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TRIPHYLETIC EVOLUTION OF VASCULAR PLANTS

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ABSTRACT

Permian Shansi flora reveals the relation between the change of plants and the environments which is shown in the principles of Growth Retardation (abbreviated G. R.). The changes of plants in Palaeozoic, Mesozoic and Cenozoic are all explained by the principles of G. R., not by the principles of Growth Acceleration, which means that the environments in geological age must have been changed to the more and more unsuitable environments for the growth of plants. These environmental changes indicate the paleoclimatic change of increasing annual range of temperature. To adapt to these climatic changes the plants might have to change successively their form and function through geological age. We call these changes — evolution. Therefore the plants might have to change their form and function grading up from spore-stage (pteridophyte) to angiosperm-stage through gymnosperm-stage.

Palaeozoic pteridophytes have three lineages, namely, Lycopsida (have microphyll), Sphenopsida (have articulate stem) and Pteropsida (have macrophyll). The plants of these three lineages in Palaeozoic must have been changed parallelly their form and function grading up from spore-stage to angiosperm-stage through ages. Therefore it is reasonable to recognize the evolution of three lineages, Microphyta, Arthrophyta and Macrophyta.

Key-words — Triphyletic evolution, Pteridophytes, Microphyta, Arthrophyta, Macrophyta, Japan.

सारांश

संवहनी पौधों का त्रिजातिवृत्तीय विकास – काज़ुश्रो श्रसामा

पर्मियन कालीन शाँसी वनस्पतिजात पौधों के परिवर्त्तन एवं वातावरण में सहसंबंध व्यक्त करता है जिसे वृद्धि मंदन (जी॰ श्रार॰) के सिद्धान्तों द्वारा प्रदर्शित किया गया है। पेलियोज़ोइक, मीसोज़ोइक एवं सीनोज़ोइक युगों में पौधों के परिवर्तनों की व्याख्या वृद्धि त्वरण के द्वारा न होकर वृद्धि मंदन के सिद्धान्तों से होती है। जिसका श्रर्थ है कि भूवैज्ञानिक काल में पौधों की वृद्धि हेतु वातावरण श्रधिक से श्रधिक प्रतिकूल होते गये होंगे। ये वातावरणीय परिवर्तन तापक्रम की विस्तीर्यमान वार्षिक सीमा का पुरातापक्रमी परिवर्तन इंगित करते हैं। भूवैज्ञानिक काल में इन जलवायवी परिवर्तनों के श्रनुकूलित होने हेतु पौधों को श्रपने प्ररूप एवं कार्य को क्रमश: बदलना पड़ा होगा। इन परिवर्तनों को हम विकास कहते हैं। श्रतएव पौधों को बीजाणु श्रवस्था (टेरिडोफ़ाइट) से श्रनावृतबीजी-श्रवस्था द्वारा श्रावृतबीजी-श्रवस्था तक श्रपना प्ररूप एवं कार्य बदलना पड़ा होगा।

पेलियोज़ोइक टेरिडोफ़ाइटीयों के तीन वंशानुक्रम – लाइकोप्सीडा (लघुपर्ण वाले), स्फ़ीनॉप्सीडा (संधियुत तने वाले) एवं टेरोप्सीडा (बृहत् पर्ण वाले) – हैं। पेलियोज़ोइक युग में विभिन्न कालों में इन तीन वंशानुक्रमों के पौधों ने बीजाणु-श्रवस्था से श्रावृतबीजी-श्रवस्था तक विकसित होंने में श्रपने प्ररूप एवं कार्य को समानान्तर ढंग से परिवर्तित किया होगा। श्रतएव तीन वंशानुक्रमों – माइक्रोफ़ाइटा, श्रार्थ्रोफ़ाइटा एवं मैक्रोफ़ाइटा – के विकास को मान्यता देना तर्कसंगत है।

INTRODUCTION

IN 1974, the author wrote a paper "Origin of angiosperms inferred from the evolution of leaf form" and stated that the origin of angiospermous plants was not monophyletic but polyphyletic. Recently the author published three books and discussed about the evolution of plants in detail (Asama, 1975; Asama & Kimura, 1977; Asama, 1979a).

EVOLUTION OF SHANSI FLORA AND PRINCIPLES OF GROWTH RETARDATION

I studied the Permian plants from Shansi, China which had been described earlier by Halle (1927) in detail and observed the following evolutionary series in Shansi flora (Asama, 1959):

A. *Emplectopteris* Series (Text-fig. 1, Principle A, Fusion): *Emplectopteris triangularis* — *Gigantonoclea lagrelii* — *Bicoemplectopteris hallei* — *Tricoemplectopteris taiyuanensis*

B. *Emplectopteridium* Series (Text-fig. 1, Principle A, Fusion): *Emplectopteridium alatum* — *Bicoemplectopteridium longifolium* — *Gigantopteris nicotianaefolia*

C. *Konnoa* Series (Text-fig. 1, Principle B, Enlargement); *Konnoa penchihuensis* — *Cathaysiopteris whitei*

D. *Alethopteris* Series (Text-fig. 1, Principle B, Enlargement and Principle E, Shortening-palmation): *Alethopteris norinii* — *Protoblechnum wongii* — *Psygmophyllum multipartitum*

E. *Tingia* Series (Text-fig. 1, Principle B, Enlargement): *Tingia partita* — *T. carbonica* — *T. crassinervis*

F. *Trizygia* Series (Text-fig. 1, Principle B, Enlargement): *Trizygia oblongifolia* — *T. speciosa* — *T. sinocoreana* — *T. grandifolia*

G. *Lobatannularia* Series (Text-fig. 1, Principle B, Enlargement): *Lobatannularia sinensis* — *L. lignulata* — *L. heianensis*

Through these processes of evolution, the plants changed their leaf forms. And I have classified these type of processes into seven groups in terms of Principles of Growth Retardation, abbreviated G.R. (Text-fig. 1).

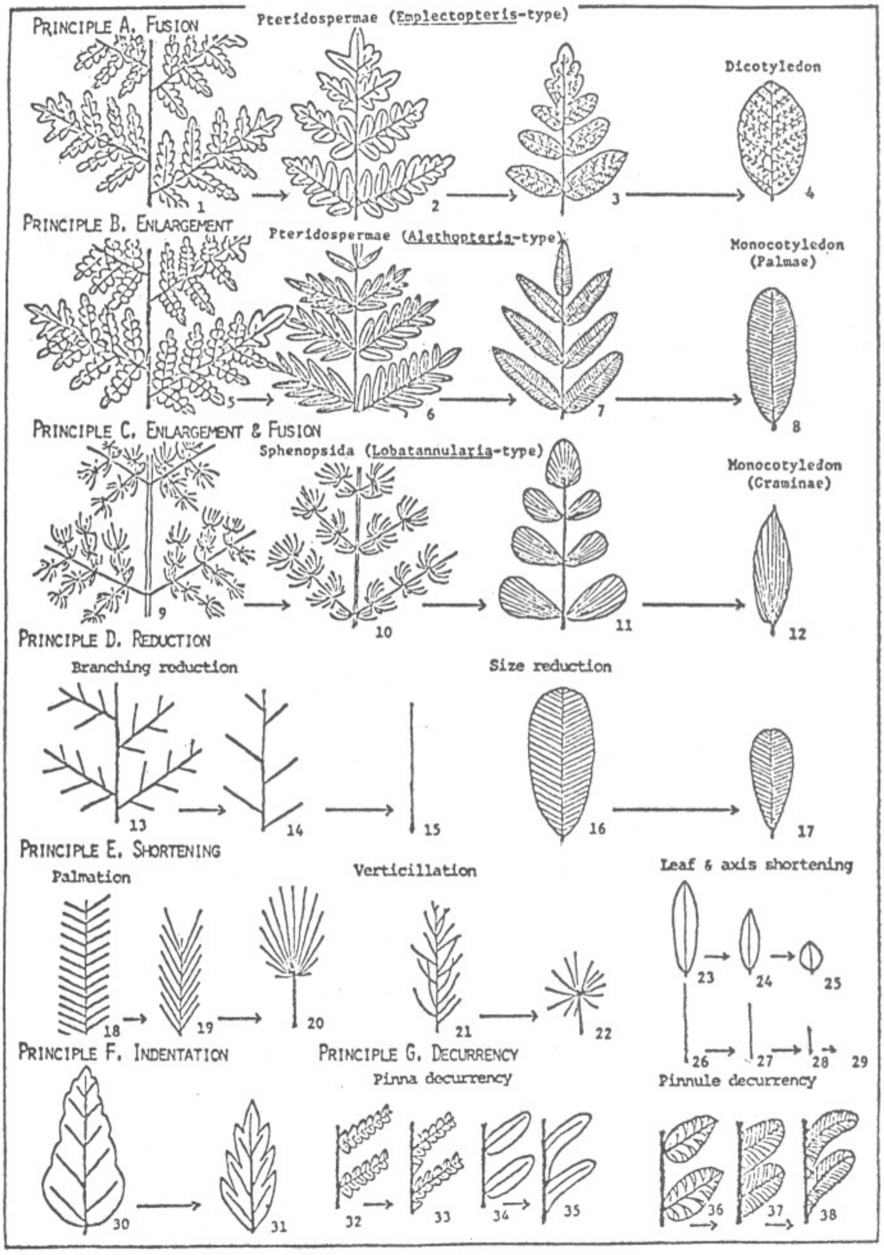
The changes explained by the principles above occurred when the plants became smaller (Text-fig. 1), by growth retardation showing the terminal abbreviation of ontogeny (the loss of late stage) (Asama, 1962; Takhtajan, 1969) and these principles may be called the principles of neoteny (Asama, 1960, 1979a). The cause of such changes among the plants of the Cathaysia flora can be found by examining the palaeogeography of the region. In the Cathaysia region the environment changed a mild oceanic climate to a continental climate by the upheaval of continent. Plants must have attained their full growth in a mild oceanic climate. But as the climate turned continental, their growth was retarded, and their size was diminished. Consequently, various changes occurred in their leaf form. Fusion and enlargement were particularly significant changes.

The principles of G.R., based on the evolution of leaf form of the plants in the Cathaysia flora, are very important, because they indicate that the environmental changes are closely related to the leaf form changes. Therefore the principles ought to be applicable to any geological ages and regions. By correlating the leaf form changes in a given geological age with the principles, the environmental change of that period causing the leaf transformation can be inferred. And, conversely, by determining the environmental changes of a certain region from certain phenomena (such as appearance of glaciers, arid climate, etc.), we can infer resultant changes of leaf form in that region.

I have examined the leaf form changes in various geological ages and found that all changes can be explained by the principles of Growth Retardation, without a single case in favour of Growth Acceleration (G.A.). This means that the environment of the geological ages responsible for the leaf form changes gradually worsened. To interpret this, the writer assumed that the environmental change of the geological ages was a climatic change in which the annual range gradually increased (Asama, 1960, 1962, 1975, 1979a, 1979b) (see Text-fig. 8).

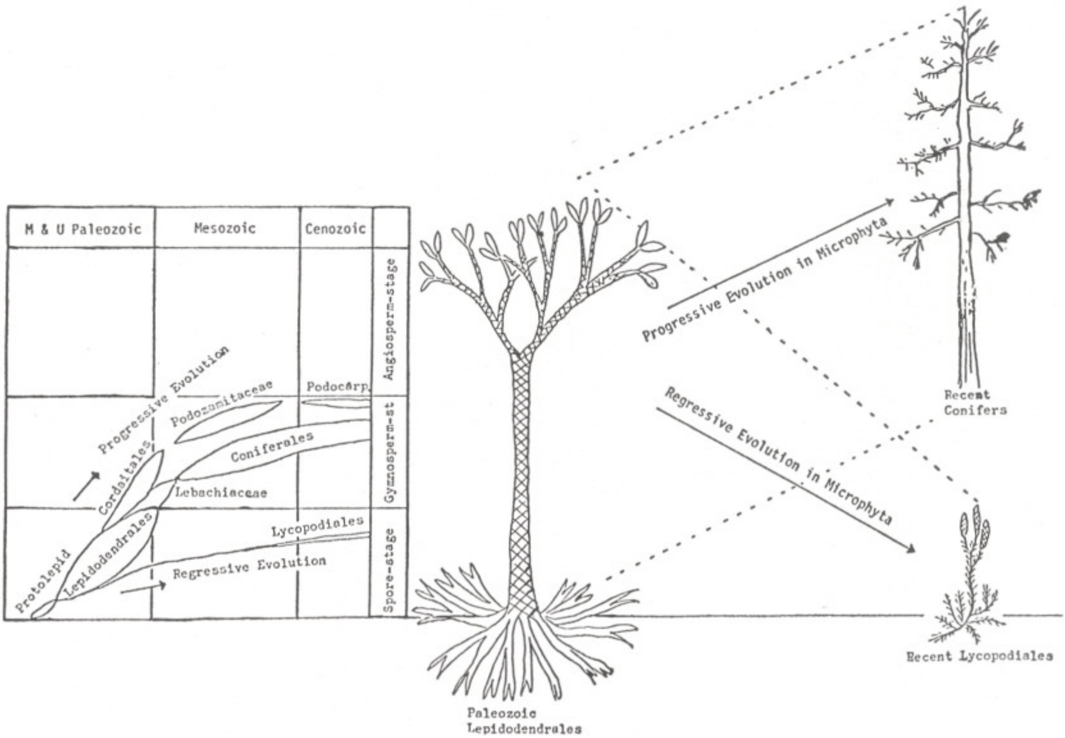
THREE LINEAGES OF VASCULAR PLANTS

Palaeozoic pteridophytes are classified into Psilophytopsida, Lycopsida, Sphenopsida and Pteropsida by the characteristics of leaves or stems such as naked stem, microphyll, articulate stem and macrophyll respectively. Psilophytopsida consists of Rhyniaceae, Zosterophyllaceae, Psilophytaceae and Asteroxylaceae. But Sporne (1975) thinks that Asteroxylaceae belongs to Lycopsida and I am also of the same opinion. Psilophytopsida, except Asteroxylaceae, is not the ancestral type of all vascular plants but only that of Pteropsida. Therefore there had been the plants of three types, Lycopsida, Sphenopsida and Pteropsida in the Early Devonian.



TEXT-FIG. 1 — 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, Palaeozoic, Mesozoic and Cenozoic will be explained by these principles indicating that the environments change successively mild to severer, simple to more complex through geological ages. Therefore the paleoclimatic change shown in Text-fig. 8 was speculated.

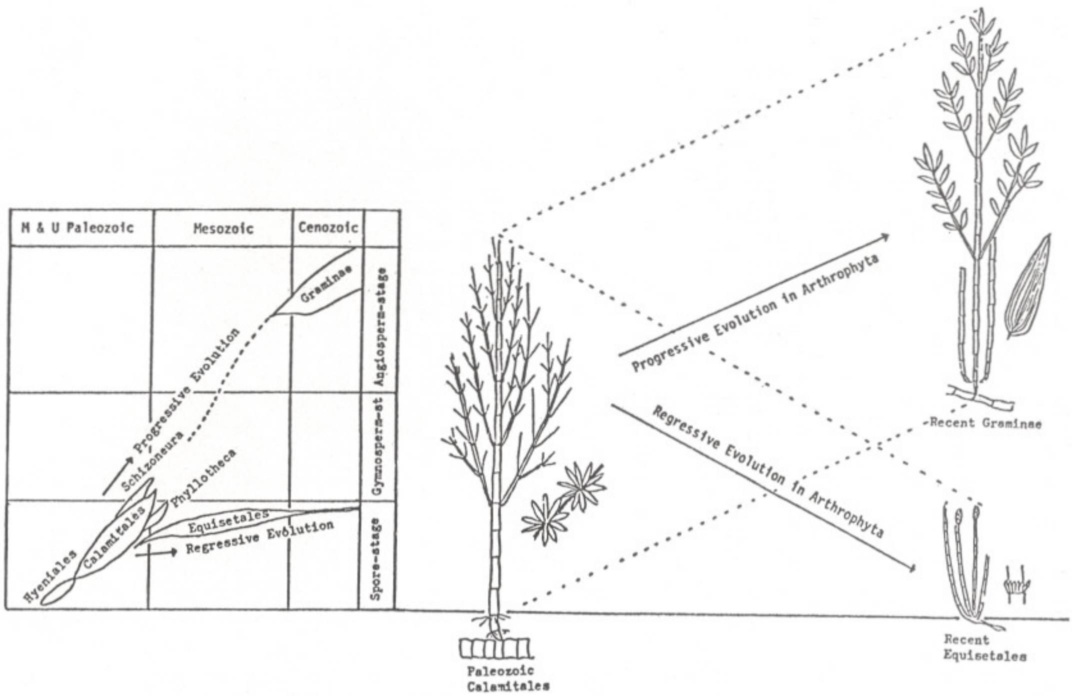
Plants of the geological age changed regularly their leaf forms in response to the environmental change in where they live. And their changes are always explained by principles of Growth Retardation. Therefore we must recognize that such characteristics as microphyll, macrophyll and articulate stem are the inherent



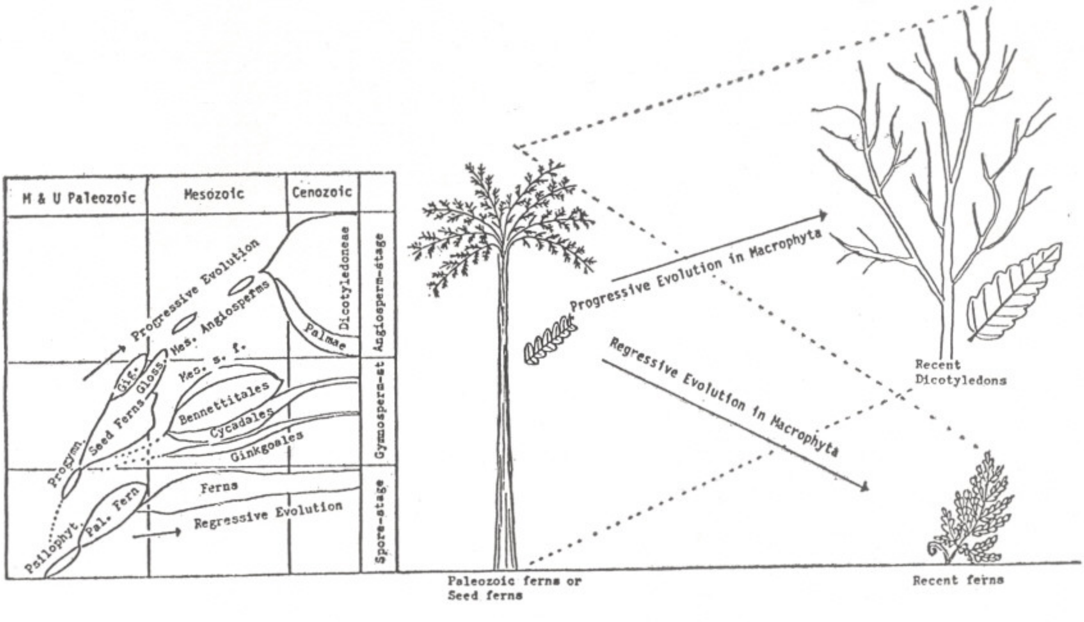
TEXT-FIG. 2 — Phylogeny of Microphyta (Asama, 1975). Showing the progressive and regressive evolution.

characters of each lineage and that these characteristics have never been lost in recent plants showing each lineage. Therefore I have classified the vascular plants into three lineages, Microphyta (Lycopsida and its descendants), Macrophyta (Pteropsida and its descendants) and Arthrophyta (Sphenopsida and its descendants). The plants of these three lineages have been evolved, parallelly from the stage of spore to the stage of angiosperms through that of gymnosperms as shown in Text-figures 2, 3 and 4.

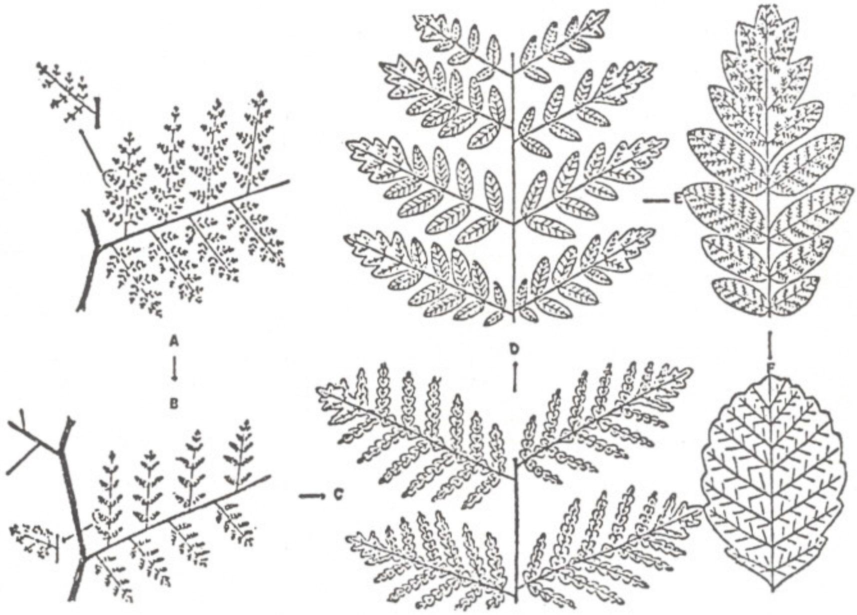
In general, the leaves of Microphyta and Arthrophyta are microphylls showing small type of leaves but they show sometimes large type of leaves gathering many microphylls (see Text-fig. 1, Principle C; such leaves as *Schizoneura*, Graminae, Cordaitales, Podozamitaceae, Podocarpaceae, etc.). The leaves of Macrophyta are macrophylls showing large type of leaves but they show sometimes small type of leaves reducing their size as shown in plants of desert. Even though plants have large type of leaves, they are the plants belonging to Microphyta, if they have the leaves derived from microphylls. Reversely even though plants have small type of leaves they are plants belonging to Macrophyta, if they have the leaves derived from macrophylls. The relation between the leaf size and lineage is very important. The plants having large type of leaves are not always plants belonging to Macrophyta and those having small type of leaves are not always plants belonging to Microphyta. Sometimes plants of Microphyta and Macrophyta may have articulate stem caused by shortening of stem (Text-fig. 1, Principle E, Shortening-Verticillation). But they do not belong to Arthrophyta because the articulate secondary stems were derived by G.R. from the non-articulate primary stems (example: a part of Palmae, etc.). The judgement of lineage must be determined by original type of leaves or stems. In general, the plants of some order belong to Arthrophyta, if they have only articulate stems and belong to Macrophyta or Microphyta, if they have mixed stems, namely some plants have



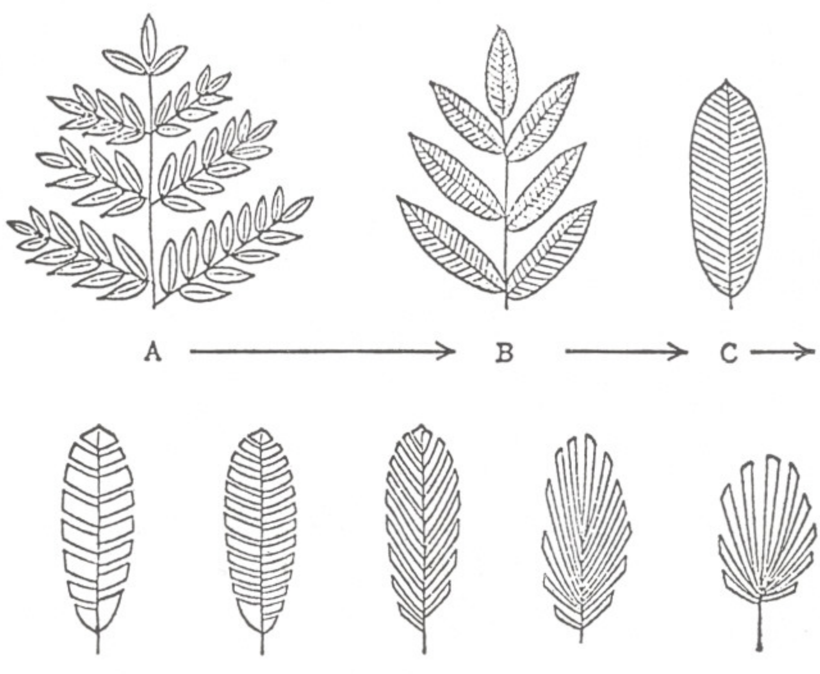
TEXT-FIG. 3 — Phylogeny of Arthrophyta (Asama, 1975). Showing the progressive and regressive evolution.



TEXT-FIG. 4 — Phylogeny of Macrophyta (Asama, 1975). Showing the progressive and regressive evolution.



TEXT-FIG 5 — Simple leaf forming process by Growth Retardation. **A.** Devonian type. **B.** Carboniferous type. **C-F.** Permian type.



TEXT-FIG. 6 — Leaf forming process in monocotyledonous plants I (Palmae).

articulate stems and other plants have non-articulate stems.

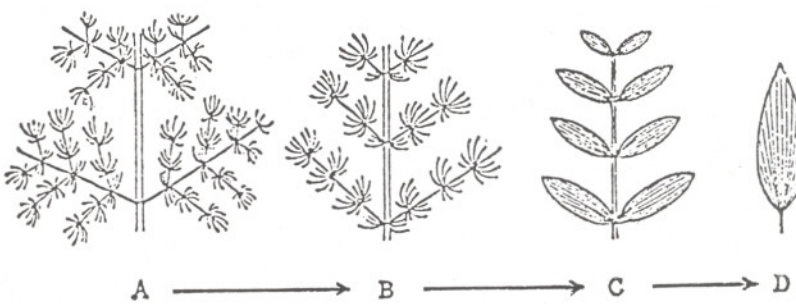
Angiosperms are the most advanced type of vascular plants and simple leaf is the basic form in angiospermous plants. Recent angiospermous plants generally have simple leaves or broad leaves in both monocotyledons and dicotyledons, so we must clear the simple leaf-forming process which had taken place in geological ages. These processes which found in dicotyledons and monocotyledons (Palmae and Graminae) are shown in Text-figures 5, 6 and 7.

Greguss (1964) proposed the triphyletic evolution of the land plants. He thought that branching has a decisive role in the history of evolution of the vegetable kingdom. He classified land plants into three lineages by such branching as monopodial, dichotomous and verticillate. But I think that such leaf or stem characters as microphyll, macrophyll and articulate stem are more important characters than branching system.

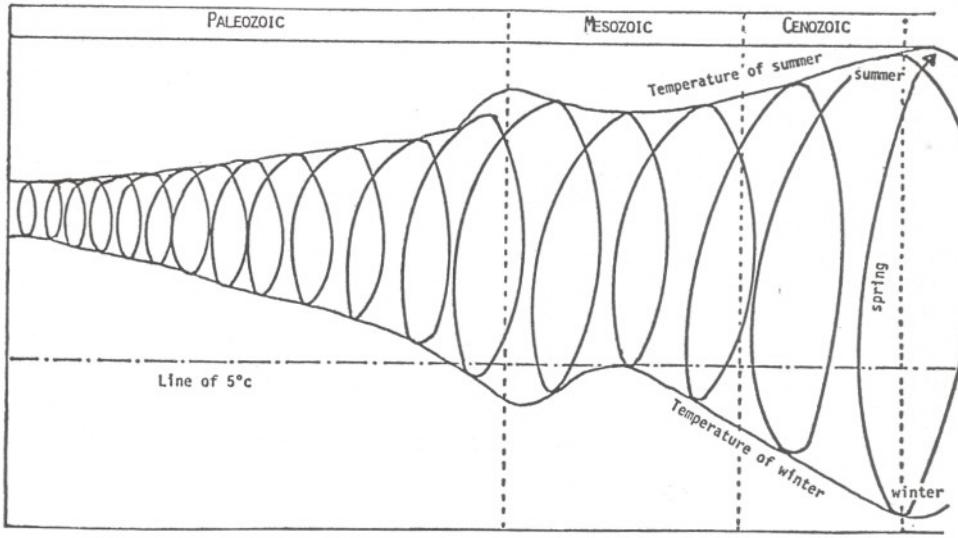
REGRESSIVE AND PROGRESSIVE EVOLUTION IN VASCULAR PLANTS AND THE CLIMATIC CHANGE THROUGH AGES

We can find two evolutionary trends in each lineage — regressive evolution and progressive evolution. As shown in Text-fig. 2, recent Lycopodiales and Coniferales are derived from the ancestral Palaeozoic Lepidodendrales. The former did not change their reproductive method and remained in the spore stage. The latter, changed their reproductive method to more advanced naked seed (Gymnosperm stage). In the case of the former we find the remarkable size reduction. Palaeozoic lycopods were giant arborescent trees but recent lycopods are very small herbaceous (see Text-fig. 2). Therefore such change may be referred as regressive evolution. In the case of the latter the reproductive organ was improved from spore to seed and new characters were added successively and these changes have been named as progressive evolution.

We can find the same manner of changes in Macrophyta and Arthrophyta as shown in Text-figures 3 and 4. In both Macrophyta and Arthrophyta the reproductive organ was improved from spore to the enclosed seed (Angiosperm-stages) that means the most advanced reproductive method. In the regressive groups of each lineage we find remarkable size reduction in the vegetative organ parallelly and this means that Palaeozoic lycopods, horsetails and ferns could grow to giant trees but recent lycopods, horsetails and ferns cannot grow to trees. From the facts, mentioned above we can recognize that the environment of Palaeozoic was so suitable for the growth of plants that Palaeozoic plants could grow to giant trees but the recent environment is so severe for the growth of plants that they cannot grow to trees and are remaining in the herbaceous condition. The plant changes in geological ages were all explained by the principles of Growth Retardation. To interpret these facts theoretically the writer proposed the assumption of palaeoclimatic change through ages (see Text-fig. 8). This assumption is that the annual range of temperature increased successively through geological ages. Therefore we cannot recognize both winter and summer in Palaeozoic and it was the end of Mesozoic to occur true winter



TEXT-FIG. 7 — Leaf forming process in monocotyledonous plants II (Graminae).



TEXT-FIG. 8 — Paleoclimatic change through ages speculated by the fossil evidence of the progressive and regressive evolution of vascular plants (in middle latitude). The bulge in the Late Palaeozoic and Early Mesozoic shows the effects by epeirogenetic movement. The environments changed successively simple to complex by the increasing annual range remaining the former environments before change. Namely, it contains only Palaeozoic environment in Palaeozoic but coexists Palaeozoic and Mesozoic environments in Mesozoic and coexists Palaeozoic, Mesozoic and Cenozoic environments at present. This is the reason why it can coexist the plants in the pteridophyte, gymnosperm and angiosperm stage at present.

in the northern hemisphere. The temperature of winter was descending through Cenozoic successively and the Quaternary glaciation occurred when the lowering of temperature attained its climax. Therefore the cause of Quaternary glaciation distributed in both hemispheres was different from that of Permian glaciation confined its distribution in southern hemisphere.

The increasing annual range of temperature made more severer environment through ages successively and to adapt these successive environmental change the vascular plants might have been changed their reproductive organ from spore to enclosed seed through naked seed successively.

Can we find any cause of regressive and progressive evolution except the palaeoclimatic change of increasing annual range ? By this palaeoclimatic change we can explain the cause of vascular plant evolution theoretically. If we accept the palaeoclimatic change mentioned above, we can explain the evolutionary processes of regression, progression and diversification theoretically.

CLASSIFICATION OF VASCULAR PLANTS

The plants of three lineages, Microphyta, Macrophyta and Arthrophyta, had been changed successively by their forms and functions to adapt to more severer environments from Palaeozoic to Cenozoic. They could adapt to the environments by decreasing their size in the regressive group and by improving their reproductive organ in the progressive group through ages respectively. Therefore they have been classified as follows (see Text-figs 2, 3, 4)..

I. Microphyta

A. Microphyll-sporophyta (Lycopsida) ...... Spore-stage

Protolepidodendrales   Lepidodendrales

Selaginellales   Isoetales

B. Microphyll-gymnospermophyta .... Gymnosperm (naked seed)-stage

Cordaitales Podozamitaceae Podocarpaceae

Lebachiaceae Coniferales

C. Microphyll-angiospermophyta .... Angiosperm (enclosed seed)-stage

unknown

II. Macrophyta

A. Macrophyll-sporophyta (Pteropsida) ...... Spore-stage

Protoperidiales Aneurophytales Coenopteridiales

Archaeopteridales Cladoxylales Noeggerathiales

Marattiales Osmundales Filicales

Ophioglossales

B. Macrophyll-gymnospermophyta .... Gymnosperm (naked seed)-stage

Pteridospermae Ginkgoales Bennettitales

Nilssoniales Cycadales Pentoxylales

Caytoniales

C. Macrophyll-angiospermophyta .... Angiosperm (enclosed seed)-stage

Dicotyledoneae

Monocotyledoneae (except Graminae)

III. Arthrophyta

A. Articulate-sporophyta (Sphenopsida) ....Spore-stage

Hyeniales Pseudoborniales Sphenophyllales

Calamitales Neocalamitales Equisetales

B. Articulate-gymnospermophyta .... Gymnosperm (naked seed)-stage

Calamocarpaceae ?

C. Articulate-angiospermophyta .... Angiosperm (enclosed seed)-stage

Graminae

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