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The Fundamental Nature of the Flower

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The fundamental nature of the flower¹

JOHN H. SCHAFFNER
(WITH PLATES 12 AND 13)

In 1925 the writer published a general account of the evolution of the flower² in which the subject was covered in a general way; but since some rather fantastic notions have recently been advanced about the origin and evolution of the angiospermous flower it was thought proper to present a further statement with the addition of certain facts and principles which must be taken into account in any comprehensive treatment. In the previous paper also no distinction was made between the epigynous flower with a tubular, epigynous hypanthium and the epigynous flower with a solid, epigynous hypanthium. With the recognition of the latter type, there are then nine fundamental, morphological types of flowers. The primary causal factor in the evolution of the flower is determinateness of the reproductive axis. If the reproductive axis of a vascular sporophyte is indeterminate, the plant is a flowerless plant. Thus the flower is definitely defined, as a determinate sporophyll-bearing shoot, or a modification of such a shoot.

The sporophyte of the Bryophyta is a radially symmetrical system and the embryonic sporophyte of the vascular plants also develops a radially symmetrical or cylindrical axis with a hemispherical mass of meristematic cells at the upper end from which lateral appendages or leaves are produced, originally in acropetal succession. The terminal bud may have a single apical cell or a group of initial cells but the development of the axis and lateral appendages results in either case in the same fundamental type, a cylinder with the leaves arranged in definite spirals when development is complete. The growing stem bud, whether terminal or lateral, is fundamentally indeterminate in growth, as appears in such simple types as *Lycopodium lucidulum* Michx. or *Osmunda cinnamomea* L. This is in marked contrast to the extreme determinateness of the sporophyte of liverworts and mosses in which the terminal bud of the sporophyte is destroyed by the reproductive process. We are not immediately concerned as to how the system of lateral appendages, including the sporophylls, was originally evolved from a stem system without appendages, but we must be cognizant of the fact that the living vascular plants from the ferns, horsetails, and clubmosses on up to the very highest angiosperms have evolved and retained the potentiality of spiralization in the production of lateral appendages with practically no exceptions.

¹ Papers from the Department of Botany, The Ohio State University, No. 388.

² Schaffner, John H. Principles of Plant Taxonomy II. Ohio Jour. Sci. 25: 219-243. 1925.

[THE BULLETIN FOR NOVEMBER (64: 499-568) WAS ISSUED NOVEMBER 1, 1937]

Fundamentally then the flower is of essentially the same nature as the vegetative shoot.

As intimated above, the reproductive process in the living vascular plants has been shifted from the stem tissues themselves to the leaves and thus the growing bud in the lower forms produces alternate zones of purely vegetative or foliage leaves and sporophylls in an indefinite succession. The production of reproductive zones or rosettes is present in *Psilotum*, in the lowest species of *Lycopodium*, in all the ferns, in the quillworts, in the carpellate plants of the genus *Cycas*, and in both carpellate and staminate plants of *Ginkgo*. In *Psilotum* there is a distinct difference between the leaves with sporangia in their axils and those without. Although the reproductive branches are determinate sooner or later, this determinateness is vegetative, like the vegetative determinateness in the branches of the higher species of *Lycopodium*, and commonly the production of sporangia has ceased sometime before growth of the branch ends, or there may be more than one reproductive zone produced. All other higher, vascular plants have determinate reproductive shoots or flowers. The reproductive reactions initiate processes which sooner or later bring about complete stopping of growth and death of the given bud. The introduction of this new, reproductive, determinate potentiality constituted the evolution of the flower and the potentiality was evolved independently in a number of phyletic lines of vascular plants. There is then no difficulty in determining whether a plant has flowers or not, since both the physiological conditions and the morphology of the flower are clearly defined. At the lower levels of the evolution of reproductive determinateness of the stem axis, stopping of growth takes place very slowly and indefinitely. Thus the number of sporophylls is not only large but varies greatly from flower to flower, while in the highest flowers determination is very prompt and definite. Because of the extreme promptness of determination and consequent shortening of the cell lineage, in the extreme types of flowers, the differentiation processes are often confused and many of the structures are so modified that it is often difficult to homologize them with the more normal organs of the primitive flowers. Unfortunately these extremely reduced and specialized flowers have often been considered to indicate direct relationships and to be directly derived from each other, when they really represent phylogenetic culminations of independent evolutionary lines. Thus it has been assumed that *Juniperus*, *Ephedra*, *Casuarina*, *Juglans*, etc. form a progressive phylogenetic line of relationship. To one accustomed to consider the evolution and taxonomy of the plant kingdom from the geological and phyletic point of view, such an arrangement seems exceedingly fantastic and un-

reasonable, since all lines of fundamental study point to evolution as an irreversible process.

On the lowest levels of floral evolution the potentiality for determinateness is not decidedly perfected and thus failure of the reaction or proliferation is frequent, as in species of *Lycopodium*, *Equisetum fluviatile*, *Selaginella*, *Araucaria*, *Cunninghamia*, *Rosa*, and other genera. The lower flowers are appropriately called strobili or cones and these two words should be used synonymously, but a strobilus should never be called a spike. Since flowers appear in two classes of homosporous pteridophytes it follows that the lowest are homosporous or neutral flowers. There is no sexual dimorphism in any lycopod or equisetum flower. But in the heterosporous plants sexual dimorphism is always present either between parts of the same flower or of separate flowers. Heterosporous flowers are bisporangiate or monosporangiate; if monosporangiate they are megasporangiate or microsporangiate and in the seed plants they should be called carpellate and staminate flowers respectively. Monosporangiate flowers may be evolved from bisporangiate flowers through a change in the time of sex determination. In these flowers vestiges of the opposite set of sporophylls are usually developed to a greater or less degree, but in extreme cases they are completely suppressed. There is a second possible mode of evolution for some monosporangiate flowers, which may have been the mode in some gymnospermous strobili. A monocious condition of the reproductive branches may have evolved before the determinate reproductive potentiality or flowers and a branching tree produced with alternating sporophylls and vegetative leaf zones and with different sexual states determined on different twigs. Now if the reproductive determinateness was introduced into such a system it would result directly in monosporangiate flowers and such flowers would show no vestiges of the opposite sporophylls. This may have been the sequence, in the evolution of the flowers of the ordinary conifers which show no vestiges of the opposite secondary sexual structures. This is in marked contrast to the monosporangiate flowers of most angiosperms together with a few gymnosperms, like *Welwitschia*, which show vestiges in the vast majority of cases either in one flower or in both. Of course, it is well known that occasionally bisporangiate flowers occur in various conifers, but these are plainly the result of accidental sex reversal and not a recapitulation of a more primitive condition.

The strobilus type of flower may show a decided disturbance in the transition zone between the vegetative and reproductive zones of the shoot, but the transition characters are for the most part much less extreme than in the angiosperms. Hereditary potentialities may be

evolved which come into play in the transition zone and give rise to peduncles, branching reactions resulting in inflorescences, simple perianths, and involucre. One or more of these characters may be observed in various species of *Equisetum*, *Lycopodium*, and *Selaginella* and also in the gymnospermous cycads, conifers and joint-firs. A definite, sterile perianth or calyx is present in the higher species of *Equisetum* and prominent involucre are present at the base of the pedicels of the staminate flowers of *Taxus* and of both staminate and carpellate flowers of *Ephedra*, *Welwitschia* and *Gnetum*. The lowest types of flowers are developed at the ends of ordinary vegetative shoots as in *Equisetum*, *Lycopodium annotinum* L., *Araucaria*, and *Magnolia*. The next step in the evolution of floral position is the axillary flower, as in *Macrozamia*, and *Asimina*.

Inflorescences result from a branching factor active in the reproductive bud and from differentiations and shortening of the inflorescence branches. The main axis below the branching system may also be involved, giving rise to such extreme angiospermous inflorescences as the heads and discs of the Compositales, the syconium or fig fruit, and the cyathium of spurges.

THE FLOWER OF ANGIOSPERMS

The most highly evolved flowers are found in the Angiospermae which contain a single phylum, the Anthophyta. The angiospermous flower is, however, fundamentally the same system as that of the strobili of horsetails, clubmosses, cycads and conifers. In the lower levels the flowers are essentially merely more elaborated strobili, as can be seen in *Echinodorus*, *Magnolia* and *Myosurus*. Probably the most advanced feature is the perianth which is usually very conspicuous in the lower types of angiosperms. The flowers are fundamentally radially symmetrical systems with lateral organs developed in spirals. The pitch of the clockwise and counter-clockwise spirals becomes equal in the more advanced forms and the parts are then developed in cycles and vertical ranks. The cyclic condition is frequently present in the perianth even if the sporophylls are still in the more primitive spiral arrangement. It will be remembered that very primitive flowers may be completely cyclic as in *Equisetum*. The angiospermous flower is fundamentally a bisporangiate system and this fundamental type may be changed to a monosporangiate condition by the progressive shifting, to an earlier stage of the ontogeny, of the time of sex determination, to the axis below the flower, as in the various kinds of monociousness and dieociousness.

The older systems of classification of the Dicotylae were based on the development and modification of the perianth, especially on the corolla, and the main divisions were thus Polypetalae, Monopetalae and Apetalae, or in the more recent Engler system Archichlamydeae (*Apetalae* and *Chori-*

petalae) and Metachlamydeae or Sympetalae, which amounts to the same thing. But this gave only a very artificial arrangement, since there are many families and even individual genera that contain species represent-

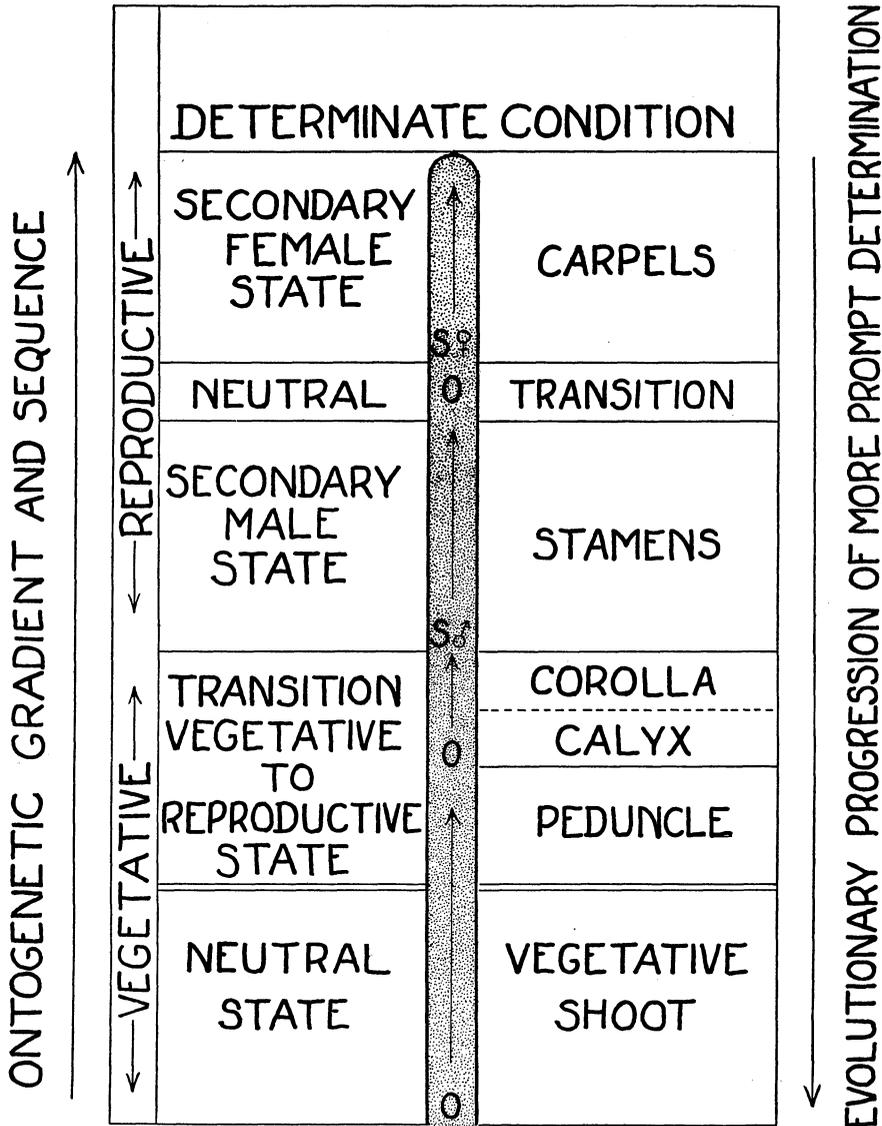


Chart 1. Diagram illustrating the general nature and development of the primitive flower of the angiosperms.

ing all the three general types. A much more fundamental morphological system is obtained by taking into account the general progressive determination of the floral axis and its expansions or other modifications.

The general nature of the development of the primitive angiospermous flower is illustrated in chart 1. As the floral bud approaches and passes through its determinate growth a definite growth gradient is developed and in consequence a definite series of activities is carried out from the beginning to the end. As the bud passes from the neutral or vegetative condition to the reproductive phase, it produces first a peduncle and then a perianth. Next, along with the reproductive reactions, the secondary male state appears and this is followed by a neuter transition zone as the bud reverses to the secondary female state, in which it normally remains until determination is complete. The neutral transition between the male and female conditions is usually so abrupt that no special developments appear. In some cases, however, a prominent internode may develop as in *Michelia* and species of *Geum* or special bracts may develop, different from both sepals and petals, as in *Aquilegia*.

The general, progressive evolution of determinateness together with the expansive growth factors operative in the floral axis have produced the fundamental morphological flower types. The determinateness of the flower bud may be brought about in two general ways. The entire mass of cells of the flower bud may stop growth uniformly or the central part of the bud may stop growing while the cortical region continues growth for a time, giving rise to the epigynous types of flowers. The expansive factors of the floral axis are active in association with the secondary sexual states developing in the axis. A careful study of living forms as well as a consideration of the possibilities under this evolutionary system show that there are nine fundamental, morphological flower types in the angiosperms. It must always be remembered that there are often transition types between the nine normal types but for the most part the types are easily recognized. There may also be more than one type of flower on a single plant.

The general ontogenetic and phylogenetic or evolutionary activities of the flower may then be reduced to a few general potentialities and summarized as follows:

1. The primary potentiality which is the cause of flower production is the determinateness of the floral axis in relation to the beginning of the reproductive reactions of a shoot. In the primitive flower types, the determination acts very slowly and indefinitely, producing a wide degree of fluctuation in the floral members. The general evolution of the flower then in all the phylogenetic lines is to a more prompt and more definite determination of the floral axis until the possible limit is reached. As stated above, the determination of the flower bud may be differential, the center of the bud stopping growth before the cortical region does. In

the extreme epigynous types the ovulary represents mainly cortical or cauline tissues, only the top with the style and stigmas and the partitions, if such are present, being cortical outgrowths or vestigial sporophylls. In the lowest flowers all the parts are usually entirely distinct but as determinateness of the floral axis advances and cell lineages are shortened, union of parts generally appears, usually first in the gynecium followed by unions in the perianth and finally all the parts may be more or less united. There is, so to speak, a telescoping of the processes of cell development and cell differentiation, and although other factors may be involved the fundamental cause appears to be especially associated with the determinate process, since no such union of parts is shown by any of the very primitive flowers, even though the plant may already have united leaf sheaths, as in *Equisetum*.

2. Hereditary factors may be evolved in the cell which have an expansive action on the flower bud as a whole or in the basal region of the floral axis which is passing into the secondary male state, or in the terminal region which is passing into the secondary female state. Such expansions may appear in the secondary male tissues of either the hypogynous or epigynous flower types, giving rise to a hypogynous hypanthium (perigynous disc) or to an epigynous hypanthium. The epigynous hypanthium must be distinguished from the ordinary perianth tube.

3. There may be adnation between the hypanthium and ovulary in the case of perigynous flowers or between the hypanthium and style, resulting in a solid growth above the ovulary in the case of epigynous flowers. This adnation is accomplished by the introduction of a factor which causes intercalary growth in the neutral transition tissues between the tissues in the secondary male state and those in the secondary female state, as in the adnate hypogynous hypanthium of the apple, and the adnate or solid epigynous hypanthium of the iris.

The interaction of these three general growth factors accounts for all the fundamental morphological flower types, and as stated above an inspection of the possibilities indicates that there can be nine types and no more. It is possible for each of the nine flower types to be developed as a radially symmetrical system or to be modified to a zygomorphic or bilateral condition through the determinateness of the bud or hypanthium developing more promptly on one side than on the other, and thus establishing peculiar physiological gradients around the flower bud which influence the expression of the shape, size, color, etc. of the general floral organs. In rare cases an isobilateral condition may evolve and zygomorphy may be superimposed on this potentiality as in *Capnoides*, or an inequilateral potentiality may be added to the zygomorphy, as in *Marantaceae*.

In addition to the general structural conditions, the flower may be modified in three general subordinate ways.

1. There may be a partial or complete suppression of one or the other sets of sporophylls (stamens or carpels) through the shifting of the time of sex determination to some point below the beginning of flower production. The same conditions may be present in the various types of monoecious and dioecious plants. The size or the absence of the vestiges will depend on the promptness and intensity of development of the secondary sexual states in the incipient tissues involved. In some cases both sets of sporophylls may become vestigial by the introduction of a hereditary factor which inhibits the development of both the secondary male state and the secondary female state in the flower, giving rise to a neutral condition.

2. There may be numerous genes evolved in the cell which give rise to complex chemical reactions with the production of various chemical compounds as pigments, odors, color patterns, deliquescent substances, etc.

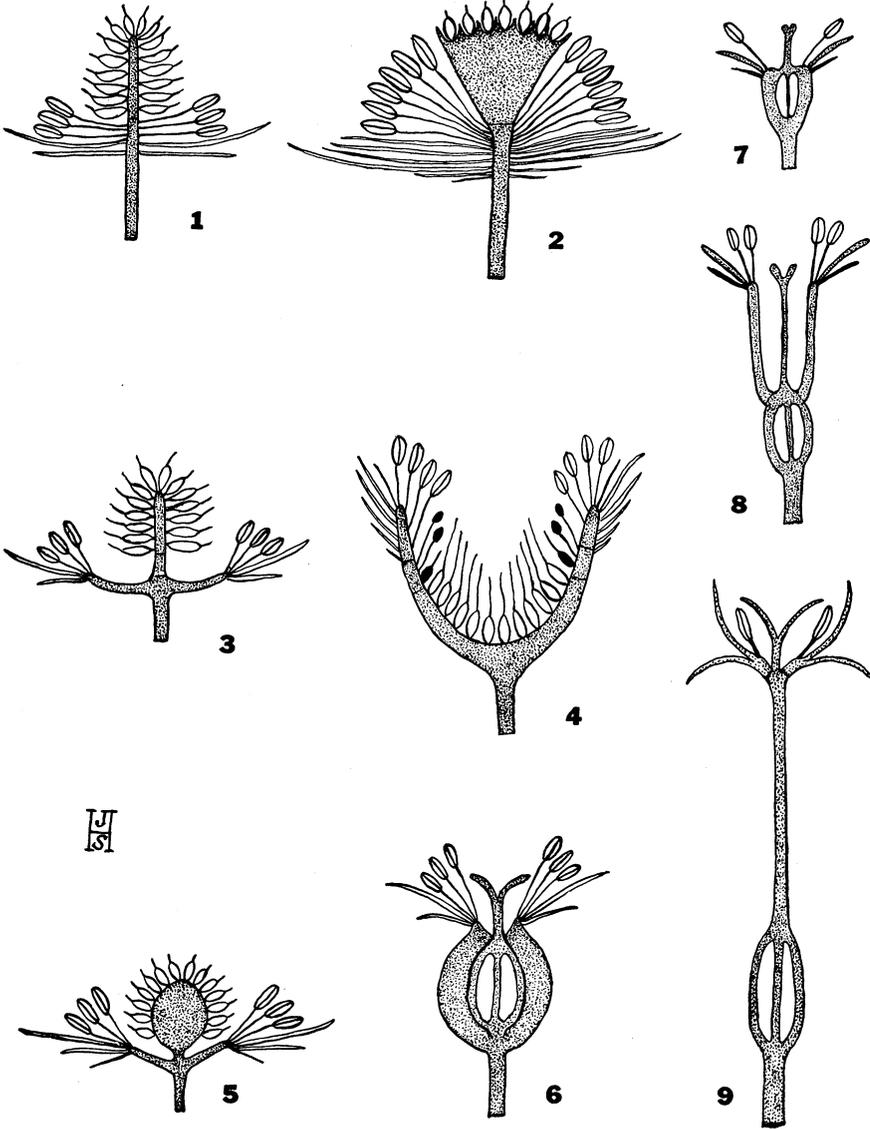
3. There may be hereditary factors or genes modifying the growth of the size, shape, surface appendages, etc. of the floral organs including the sepals, petals, stamens, and carpels and special glands. In some extreme types of floral evolution the structures may become very fantastic and complicated as in some Burmanniaceae and Orchidaceae.

In 1916, the writer published a short paper on a method of constructing floral diagrams and gave graphs representing the five most common types of flowers.³ This method has been found satisfactory for phylogenetic studies of the flower. Below a complete system is presented of the nine fundamental morphological types. With the aid of a uniform system of graphs to represent the floral structures one can read the general character of the flower and even special details may be indicated as nectar spurs, appendages, etc. One can thus easily compare a phylogenetic series of flowers and the evolutionary progression is often shown in a striking manner. It is important that the same general graph always represents the same floral organ or structure and that the diagrams can be constructed easily with the aid of compass and pen.

THE NINE FUNDAMENTAL MORPHOLOGICAL FLOWER TYPES

1. Hypogynous flower. In this first and simplest type there is no special expansion or differential growth of the floral axis. The general morphological system and mode of development is the same as in the primitive flowers of *Equisetum*, *Lycopodium*, *Selaginella*, cycads, and conifers.

³ Schaffner, John H. A general system of floral diagrams. *Ohio Jour. Sci.* 16: 360-364. 1916.



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SCHAFFNER: NATURE OF FLOWER

fers. Occasionally there is a slight enlargement of the floral axis, especially in the gynecium axis, as in the primitive *Araucaria Cookii* R. Br., but this is not taken into account unless the expansion is pronounced. Examples of the first flower type: *Echinodorus*, *Magnolia*, *Yucca*, *Tradescantia*, *Delphinium*, *Oxalis*, *Viola*, *Rhododendron*, *Catalpa*. Pl. 12, fig. 1. *Ranunculus abortivus* L. (Ranunculaceae).

2. Hypogynous flower with expanded gynecium axis. This type of flower is essentially the same as the primitive hypogynous type except that it has a hereditary potentiality which causes a decided expansion of the upper part of the floral axis which is in the secondary female state. Familiar examples are *Sagittaria latifolia* Willd. (carpellate flower) and pl. 12, fig. 2. *Nelumbo lutea* (Willd.) Pers. (Nelumbonaceae).

3. Perigynous flower with free hypogynous hypanthium and normal gynecium axis. This is the common perigynous type, all the floral organs except the carpels being borne on the perigynous disk or hypanthium. The hypanthium may vary from only a slight rim to a very prominent cup-like organ. Examples: *Rosa*, *Agrimonia*, *Lythrum*, *Amygdalus*, *Baptisia*, *Hamamelis*, *Ulmus*. Pl. 12, fig. 3. *Geum vernum* (Raf.) T. & G. (Rosaceae).

4. Perigynous flower with the entire floral axis expanded continuously. In this type the floral organs are borne on a broad cup-like disc and as the neutral transition zone between the gynecium and andrecium is about in the middle of the cup both staminodes and carpellodes may be present in a bisporangiate flower. This is apparently a rare type. Examples: *Meratia*, *Monimia*. Pl. 12, fig. 4. *Calycanthus floridus* L. (Calycanthaceae).

5. Perigynous flower with hypogynous hypanthium and separately expanded gynecium axis. In this flower type the transition zone of the floral axis in the neutral condition is not influenced by the expansion factors. Examples: *Duchesnea*, *Comarum*. Pl. 12, fig. 5. *Fragaria virginiana* Duchesne (Rosaceae).

6. Perigynous flower with adnate hypogynous hypanthium. Although this type of flower superficially resembles the ordinary epigynous type it is very different in its incipient stage, beginning its development much like an ordinary perigynous flower. In most cases also the plants with flowers of this type plainly show their relationship to typical perigynous groups, as for example the apple to the rose family. As development proceeds the neutral zone of tissue between the gynecium axis and the hypanthium also grows, thus producing a complete adnation except at the outer end where the short cup usually seen in apples represents the hypanthium developed in the incipient stage. Examples: *Pyrus*, *Amelanchier*, *Crataegus*, *Carya*, *Juglans*. Pl. 12, fig. 6. *Malus sylvestris* Mill. (Rosaceae).

7. Epigynous flower without hypanthium. In this flower type the morphological apex of the floral axis is in the base of the ovulary and

growth of the cortical tissues does not extend beyond the ovulary wall. It is a common and wide-spread type found in many groups. Examples: *Vallisneria*, *Hypoxis*, *Sisyrinchium*, *Canna*, *Cypripedium*, *Portulaca*, *Vaccinium*, *Opuntia*, *Philadelphus*, *Asarum*, *Pastinaca*, *Cornus*, *Lobelia*, *Helianthus*. Pl. 12, fig. 7. *Cynoxylon floridum* (L.) Raf. (Cornaceae).

8. Epigynous flower with tubular epigynous hypanthium. In this type the cortical tissue, as it passes into the secondary male state at the top of the ovulary, continues its growth and produces a tube of greater or less length at the end of which the sepals, petals, and stamens are borne. Examples: *Euryale*, *Crinum*, *Hymenocallis*, *Cereus*, *Epiphyllum*, *Ribes odoratum* Wendl., *Oenothera*. Pl. 12, fig. 8. *Fuchsia hybrida* Voss. (Onagraceae).

9. Epigynous flower with solid epigynous hypanthium. In this type the lower part of the hypanthium and the style, above the ovulary, develop as a continuous tissue. In most cases there is a tubular upper part of the hypanthium above the solid portion, which indicates that this type probably evolved from the tubular epigynous hypanthium. It is interesting to note that Dr. G. H. Shull obtained a mutant *Oenothera* with a solid epigynous hypanthium from the ordinary tubular epigynous hypanthium type. Examples: *Iris*, *Strelitzia* and Shull's mutant *Oenothera pollicata*. Pl. 12, fig. 9. *Iris cristata* Ait. (Iridaceae).

In some plants there is an elongation of the upper part of the ovulary, as it ripens, which simulates to some extent the solid epigynous hypanthium. Such a condition is present in *Taraxacum*, *Tragopogon*, *Lactuca virosa* L., etc., but as the structure is developed more especially in relation to the fruit rather than the flower it should not be associated with the ninth flower type. It will be noted that this elongation of the upper part of the fruit is found in plants which have the simple epigynous condition.

MORPHOLOGICAL DESCRIPTION OF THE FLOWERS WHOSE
DIAGRAMS ARE REPRESENTED IN PLATE 13

An inspection of the diagrams will readily show the character of the signs used to represent the various floral organs and structural conditions. In general a star represents a missing member; a completely black or stippled sporophyll graph indicates that the organ is vestigial to a greater or less degree, either because of determination of the floral axis, or because of the inhibitory influence produced by a secondary sexual condition in a monosporangiate flower, or because of the neutral condition produced on a zone where sex reversal is taking place. Connecting lines indicate union of parts or organs situated on a structure. If the stamens are very numerous in a perigynous or epigynous flower the connecting lines to these may be omitted, since the connecting lines from the sepals

and petals will indicate their position in the flower. The hypanthium is represented by a broad dotted circle and the inferior ovulary is drawn with an extra heavy circle. Adnation between the ovulary and hypogynous hypanthium is indicated by stippling, and the solid epigynous hypanthium both by connecting lines and stippling. An expanded gynecium axis is represented by an ordinary circle around the carpels. Union of perianth segments of two cycles forming an ordinary perianth tube is indicated by connecting lines between the ends of the successive inner and outer segment graphs. In case of a prominent spiral arrangement, this character can be indicated by drawing one or more spiral lines to connect the proper members of the spiral. Bracts of an involucre or subtending bracts are represented by ordinary lines to distinguish them from sepals. The secondary axis on which the flower is borne is indicated by a small circle with a dot in the center. The relation of the primary axis to the secondary axis is sometimes not easy to determine and in such a case it should be omitted until the relationship is definitely known. If the anthers are bilocular (with two microsporangia) the horizontal line producing four divisions in the anther graph is omitted.

In present systematic descriptions the terminology used is both improper and confusing and cannot be depended upon for learning the actual condition. Thus the anthers of *Lilium* are said to be "2-celled" and those of *Smilax* are also described as "2-celled," but the first has four microsporangia while the second has two microsporangia in each anther.

All of the figures refer to plate 13.

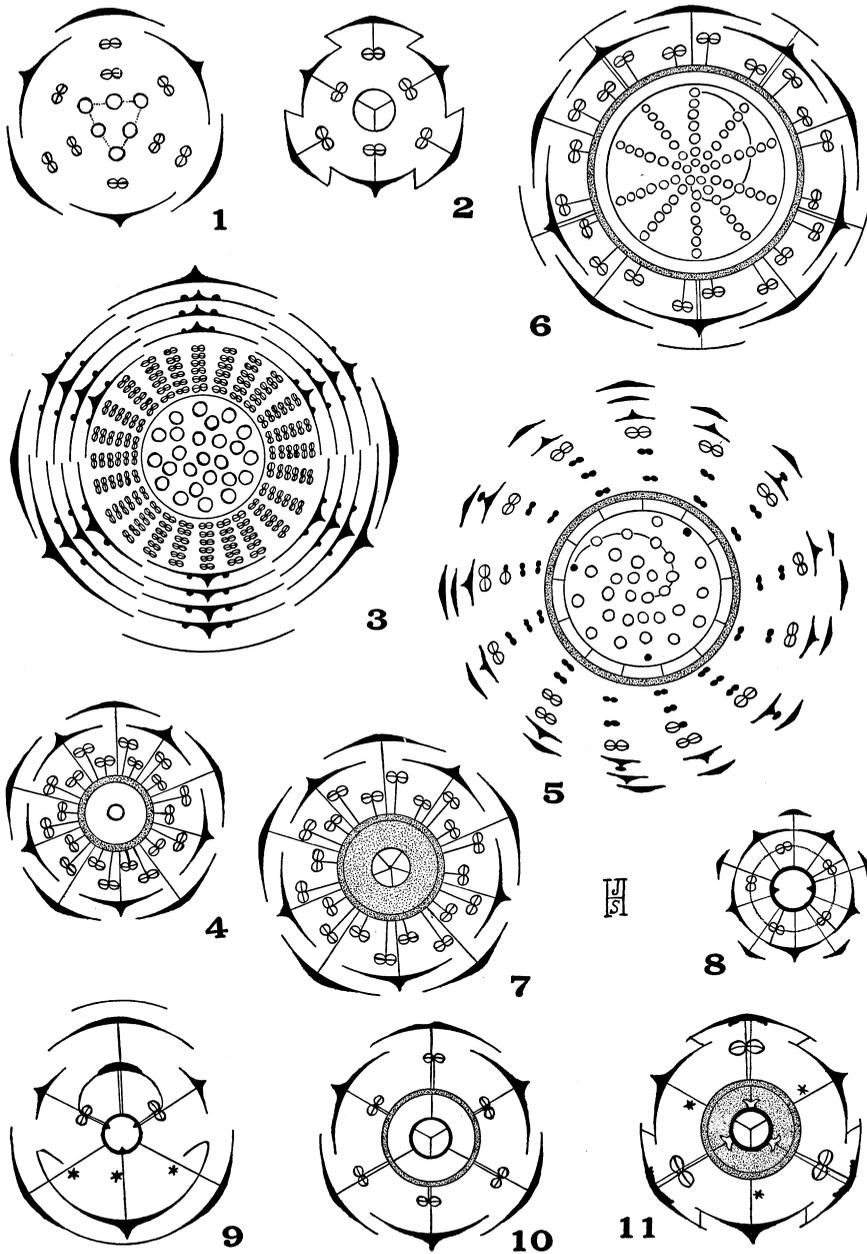
Fig. 1. *Butomus umbellatus* L. (Butomaceae). Flower hypogynous, bisporangiate, heptacyclic, trimerous, actinomorphic, choripetalous; carpels slightly united.

Fig. 2. *Polygonatum commutatum* (R. & S.) Dietr. (Liliaceae). Flower hypogynous, bisporangiate, pentacyclic, trimerous, actinomorphic; perianth segments (sepals and petals) united into a perianth tube; stamens united with the perianth; syncarpous, ovulary trilocular.

Fig. 3. *Nelumbo lutea* (Willd.) Pers. (Nelumbonaceae). Flower hypogynous, bisporangiate, choripetalous; calyx dimerous; corolla trimerous, with numerous petal-like staminodes; stamens and carpels free, in spirals, the carpels in a greatly expanded gynecium receptacle. The expansion of the receptacle is indicated by the circle surrounding the carpels.

Fig. 4. *Prunus virginiana* L. (Rosaceae). Flower perigynous with a free hypanthium, bisporangiate; perianth pentamerous, actinomorphic, choripetalous; carpel one.

Fig. 5. *Calycanthus floridus* L. (Calycanthaceae). Flower perigynous with a continuously expanded floral axis, bisporangiate, actinomorphic,



SCHAFFNER: NATURE OF THE FLOWER

the parts in spirals. The broad circle represents the expanded andrecium axis and the narrow inner one the expanded gynecium axis. The connecting lines between the two indicate that the two are continuous; on the neutral transition between the normal carpels and stamens are some staminodes and carpelodes represented in black.

Fig. 6. *Fragaria chiloensis* Duchesne. (Rosaceae). Flower perigynous with separately expanded gynecium axis and hypogynous hypanthium, bisporangiate, actinomorphic; perianth pentamerous, choripetalous, the calyx with five alternate bractlets; carpels spirally arranged; neutral zone of the floral axis not affected by the expansion potentialities.

Fig. 7. *Malus sylvestris* Mill. (Rosaceae). Flower perigynous with adnate hypogynous hypanthium, bisporangiate, actinomorphic, choripetalous, syncarpous, plurilocular; calyx, corolla, and gynecium pentamerous. The stippling between the hypanthium and the ovulary indicates adnation.

Fig. 8. *Sclerolepis uniflora* (Walt.) B. S. P. (Helianthaceae). Flower epigynous without hypanthium, bisporangiate, tetracyclic, pentamerous, actinomorphic, sympetalous; ovulary of two united carpels, unilocular; calyx (pappus) of five distinct sepals (scales); stamens synantherous, their filaments united with the corolla.

Fig. 9. *Cypripedium parviflorum* Salisb. (Orchidaceae). Flower epigynous without hypanthium, bisporangiate, pentacyclic, trimerous, choripetalous, zygomorphic; ovulary unilocular; two sepals united; lip petal large; the odd upper stamen represented by a large staminode and connected with the two fertile stamens with the style (column). The stars represent missing stamens.

Fig. 10. *Crinum asiaticum* L. (Amaryllidaceae). Flower epigynous with tubular epigynous hypanthium, bisporangiate, pentacyclic, trimerous, choripetalous, actinomorphic; ovulary trilocular. The lines connecting the hypanthium with the ovulary without stippling in between indicate an epigynous hypanthium.

Fig. 11. *Iris cristata* Ait. (Iridaceae). Flower epigynous with solid epigynous hypanthium, bisporangiate, pentacyclic with the inner cycle of stamens wanting, trimerous, actinomorphic; ovulary trilocular. The crests on the sepals are indicated and also the peculiar petal-like condition of the stigmas. The lines connecting the hypanthium with the ovulary and the stippling in between indicate a solid epigynous hypanthium. The connecting lines passing from the anthers to the perianth segments show that the stamens are united with the perianth.