PRINCIPLES OF PLANT TAXONOMY, VI.*

JOHN H. SCHAFFNER,
Ohio State University.

In the earlier papers of this series, the fact was developed that there are six, great, progressive transitions in the plant kingdom which delimit the seven fundamental stages or subkingdoms. These subkingdoms are of the greatest convenience in establishing natural classes, since it becomes much easier to segregate groups on a natural basis if the organisms to be classified are known to come within similar limits. We can then look for truly segregative characters within the limits indicated by the several transitions.

PROGRESSIVE MOVEMENTS AND STAGES WITHIN THE SUBKINGDOMS AND CLASSES.

The fifth paper of the series discussed in a general way the progressive evolutionary movements which are the basis of the taxonomic orthogenetic series. The most important of these progressive movements within the subkingdom will now be considered more definitely in relation to their importance in classification, since no proper arrangements can be made until such series are clearly understood. A given movement may affect practically all the classes and subclasses of a subkingdom or only a part of them. These subordinate series are of especial importance when one comes to the task of segregating orders and families within the class. For it frequently happens that the same progressive movement will appear in two groups long after they have become distinct through the acquisition of some segregative character. Among such movements may be mentioned the origin of heterogamy in several independent lower groups and the independent origin of the flower in a considerable number of higher groups. Other important examples are the development of unisexuality, and of moneciousness and dieciousness, which are attained in a multitude of lines with the most diverse morphological and physiological characters.

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PROTOPHYTA. The progressions in the protophytes are from the unicellular to the multicellular condition and also from the undifferentiated colonial condition of the cells to the differentiated condition. The filamentous forms show both ends differentiated alike in the lower levels while in the higher there is a distinct development of base and apex. If the Glaucocysteæ really belong to the blue-green algæ, they show a very decided advancement in the development of definite chromatophores and a highly organized nucleus with a nuclear membrane.

NEMATOPHYTA. In the evolution of the vegetative body the following progressive strata are to be recognized: (1). Unicellular organisms; (2). Colonial organisms including simple filaments with undifferentiated tips; (3). Simple filaments with differentiated base and apex; (4). Branched fllaments with differentiated base and apex and sometimes intermediate cells; (5). Solid aggregates with differentiated base and tip, usually showing a juvenile filamentous phase. In the true fungi a number of distinctly progressive developments of the mycelium are in evidence. The lower mycelia are branched systems with some differentiation; higher up in the scale, mostly in connection with the reproductive process, highly complex fruiting bodies are developed in which mycelial differentiations are accomplished comparable to the complex tissue systems of the algæ and higher plants, whose bodies represent true solid aggregates.

In the reproductive systems the stages of sexual evolution are quite prominent; first, there is the progression from isogamous to moderately heterogamous conditions and then to the extremely heterogamous gametes and differentiated gametangia; second, the transition from plants which show no sexual states beyond the gametangia to forms with well-developed secondary sexual states and dimorphisms in the vegetative tissues beyond the gametangia; and third, the highest condition in which the secondary sexual state, either male or female, is in evidence throughout the entire gametophyte.

BRYOPHYTA. The sporophyte shows a definite series of distinct advances. In the first and lowest stage the entire sporophyte is a sporangium and the interior of the sporangium is completely sporogenous. The second stage represents a sterilization of the lower part and a differentiation into foot and

stalk. At the same time sterile cells appear in the sporangium. This is the first step in the shifting of the reproductive process from the central axis to a lateral appendage. In the higher bryophytes the central part of the sporangium becomes completely vegetative, developing a central columella, as in most of the mosses and in the hornworts. A fourth definite organ also appears, the hypophysis, with true stomata. The hypophysis and photosynthetic tissues around the sporangium with the stomata are the fore-runners of a leaf, and bryophyte sporophytes which have these structures are to be regarded as the highest in the scale. There is also the development of a central strand of tissue which is a primordial vascular system. In the Anthocerotæ, the intercalation of a growing zone between the sporangium and the foot is a very decided progression and foreshaddows an indeterminate sporophyte system. This growing zone is, however, not the fore-runner of the terminal growing point of the higher plants. This was attained through the transfer of the spore-reproductive process entirely away from the stem to the lateral appendages or leaves, thus permitting the terminal bud to develop vegetatively for an indefinite period after reproduction is begun. The presence of the central columella, the basal growing zone, development of stomata, and other advanced conditions place the Anthocerotæ as a separate class far above the Hepaticæ.

The gametophyte of the bryophytes also shows marked progressive stages. In the Hepaticæ, the highest development is in the cylindrical stem with differentiated types of lateral and ventral scales. In the mosses there are several advances, the erect gametophore coming from the protonema is a culmination type while the branched creeping forms are to be regarded as the more primitive types, although there may be a progression in the branching system, especially seen in such forms as have a creeping rhizome-like stem with erect aerial branches.

Several distinct stages are also to be observed in the progression of sexual evolution. The lower are hermaphrodites, the higher are unisexual. The unisexual condition is attained independently in many lines. The hermaphrodites fall into an ascending series approaching the unisexual forms. This series is in general: 1, synoicous condition, 2, paroicous, 3, autoicous, 4, unisexual; with various intergrading conditions. The series represents the actual evolutionary advancement not only in these plants but also in the progression upwards through the

higher subkingdoms and the species and groups are always to be arranged in this sequence, other things being equal.

PTERIDOPHYTA HOMOSPORÆ. There are three well segregated phyla represented in this subkingdom. In general there are two stages in the advancement of the gametophyte. The lower species have hermaphroditic gametophytes which give way to unisexual individuals in the highest species of the series. These movements are usually in the same direction as the progressive movements in the sporophyte. Thus the highest ferns like the sensitive fern and ostrich fern have unisexual gametophytes and the same seems true also for Equisetum, in which extreme species, like *Equisetum arvense*, have unisexual gametophytes while more primitive species, like *Equisetum laevigatum*, have hermaphroditic gametophytes.

The sporophyte of the lycopods shows progressive stages from indeterminate growth in the reproductive system to a definite, determinate flower; from very little difference between the foliage leaves and sporophylls in the lower species to decided dimorphism in the higher; from no peduncle developed below the cone or inflorescence to a very prominent peduncular development; from one type of foliage leaf to a complex system; from a simple, uniform reaction of the stem buds to light and gravity to a complex reaction; from a very simple branching system to a complex branching system, developed both in the vegetative part and in the inflorescence.

EQUISETEÆ. The living Equiseta show several definite progressive stages; from perennial aerial stems to annual aerial stems, attained independently several times; from no special dimorphism between the sterile and fertile shoots to a very decided dimorphism in some lines; from no peduncle to a prominent peduncle; from a sporangium-bearing ring or calyx to a completely sterile calyx; from a green sporophyll to a non-green sporophyll and finally to a completely non-green fertile shoot; from the aerial development of the flower to the completely geophilous development of the flower. All these movements correspond to the progressive movements evolved in plants in the higher subkingdoms.

PHYLLOPTERIDÆ. The ferns show various detailed progressive movements. Among these, the evolution of the sporophyll is conspicuous and represents a definite character which

will show lower and higher levels. In general one can distinguish three phases: 1. Undifferentiated sporophylls, or such as show no very distinct dimorphism with the foliage leaf; 2. Sporophylls that are partially distinctly differentiated, either at the tip, at the base, or in the middle; 3. completely differentiated sporophylls showing a decided dimorphism with the foliage leaf as in *Onoclea sensibilis*, *Osmunda cinnamonea*, and *Lorinseria areolata*. The vascular system with open bundles, cylindrical cambium, and a central pith is associated with the more primitive general morphology and is for this and other reasons regarded as the more primitive condition in the Ptenophyta while the various types of concentric bundle systems are specializations from this. The open system was carried up through the gymnosperms and angiosperms, and at various points bundle systems with short-lived cambiums and closed bundles like these of the monocotyls were evolved. The indeterminate perennial types represent the primitive Pteridophyta and from those in various lines the progression leads up to biennials and annuals which are the culmination types in the evolution of length of life of the individual.

PTERIDOPHYTA HETEROSPORÆ. In the Selaginelleæ, those species with very slowly determinate cones represent the primitive condition while the quickly determinate cones represent the advanced type of floral development. As in the lycopods, the radially symmetrical spiral arrangement of the leaves is the primitive condition while the species which have more or less flattened stems with the leaves spreading into two ranks are more advanced. The species with solid stems are more primitive than those of the same series having the vascular bundles in hollow tubes.

Isoëtes does not show any striking linear series, the species all having practically the same fundamental morphology, but the water-ferns indicate several progressive movements. The species which have creeping rhizomes are more primitive than those with floating bodies. The genera which have both megasporangia and microsporangia in the same sorus are more primitive than those which have monosporangiate sori. The quillworts and selaginellas with the entire leaf differentiated as a megasporophyll or a microsporophyll are to be regarded as more advanced in their sexual evolution than the water-ferns although they may be lower in some other respects.

GYMNOSPERMÆ. All living gymnosperms, except the two genera, Cycas and Ginkgo, have evolved the determinate reproductive axis or the flower. In Cycas the flower is really present, but is expressed only in the staminate plant under the influence of the secondary male state. The flower shows a general progressive movement in all lines to a more prompt and definite determination, thus producing a decreasing number of sporophylls. In the extreme condition the entire flower is reduced to one sporophyll. There is also a definite progressive movement in the greater dimorphism shown between sporophyll and foliage leaf. Among the living species there are none with normal bisporangiate flowers but such a condition is found in some fossil groups. The two main stages are, therefore: 1, moneciousness and 2, dieciousness. In the conifers at least the diecious condition has plainly come out of the monecious condition and the series should always be arranged in this order, wherever the two conditions appear in the same line. There are many subordinate progressive series in the various lines which show in the vegetative parts as well as in the reproductive systems. One such vegetative advance is shown, as in the two preceding subkingdoms, by the development of internodes. The lower stages are without internodal development; the higher have very prominent internodes. Another progression is shown in the complexity of the branching system. The movement in leaf arrangement is from alternate, spiral arrangements in the lower forms to opposite and whorled arrangements in the higher groups. In various lines the progression is from two cotyledons to numerous cotyledons, rarely to one by the suppression of the second member. There is also a progression in certain lines, especially of the Pinales, from simple embryos to multiple embryos from one egg.

ANGIOSPERMÆ. The stages in the progressive advancement of the angiosperm series are mostly definite and are often repeated independently a great number of times. The main movements are as follows: In the line of sex determination, the three progressive steps are, 1, bisporangiate flowers; 2, various degrees of moneciousness; 3, dieciousness. The third condition sometimes follows the second and sometimes originates directly from the first. In duration, the general movement is from trees to shrubs and lianas, to perennial herbs, to biennial and annual herbs. This movement is repeated in a great number

of independent lines. The inflorescence usually proceeds from single flowers at the end of leafy branches or in the leaf axils, to loose flower clusters of various kinds, to very compact clusters; and occasionally the reduction brings about single flowers again. The flower shows very definite progressive stages. 1. Just as in previous subkingdoms, the evolutionary movement brings out all gradations from numerous floral parts to single sporophylls. Only rarely are the parts multiplied for a special reason in the more advanced groups, as in cacti for example. 2. The lower forms are hypogynous, the higher epigynous. 3. The lowest flowers are apocarpous, the intermediate are syncarpous, commonly with as many cavities as developed carpels, while the highest are syncarpous and have unilocular ovularies whether they are hypogynous or epigynous. 4. The lowest flowers have distinct perianth segments, and the higher united segments; or there is a gradual loss until the apetalous, asepalous or, completely naked flowers are attained in various lines. 5. The andrecium also often shows progressions from completely distinct organs to various types of unions in the highest members of the series. 6. The symmetry is almost invariably from the spiral, actinomorphic condition to a monosymmetrical or zygomorphic condition, through the unequal determinate growth of the upper and lower parts of the flower bud. 7. In some lines also hypogynous and epigynous hypanthia appear, which show progressive developments, or in some cases a reduction series, since the hypanthium, along with all the floral structures, is finally involved in the inevitable evolutionary progression of the earlier and earlier determination of the floral axis. 8. In general, the primitive angiosperms are insect pollinated with no special adaptations to special conditions. This condition leads on to the specialized flowers which can only be successfully pollinated by special types of insect visitors; or to wind pollination; or to water pollination if the plants are moving down under the water in their evolutionary progression. Either the anemophilous type or the entomophilous may finally end in self-pollination or cleistogamy, or in various types of parthenogenetic developments. These specializations appear many times, independently, in unrelated groups.

The movements indicated above are correct criteria for the serial arrangement of larger and smaller groups after the proper phyletic segregations have been made.

PROPER ARRANGEMENT OF THE GROUPS IN SERIAL SEQUENCE

In general, the groups are to be taken in the order of their several evolutionary advancements as indicated by the totality of their important characters. If two lines are at about the same level at their bases but the one shows a much longer evolutionary progression than the other, the one that attains the highest level at the end is to be taken up last. Even if a group is a little more advanced at the base than its next nearest segregate, it is to be taken up first, if the second one shows a much higher level at the end. In this method of arrangement, the ends of the series will always show the culmination types. This is very desirable if one is to acquire a general knowledge of plants in relation to the advancing evolutionary movements. It is evident that when we are following out lines of development we can only acquire a clear comprehension of the process when the end of the pursuit actually brings us to the highest type attained in the series as a whole as well as in each subordinate series.

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