoid compounds Calyceraceae resemble Dipsacaceae and were placed near Dipsacaceae by Wettstein (1935), Hutchinson (1959, 1969), Cronquist (1968), Thorne (1968, 1976), Stebbins (1974), and Dahlgren (1975, 1977a, 1977b). But from Dipsacaceae and the whole order Dipsacales they differ in having an Asteraceae-like racemose inflorescence, in the valvate corolla lobes, in the filaments and anthers usually more or less connate around the style, in two-celled pollen grains, in the alternate leaves, and in the absence of glandular hairs. According to Skvarla et al. (1977), "the Calyceraceae possess a pollen morphology which is strikingly similar to the Compositae." According to Avetisian (1980), pollen grains of the Calyceraceae strongly differ from those of the Dipsacaceae and resemble pollen grains of the Asteraceae and especially of the Goodeniaceae (but not those of the Campanulaceae). However, pollen grains of the Calyceraceae are more advanced than those of Goodeniaceae. In many respects Calyceraceae occupy a somewhat intermediate position between Campanulales and Asterales but are nearer to Asterales (Takhtajan, 1966, 1969).

1. Calyceraceae.

Order 71. Asterales.

Related to both Campanulales and Calycerales. From Calycerales this order differs in the basal attachment of ovule, in the two-lobed or bifid style, in the absence of endosperm from the seeds, in three-celled pollen grains, in the presence of external glands and secretory cavities, in the absence of iridoid compounds, and in the presence of inulin and acetylenes. From Campanulales it differs in flowers aggregated into capitulum surrounded by an involucre of bracts, in commonly connate anthers, in definite number of carpels, in the two-lobed or two-fid style, in definite number of ovules, in the Asterad type of embryogeny, in the absence of both micropylar and chalazal haustoria, in the absence of endosperm from the seeds, in the type of fruit, and in three-multilacunar node. Delpino (1871), Small (1919), Rosén (1946, 1949) and others concluded that Asteraceae (Compositae) derived from Campanulaceae-Lobelioideae (Lobeliaceae). The ancestral corolla form in Asteraceae "was probably a zygomorphic bilabiate pentamerous type," and the disc flower "appears as a neotenous derivative form, probably evolved in parallel with the evolution of a capitate inflorescence" (Jeffrey, 1977).

1. Asteraceae or Compositae. Subfamilies Asteroideae and Cichorioideae.

CLASS LILIOPSIDA OR MONOCOTYLEDONES

Subclass A. Alismatidae

Superorder I. Alismatanae

Order 1. Alismatales (incl. Butomales and Hydrocharitales).

A very heterobathmic group, which combines some archaic features (especially in gynoecial structures) with highly specialized characters (including seeds without endosperm). The majority of Alismatales are apocarpous and their most primitive members have conduplicate carpels with lateral-laminar placentation and frequently with more or less decurrent stigmas on the undifferentiated carpel or on the style. Have some definite similarities with Nymphaeales (Hallier, 1905; Schaffner, 1929, 1934; Eber, 1934; Takhtajan, 1954, 1966, 1969; Kimura, 1956; Kaul, 1967, 1968b, 1969; Moseley, 1971). As long ago as 1905, Hallier suggested that the Nymphaeaceae s.l. were the "ancestors of Helobiae and of the whole division of monocotyledons" though later (Hallier, 1912) he changed his opinion. It is much more probable that Nymphaeales and Alismatales (together with other primitive liliopsids) have a common origin from a hypothetical extinct terrestrial herbaceous group of Magnoliidae. Though the Alismatales have some primitive characters, they should be regarded as only an ancient side-branch of monocot development and not as a basic ancestral group (see Takhtajan, 1959, 1969; Cronquist, 1965, 1968).

Suborder Butomineae.

1. Butomaceae (*Butomus*). The only member of the order with monocolpate pollen grains. The basally connate carpels are conduplicately appressed but not fused, the prominent stigmatic area is decurrent on the style for some distance, and the placentation is lateral-laminar (Zazhurilo and Kuznetsova, 1939; Eames, 1961; Singh and Sattler, 1974; Kaul, 1976).

Suborder Alismatineae.

2. Limnocharitaceae (*Limnocharis, Hydrocleys, Tenagocharis,* and *Ostenia*). Related to Butomaceae, but differ in many respects, including leaves differentiated into blade and petiole, the occurrence of laticifers, green sepals, deciduous petals, inaperturate or 3–4-porate pollen grains, Allium type embryo sac (Polygonum type in *Butomus*), and horseshoe-shaped embryo (straight in *Butomus*). Carpels are open or partially conduplicately closed (Kaul, 1967, 1968b), the stigmatic area is more or less decurrent on the carpel (*Limnocharis*) or on the style, and placentation is lateral-laminar.

3. Alismataceae. Very closely related to Limnocharitaceae, especially to the genus *Limnocharis*. The genus *Alisma* is the only member of Alismataceae with carpels opened at anthesis: the margins of the carpel come close to each other by the activity of the marginal meristem, but

they remain free and do not fuse even in the mature state (Singh and Sattler, 1972). The flared stigmatic crest is decurrent on the style (Kaul, 1976). In *Alisma* each carpel has only one basal ovule. *Damasonium polyspermum* is the only member of the family with many ovules, lateral-laminar placentation and clearly limnocharitaceous vasculature (Kaul, 1976), though carpels are closed. The genus *Damasonium* shows a series of stages in reduction from many ovules to one and from laminar to basal placentation (Eames, 1961). *Ranalisma humile* is also somewhat transitional between Limnocharitaceae and Alismataceae and its inflorescence being quite comparable with that of *Hydrocleys nymphoides* (Charlton and Ahmed, 1973).

Suborder Hydrocharitineae.

4. Hydrocharitaceae. Near to Limnocharitaceae and especially to Butomaceae (the embryo sac is also of the Polygonum-type) and have a common ancestry with them. Vessels absent from all organs. Pollen grains in some Vallisnerioideae are 1-colpate (as in *Butomus*), but mostly inaperturate. Usually they are three-celled at release, but in *Blyxa* and *Ottelia* are two-celled. In *Blyxa oryzetorum,* in contrast with all other investigated Alismatales, the micropyle formed by both integuments (Davis, 1966). Gynoecium is basically apocarpous (Troll, 1931; Eames, 1961; Tomlinson, 1969a), but in contrast with the usual type of the apocarpous gynoecium it is inferior (according to Kaul, 1969, the inferior ovary of Hydrocharitaceae is appendicular in nature). Some genera, like *Enhalus* and *Stratiotes,* are fully apocarpous but most genera are at least slightly syncarpous, and in *Limbobium spongia* the total fusion of adjacent carpel walls is obvious (Kaul, 1969). Placentation is lateral-laminar, as in Butomaceae and Limnocharitaceae. Subfamilies Hydrocharitoideae, Vallisnerioideae, Thalassioideae, Halophiloideae.

Order 2. Najadales (incl. Aponogetonales, Potamogetonales and Zosterales).

Near to Alismatales and probably derived from their immediate ancestor. Pollen grains usually three-celled when shed, but in some genera they are two-celled (*Lilaea, Triglochin, Zostera*).

Suborder Aponogetonineae.

1. Aponogetonaceae. The only family within the order with typical monocolpate pollen grains. Gynoecium apocarpous, stigmas of primitive decurrent type, and fruit is a multifolliculus. The nearest family to Alismatales.

Suborder Scheuchzeriineae.

2. Scheuchzeriaceae (*Scheuchzeria*). A comparatively primitive family, which also exhibits some definite links with Alismatales especially with

the Alismataceae (see Hutchinson, 1934, 1959). Stomata tetracyclic and pollen grains inaperturate.

Suborder Potamogetonineae.

3. Juncaginaceae (incl. Lilaeaceae, ? Maundiaceae, and Triglochinaceae). Related to Scheuchzeriaceae, but bracts absent, pollen grains two-celled when shed, and ovule solitary in each carpel.
4. Posidoniaceae (*Posidonia*). Probably represents an extreme marine stage of the Juncaginaceae (see Hutchinson, 1934, 1959).
5. Potamogetonaceae. Related to Juncaginaceae and probably derived from them.
6. Ruppiaceae (*Ruppia*). Closely related to Potamogetonaceae, but perianth absent, ovule pendulous from the apex of each carpel, the micropyle formed by both integuments, and fruiting carpels stipitate.
7. Zannichelliaceae. Closely related to Potamogetonaceae and Ruppiaceae (see Singh, 1965, and Posluszny and Sattler, 1976) and had a common origin. Singh (1965) had even argued for keeping *Zannichellia* together with *Potamogeton* and *Ruppia* in one family.
8. Cymodoceaceae. Closely related to the Zannichelliaceae.

Suborder Zosterineae.

9. Zosteraceae. Highly advanced submerged marine plants, the systematic position of which is not fully clear. Probably derived from some Juncaginaceae-like ancestor. The filamentous and exineless pollen grains are still two-celled when shed (as in Juncaginaceae), and as Hutchinson (1934) notes, the sagittate fruit of *Phyllospadix* is reminiscent of somewhat similar fruits in the Juncaginaceae.

Suborder Najadineae.

10. Najadaceae (*Najas*). Small submerged annual plants, which evidently represent the most advanced family within the order. But male and female flowers are extremely reduced, "too reduced in fact to enable us to be very sure of its relationship" (Hutchinson, 1934, 1959). Pollination occurs under water as in Zosteraceae, but pollen grains are spherical, not filamentous, and three-celled at release. Probably related to Juncaginaceae or (and) Zannichelliaceae.

Subclass B. Liliidae (incl. Commelinidae and Zingiberidae)

Superorder II. Triuridanae

Order 3. Triuridales.

Despite the fact that the gynoecium is apocarpous and seeds have copious endosperm, the order as a whole is very specialized (small achlorophyllous saprophytes with leaves reduced to scales and with very small and generally unisexual flowers). Vessels are lacking in Triuridales, which is probably due to the saprophytic habit (Carlquist, 1975; Wagner, 1977). Has much in common with the lower members of the next order, especially with the Colchicaceae-Petrosavieae (and Tofieldieae), but pollen grains are three-celled when shed and styles are nearly basal. There are also some similarities with Alismatales, from which it differs by endospermous seeds.

1. Triuridaceae.

Superorder III. Lilianae

Order 4. Liliales.

The presence of endosperm and usually two-celled pollen grains indicates that the order Liliales could not have originated from the Alismatales. Both these orders, together with the Triuridales, have more probably a common origin from a hypothetical extinct group with endospermous seeds and two-celled pollen grains, as in the Liliales, and an apocarpous gynoecium, as in the Alismatales. The subfamily Melanthioideae of the family Colchicaceae is the most primitive group within the Liliales (Lotsy, 1911; Takhtajan, 1959, 1966; Eames, 1961; Radulescu, 1973d) and is nearest to the ancestral type.

Suborder Liliineae.

1. Colchicaceae (nom. cons.) (incl. ? Calochortaceae, Melanthiaceae, Nartheciaceae, Petrosaviaceae, Protoliriaceae, Tricyrtidaceae, Uvulariaceae). The most primitive subfamily of the Colchicaceae is Melanthioideae. Vessels in the Melanthioideae only in roots, being exclusively with scalariform perforations (Cheadle and Kosakai, 1971). No vessels occur in the saprophytic genus *Petrosavia* (*Protolirion*). In some members of the Melanthioideae the gynoecium is of the most primitive type within the Liliales (see El-Hamidi, 1952, and Eames, 1961) and pollen grains are usually more primitive than in other two subfamilies. But like many other primitive taxa, the subfamily Melanthioideae is heterobathmic and some of its members are characterized by features of specialization (the saprophytic and almost apocarpous genus *Petrosavia* being the best example). From the chemical point of view the family Colchicaceae is remarkably heterogenous (see C. Williams, 1975). It is very diversified and exceedingly variable both in appearance and in morphology. Thus endosperm is helobial in the Melanthioideae and nuclear in the Calochortoideae and Colchicoideae, and pollen grains of the tribe Colchiceae markedly differ from those of the other tribes of the family (Kuprianova, 1948; Erdtman, 1952; Radulescu, 1973c). But despite their diversity the Colchicaceae represents a natural group. The family (most frequently under the earlier name Melanthiaceae) was already correctly defined by the last century botanists, including Lindley (1836, 1846), Endlicher (1836, 1841),

and le Maout and Decaisne (1868). Subfamilies Melanthioideae: Tofieldieae, Petrosavieae (*Petrosavia*), Helonieae (incl. Chionographideae), Aletrideae (*Aletris*), Melanthieae (Veratreae), Calochortoideae (*Calochortus*) (sometimes is considered as a family—see Huber, 1969) and Colchicoideae (Wurmbaeoideae); Uvularieae (related to the Tofieldieae—see Buxbaum and Schnarf, 1929) and occupy a somewhat intermediate position between subfamilies Melanthioideae and Colchicoideae), Glorioseae, ? Scolopieae (*Scolopius*—see Berg, 1962) Tricyrtideae (*Tricyrtis,* stands near to the Glorioseae and karyotype resembles *Littonia* and *Gloriosa*—see Satô, 1942), Scolopieae (*Scolopius*—see Berg, 1952), Anguillarieae (incl. Beometreae, Burchardieae, Iphigenieae and Neodregeae) and Colchiceae (incl. *Androcymbium,* which is a connecting link between Colchiceae and Anguillarieae; according to Cave, 1967), on embryological data *Androcymbium* is closely related both to *Gloriosa* and to *Iphigenia* and *Colchicum,* but pollen grains are of the same type as those of the other members of the Colchiceae—see Erdtman, 1952 and Radulescu, 1973c).

2. Herreriaceae (*Herreria* and *Herreriopsis*). The affinity is not fully clear. Probably related to the Colchicaceae-Melanthioideae, but alkaloids are lacking (C. Williams, 1975), vessels with scalariform perforations in both roots and stems (Wagner, 1977), erect or climbing stems sometimes with prickles, leaves rather rigid, cladode-like, and fruit a laterally deeply three-lobed capsule. Pollen grains 1-colpate, resemble those of the Melanthioideae (Kuprianova, 1948). According to Satô (1942) the karyotype of *Herreria salsaparilha* somewhat resembles that of Yucca-Agave type (parallel evolution?).

3. Liliaceae (incl. Hyacinthaceae and Scillaceae). Related to the Colchicaceae and have many similarities with them, especially with the Anguillarieae. Bulbous plants. Vessels in roots only, always with scalariform perforations (Cheadle and Kosakai, 1971). Stem bearing one or more leaves (Lilioideae) or stem leafless (Scilloideae). Pollen grains 1-colpate, rarely 2(3)-colpate, with a variety of patterns in exine surface (Kuprianova, 1948; Erdtman, 1952; Radulescu, 1973c). Endosperm nuclear. There are considerable chemical differences between the two subfamilies: alkaloids are present in the Lilioideae and are lacking in the Scillioideae, whereas chelidonic acid, cardiac glycosides and raphides are found only in the Scilloideae (C. Williams, 1975). According to Williams, the Lilioideae is chemically homogenous (like Colchicoideae in the Colchicaceae), but Scilloideae is chemically very heterogenous (like Melanthioideae). Subfamilies Lilioideae, Lloydieae, (*Gagea* and *Lloydia*), ? Medeolae (*Medeola*—see Berg, 1962; Björnstad, 1970) Lilieae and Tulipeae and Scilloideae (Hyacinthaceae): Chlorogaleae (including *Camassia,* in which the karyotype strikingly resembles that of *Chlorogalum*; in fact, the karyo-

type of some species of *Camassia* is nearly indistinguishable from species of *Chlorogalum* with $n = 15$—Sen, 1975), ? Bowieae (*Bowiea* and *Schizobasis*), Scilleae, Hyacintheae. Systematic position of the Bowieae is uncertain.

4. Alstroemeriaceae. Related to the Liliaceae, but differ by rhizomatous rootstock, by the leaves usually twisted through 180°, by the presence of chelidonic acids and raphides (but similar in containing only flavonols) (see C. Williams, 1975), by morphology of pollen grains (Radulescu, 1973c), karyologically (Sen, 1975), by the Polygonum-type embryo sac (Fritillaria-type in Liliaceae), etc.

5. Alliaceae (incl. Agapanthaceae, Gilliesiaceae, ? Hesperocallidaceae, Milulaceae and Tulbaghiaceae). Related to the Liliaceae-Scilloideae, but differ in the absence of cardiac glycosides and the presence of the strong-smelling allyldisulphides and propy- and vinil-sulphides (C. Williams, 1975), the presence of the laticifers, and in the inflorescence which is usually umbellate and subtended by a pair of more or less leaf-like bracts (rarely a raceme—*Hesperocallis* and *Milula*). They also show some similarities with the Liliaceae-Lloydieae. Lotsy (1911) included a monotypic genus *Hesperocallis* (deserts of California and Arizona) in his Alliaceae, which is confirmed by the presence of laticifers and unique alliaceous scent present when the tissue are broken (see Traub, 1972a). However, cytologically and embryologically it is close to *Hosta* (Cave, 1948, 1970) which reflects some relationships between the Alliaceae and some primitive Agavaceae. Vessels only in roots, with simple, simple and scalariform or (in *Agapanthus*) scalariform perforations (Cheadle, 1969; Cheadle and Kosakai, 1971). Tribes Agapantheae (*Agapanthus*), Allieae (incl. Miluleae), Hesperocallideae (*Hesperocallis*), Gilliesieae, Milleae and Brodiaeeae.

6. Hemerocallidaceae (*Hemerocallis* and ? *Leucocrinum*). Probably derived from the liliaceous stock. Rootstock a rhizome. Vessels only in roots and with scalariform perforations (Cheadle and Kosakai, 1971). Perianth-segments connate into a tube. Pollen grains somewhat resemble *Hosta* (Radulescu, 1973a) and *Hesperocallis,* karyotype resembles that of Amaryllis type (Satô, 1942). Serologically it shows some relationship with *Phormium* and *Dianella* (Chupov and Cutjavina, 1978, 1980b). The monotypic genus *Leucocrinum* (SW. U.S.A.), which Hutchinson (1934, 1959) put near *Hemerocallis,* resembles it in many respects, but differs by some embryological characters (Cave, 1948; Fulvio and Cave, 1964).

7. Amaryllidaceae (incl. Ixioliriaceae). Related to the Alliaceae and presumably also to the Hemerocallidaceae and probably had a common origin with them from the liliaceous stock. The Amaryllidaceae differ from the Liliaceae mainly in their umbellate inflorescence and inferior ovary, and also chemically (Gibbs, 1974). The Asiatic genus *Ixiolirion* is

somewhat isolated within the family and differs from its other members by subumbellate inflorescence and cormous rootstock. Subfamilies Ixiolirioideae (*Ixiolirion*) and Amaryllidoideae.

8. Phormiaceae (incl. Dianellaceae and *Blandfordia*). Probably had a common ancestry with the Hemerocallidaceae. Rhizomatous with linear and more or less rigid leaves. Pollen grains 1-colpate (*Blandfordia*) or trichomatocolpate (*Phormium* and Dianelleae—Erdtman, 1952; Radulescu, 1973c). Fruit a loculicidal capsule (*Blandfordia, Phormium* and *Excremis*) or a berry (*Dianella* and *Stypandra*). The embryological characteristics of the Australian genus *Blandfordia* show some similarities with *Phormium* (and *Hosta*) (Fulvio and Cave, 1949). Both serological (Chupov and Cutjavina, 1978, 1980b) and morphological data show relationship between *Phormium* and *Dianella*. The genus *Blandfordia*, which is somewhat isolated within the family, needs further studies. Tribes Blandfordieae (*Blandfordia*), Phormieae (*Phormium*) and Dianelleae.

9. Agavaceae (incl. Yuccaceae and *Hosta* and excl. Dracaenaceae and *Doryanthes*). Related to the Hemerocallidaceae and Phormiaceae and probably had a common origin. Rhizomatous plants with usually arborescent stem (herbaceous in primitive genus *Hosta*). Vessels only in roots; perforations scalariform in *Hosta* and simple in *Agave* (Cheadle and Kosakai, 1971). Ovary superior or inferior. In its appearance *Hosta* differs from all other members of the family, but it probably belongs to Agavaceae (Traub, 1972b; Chupov and Cutjavina, 1978, 1980b) and its chromosome number and morphology strikingly resemble the Yucca-Agave type (Whitaker, 1934; Satô, 1942; Sharma, 1969; Sen, 1975). However in *H. aromatica* chromosome number has been found to be $x = 10$, with only slight difference in chromose complement. This species may be considered as a primitive type, from which gradual asymmetry has been evolved (Sen, 1975). Tribes Hosteae (*Hosta*), Yucceae and Agaveae.

10. Doryanthaceae. The oligotypic Australian genus *Doryanthes*, which usually included in the Amaryllidaceae, has been transferred by Hutchinson (1934, 1959) to the Agavaceae. But it markedly differs from all other members of the Agavaceae by bulbous rootstock, paracytic stomata (Blunden and Jewers, 1973), by very peculiar morphology of leaves (Newman, 1928), simultaneous type of microsporogenesis, the presence of nucellar cap (Cave, 1955), seed coat anatomy, and by some other features. Serologically it is very isolated within the Liliales (Chupov and Cutjavina, 1980b). It was raised to family rank by Huber (1969).

Suborder Asphodelineae.

11. Asphodelaceae (incl. Aloeaceae, ? Anthericaceae and Johnsoniaceae). Related to the Colchicaceae, but alkaloids are absent and mor-

phologically more advanced. Vessels are present in the roots and in seven of the genera studied also in the stems; perforations in the root almost exclusively simple, except in Kniphofieae and related genera, in which both scalariform and simple perforations are found, and in *Borya* in which the perforations are scalariform; the perforations in the stem vessels are scalariform except in *Tricoryne* in which also simple perforations occur (Cheadle and Kosakai, 1971; Wagner, 1977). Microsporogenesis simultaneous (Asphodeloideae) or successive (Anthericoideae). Endosperm formation helobial. Seeds with an arillus (Asphodeloideae) or without (Anthericoideae). Subfamilies Asphodeloideae: Asphodeleae, Aloineae, Kniphofieae and Anthericoideae: Anthericeae, Thysanoteae, Hodgsonioleae, Simethideae, Johnsonieae.

12. Xanthorrhoeaceae (incl. Baxteriaceae, Calectasiaceae, Dasypogonaceae, Kingiaceae, Lomandraceae, Xerotaceae). Related to the Asphodelaceae-Anthericoideae (especially to Johnsonieae) and probably derived from the asphodelaceous stock. A specialized and usually xeromorphic group with thick woody caudex or rhizome. Vessels usually only in roots and usually only with simple perforations, except *Baxteria* and *Kingia* which have only scalariform perforations; in *Acanthocarpus* and *Xanthorrhoea* vessels with scalariform perforations are found in leaves (Fahn, 1954a; Wagner, 1977). Stomata paracytic (*Baxteria* and *Xanthorrhoea*) or anomocytic. Perianth segments usually dry and glumaceous. Pollen grains 1-colpate or zonocolpate, sometimes more or less spiraperturate (Kuprianova, 1948; Erdtman, 1952; Radulescu, 1973a, 1973c; Chanda and Ghash, 1976). Subfamilies Kingioideae (*Kingia* and *Baxteria*), Dasypogonoideae (*Dasypogon* and *Calectasia*), Xanthorrhoeoideae (*Xanthorroea*) and Lomandroideae.

13. Aphyllanthaceae (*Aphyllanthes*). Near to the Xanthorrhoeaceae (Tomlinson, 1965) and probably share a common ancestry (Takhtajan, 1966). The monotypic West Mediterranean genus *Aphyllanthes* is a specialized xeromorphic perennial tufted herb with stiff, rush-like and usually leafless stems. Vessels only in roots and usually with simple perforations (Tomlinson, 1965). Pollen grains more or less spiraperturate and are very similar to those of *Lomandra endlicheri* (Chanda and Ghash, 1976).

14. Hanguanaceae (*Hanguana*). The monotypic tropical Asiatic genus *Hanguana* is related to the Xanthorrhoeaceae. Formerly included in the Flagellariaceae, but anatomy and morphology of pollen grains separate *Hanguana* from the Flagellariaceae and suggest a certain relationship with the Xanthorrhoeaceae. Thorne (1976) includes *Hanguana* in his subfamily Xanthorrhoeoideae of Liliaceae s.l. but Cronquist (1979) more appropriately accepts Airy Shaw's new family Hanguanaceae and places it after the Xanthorrhoeaceae. I do not think that these two families are

very closely related, but they probably share a common ancestry. It is interesting to note that stomata in *Hanguana* are tetracytic (Tomlinson, 1969b; Baranova, 1975), and the fruit is a 1–3-seeded drupe. Vessels only in roots (Tomlinson, 1969b), but the perforation plates are not studied yet.

Suborder Asparagineae.

15. Asparagaceae (nom. cons.) (incl. Aspidistraceae, Convallariaceae, Ophiopogonaceae, Peliosanthaceae, Polygonataceae, Ruscaceae). Related to the Colchicaceae, especially to the Uvularieae (see Lotsy, 1911). Rhizomatous plants. Alkaloids are lacking (C. Williams, 1975). Vessels only in roots and with scalariform perforations (Aspidistreae, Peliosantheae, *Ruscus*); in *Danae* vessels both in roots and stems and with scalariform perforations, but in *Semele* and *Asparagus* vessels in roots with simple perforations, while in stems they have scalariform perforations (Cheadle, 1970; Cheadle and Kosakai, 1971; Wagner, 1977). Fruit a berry. Subfamilies Convallarioideae: Aspidistreae, Peliosantheae (*Peliosanthes*), Ophiopogoneae, Polygonateae, Streptopodeae, Convallarieae, Ruscoideae: Rusceae, and Asparagoideae: Asparageae (*Asparagus*). Serologically Rusceae are close to Convallarieae, but *Asparagus* is far from both (Chupov and Cutjavina, 1978, 1980b).

16. Dracaenaceae (incl. Asteliaceae, Nolinaceae, Sansevieriaceae). Related to the Asparagaceae-Ophiopogoneae and probably had a common origin. Cytologically Dracaenaceae are close to the Ophiopogoneae (cytological data "confirm the relationship between *Sansevieria* and *Ophiopogon* and suggest their affinity with *Dracaena*"—Sharma and Chaudhuri, 1964, see also Sen, 1975), but serologically nearer to Polygonateae (Chupov and Cutjavina, 1978, 1980b). Vessels only in roots (*Astelia*) or in roots and leaves (but not in stems). In *Astelia* perforations scalariform, in all other investigated genera vessel perforations in leaves are scalariform, but probably simple in roots (Cheadle, 1942; Cheadle and Kosakai, 1971; Wagner, 1977). Fruit a loculicidal capsule or a berry. Subfamilies Astelioideae: Astelieae (*Milligania* and *Astelia*) and Dracaenoideae: Dracaeneae (*Cordyline* and *Dracaena*), Nolineae (*Nolina, Dasylirion* and *Calibanus*), Sansevierieae (*Sansevieria*).

Suborder Iridineae.

17. Tecophilaeaceae (incl. Cyanastraceae, ? Eriospermaceae, ? Walleriaceae). According to Hutchinson (1934, 1959) probably derived from the Liliaceae s.l. Occupy a somewhat intermediate position between Colchicaceae-Melanthioideae and Iridaceae, but seemingly nearer to the latter. *Tecophilaea cyanastrum* especially resemble some members of the Iridaceae. Vessels only in roots with exclusively scalariform perforations (Cheadle, 1969). Pollen grains usually 1-colpate, occasionally trichoma-

tocolpate, with thin exine (Erdtman, 1952). Ovary half-inferior or nearly superior (*Zephyra*). Fruit a three-grooved loculicidal capsule. Tribes Eriospermeae (*Eriospermum*), Wallerieae (*Walleria*) and Tecophilaeeae (*Cyanastrum, Cyanella, Conanthera, Tecophilaea, Zephyra, Odontostomum*).

18. Iridaceae (incl. Campynemataceae, Geosiridaceae, Hewardiaceae, Isophysidaceae). According to Hallier (1912) and Hutchinson (1934, 1959) derived from the Liliaceae s.l., most probably from the Colchicaceae-Melanthioideae (Takhtajan, 1959, 1966). Very likely had a common origin with the Tecophilaeaceae. Vessels only in roots and usually are highly specialized except those in the tribe Aristeae, where they are primitive (*Schizostylis* has simple perforations, however) (Cheadle, 1963). Stamens usually three (the outer whorl), rarely six (Campynematoideae). Pollen grains of various type, but basically 1-colpate (Kuprianova, 1948; Erdtman, 1952; Radulescu, 1970). Ovary mostly inferior, rarely superior (*Isophysis*). The monotypic Malagasy genus *Geosiris* was correctly placed by its author (Baillon, 1890) in the Iridaceae (see also Thorne, 1968, 1976). From all other members of the family it differs by its saprophytic habit, scaly rhizome and dendriform placenta. Subfamilies Isophysidoideae (*Isophysis*), Campynematoideae (*Campynema* and *Campynemanthe*), Crocoideae, Iridoideae (Sisyrinchieae, Mariceae, Irideae, Tigridieae, Aristeae, Cipureae), Ixioideae and Geosiridoideae (*Geosiris*).

Suborder Haemodorineae.

19. Haemodoraceae (incl. Conostylidaceae and excl. *Lanaria* ? and *Lophiola* ?). Related to the Asparagaceae-Ophiopogoneae and probably had a common origin. Short rhizomes or tubers. Stomata paracytic (Stebbins and Khush, 1961). Vessels in some genera (*Dilatris, Tribonanthes*) only in roots and with scalariform perforations; only in *Lachnanthes* and *Xiphidium* are vessels present in the shoot system (Cheadle, 1942, 1968, 1969; Fahn, 1954b). Pollen grains 1-colpate (some members of Haemodoreae) or 2–3(4)-porate (Erdtman, 1952; Radulescu, 1973b). Ovary superior to inferior. Tribes Haemodoreae and Conostylideae (*Anizoganthus, Macropidia, Conostylis, Tribonanthes*).

20. Hypoxidaceae. Related to the Haemodoraceae and probably had a common origin from the Asparagaceae-Ophiopogoneae. The origin of Hypoxidaceae from the Ophiopogoneae is also supported by cytological data (Sen, 1975). Large, hard tuberous vertical rhizome or small monocarpic corm. Stomata paracytic (Stebbins and Khush, 1961). Vessels only in roots and with scalariform perforations (Cheadle, 1968). Pollen grains 1-colpate, not operculate, with fairly thin exine (Erdtman, 1952). Ovary inferior.

21. Velloziaceae. Related to the Haemodoraceae and the Hypoxida-

ceae. Xerophytes with pseudodichomotously branched stems and leaves crowded at the ends of branches. Stomata paracytic. Vessels both in roots and leaves, but in *Vellozia elegans* also in stems; vessels in roots with simple perforations; vessels in leaves and stems with scalariform perforations (Ayensu, 1968b). Pollen grains 1-colpate, free or united in tetrads (Kuprianova, 1948; Erdtman, 1952; Radulescu, 1973a). Ovary inferior.

Suborder Pontederiineae.

22. Pontederiaceae. Related to the Liliaceae (Solms-Laubach, 1883; Bessey, 1915; Wettstein, 1935; Hutchinson, 1934, 1959; Kimura, 1956; Takhtajan, 1959, 1966). They show many similarities with the Liliaceae, including septal nectaries (Brown, 1938; Daumann, 1965) and vegetative anatomy (Schwartz, 1926, 1930) and probably originated from the liliaceous stock. There are some embryological similarities with the Liliaceae, but the micropyle formed by both integuments. They differ also by paracytic stomata (Stebbins and Khush, 1961). Cytological data support the inclusion of Pontederiaceae in the Liliales (Sen, 1975).

Suborder Philydrineae.

23. Philydraceae. A somewhat isolated family, which is related to Pontederiaceae (Hallier, 1912; Takhtajan, 1959, 1966; Hamann, 1963, 1966; Cronquist, 1968; Huber, 1969) and probably share a common ancestry. According to Hamann (1966), "In consideration of many characters there seem to exist relations the easiest to the Pontederiaceae, perhaps also to the Haemodoraceae and Hypoxidaceae." In both families stomata paracytic (in some Philydraceae also tetracytic) (Stebbins and Khush, 1961), but vessels with scalariform perforations only in roots (Cheadle, 1968; Fahn, 1954b) and in this respect Philydraceae are more primitive than Pontederiaceae. Some embryological characters of Philydraceae, as the structure of anther wall, pollen grains and ovules, the successive type of microsporogenesis, and the development of female gametophyte and endosperm are apparently similar to those of Pontederiaceae (see Kapil and Walia, 1965; Hamann, 1966). In both families endosperm is starchy and consists of single grains. But Philydraceae differ from Pontederiaceae in more or less zygomorphic flowers, androecium reduced to one stamen, the absence of septal nectaries, the Onagrad-type of embryogenesis (in Pontederiaceae it is of Asterad type), and in carunculate seeds.

Order 5. Smilacales ("Smilales"—Lindley, 1833. Incl. Dioscoreales, Stemonales, and Taccales).

Closely related to Liliales, especially to Asparagaceae (=Convallarioideae), and probably derived from them.

1. Philesiaceae (incl. Lapageriaceae, Luzuriagaceae, and Petermanniaceae). Erect shrubs or tall climbers. Stomata anomocytic. Vessels only in roots (*Behnia*) or in roots and stems or in roots, stems and leaves (*Eustrephus, Geitonoplesium*); vessels in roots with scalariform perforations (*Petermannia*), with scalariform and simple perforations, or with simple or mostly simple perforations (*Eustrephus, Behnia*); vessels in stems and leaves with scalariform perforations (Cheadle and Kosakai, 1975; Wagner, 1977). Pollen grains two-celled when shed, 1-colpate or trichomatocolpate or nonaperturate and spiniferous (*Lapageria, Philesia*) (Erdtman, 1952). Gynoecium syncarpous or paracarpous; ovary superior or inferior. Fruit a berry. Subfamilies Luzuriagoideae, Philesioideae (*Philesia, Lapageria*), Petermannioideae (*Petermannia*). *Petermannia* is rather isolated within the family, but probably does not deserve a family rank (see Schlittler, 1949; Tomlinson and Ayensu, 1969).

2. Stemonaceae (incl. Croomiaceae and Roxburghiaceae). Probably related to Philesiaceae and had a common origin. Stems erect from a rhizome or climbing (*Stemona*). Alkaloids occur only in *Stemona* (Gibbs, 1974). Stomata anomocytic. Vessels only in roots (*Croomia*) or also in stems; perforations scalariform; vessels in *Croomia* with long perforation plates on very oblique end walls (Tomlinson and Ayensu, 1968). Flowers bisexual, dimerous. Pollen grains 1-colpate. Gynoecium of two carpels. Ovary superior or rarely half inferior, one-locular. Fruit a two-valved capsule, in *Croomia* berry-like. Tribes Stemoneae (*Stemona*) and Croomieae (*Croomia, Stichoneuron*).

3. Trilliaceae (*Paris* and *Trillium*). Related to the Stemonaceae (see Huber, 1969), but have also similarities with the Asparagaceae. Rhizomatous herbs with verticillate and more or less reticulate-veined leaves. Stomata anomocytic. Vessels only in roots, perforations scalariform (Cheadle, 1970). Anthers basifixed. Pollen grains 1-colpate. Ovary superior. Fruit a berry or fleshy loculicidal capsule.

4. Smilacaceae (incl. Rhipogonaceae). Closely related to Philesiaceae-Luzuriageae (Schlitter, 1949). Mostly climbing rhizomatous plants with woody, often prickly stems. Stomata anomocytic. All the species investigated have vessels in the roots, 7 of 11 in the stems and 8 of 15 in the leaves; vessels always with scalariform perforations (Cheadle, 1970; Wagner, 1977). Flowers mostly dioecious. Pollen grains 1-colpate, trichotomocolpate or inaperturate, spinuliferous (Nair and Sharma, 1965). Ovary superior. Fruit a berry. Subfamilies Rhipogonoideae (*Rhipogonum*) and Smilacoideae (*Smilax, Heterosmilax*).

5. Dioscoreaceae (incl. Stenomeridaceae and Trichopodaceae). Closely related to Smilacaceae and Stemonaceae (Burkill, 1960) and had a common origin. Burkill (1960) pointed out the close relationship of Dioscoreaceae with Stemonaceae. Usually climbers with thick rhizomes or tu-

bers. Vessels with scalariform perforations are present in roots, aerial stems and petioles, but absent in leaf laminae and rhizomes (Ayensu, 1972). Flowers mostly unisexual. In *Stenomeris* and *Avetra* the connective produced above loculi into an elongated appendage (supraconnectivum), as in *Stemona*. Pollen grains 1-colpate, 2(3)-colpate or 4(5?)-foraminoidate (*Avetra*) (Kuprianova, 1948; Erdtman, 1952). Ovary inferior, three-locular. Fruit a three-valved capsule or a berry. Subfamilies Dioscoreoideae (Stenomerideae, Dioscoreae) and Trichopodoideae (*Trichopus*). Burkill (1951: 297) describes *Trichopus* as "preserving through life the habit of the first-year seedling of *Dioscorea,* which lies in the arrest of the second leaf of a stem to the advantage of the first."

6. Taccaceae (*Tacca*). Closely related to Dioscoreaceae and share a common origin (Hallier, 1912, see also Schlittler, 1949). Stomata anomocytic (Stebbins and Khush, 1961). Vessels only in roots with long scalariform perforation plates (Fahn, 1954b; Cheadle, 1968). Flowers bisexual, in umbellate inflorescence. Pollen grains 1-colpate. Ovary superior. Fruit berry-like.

Order 6. Burmanniales.

Closely related to Liliales, especially to Iridaceae and evidently derived from them. Mostly saprophytic plants with leaves reduced to scales. Ovules tenuinucellate. Embryogeny is arrested at 4–10-celled stage. Seeds numerous, minute, with little endosperm.

1. Burmanniaceae (incl. Thismiaceae). Linked with Iridaceae, especially with Ixioideae, through the autotrophic section *Foliosa* of the genus *Burmannia* (see Jonker, 1938). They represent a parallel line with the saprophytic Geosiridoideae. Two autotrophic species (*Burmannia disticha* and *B. longifolia*), which are the only ones anatomically studied, have vessels with scalariform perforations in roots, stems and leaves (Carlquist, 1975). Pollen grains three-celled when shed. Tribes Burmannieae, Haplothismieae, Thismieae.

2. Corsiaceae. Closely related to Burmanniaceae.

Order 7. Orchidales.

Closely related to and derived from Liliales. Shows closest connections with Hypoxidaceae (Rolfe, 1909, 1910; Hallier, 1912; Gobi, 1916; Hutchinson, 1934, 1959; Garay, 1960; Rao, 1969), especially with the genera *Hypoxis* and *Curculigo*. There are many similarities between Hypoxidaceae and Orchidaceae and *Curculigo orchioides,* for example, strongly resembles orchids. Besides, chromosomes of Hypoxidaceae resemble those of Orchidaceae (Sharma, 1969). The connecting link between Hypoxidaceae and Orchidales is the most primitive subfamily of Orchidaceae, the Apostasioideae. This intermediate position of apostasiads was already mentioned by Lindley (1833) in his *The Vegetable Kingdom* ("The order seems as if connecting Orchids with Hypoxids"). In the most primitive genus of Apostasioideae, *Neuwiedia,* there are three fertile stamens. The two lateral are in the same position as in Cypripedioideae, being opposite the lateral petals and hence belonging to the inner staminal whorl. The dorsal (anterior) stamen of *Neuwiedia* (and the dorsal staminode of *Apostasia*) is in the same position as in all remaining orchids (except the genus *Satyrium*), being opposite the dorsal sepal, hence belonging to the outer staminal whorl. The genus *Adactylus* with only two lateral stamens and no staminode is closest to Cypripedioideae. Among the Apostasioideae we can also see the first steps toward the formation of gynostemium. The subfamilies Cypripedioideae and Orchidoideae had probably derived from some ancient Apostasioideae, which had flowers of *Neuwiedia* type and seeds of *Apostasia* and *Hypoxis* type. Orchidales have no direct relationship with Burmanniales and some similarities between these two orders are the result of parallel evolution. There are some basic differences between the flowers of Orchidales and Burmanniales, especially in aestivation of perianth-segments and in structure of their androecia. As Rao (1969, 1974) pointed out, in Burmanniaceae stamens are epipetalous and their adnation is with the corolla. In the Orchidaceae (including Apostasiaceae), there is absolutely no fusion between the perianth members and the stamens, and the adnation is only with style to form a gynostemium (see also Jonker, 1938).

1. Orchidaceae (incl. Apostasiaceae and Cypripediaceae). Subfamilies Apostasioideae, Cypripedioideae, Orchidoideae.

Order 8. Bromeliales.

Related to Liliales (especially to agavaceous stock) on one side and to Commelinales (especially to Rapateaceae—see Smith, 1934) on the other. Among the similarities between bromeliads and many members of Liliales are the presence of raphides, steroidal sapogenins and flavonoids, mostly scalariform perforations in root vessels, the usual presence of septal nectaries, and helobial endosperm. Besides, according to my observations, there are definite similarities between pollen grains of Bromeliaceae and of some lilealean families, especially those of Agavaceae (particularly the genus *Agave*). From the majority of lilealean families, except Haemodoraceae, Pontederiaceae and Philydraceae, bromeliads differ by starchy endosperm. From the majority of Liliales they also differ by their stomata usually with two narrow lateral and two short terminal subsidiary cells (see Ziegenspeck, 1944; Tomlinson, 1969). They differ also by the presence of silica-bodies. Probably Bromeliaceae had a common ancestry with the agavacean stock from an ancient lilialean ancestor. In bromeliads the embryo usually small, mostly lateral, with the radicle next to the hilum, in a hollow of the copious starchy endosperm (starch in compound grains).

1. Bromeliaceae. Subfamilies Pitcairnioideae (incl. Navioideae?), Tillandsioideae, Bromelioideae.

Superorder IV. Juncanae

Order 9. Juncales.

Most probably derived directly from lilialean stock. Already Beuchenau (1871) considered Juncaceae as a reduced group nearest to Xeroteae and Calectasieae. According to Lotsy (1911) Juncaceae are reduced derivatives of Lomandraceae (included here in Xanthorrhoeaceae). Hallier (1912), who derived Juncaceae from Liliaceae-Asphodeloideae ("près des Johnsoniées, Dasypogonées, Lomandrées et Calectasiées"), marks "une grande resemblance" between *Juncus* and the genus *Laxmannia* (Liliaceae-Johnsonieae). Rendle (1953) also derives Juncaceae from Liliaceae s.l. "So close is the relation between the two families that several genera with a membranous perianth, e.g. *Xanthorrhoea, Calectasia* and others, are included indifferently in either," says Rendle. *Rostkova* (Juncaceae) and *Thurnia* (Thurniaceae) have vessels with scalariform perforations in roots, stems and leaves (Cutler, 1969) and thus as regards vessel characteristic are the most primitive members of Juncales (Wagner, 1977). The genera *Borya* (Liliaceae-Johnsonieae) and *Kingia* (Xanthorrhoeaceae) have only root vessels with exclusively scalariform perforation and therefore as regards vessel distribution are less advanced than the most primitive genera of Juncales. Stomata usually paracytic, as in some members of Xanthorrhoeaceae. Pollen grains are very specialized, usually united in tetrahedral tetrads, which are surrounded by the general tetrad wall consisting of sporopollenin; the grains have only a reduced distal aperture (see Meyer and Yaroshevskaya, 1976). Seeds with a very minute straight embryo in the axis of a starchy endosperm.

1. Juncaceae.
2. Thurniaceae (*Thurnia*). Very closely related to Juncaceae.

Order 10. Cyperales.

Evidently derived directly from the most primitive Juncaceae. Generally speaking, Cyperaceae exhibit more advanced vessel features than Juncaceae (Metcalfe, 1971; Cheadle and Kosakai, 1972; Wagner, 1977). The wall of microsporocyte becomes the wall of the tetrad in which only one microspore develops and the tetrads thus transformed to pseudomonads, containing a functional microspore and three non-functional nuclei of the other three microspores of the tetrad (see Wulff, 1939; Shah, 1962, 1967). Besides, members of both families have chromosomes in which centromeric activity is spread over a considerable part of the chromosome (so called "diffuse centromere"—see Battaglia and Boyes, 1955; Stebbins, 1971). But endosperm formation is nuclear, not helobial as in Juncales.

1. Cyperaceae. Subfamilies Cyperoideae and Caricoideae.

Superorder V. Commelinanae

Order 11. Commelinales.

Related to both Bromeliales and Liliales and probably had a common origin with bromeliads from lilialean stock. Commelinales characteristically have paracytic stomata or stomata with four or six subsidiary cells (Stebbins and Khush, 1961; Tomlinson, 1969), nuclear endosperm, seeds with copious starchy, usually mealy, endosperm, and lateral embryo situated at the opposite end to the hilum.

Suborder Xyridineae.

1. Rapateaceae. A very heterobathmic family with comparatively primitive vessel characteristics (the majority of genera have vessels with scalariform perforations, in roots and stems—see Carlquist, 1966, 1969), but a rather advanced inflorescence and flowers (calyx hyaline, corolla tubular, stamens inserted in the tube, style simple, ovules few to solitary in each locule, etc.). According to Carlquist (1966) from the evidence of root and stem anatomy, Rapateaceae show numerous resemblances to the families Bromeliaceae and Xyridaceae. In particular, as Carlquist points out, the ergastic materials (tannin, silica bodies) of Rapateaceae occur also in Bromeliaceae, and the schizogenous slime cavities such as found in Schoenocephalieae of Rapateaceae have also been reported in Bromeliaceae. But pollen grains are different from those in Bromeliaceae and Xyridaceae. Subfamilies Saxofridericioideae (Schoenocephalieae, Saxofridericieae) and Rapateoideae (Monotremeae, Rapateeae).

2. Xyridaceae (incl. Abolbodaceae). Near to Rapateaceae, but more advanced (flowers in heads, stamens three, and vessels in all parts with simple perforations—see Tomlinson, 1969b).

Suborder Commelinineae.

3. Commelinaceae (incl. Cartonemataceae—see Hamann, 1961; Brenan, 1966; Rohweder, 1969). Related to Rapateaceae and probably had a common origin. Vessels more advanced than in Rapateaceae and more or less at the same level as in Xyridaceae (vessels in roots, stems and leaves mostly with simple perforations—Tomlinson, 1969b). Embryo is

covered with embryotega—small hardened cup-like portion of seed-coat which seperates like a little lid (germinal lid) at period of germination.

4. Mayacaceae (*Mayaca*). Very closely related to Commelinaceae and in general more advanced, though vessels in all parts with scalariform perforations (Tomlinson, 1969b).

Order 12. Eriocaulales.

Near to and derived from Commelinales. Vessels in all parts with mostly simple perforations (Tomlinson, 1969b). Endosperm development nuclear.

1. Eriocaulaceae. Subfamilies Eriocauloideae and Paepalanthoideae.

Order 13. Restionales.

Closely related to Commelinales and probably has a common origin with them. Stomata paracytic and frequently with "graminoid" guard cells, vessels mostly in all parts, perforations scalariform or simple. Pollen grains 1-porate, of "graminoid" type. Ovules orthotropous. Endosperm development nuclear. Seeds with small lateral or peripheral lentiform embryo opposite the hilum at the apex of copious starchy endosperm. The most notable feature of the order is the appearance of some typical graminoid characters.

1. Flagellariaceae (*Flagellaria*).
2. Joinvilleaceae (*Joinvillea*). Very closely related to Flagellariaceae.
3. Restionaceae (incl. Anarthriaceae). Subfamilies Restionoideae and Anarthrioideae (*Anarthria*).
4. Ecdeiocoleaceae (*Ecdeiocolea*). Near Restionaceae, but differ by "xyridaceous" habit, anatomy of vegetative organs and morphology of inflorescence (see Cutler and Airy Shaw, 1965).
5. Centrolepidaceae. Closely related to Restionaceae (see Hamann, 1962a, 1975), but flowers minute, without perianth, the male consisting of a single stamen, the female of a single carpel (or pseudomonomerous?).

Order 14. Hydatellales.

The genera *Trithuria* and *Hydatella* were included in Centrolepidaceae, but recently they have been segregated into a new family Hydatellaceae by Hamann (1976), and a new order by Cronquist[4] (1979, unpublished). From Centrolepidaceae and the whole order Restionales it differs by many important characters, including anomocytic stomata of *Trithuria*

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[4] Hydatellales Cronq. ord. nov. Based on and coextensive with family Hydatellaceae Hamann, New Zealand J. Bot. **14:** 193–196. 1976.

(no stomata in *Hydatella,* which probably is the result of adaptation to a submersed habitat) (Cutler, 1969; Hamann, 1976), basifixed and four-sporangiate anthers, anatropous ovules with micropyle directed upwards, probably cellular endosperm, seeds with copious starchy perisperm developing from the large nucellus, and a reduced endosperm consisting of a few cells without starch surrounding an incompletely developed lentiform embryo, seed coat with enlarged outer layer of outer integument and with an operculum from inner integument (Hamann, 1976). These differences are so significant that any close affinity between Hydatellaceae and Centrolepidaceae is out of question. Even the inclusion of the Hydatellales in the Commelinales is somewhat doubtful. The systematic position of this order is still uncertain and it badly needs further studies.

1. Hydatellaceae.

Order 15. Poales.

Very closely related to and derived from Restionales, most probably from some extinct ancestor of the type of the living genus *Joinvillea.* Hallier (1902, 1912) included grasses in Enantioblastae and even placed them between Flagellariaceae and Restionaceae, and Wettstein (1908, 1935) derived them from Enantioblastae. Various anatomical, palynological and embryological studies confirm the close affinity between Poales and Restionales (see Wodehouse, 1936; Erdtman, 1944, 1952; Kuprianova, 1948; Yakovlev, 1950; Smithson, 1957). Relationships are especially close between *Joinvillea* and such a primitive grass as the genus *Streptochaeta.*

1. Poaceae. Subfamilies Bambusoideae (incl. Anomochloideae), Oryzoideae, Pooideae (Festucoideae), Arundinoideae, Eragrostoideae, Panicoideae, Andropogonoideae.

Superorder VI. Zingiberanae

Order 16. Zingiberales.

Related to Liliales and Bromeliales and probably have a common origin with Bromeliales from ancient lilealean stock. The chemistries of Zingiberales and Liliales are not very different and both have raphides and chelidonic acid (Gibbs, 1974), vessel characters are on more or less the same level (Wagner, 1977) and both orders have septal nectaries and cylindrical embryo. Zingiberales have also some similarities with Commelinales (including the position of embryo and starchy food reserves, which in Zingiberales (as well as in Hydatellales), are of two kinds—copious perisperm and reduced endosperm). Flowers highly advanced, more or less zygomorphic or even asymmetric (Cannaceae and Marantaceae) and androecium is characterized by progressive specialization and reduction from six fertile stamens to one stamen (the remainder represented by various petaloid staminodes). In Cannaceae and Marantaceae even the only fertile stamen is half petaloid. Ovary inferior. A very distinctive group which deserves a superordinal rank (Dahlgren, 1975, 1980). According to Tomlinson (1962), the family Strelitziaceae may be considered to represent the nearest approach to the ancestral stock from which the whole order has evolved.

1. Strelitziaceae (*Phenakospermum, Ravenala, Strelitzia*). *Ravenala* is the only genus within the order with six fertile stamens.
2. Musaceae (*Musa* and *Ensete*).
3. Heliconiaceae (*Heliconia*).
4. Lowiaceae (*Orchidantha*).
5. Zingiberaceae. Tribes Globbeae, Zingibereae, Alpinieae.
6. Costaceae.
7. Cannaceae (*Canna*).
8. Maranthaceae. The most advanced family in the order.

Subclass C. Arecidae

Superorder VII. Arecanae

Order 17. Arecales.

The order Arecales and the whole subclass Arecidae has a common origin with Alismatidae and Liliidae. All three subclasses derived from a hypothetical extinct common ancestor, which most likely was a terrestrial rhizomatous herb without vessels and with primitive paracytic stomata, 1-colpate pollen grains (two-celled when shed), and with nectarless flowers with primitive conduplicate free carpels. In all three subclasses there are still forms with apocarpous gynoecium and primitive carpels. Amongst Arecales some coryphoid palms (including *Trithrinax, Trachycarpus,* and *Chamaerops*), *Phoenix* and *Nypa* have apocarpous gynoecium and in some of them carpels are conduplicate and stipitate, with open sutures and laminar or sublaminar placentation (see Uhl and Moore, 1971; Moore, 1973). In *Trachycarpus fortunei* trichomes are present along and to some extent within the unsealed suture, as in some species of primitive dicotyledons (Uhl and Moore, 1971). Stigmas are sessile or subsessile. In Arecales septal nectaries developed independently and as Eames (1961) says "the story here parallels that in the Liliaceae."

1. Arecaceae or Palmae. Subfamilies Coryphoideae, Phoenicoideae, Borassoideae, Caryotoideae, Lepidocaryoideae, Arecoideae, Cocosoideae, Phytelephantoideae, Nypoideae.

Order 18. Cyclanthales.

Evidently has a common origin with Arecales.

1. Cyclanthaceae. Subfamilies Carludovicoideae and Cyclanthoideae.

Order 19. Pandanales.

Stands near to Cyclanthales and has a common origin.

1. Pandanaceae.

Order 20. Typhales.

Very closely related to Pandanales and has a common origin, but stomata paracytic (tetracytic in Pandanaceae), flowers monoecious, gynoecium always pseudomonomerous (in Pandanaceae usually paracarpous, occasionally pseudomonomerous), fruit dry and indehiscent (in Pandanaceae berry or multi-locular drupe), and endosperm starchy and mealy (in Pandanaceae endosperm fleshy and oily). Despite these differences there are also many similarities, including vessel characteristics (Wagner, 1977), close resemblances between the branching in *Sparganium* and that in *Pandanus,* and striking resemblances in the arrangement of flowers (see Rendle, 1953). As Rendle points out, the inflorescence of *Sparganium* recalls that of *Pandanus* on a smaller scale. According to Müller-Doblies (1969) there is "die frappierende Ähnlichkeit der köpfchenförmigen Partialinfloreszenzen von *Sparganium* mit jenen mancher Pandani (Z.B. *Pandanus sparganioides* Bak.)." The close affinity between these two orders is supported also by cytological data (Sharma, 1964; Mallick and Sharma, 1966). In both of them $x = 15$. "Moreover, in the morphology of the chromosomes too, homogeneity is evident, all being characterized by very small chromosomes, with nearly identical types of constrictions. It is very difficult to distinguish the three genera on the basis of their karyotypes as they look very similar to each other" (Sharma, 1964). Therefore Sharma even suggests the inclusion of all of them under one order Pandanales.

1. Typhaceae (incl. Sparganiaceae—see Hallier, 1912; Müller-Doblies, 1970; Thorne, 1976; Ehrendorfer, 1978). Subfamilies Sparganioideae and Typhoideae.

Superorder VIII. Aranae

Order 21. Arales.

Most likely has a common origin with Arecales and Cyclanthales from an apocarpous and multiovulate protolilealean ancestor. It would have vessels only in roots and with only scalariform perforations. According to Eyde et al. (1967) the origin of syncarpy occurred independently in several evolutionary lines in Araceae. The genus *Philodendron,* which has multicarpellate gynoecium, shows nearest approach to apocarpy, but its flowers are naked and unisexual.

1. Araceae (incl. Acoraceae and Pistiaceae). Subfamilies Pothoideae, Acoroideae (*Acorus*—see Eyde et al., 1967), Monsteroideae, Calloideae, Lasioideae, Philodendroideae, Calocasioideae, Aroideae, Pistioideae.
2. Lemnaceae. Close to and descended from Araceae-Pistioideae by neotenous retention of embryonic features of *Pistia*-like ancestor (see Takhtajan, 1943). Subfamilies Lemnoideae and Wolffioideae.

IV. ACKNOWLEDGMENTS

My thanks to Arthur Cronquist with whom I have carried on a dialogue on phylogenetic systematics for many years, for his kind suggestion that I write this outline of my system for Botanical Review, and for his most useful comments on the manuscript. I also thank my colleagues who kindly sent me their published works and preprints, which have been very helpful to me.

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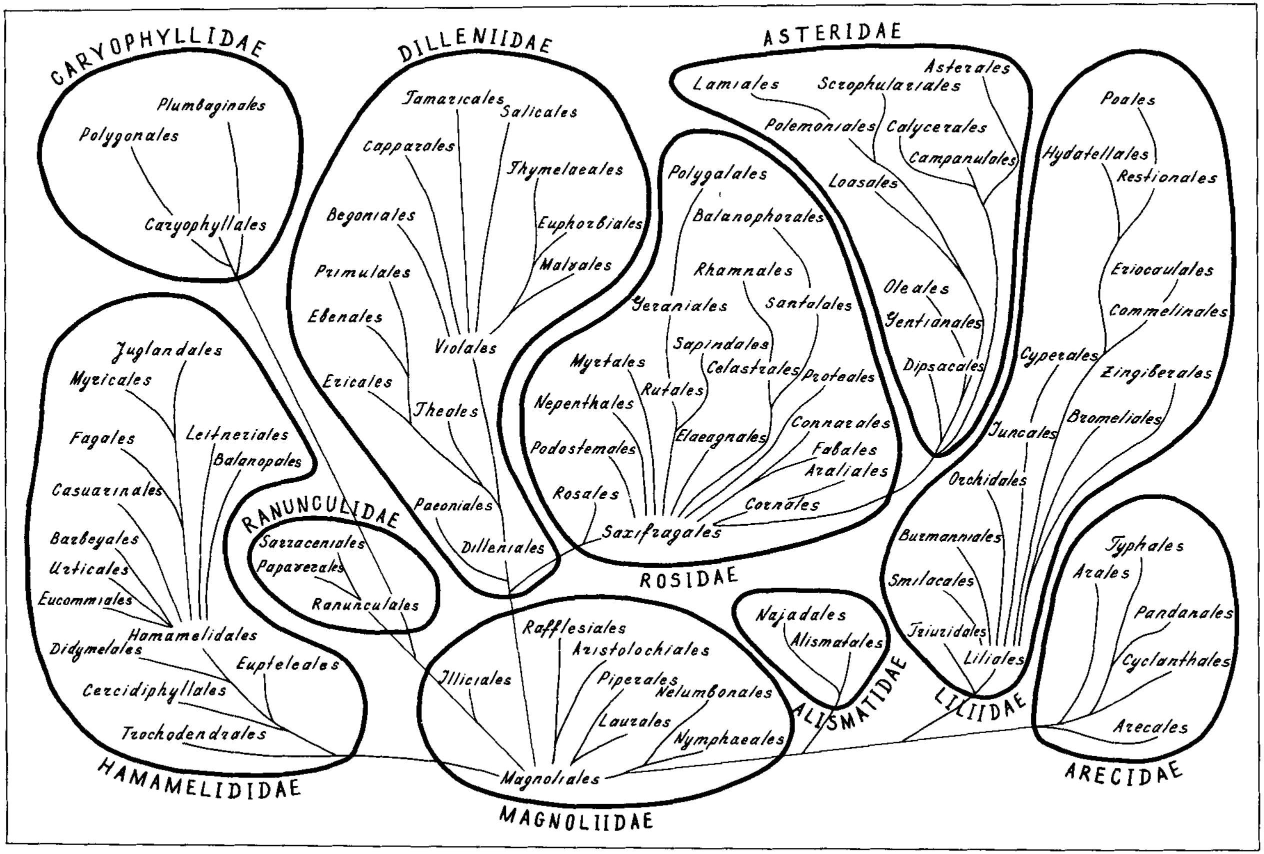

Putative relationships among the classes, subclasses and orders of flowering plants.

VI. LIST OF THE CLASSES, SUBCLASSES, ORDERS AND FAMILIES OF THE MAGNOLIOPHYTA

CLASS MAGNOLIOPSIDA OR DICOTYLEDONES

Subclass A. Magnoliidae

Order 1. Magnoliales

1. Winteraceae
2. Degeneriaceae
3. Eupomatiaceae
4. Himantandraceae
5. Magnoliaceae
6. Annonaceae
7. Canellaceae
8. Myristicaceae

Order 2. Illiciales

1. Illiciaceae
2. Schisandraceae

Order 3. Laurales

1. Austrobaileyaceae
2. Amborellaceae
3. Trimeniaceae
4. Monimiaceae
5. Gomortegaceae
6. Calycanthaceae
7. Chloranthaceae
8. Lactoridaceae
9. Lauraceae
10. Hernandiaceae

Order 4. Piperales

1. Saururaceae
2. Piperaceae

Order 5. Aristolochiales

1. Aristolochiaceae

Order 6. Rafflesiales

1. Hydnoraceae
2. Rafflesiaceae

Order 7. Nymphaeales

1. Cabombaceae
2. Nymphaeaceae
3. Ceratophyllaceae

Order 8. Nelumbonales

1. Nelumbonaceae

Subclass B. Ranunculidae

Order 9. Ranunculales

1. Lardizabalaceae
2. Sargentodoxaceae
3. Menispermaceae
4. Berberidaceae
5. Ranunculaceae
6. Glaucidiaceae
7. Circaeasteraceae

Order 10. Papaverales
  1. Papaveraceae
Order 11. Sarraceniales
  1. Sarraceniaceae

Subclass C. Hamamelididae
Order 12. Trochodendrales
  1. Trochodendraceae
  2. Tetracentraceae
Order 13. Cercidiphyllales
  1. Cercidiphyllaceae
Order 14. Eupteleales
  1. Eupteleaceae
Order 15. Didymelales
  1. Didymelaceae
Order 16. Hamamelidales
  1. Hamamelidaceae
  2. Platanaceae
  3. Myrothamnaceae
  4. Daphniphyllaceae
  5. Buxaceae
  6. Simmondsiaceae
Order 17. Eucommiales
  1. Eucommiaceae
Order 18. Urticales
  1. Ulmaceae
  2. Moraceae
  3. Cannabaceae
  4. Cecropiaceae
  5. Urticaceae
Order 19. Barbeyales
  1. Barbeyaceae
Order 20. Casuarinales
  1. Casuarinaceae
Order 21. Fagales
  1. Fagaceae
  2. Betulaceae
Order 22. Balanopales
  1. Balanopaceae
Order 23. Leitneriales
  1. Leitneriaceae
Order 24. Myricales
  1. Myricaceae
Order 25. Juglandales
  1. Rhoipteleaceae
  2. Juglandaceae

Subclass D. Caryophyllidae
Order 26. Caryophyllales
  1. Phytolaccaceae
  2. Achatocarpaceae
  3. Nyctaginaceae
  4. Aizoaceae

5. Cactaceae
6. Portulacaceae
7. Hectorellaceae
8. Basellaceae
9. Didiereaceae
10. Stegnospermataceae
11. Molluginaceae
12. Caryophyllaceae
13. Amaranthaceae
14. Chenopodiaceae

Order 27. Polygonales

1. Polygonaceae

Order 28. Plumbaginales

1. Plumbaginaceae

Subclass E. Dilleniidae

Order 29. Dilleniales

1. Dilleniaceae
2. Crossosomataceae

Order 30. Paeoniales

1. Paeoniaceae

Order 31. Theales

1. Ochnaceae
2. Sauvagesiaceae
3. Strasburgeriaceae
4. Diegodendraceae
5. Ancistrocladaceae
6. Dioncophyllaceae
7. Theaceae
8. Oncothecaceae
9. Pentaphylacaceae
10. Tetrameristaceae
11. Caryocaraceae
12. Asteropeiaceae
13. Marcgraviaceae
14. Pelliceriaceae
15. Quiinaceae
16. Medusagynaceae
17. Bonnetiaceae
18. Clusiaceae
19. Elatinaceae

Order 32. Violales

1. Flacourtiaceae
2. Passifloraceae
3. Stachyuraceae
4. Violaceae
5. Bixaceae
6. Cistaceae
7. Peridiscaceae
8. Scyphostegiaceae
9. Dipentodontaceae
10. Turneraceae

11. Malesherbiaceae
12. Achariaceae
13. Caricaceae
14. Cucurbitaceae

Order 33. Begoniales

1. Datiscaceae
2. Begoniaceae

Order 34. Capparales

1. Capparaceae
2. Tovariaceae
3. Brassicaceae
4. Resedaceae
5. Moringaceae

Order 35. Tamaricales

1. Frankeniaceae
2. Tamaricaceae
3. Fouquieriaceae

Order 36. Salicales

1. Salicaceae

Order 37. Ericales

1. Actinidiaceae
2. Clethraceae
3. Ericaceae
4. Empetraceae
5. Epacridaceae
6. Diapensiaceae
7. Cyrillaceae
8. Grubbiaceae

Order 38. Ebenales

1. Styracaceae
2. Symplocaceae
3. Lissocarpaceae
4. Ebenaceae
5. Sapotaceae

Order 39. Primulales

1. Myrsinaceae
2. Theophrastaceae
3. Primulaceae

Order 40. Malvales

1. Elaeocarpaceae
2. Tiliaceae
3. Sterculiaceae
4. Huaceae
5. Scytopetalaceae
6. Dipterocarpaceae
7. Sarcolaenaceae
8. Sphaerosepalaceae
9. Bombacaceae
10. Malvaceae

Order 41. Euphorbiales

1. Euphorbiaceae
2. Pandaceae

3. Dichapetalaceae
4. Aextoxicaceae

Order 42. Thymelaeales

1. Thymelaeaceae

Subclass F. Rosidae

Order 43. Saxifragales

1. Brunelliaceae
2. Cunoniaceae
3. Davidsoniaceae
4. Eucryphiaceae
5. Escalloniaceae
6. Hydrangeaceae
7. Montiniaceae
8. Columelliaceae
9. Roridulaceae
10. Pittosporaceae
11. Byblidaceae
12. Bruniaceae
13. Alseuosmiaceae
14. Pterostemonaceae
15. Saxifragaceae
16. Crassulaceae
17. Cephalotaceae
18. Grossulariaceae
19. Vahliaceae
20. Eremosynaceae
21. Greyiaceae
22. Francoaceae
23. Parnassiaceae
24. Droseraceae
25. Gunneraceae ?

Order 44. Rosales

1. Rosaceae
2. Chrysobalanaceae
3. Neuradaceae

Order 45. Fabales

1. Fabaceae

Order 46. Connarales

1. Connaraceae

Order 47. Podostemales

1. Podostemaceae

Order 48. Nepenthales

1. Nepenthaceae

Order 49. Myrtales

1. Crypteroniaceae
2. Lythraceae
3. Sonneratiaceae
4. Punicaceae
5. Melastomataceae
6. Oliniaceae

7. Penaeaceae
8. Myrtaceae
9. Combretaceae
10. Onagraceae
11. Trapaceae
12. Haloragaceae
13. Rhizophoraceae
14. Lecithydaceae

Order 50. Rutales

1. Rutaceae
2. Rhabdodendraceae
3. Cneoraceae
4. Simaroubaceae
5. Zygophyllaceae
6. Nitrariaceae
7. Balanitaceae
8. Meliaceae
9. Kirkiaceae
10. Ptaeroxylaceae
11. Burseraceae
12. Anacardiaceae
13. Julianiaceae
14. Podoaceae
15. Coriariaceae

Order 51. Sapindales

1. Staphyleaceae
2. Sapindaceae
3. Aceraceae
4. Hippocastanaceae
5. Stylobasiaceae
6. Gyrostemonaceae
7. Bataceae
8. Emblingiaceae
9. Bretschneideraceae
10. Melianthaceae
11. Akaniaceae
12. Sabiaceae
13. Physenaceae (**fam. nov.**)

Order 52. Geraniales

1. Linaceae
2. Houmiriaceae
3. Erythroxylaceae
4. Oxalidaceae
5. Geraniaceae
6. Balsaminaceae
7. Tropaeolaceae
8. Limnanthaceae

Order 53. Polygalales

1. Malpighiaceae
2. Trigoniaceae
3. Vochysiaceae

4. Polygalaceae
5. Krameriaceae
6. Tremandraceae

Order 54. Cornales

1. Davidiaceae
2. Nyssaceae
3. Alangiaceae
4. Cornaceae
5. Aucubaceae
6. Garryaceae
7. Melanophyllaceae
8. Griseliniaceae
9. Toricelliaceae
10. Helwingiaceae

Order 55. Araliales

1. Araliaceae
2. Apiaceae

Order 56. Celastrales

1. Icacinaceae
2. Sphenostemonaceae
3. Aquifoliaceae
4. Phellinaceae
5. Paracryphiaceae
6. Cardiopterygaceae
7. Medusandraceae
8. Celastraceae
9. Stackhousiaceae
10. Siphonodontaceae
11. Goupiaceae
12. Geissolomataceae
13. Salvadoraceae
14. Corynocarpaceae
15. Lophopyxidaceae

Order 57. Santalales

1. Olacaceae
2. Opiliaceae
3. Santalaceae
4. Misodendraceae
5. Loranthaceae
6. Viscaceae

Order 58. Balanophorales

1. Cynomoriaceae
2. Balanophoraceae

Order 59. Rhamnales

1. Rhamnaceae
2. Vitaceae
3. Leeaceae

Order 60. Elaeagnales

1. Elaeagnaceae

Order 61. Proteales

1. Proteaceae

Subclass G. Asteridae

Order 62. Gentianales

1. Loganiaceae
2. Rubiaceae
3. Theligonaceae
4. Apocynaceae
5. Asclepiadaceae
6. Gentianaceae
7. Menyanthaceae
8. Dialypetalanthaceae

Order 63. Oleales

1. Oleaceae

Order 64. Dipsacales

1. Caprifoliaceae
2. Adoxaceae
3. Valerianaceae
4. Morinaceae
5. Dipsacaceae

Order 65. Loasales

1. Loasaceae

Order 66. Polemoniales

1. Convolvulaceae
2. Cuscutaceae
3. Polemoniaceae
4. Hydrophyllaceae
5. Boraginaceae
6. Lennoaceae
7. Hoplestigmataceae

Order 67. Lamiales

1. Verbenaceae
2. Lamiaceae
3. Callitrichaceae

Order 68. Scrophulariales

1. Solanaceae
2. Duckeodendraceae
3. Buddlejaceae
4. Retziaceae
5. Scrophulariaceae
6. Bignoniaceae
7. Pedaliaceae
8. Martyniaceae
9. Orobanchaceae
10. Gesneriaceae
11. Plantaginaceae
12. Lentibulariaceae
13. Myoporaceae
14. Acanthaceae
15. Hydrostachyaceae
16. Hippuridaceae

Order 69. Campanulales

1. Campanulaceae

2. Stylidaceae
3. Donatiaceae
4. Goodeniaceae

Order 70. Calycerales

1. Calyceraceae

Order 72. Asterales

1. Asteraceae

CLASS LILIOPSIDA OR MONOCOTYLEDONES

Subclass A. Alismatidae

Order 1. Alismatales

1. Butomaceae
2. Limnocharitaceae
3. Alismataceae
4. Hydrocharitaceae

Order 2. Najadales

1. Aponogetonaceae
2. Scheuzeriaceae
3. Juncaginaceae
4. Posidoniaceae
5. Potamogetonaceae
6. Ruppiaceae
7. Zannichelliaceae
8. Cymodoceaceae
9. Zosteraceae
10. Najadaceae

Subclass B. Liliidae

Order 3. Triuridales

1. Triuridaceae

Order 4. Liliales

1. Colchicaceae
2. Herreriaceae
3. Liliaceae
4. Alstroemeriaceae
5. Alliaceae
6. Hemerocallidaceae
7. Amaryllidaceae
8. Phormiaceae
9. Agavaceae
10. Doryanthaceae
11. Asphodelaceae
12. Xanthorrhoeaceae
13. Aphyllanthaceae
14. Hanguanaceae
15. Asparagaceae
16. Dracaenaceae
17. Tecophilaeaceae
18. Iridaceae
19. Haemodoraceae
20. Hypoxidaceae
21. Velloziaceae

22. Pontederiaceae
23. Philydraceae

Order 5. Smilacales

1. Philesiaceae
2. Stemonaceae
3. Trilliaceae
4. Smilacaceae
5. Dioscoreaceae
6. Taccaceae

Order 6. Burmanniales

1. Burmanniaceae
2. Corsiaceae

Order 7. Orchidales

1. Orchidaceae

Order 8. Bromeliales

1. Bromeliaceae

Order 9. Juncales

1. Juncaceae
2. Thurniaceae

Order 10. Cyperales

1. Cyperaceae

Order 11. Commelinales

1. Rapateaceae
2. Xyridaceae
3. Commelinaceae
4. Mayacaceae

Order 12. Eriocaulales

1. Eriocaulaceae

Order 13. Restionales

1. Flagellariaceae
2. Joinvilleaceae
3. Restionaceae
4. Ecdeiocoleaceae
5. Centrolepidaceae

Order 14. Hydatellales

1. Hydatellaceae

Order 15. Poales

1. Poaceae

Order 16. Zingiberales

1. Strelitziaceae
2. Musaceae
3. Heliconiaceae
4. Lowiaceae
5. Zingiberaceae
6. Costaceae
7. Cannaceae
8. Maranthaceae

Subclass C. Arecidae

Order 17. Arecales

1. Arecaceae

Order 18. Cyclanthales
  1. Cyclanthaceae
Order 19. Pandanales
  1. Pandanaceae
Order 20. Typhales
  1. Typhaceae
Order 21. Arales
  1. Araceae
  2. Lemnaceae