

Flowering Plants

Armen Takhtajan

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Foreword

Professor Armen Takhtajan, a giant among botanists, has spent a lifetime in the service of his science and of humanity. As a thoroughgoing internationalist, he promoted close relationships between botanists and people of all nations through the most difficult times imaginable, and succeeded with his strong and persistent personal warmth. He also has stood for excellent modern science throughout this life, and taught hundreds of students to appreciate the highest values of civilization whatever their particular pursuits or views, or the problems they encountered.

Takhtajan has made multiple contributions to our understanding of plant evolution, particularly concerning angiosperms and their classification. As early as 1943, in his paper “Correlations of Ontogenesis and Phylogenesis in Higher Plants,” he put forward a theory of the macroevolution of many groups of plants through neoteny; he elaborated this theory in later publications. Takhtajan’s ideas on macroevolution as a result of changes in developmental timing (heterochrony or heterobotmy) has been viewed favorably by a number of outstanding biologists, including Agnes Arber (in “The Natural Philosophy of Plant Form”, 1950) and Stephen Gould (in “Ontogeny and Phylogeny”, 1977). His principal ideas were that the origin of herbaceous angiosperms was the result of neoteny and that the origin of some arborescent forms was secondary. He also offered hypotheses about the way in which monocot leaves, with their characteristic parallel venation, and discussed well the patterns involved in the origin of stomata. Takhtajan produced a novel classification for the structural types of gynoecium and of their placentation. He also wrote on the evolution of inflorescences, the evolution of pollen grains, and the evolutionary classification of fruit types. His theory of the evolution of inflorescences, in which he postulated that a leafy cyme was the original type, was accepted by Stebbins (“Flowering Plants, Evolution Above the Species Level,” 1974: 263). One of his most important contributions was the idea that the origin and evolution of male and female gametophytes of the angiosperms came about through evolutionary changes in developmental timing accompanied by drastic modifications of the ontogenetic processes involved.

Takhtajan’s most important achievement has been the development of his phylogenetic system of the flowering plants, a system that has greatly influenced all other recent systems of classification; in turn, Takhtajan was inspired by Hans Hallier’s earlier theories. He published a preliminary phyletic diagram of the orders of angiosperms as early as in 1942, and this diagram was mentioned by Gundersen in his “Families of Dicotyledons” (1950). Later in his large book, “A System and Phylogeny of the Flowering Plants” (1966) and in his “Systema Magnoliophytorum” (1987), both in Russian, as well as in “Diversity and Classification of Flowering Plants” (1997), in English, Takhtajan provided a detailed exposition of his system as well as

the reasons for his delimitation and arrangement of families and orders. One of his main innovations was the subdivision of both the dicots and monocots into subclasses, which was widely accepted as a major advance in angiosperm classification and introduced into some textbooks, including the last edition of Strasburger's "Lehrbuch der Botanik".

Takhtajan's system of classification is a synthetic, integrated one based on all available data, including recent studies in embryology, palynology, comparative anatomy, cytology, phytochemistry, and molecular data, as well as on cladistic analyses of many taxa. This new book, as well as "Diversity and Classification of Flowering Plants", includes also intrafamilial classification (subfamilies and tribes).

Armen Takhtajan has worked for many years at the Komarov Botanical Institute, St. Petersburg, Russia (LE), where he had access to its great herbarium collections and library. He used these rich resources to supplement his field experience in many regions in the world. As a result of his studies and the observations he was able to make during the course of his travels, he prepared a book entitled "Floristic Regions of the World," in which he presented not only floristic divisions for the whole world, but also listed endemic families and genera and provided examples of endemic species for each province.

At the present, the classification of angiosperm families and our ideas of their relationships are moving forward rapidly; current studies have led and are leading to many significant changes in our interpretations, largely following the important clues about relationship that have come from molecular comparisons between taxa. Because of the numerous examples of parallelism and evolutionary convergence among the angiosperms and their individual structures, some of the ideas gained by earlier, often meticulous analyses of morphological, anatomical, and even chemical features. The classification presented in the current book should be understood as a summary of a life's study of plants and the system that his insights support – the work of a very great botanist that takes into account not only his own meticulous studies but as much of the contemporary information as he was able to assimilate and take into account. Although future classifications will clearly go beyond the stage of development represented here, it is important to be able to benefit from Armen Takhtajan's insights into the features of flowering plants and the ways in which the suites of characteristics they present can be viewed in an evolutionary context.

Takhtajan is a botanist of the 20th century, and the views developed from his vast experience – he is nearly 100 years of age – richly deserve publication. Younger research workers and students will appreciate the opportunity to be informed of Armen Takhtajan's ideas, and to be acquainted with the wide ranging data on where they are based. This book naturally draws extensively on the rich Russian literature in the field of plant classification, and many readers will find ideas expressed that are of interest to them. The new insights and ideas in the book likewise will inspire new levels of thinking about the relationships between the families of angiosperms and their evolutionary history, including the convergent and parallel evolution of particular features.

Peter Stevens, one of the reviewers, has pointed out that additional evidence has accumulated regarding the relationships of many angiosperm families, and that comparisons of their DNA have revealed unsuspected similarities. Armen Takhtajan has taken into consideration some, but not all, of this evidence, and future treatments will result in major revisions of some of the concepts presented here. Importantly, he brings to our attention the pertinent Russian botanical literature, which is poorly

known in the West. This book presents challenging new ideas and insights clearly, and it is very important to publish for its demonstrated value as the final work of a great scientist, representing the culmination of his experience and study.

It is also important to mention that this book summarizes the ideas and understanding of a lifetime of investigation and thought by one of the most able and influential botanists of our time. Considering his age, it will probably be the last one. – Peter H. Raven, President and Director, Missouri Botanical Garden, St. Louis, Missouri, USA.

Short Biography

Armen Takhtajan was born on June 10, 1910 in Shusha, Nagorny Karabakh. He was graduated from the Institute of Subtropical Cultivation in Tbilisi (1929–1932). He got his Ph.D. (candidate of sciences) in Leningrad, 1938; and his Dr. Sci. (Doctor of Sciences) at the Yerevan State University, Armenia in 1943. He worked as Research fellow, at the Natural History Museum in Yerevan (1932–1937), and as Senior Botanist, at the Biological Institute in Armenia (1935–1943). He was also Lecturer and later Professor of Botany at the Yerevan State University (1936–1948); Director of Botanical Institute, Armenian Academy of Sciences (1943–1948); and Professor of Botany, Leningrad State University (1949–1960). He has been a member of the staff at the Komarov Botanical Institute, Russian Academy of Sciences since 1955, first as a Chief of the Laboratory of Palaeobotany (1955–1987) and also as Director of the Institute (1976–1986). Now he is an Advisor of the Komarov Botanical Institute.

He is a full member (Academician) of the Armenian Academy of Sciences and of the Russian Academy of Sciences, foreign associate of the National Academy of Sciences of the United States of America, foreign member of Finnish Academy of Sciences and Letters, German Academy of Naturalists (Leopoldina), Polish Academy of Sciences, Norwegian Academy of Sciences, foreign member of the Linnaean Society of London. For many years he was President of the Soviet Union Botanical Society.

Armen Takhtajan was awarded the A.L. Komarov Award (1969), Russian State Award (1981), the Allerton Medal (1990) and Henry Shaw Medal (1997) for Botany, and he has 20 books and more than 300 scientific papers to his name. He served as editor for many books and series published in Russia, including the *Botaniskiy Zhurnal*. As an editor, he read and corrected the entire text line by line. The recent publication of this kind was the 6-volume series “Plant Life,” which serves for many high school and university students as a wonderful textbook.

Armen Takhtajan has been and is an individual of outstanding accomplishment and influence on the biological sciences both in Russia and throughout the world.

Preface

This book is a result of my almost half-century study of the morphology and systematics of flowering plants. It continues my work published in several of my previous books, especially “Systema Magnoliophytorum” (1987), published in Russian, and its continuation and expansion – “Diversity and Classification of Flowering Plants” (1997), published in English. However, when writing this book of mine, I have inevitably analyzed and considered the matter again and in many cases considerably changed the former conclusions. Here I present an essentially new version of my system.

My new revision of the system is based on a great amount of new information published in the last decade as well as on discussions and consultations with many of my colleagues. New taxonomic revisions of large groups, including families, and new comparative-morphological studies of various groups, including an increasing number of micromorphological (ultrastructural) studies, were especially important for phylogenetic inferences.

No less important was a rapidly increasing number of molecular taxonomic studies, provided that they did not contradict the totality of other evidence.

I would like to thank Dr. Peter Stevens and Dr. James Reveal for reading the manuscript. Both of them made valuable suggestions that were very helpful during the preparation of the final version of the book.

My work on this book would be impossible without the great help of Tatiana Wielgorskaya. She has helped me not only in all kinds of computer work but also in the search of literature.

November, 2008

Armen Takhtajan

Introduction

Main Vectors of Evolution in Flowering Plants (The Criteria Used in Evaluating the Relative Degree of Their Advancement)

The vegetative characters there are many easily reversible characters, such as growth habit, arrangement, size and form of leaves, but there are also many trends which either can be reversible with great difficulty or are completely irreversible. In general, vegetative organs are characterized by more reversibility than reproductive organs. However, even the most reversible characters usually reveal more or less definite evolutionary trends.

Growth habit: The most primitive magnoliophytes are woody plants, and the herbaceous growth habit is always secondary (Jeffrey 1899, 1917; Hallier 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). 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”.

Branching: There are two main morphological types of branching in flowering plants – monopodial and sympodial. Both these types are met in many families and even within one and the same genus and change from one to the other with great ease. This makes the determination of the main direction of evolution of the branching in flowering plants somewhat difficult. The study of the most archaic extant magnoliophytes indicates that perhaps the original type has a combination of monopodial and sympodial branching – well expressed, for example, in *Magnolia*. The vegetative branches of *Magnolia* are monopodial, but the short branches carrying the terminal flowers develop in a strictly sympodial manner, and the apparently simple axis of such a branch is in fact a sympode of a certain number of shoots of an ascending series. The sympodial

nature of a reproductive branch is determined by the fact that each of the component axes ends in a terminal flower, arresting its subsequent development. So the sympodial nature here is primary and not secondary as in the evolution of the vegetative branches. Monopodial branching is characteristic of many trees of the humid subtropical and particularly the humid tropical forest (Serebryakov 1955: 75). This is explained by the fact that the conditions of humid tropical and subtropical climates help in prolonged preservation of the terminal meristems of the stems so that the growth of the vegetative shoot occurs all the time through a continuously operating apical meristem, which leads to a vigorous development of the main axis and to a greater or lesser suppression of the lateral shoots. But in the extratropical regions as well as in the mountains of tropics and under the conditions of a dry tropical climate, the sympodial branching arises out of monopodial (Takhtajan 1948, 1964; Serebryakov 1955). The growth of the annual shoots ends in the disappearance of their terminal bud, which inevitably leads to the development of a large number of lateral buds and the formation of a larger number of lateral shoots. The main axis ceases to hinder the development of the lateral shoots, the intensity of branching is amplified, and the crown becomes denser. The process of the origin of sympodial branching out of the monopodial type is realized in the most diverse phyletic lines and at various levels of specialization. Sympodial branching is very widespread in the herbaceous angiosperms. It is observed in almost all monocotyledons, where it is a direct result of the reduction of the cambium (Holtum 1955), and quite typical of the herbaceous dicotyledons as well. The biological advantages of sympodial branching is emphasized by Zhukovsky (1964: 125), who thinks that the successive dying off of the terminal buds should be considered as a very useful adaptation. According to Serebryakov, sympodial renewal was in addition a vigorous tool for intensifying vegetative reproduction (1952: 278). Lastly, in his opinion, the dying off of the shoot apex or the terminal buds under sympodial growth provides for an earlier “maturing” of the shoots, their transition to the state of dormancy, and an intensification of the hardiness of the trees and shrubs.

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 Winteraceae, Canellaceae, Magnoliaceae, and Himantandraceae. 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 venation (ptyxis) the most primitive is conduplicate venation 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: The stomatal apparatus of flowering plants is characterized by diversity of structure. Stomata may be surrounded either by ordinary epidermal cells (the anomocytic type characteristic of Ranunculaceae, Berberidaceae, Liliaceae, and many other families), or by two or more subsidiary cells morphologically distinct from the other epidermal cells (paracytic, tetracytic, anisocytic, diacytic, actinocytic, and other types).

There are two basic types of development of stomata with subsidiary cells – perigenous and mesogenous. There is also an intermediate mesoperigenous (Pant 1965). In the evolution of seed plants the perigenous type preceded the mesogenous type (Florin 1933, 1958), but the flowering plants most probably began with the mesogenous type. This is supported by the occurrence of the mesogenous (and mesoperigenous) type in such archaic families as Degeneriaceae, Himantandraceae, Magnoliaceae, Eupomatiaceae, Annonaceae, Canellaceae, Winteraceae, and Illiciaceae. Moreover, the stomatal apparatus of the mesogenous and mesoperigenous Magnoliidae is of the paracytic type (accompanied on either side by one or more subsidiary cells parallel to the long axis of the pore and guard cells). Mesogeneous paracytic stomata are the most primitive and initial type of the magnoliophyte stomatal apparatus (Takhtajan 1966, 1969; Baranova 1972, 1985, 1987a, b). All other types of stomata, including the anomocytic type which is devoid of subsidiary cells, are derived.

As regards stomatal ontogeny, most of the morphological types of stomatal complexes with subsidiary cells are in fact ontogenetically heterogeneous (Baranova 1987a).

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 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 tripentalacunar (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-traces 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 Magnolianaes 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* 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 Plan-taginaceae 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. 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).

As comparative anatomical studies of the phloem from Hemenway (1913) onwards have shown, the sieve elements of primitive angiosperms are long and narrow with very oblique end wall, as, for example, in *Drimys*. This is in agreement with the finding that the sieve elements in ferns and gymnosperms are long and pointed with no pronounced differences between the side and end walls. The absence of companion cells in the phloem of gymnosperms and ferns gives us good reason to suspect that the earliest angiosperms were also devoid of them.

Wood parenchyma (occurring as longitudinal parenchyma strands) in early angiosperms was either very scanty (Hallier 1908, 1912) and apotracheal (independent of the tracheal elements in distribution) or, more probably, was absent. Carlquist (1962) considers absence of parenchyma as primitive. The most primitive type of ray tissue system is a heterogenous ray system which consists of two kinds of rays: one heterocellular-multiseriate composed of elongated or nearly isodiametric cells in the multiseriate part and upright cells in the uniseriate marginal parts which are longer than the multiseriate part; the other homocellular-uniseriate composed entirely of upright (vertically elongated) or of upright and square cells. Such rays are met with in many living angiosperms with relatively primitive wood (Kribs 1935; Metcalf and Chalk 1950; Eames 1961; Esau 1965).

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 1945).

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). Weberling (1965) also comes to the conclusion that in general the polytelic type is more highly evolved than and perhaps derived from the monotelic type. 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.

The diversity of the types of inflorescences is strengthened by the presence of different and sometimes very complex combinations of their basic types. Examples of such secondary or composite inflorescences (inflorescentiae compositae) are compound umbels of Apiaceae or catkinlike compound inflorescences of *Betula*, *Alnus*, or *Corylus*.

It is most interesting that frequently the ways and trends of evolution of secondary inflorescences repeat those of primary inflorescences. In many cases, the secondary inflorescences imitate the architecture of the primary one. Such are, for example, the catkinlike inflorescences of Betulaceae, which are so similar to aments of *Salix*. Even more remarkable are the secondary capitula of some Asteraceae, for example those of *Echinops*, which are externally almost indistinguishable from the simple (elementary) capitula. It is also interesting that there is a remarkable parallelism in evolution of composite and elementary capitula of Asteraceae.

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. 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). 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, of Peruvian ranunculaceous *Laccopetalum giganteum*, 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 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 archaic 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 the majority of flowering plants, 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”. Bracteopetals occur in more archaic taxa and evidently appeared earlier, they also connected with generally more primitive pollination mechanisms and with less specialized pollinators. Andropetals, on the contrary, are usually connected with more advanced types of pollination.

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 leaf-like 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 microsporangiote organ (see Eames 1961).

During evolution changed not only the number and arrangement of stamens but also the mode of their sequence of ontogenetic development (Payer 1857; Corner 1946). The initial and most widespread type of development is the centripetal (acropetal), when the development of androecium follows the development of the perianth in the normal sequence, spiral or cyclic. The first to develop in this case are the outermost (lowermost) stamens and then, successively, the inner ones. This type is characteristic for all spiral androecia (like those of Magnoliaceae, Annonaceae, Nymphaeaceae, Nelumbonaceae, Ranunculaceae), for cyclic oligomerous androecia, such as those of the Papaveraceae, Rosaceae, Fabaceae – Mimosoideae, or Myrtaceae. In the centrifugal androecium, there is a break between the order of development of perianth and androecium caused by the intercalation of new stamens. The centrifugal development arose from the centripetal (Corner 1946; Ronse Decraene and Smets 1987). It is characteristic of the Glau-cidiaceae, Paeoniaceae, probably some Phyto-laccaceae with numerous stamens, Aizoaceae, Cactaceae, Dilleniaceae, Actinidiaceae, Theaceae, Clusiaceae, Lecythidaceae, many Violales, some Capparaceae, Bixaceae, Colchosperrmaceae, Cistaceae, Tiliaceae, Bombacaceae, Malvaceae, the genus *Lagerstoemia* (Lythraceae), Punicaceae, Loasaceae, Limnocharitaceae, and some other taxa. In some families such as Ochnaceae, Begoniaceae, Lythaceae, and Loasaceae, there are both types of stamen development. Therefore, the distinction between centrifugal and centripetal types of development is by no means clear-cut and there are some transitional forms (Sattler 1972; Philipson 1975; Sattler and Pauzé 1978; Ronse Decraene and Smets 1987). According to Leins (1964, 1975), the difference between centripetal and centrifugal development depends on the shape of the receptacle: a concave receptacle would give rise to a centripetal development, while on a convex receptacle only a centrifugal development would be possible. But this is not a general rule (Hiepkö 1964; Mayr 1969; Ronse Decraene and Smets 1987).

Microsporangia, microsporogenesis and pollen grains: Stamens most commonly contain four microsporangia arranged in two pairs. Only in some taxa, such as Circaeasteraceae, Epacridaceae, certain Diapensiaceae, Bombacaceae, Malvaceae, Adoxaceae, Philydraceae, Restionaceae, the stamens contain only two microsporangia. Very rarely, as in *Arceuthobium* (Viscaceae) there is only one microsporangium. Multisporangiate stamens of some taxa, e.g., in Rhizophoraceae, result from partition of the sporogenous tissue by sterile plates.

There are two structural and functional types of tapeta, distinguished on the basis of cell behavior during microsporogenesis: the secretory or glandular tapetum, the cells of which remain intact and persist in situ but, after meiosis at the tetrad stage, or at the beginning of the free microspore stage, and sometimes as late as at the stage of two-celled pollen grains, become disorganized and obliterated, and the plasmodial or amoeboid tapetum, characterized by the breakdown of the cell walls before meiosis and protrusion of the protoplasts into the locule and fusion to form a multinucleate plasmodium. Besides, unusual cyclic-invasive type of tapetum has been found lately (Rowley et al. 1992; Gabarayeva and El-Ghazaly 1997). The overwhelming majority of families of flowering plants, including the majority of the most archaic taxa, is characterized by the secretory tapetum. In additions, some primitive characters are correlated with a secretory tapetum (Sporne 1973; Pacini et al. 1985). On the other hand, the plasmodial type usually occurs in relatively more advanced groups. As Schürhoff (1926) pointed out, the presence of plasmodial tapetum is closely correlated with an advanced character such as tricelled pollen grains.

The ways of dehiscence of the mature anther has also some systematic and evolutionary significance. The commonest and the most primitive dehiscence is the longitudinal dehiscence along the fissure (stomium), situated between a pair of microsporangia. The longitudinal dehiscence is of two types: by one simple longitudinal slit or by two longitudinal valves. The second type is characterized by additional, transverse slits usually at both ends of the longitudinal slit, which results in two windowlike lateral valves (see Endress and Hufford 1989; Hufford and Endress 1989). Whereas the dehiscence by simple longitudinal slit is very common, the second type is characteristic of many Magnoliidae and Hamamelididae with more or

less massive anthers and evidently derived from the first type. “Possibly, only the predisposition for easily developing valvate dehiscence was present in the original angiosperm stamen that dehisced via simple longitudinal slits. This predisposition would have been lost in more advanced angiosperms” (Endress and Hufford 1989: 79). More specialized is a valvate dehiscence in Laurales and Berberidaceae, which typically arises by the opening of the thecal wall outward producing apically hinged flaps that lift upward at dehiscence. One of the most advanced types of dehiscence is the poricidal dehiscence, when pollen is released from a small opening situated at one end (distal or proximal). Examples of the latter are: Ochnaceae, Ericaceae, Myrsinaceae, some Fabaceae, the majority of Melastomaceae, Tremandraceae, Solanaceae. There are also other specialized modes of dehiscence including transverse dehiscence (e.g., *Alchemilla*, *Hibiscus*, *Euphorbia*, *Chrysosplenium*).

The microspore tetrads are formed by two patterns determined by the mechanism of cytokinesis in microspore mother cells. In the successive type, the developing cell plate is formed at the end of meiosis I, dividing the microsporocyte into two cells; in each of these two cells, the second meiotic division takes place, followed again by centrifugal formation of cell plates. In the simultaneous type, on the other hand, no wall is formed after meiosis I; division occurs by centripetally advancing constriction furrows, which usually first appear after the second meiotic division, meet in the center, and divide the mother cell into four parts. The constriction furrows originate at the surface of the mother cell and develop inwardly, resulting in the formation of walls that divide the microsporocyte into four microspores.

It is difficult to say which of the two types of microsporogenesis is more primitive. Although some authors (including Schürhoff 1926 and Davis 1966) consider the successive type as the more primitive, there is no definite correlation between this type and archaic Magnoliidae and Ranunculidae. The majority of Magnoliidae and Ranunculidae are characterized by simultaneous microsporogenesis.

The pollen wall, as a rule, consists of two main layers – the inner one, called intine, and the outer one, called exine. The exine typically consists of two layers – the inner layer endexine and the outer layer ectexine. Endexine may be found as a continuous layer (sometimes very thick, as in Lauraceae) or only in apertural regions, in some taxa it is absent.

In an overwhelming majority of flowering plants the ectexine is well developed and stratified. The exine structure and ornamentation (sculpturing) is extremely varied and, at the same time, very constant within the taxonomic groups and has a large systematic and evolutionary significance. The ectexine consists of two basic layers – a roof-like outer layer or tectum and an infratectal layer. The latter is of two main types – granular and columellar. Granular structure is characterized by an infratectal layer consisting of more or less densely aggregated, equidimensional granules of sporopollenin. The tectum, which is not always noticeable, is composed of more densely aggregated granules. Doyle et al. (1975: 436) suspect that at least some of the apparently homogenous “atectate” exine of Walker and Skvarla (Walker and Skvarla 1975), revealed in some of the most archaic Magnoliidae such as *Degeneria* and *Eupomatia*, are extreme members of the granular category, with very closely aggregated granules. The predominant type of infratectal structure is columellar, which is characterized by radially directed rods of linearly fused sporopollenin granules, the columellae. Comparative studies of the ectexine ultrastructure suggest an evolutionary trend from granular ectexine to incipient rudimentary columellae and from the incipient columellae to fully developed columellar structure. The great majority of flowering plants have tectate columellate pollen (the heads of the columellae extend laterally over the intercolumnellar spaces forming tectum). In the most primitive type of columellar ectexine the tectum is devoid of any kind of holes or perforations (Walker 1974a). The tectate-imperforate (Walker 1974a) or completely tectate ectexine (Hideux and Ferguson 1976) is found in various groups of flowering plants both archaic and advanced. The next evolutionary stage of the tectum structure is the perforate (Walker 1974a, Hideux and Ferguson 1976). In the perforate tectum, the holes or tectal perforations (lumina) are always small (e.g., in some Annonaceae and Myristicaceae) and the columellae are invisible through them. When perforations enlarge so that their diameter becomes greater than the width of the pollen wall between them (muri), e.g., in Winteraceae, Illiciaceae, and Schisandraceae, the exine becomes semitectate (Walker 1974a). For this partial tectum, the visibility of columellae in oblique view through the lumina is characteristic (Hideux and Ferguson 1976). When the tectum is completely lost, e.g., in some Annonaceae, Myristicaceae, and Salicaceae, and there

are only free, exposed columellae or their modified derivatives, we have intectate exine (Walker 1974a). The culmination of an evolutionary trend is the origin of the almost exinless pollen with a much expanded and highly structured intine.

Most pollen grains have specially delimited apertures—generally thin-walled areas or openings in the exine which serve as exits through which the pollen tubes usually emerge. The apertures of flowering plants pollen grains are characterized by a great diversity and are of various types. Various types of apertures correspond to different levels of specialization, and the significance of these types is very important in determining the general level of organization of some taxon or other. The apertural arrangement in the angiosperm pollen grains evolved from distal through zonal to global.

As long ago as 1912 Hallier concluded that the most primitive type of pollen grain is characterized “par une seui 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; Stebbins 1974; Walker 1974b, 1976a, b; 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 “zonasulcate” 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 (“disulcate”), 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, triporate, polyporate (including panporate). The highest stage of the evolution of the pollen grains in dicotyledons is trimultiaperturate pollen with composite apertures.

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.

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 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 syncarpous (coenocarpous) gynoecium. As a result, forms with more or less syncarpous gynoecia appear even in such families as Winteraceae, Magnoliaceae, Annonaceae, etc. The overwhelming majority of the magnoliophytes has one or another type of syncarpous gynoecium.

I distinguish three main types of syncarpous gynoecium: eusyncarpous, paracarpous, and lysicarpous. An eusyncarpous gynoecium emerged independently in many lines of evolution from an apocarpous gynoecium by lateral concrescence of closely connivent carpels. The eusyncarpous gynoecium usually originates from a more advanced cyclic apocarpous gynoecium. The most primitive forms of eusyncarpous gynoecium still have free upper portions of the fertile regions of the carpels. With specialization of the eusyncarpous 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 syncarpous gynoecium that has a parietal arrangement of ovules (Takhtajan 1942, 1948, 1959, 1980). 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 Lillianaes, the paracarpous gynoecium arises from the primitive type of eusyncarpous

gynoecium in which the margins of individual carpels are not fused yet. As a result of unfolding of these unsealed carpels the eusyncarpous 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 eusyncarpous 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 and some Caryophyllaceae, 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 syncarpous 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 syncarpous 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, 1991):

- A. Laminar (superficial) placentation. The ovules occupy the side portions of the inner face of the carpel or are scattered over almost the entire surface, rarely occupy only its back side.
 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 pseudo-medially, occupying the back of the carpel. Examples: *Nelumbo*, *Ceratophyllum*, Cabombaceae.
- B. Submarginal (sutural) placentation. The ovules occupy morphologically sutural areas of the carpel.
 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 *Zygogynum*. 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 submarginal. 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 submarginal placentation can be found in syncarpous gynoecia. Two basic types of submarginal placentation are the axile and the parietal types. Their origin and evolution is correlated with the origin and evolution of eusyncarpous 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; Kozo-Poljanski 1948; 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 magnoliophytes. Some confirmation of this conjecture mentioned by Stebbins (1974: 232) is the fact that in many families of flowering plants – including the relatively archaic groups – the outer and inner integuments of the ovule differ greatly from each other in their morphology and their histological structure. In these forms, the outer integument is thicker than inner one and has specialized epidermal cells, in some cases including stomata. Moreover, the micropyle may be differently shaped in the two integuments. Stebbins mentions also the lobed distal portion of the outer integument in a few genera. Lobed integuments have been observed in Berberidaceae, Juglandaceae, Rosaceae, and Flacourtiaceae (van Heel 1970, 1976). Distal lobing may involve either the outer or the inner integument, or both. "The lobing suggests that the integuments are compound organs," states Bouman (1984: 144). The cupular origin of the outer integument of the angiosperm ovule was suggested by Gaussen (1946), Takhtajan (1950, 1959, 1964), and Walton (1953).

Unitegmic ovules arose from the bitegmic ones in various lines of flowering plants evolution. As the single integument of the sympetalous magnoliopsids (except for Plumbaginales, Primulales, and Cucurbitales) and some choripetalous ones is usually as massive or even more massive than the double, a suggestion was made (Coulter and Chamberlain 1903), that the single massive 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 many 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. Thus, in *Filipendula*, *Rubus*, *Rosa*, *Potentilla*, *Fragaria*, *Alchemilla*, and some other Rosaceae, the envelope resulted from the incomplete development of the inner integument; while in *Peperomia*, *Hydnoraceae*, *Rafflesia*, *Mitrastemon*, *Cytinus*, and some others, it resulted from the underdevelopment of the outer integument. Another pathway of the origin of unitegmy, integumentary shifting, has been described in Ranunculaceae (Bouman and Calis 1977). According to Bouman (1984: 140), integumentary shifting is a complicated ontogenetic process involving (1) a fusion of primordia, in the sense that the initials of the two integuments give rise to a common structure; (2) a shifting of the inner integument; and (3) an arrested growth of the latter. 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, as a result of reduction, 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-wcrassinucellate (e.g. Cornaceae and Araliaceae) (see Philipson 1974, 1977).

There is also a definite evolutionary trend in the form and orientation of the ovule. Anotropous ovules characterize a majority of flowering plants, including Magnoliales, and are presumably the initial type (Netolizky 1926; Takhtajan 1959; Eames 1961;

Cronquist 1968, 1988; Corner 1976). The orthotropous type, as well as campylotropous and amphitropous ones, arose from the anotropous ovule.

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, 1983, 1991).

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 magnoliophytes 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 non-archegoniate 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.

Following triple fusion, both the zygote and the primary nucleus of the endosperm develop further.

The development of the seed begins with the divisions of the primary endosperm nucleus, followed by the emergence of embryo. Three major types of the endosperm development are recognized – cellular, nuclear, and helobial.

In the cellular type, at least the first few divisions of the primary endosperm nucleus are accompanied by wall formation. The cellular pattern of development is found in many families of magnoliopsids (both archaic and advanced) and occurs only in four monocotyledonous families – Hydatellaceae, Araceae, Lemnaceae, Acoraceae.

In the helobial type, which is usually considered as somewhat intermediate between the cellular and nuclear type, the primary endosperm nucleus is always found at the chalazal end of the gametophyte; and, therefore, when it divides, two unequal cells or chambers are produced – a small chalazal cell and a much larger micropylar cell. The nucleus in the chalazal cell either does not divide further (a basic type, according to Swamy and Parameswaran 1963) or undergoes a usually restricted number of free nuclear divisions, whereas the larger micropylar cell undergoes numerous free nuclear divisions. Commonly, the cell-wall formation ultimately takes place in the micropylar chamber. The helobial type is common in liliopsids and is much less frequent in magnoliopsids.

In the nuclear type, the division of the primary endosperm nucleus is followed by a series of free nuclear divisions, resulting in the formation of a large multinucleate cell, which usually becomes cellular in a later phase of development. The nuclear type is widespread in both magnoliopsids and liliopsids.

The helobial type of endosperm development is probably apomorphic, derived either from nuclear or, more likely, from cellular type. But it is much more difficult to decide which of the two types – nuclear or cellular – is the more primitive. The main reason for this difficulty is that the formation of the endosperm is subject to reversal and that there are also many intermediates (Schnarf 1929, 1931; Brink and Cooper 1947). But, in spite of the reversibility of the types of endosperm development, the first flowering plants must have had either cellular or nuclear endosperm.

Seeds: The seeds of primitive flowering plants are of medium-size, 5–10mm 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 1912).

There are two main types of the specialization of endosperm – rumination and the development of haustoria. The outer surface of the ruminant endosperm tissue is irregularly ridged and furrowed to varying degrees, often very deeply. This furrowing occurs in a number of magnoliopsid families, especially in Magnoliales, and in some liliopsids (some genera of Dioscoreales, Cyclanthaceae, and Arecaceae) (Tamamschian 1951; Periasamy 1962; Corner 1976). Rumination is due to irregular growth activity of the seed coat or endosperm itself, during later stages of seed development (Boesewinkel and Bouman 1984). According to Vijayaraghavan and Prabhaker (1984: 343), ruminant endosperm could be an ancestral character still occurring in present-day seeds, belonging to both primitive and advanced taxa.

Another and more remarkable type of endosperm specialization is the formation of endosperm haustoria. The haustoria may arise at the chalazal or micropylar end, or at both ends of the developing endosperm. Endosperm haustoria are especially characteristic for taxa that develop the cellular type of endosperm. In the most archaic groups of flowering plants, including Magnoliaceae, endosperm haustoria are usually absent. In those rare cases, when haustoria are present in them, as in *Magnolia obovata* and in Saururaceae, they are chalazal.

Endosperm haustoria evolved independently in various lines of angiosperm evolution. The presence or absence of haustoria is a taxonomically useful embryological character, but the evolutionary trends in endosperm haustoria are not yet well known.

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 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 syncarpous fruit types (see Takhtajan 1991).

Karyotype: As was proposed as long ago as 1931 by Lewitsky (1931), the morphologically more primitive and basic type of chromosome of the flowering plants was one which had equally developed arms and a median or submedian centromere. Such symmetrical (or, in contemporary terminology, 'metacentric') chromosomes were those from which in course of evolution arose asymmetrical (acrocentric) chromosomes, in which the centromere is situated very close to one end.

The original karyotype of flowering plants was probably characterized by a comparatively small number of medium-sized chromosomes. But it is very difficult to say what in fact was the ancestral basic number of chromosomes in the flowering plants.

In the Magnoliaceae $2n = 38, 76$ and 114 ; consequently, in this family $n = 19$. In the Eupomatiaceae $n = 10$, i.e. the basic number differs both from that of the Magnoliaceae and from that of the Degeneriaceae and Himantandraceae. In the Annonaceae $n = 7, 8, 9$; in the Canellaceae $n = 11, 13, 14$.

It appears highly probable that the basic number of chromosomes of the early flowering plants was a low one. Darlington (Darlington and Mather 1949: 324) came to the conclusion that the basic number relationships of the chief families of woody flowering plants showed 7 as the common ancestral chromosome number of flowering plants. 'From this origin, 8, 9 and an increasing series have arisen on only a few occasions, whereas 14, with its diminishing series, has arisen very frequently. In this series 12 has often been stabilized, and, from its addition to 7, 19 has appeared several times'. Later, Raven and Kyhos (1965) and Ehrendorfer et al. (1968) reached a similar conclusion. The probability is very high that Darlington's proposal was correct and that the basic number was indeed 7. Yet on the other hand, in such extremely primitive families as Himantandraceae ($n = 6$), in some Winteraceae, Degeneriaceae, Cetrarophyllaceae, in

some Hernandiaceae $n = 12$, in the primitive family Eupomatiaceae $n = 10$. Moreover, in the ancient family Lauraceae is characterized by a basic number of 12. These data occasion some doubt that the basic number of chromosomes in the evolution of the karyotype of the flowering plants was in fact 7; a figure of 5, or better 6 is just as likely. Stebbins (1966) has suggested that the original number was $x = 7$ or $x = 6$.

The Significance of Primitive Characters

Evolutionary systematists consider both derived (apomorphic) and primitive (plesiomorphic) characters. For evolutionary taxonomists the retention of a large number of ancestral characters is just as important an indicator of phylogenetic relationships as the joint acquisition of a few apomorphic characters. Plesiomorphic characters are often among the most evident key characters of a taxon and are used for the delimitation and ranking of taxa.

Evidently the information content of primitive and derived characters is different and of different significance. Whereas the ancestral characters cannot be used in cladistic analysis to locate branching points, they have great importance in classification when they represent the dominant characters of a taxon. Often they are even more important in classification than rapidly changing derived characters. The conservative ancestral characters may actually tell us more about the total genotype. Often the discovery of ancestral, plesiomorphic features in some generally advanced groups indicates their phyletic links with less specialized taxa. The presence of distally monocolpate or distally dicolpate pollen grains in such specialized groups as Piperales, Aristolochiales, Hydnorales, and Rafflesiales provides important confirmation of their affinities with the orders of the archaic subclass Magnoliidae. The very definition of the Magnoliidae is based on the fact that they have the greatest number of primitive characters.

For the classification of taxa within individual lineages a systematist uses both the primitive and derived characters. Every new stage of evolution, and consequently every new taxon, differs from the ancestral taxon by an acquisition of some new, derived characters. The ancestral taxon, on the other hand, will differ from its descendants by the absence of these derived characters. For example, prokaryotes differ from the

eukaryotes just in their fundamental plesiomorphic character, namely, the absence of the nucleus. The situation is different in the case of cladogenesis. Sister groups differ from each other essentially in derived characters acquired during the process of divergence.

Primitive characters are no less important for the hypothetical reconstruction of the ancestral groups, which was especially emphasized by the paleontologist Tatarinov (1984: 11). Thus knowing the basic evolutionary trends in flowering plants we may by extrapolation extend the transformation series into the past to the lowest level of specialization. In the absence of reliable fossil records this is the only way to reconstruct ancestral types. Out-group comparisons are especially important in these cases.

Convergence and Parallelism

It is generally accepted that a convergence is the origin of apparently similar apomorphies from different plesiomorphic states while parallelism is the independent development of similar apomorphies from the same plesiomorphic state.

The term *convergence* is usually applied to the occasional tendency for distantly related taxa to acquire some similar characters and thus in one or more respects to come to simulate one another and be more nearly alike than were their ancestors. Convergence is an independent analogous adaptation of different organisms to similar environmental conditions in response to similar functional needs. Therefore convergence is usually limited to the organs and tissues that are directly connected with similar environmental factors. However, convergent similarity is never very deep and mostly concerns only a few organs. There is only a very low probability of an independent development of similarity in the total morphological pattern in different lineages. As a rule, the more organisms are differentiated, the less probable is their complete convergence. It is also quite natural that the chance of partial convergence is much higher than that of overall convergence. But even so, any kind of convergent similarity is more or less easily distinguishable by detailed comparative studies. For example, the similarity in general habit between *Cuscuta* and *Cassytha* does not obscure the fact that in the basic characters of their flowers, fruit, pollen morphology, and vegetative

anatomy as well as in their chemistry they belong to different subclasses of flowering plants.

The problem of parallelism is much more difficult than that of convergence. In flowering plants parallel evolutionary changes are very common. Similarities due to parallel evolution occur not only in the structure of the vegetative organs but also in flowers, inflorescences, fruits, seeds, pollen grains, and even chemical characters. The phenomenon of parallelism is usually defined as the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characters of that ancestry (see Simpson 1961: 78). In contrast to convergence, parallelism is based on an initial similarity of structure and an initial homology of mutations and common evolutionary trends. It is highly improbable that two unrelated taxa will have a large number of parallel characters. This means that the parallel development of characters implies an evolutionary relationship. Thus the closeness of parallelism in the evolution of given taxa depends on the closeness of their affinity (Takhtajan 1947: 106; Cronquist 1968, 1987, 1988), and therefore we come to the general principle that evolutionary parallelism tends to indicate relationships, and accordingly it should be given due weight, along with other factors, in arriving at conclusions (Cronquist 1988: 32).

Weighting of Taxonomic Characters and Heterobathmy

Every practicing systematist knows the importance of detection, selection, and weighting of characters. He or she knows that some characters have a greater diagnostic value and therefore have greater weight than others. For a systematist different characters hold different information content, and many of them are merely “noise” (Mayr 1969: 208). It is therefore more important to deal with a small number of carefully selected and weighted characters than to deal with a large number of random characters. In addition, the same characters can have a different weight in various related taxa and especially in unrelated ones. It is well known that weighting can be only a posteriori, that is, based on experience. The relative weight of the characters is determined by the trial-and-error method, based on the personal experience of a systematist as well as

on the experience of his or her predecessors and colleagues. Weighting is a specific taxonomic problem that can be solved only by the systematist. It is also well known that the higher the rank of a taxon, the more important weighting becomes (Mayr 1969: 211). Unfortunately, the weighting of characters and the selection of characters to use is not completely free of subjective elements. No technique or procedure (including the cladistic one) is immune to the necessity for subjective decisions. I agree with Cronquist (1988: 39) that “complete objectivity in taxonomy or any other complex subject is an unattainable will-o’-the-wisp.” There is always room for subjective and even intuitive decisions, but we should always strive for objectivity.

The problem of weighting would not be so difficult if all the characters of an organism evolved harmoniously, at an equal rate and the same level of evolutionary development. But as is well known, the rates of evolution of different organs and parts of an organism are different, often drastically so, and the evolution of one structure may be faster or slower compared to that of other structures in the same taxon. This phenomenon of unequal rates of evolution of different features within one lineage is known under different names, of which the best known is mosaic evolution (De Beer 1954; Simpson 1961; Mayr 1963; Takhtajan 1991). As a result of mosaic evolution an organism may represent a disharmonious combination of characters of quite different evolutionary grade.

These differences in the grades of characters within the same taxon have been designated heterobathmy (from Greek *bathmos* – “step,” “grade”) (Takhtajan 1959, 1991). Heterobathmy may be expressed not only within the organism as a whole but also within its parts, such as flowers or xylem and their components, such as perianth, stamens, carpels, vessels, rays, and axial parenchyma.

The concept of heterobathmy is of the greatest importance for phylogenetical reconstructions. Thus if two taxa differ from each other by a pair of characters *A* and *B*, in one taxon character *A* may be primitive (plesiomorphic) while character *B* may be comparatively advanced (apomorphic), whereas in the other taxon the situation may be the reverse. In such a case of heterobathmy, the phyletic interrelationship between the two taxa can be reconstructed 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 long ago Dollo (1893) emphasized the importance of the *chevauchement des specialisations* (“crossing of specializations”) when establishing cladistic relationships of recent organisms.

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 archaic groups of the flowering plants, where heterobathmy is most clearly expressed (as in the Magnoliaceae and Winteraceae, and especially in *Amborella*), we cannot establish phyletic relationships and construct phyletic lineages using only floral characters. It is all the more impossible to reconstruct phyletic lineages on the basis of the characters of vegetative organs only, as, for example, on the basis of wood anatomy or leaf architecture. In such cases, instead of phyletic lineages we usually obtain only 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 reconstructions, the closer we shall approach phyletic interrelationships. Studying the evolution of an adequate number of independent noncorrelated characters belonging to a sufficient number of different high-weight character complexes enables us to establish the basic trends of the evolution of a given taxon, to discover those of its members nearest to the phylogenetically initial forms and those more distant, and to deduce the cladistic relationships among orders, families, and subfamilies 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 all-around must be its study. Only the application of various methods and techniques can reveal those “critical characters” and “critical tendencies” (Wernham 1912) that are reliable phyletic markers. Correct weighting of the characters and their evolutionary trends takes on special significance in such cases and largely depends on the experience of a systematist and his or her erudition.

In many different lines of the evolution of the flowering plants there occurs a simplification of various

structures accompanied by the loss of characters. During this regressive evolution many structures were not only reduced but even completely disappeared, which often represents an irretrievable loss of information. Extreme simplification and loss of information are typical of many aquatic plants and especially of parasites. A considerable loss of information is also characteristic of many specialized anemophilous flowers.

The Linnean Hierarchy

Any evolutionary classification is inevitably a more or less simplified representation of the phylogram in the form of nested hierarchies of increasingly more inclusive monophyletic taxa of different categorical rank. The hierarchical arrangement of taxa is a special information storage system that facilitates information retrieval by permitting an easy survey of taxa. However, from any given phylogenetic tree a number of different classifications can be derived. Nevertheless, there are some requirements essential to any practical and applicable hierarchical classification system. The most important requirement is the manageable number of ranks. A form of hierarchy that has been adopted for usual botanical classifications represents a sequence of basically seven levels (kingdom, phylum or division, class, order, family, genus, and species) with additional levels designated as super- (above the basic levels) and sub- (below them).

While taxa and the branches of phylogenetic trees are realities, taxonomic categories and their hierarchy are based on concepts. The use of any particular number of levels is therefore arbitrary. “It does not correspond with anything in nature but is an artifice imposed by practical necessity in the use of any hierarchy” (Simpson 1961: 17–18). To arrange the system in the form of the Linnean hierarchy is the only way to make it manageable and to achieve economy of memory.

The hierarchical classification is based on the gaps between taxa and the size of the gaps. Evolutionary systematists follow Mayr’s recommendation (1969: 92) that the size of the gap be in inverse ratio to the size of the taxon. This is especially important in the recognition of higher taxa, particularly of monotypic higher taxa. According to Ashlock’s definition (1979: 446), “A higher taxon is a monophyletic group of species (or a single species) separated from each phylogenetically

adjacent taxon of the same rank by a gap greater than any found within these groups”.

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SYNOPSIS of families and suprafamilial taxa of the Magnoliophyta

Phylum MAGNOLIOPHYTA (FLOWERING PLANTS)

Class MAGNOLIOPSIDA (DICOTYLEDONS)

Dicotyledonous family of incertae position

1. HAPTANTHACEAE

Subclass I. Magnoliidae

SUPERORDER NYMPHAEANAE

Order 1. Amborellales

Family 1. *Amborellaceae*

Order 2. Nymphaeales

- Family 1. *Hydropeltidaceae*
2. *Cabombaceae*
3. *Nymphaeaceae*
4. *Barclayaceae*

Order 3. Austrobaileyales

Family 1. *Austrobaileyaceae*

Order 4. Illiciales

- Family 1. *Illiciaceae*
2. *Schisandraceae*

Order 5. Trimeniales

Family 1. *Trimeniaceae*

Order 6. Chloranthales

Family 1. *Chloranthaceae*

Order 7. Ceratophyllales

Family 1. *Ceratophyllaceae*

SUPERORDER MAGNOLIANAE

Order 8. Canellales

- Family 1. *Winteraceae*
2. *Canellaceae*

Order 9. Magnoliales

- Family 1. *Degeneriaceae*
2. *Magnoliaceae*

Order 10. Himantandrales

Family 1. *Himantandraceae*

Order 11. Annanales

- Family 1. *Eupomatiaceae*
2. *Annonaceae*

Order 12. Myristicales

Family 1. *Myristicaceae*

SUPERORDER LAURANAE

Order 13. Laurales

- Family 1. *Monimiaceae*
2. *Idiospermaceae*
3. *Calycanthaceae*
4. *Atherospermataceae*
5. *Siparunaceae*
6. *Comortegaceae*
7. *Hernandiaceae*
8. *Lauraceae*

SUPERORDER PIPERANAE

Order 14. Piperales

- Family 1. *Lactoridaceae*
2. *Saururaceae*
3. *Piperaceae*
4. *Peperomiaceae*
5. *Aristolochiaceae*

Order 15. Hydnorales

Family 1. *Hydnoraceae*

SUPERORDER RAFFLESIANAE

Order 16. Mitrostemonales

Family 1. *Mitrostemonaceae*

Order 17. Rafflesiales (Cytinales)

- Family 1. *Apodanthaceae*
2. *Rafflesiaceae*
3. *Cytinaceae*

Subclass II. Ranunculidae

SUPERORDER PROTEANAE

Order 18. PlatanalesFamily 1. *Platanaceae***Order 19. Proteales**Family 1. *Proteaceae***Order 20. Nelumbonales**Family 1. *Nelumbonaceae*

SUPERORDER RANUNCULANAE

Order 21. EuptelealesFamily 1. *Eupteleaceae***Order 22. Lardizabalales**Family 1. *Lardizabalaceae***Order 23. Menispermiales**Family 1. *Menispermaceae***Order 24. Berberidales**

- Family 1. *Nandinaceae*
- 2. *Berberidaceae*
- 3. *Ranzaniaceae*
- 4. *Podophyllaceae*

Order 25. Ranunculales

- Family 1. *Hydrastidaceae*
- 2. *Ranunculaceae*

Order 26. Circaeasterales

- Family 1. *Kingdoniaceae*
- 2. *Circaeasteraceae*

Order 27. Papaverales

- Family 1. *Papaveraceae*
- 2. *Pteridophyllaceae*
- 3. *Hypecoaceae*
- 4. *Fumariaceae*

Order 28. GlaucidialesFamily 1. *Glaucidiaceae***Order 29. Paeoniales**Family 1. *Paeoniaceae*

Subclass III. Hamamelidae

SUPERORDER TROCHODENDRANAE

Order 30. Trochodendrales

- Family 1. *Trochodendraceae*
- 2. *Tetracentraceae*

Order 31. CercidiphyllalesFamily 1. *Cercidiphyllaceae*

SUPERORDER MYROTHAMNANAE

Order 32. MyrothamnalesFamily 1. *Myrothamnaceae*

SUPERORDER HAMAMELIDANAE

Order 33. Hamamelidales

- Family 1. *Hamamelidaceae*
- 2. *Altingiaceae*

Order 34. DaphniphyllalesFamily 1. *Daphniphyllaceae***Order 35. Balanopales**Family 1. *Balanopaceae***Order 36. Buxales**

- Family 1. *Buxaceae*
- 2. *Didymelaceae*

Order 37. Fagales

- Family 1. *Fagaceae*
- 2. *Nothofagaceae*

Order 38. Betulales (Corylales)

- Family 1. *Betulaceae*
- 2. *Ticodendraceae*

Order 39. CasuarinalesFamily 1. *Casuarinaceae*

SUPERORDER JUGLANDANAE

Order 40. MyricalesFamily 1. *Myricaceae***Order 41. Juglandales**

- Family 1. *Rhoipteleaceae*
- 2. *Juglandaceae*

Subclass IV. Caryophyllidae

SUPERORDER CARYOPHYLLANAE

Order 42. Caryophyllales

- Family 1. *Phytolaccaceae*
- 2. *Rhabdodendraceae*
- 3. *Gisekilaceae*
- 4. *Sarcobataceae*
- 5. *Barbuiaceae*
- 6. *Achatocarpaceae*
- 7. *Nyctaginaceae*
- 8. *Aizoaceae*
- 9. *Stegnospermaceae*
- 10. *Portulacaceae*
- 11. *Hectorellaceae*
- 12. *Basellaceae*
- 13. *Halophytaceae*
- 14. *Cactaceae*
- 15. *Didiereaceae*
- 16. *Molluginaceae*
- 17. *Limeaceae*
- 18. *Caryophyllaceae*

19. *Simmondsiaceae*
20. *Amaranthaceae*
21. *Chenopodiaceae*

Order 43. Physenales

- Family 1. *Asteropeiaceae*
2. *Physenaceae*

SUPERORDER POLYGONANAE

Order 44. Polygonales

- Family 1. *Polygonaceae*

Order 45. Plumbaginales

- Family 1. *Plumbaginaceae*

Order 46. Tamaricales

- Family 1. *Tamaricaceae*
2. *Frankeniaceae*

SUPERORDER NEPENTHANAE

Order 47. Nepenthales

- Family 1. *Ancistrocladaceae*
2. *Dioncophyllaceae*
3. *Nepenthaceae*
4. *Drosophyllaceae*
5. *Droseraceae*

Subclass V. Dilleniidae

SUPERORDER DILLENIANAE

Order 48. Dilleniales

- Family 1. *Dilleniaceae*

SUPERORDER ERICANAE

Order 49. Paracryphiales

- Family 1. *Paracryphiaceae*

Order 50. Theales

- Family 1. *Stachyuraceae*
2. *Sladeniaceae*
3. *Pentaphragmaceae*
4. *Ternstroemiaceae*
5. *Theaceae*
6. *Oncothecaceae*
7. *Caryocaraceae*

Order 51. Balsaminales

- Family 1. *Balsaminaceae*
2. *Marcgraviaceae*
3. *Tetrameristaceae*
4. *Pellicieraceae*

Order 52. Hypericales

- Family 1. *Bonnetiaceae*
2. *Clusiaceae*
3. *Hypericaceae*
4. *Elatinaceae*

Orders 53. Ochnales

- Family 1. *Strasburgeriaceae*
2. *Sauvagesiaceae*
3. *Lophiraceae*
4. *Ochnaceae*
5. *Medusagynaceae*
6. *Quinaceae*

Order 54. Ericales

- Family 1. *Actinidiaceae*
2. *Clethraceae*
3. *Cyrillaceae*
4. *Ericaceae*

Order 55. Diapensiales

- Family 1. *Diapensiaceae*

Order 56. Fouquieriales

- Family 1. *Fouquieriaceae*

Order 57. Polemoniales

- Family 1. *Polemoniaceae*

Order 58. Lecythidales

- Family 1. *Scytotetalaceae*
2. *Lecythidaceae*
3. *Napoleonaceae*

Order 59. Sarraceniales

- Family 1. *Sarraceniaceae*

Order 60. Roridulales

- Family 1. *Roridulaceae*

SUPERORDER PRIMULANAE

Order 61. Styrcacales (Ebenales)

- Family 1. *Styracaceae*
2. *Symplocaceae*
3. *Ebenaceae*

Order 62. Sapotales

- Family 1. *Sapotaceae*

Order 63. Primulales

- Family 1. *Myrsinaceae*
2. *Maesaceae*
3. *Aegicerataceae*
4. *Theophrastaceae*
5. *Primulaceae*
6. *Coridaceae*

SUPERORDER VIOLANAE

Order 64. Berberidopsidales

- Family 1. *Berberidopsidaceae*

Order 65. Aextoxicales

- Family 1. *Aextoxicaceae*

Order 66. Violales (Passiflorales)

- Family 1. *Flacourtiaceae*
2. *Salicaceae*
3. *Lacistemataceae*

4. *Peridiscaceae*
 5. *Violaceae*
 6. *Dipentodontaceae*
 7. *Scyphostegiaceae*
 8. *Passifloraceae*
 9. *Turneraceae*
 10. *Malesherbiaceae*
 11. *Achariaceae*
 12. *Aphloiaceae*
- Order 67. *Elaeocarpales***
Family 1. *Elaeocarpaceae*
- Order 68. *Cucurbitales***
Family 1. *Cucurbitaceae*
2. *Datisceae*
3. *Tetramelaceae*
4. *Begoniaceae*
- SUPERORDER CAPPARANAE
- Order 69. *Acaniales***
Family 1. *Akaniaceae*
2. *Bretschneideraceae*
- Order 70. *Tropaeolales***
Family 1. *Tropaeolaceae*
- Order 71. *Limnanthales***
Family 1. *Limnanthaceae*
- Order 72. *Caricales***
Family 1. *Caricaceae*
- Order 73. *Moringales***
Family 1. *Moringaceae*
- Order 74. *Capparales (Resedales, Brassicales)***
Family 1. *Capparaceae*
2. *Cleomaceae*
3. *Brassicaceae*
4. *Resedaceae*
5. *Gyrostemonaceae*
6. *Pentadiplandraceae*
7. *Koerberliniaceae*
8. *Bataceae*
9. *Salvadoraceae*
10. *Tovariaceae*
11. *Setchellanthaceae*
12. *Emblingiaceae*
- SUPERORDER MALVANAE
- Order 75. *Malvales***
Family 1. *Muntingiaceae*
2. *Tiliaceae*
3. *Dipterocarpaceae*
4. *Monotaceae*
5. *Sarcolaenaceae*

6. *Neuradaceae*
 7. *Sterculiaceae*
 8. *Diegodendraceae*
 9. *Sphaerosepalaceae*
 10. *Bombacaceae*
 11. *Malvaceae*
 12. *Bixaceae*
 13. *Cochlospermaceae*
 14. *Cistaceae*
 15. *Tepuianthaceae*
 16. *Thymelaeaceae*
- Order 76. *Urticales***
Family 1. *Ulmaceae*
2. *Moraceae*
3. *Cannabaceae*
4. *Cecropiaceae*
5. *Urticaceae*
- SUPERORDER EUPHORBIANAE
- Order 77. *Euphorbiales***
Family 1. *Phyllanthaceae*
2. *Putranjivaceae*
3. *Picrodendraceae*
4. *Euphorbiaceae*
5. *Pandaceae*
- Subclass VI. Rosidae
- SUPERORDER ROSANAE
- Order 78. *Cunoniales***
Family 1. *Cunoniaceae*
2. *Brunelliaceae*
- Order 79. *Anisophylleales***
Family 1. *Anisophylleaceae*
- Order 80. *Cephalotales***
Family 1. *Cephalotaceae*
- Order 81. *Saxifragales***
Family 1. *Tetracarpaeaceae*
2. *Aphanopetalaceae*
3. *Penthoraceae*
4. *Crassulaceae*
5. *Haloragaceae*
6. *Gunneraceae*
7. *Saxifragaceae*
8. *Grossulariaceae*
9. *Pterostemonaceae*
10. *Iteaceae*
- Order 82. *Podostemales***
Family 1. *Podostemaceae*

- Order 83. Vitales**
 Family 1. *Vitaceae*
 2. *Leeaceae*
- Order 84. Rosales**
 Family 1. *Rosaceae*
 2. *Quillajaceae*
- Order 85. Crossosomatales**
 Family 1. *Crossosomataceae*
- Order 86. Chrysobalanales**
 Family 1. *Chrysobalanaceae*
 2. *Dichapetalaceae*
 3. *Trigoniaceae*
 4. *Euphroniaceae*
- SUPERORDER MYRTANAE
- Order 87. Myrtales**
 Family 1. *Alzateaceae*
 2. *Rhynchoalycaceae*
 3. *Geissolomataceae*
 4. *Penaeaceae*
 5. *Oliniaceae*
 6. *Combretaceae*
 7. *Crypteroniaceae*
 8. *Memecylaceae*
 9. *Melastomataceae*
 10. *Lythraceae*
 11. *Trapaceae*
 12. *Onagraceae*
 13. *Myrtaceae*
 14. *Vochysiaceae*
- SUPERORDER FABANAE
- Order 88. Fabales**
 Family 1. *Fabaceae*
- Order 89. Polygalales**
 Family 1. *Polygalaceae*
- SUPERORDER RUTANAE
- Order 90. Oxalidales (Connarales)**
 Family 1. *Connaraceae*
 2. *Oxalidaceae*
- Order 91. Sapindales**
 Family 1. *Staphyleaceae*
 2. *Tapisciaceae*
 3. *Sapindaceae*
 4. *Hippocastanaceae*
 5. *Aceraceae*
- Order 92. Sabiales**
 Family 1. *Sabiaceae*
- Order 93. Biebersteiniales**
 Family 1. *Biebersteiniaceae*
- Order 94. Rurales**
 Family 1. *Rutaceae*
2. *Cneoraceae*
 3. *Simaroubaceae*
 4. *Picramniaceae*
 5. *Leitneriaceae*
 6. *Surianaceae*
 7. *Irvingiaceae*
 8. *Kirkiaceae*
 9. *Pteroxylaceae*
 10. *Meliaceae*
 11. *Burseraceae*
 12. *Anacardiaceae*
 13. *Podoaceae*
- Order 95. Coriariales**
 Family 1. *Coriariaceae*
- Order 96. Corynocarpales**
 Family 1. *Corynocarpaceae*
- Order 97. Geraniales**
 Family 1. *Hypseocharitaceae*
 2. *Geraniaceae*
 3. *Vivianiaceae*
 4. *Ledocarpaceae*
 5. *Melianthaceae*
 6. *Greyiaceae*
 7. *Francoaceae*
- Order 98. Zygophyllales**
 Family 1. *Zygophyllaceae*
 2. *Balanitaceae*
 3. *Peganaceae*
 4. *Nitrariaceae*
 5. *Tetradiclidaceae*
- Order 99. Linales**
 Family 1. *Hugoniaceae*
 2. *Linaceae*
 3. *Ctenolophonaceae*
 4. *Ixonanthaceae*
 5. *Humiriaceae*
 6. *Erythroxylaceae*
 7. *Rhizophoraceae*
- Order 100. Malpighiales**
 Family 1. *Malpighiaceae*
 2. *Krameriaceae*
- SUPERORDER CELASTRANAE
- Order 101. Celastrales**
 Family 1. *Goupiaceae*
 2. *Lepidobotryaceae*
 3. *Brexiaceae*
 4. *Celastraceae*
 5. *Plagiopteraceae*
 6. *Lophopyxidaceae*
 7. *Stackhousiaceae*

8. *Parnassiaceae*
9. *Huaceae*
- SUPERORDER SANTALANAE
- Order 102. Santalales**
Family 1. *Olacaceae*
2. *Opiliaceae*
3. *Aptandraceae*
4. *Octoknemaceae*
5. *Medusandraceae*
6. *Santalaceae*
7. *Misodendraceae*
8. *Loranthaceae*
9. *Viscaceae*
10. *Eremolepidaceae*
- SUPERORDER BALANOPHORANAE
- Order 103. Cynomoriales**
Family 1. *Cynomoriaceae*
- Order 104. Balanophorales**
Family 1. *Balanophoraceae*
- SUPERORDER RHAMNANAE
- Order 105. Rhamnales**
Family 1. *Rhamnaceae*
2. *Elaeagnaceae*
3. *Barbeyaceae*
4. *Dirachmaceae*
- Subclass VII. Asteridae
- SUPERORDER CORNANAE
- Order 106. Desfontainiales**
Family 1. *Escalloniaceae*
2. *Eremosynaceae*
3. *Abrophyllaceae*
4. *Ixerbaceae*
5. *Tribelaceae*
6. *Kaliphoraceae*
7. *Montiniaceae*
8. *Columelliaceae*
9. *Desfontainiaceae*
10. *Vahliaceae*
- Order 107. Bruniales**
Family 1. *Bruniaceae*
- Order 108. Loasales (Hydrangeales)**
Family 1. *Hydrangeaceae*
2. *Loasaceae*
- Order 109. Cornales**
Family 1. *Davidiaceae*
2. *Nyssaceae*
3. *Mastixiaceae*
4. *Curtisiaceae*
5. *Grubbiaceae*
6. *Cornaceae*
7. *Alangiaceae*
- Order 110. Garryales**
Family 1. *Garryaceae*
2. *Aucubaceae*
- Order 111. Eucommiales**
Family 1. *Eucommiaceae*
- Order 112. Dipsacales**
Family 1. *Viburnaceae*
2. *Sambucaceae*
3. *Adoxaceae*
4. *Caprifoliaceae*
5. *Valerianaceae*
6. *Triplostegiaceae*
7. *Dipsacaceae*
8. *Morinaceae*
- Order 113. Aquifoliales**
Family 1. *Aquifoliaceae*
2. *Icacinaceae*
3. *Helwingiaceae*
4. *Phyllonomaceae*
5. *Sphenostemonaceae*
6. *Cardiopteridaceae*
- Order 114. Apiales**
Family 1. *Pennantiaceae*
2. *Griselinaceae*
3. *Aralidiaceae*
4. *Toricelliaceae*
5. *Melanophyllaceae*
6. *Pittosporaceae*
7. *Araliaceae*
8. *Myodocarpaceae*
9. *Apiaceae*
- SUPERORDER ASTERANAE
- Order 115. Rouseales**
Family 1. *Rousseaceae*
2. *Carpodetaceae*
- Order 116. Campanulales**
Family 1. *Pentaphragmataceae*
2. *Sphenocleaceae*
3. *Campanulaceae*
- Order 117. Stylidiales**
Family 1. *Donatiaceae*
2. *Stylidiaceae*
- Order 118. Phellinales (Alseuosmiales)**
Family 1. *Phellinaceae*

2. *Argophyllaceae*
3. *Corokiaceae*
4. *Alseuosmiaceae*

Order 119. Asterales

- Family 1. *Goodeniaceae*
2. *Brunoniaceae*
 3. *Menyanthaceae*
 4. *Calyceraceae*
 5. *Asteraceae*

Subclass VIII. Lamiidae

SUPERORDER LAMIANAE

Order 120. Rubiales (Gentianales)

- Family 1. *Gelsemiaceae*
2. *Loganiaceae*
 3. *Strychnaceae*
 4. *Antoniaceae*
 5. *Spigeliaceae*
 6. *Dialypetalanthaceae*
 7. *Rubiaceae*
 8. *Theligonaceae*
 9. *Gentianaceae*
 10. *Geniostomaceae*
 11. *Apocynaceae*

Order 121. Solanales

- Family 1. *Solanaceae*
2. *Nolanaceae*
 3. *Sclerophylacaceae*
 4. *Duckeodendraceae*
 5. *Goetzeaceae*
 6. *Hydroleaceae*
 7. *Convolvulaceae*
 8. *Cuscutaceae*
 9. *Humbertiaceae*

Order 122. Boraginales

- Family 1. *Hydrophyllaceae*
2. *Boraginaceae*
 3. *Hoplostigmataceae*
 4. *Lennoaceae*

Order 123. Oleales

- Family 1. *Oleaceae*

Order 124. Lamiales

- Family 1. *Buddlejaceae*
2. *Polypremaeae*
 3. *Tetrachondraceae*
 4. *Calceolariaceae*
 5. *Stilbaceae*

6. *Scrophulariaceae*
7. *Bignoniaceae*
8. *Gesneriaceae*
9. *Plocospermataceae*
10. *Carlemanniaceae*
11. *Globulariaceae*
12. *Plantaginaceae*
13. *Callitrichaceae*
14. *Hippuridaceae*
15. *Pedaliaceae*
16. *Martyniaceae*
17. *Trapellaceae*
18. *Myoporaceae*
19. *Ofiaceae*
20. *Acanthaceae*
21. *Avicenniaceae*
22. *Byblidaceae*
23. *Lentibulariaceae*
24. *Verbenaceae*
25. *Phrymataceae*
26. *Cyclocheilaceae*
27. *Nesogenaceae*
28. *Symphoremataceae*
29. *Lamiaceae*

Order 125. Hydrostachyales

- Family 1. *Hydrostachyaceae*

Class LILIOPSIDA (MONOCOTYLEDONS)

Subclass I. Alismatidae

SUPERORDER PETROSAVIANAE

Order 1. Petrosaviales

- Family 1. *Japonoliriaceae*
2. *Petrosaviaceae*
 3. *Tofieldiaceae*
 4. *Nartheciaceae*

SUPERORDER ALISMATANAE

Order 2. Hydrocharitales

- Family 1. *Aponogetonaceae*
2. *Butomaceae*
 3. *Najadaceae*
 4. *Hydrocharitaceae*

Order 3. Alismatales

- Family 1. *Limnocharitaceae*
2. *Alismataceae*

Order 4. Potamogetonales

- Family 1. *Scheuchzeriaceae*
 2. *Juncaginaceae*
 3. *Potamogetonaceae*
 4. *Posidoniaceae*
 5. *Ruppiceae*
 6. *Zannichelliaceae*
 7. *Cymodoceaceae*
 8. *Zosteraceae*

SUPERORDER ARANAE

Order 5. Arales

- Family 1. *Acoraceae*
 2. *Araceae*
 3. *Pistaceae*
 4. *Lemnaceae*

Subclass II. Liliidae

SUPERORDER LILIANAE

Order 6. Melanthiales

- Family 1. *Melanthiaceae*

Order 7. Trilliales

- Family 1. *Trilliaceae*

Order 8. Liliales

- Family 1. *Campynemataceae*
 2. *Colchicaceae*
 3. *Tricyrtidaceae*
 4. *Scoliopaceae*
 5. *Calochortaceae*
 6. *Liliaceae*
 7. *Medeolaceae*

Order 9. Burmanniales

- Family 1. *Burmanniaceae*
 2. *Thismiaceae*
 3. *Corsiaceae*

Order 10. Alstroemeriales

- Family 1. *Luzuriagaceae*
 2. *Behniaceae*
 3. *Alstroemeriaceae*
 4. *Petermanniaceae*

Order 11. Smilacales

- Family 1. *Philesiaceae*
 2. *Ripogonaceae*
 3. *Smilacaceae*

Order 12. Orchidales

- Family 1. *Blandfordiaceae*
 2. *Asteliaceae*
 3. *Lanariaceae*

4. *Hypoxidaceae*

5. *Orchidaceae*

Order 13. Iridales

- Family 1. *Ixioliriaceae*
 2. *Walleriaceae*
 3. *Tecophilaeaceae*
 4. *Cyanastraceae*
 5. *Doryanthaceae*
 6. *Geosiridaceae*
 7. *Iridaceae*

Order 14. Amaryllidales

- Family 1. *Hemerocallidaceae*
 2. *Phormiaceae*
 3. *Xeronemataceae*
 4. *Asphodelaceae*
 5. *Xanthorrhoeaceae*
 6. *Anthericaceae*
 7. *Anemarrhenaceae*
 8. *Hyacinthaceae*
 9. *Agavaceae*
 10. *Themidaceae*
 11. *Agapantaceae*
 12. *Alliaceae*
 13. *Amaryllidaceae*
 14. *Herreriaceae*
 15. *Aphyllanthaceae*

Order 15. Asparagales

- Family 1. *Convallariaceae*
 2. *Dracaenaceae*
 3. *Nolinaceae*
 4. *Ruscaceae*
 5. *Asparagaceae*
 6. *Eriospermaceae*

SUPERORDER PANDANANAE

Order 16. Pandanales

- Family 1. *Pandanaceae*

Order 17. Cyclanthales

- Family 1. *Cyclanthaceae*

Order 18. Triuridales

- Family 1. *Triuridaceae*

Order 19. Velloziales

- Family 1. *Velloziaceae*
 2. *Acanthochlamydeaceae*

Order 20. Stemonales

- Family 1. *Stemonaceae*
 2. *Pentastemonaceae*

SUPERORDER DIOSCOREANAE

Order 21. Dioscoreales

- Family 1. *Taccaceae*
- 2. *Stenomeridaceae*
- 3. *Dioscoreaceae*
- 4. *Trichopodaceae*

Subclass III. Arecidae

SUPERORDER ARECANAE

Order 22. Arecales

- Family 1. *Arecaceae*

Subclass IV. Commelinidae

SUPERORDER BROMELIANAE

Order 23. Bromeliales

- Family 1. *Bromeliaceae*

SUPERORDER ZINGIBERANAE

Order 24. Zingiberales (Canales)

- Family 1. *Strelitziaceae*
- 2. *Lowiaceae*
- 3. *Musaceae*
- 4. *Heliconiaceae*
- 5. *Zingiberaceae*
- 6. *Costaceae*
- 7. *Cannaceae*
- 8. *Marantaceae*

SUPERORDER COMMELINANAE

Order 25. Commelinales

- Family 1. *Hanguanaceae*
- 2. *Commelinaceae*

- 3. *Philydraceae*
- 4. *Pontederiaceae*
- 5. *Haemodoraceae*

Order 26. Xyridales

- Family 1. *Mayaceae*
- 2. *Xyridaceae*
- 3. *Rapateaceae*
- 4. *Eriocaulaceae*
- 5. *Hydatellaceae*

Order 27. Dasypogonales

- Family 1. *Baxteriaceae*
- 2. *Lomandraceae*
- 3. *Dasypogonaceae*
- 4. *Calectasiaceae*

SUPERORDER JUNCANAE

Order 28. Juncales

- Family 1. *Thurniaceae*
- 2. *Juncaceae*
- 3. *Cyperaceae*

SUPERORDER POANAE

Order 29. Typhales

- Family 1. *Sparganiaceae*
- 2. *Typhaceae*

Order 30. Restionales

- Family 1. *Flagellariaceae*
- 2. *Joinvilleaceae*
- 3. *Restionaceae*
- 4. *Anarthriaceae*
- 5. *Ecdeiocoleaceae*
- 6. *Centrolepidaceae*

Order 31. Poales

- Family 1. *Poaceae*