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# Trends in the evolution of the angiosperm flowers

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The flower is classically defined as a determinate shoot that bears modified leaves. It is believed that the primitive flowers are those which possess numerous floral parts, all spirally arranged on the floral axis. Discussing the origin of the flowers it is claimed that the flowering plants might have evolved from the hypothetical 'Proangiosperms' that existed in the Late Mesozoic Era and had characters of both gymnosperms and angiosperms. Among other factors, seasonal climate is believed to have caused the angiospermatization in the early proangiosperms.

Primitive flowers, such as those of Magnoliales, are all solitary, regular and moderately-sized in which the floral parts are all separate and indefinite in number. It is stressed that the evolution of the flower is guided by (a) principle of progressive economy in the production of floral parts, and (b) principle of progressive adaptation to insect visitors. Adaptations of angiosperms to insect visitors include development of conspicuous flowers (either by enlargement of individual flowers or by aggregation of separate flowers), development of zygomorphy and fusion of floral parts. Primitive flowers lack a differentiation between calyx and corolla. Derived perianth features are said to include (a) evolution of two distinct whorls of perianth—calyx and corolla, (b) establishment of a regular number of floral parts, (c) fusion of sepals and petals, and (d) development of zygomorphy.

Primitive stamens, characteristics of the genus *Degeneria* (Degeneriaceae : Magnoliidae) are broad and laminar and evolution proceeded towards transformation of such laminar stamens to a distinct filament and anther. Tendency towards reduction in the number of stamens is also quite evident. Similarly the flowers with many free carpels (as in Magnoliales) have given rise to flowers with syncarpous gynoecia which have further evolved to give rise to inferior ovary by the fusion of gynoecial walls to the calyx and receptacle.

Finally it is said that the above evolutionary modifications in the flowers/flower parts are fundamentally guided by the mode of pollination and pollination mechanism and have been attempted independently by different groups of plants—a fact that suggests the polyphyletic nature of angiosperms.

**Key-words**—Trends, Evolution, Angiosperms, Flower.

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## सारांश

### आवृतबीजी पुष्पों में वैक्सिक प्रवृत्तियाँ

आर० आर० राव

पुष्प की परिभाषा एक निर्धारि प्ररोह के रूप में की गई है जो परिवर्तित पत्तियाँ उत्पन्न करता है। ऐसा मत है कि आद्य पुष्प वे पुष्प हैं जिनमें अत्याधिक पुष्पी भाग हैं तथा सभी पुष्पी अक्ष पर बलयाकार रूप में विन्यस्त रहते हैं। ऐसी धारणा है कि पुष्पी पौधों का विकास परिकल्पनात्मक 'प्रोएन्जिऑस्पर्मों' से हुआ है जो कि अर्न्तम मध्यजीवी कल्प में विद्यमान थे तथा ये आवृतबीजी एवं अनावृतबीजी दोनों ही समूहों के लक्षणों से युक्त थे। अन्य कारकों में जलवायु का भी महत्वपूर्ण योगदान रहा है।

आद्य पुष्प, जैसे कि मैग्नोलिएल्स में, एकल, नियमित एवं औसतन आकार के होते हैं तथा इनमें सभी भाग अलग-अलग एवं संख्या में अगण्य होते हैं। ऐसा प्रस्तावित किया गया है कि पुष्पों का विकास (अ) पुष्पी भागों के उत्पादन में मित्त्व्ययिता के सिद्धान्त, तथा (आ) कीट परागणीयों हेतु अनुकूलनता के सिद्धान्त पर हुआ है। आद्य पुष्पों में बाह्यदलपुंज एवं दलपुंज दोनों ही में कोई भेद नहीं होता। व्युत्पादित परिदलपुंज में (अ) बाह्यदलपुंज एवं दलपुंज के दो स्पष्ट चक्र, (आ) पुष्पी भागों की नियमित संख्या, (इ) बाह्यदलों एवं दलों का संयोजन, तथा (ई) एकव्यास सममिति का विकास नामक लक्षण हैं।

आद्य पुंकेसर, जैसा डीजेनेरिया प्रजाति में है, चौड़े एवं पटली प्रकार के हैं तथा इनसे अलग पुंतन्तु एवं परागकोष वाले पुंकेसरो का विकास हुआ है। अन्त में समग्र रूप से यह प्रस्तावित किया गया है कि पुष्पों अथवा पुष्पों के भागों में उक्त विकासीय परिवर्तन परागण एवं परागण-क्रिया के फलस्वरूप हुए हैं तथा पौधों के विभिन्न समूहों में स्वतंत्र रूप से विकसित हुए हैं जिससे आवृतबीजीयों की बहुजातिवृत्तीय प्रकृति व्यक्त होती है।

SINCE the publication of the monumental work "Origin of Species" by Charles Darwin (1859) his basic principles of evolution have been the basis for the determination of the history and evolution of all taxa, both extinct and extant. In this process of determination of the phylogeny of organisms an analysis of characters from both living and fossil organisms is highly essential. But the fossil records of angiosperms in many cases are so fragmentary that all hypothesis so far proposed by palaeobotanists and morphologists as regards the origin of any group seem to be unsatisfactory. Even the origin of angiosperms, which was an 'abominable mystery' to Charles Darwin remains so to modern evolutionists, in spite of tremendous advancements practically in every discipline of biology. Nevertheless, a knowledge of phylogenetic relationships may be invaluable to understanding structural evolution as well as gaining insight into the possible adaptive significance of the evolutionary changes acquired by different plant parts such as flowers, leaves, pollen, etc. Due to paucity of substantial fossil records one has to largely depend on the comparative study of living forms. Speaking on the numerous available fossil records mainly of leaves, wood, and dispersed fruits, seeds, and pollen, Takhtajan (1980) remarks "such material though very important for the geological history of angiosperm flora and vegetation...has almost no significance for the phyletic interpretation of taxa". Yet the fossil records' unique position as the only body of data that can provide concrete evidence of mosaics of characters not present in modern groups, or character states that are now not seen, cannot be overestimated.

Evolution of the flower refers to the historical changes in the morphology of a flower and reflects changes in genetic composition recognised as a transition from an ancestral (primitive) type to the derived type (advanced). The study of such structural modifications may be important to understand the possible adaptive significance of changes in the evolution of organisms within a particular environment and with reference to interactions with other organisms. The evolution of the flower is always studied with regard to a group of organisms and, therefore, can be determined by using the methodology of phylogenetic systematics.

Here I have attempted to briefly summarise the available scattered information on the subject of evolution of flower in angiosperms and in doing so I have confined to mainly the terminology and classification of Takhtajan (1969, 1980) and Cronquist (1968).

## NATURE AND ORIGIN OF EARLY ANGIOSPERM FLOWER

The angiosperm flower is classically defined as a determinate shoot bearing modified leaves. In other words, flower parts are believed to be homologous with vegetative leaves (Puri, 1951, 1961). The primitive angiosperm flower may be visualised as having numerous spirally arranged tepals, laminar stamens and unsealed carpels (Cronquist, 1968). Such characteristics can be found in certain members of Magnoliales. Primitive angiosperms had either solitary, moderate sized flowers at the ends of branches or loosely organised cymes like those of the species of *Paeonia* (Stebbins, 1974; Cronquist, 1968; Takhtajan, 1969).

The origin of angiosperm flower is still an unsolved mystery. All the hypotheses proposed for the origin of angiosperms can be considered for discussion on the origin of the angiosperm flower. Although it is not relevant to discuss the origin of angiosperms here, a brief reference to the hypothetical 'proangiosperms' is considered necessary. It is certain that such a group of plants existed sometime in the Late Mesozoic Era and had characters of both gymnosperms and angiosperms. Krassilov (1977) has opined that about three large groups—Caytoniales, Czekanowskiales and Dirhoplostachyaceae constituted the 'proangiosperms'. These groups belonged to different lineages but in the same grade of angiospermatization, their ovules were enclosed in capsules and provided with some devices for pollination and dehiscence. Some of these angiospermous characters among proangiosperms and other lineages such as Bennettiales, constituted a character pool from which early angiosperms were derived. At the same time, identifications of Jurassic plants as proangiosperms have also been questioned by some palaeobotanists (Hickey & Doyle, 1977). Considering the vast number of advanced and diverse proangiosperm fossils from the Siberian localities this region could be concluded as one of the major world centres of diversification of early angiosperms. Tectonic events and environmental instability perhaps could have played a major role in the adaptive strategies of these ancestral populations.

Seasonal climate could be taken as one of the major factors for the hypothetical derivation of angiosperm flower. The closure of the carpel could have evolved as an adaptation to seasonal drought (Axelrod, 1970; Stebbins, 1974). The closed carpel could provide protection and effective pollination though it would seem it would be harder (longer) to

pollinate a closed carpel. A shift from wind pollination (gymnosperm character) to insect pollination could also be attributed to seasonal drought. Evidence from functional analysis of pollen morphological features of early angiosperms strongly supports this view, as well developed reticulate exine sculptured fossil pollen grains have been unearthed from the beds of Potomac Group and the Barremian of England (Hickey & Doyle, 1977), and from many other localities. The view of Arber and Parkin (1907) that a strobiloid flower of Magnoliaceae is a direct derivation from the strobilii of the gymnosperms such as the conifers, cycads or the fossil Bennettitales has now been put to serious objections mainly based on the vascular anatomy and developmental pattern of the magnoliaceous flower as also its reproductive biology. It can, therefore, be concluded that the strobilii of conifers, cycads and Bennettitales and the strobiloid flowers of Magnoliaceae are analogous and not homologous and have different origins probably as a result of similar selection pressure. Nevertheless, that the Magnoliales are among the most primitive angiosperms cannot be denied. Certainly Magnoliales are among the most primitive angiosperms and the original angiosperm flower was of moderate size and was a reproductive shoot, in which the floral parts were all separate and indefinite in number, not necessarily of a strobiloid form (Stebbins, 1974; Cronquist, 1968). Some exceptions are the Rose Greek flower of Basinger and Dilcher, the chloranthaceous flower of Taylor and Hickey, or the buxaceous flowers of Drinaan Crane.

#### GUIDING PRINCIPLES OF FLOWER EVOLUTION

Having considered the nature of the early angiosperm flower let me now trace the evolution of such a simple, solitary and regular flower in which all floral parts were separate and indefinite in number to highly complex and reduced flowers as those of the flowers of Asteraceae with highly reduced and adnate floral parts. The evolution of the flower was certainly one of the major factors for the success and diversity of angiosperms. One of the early but less publicised morphologists to propose some of the broad evolutionary principles which underline the floral development and evolution was Wernham (1913), whose basic principles of floral evolution have been considered by all subsequent phylogeneticists (Cronquist, 1968; Takhtajan, 1969; Stebbins, 1974; Thorne, 1976; Van der Pijl, 1960, 1961).

The evolutionary process in flowers of angiosperms is fundamentally guided by two basic principles which are subserved by three tendencies. These are:

1. Principle of progressive economy' in the production of reproductive parts.
2. Principle of progressive adaptation to the insect visitors (Wernham, 1913).

The first principle refers to the reduction in number of not only floral parts (both male and female organs) but in the overall size of the flower itself. This would simply mean a decreased chance of pollination, which is against the norms of natural selection. It is therefore, the second principle, the principle of progressive adaptation to insect visitors that comes to subserve the first principle.

The above two fundamental principles are constantly being subserved by three tendencies, namely:

- (i) tendency to increased conspicuousness flowers of angiosperms have evolved in two directions—(a) by enlargement of the individual flower, (b) aggregation of flowers into dense inflorescences.

Increased conspicuousness of flowers is reflected in the petaloid perianth, perhaps from Cycadioidea to early Magnoliales. Such petaloid perianth gradually led to the heterochlamydeous flowers with the differentiation of the perianth into an outer protective green calyx and an inner attractive corolla. In the primitive Magnoliales increased conspicuousness of flowers is certainly achieved but at a huge cost (in terms of energy) with indefiniteness of all floral parts, the resultant of which is effective pollination but of only one flower although each flower produces indefinite (large number) carpels that mature resulting in many offsprings from each flower.

Aggregation of flowers into dense inflorescences by repeated branching of the floral axes is also coupled by the reduction in the general size of flowers. While economy is achieved, pollination of more than one flower, often numerous flowers, as in the case of Apiaceae or Asteraceae is also achieved. It is in the less specialised families of Polypetalae that the principle of economy and its subserving tendencies are at their fullest activity.

- (ii) tendency towards flower modification in relation to visiting insects:

The second tendency to subserve the second fundamental principle of progressive

adaptation to insect visitors is accomplished by the flowers by development of zygomorphy. Perhaps because of functional or morphological constraints zygomorphy is less developed in Polypetalae while well-developed in sympetalous families. Zygomorphic flowers are relatively large and solitary or loosely aggregated indicating that the zygomorphy in angiosperm flowers goes hand in hand with insect pollination. Zygomorphy, often coupled with aggregation of flowers into compact inflorescences, is another advancement in the evolutionary tree. In certain families like Asteraceae, both the principle of economy and principle of progressive adaptation to visiting insects are best achieved.

(iii) tendency towards fusion of floral parts:

The third tendency subserves both the fundamental principles of floral evolution and relates to that of fusion of floral parts. Fusion of floral parts serves the economy on space and material. Material is saved by the fusion of carpels with the receptacle as in the case of several families of Rosidae (Saxifragaceae, Rosaceae, Leguminosae, Connaraceae, Podostemaceae, etc.).

Material economy is also achieved by the development of short filaments or subsessile anthers as in several epipetalous flowers (Primulaceae, Myrsinaceae, Plumbaginaceae, etc.). Development of such short filaments also help in accommodating some kind of specific pollinators.

Fusion of petals to form a tube is connected with the principle of adaptation to certain types of insect-visitors. A compact corolla tube is certainly helpful in concealment of nectar. Throughout the Polypetalae, at various levels there have been evolutionary attempts towards development of sympetalous corolla, a fact that supports polyphyletic origin of Sympetalae or just multiple evolutionary events to the same end in different groups of a monophyletic clade.

Fusion of stamens to form a staminal tube is another adaptation to insect visits, and remarkably expressed in such families as Fabaceae, Geraniaceae, and the less specialised families of Malvales. Development of gynostegium in the highly specialised flowers of Asclepiadaceae is a similar adaptation.

### EVOLUTIONARY MODIFICATIONS IN FLORAL PARTS

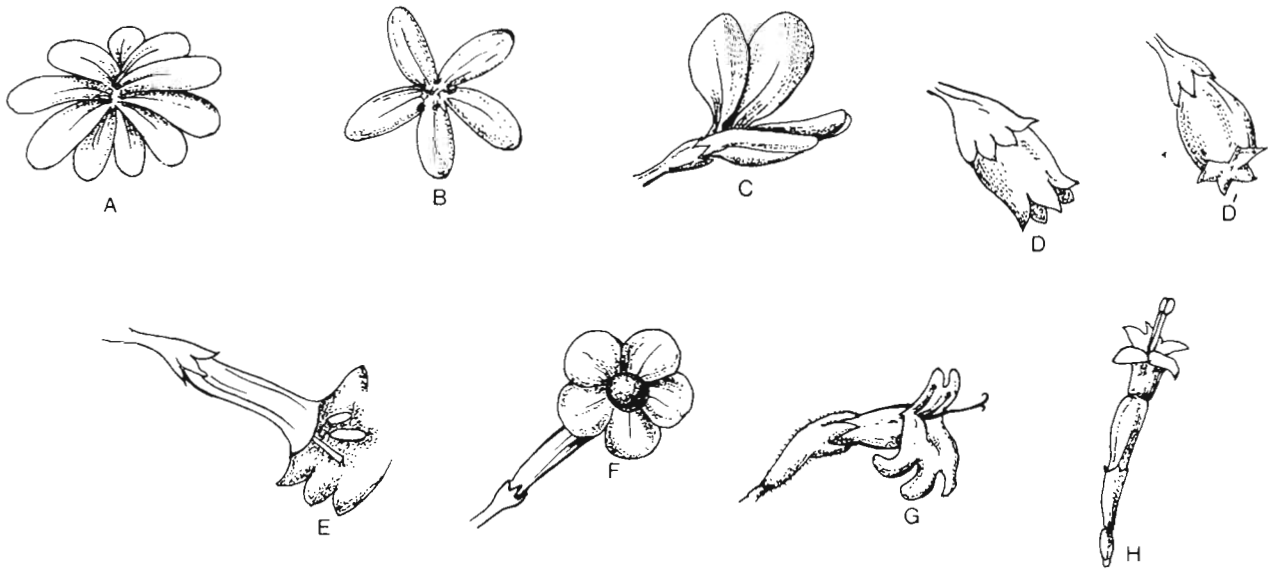
*Petals*—The two principles discussed above are

least supported by the classical interpretation of the primitive or prototypical angiosperm flower. Primitive flowers lack differentiation of calyx and corolla, exhibit no economy in the production of indefinite number of floral parts, have no specializations for insect visitors such as aggregation, chorisis, zygomorphy or fusion of parts. Yet, a gradual transition between outer green, leaf-like parts and inner coloured whorls can be marked even in several primitive extant angiosperms, such as Magnoliales, Illiciales and Paeoniales indicating petals are a later acquisition with their origin in bracts. This view is supported largely by the doctrine of correlation. In addition, certain primitive taxa (Nymphaeales, Ranunculales, Papaverales, Caryophyllales) have a well-differentiated calyx and corolla but show a transition between outer petal-like structures and inner fertile stamens, indicating their staminal origin. Petals in flowering plants are thus of a dual origin.

Derived perianth features are generally accepted to include: (i) evolution of two distinct whorls of perianth (calyx and corolla), (ii) establishment of a regular number of floral parts, (iii) fusion of sepals and petals, and (iv) zygomorphy and development of calyx or corolla spurs, and tubes (Text-figure 1A-H). These derived features are certainly the resultant of the selective pressure towards a variety of specialised pollination mechanisms and each of these trends has occurred independently and repeatedly in many different evolutionary lines.

The origin of zygomorphy is a clear indication of the adaptation of flowers for insect pollination. A number of independent evolutionary lines can be traced in flowering plants. Stebbins (1974) estimated about 10 separate origins of zygomorphy at the familial level. Bilaterally symmetrical flowers in a terminal raceme or a panicle, where the lower petals and sepals are fused and placed in such a way as to form a platform for the insects to alight are certainly advanced over the radial flowers in similar inflorescences.

*Stamens*—A great majority of stamens consist of a delimited anther, composed of two longitudinally dehiscing thecae, to which is attached a terete or feebly flattened uninerved filament. It is generally accepted that within the angiosperms the most primitive type of stamen is broad, laminar (flattened) 3-nerved structure, on one side of which are borne the two thecae either embedded or superficial (Eames, 1961; Takhtajan, 1980; Cronquist, 1968). From such a most primitive angiosperm stamen type as in the case of *Degeneria* (Degeneriaceae) evolution has generally proceeded towards a transformation of stamen-supporting



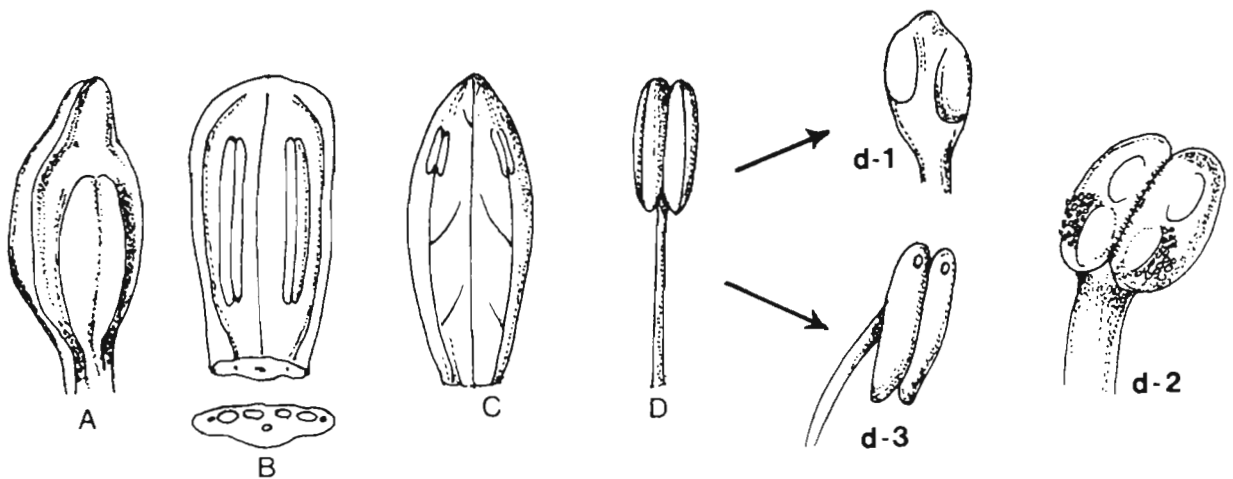
**Text-figure 1**—Evolution of flower types: **A**, Numerous free perianth lobes; **B**, Pentamerous free perianth lobes; **C**, Zygomorphic corolla with free petals; **D, D'**, Sympetalous urceolate corolla; **E**, Infundibuliform corolla; **F**, Salverform corolla; **G**, Bilabiate corolla; and **H**, Tubular corolla.

structure into a distinct filament (Text-figure 2 A-D,  $d_1$ - $d_3$ ). According to Takhtajan (1980) both abaxial and adaxial positions of microsporangia have been derived from a common ancestral type, which could only have been the marginal, as in the case of the ancestors of living Magnoliales. Additional derived features in stamen evolution are the development of specialised dehiscence mechanism (valvular or poricidal dehiscence) and of various types of stamen fusion such as monodelphy, diadelphly and even epipetaly (Text-figure 3 A-E). The evolution of stamen size, number and adnation are all related to their function—function of effective discharge of pollen. Elongation of stamen filaments in most wind pollinated flowers is to raise the anthers much above

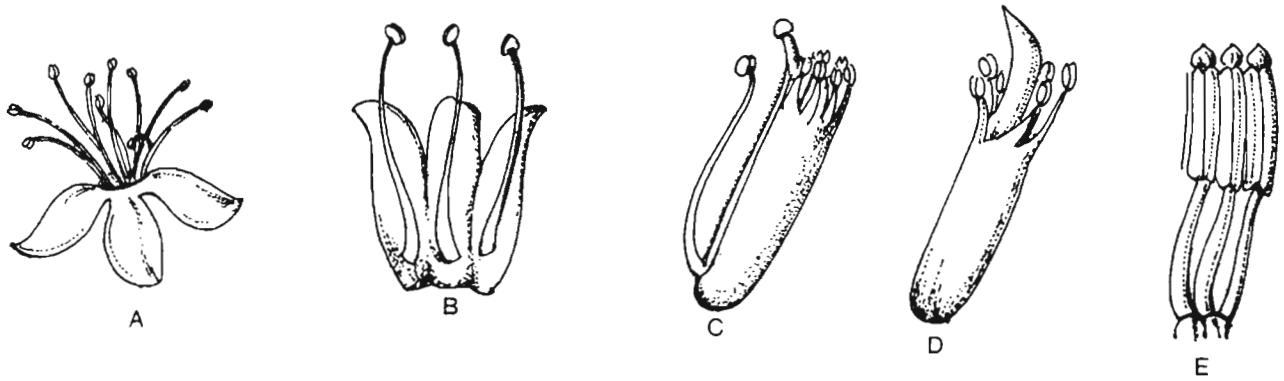
the other floral parts, so that the pollen are carried by air without any obstacles. In the case of insect-pollinated bilateral flowers the stamens are placed in such a way that the anthers are able to touch the body of insects.

Reduction in stamen number is a general trend as per the economy principle discussed above. But certain families such as Rosaceae (*Rosa*) otherwise having advanced features have numerous stamens, where stamens are relatively flat and are capable of attracting the insects. Investigations on the pollination biology of angiosperm flowers certainly throw light on the structural evolution of floral parts in relation to their function.

*Carpels*—The carpel in flowering plants is



**Text-figure 2**—Stamen structural types: **A**, Appendicular; **B**, Laminar; **C**, Petaloid; **D**, Typical; **d<sub>1</sub>-d<sub>2</sub>**, Valvular dehiscence; **d<sub>3</sub>**, Poricidal dehiscence.



**Text-figure 3**—Stamen arrangement: **A**, Fascicled; **B**, Epipetalous; **C**, Diadelphous; **D**, Monadelphous; **E**, Syngenesious.

defined as the unit of gynoecium, consisting of a modified, conduplicate megasporophyll with fused or interlocking margins enclosing one or more ovules. The most primitive carpels are unsealed, conduplicate and more or less stipitate structure, containing relatively large number of ovules as noticed in such archaic genera as *Degeneria* (Takhtajan, 1980; Bailey & Swamy, 1951; Eames, 1961).

Carpel evolution was an important factor for the success and diversity of the angiosperms. Various theories are proposed on the origin of the carpel in flowering plants from many hypothetical or known gymnospermous reproductive bodies. According to Takhtajan (1980) the carpel had a neotenic origin. The ontogeny of a typical carpel shows a gradual transition from a leaf-like structure by fusion of margins and apical extension growth, forming the style and stigma. The primitive carpel is generally believed to be that which is leaf-like, lacking a differentiated style and having relatively unfused margins with the decurrent stigmatic surface (Parkin, 1955; Eames, 1961; Takhtajan, 1980). In the course of evolution, the primitive decurrent stigma was transformed into a more localised subapical and then apical stigma (Text-figure 4). Further, it is quite logical to believe that as the stigma localised in the apical part of the carpel the stigmatic surface had to be raised above by the development of a style in order to receive the pollen grains with ease.

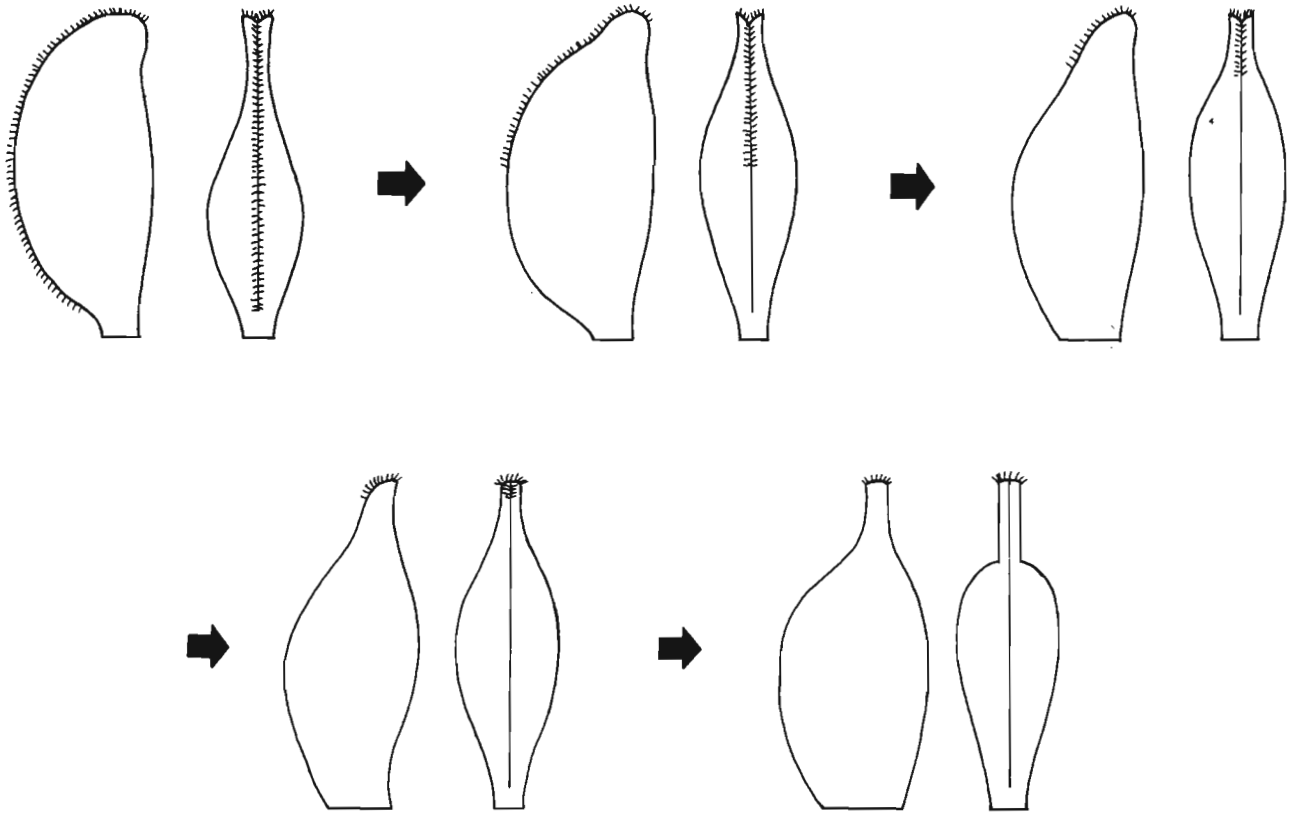
As in the case of stamens, carpel evolution is also guided by two basic features, i.e., the number of carpel per flower and fusion of carpels either with other carpels or with other floral parts. Traditionally, flowers, with many free carpels (apocarpous gynoecium) as we find in many primitive taxa of Winteraceae, Magnoliaceae, Annonaceae, etc., are widely thought to be most primitive or ancestral to flowers with fewer and fused carpels (syncarpous gynoecium). This reasoning follows the doctrine of

association. The relative ancestry of the number of carpels per flower is also not very clear as this tendency towards a greater or lesser union of carpels is already set in the most primitive families as Winteraceae, Magnoliaceae, etc. Because of the paucity of information from the fossil record, the relative ancestry of carpel number is largely speculative and requires further investigation.

Other derived features of carpel evolution include the union of carpels, shifts in the nature of placentation and ovules and the evolution of an inferior ovary by the fusion of the gynoecial walls to the calyx and the receptacle. Union of carpels in angiosperm flowers has occurred independently in as many as 20 to 25 different evolutionary lines via synovarious (fusion of ovaries) to synstylovarious (fusion of styles and ovaries but not stigmas) to completely syncarpous condition (Text-figure 5 A-C). The attainment of a uniformly syncarpous condition in certain groups of primitive families such as Magnoliaceae, Annonaceae (*Annona*), Ranunculaceae (*Nigella*) and Nymphaeaceae has rendered these groups as dead ends of these lines of evolution (Stebbins, 1974).

A syncarpous gynoecium is said to be more efficient than an apocarpous gynoecium in terms of reproductive efficiency (pollination & fertilization). As per the economy principle just discussed a syncarpous gynoecium requires less energy to elaborate a smaller amount of wall tissue than to separate carpels.

Trends of evolution in placentation types have been reviewed by Puri (1952), Parkin, (1955), Takhtajan (1969), Cronquist (1968) and Stebbins (1974). The evolutionary fusion of two or more carpels bearing a number of marginal ovules is believed to have given rise to either axile placentation if fusion of each carpel margins occurs prior to fusion between carpels or parietal if fusion between carpels occur by fusion of carpel margins.



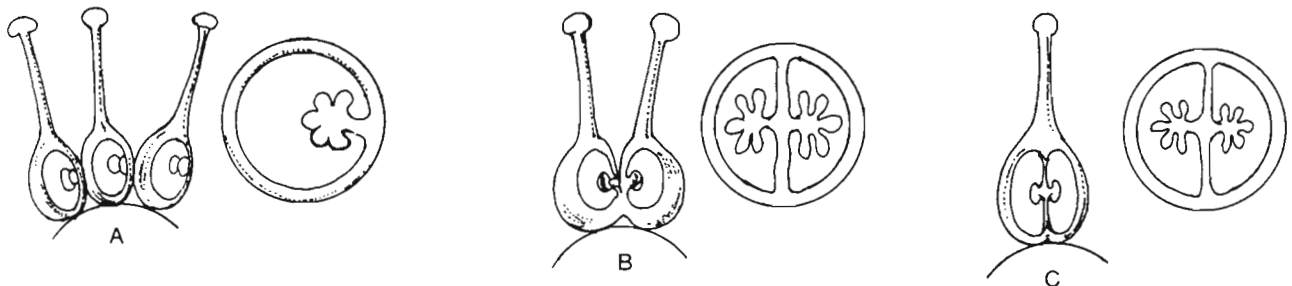
**Text-figure 4**—Diagrammatic representation of the derivation of a simple carpel from the conduplicate unsealed carpel type of *Degeneria* (after Cronquist, 1968).

From such axile or parietal placentation derived type such as free-central placentation (noticed in Primulaceae) is believed to have evolved. The evolution of placentation type in angiosperm carpels is primarily governed by the seed number and the size.

**EVOLUTION OF EPIGNY**

A final derived feature of carpel evolution is the evolution of epigyny or the inferior ovary through perigyny. An inferior ovary results by the fusion of a superior ovary with calyx, corolla and androecium. In the primitive families, the flowers are hypogynous

(superior ovary), i.e., the sepals, petals, stamens and gynoecium are inserted separately on the receptacle. The formation of a hypanthium or calyx tube by the adnation of sepals to which petal bases and filaments are fused is considered to be the derived feature rendering the flowers perigynous, as in the families of Rosales (Rosaceae, Saxifragaceae and Leguminosae). A further trend in the same direction brings about the adnation of hypanthium with the gynoecium leading to epigynous condition (inferior ovary). Distinct trends from perigyny to epigyny can be traced in different taxa of Rosales and infact the genus (*Saxifraga* is known to possess all possible conditions from perigyny with superior ovaries



**Text-figure 5**—Gynoecial types: **A**, Apocarpous; **B**, Semicarpous; and **C**, Syncarpous.

through half inferior ovaries to complete epigyny (Stebbins, 1974). It can, therefore, be concluded that the perigyny might have been derived from a common ancestry with the Rosales but the trends towards epigyny from perigyny have taken place independently many times in different groups of angiosperms.

The origin of epigyny from hypogyny is also controversial. In many families the inferior ovary has evolved independently. This is primarily based on evidence derived from monophyletic families like Ericaceae, Caryophyllaceae, Loganiaceae and Rubiaceae, where both epigyny and hypogyny are prevalent. Developmental evidence also corroborates the independent evolution of the inferior ovary. Most inferior ovaries are appendicular, and the androperianth traces traverse the peripheral tissue of the flower vertically. However, some taxa (Cactaceae, Aizoaceae) have a receptacular (axial) inferior ovary; the peripheral vascular traces curve inward towards the locules before traces are initiated to the androperianth. Though not accepted by some botanists (Kaplan, 1967; Stebbins, 1974), the differences between the receptacular versus appendicular inferior ovary represents a distinct difference in the developmental origin of each supporting a hypothesis of independent evolutionary origin.

### CONCLUDING REMARKS

Any discussion on the evolution of the flower and consequent success of modern angiosperms would be incomplete without a study of the adaptive value of floral modifications in relation to natural selection. A flower is but a reproductive shoot assigned the functions of pollination, fertilization and subsequent production of fruits and seeds. These important functions are necessary to maintain the continuity of generations and to multiply and extend the domain of the particular species. Therefore, all evolutionary modifications in the structure of a flower are attempts to optimize the success of one or more of the functions listed above. The various modifications of the flower that we have just discussed (evolution of two distinct perianth whorls, establishment of a regular number of floral parts, fusion of floral parts, zygomorphy and development of spurs) occur in flowers of very many groups of plants, groups which may be related or unrelated, primitive or advanced. Environment-organism interactions have been so complex and diverse that in some cases it is very difficult to determine the direction of the evolution of particular characters. In other words, various

parameters and sometimes even combinations of several parameters must be considered when attempting to determine the trends in the evolution of flowers. Added to this, the pollination biology of several groups of plants have scarcely been studied.

The palaeobotanical record of flowers has been analyzed by various researchers (Dilcher, 1979; Dilcher & Crane, 1984; Crane & Dilcher, 1984; Taylor & Hickey, 1990). The evolution of early angiosperm reproduction has been largely a speculation, not based on findings from fossil record. But recently Dilcher (1979) has provided an excellent account of fossils of angiosperm reproductive systems. He is of the opinion that primitive angiosperms, some with diclinous (unisexual) flowers and some with monoclinal (bisexual) flowers followed a course of parallel evolution in their modifications and specialization of vegetative form. This is because early lineages of both diclinous wind pollinated flowers and monoclinal, mainly insect pollinated flowers co-exist in the early fossil history of angiosperms. Based on the present fossil record of early angiosperm reproduction he further opines that (a) Magnoliales should no longer be thought to epitomize the primeval angiosperm flowers. The Ranalian complex may represent one of the early lines of angiosperm evolution, but not singularly the most primitive, (b) The so-called 'reduced' flowers of such orders as the Trochodendrales, Cercidiphyllales, Eupteleales, Hamamelidales and Piperales may be considered initially simple rather than reduced from a monoclinal ancestor. Independent lineages of some anemophilous flowers developed early and perhaps separately from entomophilous flowers from a common diclinous ancestral stock.

The recent fossil records indicate an extremely rapid radiation of types of angiosperm reproduction during the Early Cretaceous itself. An Aptian plant with attached leaves and flowers discovered from the Lower Cretaceous strata from Australia (Taylor & Hickey, 1990) is perhaps the oldest direct evidence of flowers which show clear evidences of their relationship to the extant Chloranthaceae. Dilcher and Crane (1984) and Crane and Dilcher (1984) described two interesting fossil genera of early angiosperms (*Archaeanthus* and *Lesqueria*) from the Mid-Cretaceous Dakota Formation of Central Kansas and the Woodbine Formation of northeastern Texas. The two fossil groups had multifollicular fructification, most closely related to Recent Magnoliidae and in some features comes close to the hypothetical angiosperm archetype predicted by magnoliid floral theory. The discovery of these unique and extinct genera led to the conclusion that



the basic magnoliid flower was one of the earliest kinds of floral organization to be developed during the Mid-Cretaceous radiation of flowering plants.

The method of pollination and its optimization has resulted in certain alterations in the structure of flowers or flower parts. It is believed that self-pollinating flowers were the precursors to cross-pollination. But there are innumerable instances where self-fertilizing species have evolved from obligate outcrossing species as in certain members of Cruciferae, Leguminosae, Onagraceae, and the advanced Compositae and Graminae. At the same time, there are many entirely self-fertilizing species which have successfully perpetuated over millions of years.

It is again difficult to say whether wind pollination or insect pollination is a derived feature, as there are noticeable shifts from insect to wind pollination and vice versa. These shifts are accompanied by characteristic alteration in the floral morphology (Faegri & Van der Pijl, 1966). Wind pollinated flowers are normally small and form dense inflorescences. The perianth in these flowers is either reduced or absent with anthers producing abundant pollen. The apparent similarity between wind pollinated 'flowers' of gymnosperms and those of 'Amentiferae' is one of several lines of evidence of derivation of angiosperms from gymnosperms (Engler & Prantl, 1928).

Wind pollination in flowering plants has been accomplished independently in several families or genera of certain families which are otherwise adopted to insect pollination, e.g., *Thalictrum* (Ranunculaceae) tribe Poterieae (Rosaceae); Ambrosiinae of the tribe Heliantheae and *Artemisia* of the tribe Anthemidae (Compositae). Similarly there are several instances of shifts from wind pollination to insect pollination in groups that are otherwise predominantly adopted to wind pollination, e.g., *Dichromena* (Cyperaceae) and Moraceae of Urticales (Leppik, 1955; Stebbins, 1974). The final conclusion, therefore, is that the evolution of the flower in angiosperms is primarily guided by the mode of pollination and pollination mechanism. In achieving optimal results, all groups of plants, whether primitive or advanced have attempted to acquire the various modifications such as reduction in general size of flower, and number of floral parts, fusion of floral parts, and zygomorphy. These characters have arisen independently, suggesting the polyphyletic nature of their origin. While some groups evolved in the direction of zygomorphy and reduction of floral parts for insect pollination, yet other groups specialised for wind pollination.

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