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# Evolution of the Leaf Forms through the Ages Explained by the Successive Retardation and Neoteny

## Part 1. Outline of Retardation

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### 1. INTRODUCTION AND ACKNOWLEDGEMENTS

In the former paper (Asama, 1959) it was explained that the so-called *Gigantopteris* was not derived monophyletically from one primitive *Gigantopteris*-like plant but polyphyletically from many ancestors. Therefore, the relation between these so-called *Gigantopteris* is parallel evolution. It was also stated that the successive changes in the climate cause orthogenesis and parallel evolution in coherent leaf plants (so-called *Gigantopteris*) and that similar environments produce similar leaf forms in different regions. For example, *Gigantopteridium americanum* (White) from North America differs essentially from the Cathaysian "*Gigantopteris*" but the similar climatic conditions in these regions produced similar leaf forms.

The increasing dry climate retarded the growth of the fronds of the so-called *Gigantopteris* and gave rise to the coherent leaf plants with cohering adjacent pinnules and pinnae step by step and thus the frond reduced its leaf areas but the coherent pinna became larger than the former pinnule, because the former corresponds to the pinna of the former. A tripinnate frond changed to a simple frond by cohering step by step, thus reducing its leaf area. The coherent leaf plants were derived from the pinnate frond by retardation. Such coherent leaf plants as mentioned are derived from the pinnate frond by successive retardation. Such are found in the Paleozoic, Mesozoic and Cenozoic eras, from which we can recognize the successive retardation as the main cause of leaf form evolution. We can find many coherent leaf plants not only in different regions of the same geological age but also in that of dissimilar geological ages.

Fossil plants collected from many localities of different geological ages were leaves or fronds and the fructifications and woods preserving their inner structures were few. However, the phylogenetic classification was based on them because the leaf forms were considered to be less important for their variability. The leaves are sterile organs and are subjected to easy change in their forms by the influence of the outer condition. If the environments change, the plants from adaptation to the new environment change their leaf form. Therefore it may be inferred that the leaf forms are the most effective organ for

indication of the environments. Although the structure of fructification and the inner structure of woods changed with age, that of the leaf forms were greater. The plants and their environments are in intimate relationship as evidenced by them at present and a plant to survive must become adapted to the environments. This means that the plants must change in their form and structure of their organs to meet the new requirements. It is known that the climate of geological ages changed many times, therefore from the transformation of leaf form, we can speculate the climate of that time. Although the leaf forms are variable, their forms are changed only with reason. When their forms change, the new leaf forms retain relationship with their previous one and from such reasons their trends can be understood. It is natural that Mesozoic plants were derived from Paleozoic plants and Cenozoic plants from Mesozoic ones respectively. Comparative morphology in the leaf forms of the three eras provide evidence for constructing their evolutionary trends as reflected in their leaf form and conversely also the environmental conditions leading to those changes.

In this paper the writer attempts to explain the transformation of leaf forms through the ages by successive retardation. Orthogenesis and parallel evolution which is found in many regions and many geological times will also be explained by successive retardation. These phenomena can easily be understood from inference of continuous and uni-directional change in the environment. Such change has led to successive retardation in leaf development with remarkable correspondence with the change of environments. Cenozoic broad leaf is the coherent leaf derived from the pinnate seed bearing fronds of the Mesozoic or Paleozoic Pteridosperms. The evolution of the Cenozoic Dicotyledon is polyphyletic and the origin of the broad leaved trees were many plants belonging to Pteridosperms of the Mesozoic or Paleozoic and they were derived parallel from the many kinds of leaf forms of Pteridosperms.

In this paper the writer presents his opinions on explosive evolution of Schindewolf. In plant evolution the coherent leaf plants are a good example. The evolution of the so-called *Gigantopteris* in the Paleozoic and the broad leaves in the Cenozoic were very rapid and the coherent leaf plants of both ages appeared rapidly. Therefore to explain the evolution of coherent leaf plants monophyletically we must accept explosive evolution. Since the coherent leaf plants have many origins, their evolution is polyphyletical. The writer agrees with Schindewolf's opinion that the process of appearance of new types does not begin with variety but with family or genus. (Tokuda, 1951, p. 231)

The writer has treated only the transformation of leaf forms and opinions concerning the fructification and the anatomy of the wood will be reserved for another paper. As the conclusion, we must accept the continuous lowering of the lowest temperature of the year through geological ages, namely the successive increase of annual range and the transformation of leaf forms to be neotenic evolution. And the cause of the successive change of leaf form is continuous retardation and it is also supported by the writer's conclusion which is conducted from the study of the fructification and anatomy of plants.

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## 2. ONTOGENY AND PHYLOGENY

### 1) Branched vein plants

#### (1) Ontogeny of *Dryopteris lepigera* O. Kuntze and *Diplazium esculentum* Swartz

In brief, pteridophytes involves the occurrence of two distinct phases in life history, each of which produces the other. One is the sexual phase or generation, the gametophyte, which bears male and female sexual organs and in which fertilization is effected. The fertilized spore does not develop into another gamete-bearing individual, but into a non-sexual phase, the sporophyte, which does not bear sex organs but produces instead a large number of single celled spores, each of which without any sexual process develop directly into a new gametophyte. In ferns and pteridosperms it is the sporophyte rather than the gametophyte which is large and conspicuous. The greater part of the fossil plants are the sporophyte and not the gametophyte, so the process of growth of sporophyte will be discussed here.

The frond of *Dryopteris lepigera* (Fig. 1; Ogata, 1936, Vol. 6, pl. 312) is quadripinnate in the lowest part and tripinnate in the lower, bipinnate in the middle and unipinnate in the upper parts. A pinnule of unipinnate pinna in the youngest stage will become a unipinnate pinna, bipinnate pinna and tripinnate pinna as it grows. Therefore a pinnule of unipinnate pinna in the youngest stage has a potential energy to become a unipinnate pinna, bipinnate pinna and tripinnate pinna in the future. The first pinnule will become uni-pinnate pinna differentiating pinnules from the base of the first pinnule as it grows and it will become bi- and tripinnate pinna repeating the same process of pinnules-differentiation.

If we remove this plant to another place where the environment differs, the growth of this plant will be accelerated if the new environment is favorable for that plant and will be retarded if it is unfavorable. The life of plants and their environments are closely united as we see in the present distribution of plants and, if the environments change, the plants also will change their leaf form corresponding with the new environment. Because the leaf is extremely sensitive to the environment. If the growth of the frond of *Dryopteris lepigera* is accelerated by favorable conditions of the new environment, it will continue to grow beyond the quadripinnate frond. However, it may not continue to grow to develop the former quadripinnate if it is retarded by unfavorable conditions of the new environment. The frond of this plant is quadripinnate and this represents its most adaptive state in the

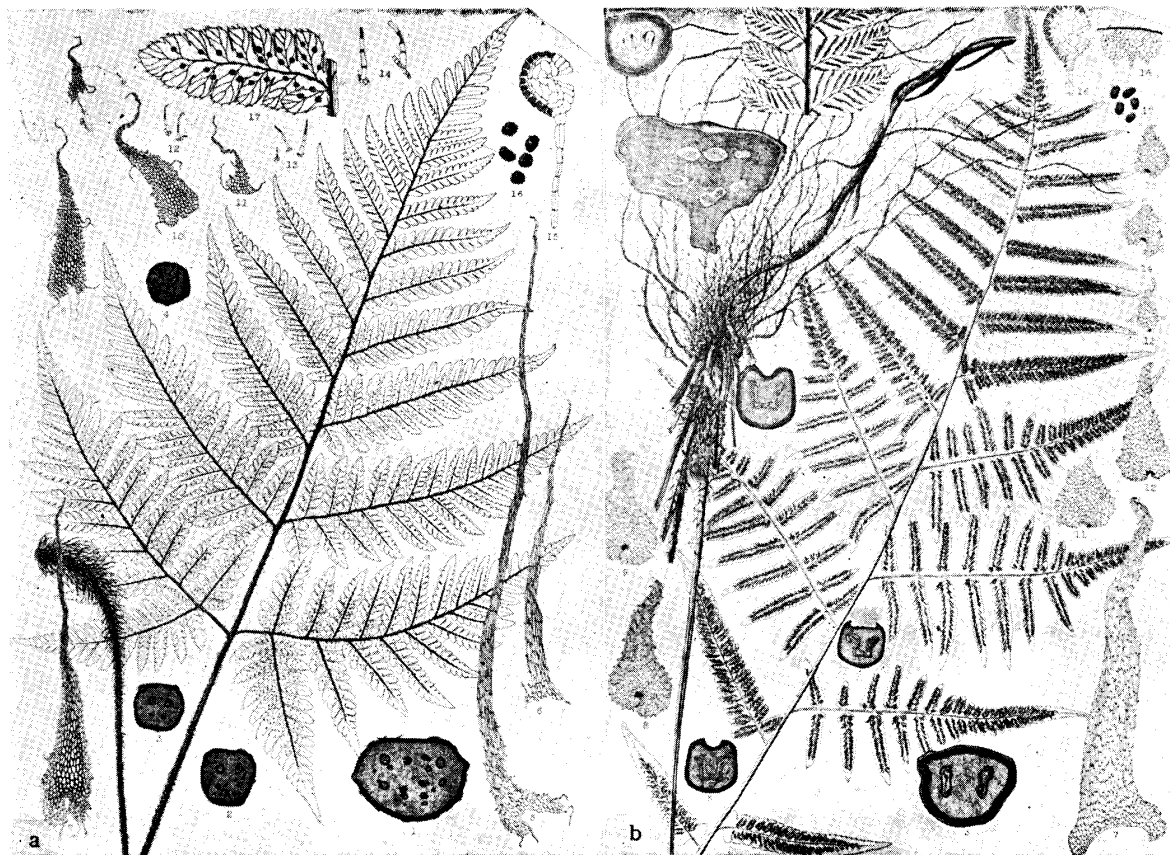


Fig. 1. Ontogeny of recent ferns.

a: *Dryopteris lepigera* O. Kuntze (from Ogata, 1936, pl. 312)

b: *Diplazium esculentum* Swartz (from Ogata, 1936, pl. 308)

present environment, but the plant has potential energy to change its leaf form in any direction within the limits of its living ability if the environment changes. The French botanist Bonnier (Bonnier, 1895; Ikeno, 1948, p. 41; Tokuda, 1957, p. 204) and the American botanist Clements (Clements, 1950; Tokuda, 1957, p. 205) show many examples where plants have changed to other forms corresponding with the new environments.

The frond of *Diplazium esculentum* Swartz (Fig. 1; Ogata, 1936, Vol. 6, pl. 308) is bipinnate and the plinnules are very long, corresponding with the unipinnate pinna of *Dryopteris lepigera* in form, but the cutting of the pinnules margin of the former species does not reach the rachis, so we must use the term pinnules for them. This frond is unipinnate in the upper part, bipinnate in the middle and unipinnate in the lower part. The pinnules of the upper and lower parts are larger than that of the middle part and a pinnule of the upper part will become a unipinnate pinna of the middle part as it grows. The pinnules of the unipinnate pinna of the middle part are attached to the rachis by the whole base of the pinnules in the upper and by the midrib in the lower. This means that the whole base-attachment will become the midrib-attachment as it grows.

## (2) Ontogeny of *Angiopteris lygodiifolia* Rosenst

This fern was removed by Dr. K. Soma of the Institute of Biology of the Tohoku

University from the Koshiki islands (31°40'N. Lat.; 129°50'E. Long.) in Kagoshima Prefecture to the hothouse of the Institute of Biology of the Tohoku University, Sendai (37°15'N. Lat.; 140°50'E. Long.), in November of 1958. At that time the frond was normal and bipinnate. The steaming of the hothouse begins in late November and closes in early April every year. The new fronds began to sprout since late June and the old fronds withered. The photographs shown in Pls. 26-28 were taken in the middle of September of 1959. Pl. 26 fig. 3 is a complete view of *Angiopteris lygodiiifolia* removed from the Koshiki islands and two old fronds are shown in the right and left hands and the others are new fronds which sprouted in Sendai since late June. Pl. 27, fig. 1 shows the old bipinnate frond with three pairs of pinnae and each pinna has 13-18 pairs of pinnules and each pinnules have many sporangium on their margin. The frond shown in Pl. 28, fig. 3 is the largest of the new fronds and is also shown in the center of Pl. 26, fig. 3. This frond is bipinnate and resembles the old one in the essential points but it is smaller, namely it has three pairs of pinnae and each pinna has about 11 pairs of pinnules without sporangium and the serration of the margin is larger. Some pinna have uncomplete pinnules at its base. Pl. 28, fig. 1 shows the unipinnate frond; it corresponds with the bipinnate one shown in Pl. 28, fig. 3, namely one pinnule of the former corresponds to one unipinnate pinna of the latter. Each pinnule is larger and longer than that of the latter and its outline is similar to the pinnule of unipinnate pinna, namely the exterior of the former shows the form of an enlarged pinnule of the latter. The writer uses the word "enlarged pinna" for such pinnule (Fig. 4-B). The fronds shown in Pl. 26, figs. 1, 2, 4; Pl. 27, figs. 2-4 and Pl. 28, figs. 2, 4, are types intermediate between the bipinnate frond in Pl. 28, fig. 3 and the unipinnate one in Pl. 28, fig. 1. In Pl. 26, fig. 1 the frond has three pairs of pinnae and two pinnae in the upper part of frond are unipinnate pinna and two pinnae in the middle part of frond are enlarged pinna and in the lower part the right one is the enlarged pinna, the left one the unipinnate pinna. In Pl. 26, figs. 2, 4 the uppermost pinnae are differentiated to pinnules in some part, namely these pinnae are the intermediate type between the unipinnate pinna and the enlarged pinna. Such pinna of the intermediate type are found in Pl. 26, fig. 4; Pl. 27, figs. 3-4.

The unipinnate pinnae of the old frond have many sporangium on the lower surface of the pinnules but the unipinnate pinnae of the new frond have almost no sporangium. On the contrary the enlarged pinnae have many sporangium. All of the new fronds are smaller than the old one in form of frond, unipinnate pinna, pinnules of unipinnate pinna and enlarged pinna. The cause of such variety of leaf form is due to the change of environment. The environment in Sendai differs from that of the Koshiki islands, especially in temperature. The mean temperature of June is 17.7°C in Sendai and 22.5°C in Kagoshima (70 km east of Koshiki islands). Thus, the environment in Sendai is not so suitable for this fern, because the new fronds are smaller than the old one and do not grow as in the Koshiki islands. This means that the development of fronds has retarded and therefore in Sendai it can not grow as in the Koshiki islands. Bipinnate frond in Koshiki islands corresponds with the unipinnate frond in Sendai. The pinna, which is differentiated to pinnules and produces a unipinnate pinna, remains as an enlarged pinna without

differentiating to pinnules in Sendai. But it has the potential energy to develop as in the Koshiki islands and it will develop unipinnate pinna if the environment in Sendai is favorable. As shown in the plates the frond of this fern grows not only to the state of enlarged pinna but to that of unipinnate pinna in Sendai too. Bipinnate frond in Pl. 28, fig. 3 is that of the younger stage, because it has no sporangium. The fronds in Pl. 26, figs. 1-2, 4; Pl. 27, figs. 2-4 and Pl. 28, fig. 4, which are the enlarged pinna without differentiating to pinnules, are of the mature stage, because they have sporangium. This means that they can not continue to grow the mature stage in the differentiated pinnules as in the Koshiki islands but they can attain maturity in the non-differentiated enlarged pinna as in Sendai. This is most important, because they cannot continue to live in Sendai if they cannot produce sporangium. Therefore the non-differentiated enlarged pinnae are the most adaptive form for this fern in Sendai. The difference of temperature in the Koshiki islands and Sendai has caused such variety of leaf form as mentioned above. It is no doubt that the frond in Sendai has not developed completely as in the Koshiki islands and this means that the growth of frond retarded by the lowering of the temperature. Pl. 28, fig. 2 shows the frond of a young stage and one pinna shows the enlarged pinna, three pinnae uni-pinnate pinna, namely the leaf form to be attained in the future has already been decided before the present stage. The leaf forms of frond are decided by the environment (temperature) in the earlier stage of ontogeny. The temperature and water are the most important factors for the growth of plants. The temperature in the earlier stage of ontogeny is the most essential factor for this fern.

New fronds begun to sprout in June when the temperature in Sendai is five degrees lower than in the Koshiki islands, therefore the lowering of temperature caused various kinds of leaf form not normal in the Koshiki islands. It is concluded that the growth of frond was retarded by the lowering of temperature and the enlarged pinna was derived from the unipinnate pinna by retardation. The change from the unipinnate pinna to the enlarged pinna is by the lowering temperature in the earlier stage of ontogeny and the change is rather abrupt. The pinna of intermediate type is found but few. This is important, because it is difficult to trace the change of leaf form from one type to another type without the pinna of the intermediate type in the case of fossil plants (Fig. 4-B). The enlarged pinna is similar to one pinnule of unipinnate pinna in form which corresponds with the enlarged pinna and it is larger than that pinnule but smaller than the unipinnate pinna.

From the above mentioned we can summarize as follows :

1. The variety of leaf form in Sendai is explained to be caused by retardation.
2. The main cause of retardation is the lowering temperature.
3. The leaf form changes completely to another form by retardation.
4. The environment in the earlier stage of ontogeny decides the leaf form in the future. The most important change occurs in the earlier stage of ontogeny.
5. The enlarged pinna corresponds with unipinnate pinna before change.
6. The enlarged pinna is smaller than the unipinnate pinna before change and larger than the pinnule of the latter.
7. The venation of the enlarged pinna is similar to that of pinnule of the unipinnate

pinna before change.

8. The pinna of the intermediate type between the enlarged pinna and the unipinnate pinna before change is few in number.

9. When the leaf form of frond does not change to an enlarged pinna bearing frond by retardation, the frond, which is retarded, is smaller than the former and the pinnules of one pinna are less than that of the former one in number and the serration of margin of pinnules is more larger than the former.

10. In any cases the surface areas of a frond are reduced by reatardation.

These change of leaf form mentioned above are the transformation observed in a year and if we return this plant to the Koshiki islands, the fronds will grow in normal aspect. But if this fern is retained in Sendai for a long time as we see in geological ages, it will change to another species or genus. These examples were examined by a French botanist Bonnier and American botanist Clements.

The change shown in *Angiopteris lygodiifolia* is the transformation in ontogeny of the fern brought about by the change of environment. The unsuitable condition environmental caused retardation of the frond. The environments of geological ages have changed many times, therefore it is expected that the change seen in the ontogeny of *Angiopteris lygodiifolia* will occur in the phylogeny of many kinds of fern-like fronds. The phylogeny seen in the so-called *Gigantopteris* is the best example.

Dr. Sohma has removed *Cyathea boninsimensis* Copel with *Angiopteris lygodiifolia* from the Koshiki islands to the hothouse of the Institute of Biology of the Tohoku University in November, 1958. The leaf form of *Angiopteris lygodiifolia* has largely changed, but the leaf form of *Cyathea boninsimensis* has not changed in the same hothouse. This depends entirely on the adaptive ability against the environment. Such examples as mentioned above are found in fossil plants in geological times and it is natural that when the environment changed, some plants will and others will not transform their leaf form to become adapted to the new environment. The adaptative ability is limited and will not continue without change in leaf form for a long time geologically. The adaptability to the new environments saves the plant from extinction and those able to change their leaf form for such reasons will continue to persist. This is well shown in the evolution of leaf form. Examples of the enlarged pinna or leaf: *Taeniopteris*, *Gangamopteris*, *Protoblechnum* and etc.

### (3) Ontogeny and phylogeny of the so-called *Gigantopteris*

In the previous paper the writer wrote on the evolution of the so-called *Gigantopteris* (Asama, 1959). There are many series in the so-called *Gigantopteris* and the *Emplectopteris* series is the best example as the same directional evolution (Orthogenesis). In the *Emplectopteris* series they transformed from *Emplectopteris triangularis* to *Gigantonoclea Lagrelii*, from *G. Lagrelii* to *Bicoemplectopteris Hallei* and from *B. Hallei* to *Tricoemplectopteris taiyuanensis*. The pinnae of the upper part of penultimate pinna of *Emplectopteris triangularis* are not differentiated to pinnules but that of the lower part are differentiated to pinnules, namely the pinnae are dissected to pinnules from the base of pinna as it grows



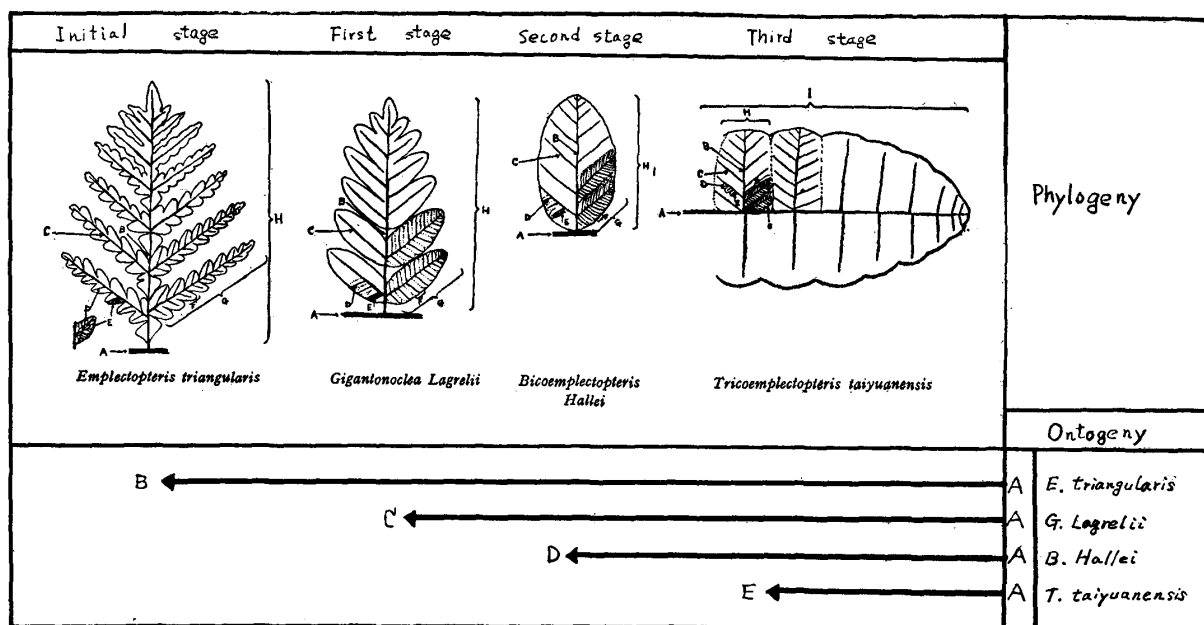


Fig. 2. Ontogeny and phylogeny of the *Emplectopteris* Series.

(Figs. 2 and 5-C). The pinnae of the upper part of *Gigantonoclea Lagrelii* are not differentiated into pinnae and cohering each other but that of the lower part are separated into pinnae, namely the frond of this plant grows separating each pinnae from the base. The pinna of *G. Lagrelii* corresponds with the unipinnate ultimate pinna of *E. triangularis* and it is produced by the non-differentiation of the pinna of the latter, namely the leaf form of the young *E. triangularis* had become the leaf form of the mature *G. Lagrelii* (Figs. 2 and 5-D). The pinnae of *B. Hallei* are uniting with each other in the upper part but they are separated to each pinnae in the lower part and therefore the united pinnae are dissected to each pinnae from the base as they grow. The ultimate pinna of *B. Hallei* corresponds with the penultimate pinna of *G. Lagrelii* and it is produced by the non-differentiation of the penultimate pinna of the latter. The leaf form of young *G. Lagrelii* had changed to the leaf form of the mature *B. Hallei* (Figs. 2 and 5-E). The frond of *T. taiyuanensis* is simple (Figs. 2 and 5-F). If the development of simple frond of *T. taiyuanensis* is accelerated, it will grow to a simple pinnate frond by separating each pinna from the base of simple frond and this is the frond of *B. Hallei*. If the development of unipinnate frond of *B. Hallei* is accelerated, it will grow to bipinnate frond by separating the pinnules from the base of pinna and this is the frond of *G. Lagrelii*. In this way *G. Lagrelii* will change to *E. triangularis* by acceleration. On the contrary, if the development of pinna of *E. triangularis* is retarded, it will grow to *G. Lagrelii* by cohering the pinnules, from *G. Lagrelii* to *B. Hallei* and from *B. Hallei* to *T. taiyuanensis*. Namely by successive retardation of development of the frond, *E. triangularis* changes to *G. Lagrelii*, *B. Hallei* and *T. taiyuanensis* successively. Geologically *E. triangularis* is found in the lower part of the Lower Shihhotse Series, *G. Lagrelii* in the upper part of the Lower Shihhotse Series and *B. Hallei* in the lower part of the Upper Shihhotse Series. Therefore the change of leaf form of these plants to another is not by acceleration but by

retardation. As already mentioned the leaf form of *Angiopteris lygodiifolia* has largely changed its leaf form by retardation and its unipinnate pinna changed to an enlarged pinna resembling the pinnule of the former. *E. triangularis* changed to *G. Lagrelii* by retardation and the unipinnate pinna of the former changed to the coherent pinna (Fig. 4-A) shown by the united pinnules of pinna of the former. These relations are shown in Figs. 2 and 5, C-D-E-F. Ontogeny of *E. triangularis*, *G. Lagrelii*, *B. Hallei* and *T. taiyuanensis* are shown by the lines of A-B, A-C, A-D and A-E respectively (Fig. 2). Ontogeny of *G. Lagrelii* ends one stage before the ontogeny of *E. triangularis* and that of *B. Hallei* one stage before that of *G. Lagrelii* and also that of *T. taiyuanensis* one stage before that of *B. Hallei*. We can call these changes neoteny (Tokuda, 1957, p. 131). The main cause of these neoteny or successive transformation shown in the *Emplectopteris* series was the dry climate and the development of these plants had been retarded by successive dry climate. The leaf form of these plants had changed abruptly to that of the next stage without having the leaf form of the type intermediate between the coherent pinna and the unipinnate pinna (Fig. 4-A). The facts mentioned above are summarized as follows:

1. The transformation of the leaf form in the *Emplectopteris* series can be explained to be the effect of retardation.
2. The main cause of the retardation is the successive dry climate.
3. The successive change of leaf form is by successive retardation and the effect can be explained by the theory of neoteny. Namely the cause is retardation and the effect is neoteny.
4. The leaf form of these plants had changed to the form of the next stage without producing the leaf form of a type intermediate between the coherent pinna and the unipinnate pinna.
5. The coherent pinna corresponds with the unipinnate pinna before change.
6. The coherent pinna is smaller than the unipinnate pinna before change and larger than the pinnule of the latter.
7. The venation of the coherent pinna is similar to that of the unipinnate pinna before change.
8. The surface areas of a frond are reduced by retardation.

Examples of the coherent pinna or leaf: so-called *Gigantopteris*, broad leaf of Dicotyledon, simple frond of fern and etc.

#### (4) Ontogeny of *Callipteridium pteridium* Franke

This plant (Franke, 1912, p. 108, figs. 1-2) has one or more intermediate pinnules on the rachis between two adjacent pinnae and this is the most characteristic in the Genus *Callipteridium*. The venation of *Callipteridium* resembles that of *Alethopteris* but differs in having intermediate pinnule (Fig. 4-G). The intermediate pinnule is characteristic in *Callipteridium* but are not always found on the rachis between the two adjacent pinnae. For example in *C. pteridium* the rachis of the upper part of the frond has the intermediate pinnule but not the rachis of the lower part. In any *Callipteridium* there are intermediate pinnules on the rachis between the two adjacent pinnae in the upper part of frond and less in number in the middle part and not always found in the lower part. Genus *Alethopteris*

has no intermediate pinnule as a rule but they sometimes have intermediate pinnule or decurrent wing on the rachis between the adjacent two pinnae in the most upper part of frond. This means that the pinnae of the lower part of frond have developed completely but that of the upper part of frond have not completed their development yet and if the upper part continue to grow the intermediate pinnule will ascend along the rachis and merge into the pinna-rachis. But the environment and leaf form or structure of frond indicate that they cannot continue to develop farther and the intermediate pinnules remain on the rachis. Therefore the intermediate pinnules are not the fixed one but the moving one and they depend entirely on the plant environments. If the development of *Alethopteris* is accelerated they will change their leaf form to that of *Neuropteris* and if that of *Alethopteris* is retarded they will change their leaf form to that of *Callipteridium*.

These facts are summarized as follows :

1. The intermediate pinnules are produced by retardation from fronds without them.
2. The intermediate pinnules are better shown in the upper part of frond than in the lower part.

Examples of the intermediate pinnules : *Callipteridium*, *Konnoa*, *Callipteris*, *Emplectopteris*, *Emplectopteridium*, *Linopteris* and etc.

(5) Ontogeny of *Protoblechnum Wongii* Halle

Reported from the Upper Shihhotse Series of Shansi by Halle (1927, p. 131, pls. 35-36), this plant has the frond unipinnate and pinnae very long and large and attached by a broad base, except in the lowermost part of the frond decurrent on the rachis, sometimes almost to the next lower pinna. Decurrent wings (Fig. 4-H) broad, in the upper part of the frond flat and often broader than the rachis, in the lower part curving up on the upper side of the rachis in an auriculate manner, becoming gradually more indistinct towards the base and entirely lacking in the lowermost part.

As described the decurrent wings are better developed in the upper part of the frond than in the lower part. Like *Callipteridium* this means that the decurrent wings entirely depend on their living environment and if this plant continues to grow the decurrent wings will merge into the pinna-rachis. But in their environment and with the present structure of frond they cannot continue their development. Therefore the decurrent wings are produced by retardation.

What is the significance of the long pinna of this plant? Such long pinnae as seen in *P. Wongii* have never been found in the lower Shihhotse Series, therefore they must have been derived from a frond having short pinnules. In the previous paragraph was described the transformation of the leaf form of *Angiopteris lygodiiifolia* using the word "enlarged pinna". The long pinnae of this plant are the enlarged pinna derived from *Alethopteris Norinii* Halle by retardation. The decurrent wings are produced by retardation, and it is considered that the long pinnae of *P. Wongii* are produced by retardation from other pinnae. If the long pinnae thus produced, the former pinnae must have been larger than the one of *P. Wongii* and each pinnules resemble the long pinna of the latter and are smaller. Such pinnules are those of *Alethopteris Norinii*, which is found in beds 10 and 16 of

the Lower Shihhotse Series and *Protoblechnum Wongii* is found in beds 18, 21 and 25 of the Upper Shihhotse Series. This means that the latter was derived from the former by retardation.

The facts mentioned above are summarized as follows :

1. The decurrent wings are produced by retardation from the frond without them.
2. The long pinnae are derived from the pinnate one by retardation.

Examples of the decurrent wings and long pinnules: *Protoblechnum*, *Danaeopsis*, *Glenopteris*, *Megalopteris*, *Supaia*, *Brongniartites*, *Thinfieldia* and etc.

#### (6) Ontogeny of *Neuropteris* and *Alethopteris*

The pinnules of *Neuropteris* (Gothan and Remy, 1957, p. 128, fig. 122) have contracted base and therefore attach to the rachis with the midrib and the veins extend only from the midrib. The pinnules of *Alethopteris* (Gothan and Remy, 1957, p. 119, fig. 111) attach to the rachis with their whole base of pinnules and the veins extend from the midrib and directly from the rachis. But these relations are not the fixed one but the living one. Namely these facts entirely depend on the environments where plants live and if the environments change, the relation will change. In the pinna of the upper part of frond the pinnules of *Alethopteris* attach to the rachis with the whole base and also in the middle part but in the lowest part sometimes the pinnules attach to the rachis with midrib only and their bases are contracted. In the pinna of the lower part of the frond of *Neuropteris* the pinnules are always attached to the rachis with midrib and their bases are contracted but in the upper part they are always attaching to the rachis with the whole base and the veins extend directly from the rachis. Namely if the development of pinnules of *Alethopteris* are accelerated, the leaf form will change to that of *Neuropteris* and if the development of pinnules of *Neuropteris* are retarded, the leaf form will change to that of *Alethopteris*.

The facts mentioned above are summarized as follows :

1. The midrib-attachment of pinnules change to the whole base-attachment by retardation.
2. The veins extending from the rachis are due to retardation from the pinnules which have them extending directly from the midrib only.

Examples of the whole base-attachment and the axial veins: *Alethopteris*, *Callipteris*, *Callipteridium*, *Konnoa*, *Neuropteridium* and etc.

#### (7) Ontogeny of *Zeilleropteris yunnanensis* Koidzumi

This plant was reported by Zeiller (1907, p. 13, pl. 14, fig. 15) from Yunnan as *Gigantopteris nicotianaefolia* and later named *Zeilleropteris yunnanensis* by Koidzumi. This is one of the so-called *Gigantopteris* and a coherent leaf plant. It shows the second stage of leaf cohesion and the pinnules of the initial stage are *Pecopteris*-type in which the veins are not given off directly from the rachis. The veins of pinnules of *Pecopteris*-type are not anastomosed, but those of *Z. yunnanensis* (Fig. 4-K), and such venation was derived by the cohesion of pinnules from the non-anastomosed veins of the initial *Pecopteris*-type pinnules. The cohesion of pinnules was conducted by retardation. The anastomosed veins are produced when the pinnules of pinnae become coherent with each other by retarda-

tion to make coherent pinna, but are not produced when the pinnae change to the enlarged pinna by retardation.

The facts mentioned above are summarized as follows :

1. The anastomosed veins are produced in the coherent pinna by retardation.
2. The enlarged pinna do not make anastomosed veins.

Examples of the anastomosed veins : *Zeilleropteris yunnanensis*, *Linopteris*, *Lonchopteris*, *Emplectopteris*, *Emplectopteridium*, *Palaeoweichselia* and etc.

## 2) Parallel vein plants

### (8) Ontogeny of *Trachycarpus* and *Phoenix*

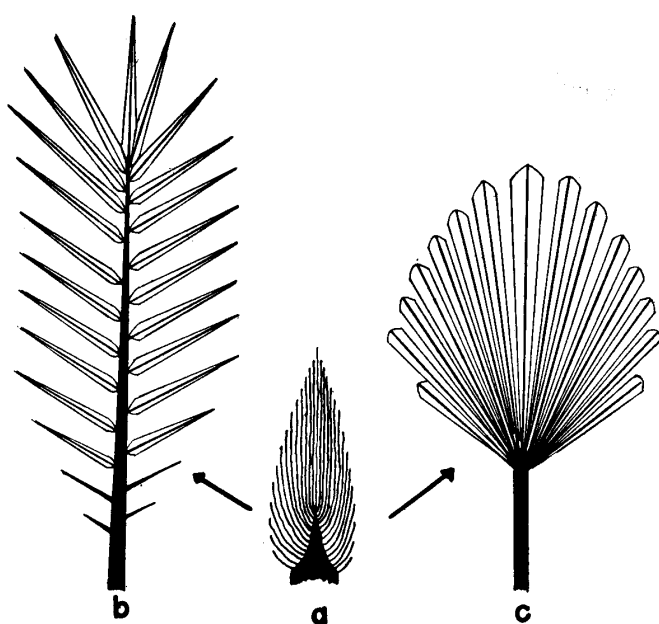


Fig. 3. Ontogeny of *Phoenix* and *Trachycarpus*.

- a: Young stage of both genera  
 b: Mature stage of *Phoenix*  
 c: Mature stage of *Trachycarpus*

In the first stage of development of these plants the leaf forms are similar and the polyfolded leaf in which each segments are united in a leaf attaches to the axis (Fig. 3-a). In *Phoenix* the development of leaf and axis comes simultaneously into operation and each segments are separated as it grows, therefore its leaf form is unipinnate (Fig. 3-b). In *Trachycarpus* the development of leaf and axis is not simultaneously in operation and the leaf segments continues to grow but not the axis, therefore its leaf form shows palmate arrangement separating each segments as it grows (Fig. 3-c). Whether the leaf forms of plants show the pinnate or the palmate arrangement depends entirely on the development of the axis. If the axis continues to grow the leaf form will become pinnate and if the axis stops to grow the leaf form will show palmate arrangement. It is possible to postulate whether the development of axis is retarded by comparison with leaf segments or whether it stopped, if the environment changes to another not suitable for the development of their leaves (Ikeno, p. 40, fig. 15). The facts mentioned above are summarized as follows :

1. Axis changes the rate of development by retardation.

2. Palmate arrangement is derived from a pinnate one by retardation.

Examples of the retarded axis: *Trachycarpus*, *Sabalites*, *Goenomites*, *Clathropteris*, *Dictyophyllum*, *Camptopteris*, *Thaumatopteris*, *Hausmannia* and etc.

(9) Ontogeny and phylogeny of *Calamites*, *Lobatannularia*, *Schizoneura* and *Neocalamites* (Figs. 4-A, d, e, f and 4-B, d, e)

*Lobatannularia sinensis*, *L. lingulata* and *L. heianensis* are described from Shansi by Halle (1927), and Kon'no and Asama (1950, p. 18) who made clear that the leaf whorls of these plants have some trend in extending from the axis, namely the cohesion of leaf segments increased with ages. In *L. sinensis* (Fig. 4-A, d) the leaf segments are separated but those of *L. heianensis* (Fig. 4-A, f) are completely united separating into two lobes. *L. sinensis*, *L. lingulata* (Fig. 4-A, e) and *L. heianensis* are found in the Lower Shihhotse, lower part of Upper Shihhotse and upper part of Upper Shihhotse Series respectively. Therefore it is possible to postulate that these plants had changed from *L. sinensis* to *L. lingulata*, from *L. lingulata* to *L. heianensis* increasing the cohesion of their leaf segments with ages.

In *Schizoneura* the leaf segments are completely united separating into two lobes but in the lowest part of axis they are separated in each leaf segments and this means that they were derived by retardation from the plant which has separating leaf segments.

In *Calamites* (Fig. 4-B, d) the axis branches twice or more from the main axis and in *Neocalamites* (Fig. 4-B, e) branches once. The leaf whorls of *Calamites* are called *Annularia* and *Lobatannularia* and the latter is characteristic in the Gigantopteris flora. The whorls and the branching of the latter are anisophyllous and this is caused by retardation. When *Calamites* changed to *Lobatannularia*, they reduced half of their branching and therefore their branchings are anisophyllous. When *Calamites* changed to *Neocalamites*, they reduced the one stage of their branching and therefore *Calamites* branches twice or more from the main axis but *Neocalamites* only once. This is similar with the facts in which the coherent leaf plants reduced their branching by the cohesion of pinnules or pinnae step by step. The leaf areas of frond reduced step by step by the cohesion but the areas of each segments increased step by step by the cohesion and they changed to simple frond or leaf at last. In *Calamites*, *Lobatannularia* and *Neocalamites* the leaf segments have become larger, reducing their branching step by step.

The facts mentioned above are summarized as follows :

1. The united leaf is produced from the separated leaf segments by retardation.
2. The branching of axis from the main axis was reduced by retardation step by step but the leaf segments were increased in their length as they reduce their branching. Examples of the cohesion of leaf segments of parallel vein plants and the reduced branching: *Lobatannularia*, *Schizoneura*, *Neocalamites* and etc.

### 3. PRINCIPLES OF RETARDATION

As mentioned the leaf forms are transformed by retardation in many ways. By retardation in the leaves not only retarded their development but also changed their leaf forms, namely the new ontogeny, which differs already in the very young stage from that of the former plants, occurs. The retardation, which acted to the plants in the very

young stage, controls largely the future leaf forms of that plants.

Here the many principles seen in the cases of retardation are mentioned, because there are no examples explained by acceleration in geological ages about the evolution of the leaf forms. It is natural that in the cases of acceleration the opposite phenomenon will occur. The leaf forms of plants will become simpler by retardation and more complex by acceleration. The leaf areas of one leaf will become larger by acceleration and smaller by retardation but the area of the segments of one leaf will become larger by retardation and be a simple frond or leaf at last. Three fundamental principles of retardation and acceleration are as follows :

#### **Fundamental principles of retardation and acceleration**

- 1. The area of one leaf will be reduced by retardation and increased by acceleration.**
- 2. The leaf forms derived by retardation resemble that of the youngest stage before change and that derived by acceleration resemble that of the oldest stage before change.**
- 3. Leaf segments are united by retardation and differentiated by acceleration, therefore each segments of the later stage will become larger than that of the former stage by retardation and will become smaller by acceleration.**

#### **Principles of retardation**

##### **Principle A. Coherent pinna or leaf (Fig. 4-A)**

The coherent pinna or leaf is produced from the pinnate pinna by retardation (chap. 2-3).

##### **Principle B. Enlarged pinna or leaf (Fig. 4-B)**

The enlarged pinna or leaf is produced from the pinnate pinna by retardation (see chap. 2-2).

##### **Principle C. Branching reduction (Fig. 4-C)**

The branching is reduced by retardation (chap. 2-2, 3, 9).

##### **Principle D. Palmate arrangement (Fig. 4-D)**

The palmate arrangement is produced from the pinnate one by retardation of axis (chap. 2-8).

##### **Principle E. Smaller form (Fig. 4-E)**

The leaf becomes smaller in form by retardation (chap. 2-2, 3).

##### **Principle F. Serration deepening (Fig. 4-F)**

The serration of the leaf becomes deeper by retardation (chap. 2-2).

##### **Principle G. Intermediate pinnule (Fig. 4-G)**

The intermediate pinnule is produced by retardation (chap. 2-4).

##### **Principle H. Decurrent wing (Fig. 4-H)**

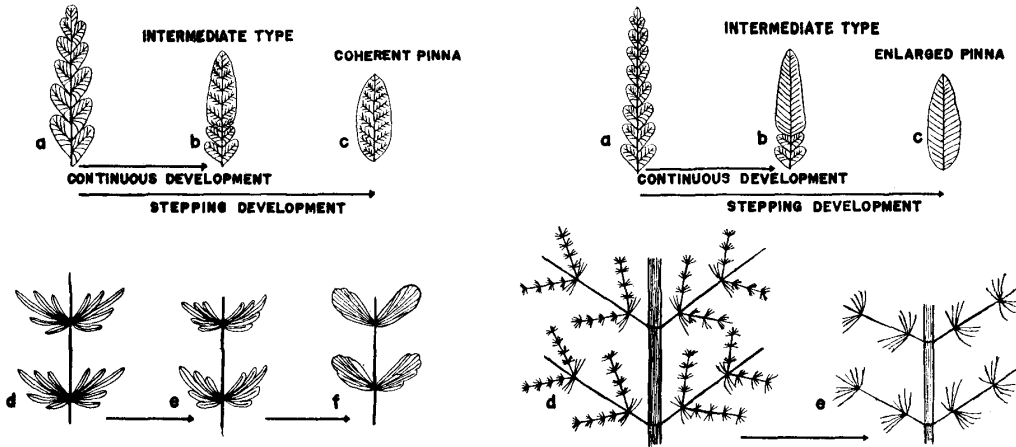
The decurrent wing is produced by retardation (chap. 2-5).

##### **Principle I. Whole base attached (Fig. 4-I)**

The midrib attachment becomes the whole base attachment by retardation (see chap. 2-6).

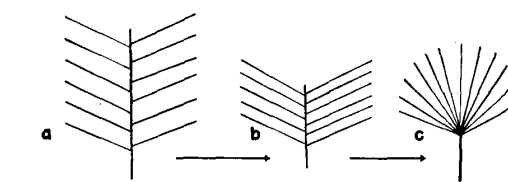
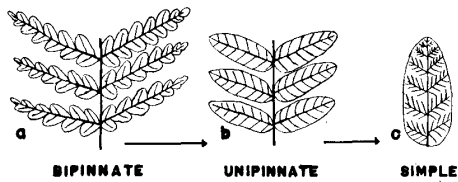
# PRINCIPLES OF RETARDATION

PRINCIPLE A. COHERENT PINNA OR LEAF    PRINCIPLE B. ENLARGED PINNA OR LEAF



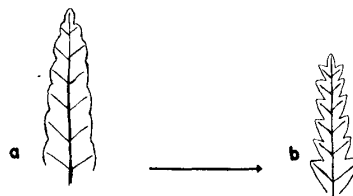
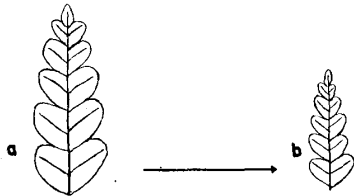
PRINCIPLE C. BRANCHING REDUCTION

PRINCIPLE D. PALMATE ARRANGEMENT



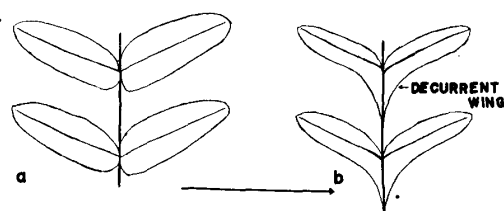
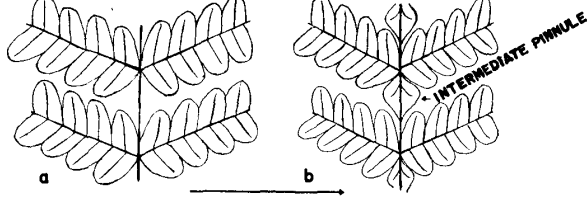
PRINCIPLE E. SMALLER FORM

PRINCIPLE F. SERRATION DEEPENING



PRINCIPLE G. INTERMEDIATE PINNULE

PRINCIPLE H. DECURRENT WING



PRINCIPLE I. WHOLE BASE ATTACHED

PRINCIPLE J. AXIAL VEINS

PRINCIPLE K. ANASTOMOSED VEINS

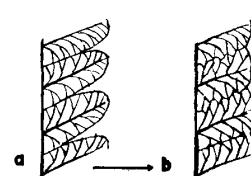
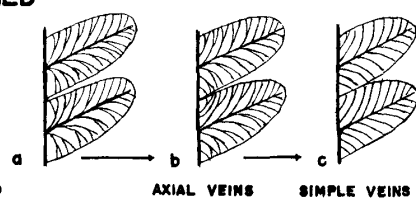
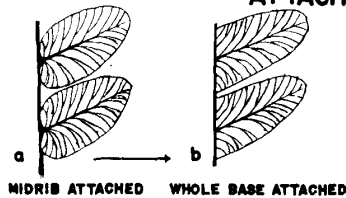


Fig. 4. Principles of retardation



**Principle J. Axial veins (Fig. 4-J)**

The axial veins are produced by retardation (chap. 2-6).

**Principle K. Anastomosed veins (Fig. 4-K)**

The anastomosed veins are produced by the cohesion of pinnules (chap. 2-7).

#### 4. SUCCESSIVE TRANSFORMATION OF THE LEAF FORMS THROUGH THE AGES

The majority of fossil plants found in geological ages are the leaf impression which have not been regarded important for classification or phylogeny. The leaf forms of Paleozoic plants are entirely different from those of the Mesozoic and the latter from that of the Cenozoic. However, the relation between them have not been explained clearly to date. The writer tried to explain the phylogenetic relation between them by using the principles of retardation. The leaf forms of the Mesozoic plants were derived from those of the Paleozoic and therefore the ancestor of the former should be found in the latter. The environments of the plants had changed through ages. If the environments change from age to age, the plants must also change their leaf forms to adapt to the new environments. Therefore the leaf forms of the Mesozoic plants differ from that of the Paleozoic. But the leaf forms do not change without reason and not irregularly. If the new environments are suitable the development of leaf will be accelerated, but otherwise they will be retarded. The leaf forms which will be change to another by acceleration or retardation are systematic and not with random direction. Therefore if we know the principles of accelertaion or retardation, we can restore the changed leaf forms to that before change. Using the principles of retardation the writer found the phylogenetic relation between the Paleozoic, Mesozoic and Cenozoic plants.

At first we must remember that the large pinnae or leaves are all derived from the pinnate one by cohesion and not derived from small forms by acceleration (Fundamental principle 3. Fig. 5). The leaf forms are differentiated by acceleration and they will become smaller in one segment but that are united by retardation and therefore become larger in one segment. The simple frond or leaf is a coherent leaf which is united by retardation and derived from the pinnate one. The leaf segments becoming larger from age to age are coherent pinna or enlarged pinna derived by retardation and this can be known from the following facts, namely their branching becomes reduced from age to age.

##### 1) Paleozoic plants

The most primitive land plants are found in the Silurian and Devonian and are few comparing with the Carboniferous plants. In the middle Devonian, *Protopteridium* and *Aneurophyton* are found, these are the most primitive ancestors of Pteridosperms or ferns. They have no true leaf and have only linear branches in the upper part of axis and pinnule-like ones are unknown. These linear branches are characteristic in all primitive plants and are found in *Protopteridium*, *Aneurophyton*, *Asteroxylon*, *Protolepidodendron*, *Calamophyton*, *Hyenia*, *Psilophyton*, *Rhynia* and *Cladoxylon*. These plants are the ancestors of the land plants which are found since the Carboniferous.

In the upper Devonian we find *Archaeopteris*, which has intermediate pinnule different from those of Permian and upper Carboniferous in origin. *Rhacopteris* is also a lower Carboniferous plant. These plants have radiate venation and it is possible to postulate that they were derived from plants having radiate branches as *Cladoxylon* in the middle Devonian by retardation (Principle B).

In the lower Carboniferous we find *Archaeopteris*, *Adiantites*, *Sphenopteris*, *Sphenopteridium*, *Rhodea*, *Cardiopteris* and etc. These plants have the true leaf instead of the linear branches of the Devonian primitive plants and this is explained by the principle A, namely each pinnules are derived from the linear branches by cohesion and to cohere they must make the stepping development, reducing their branching by retardation. This is the only way to make areal pinnules from non-areal linear branches.

In the upper Carboniferous such plants as *Pecopteris*, *Alethopteris*, *Lonchopteris*, *Odontopteris*, *Linopteris*, *Mariopteris* are found and *Sphenopteridium* and *Cardiopteris* have disappeared. The axial veins which is not seen in the lower Carboniferous plants are found in *Alethopteris* and the anastomosed veins in *Linopteris* and *Lonchopteris*. These veins were derived by retardation (Principles I and K).

In the Stephanian (late Carboniferous) the ferns and Pteridosperms become abundant: *Callipteridium*, *Pecopteris*, *Taeniopteris* and *Odontopteris*. In Gondwana land *Gondwanidium*, *Glossopteris*, *Gangamopteris* are found. It is clear that *Callipteridium* was derived by retardation from *Alethopteris*-like frond (Principle G). *Taeniopteris* and *Odontopteris* are the enlarged pinnae (Principle B). *Glossopteris* and *Gangamopteris* which are found in the *Glossopteris* flora are undoubtedly the enlarged pinnae derived from the pinnate frond by retardation (Principle B). From the climate of Gondwana land it is considered that these enlarged leaves were produced by cool temperature. These plants are simple leaf and in the last stage of the enlarged pinna, this depends entirely on the environments of Gondwanaland at that age. In Euamerican land there are no simple leaf plants, which represent the last stage of cohesion, and this means that the climate during the Stephanian was not so cool as Gondwanaland. In Euamerican land and Cathaysian land the dry climate was the more important factor for plants than the cool climate. This is well shown in the Permian.

*Callipteris* is the characteristic Permian plant and it was derived by retardation (Principle G). *Callipteris* have many kinds of plants and are comparable to the so-called *Gigantopteris*. The leaf form, which has intermediate pinnules resembles each other but their ancestors are different from each other, was derived from different ancestors by retardation. *Neuropteridium* is the characteristic Permian plants and is also found in the Triassic. This was derived from *Neuropteris*-like plants by retardation in making the stepping development (Principle B). The enlarged pinna of this plants in Cathaysia land show sometimes the pinna of the intermediate type. We can understand that *Neuropteridium* was derived by retardation from the plants of the *Neuropteris*-type which show bipinnate or more, because the former shows the simple pinnate. *Protoblechnum* and *Supaia* were derived by retardation from the plants of *Alethopteris*-type (Principles B and H). In Cathaysia land the so-called *Gigantopteris* all show the coherent pinnae

and were undoubtedly derived by retardation from the pinnate plants, as mentioned in the previous paper (Asama, 1959). The fronds of *Gigantopteris nicotianaefolia* and *Tricoem-plectopteris taiyuanensis* show the simple leaf which is the last stage of cohesion.

*Lobatannularia* is derived by retardation as already mentioned. *Schizoneura* from the Gondwana land and Cathaysia land is an articulate plant derived from that of Calamaria-type by retardation. In this way the plants of the Calamaria-type had changed their leaf forms by retardation as in that of the branched vein plants. *Lobatannularia* and *Schizoneura* have coherent leaf and that of *Phyllothea* which is found in Gondwana land and Angara land shows the semicoherent leaf, therefore *Phyllothea* is derived from the Calamaria-type by retardation (Principle A).

*Glossopteris* and *Gangamopteris* from Angara (Zalessky, 1918, 1927) land resemble that of Gondwana land in their leaf forms but they were derived from different plants by retardation. The pinnate fronds of many kinds of plants change to simple leaves by retardation, therefore they resemble each other in their leaf forms. This is the most important factor for the phylogenetical classification of fossil plants and we must always remember that the leaf forms of the branched vein or parallel vein plants change to simple forms or simple leaf by retardation. Such misleading as mentioned above have been made in many cases, as in the so-called *Gigantopteris* of other authors, *Glossopteris*, *Gangamopteris*, *Callipteris*, *Brongniartites* and etc.

The transformation of leaf forms from Devonian to Permian is by retardation and there is no examples by acceleration. The branches of the primitive Devonian plants changed to pinnules by retardation of the first stage and to larger pinnules by the second stage and finally to simple leaf by successive retardation, namely the simple leaf is made by retardation from the pinnate one and the veins of simple leaf correspond to the branches of the initial primitive Devonian plants.

As mentioned above the leaf forms of Paleozoic plants had changed by retardation and the important transformations are found in Devonian and Permian times. The universal dry climate is well known in the Devonian and Permian. Thus the Paleozoic leaf forms were affected by these dry climate, but in Gondwanaland the cool climate was the main factor for retardation.

## 2) Mesozoic plants

Although the Mesozoic plants were derived from the Paleozoic plants, their leaf forms may be different. To restore the leaf forms of Mesozoic plants which changed their form by retardation or acceleration we must trace the phylogenetic relation between them.

The fossil Dipteridaceae characteristic in the Rhaetic, have large palmate fronds. They are classified by Hirmer (1927, p. 642) into two subfamilies, Dipterideae and Camptopterideae, which are distinguished by the branching of the frond. It is well known that the dry climate prevailed universally in the Permo-Triassic and therefore to trace the relation between the leaf forms of the Paleozoic and Mesozoic the principles of the retardation must be considered.

As mentioned in chapter 2 the palmate arrangement is produced from the pinnate pinnae by retardation (Principle D). Namely if the development of the axis is retarded

or stopped, the pinnate frond will change to a palmate frond. The plants which have pinnate frond and anastomosed veins were commonly found in the Paleozoic. The palmate arrangement shown in Dipteridaceae is also explained in such a way (Principle D).

The pinnae of *Danaeopsis* and *Thinnfeldia* are enlarged pinna and these correspond with that of *Protoblechnum*, *Supaia* and *Brongniartites* of the Paleozoic in their forms.

The leaves of Bennettitales are characteristic in the Mesozoic and they have parallel veins. The transformation of leaf forms of this plants will be described in another paper with the leaves of Monocotyledon.

*Neocalamites*, characteristic in the Rhaetic, was derived from the parallel vein plants as Calamaria-type by retardation (Principle B). The leaf segments of a whorl of *Neocalamites* (Fig. 4-B, e) are longer than those of *Annularia* (Fig. 4-B, d). That of *Neocalamites* has the leaf segments on the lateral stem of the first stage but that of *Annularia* on that of the second stage, therefore the leaf segments of the former is longer than that of the latter. The lateral stem branches from the main axis twice or more in Calamaria-type of Paleozoic but once in *Neocalamites*.

There are many fern-like *Pecopteris* in the Paleozoic but in the Mesozoic it is replaced with *Cladophlebis*. The leaf forms of *Cladophlebis* were derived from the Paleozoic *Pecopteris* by retardation and this is well shown in the Rhaetic *Cladophlebis raciborskii* and *C. haiburnensis*. The leaf forms of these plants are larger than the Paleozoic *Pecopteris* and this means that the former was derived from the latter by retardation (Principle A). These *Cladophlebis* with large pinnules had changed to those with small pinnules through the Mesozoic (Principle E).

In the lower Cretaceous of western Greenland (Disko Island) there occurred what is believed to be the earliest known Angiosperm flora with *Lacopteris*, *Hausmannia*, *Cladophlebis* and *Ginkgoites*. The Angiospermous genera were chiefly *Platanus*, *Artocarpus*, *Liriodendron*, *Magnolia*, *Cinnamomum*, *Menispermites* and *Dalbergia*. In the middle Cretaceous the many of the recent families developed. Angiospermous plants are the most important in the Cenozoic.

As mentioned the leaf forms of the Mesozoic plants were derived from the Paleozoic plants by retardation.

### 3) Cenozoic plants

Angiosperms are the characteristic Cenozoic plants and they have two kinds of venation, one is the anastomosed veins and the other the parallel veins, namely Dicotyledon and Monocotyledon.

#### (1) Broad leaf of Dicotyledon and its origin

In a previous paper the writer described the so-called *Gigantopteris* (Asama, 1959) of Cathaysia land and showed that the coherent leaves were all derived from the pinnate one by cohesion. If these plants were found in the Mesozoic, the so-called *Gigantopteris* would be considered the ancestors of the recent Angiosperms, because they have seeds on the leaves and resemble the broad leaves of Angiosperm in their leaf forms. There are many coherent leaves in the Paleozoic as shown in *Glossopteris*, *Gangamopteris*, *Taeniopteris* and they are all derived from the pinnate one by retardation, namely they show the last

stage of cohesion.

Many authors believe that the Triassic *Furcula* of Greenland is the ancestor of Angiosperms and this plant resembles the broad leaves of Dicotyledon in their leaf form and venation. This plant is the coherent leaf plant and shows the uncoherent leaf stage. But this plant is not found in the succeeding Jurassic and lower Cretaceous. It may be one ancestor of some genus of Angiosperms but does not represent that of all Angiosperms. If we seek the primitive broad leaf like plants as the ancestors of Angiosperms, we shall not be able to find them, because the leaf forms of the Mesozoic plants had been changed to other forms by acceleration or retardation depending on their environments. If the Mesozoic plants had been changed by acceleration, when they passed from Mesozoic to Cenozoic, the leaf forms of them will be differentiated and the frond will become larger and also pinnae larger dissecting pinnules from the base. If they had been changed by retardation, the leaf forms will be cohered and the frond will become smaller and also pinnae smaller cohering pinnules (Fig. 2). The leaf forms changed by acceleration are excessively not different from the forms before change, because they become of larger form or differentiate to the same form. The leaf forms changed by retardation are excessively different from that before change, because they make the coherent leaf or the enlarged leaf.

The coherent leaf or enlarged leaf as shown in the broad leaf of Angiosperms is produced only by retardation and not by acceleration (Fig. 5). The majority of the broad leaves of Angiosperms are the coherent leaves or enlarged leaves, therefore they have been produced by retardation and their ancestors must have had pinnate leaves. The conclusion is that the ancestors of Angiosperms (Dicotyledon) must have been the pinnate plants of Paleozoic or Mesozoic Pteridosperms. Axelrod (1952, p. 27) pointed that the ancestors of Angiosperms had lived on the upland regions remote from lowland sites of deposition. If so, the so-called *Gigantopteris* or the Permian coherent leaf plants are enumerated at first, but the Pteridosperms lived in Mesozoic like *Lepidopteris*, *Caytonia* and etc. The pinnate fronds of *Pecopteris*-type in Paleozoic were Pteridosperms in part and ferns in part and that of *Cladophlebis*-type were Pteridosperm in part (*Lepidopteris*) and ferns in part but the majority of them remained without determination of their rank.

In the so-called *Gigantopteris* we can trace the change of their leaf forms from the initial to the third stage of cohesion, namely from *Emplectopteris triangularis* to *Tricoem-plectopteris taiyuanensis* (Fig. 2). They change to another form without making the intermediate form and abruptly, namely the thickness of sediments from *E. triangularis* bearing strata to *T. taiyuanensis* bearing strata is about 150 m. and of alternation of green or red sandstone and shale. If we cannot find these strata, we shall not be able to find *Gigantonoclea Lagrelii* and *Bicoem-plectopteris Hallei*, namely they are in the first stage of cohesion and the second stage. Therefore it is very difficult to determine the relation between *E. triangularis* and *T. taiyuanensis* (Fig. 2). The writer expects that the succeeding stage of cohesion as shown in the so-called *Gigantopteris* will be found in the cohesion stage of Angiosperms in the future. But it is very difficult to find the cohesion stage of all families of Angiosperms, because they had polyphyletically evolved from different ancestors as shown in the evolution of the so-called *Gigantopteris*. (Asama, 1959,

p. 51, Table F-A and p. 53, Table F-B). The appearance of many families of Anigospems in the upper Cretaceous will be explained by the theory of polyphyletic evolution, because such many families are not able to evolve from one origin in such a short time.

The leaves shown in Pl. 29, figs. 1-4 are *Rhus javanica* and their uppermost leaves are dissected into one or two lobes. Such dissected leaves as shown in *Rhus javanica* are found in many kinds of plants of Angiosperms and this means that those plants are derived from the pinnate leaves by retardation (Figs. 2 and 5). The leaves found in the Dakota Group are shown in Pl. 56, figs. 4-5 by Lesqureaux, 1892, and fig. 4 shows the intermediate type in lower part and this means that this plant was derived from a tripinnate plant by retardation (Principle A).

Dorf (1955) says. "In the Eocene floras the larger, thicker, entire-margined leaves with elongated drip points, are indicative of humid, subtropical conditions; these are gradually replaced in the Oligocene and Miocene by the smaller, thinner, toothed or lobed leaves characteristic of somewhat drier, more temperate conditions." (Principles E and F)

## (2) Coherent leaf of ferns

It is accepted that the recent ferns are derived from the Mesozoic ferns. There are many recent ferns showing the simple leaf. The process which makes the simple leaf has been explained, namely the simple leaf are produced only by retardation from the pinnate one. Comparing the simple leaf of recent ferns with Figs. 2 and 5, C-D-E-F of the so-called *Gigantopteris* we can understand these simple leaf producing process (Fig. 5).

From the mentioned we can know the main factor which caused the transformation of Cenozoic plants and the leaf forms had been changed by retardation not by acceleration.

## 5. RETARDATION AND CLIMATIC CHANGE

It has been stated that the leaf forms from the Paleozoic to Cenozoic had changed by retardation and not by acceleration. As stated both temperature and water are the main causes influencing the change of the leaf forms through the ages. Precipitation is the most important factor for their development and the dry climate (Devonian, Permian to Triassic and lower Cretaceous in east Asia) for the change of their leaf forms. In the Jurassic the climate returned to normal but the transformation of the leaf forms had continued by retardation. In Devonian time the dry climate was the main factor for retardation and their change also occurred in Carboniferous. Therefore we can suppose the dry climate as one of the main causes for retardation but not for successive retardation. The dry climate must have accelerated retardation but we can not find successive dry climates through the ages, therefore the main cause of the successive retardation was not the dry climate but some other factor. If we cannot admit the dry climate as the main cause of the successive retardation, the change of temperature must have been the main cause. It is well known that the distribution of recent plants are largely effected by the temperature and especially by the lowest temperature of the year. The retardation had occurred successively from the Paleozoic to the Cenozoic, namely through the ages. If the main cause of the successive retardation is the lowest temperature of the year, we must postulate the successive lowering of the lowest temperature of the year through the ages

and by doing so we can explain the successive change of the leaf forms. The lowest temperature of the year in Devonian time must have been the highest and that of Pleistocene Ice age the lowest and that of Mesozoic the intermediate temperature, namely the leaf forms had been changed successively by the successive lower of the lowest temperature of the year (change from species to species) and sometimes accelerated by the dry climate as shown in Devonian, Permian to Triassic and lower Cretaceous (change from genus to genus). We cannot postulate a great change of the highest temperature of the year through the ages, therefore it had remained without great change. The highest temperature of the year had not changed but the lowest temperature had successively changed through ages and therefore the annual range had successively increased from age to age, attaining the maximum in the Pleistocene. Plants had to increase their tolerance range adapting to the increasing annual range. To increase tolerance range successively they had to change themselves from lower plants to higher plants. The change of the leaf forms since Pleistocene were effected by acceleration, therefore we must postulate the rising of the lowest temperature of the year since the Pleistocene. The conclusion about the successive lower of the lowest temperature of the year is supported by the writer's study of the wood anatomy and the distribution of the fossil plants.

## 6. THE CAUSE OF THE EVOLUTION OF LEAF FORMS

### 1) The limits of distribution of recent plants and the cause of plant evolution

The distribution of the recent plants are limited to some extent by the temperature and the sum of precipitation and are not largely changed in the natural condition without the change of environment. The climate of geological ages had changed from ages to ages, namely the environments where the plants lived had changed. If we remove the recent plants to other places and if the new environment is suitable the development of the leaves will be accelerated but if not they will be retarded. If the new environment is diverse they will die. In geological ages the environments had changed from ages to ages and if the changed environments are suitable their growth will be accelerated and if not they will be retarded. If the changed environments are beyond the tolerance range of plants they will be perished. All plants have tolerance range in their present forms or structures and in their environment. If the environment changes they must change their forms or structures to adapt to the new environment and if not so, they must migrate by the spores or seeds to an environment similar to the former. If the plants can successively change their forms or structures to adapt to the new environments, they will be able to continue to live successively and we call these transformations of plants "evolution". We have glanced at the transformation of the leaf forms through the ages and found that the leaf forms had continuously been changed by successive retardation, without examples by acceleration. The continuous retardation means successive change of climate, namely the continuous lowering of the lowest temperature of the year. The plants had changed their leaf forms successively to adapt to the new environments and those unable to change their leaf forms perished. Therefore the plants perished by the lowering of the temperature and not by the struggle for existence. Many theories have been introduced to explain the

evolution but the writer adheres to the successive lowering of the lowest temperature of the year which means the successive increase of annual range and the successive decrease of growing period of plants of the year as the main cause of plant evolution. In this paper the writer could not discuss about the cause and the mechanism of the climatic change but this will be stated in another paper on the study of the anatomy of plants.

#### 2) The cause of neotenic evolution of the leaf forms

In the evolution of the leaf forms of plants their ontogeny must be found in the succeeding generations, namely the leaf form of the young stage of one plant becomes that of the mature stage in the next generation. This is called neoteny. (Tokuda, 1957, p. 131). The abbreviation of ontogeny will be called neoteny and the prolongation of that will be hypermorphosis. The evolution which is found in the transformation of the leaf forms are neoteny and these transformation are by retardation. We cannot find examples of hypermorphosis in the evolution of the leaf forms in any geological ages. The writer must take the retardation and the successive lowering of the lowest temperature of the year (increasing annual range) as the main cause of neotenic evolution of the leaf forms. But environments itself have no power to change the form of plants and it is plants themselves that change their form to adapt to the new environments.

#### 3) Orthogenesis and parallel evolution

The area of one leaf was reduced from the Paleozoic to the Cenozoic as found in the plant leaf evolution. The successive reduction of the leaf area through ages is the fundamental principle of leaf evolution (Fundamental principle 1), namely the leaf segments of one leaf had increased in size from ages to ages and finally developed to a simple leaf as shown in the leaves of Dicotyledon, simple leaf of fern, the leaf of the so-called *Gigantopteris*, *Glossopteris*, *Gangamopteris*, *Taeniopteris*, *Caytonia*, *Sagenopteris* and etc., but one leaf had become smaller through the ages. In this point the evolution of the leaf forms found in all geological ages and in all regions are orthogenesis, because they all had the same trend in their evolution which is the reduction of the area of one leaf. Since the leaf forms of all plants had changed successively by retardation, they had the same trend in their evolution. Retardation means that the environment had changed to an unsuitable trend for the development of leaves, thus plants must reduce their leaf areas to become adapted to the new environment. The reduction of leaf area will reduce the effects of the outer condition, therefore they reduce their leaf area to decrease the contact surface with the outer conditions.

The above mentioned is concluded that in the evolution of the leaf forms orthogenesis is normal and not a special phenomena. If orthogenesis is normal evolution in that of the leaf forms, it is natural that parallel evolution is found in many geological ages and many regions. A good example of parallel evolution is found in the so-called *Gigantopteris*. The evolution of *Glossopteris* and *Gangamopteris* in Gondwana land is parallel with that in Angara land and also the simple leaf of fern and the broad leaf of Dicotyledon are parallelly evolved from the pinnate frond, the one having sporangium and the other having seeds.

#### 4) Explosive evolution



There are two opposite conceptions about the process of the differentiation of species, one is that species differentiate from time to time and the units of a genus and families are derived by such differentiation (microevolution), the other is that such character of large types as genus and families (macroevolution) are formed at first. Schindewolf recognizes two phases in the process of evolution, one is the non-directional explosive evolution which occurs in the first stage of evolution and the other is the directional adaptive evolution which occurs through the stage from prosperity to extinction (Tokuda, 1951, p. 231; 1957, p. 127).

In the so-called *Gigantopteris* (Asama, 1959) the leaf forms of *Emplectopteris triangularis*, *Emplectopteridium alatum* and *Konnoa penchihuensis* had been changed largely by the stepping development, especially in the former two species the leaf forms extremely changed by the thrice stepping development, therefore we cannot satisfactory trace the relation between the initial *E. triangularis* and the last *Tricoemplectopteris taiyuanensis* and between the initial *E. alatum* and the last *Gigantopteris nicotianaefolia*, if we cannot find the plants of intermediate first and second stages of the leaf cohesion (Asama, 1959, p. 50, Text-fig.). These change had occurred in a very short geological time, namely there are about 150m thickness of strata from the *E. triangularis* bearing bed to the *T. taiyuanensis* bearing bed (Asama 1959, p. 29).

The conception of the non-directional explosive evolution of Schindewolf is based on the evolution of animals and it may not be appropriate to apply it to the evolution of plants.

Many authors (Asama, 1959, p. 53, Table F-B) thought that the so-called *Gigantopteris* was derived from one origin and they treated them under one genus, namely the broad leaf-like forms have been treated under *Gigantopteris*. They have all similar leaf forms but were derived parallelly from many origins (Asama, 1959, p. 51, Table F-A) by retardation and therefore their leaf forms resemble each other but their venations are remarkably different, because the leaf forms are more changeable than the venation by environments. If the so-called *Gigantopteris* was derived monophyletically from one origin as many authors thought, the evolution of them can be expressed by non-directional explosive evolution, but they had evolved polyphyletically from many origins and their evolution was directional. Therefore the evolution of them was rapid but not non-directional. If we accept the concept of the monophyletic evolution in the so-called *Gigantopteris*, the word "non-directional explosive evolution" is most suitable. This is the same case in the evolution of the broad leaves of Dicotyledon, namely the appearance of the broad leaves in the Cretaceous had developed rapidly and if we accept the conception of the monophyletical evolution of them, that will be expressed by "non-directional explosive evolution". But as already mentioned the evolution of the broad leaves of the Dicotyledon must have occurred polyphyletically by retardation from many origins.

The writer agrees with the conception of Schindewolf that the large character as shown in genus and families are formed at first. In the so-called *Gigantopteris* the leaf form of *Emplectopteris triangularis* had changed to that of *Gigantonoclea Lagrelii* by the stepping development and *G. Lagrelii* to *Bicoemplectopteris Hallei* and *B. Hallei* to

*Tricoempleopteris taiyuanensis* respectively, namely the change from genus to genus had occurred by stepping development. Such examples are found abundantly in the coherent leaf plants. *Alethopteris Norinii* changed to *Protoblechnum Wongii* by the stepping development. The pinnules of *Neuropteris*-type changed to that of *Alethopteris*-type by retardation. The new type of genus was derived from the other genus by the stepping development, and this means that the leaf forms had been changed largely by the stepping development and such examples as mentioned above are the phenomenon which is generally found in the evolution of the leaf forms.

The writer described *Empleopteris*, *Gigantonoclea*, *Bicoempleopteris* and *Tricoempleopteris* under the subfamily Empleopteroidae, the *Empleopteridium* series (*Empleopteridium*, *Bicoempleopteridium* and *Gigantopteris*) under the subfamily Gigantopteroidae, and the *Konnoa* series (*Konnoa* and *Cathaysiopteris*) under the subfamily Konnoideae. These three subfamilies were described under the family Gigantopteridaceae. This means that such characters as shown in genus, subfamilies and family had occurred at the first stage of the evolution of the so-called *Gigantopteris*.

There were three great revolutions in the transformation of plants, namely in Devonian, Permo-Triassic and lower Cretaceous. The remarkable dry climate in these three ages are correlated with the transformation of the leaf forms which had been accelerated thereby, therefore the rapid change as shown in the appearance of primitive land flora in the Devonian, the so-called *Gigantopteris*, *Gangamopteris*, *Glossopteris* and *Schizoneura* in the Permian, *Neocalamites* and Dipteridaceae in the Rhaetic and the broad leaves of Dicotyledon in the lower Cretaceous all correspond with the ages of these dry climates. The evolution of the leaf forms had been accelerated by the appearance of vast land and the dry climate which was related with the orogenic movement and marine regression. The environment enlarged by the successive marine regressions will accelerate the evolution of plants.

## 7. COMPARISON WITH OTHER THEORIES

### 1) The simple leaf-forming process by retardation

Simple leaf which is seen Angiosperms, Pteridosperms and ferns, was formed through the following process.

The leaf forms had been changed by successive retardation through the ages and the branches (Fig. 5-A) of the Devonian primitive plants changed to pinnules (Fig. 5-B), the pinnules to large pinnule (Fig. 5-C), the large pinnules to coherent pinna of the first stage (Fig. 5-D), the coherent pinnae to that of the second stage (Fig. 5-E) and to the simple leaf (Fig. 5-F) at last. The frond had become smaller step by step the leaf segment had become larger age by age. Therefore the simple leaf had been changed from pinnate one by retardation and had never been changed by acceleration. In *Bicoempleopteris Hallei* the frond is pinnate, in *Gigantonoclea lagrelii* bipinnate, in *Empleopteris triangularis* bipinnate or tripinnate (Halle, 1927 p. 122). The very stout axis of *G. Lagrelii* have been found in Shansi and this may mean that the axes of coherent leaf plants had secondary xylem as shown in other Pteridosperms. The axis of simple

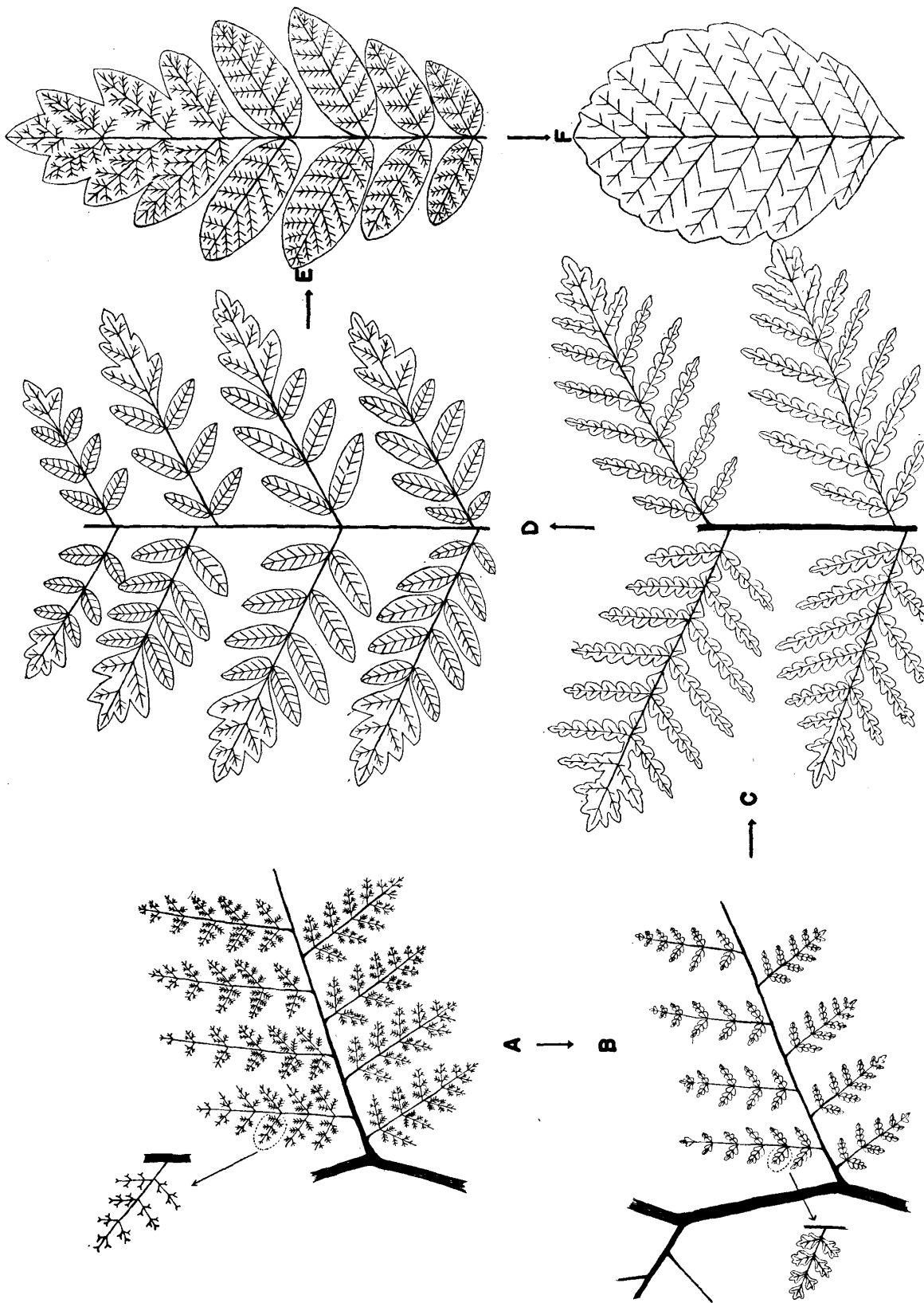


Fig. 5. Simple leaf forming process by retardation

leaf of *T. taiyuanensis* have not been found but it is not impossible to postulate that this plant had secondary xylem bearing axis.

The branching system shown in Fig. 5-A is not found in the Devonian plants and therefore the tripinnate or quadripinnate fronds must have been derived from the polydichotomized branching system by retardation reducing their branching.

## 2) Comparison with Telome theory

The writer has explained the change of leaf forms through the ages by retardation and finds that there are no examples which could be explained by acceleration. Ontogeny has not only been reduced but also changed to new type by retardation.

Zimmermann (1949, p. 60 ; Florin, 1950, p. 378) showed five main types of morphological trends, but he did not make clear the reason why these trends had occurred in the development of plants. The writer thinks that Zimmermann's overtopping and reduction correspond with principle C and fusion with principles A and B of retardation respectively and these overtopping, fusion and reduction were all due to retardation. He also thinks that fusion is derived by reducing their branching step by step (see Principles A, B, C and Fig. 6). Therefore some principles of retardation can be explained by Zimmermann's Telome theory.

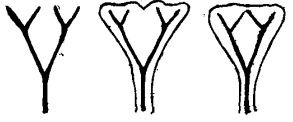

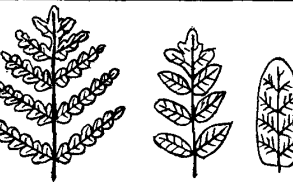

<b>TELOME TH.</b>	<b>FUSION</b>	<b>REDUCTION</b>
		
<b>RETARDATION</b>	<b>FUSION AND REDUCTION</b>	<b>BRANCHING REDUCTION</b>
		

Fig. 6. Comparison of Telome theory and retardation.

Florin (1950 p. 382, and 384) has explained a part of the results of his study in Cordaites and Conifers by the Telome theory. The transformation of leaf of conifers can be explained by retardation. Therefore the change of leaf forms can be understood by retardation not only in Pteropsida but also in all leaf forms, because all plants must have changed their leaf forms to adapt the successive change of environments which had the same trend.

## 8. CONCLUSION

1) If the environment of plants changes to another condition, the development of the leaf will be accelerated if suitable but retarded if unsuitable and the plants will perish if the environment is beyond the tolerance range of plants.

2) All plants have tolerance range in their present leaf forms and structures and are adapted to the present environment and will be able to adapt to the new environment by changing their leaf forms or structures.

3) The phenomena resulting by retardation are summarized in the three fundamental principles and the 11 principles of retardation.

4) The transformation of leaf forms through the ages can be explained by the principles of retardation and there are no examples which can be explained by acceleration. This means that the environments had changed in the same trend which was not suitable for the development of the leaf.

5) Dry climate and the lowering temperature are the main causes of retardation.

6) It is reasonable to postulate from the evolution of the leaf forms that the climate of geological ages had changed in the same trend through the ages, namely lowering of the lowest temperature of the year. (increase in annual range)

7) The plants had changed their leaf forms corresponding with the successive change of environments and those unable to change their leaf forms and structures to adapt to the changing environments perished, therefore the main cause of the evolution of leaf forms is the climatic change and that of extinction is also the climatic change.

8) The leaf area had been reduced by successive retardation from age to age but the leaf segments of a leaf had become larger step by step by the successive cohesion and had finally become a simple leaf.

9) Orthogenesis and parallel evolution in leaf forms is the general phenomenon, because the environments had changed in the same trend. Therefore we can recognize the rapid directional evolution of leaf forms but cannot recognize the explosive non-directional evolution in geological ages.

10) All simple leaf are derived from the pinnate one by successive retardation and one vein of that corresponds with one branch of primitive plants which is found in the Devonian and Silurian.

11) The leaf forms had changed through the ages by successive retardation and were accelerated by dry climate in the Devonian, Permo-Triassic and Lower Cretaceous.

12) The simple leaf or the pinnate coherent leaf of the coherent leaf plants in the Paleozoic (so-called *Gigantopteris*), had polyphyletically given off many kinds of pinnate fronds and the broad leaves of Dicotyledon must have been polyphyletically derived from many kinds of pinnate fronds of the Paleozoic or Mesozoic Pteridosperms.

13) The great change of ontogeny occurs by retardation in their young stage.

14) The transformation of leaf forms can be all explained by neotenic evolution.

15) The writer mentioned the retardation as the main cause of neoteny in the evolution of leaf forms.

16) The writer agrees fully with Schindewolf's opinion that the great characters which characterize genus, families, and order have been formed in the first stage and then differentiated to species.

17) The principles of retardation can be explained by Zimmermann's Telome theory.

18) The change of leaf form shown in *Angiopteris lygodiiifolia* occurs not in the next

generation but in the same generation without passing sexual generation and it is such a change as mentioned above that we find in geological ages.

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## PLATE 26

### *Angiopteris lygodiifolia* Rosenst

This fern has been removed from the Koshiki islands to the hothouse of the Institute of Biology, Tohoku University, Sendai.

- Fig. 1. Two pinnae of the upper part of frond are showing unipinnate but the pinnules of pinna of left hand side are not completely formed. Two pinnae of the middle part of frond are showing enlarged pinnae.
- Fig. 2. Terminal pinna is showing intermediate type of unipinnate pinna and enlarged pinna. Three pinnae of the middle part of frond are showing enlarged pinnae and two of the lower part unipinnate pinna.
- Fig. 3. Showing all fronds of *Angiopteris lygodiifolia*. Two large fronds of right and left hand side have developed in the Koshiki islands and others in Sendai.
- Fig. 4. Three pinnae of the middle part of frond are showing enlarged pinnae and others intermediate type.

## PLATE 27

### *Angiopteris lygodiifolia* Rosenst

This fern has been removed from the Koshiki islands to the hothouse of the Institute of Biology, Tohoku University, Sendai.

- Fig. 1. Showing normal pinnae which developed in the Koshiki islands and they have many sporangium on lower surface.
- Fig. 2. Two pinnae of the lower part of frond are showing unipinnate and others enlarged pinnae with sporangium on lower surface of them.
- Fig. 3. Terminal pinna is showing unipinnate and two of the middle part of frond are enlarged pinnae and two of the lower part are intermediate type which have two pinnules in the lower part of them.
- Fig. 4. Showing enlarged pinnae with sporangium on lower surface.





## PLATE 28

*Angiopteris lygodiifolia* Rosenst

This fern has been derived from the Koshiki islands to the hothouse of the Institute of Biology, Toholu University, Sendai.

- Fig. 1. This frond is showing unipinnate and corresponds with bipinnate one of the Koshiki islands.
- Fig. 2. Showing the frond of young stage and three pinnae show unipinnate and one of right hand side of the middle part shows enlarged pinna.
- Fig. 3. This frond is showing bipinnate but smaller than that of the Koshiki islands in pinnules and pinnae.
- Fig. 4. Showing enlarged pinnae in the upper part of frond and unipinnate pinnae in the lower part.



**PLATE 29**

*Rhus javanica* L.

Fig. 1. Showing the terminal leaf dissecting a segment on the right hand side.

Fig. 2. Showing the terminal leaf dissecting a large segment on the left hand side.

Fig. 3. Showing the terminal leaf dissecting two segments and a shortened internode.

Fig. 4. Showing the normal terminal leaf.

