

Evolution and Phylogeny of Vascular Plants based on the Principles of Growth Retardation. Part 1. Principles of Growth Retardation and Climatic Change through Ages

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Introduction

In 1960 the writer proposed the idea of Growth Retardation and tried to make clear the phylogenetic relationships of vascular plants on the basis of the principles of Growth Retardation (ASAMA, 1959, 1960, 1962, 1965, 1966a, 1966b, 1966c, 1967, 1968, 1969, 1972, 1975, 1977, 1979a, 1979b, 1979c, 1980; ASAMA and KIMURA, 1977). As the writer's theory, the triphyletic evolution of vascular plants, was so different from others, he wrote most of papers on his theory in Japanese expecting that the theory would be commented by obtainists and paleobotanists in Japan first.

It is no doubt that the recent vascular plants of about 260,000 species have been derived from ancestral Devonian pteridophytes continuously changing forms of their leaves, stems and reproductive organs through Upper Paleozoic, Mesozoic and Cenozoic. If their changes through ages have been at random, it is very difficult to find the true lines of vascular plants. If they had regularly changed their organs according to some principles, it is not so difficult to decide their lines. Their changes must have been gradual in any ages and must not have been so abrupt as we are unable to find out their lines.

From the fossil evidence (Fig. 1) of Taiyuan coal field, Shansi, China, which ranges from Carboniferous to Permian (HALLE, 1927), the writer found the principles for changes of leaf-forms in environmental changes. The writer calls them "Principles of Growth Retardation" (Principles of G. R.) (Fig. 2). The principles always teach us the change of leaf-forms derived from the ancestral plants by the retardation of growth for the unfavorable environment. The changes of leaf forms found in Upper Paleozoic, Mesozoic and Cenozoic are all explainable by the principles of G. R. and not by the principles of Growth Acceleration. This means that the environments had successively changed to unfavorable condition for the growth of plants through ages. On the basis of these and many other geological and paleontological evidences the writer postulated the paleoclimatic change increasing annual range through ages. (Fig. 9).

Paleozoic pteridophytes are divided into three types by the characters of leaves

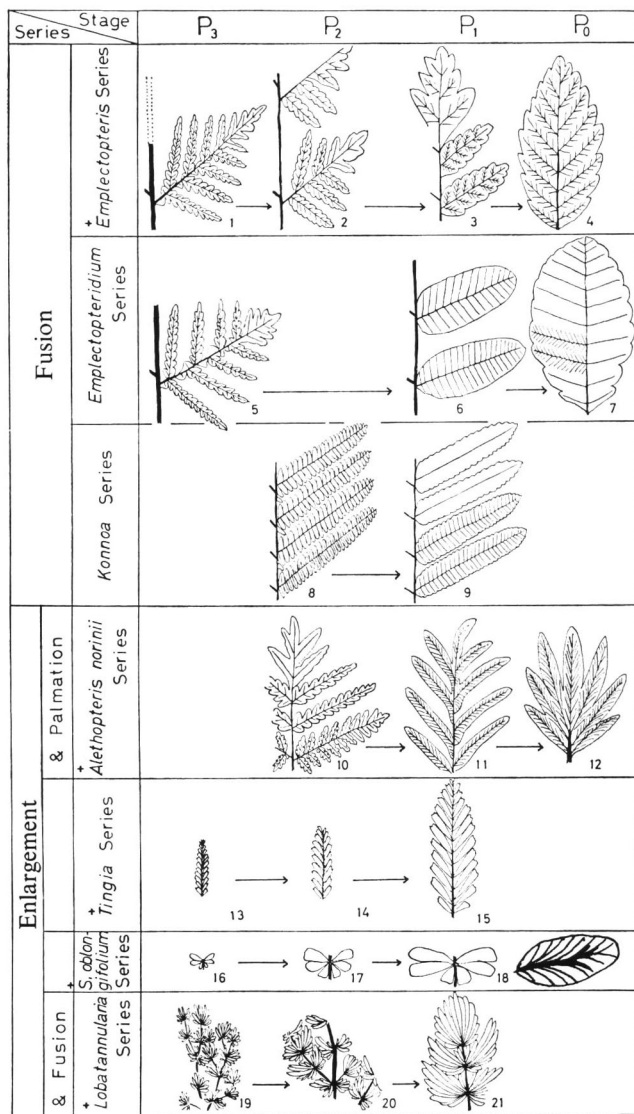


Fig. 1. Evolution of leaf forms in Cathaysia flora. + The evolutionary series found in the Taiyuan coal field, Shansi, China. 1. *Emplectopteris triangularis*...2. *Gigantonoclea lagrelli*...3. *Bicoemplectopteris hallei*...4. *Tricoemplectopteris taiyuanensis*. 5. *Emplectopteridium alatum*...6. *Bicoemplectopteridium longifolium*...7. *Gigantopteris nicotianaefolia*. 8. *Konnoa penchiuensis*...9. *Cathaysiopteris whitei*. 10. *Alethopteris norinii*...11. *Protoblechnum wongii*...12. *Psymophyllum multipartitum*. 13. *Tingia partita*...14. *Tingia carbonica*...15. *Tingia crassinervis*. 16. *Trizygia oblongifolia*...17. *T. speciosa*...18. *T. sinocoreana*...*T. grandifolia*. 19. *Lobatannularia sinensis*...20. *L. lingulata*...21. *L. heianensis*.

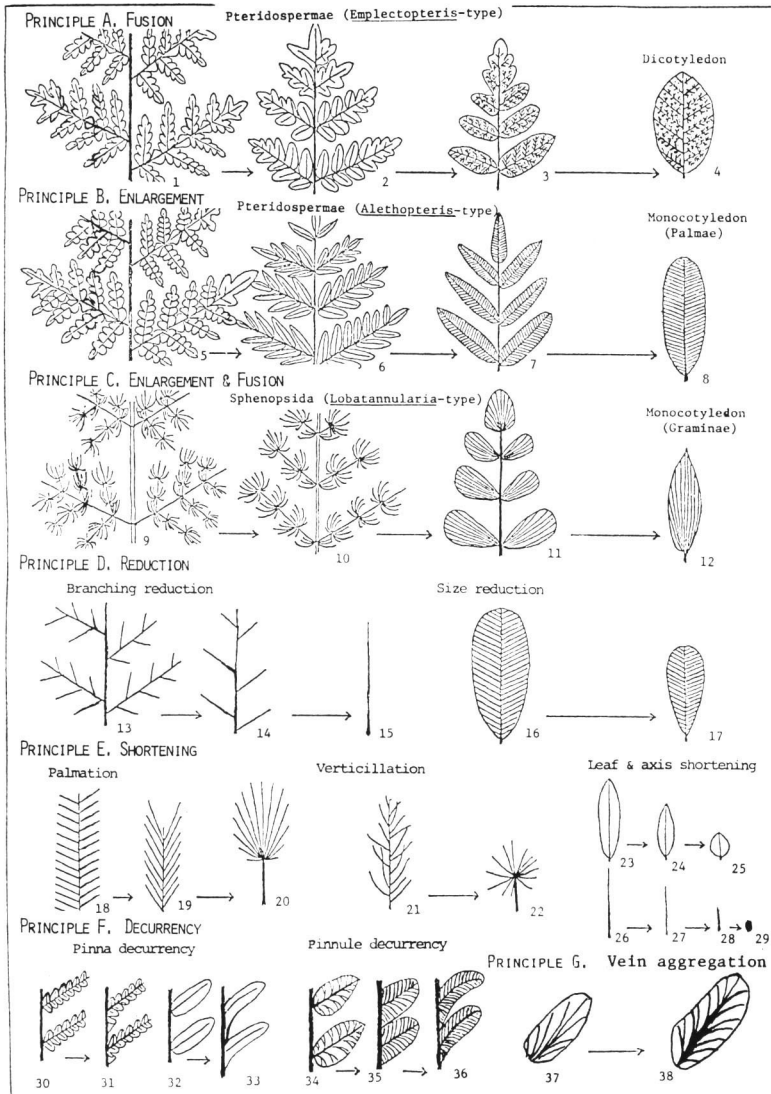


Fig. 2. Principles of Growth Retardation (Principles of G.R.). (Adapted from ASAMA, 1960, 1962, 1975). A great part of changes found in fossil plants through ages, Paleozoic, Mesozoic and Cenozoic will be explained by these principles indicating that the environments changed successively mild to severer, simple to more complex through geological ages. Therefore the paleoclimatic change shown Fig. 9 was speculated.

and stems Lycopsidea (with microphyll), Pteropsida (with macrophyll) and Sphenopsida (with articulate stem).

Many paleobotanists do not recognize microphyll, macrophyll and articulate stems as original characters. So they use these words only in pteridophytes and do not use in gymnosperms and angiosperms. The writer recognized microphyll, macrophyll and articulate stems as the original characters, which the earlier plants had in the late Silurian and early Devonian and had continuously been the basic characters through Paleozoic, Mesozoic and Cenozoic. From the viewpoint stated above the writer classified the vascular plants into three lines, Microphylllophyta (with microphyll), Macrophylllophyta (with macrophyll) and Arthrophyta (with articulate stem) and thought that the Paleozoic plants of these three lines had parallelly evolved grading up their evolutionary stages from the spore stage to gymnosperm (naked seed) and angiosperm (enclosed seed) stage, step by step through ages. The writer calls these improvement of reproductive organ the progressive evolution. On the other hand some Paleozoic plants of these three lines had remained in the spore stage without improving their reproductive organs. In this case they had remarkably reduced the size of their vegetative organs through ages. The writer calls them the regressive evolution (Figs. 6-8).

From the reason stated above the writer classified the vascular plants considering lines and evolutionary stages as follows:

I. Microphylllophyta

- A. Microphyll-sporophytina (Lycopsidea) — Spore-stage
Protolepidodendrales, Lepidodendrales, Pleuromeiales, Isoetales, Selaginellales, Lycopodiales
- B. Microphyll-gymnospermophytina — Gymnosperm (naked seed)-stage
Cordiales, Coniferales
- C. Microphyll-angiospermophytina — Angiosperm (enclosed seed)-stage
unknown

II. Macrophylllophyta

- A. Macrophyll-sporophytina (Pteropsida) — Spore-stage
Protopteridiales, Aneurophytales, Coenopteridiales, Archaeopteridiales, Filicales, etc.
- B. Macrophyll-gymnospermophytina — Gymnosperm (naked seed)-stage
Pteridospermae, Bennettitales, Cycadales, Ginkgoales, etc.
- C. Macrophyll-angiospermophytina — Angiosperm (enclosed seed)-stage
Dicotyledoneae
Monocotylendoneae (except Graminae)

III. Arthrophyta

- A. Articulate-sporophytina (Sphenopsida) — Spore-stage
Sphenophyllales, Calamitales, Equisetales, etc.
- B. Articulate-gymnospermophytina — Gymnosperm (naked seed)-stage
Calamocarpaceae ?

C. Articulate-angiospermophytina — Angiosperm (enclosed seed)-stage
Graminae

The writer takes this opportunity to express his sincere gratitude to Dr. Teruya UYENO of National Science Museum, Tokyo, for the reading of this manuscript.

Principles of Growth Retardation

1. Fossil evidences and interpretation

Principles of Growth Retardation are basic concept in order to interpret the evolution and phylogeny of vascular plants. The writer wrote several papers about these principles (1960, etc.), and without realizing these principles we cannot understand the evolution and phylogeny which are stated in the following chapter. Therefore their outlines are summarized here.

Principles of Growth Retardation consists of 7 principles, which are mainly based on the study of the Shansi flora. The geology of Taiyuan, Shansi, China was surveyed by NORIN who recognized three series, the Yuehmenkou Series, the Shihhotse Series and the Shihchienfeng Series in ascending order. He collected abundant fossil plants from 33 plant beds (Yuehmenkou Series, bed 3–10; lower part of Lower Shihhotse Series, bed 11–14; upper part of Lower Shihhotse Series, bed 15–18; lower part of Upper Shihhotse series, bed 19–22; upper part of Upper Shihhotse Series, bed 28–33) and these plants were reported by HALLE (1927) in detail. The present writer visited the Taiyuan coal field in 1944 and surveyed the stratigraphy and collected fossils of this area for about three months. The Taiyuan coal field is distributed in the east (Tung-shan) and west (Si-shan) of Taiyuan and the best section are found in the Shihhotse valley of Tung-shan. In the Shihhotse valley all fossil plants-bearing sediments are deposited conformably without any geological disturbance, and they range from Carboniferous to Triassic in age. Therefore it is no doubt that the fossil plants collected from the continuous section of the Shihhotse valley indicate the transformation of plants through ages.

(1) *Emplectopteris* Series (Figs. 1, 1–4)

Emplectopteris triangularis (1) → *Gigantonoclea lagrelli* (2) → *Bicoemplectopteris hallei* (3) → *Tricoemplectopteris taiyuanensis* (4)

In the Shihhotse valley the tripinnate *Emplectopteris triangularis* (1) (Lower Shihhotse Series, bed 9–16) appeared at first and succeeded by the bipinnate *Gigantonoclea lagrelli* (2) (upper part of the Lower Shihhotse Series—the lowest part of the Upper Shihhotse Series, bed 18–20), the unipinnate *Bicoemplectopteris hallei* (3) (the Upper Shihhotse Series, bed 20–22), and simple leaf *Tricoemplectopteris taiyuanensis* (4) (the Upper Shihhotse Series, bed 21). From the order of appearance mentioned above, the writer interpreted that simple leaf *Tricoemplectopteris taiyuanensis* was derived successively from unipinnate *Bicoemplectopteris hallei*, *B. hallei* from bipinnate *Gigantonoclea lagrelli*, and *G. lagrelli* from tripinnate *Emplectopteris triangularis* by fusing their contact segments (pinnules and pinnae) and reducing their branches step by step.

The writer calls these process "Fusion". Fusion is the most important principle in the principles of Growth Retardation.

Tripinnate *Emplectopteris triangularis* (1) has abundant small segments (pinnules), whereas simple leaf *Tricoemplectopteris taiyuanensis* (4) derived from the former has only one large segment. Segments became larger and larger from *E. triangularis* to *G. lagrelii*, *B. hallei*, and to *T. taiyuanensis* step by step by reduction of branches. It looks that the plants became larger in *Emplectopteris* Series, but this interpretation is not correct. Segments became larger step by step to be one segment at the latest stage, but plants became smaller. *E. triangularis* is very large tripinnate plants but *T. taiyuanensis* is small simple leaf plants. The direction of change in *Emplectopteris* Series is reduction in size.

(2) *Emplectopteridium* Series (Figs. 1, 5-7)

Emplectopteridium alatum (5)→*Bicoemplectopteridium longifolium* (6)→*Gigantopteris nicotianaefolia* (7)

Emplectopteris Series is well developed in Shansi, whereas *Emplectopteridium* Series is found in Korea and other districts. *Emplectopteridium alatum* was reported by KAWASAKI (1934) from the Jido Series of Korea, and later LEE (1963) described it from the Shansi Series (lower part of Lower Shihhotse Series of HALLE, 1927) of the southern Shansi. *Bicoemplectopteridium longifolium* was reported from Kobosan Series (comparable to the Upper Shihhotse Series) of Korea and *Gigantopteris nicotianaefolia* was described from the Upper Shihhotse Series of China and the Kobosan Series of Korea.

The segments (pinnules) of *Emplectopteridium alatum* are very similar to those of *Emplectopteris triangularis* but the former have the veins rising from both midrib and axis and the latter have veins rising from midrib only.

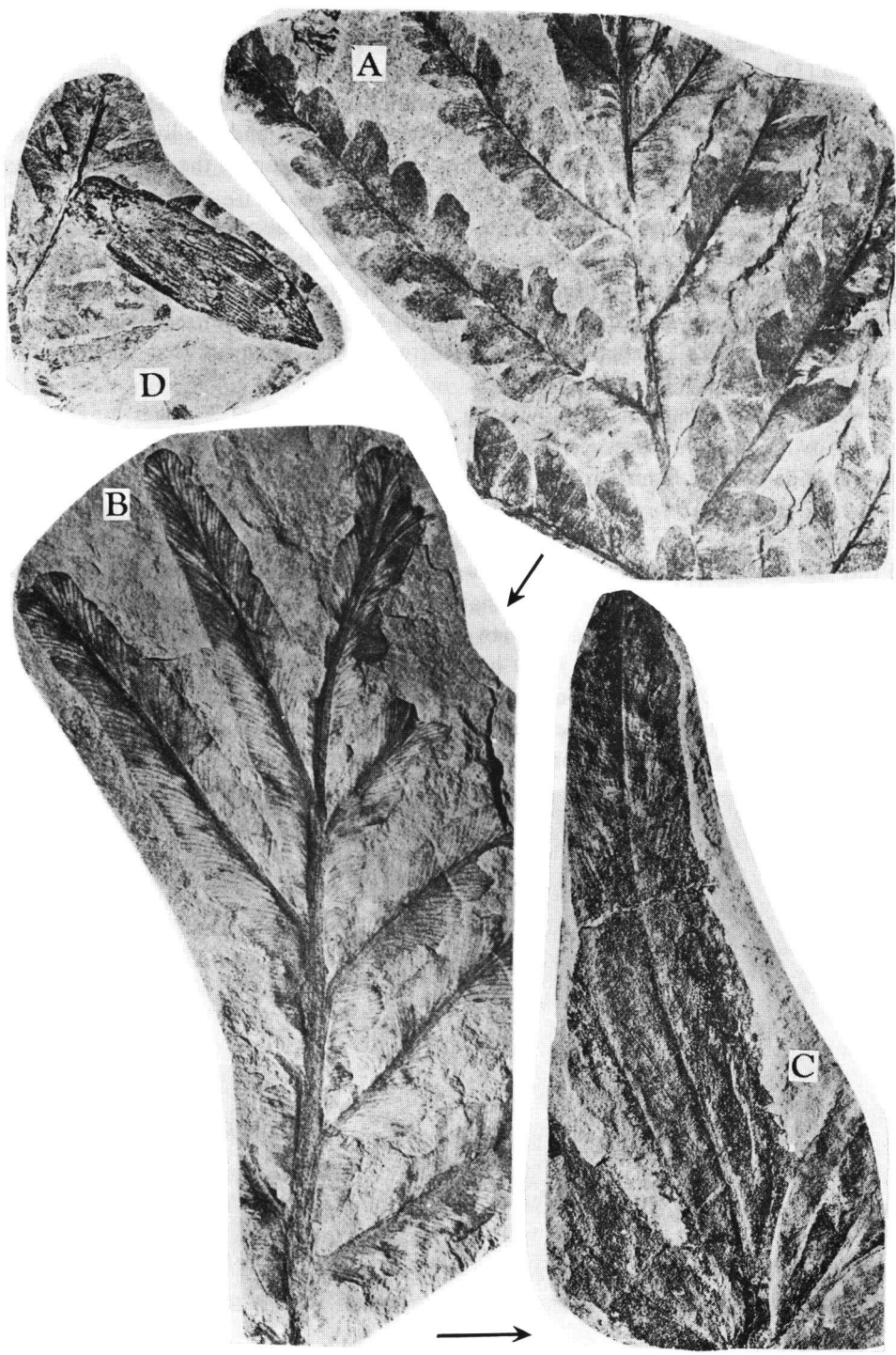
Emplectopteris Series was found in the section of Shihhotse valley, therefore it was not hard to recognize the transformation of plants of this series. *Emplectopteridium* Series was found in Korea but it was not in one successive section. So there is some question about the succession of this series, but there is no doubt that the similarity of venation between these three species indicates the same lineage and that the changes from *E. alatum* to *B. longifolium* and *G. nicotianaefolia* are explainable by the same process occurred in *Emplectopteris* Series.

(3) *Konnoa* Series (Fig. 1, 8-9)

Konnoa penchihuensis (8)→*Cathaysiopteris whitei* (9)

Konnoa penchihuensis was reported by ASAMA (1959) from the Huangchi Series (comparable to the Yuehmenkou Series of HALLE) of Penchihu, northeastern China, and *Cathaysiopteris whitei* was described by HALLE (1927) from the lower part of the Lower Shihhotse Series of Taiyuan. The writer interpreted that *C. whitei* was derived from *K. penchihuensis* by fusion of segments.

Fig. 3. Evolution of *Alethopteris norinii* Series. A: *Alethopteris norinii* HALLE. B: *Proto-blechnum wongii* HALLE. C: *Psymphyllum multipartitum* HALLE. D: *Alethopteris norinii* with seed.



(4) *Alethopteris norinii* Series (Fig. 1, 10–12 and Fig. 3, A–D)

Alethopteris norinii (10)→*Protoblechnum wongii* (11)→*Psymphyllum multipartitum* (12)

This series was found in the section of Shihhotse valley, namely *A. norinii* in the Lower Shihhotse Series, *P. wongii* in the Lower Shihhotse, and the lower part of the Upper Shihhotse Series, and *P. multipartitum* in the upper part of the Upper Shihhotse Series.

Protoblechnum wongii reported from the Upper Shihhotse Series by HALLE (1927) has the unipinnate frond and pinnae are very long and large attaching to rachis by broad base (decurrent wing) (Fig. 3, B). Decurrent wings are broad in the upper part of the frond, becoming more indistinct towards the base and entirely missing in the lowermost part. This means that the decurrent wings are produced when growth was retarded.

What is the significance of the long pinnae of this plant? Such long pinnae as seen in *P. wongii* have never been found in the Lower Shihhotse Series, therefore they must be derived from a frond having short pinnules. The writer reported about the growth of Recent *Angiopteris lygodifolia* (1960). This fern has the bipinnate frond in the mature stage, and the unipinnate frond in the young stage. If the growth of this fern is disturbed by some unfavorable environmental changes, the new frond coming up from the rhizome in the mature stage grows to be unipinnate (Fig. 4). Ordinary fronds show bipinnate and new fronds show unipinnate in the same rhizome. Pinnae of ordinary fronds (Fig. 4, A) have many short segments (pinnules) and that of new fronds (Fig. 4, B) have only one very large segment (pinna). This means that pinnate pinna with small pinnules changed to a single pinna without pinnules by the retardation of growth. Therefore the very long pinnae indicate that they were the



Fig. 4. *Angiopteris lygodifolia* ROSENST. A: Ordinary pinna. B: Changed pinna.

pinnate pinnae with short pinnules before the change. The writer calls these process of growth "Enlargement", because the new very long pinnae resemble the enlarged form of small ordinary pinnules before the change.

If the process seen in the growth of living *Angiopteris lygodiifolia* can be applicable to those of Permian *Protoblechnum wongii*, the ancestral plants of *P. wongii* (Fig. 3, B) have had small pinnules similar to the pinnae of *P. wongii*. If so, the ancestral plants of *P. wongii* must have been *Alethopteris norinii* (Fig. 3, A) which is found in the lower plant bed than that of *P. wongii*.

Psymphyllum multipartitum (Fig. 3, C) described by HALLE (1927) from the uppermost of the Upper Shihhotse Series are very large and show a palmate aspect in habit, but some show the division by dichotomy. Which plants are the ancestor of *P. multipartitum*? In plants removed from plain and planted on high mountains, the axis is shortened and leaves spread out to show verticillate condition in the arrangement (Fig. 2, 21–22). Therefore it is not surprised to assume that *Protoblechnum wongii* (Fig. 3, B) had changed to *P. multipartitum* (Fig. 3, C) by the shortening of the axis. Comparing the segments of the both plants we find many similarities. There is a great variation in the form of *P. multipartitum*, and some show fusion in the larger part of the segments and some in a smaller part of segments.

From the above mentioned reasons, the writer suggests that *Psymphyllum multipartitum* was derived from *Protoblechnum wongii*, and *P. wongii* from *Alethopteris norinii* by the shortening of the axis and the enlargement of segments respectively.

(5) *Tingia* Series (Fig. 1, 13–15)

Tingia partita (13) → *Tingia carbonica* (14) → *Tingia crassinervis* (15)

This series is found in the section of Shihhotse valley. HALLE (1927) described three species of *Tingia* from Shihhotse valley, *Tingia partita* from the lower part of the Lower Shihhotse Series, *Tingia carbonica* from the upper part of Lower Shihhotse Series, and *T. crassinervis* from the Upper Shihhotse Series. *Tingia* has leaves arranged in four rows, two on the upper and two on the lower side of the axis. Leaves of the two rows on the upper side are large and those of the two rows on the lower side are smaller. In general we can see the leaves of two rows on the upper side.

The leaves of *Tingia partita* (Fig. 1, 13) are small in size, 2–2.5 cm long and 1 cm wide, those of *T. carbonica* (14) are large in size, 5–6 cm long, and those of *Tingia crassinervis* (15) are very large attaining the length of 10 cm. There is no doubt that *T. crassinervis* was derived from *T. carbonica*, and *T. carbonica* from *T. partita* respectively.

The segments (leaves) of *Tingia* became larger and larger through ages and this does not mean that these plants became larger through ages. As seen in *Emplectopteris* Series, *Emplectopteridium* Series, *Konnoa* Series and *Alethopteris norinii* Series, the segments (pinnules and pinnae) became larger and larger by reducing numbers of branches and segments. Therefore the enlargement of segments indicates the reduction of branches, number of segments and plant size before change.

(6) *Sphenophyllum oblongifolium* (*Trizygia oblongifolia*) Series (Fig. 1, 16–18)

Trizygia oblongifolia (16)→*Trizygia speciosa* (17)→*Trizygia sinocoreana* (18)

This series is found in the section of Shihhotse valley. These plants were all reported from Shihhotse valley and other regions. *Trizygia oblongifolia* (HALLE, 1927) reported from the uppermost of the Yuehmenkou Series and the lower part of the Lower Shihhotse Series, *Trizygia speciosa* (ASAMA, 1970) from the lower part of the Upper Shihhotse Series and *Trizygia sinocoreana* (ASAMA, 1970) from the upper part of the Upper Shihhotse Series, respectively. From the order of appearance of these species the writer assumed that *T. sinocoreana* was derived from *T. speciosa*, and *T. speciosa* from *T. oblongifolia* succeedingly. As seen in the *Tingia* Series the leaf segments of *Trizygia* Series had been enlarged step by step indicating that the branches of *Trizygia* were reduced in size step by step.

(7) *Lobatannularia* Series (Fig. 1, 19–21)

Lobatannularia sinensis (19)→*Lobatannularia lingulata* (20)→*Lobatannularia heianensis* (21)

This series is found in the section of Shihhotse valley.

HALLE (1927) described four species of *Annularia* type of shoots from Taiyuan, *Annularia stellata* from the Yuehmenkou Series, *Lobatannularia sinensis* from the lower part of the Lower Shihhotse Series, *Lobatannularia lingulata* from the lower part of the Upper Shihhotse Series and *Lobatannularia heianensis* from the upper part of the Upper Shihhotse Series, respectively.

The order of appearance of these *Annularia* type shoots suggests that *Lobatannularia heianensis* was derived from *Lobatannularia lingulata*, *L. lingulata* from *Lobatannularia sinensis* and *L. sinensis* from *Annularia stellata*, respectively. The length of leaves of the ultimate whorl are 13–18 mm in *L. sinensis*, 21–28 mm in *L. lingulata* and 13–35 mm in *L. heianensis*, respectively. This means that the length of leaves increased step by step.

The leaves arranged in a whorl spread more or less equally in all direction in *Annularia stellata*, making small gap at the proximal side in *L. sinensis*, and making wide gaps in front and rear in *L. heianensis*. Therefore the whorls in *L. heianensis* are divided into two lobes uniting leaves for nearly their whole length along distinct suture lines. We can see the process of both enlargement and fusion of leaves in *Lobatannularia* Series.

2. Principles of Growth Retardation

In the previous chapter the writer enumerated many fossil evidences on the change of Permian plants observed mainly in the section of Shihhotse valley, and interpreted the process of change. These fossil plant evidences described by HALLE (1927) are undoubtedly facts indicating the transformation of Permian plants which had been resulted from the relation between the environmental change and the reaction of plants.

The palaeogeographic maps of China (LIU, 1959) and the sediments in Taiyuan coalfield from Carboniferous to Triassic show that the paleoclimate of Taiyuan had changed from a wet marine climate to a dry continental climate during Carboniferous to Triassic (ASAMA, 1962). These climatic changes must have been the main cause of the

transformation of Permian plants in Taiyuan. The wet climate accelerates and the dry climate retards the growth of plants. The growth of plants in the periods from Carboniferous to Triassic must have been retarded by the climatic change from wet to dry. Therefore we must postulate that the transformation of Permian plants in Taiyuan area were changes taken places when the growth of plants were retarded by the unfavorable environment.

The fossil evidences in Taiyuan coal field are teaching us the principles that how the environmental changes toward the unfavorable condition affect the growth of plants. There are three basic principles to be observed when the growth of plants are retarded by the unfavorable environmental changes, and accelerated by the favorable environmental change.

(1) The area of a single leaf is reduced by growth retardation, and increased by growth acceleration.

(2) The leaf forms derived by growth retardation resemble that of the youngest stage before change (neoteny) and that derived by growth acceleration resemble that of the latest stage before change.

(3) Leaf segments are united by growth retardation and differentiated by acceleration, therefore each segments of the later stage become larger than that of the former stage by the growth retardation, and become smaller by the growth acceleration.

The writer discussed the principles of growth retardation (Fig. 2) on the basis of the fossil evidence (Fig. 1) in Taiyuan coal field and other areas in Cathaysia land. These principles consist of the following 7 principles.

Principle A. Fusion (Fig. 2, 1-4)

This principle was derived from the change of plants shown in *Emplectopteris* Series (Fig. 1, 1-4), *Emplectopteridium* Series (Fig. 1, 5-7) and *Konnoa* Series (Fig. 1, 8-9). This is the most important principle when we study the origin of angiospermous plants which have simple leaf as shown in *Gigantopteris*. It indicates that the simple leaf was derived from the pinnate frond by the reduction of branches and segments.

Principles B. Enlargement (Fig. 2, 5-8)

This principle was derived from the change of plants shown in *Alethopteris norinii* Series, (Fig. 1, 10-12), *Tingia* Series (Fig. 1, 13-15), *Sphenophyllum oblongifolium* (*Trizygia oblongifolia*) Series (Fig. 1, 16-18) and *Lobatannularia* Series (Fig. 1, 19-21).

Very large type of *Taeniopteris* (14-20 cm wide) such as *T. nystroemii*, *T. latecostata* and *T. shansiensis* are described by HALLE (1927) from the lower part of the Lower Shihhotse Series, and small type (3.5-7 cm wide) from the Upper Shihhotse Series. We do not know the ancestral plants of these *Taeniopteris*, which should be found in the Yuehmenkou Series. Unfortunately fossil plants reported from the Yuehmenkou Series are meager. The process shown in *Emplectopteris* Series and *Alethopteris norinii* Series indicates that *Taeniopteris* was derived from the pinnate plants by reduction of branches and segments (pinnules and pinnae) as shown in Fig. 2, 5-8. The process making simple leaf in *Emplectopteris* Series began from the Lower Shihhotse Series and the process from tripinnate *Alethopteris* to simple leaf *Taeniopteris* had

already been finished before the Lower Shihhotse Series.

Principle C. Enlargement and Fusion (Fig. 2, 9–12)

This principle was found in the *Lobatannularia* series (Fig. 1, 19–21). Enlargement of segments were observed in *Alethopteris norinii* Series, *Tingia* Series, *Sphenophyllum oblongifolium* (*Trizygia oblongifolia*) Series and *Lobatannularia* Series. Fusion of segments were found in *Emplectopteris* Series, *Emplectopteridium* Series, *Konnoa* Series, *Alethopteris norinii* Series and *Lobatannularia* Series. Fusion and enlargement of segments are the most important principles observed when the growth of plants are retarded by unfavorable environment, reducing their branches and number of segments.

In the *Emplectopteris* Series and *Emplectopteridium* Series simple leaf indicates the last stage (Fig. 1, P₀) of these series. As *Lobatannularia heianensis* (Fig. 1, 21), and *Schizoneura manchuriensis* indicates P₁ stage (Fig. 1, 21 and Fig. 2, 11). The occurrence of the next stage of plants in P₀ stage (Fig. 2, 12) should be expected as the plants of the last stage of Calamarian series (*Lobatannularia* Series).

Principle D. Reduction (Fig. 2, 13–17)

Reduction in branching was observed in the *Emplectopteris* Series, *Emplectopteridium* Series and etc. In the case of fusion the branching before change remain as venation in the plants of the next stage (Fig. 2, 1–4) and not remained in the case of enlargement (Fig. 2, 5–8).

The plants of last stage in pinnate plants have simple leaves (Fig. 2, 4, 8). If the growth of these plants are retarded by unfavorable environment, the size of simple leaves would be reduced (Fig. 2, 16–17).

Principle E. Shortening (Fig. 2, 18–29)

This process was observed in the *Alethopteris norinii* Series and the shortening of the axis is well found in the plants transplanted to an unfavorable environment (for example; from plain to high mountains). The pinnate leaves are arranged in palmate (Fig. 2, 18–20) and the surrounded leaves around the axis are arranged in verticillate (Fig. 2, 21–22) by the shortening of the axis.

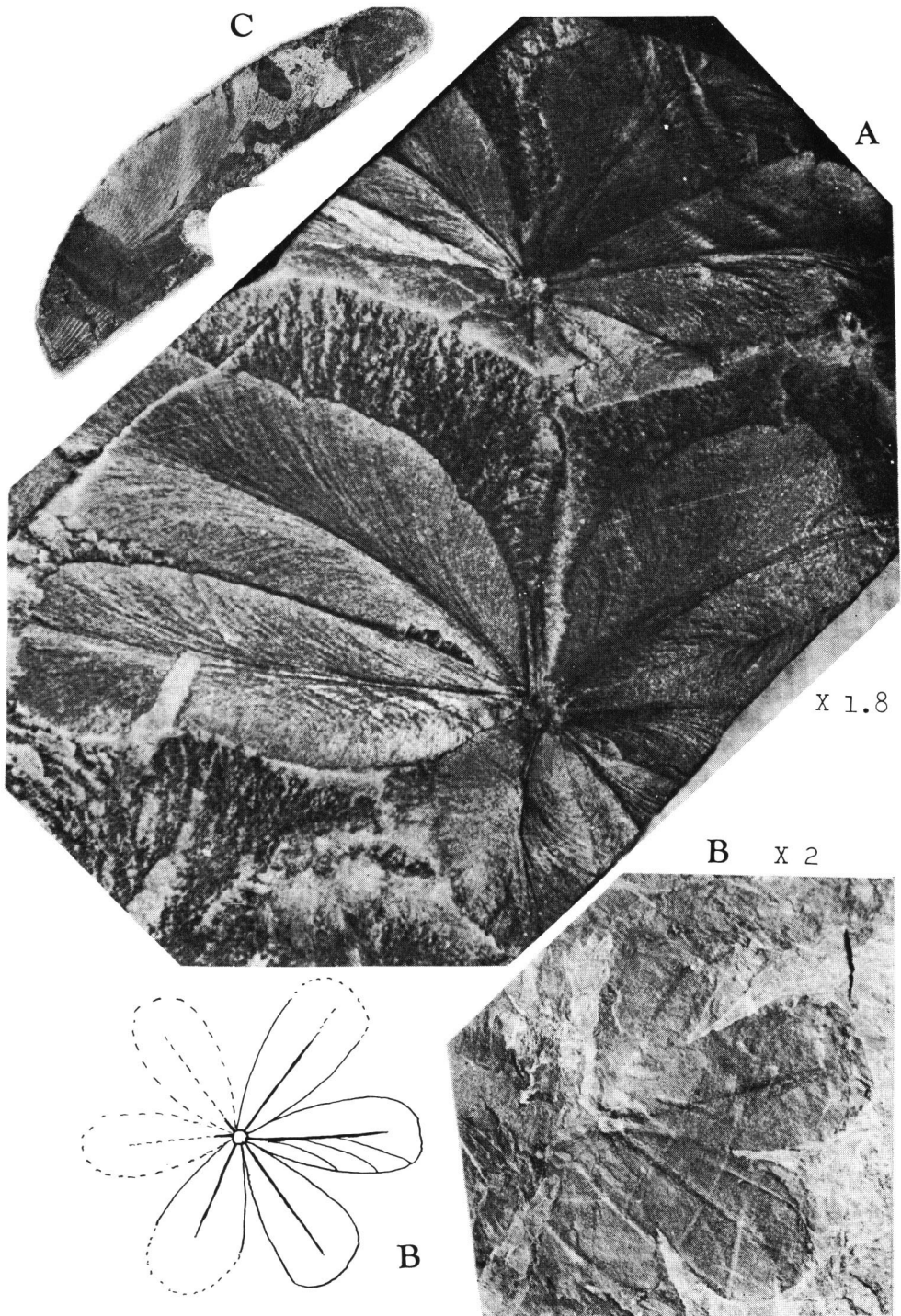
Principle F. Decurrency (Fig. 2, 30–36)

The intermediate pinnules made by pinna decurrency are not rare in Paleozoic plants and they are shown in *Callipteris*, *Callipteridium*, *Konnoa*, *Emplectopteris*, *Emplectopteridium* and *Jidopteris* in Cathaysia flora. The decurrent wings are observed in pinnules of *Alethopteris* and pinnae of *Protoblechnum wongii*.

Principle G. Vein aggregation (Fig. 2, 37–38 and Fig. 5, A, B)

The writer (ASAMA, 1970) classified *Sphenophyllum* into four lines by the arrangement and venation of leaves, *Sphenophyllum* (non-trizygoid and straight vein), *Parasphenophyllum* (non-trizygoid and curved vein), *Trizygia* (trizygoid and straight vein) and *Paratrizygia* (trizygoid and curved vein). The plants of four lines in *Sphenophyl-*

Fig. 5. Vein aggregation shown in *Paratrizygia* and *Parasphenophyllum*. A: *Paratrizygia koboensis* (KOBATAKE) from Kobosan Series, Korea. B: *Parasphenophyllum okafujii* ASAMA et OISHI from the Upper Triassic of Japan. C: *Paratrizygia maiyaensis*.



laes evolved parallelly and the median vein appeared in the latest stage of both *Paratrizygia* and *Parasphenophyllum* Series. They are shown in Fig. 5, A (*Paratrizygia koboensis* from Kobosan Series of Korea, KIM et ASAMA, 1970) and Fig. 5, B (*Parasphenophyllum okafujii* from the Upper Triassic bed of Japan, ASAMA et OISHI, 1980). These median veins (midribs) in *Paratrizygia koboensis* and *Parasphenophyllum okafujii* were derived from the ancestral *Paratrizygia* and *Parasphenophyllum* by aggregating veins.

Principles of Growth Retardation (Principles of G. R.) mentioned above indicate the relation between plants and environmental change. Therefore these principles can be applicable to the plants in anywhere and any geological time. If we know the environmental changes through ages, we can deduce the change of plants and controversially we can deduce the change of environments from the change of fossil plants by using the principles of growth retardation and growth acceleration.

The ideas about phylogeny of vascular plants proposed by many botanists and paleobotanists differ from each other, and the present writer thinks that this disagreement of ideas depends upon the difference of each writer's standpoint. One author thinks reproductive organs to be most important character, and the other author thinks stem-structure to be more basic character for the determination of phyletic lines, and etc. Such characters as reproductive organs, vegetative organs and stem structures, had been changed through ages. The environments changed through Upper Paleozoic, Mesozoic and Cenozoic. Therefore plants must have changed their reproductive organs, vegetative organs and stem structures to adapt to new environments through ages. If the change of plants through ages are depending upon the environmental change, we can infer the phylogeny of plants by the principles of Growth Retardation.

Climatic change through ages and macro-evolution of vascular plants

Both principles of Growth Retardation described above and the climatic change postulated by the principles of G. R. are the basic concept for the research of phylogeny of vascular plants in this paper.

The majority of fossil plants found in geological ages are the leaf impression which have not been regarded important for the 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 clearly explained until present. The writer tried to explain the phylogenetic relation between them by using the principle of G. R.

The leaf forms of the Mesozoic plants were derived from those of the Paleozoic and ancestor of the former should be found in the latter.

If the environments change from age to age, the plants must also change their leaf form 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 changes of leaf forms by acceleration or retardation are systematic and not with random direction. Therefore if we know the principles of acceleration or retardation, we can restore the changed

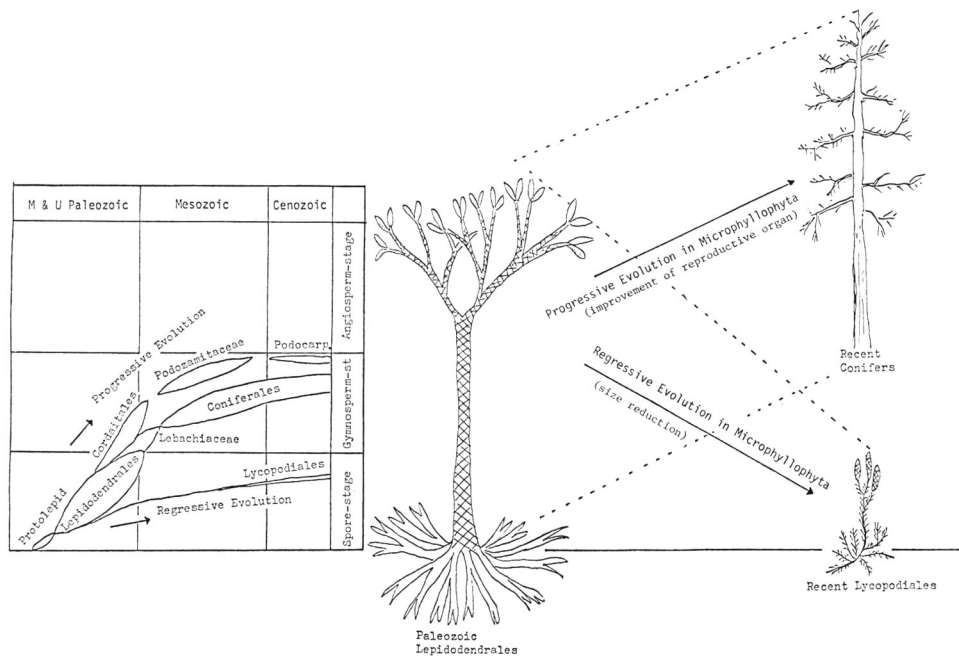


Fig. 6. Phylogeny of Microphyllphyta. Showing the progressive and regressive evolution.

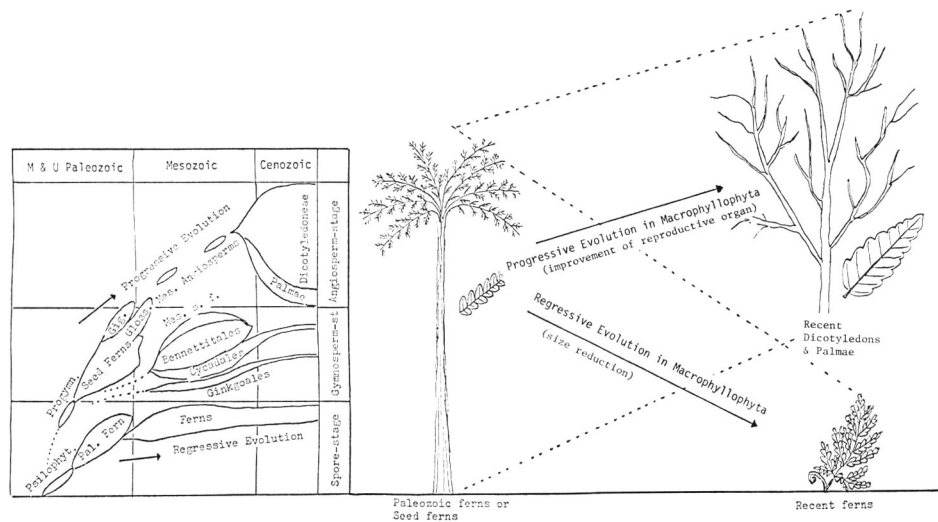


Fig. 7. Phylogeny of Macrophyllphyta. Showing the progressive and regressive evolution.

leaf forms to those before change. Using the principle of G. R. the writer found the phylogenetic relation between the Paleozoic, Mesozoic and Cenozoic plants.

1. Regressive evolution in pteridophytes

(1) Size reduction in Microphyllrophyta of spore-stage (Lycopsidea) (Fig. 6)

The most primitive land plants are found in the Silurian and Devonian, and are fewer comparing with the Carboniferous plants derived from them. It was Carboniferous that the land plants developed in maximum. The luxuriance of Carboniferous vegetation of spore-stage plants is well known and they are classified into three lines, Lycopsidea, Pteropsida and Sphenopsida by the characters of leaves and stem structure.

The most dominant lycopods in Upper Paleozoic are Lepidodendrales which contains Lepidodendraceae, Bothrodendraceae and Sigillariaceae. These plants were very tall arborescent trees attaining 20–30 m or more in height. But Recent lycopods are very small herbaceous plants and Triassic lycopods, *Pleuromeia*, are about 1 m in height. This means that Upper Paleozoic lycopods could grow to be very tall arborescent trees but Recent lycopods cannot grow to be trees and remains in small herbaceous condition. Mesozoic lycopods were derived from Paleozoic lycopods and Recent lycopods were derived from the Mesozoic ones. We must recognize the great size reduction in these lycopods-line.

(2) Size reduction in Macrophyllrophyta of spore-stage (Pteropsida) (Fig. 7)

In plants belonging to Macrophyllrophyta of spore-stage, such tall tree ferns as *Eospermatopteris* and *Archaeopteris* appeared as early as Middle or Upper Devonian. The former attained a height of 40 feet and the latter 100 feet (BANKS, 1970). These plants had homosporous or heterosporous like ferns but produced secondary xylem like that of gymnosperms. Therefore BECK (1962, etc.) has defined them as progymnosperms which must have been the ancestral plants of gymnosperms.

The marattiaceous tree ferns such as *Psaronius*, *Megaphyton* and *Cauropteris* were one of the dominating elements of the Upper Carboniferous and Permian forests. Their unbranched trunks attained a height of probably 50 feet or more. The recent marattiaceous ferns are all small herbaceous. Such Paleozoic ferns as *Archaeopteris* and marattiaceous ferns could grow to be tall tree ferns but Recent ones cannot grow to be tree ferns and remained in herbaceous habit. We must recognize the great size reduction in these marattiaceous ferns.

(3) Size reduction in Arthrophyta of spore-stage (Sphenopsida) (Fig. 8)

The representative plants of Arthrophyta of spore-stage are the Carboniferous *Calamites*, which attained the stem height of 20–30 meters and the pith casts 10–20 cm in diameter.

Paleozoic horsetails such as *Calamites* and *Phyllothea* had the more or less long whorled leaves and Mesozoic *Equisetites* which must have been derived from the Paleozoic horsetail had small leaves which were fused at the base. We must recognize the size reduction of leaves. In the Upper Triassic or the Early Jurassic the horsetails had attained a height of more than 10 m with hollow trunks whose internal diameter was up to 10 cm. Recent horsetails, *Equisetum*, are all small herbaceous plants.

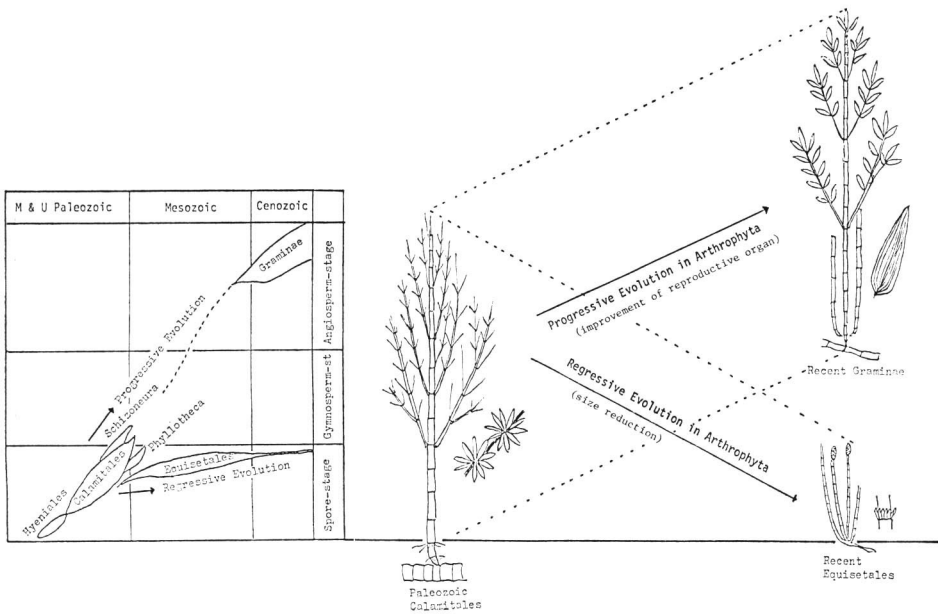


Fig. 8. Phylogeny of Arthropitya. Showing the progressive and regressive evolution.

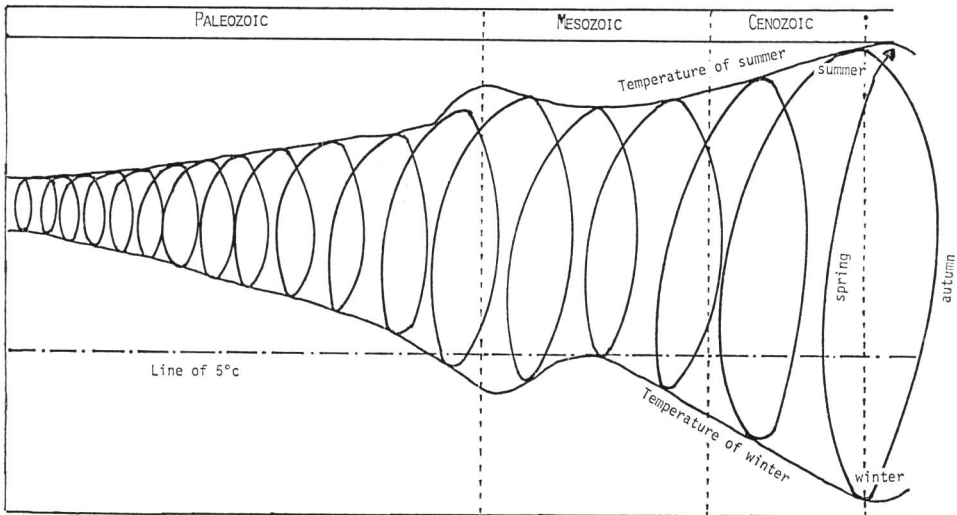


Fig. 9. Paleoclimatic change through ages speculated by the fossil evidence of the progressive and regressive evolution of vascular plants (in the middle latitude). The bulge in the Late Paleozoic and Early Mesozoic shows the effects by epirogenetic movement. The environments changed successively from simple to complex increasing annual range, but the former environment persisted in the later age. Namely, it contains only Paleozoic environment in Paleozoic, but Paleozoic and Mesozoic environments coexist in Mesozoic, and Paleozoic, Mesozoic and Cenozoic environments coexist at present. This is the reason why the pteridophyte, gymnosperm and angiosperm stages coexist at present.

The most characteristic feature in the horsetail line through ages is the great size reduction in both leaves and stems.

2. Progressive evolution of vascular plants.

As mentioned above the plants of three lines of spore-stage had reduced their size through ages without improving their reproductive organs. They had been adapted to the changing environments by reducing their size. The writer calls these change the regressive evolution. On the other hand, some plants of three lines had been adapted to the changing environments by grading up their reproductive organs. Reproductive organs had changed from homospore to heterospore, naked seed and pollen, enclosed seed and pollen, namely from pteridophytes to gymnosperms and angiosperms. Such grading up of reproductive organs had occurred parallelly in the plants of three lines. Therefore, the names of pteridophyte, gymnosperm and angiosperm correspond to the level of reproductive organs of vascular plants. The writer calls these leveling up of reproductive organs the progressive evolution.

3. Climatic change through ages

Vascular plants had two methods of adaptation for the changing environments. The one method is to reduce their size and the other method is to improve their reproductive organs. The former is the regressive evolution and the latter is the progressive evolution.

Judging from the regressive evolution of vascular plants the Upper Paleozoic environments were very mild for the growth of plants and even the plants of spore-stage could grow to be tall arborescent trees, but the recent environments are very severe for their growth and they cannot grow to be tall trees and remained in herbaceous habit. This means that the climate had changed from mild to severe for the growth of plants through ages. Considering the facts mentioned above and other evidences such as the change of paleobotanical provinces, the character of sediments, etc. the writer proposed the assumption of paleoclimatic change through ages (see Fig. 9). This assumption is that the annual range of temperature increased successively through geological ages. Therefore we cannot recognize either winter or summer in Paleozoic except Gondwanaland and it was the end of Mesozoic in which the true winter came in the northern hemisphere. The temperature of winter descended through Cenozoic successively, and the Quaternary glaciation process occurred when the lower ing of temperature attained its climax. Therefore, the cause of Quaternary glaciation distributed in both hemisphere was different from that of Permian glaciation which was confined its distribution to the southern hemisphere. The intense widening of the annual range of temperature successively made severe environments through ages, and to adapt these successive changes the vascular plants had to reduce their size in spore-stage and to change their reproductive organs from the spore to the naked seed and to the enclosed seed successively. If we accept the paleoclimatic change mentioned above, we can logically explain the evolutionary processes of regression, progression and diversification.

References

- ASAMA, K., 1959. Systematic study of so-called *Gigantopteris*. *Sci. Rep., Tohoku Univ.*, 2nd Ser. (Geol.), **31** (1): 1–72, pls. 1–20.
- 1960. Evolution of the leaf forms through the ages explained by the successive retardation and neoteny. *Ibid.*, Spec. Vol., **4**: 252–280, pls. 26–29.
- 1962. Evolution of Shansi flora and origin of simple leaf. *Ibid.*, Spec. Vol., **5**: 247–273, pls. 41–42.
- 1965. Cause and mechanism of plant evolution, Part 1. GR (Growth Retardation). *Natural Science and Museums*, **32** (1–2): 113–124. (In Japanese).
- 1966 a. Cause and mechanism of plant evolution, Part 2. Fusion and fused leaf. *Ibid.*, **33** (5–6): 65–77. (In Japanese).
- 1966 b. Cause and mechanism of plant evolution, Part 3. Enlargement and enlarged leaf. *Ibid.*, **33** (7–8): 135–146. (In Japanese).
- 1966 c. Cause and mechanism of plant evolution, Part 4. Mechanism of evolution; Shortening and Palmation. *Ibid.*, **33** (11–12): 185–200. (In Japanese).
- 1967. Cause and mechanism of plant evolution, Part 5. Cause of evolution; Directed evolution, parallel evolution and explosive evolution. *Ibid.*, **34** (1–2): 17–32. (In Japanese).
- 1968. Evolution of plants. *Biol. Sci.*, **19**: 145–152, **20**: 9–16. (In Japanese).
- 1969. What is evolution? *Natural Science and Museums*, **36** (5–6): 135–144. (In Japanese).
- 1970. Evolution and Classification of Sphenophyllales in Cathaysia Land. *Bull. Nat. Sci. Mus., Tokyo*, **13** (2): 291–317, pls. 1–7.
- 1972. Transformation of plants and environments through the geological ages. *Genetic*, **26** (1): 46–52. (In Japanese).
- 1975. Origin of Angiosperms. 1–400 pp., 164 figs. Tokyo, Sanseido. (In Japanese).
- 1977. Gondwanaland. 1–201 pp. Tokyo, Tairikushobo. (In Japanese).
- 1979 a. Why evolved plants and animals? 1–258 pp., 68 figs. Tokyo, Kodansha. (In Japanese).
- 1979 b. Evolution of Gymnosperms based on fossils. *Genetic*, **33** (6): 38–45. (In Japanese).
- 1979 c. Evolution and phylogeny of vascular plants. *Ann. Rep. Inst. Evol. Biol.*, **4–5**: 3–48. (In Japanese).
- 1980. Similarities in the patterns of macro-evolution of vascular plants and vertebrates. Prof. Saburo KANNO Memorial vol., 415–434.
- and T. KIMURA, 1977. Evolution of Plants. 1–321 pp., 123 figs. Kodansha. (In Japanese).
- and T. OISHI, 1980. Upper Triassic *Parasphenophyllum* (Order Sphenophyllales) from Omine, Western Japan. *Bull. Nat. Sci. Mus. Tokyo*, Ser C, **6** (4): 115–118.
- BANKS, H. P., 1970. Evolution and plants of the past. 1–170 pp., 81 figs. Belmont (California), Wadsworth Pub. Comp.
- BECK, C. B., 1962. Reconstructions of Archaeopteris, and further consideration of its phylogenetic position. *Amer. Jour. Bot.*, **49**: 373–382.
- HALLE, T. G., 1927. Paleozoic Plants from Central Shansi. *Palaeont. Sinica*, (A), **2** (1): 1–316, pls. 1–62.
- KAWASAKI, S., 1934. The flora of Heian System. Part. 4. *Bull. Geol. Surv. Korea*, **6** (4): 47–311.
- KIM, B. K. & K. ASAMA, 1970. Permian Sphenophyllales from the Eunseong Coal Mine. *Bull. Nat. Sci. Mus. Tokyo*, **13** (2): 319–330, pls. 1–2.
- LEE, H. H., 1963. Fossil plants of the Yuehmenkou Series, North China. *Paleont. Sinica*, New Series A, **6**: 1–185, pls. 1–45.
- LIU, H., 1959. Palaeogeographical map of China. 1–69 pp., 20 maps. Peking, Science Press.

