A Phylogenetic Consideration on the Vascular Plants, Cotyledonary Node Including Hypocotyl Being Taken as the Ancestral Form[1]

(A Preliminary Note)

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Introduction

The phylogeny of a plant is the 4th-dimensional extension of the plant in which the generations are continuously repeated. One generation is the three-dimensional extension of the protoplast at a period in the phylogenetic course, and it is limited by a resting stage accompanied by a special phase called the reproduction. Such supression of the physiological activities in the protoplast may be caused by something like the self-poisoning influenced by its own metabolites, the products of the metabolism. After a period the resting cells discharged from the influence resumes the activity, namely the next generation begins. Provided that nothing happened in the constituents of the protoplast in certain generation, the next generation will repeat the last generation, while certain deviation has happened the reaction had to appear at the special part in a certain stage in the next generations, i.e., the ontogeny in the next generation may show us the deviated characters. Consequently, we can analyse the course of the phylogeny of a protoplast by means of the studies of the ontogeny considering the supposed physiological environments which the protoplast has passed in the phylogeny and compare with those plants which are now living in the similar environments. Following consideration is the results of my analytical studies on the phylogeny of the vascular plants. The present paper mostly concerns the seed plants, especially the sporophyte. On the gametophyte of the seed plants and on the Pteridophyte the writer wishes to write a special paper.

Phylogeny of the Seed Plant

A. The vegetative phase. 1. *The ancestor.* It is considered that the phylogenetic ancestor of the seed plant was a hygrophytic multinuclear thallus (Yasui 1944), later it developed as a uninuclear multi-

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cellular one. The term "cell" in this paper is defined as one of the septate chambers in the thallus including its contents and the derivatives with the same structure. The structure of the thallus resembles the cotyledonary ring or set including the hypocotyl of the embryo. Namely it has a disk like thallus having certain number of lobes, and short stalk underneath of the central part of the disk. The thallus attached on the surface of the earth under the water with the end of the stalk. The stocker is represented now with the suspensor. The ordinary leaves above the cotyledonary node is considered as a derivative.

The reasons are: a. Cotyledon finishes the most part of its development in the very early stage of the development of the embryo and before any other organ developed yet in the ontogeny of the plants of the present age.

b. The cotyledonary ring has unique structure which is rather common in the almost all of the seed plant compared with those leaves showing the differentiation not only in the structure of the blade but also in the numbers of the lobes.

In short, these characters had to be the representation of the characters of the ancestral form in certain definite stage in the phylogeny.

The present writer reported already (1944) that the ancestor of the seed plant once existed as a hygrophytic multinuclear thallus which is represented in the beginning of the ontogeny of the plants in the present age as the multinuclear stage. The nuclear division in such thallus had to be simultaneous type at first, while when the development proceeds the rates of the nuclear division become different in the different parts of the body, and also the rates in the different dimension, e.g., in the outermost layer, the nucleus divides in two dimensions only parallel to the surface of the body. Consequently there appears different parts having different nuclear arrangements, the outer, the central and the middle layers. The similar figure we can see in the body of *Caulerpa*, but such a stage is not represented now in the ontogeny of the seed plants, namely such a stage is suppressed, probably due to the appearance of the septation in the body in certain generation in the phylogeny induced in the early stage of the ontogeny of the proper generation.

2. *Second stage.* Here we have a new problem to concern. That is the problem on the cause of the nuclear and cell division in the thallus. However, it needs too much space to discuss here, so that I will give only the definition of the term "activator" going to be used in the following items. The activator is certain metabolite of the protoplast which activates the resting nucleus to start to divide, and it is conductable from one cell to the other.

In this stage the thallus became uninuclear multicellular body. This change made the three layers mentioned above more distinctive, and also influenced on the growth of the cells. One of the results is the development of the intercellular space among the cells. Another, differences appeared between the two daughter cells derived from one, one continues the further division while the other stops. Consequently there results a series of cells from older to younger, though finally they all stop to divide. Such differentiation takes place parallel all over the body at first, but in the thallus as a whole the differentiation proceeds from the distal to proximal part, so that in the proximal part of the thallus undifferentiated cells always remain. This course of differentiation clearly represents in the ontogeny.

The separation of the cells due to the development of the cell membrane strengthens the differences in the physiological nature in cells too, e.g., the appearance of the storage cells in the central part of the lobes, one for nutrients (the phloem in the later stage) and another for the water (the xylem). Especially the latter gave the plant the aerophytic habit.

3. *The third stage*. The aerophytic habit gave the great influence to the thallus not only in the structural characters but also in the physiological activities. The *first* is the appearance of the intercellular space (the *stomata*) among the outermost layer cells and serves as the passage for the aqueous vapour to go out from the intercellular space inside. The guard cells of the stomata are the sister cells of the last division in a series of the cells mentioned above (cf. the item 2). The stomata is the intercellular space formed between the youngest sister cells. The *second* is arrest to the escape of certain metabolites from the surface of the thallus, such escape was very easy in the water, consequently certain metabolites, e.g., the cutin which came out from the cells fixes on the surface of the body, so that there arose a very distinct cell layer, the *epidermis*. The *third* is the appearance of the mesophyll, the photosynthetic layer. In water the most active photosynthesis takes place in the outermost layer as we see in those hygrophytic plants, but in the air too strong ray suppresses the development of the chlorophyll in the plastids, and the cells in the middle layer which receive the weakened visible ray passing through the epidermis just like the outermost layer cells in the water receive the weakened visible ray passing through the water, develops as the photosynthetic tissue, namely the mesophyll. It is the mesophyll which keeps the most fundamental and primitive character of the plant protoplast. The *fourth*, the accumulation of the photosythetic products and the metabolites. Namely those materials transfered into the central portion of the lobes of thallus, the phloem, from the mesophyll and then into

the proximal part of the thallus where the products are small. Thus the phloem now acts as the *conductive tissue*. The *fifth*, the evaporation of water took place through the stomata of the epidermis, especially it is stronger at the distal part of the lobes, consequently the water in the water storage cells transfers into the outer part of the lobes and the loss is filled up from the proximal portion. Thus the water storage cells serve now as the *water conductor*, and the stocker as the *sucker* just we see in the developing embryo.

4. *The fourth stage*. Now in the thallus in which the conductive tissue is differentiated the *local meristems* due to the influence of the activator conducted through the phloem. Therefore the activated points always relate with the phloem, though the cells to be activated must be rather young undifferentiated cells. Meristem produced under such circumstances had to be called the secondary meristem just like the cambium. However, strictly speaking, there are no such fixed primary meristem in the thallus, which is derived from the multinuclear cell.

One of the activated points is the proximal part of the thallus and another appears at the somewhat interior point related to the distal end of the phloem in the stalk, the hypocotyl in the plant of the present age. In the latter the activator comes through the distal end of the phloem in the stalk, so that the influence is terminal, consequently the meristem arises at one point endogenously. Such endogeous appearance of the meristem, the growing point of the root, may be due to that the surface cells which are serving as the stocker were too old already when the activator is transfered.

On the upper side of the proximal part of the thallus the influence of the activator is rather lateral at first, in other words it is interfassicular, later the activation proceeds toward the upper surface, and still later the cells at the outside of the vascular system also become active so that there arises a circle of the meristem on the proximal part of the thallus. This meristem grows as the second thallus, i.e., the 1st node of the stem, surrounding the remained undifferentiated central part, resembling the 1st thallus.

In the new meristematic ring the most activated point or points appear at the point or points where the activated tissues preceded from the opposite sides meet with, in other words, at the point just inferior to the notch of the lobes of the thallus, and grow as the primordia of the lobes or the leaves of the 1st node of the stem. Consequently, the theoretical number of the leaves of the 1st node is to be the same with number of lobes of the thallus, and appear alternately with the lobes or the cotyledonary leaves. Those deviations in the shapes of leaves we found now in several plants and also the deviated arrangement of the leaves on the stem is to be the results due to many other influences. The part which corresponds to the stalk of the thallus develops as the 1st internode of the stem.

In the primordia of the leaf conductive tissues differentiate rather soon and connect with the older ones in the thallus through which the acting parts receive the materials for growth. The processes mentioned above repeat upwards surrounding the very young central portion, the so-called growing point of the stem, thus the ordinary leaves including the stem are formed. Consequently the leaves on the stem are the emergencies of the lobes of the thallus and the internode is that of the part of the stalk.

The repetition of the node formation is the vegetative growth, while on one hand those processes in the early stage of the ontogeny takes place in the mother plant in the compressed manner receiving the material for the formation from the mother plant, due to the parasitic habit of the macrospore: that is the embyo formation. On the other hand the plant gets the habit to repeat the processes resembling the embryo formation on the certain points of the body generally at the end of the seasonal vegetative growth, namely the bud formation. It is considered that the latter is to be one of the caenozoic characters in the phylogeny of the seed plants.

B. **The reproductive phase.** On the mechanism of the sporogenesis itself we do not find out much evolution in the phylogeny of the seed plants. It is a primitive phenomenon repeated through the phylogeny. This may be due to the constancy of the metabolites which concern the sporogenesis. However, the bud which appeared in the certain later stage of the phylogeny, influenced by the activator of the sporogenesis (we will call the substance as the sporogenesis inducer, and abridged as SI) which was transfered from the old leaf, and developed specially complicated organ called the flower. On these bud some leaf primordia devoted to the sporogenesis but not developed as the vegetative leaves, i.e., there the differentiation of the vegetative and the reproductive leaf occurred. And there some develop as the microsporophylls, the anthers, and certain others as macrosporophylls, the carpel in the angiosperm.

Here I wish to specially emphasize one thing on the flower formation. That is, the flower formation is preceded always with the bud formation. And the latter is induced by the activator (here we wish to call the activator as the bud inducer or BI) as mentioned above (cf. item 4, p. 78). Several experiments on the flower formation such as the photoperiodism lead the writer to consider that if there were many factors in the floral inducer the BI must be an important one.

In the Gymnosperm the floral organ is rather simple, and the microsporophyll appears earlier than the macrosporophyll and at the different part. These data lead us to consider that SI for microsporogenesis (MiSI) is different from the SI for macrosporogenesis (MaSI) qualitatively, but not only quantitatively.

The complicated floral structure in the Angiosperm may be due to that the leaf primordia on the bud were beginning already toward the vegetative leaves, while their developmental stages were different when they receive the MiSI. Consequently some of them which were in the fittest stage to be influenced with the MiSI develop to the anthers, those on the upper region of the bud were too young to be influenced develop without reaction and later receive the MaSI so develop as the carpels, and those which were situated below the anthers develop petals and calyces according to the degrees of their earlier developmental stages towards the vegetative leaf.

The present writer reported before (Yasui 1946) that those inducer produced in the leaf transfer once into the root where it gets certain change then goes up to the bud through the xylem. Now she is considering that the inducer produced in the leaf is not perfect before it has changed at the root tip receiving certain mineral substance, e.g. the barium. By the lack of the latter an abortion of the flower happens in some plants. Such deficiency may be caused by the aerophytic habit. In water the plant gets easily such minerals from surrounding water, but aerophyte has no such circumstances except root.

Phylogeny of the Pteridophyte

It is considered that the ancestor of the Pteridophyte is to be entirely different from that of the seed plants. It might be multicellular plants grown attached on the surface of the earth with one end of the body and on the other end it had the apical cell which ever divides dichotomously. The differentiation proceeds from the proximal to apical part of the body.

Summary

1. The phylogeny map is the 4th-dimensional extension of a protoplast in which the generations repeated continuously. One generation in the phylogeny is the three-dimensional extension of the protoplast in certain period which is limited by a resting stage accompanying the reproductive phase.

2. It is considered that the ancestor of the seed plants was a hygrophytic multinuclear thallus having the structure like the cotyledonary ring including the hypocotyl in the plants of the present age.

3. In the second stage of the development in the phylogeny the thallus became uninuclear multicellular one, and the water storage cells differentiated in the body which gave the aerophytic habit for the plant.

4. Aerophytic habit gave the great change to the plant not only morphologically but also in the physiological natures. The epidermis having stomata differentiated. The mesophyll became to serve for the photosynthesis instead of the epidermis. The arrest of the escape of the metabolites from the surface of the body, the accumulation of the photosynthetic products, and the evaporation of water from the body surface lead the differentiation of conductive tissues, the phloem and xylem.

5. The transfer of the nutrients and also the metabolites, especially such as the activator of the nuclear division, influenced to differentiate the secondary meristem. The growing point of the root and the primordium of the first node of the stem including the leaves and internode produced from the meristems. The embryo and bud formation are considered.

6. The appearance of the bud lead the formation of the complicated reproductive organ called the flower. The qualitative differences between the MiSI, and MaSI, and the migration of the SI were considered.

7. The ancestor of the Pteridophyte must be entirely different from that of the seed plants. It was a uninuclear multicellular plant having the growing point at the distal end of the body.

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Further references will appear in the full paper.