Bull. Natn. Sci. Mus., Tokyo, Ser. C, 9 (1), March 22, 1983

Evolution and Phylogeny of Vascular Plants based on the Principles of Growth Retardation. Part 7. Conclusion— Considerations on the Continuous Growth Retardation and Evolutionary Thoughts

By

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The writer discussed on the evolution and phylogeny of vascular plants in the following papers:

Part 1. Principles of Growth Retardation and climatic change through ages (1981a)
Part 2. Phylogeny of Microphyllophyta (1981b)
Part 3. Phylogeny of Macrophyllophyta in Devonian (1981c)
Part 4. Phylogeny of Macrophyllophyta inferred from the evolution of leaf forms (1982a)
Part 5. Origin of angiosperms inferred from the evolution of leaf forms (1982b)
Part 6. Triphyletic evolution of vascular plants (1982c)
Part 7. Conclusion — Considerations on the continuous Growth Retardation and evolutionary thoughts (this paper)

In these papers the writer tried to discuss on the relation between the macroevolution of vascular plants and the macroclimatic changes through ages, and found the facts that the evolution of vascular plants have been the adaptable changes to the changing environments, which means the climatic changes from mild to severe. The writer proposed the Principles of Growth Retardation to explain the evolutionary changes of vascular plants through the ages, and proposed the new idea of the macroclimatic change of increasing annual range through the ages using these principles.

Phylogenetic trees of vascular plants

1) Phylogeny and supposed ontogeny of macrophyll series in the multiplication stage

BANKS (1970, 1975) suggested the evolutionary line from *Rhynia*-type to *Psilophyton*-type, Progymnosperms and to seed ferns. If so, we are able to consider the evolutionary line from Rhyniales to Trimerophytales, Aneurophytales and to Archaeopteridales, which is shown in Fig. 1. Rhyniales are characterized by dichotomous branches, Trimerophytales by main stem with lateral dichotomous branches, Aneurophytales by main stem and primary branches with lateral dichotomous branches, and Archaeopteridales by bipinnate compound leaf. These evolutionary process are

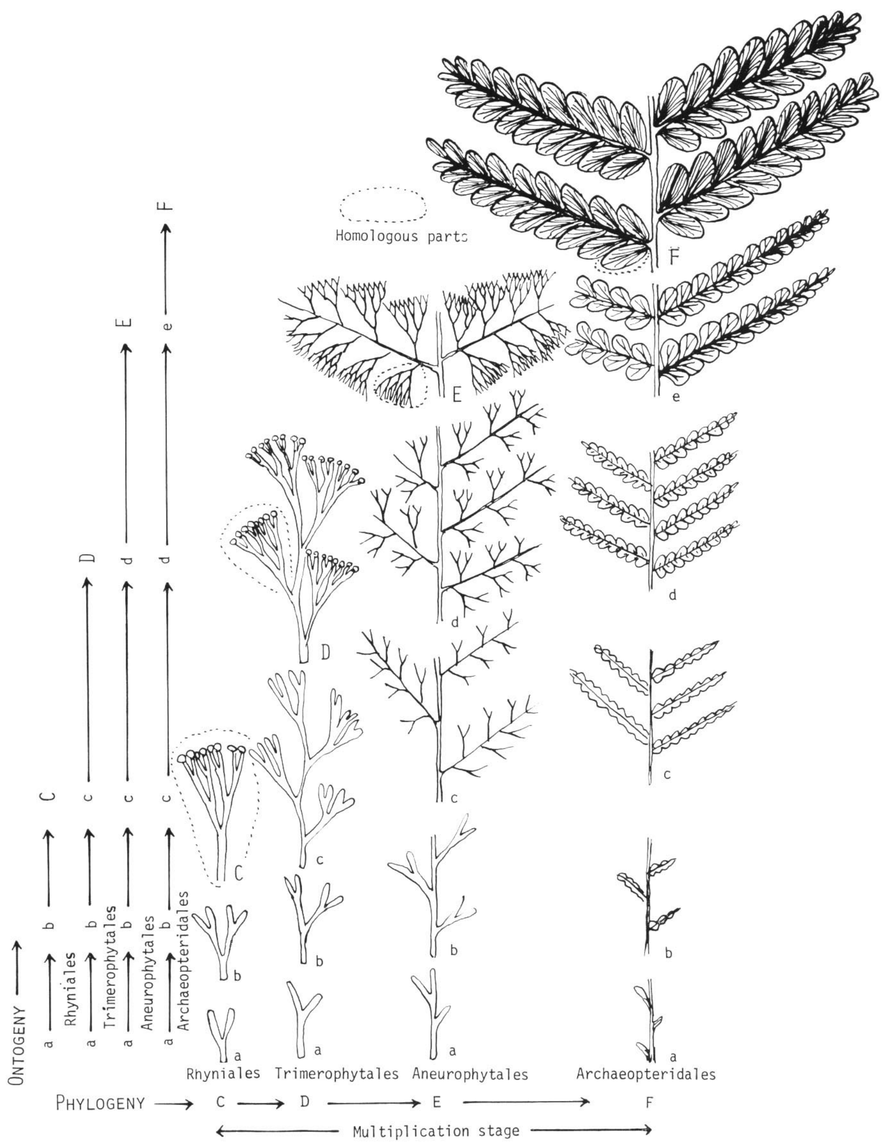
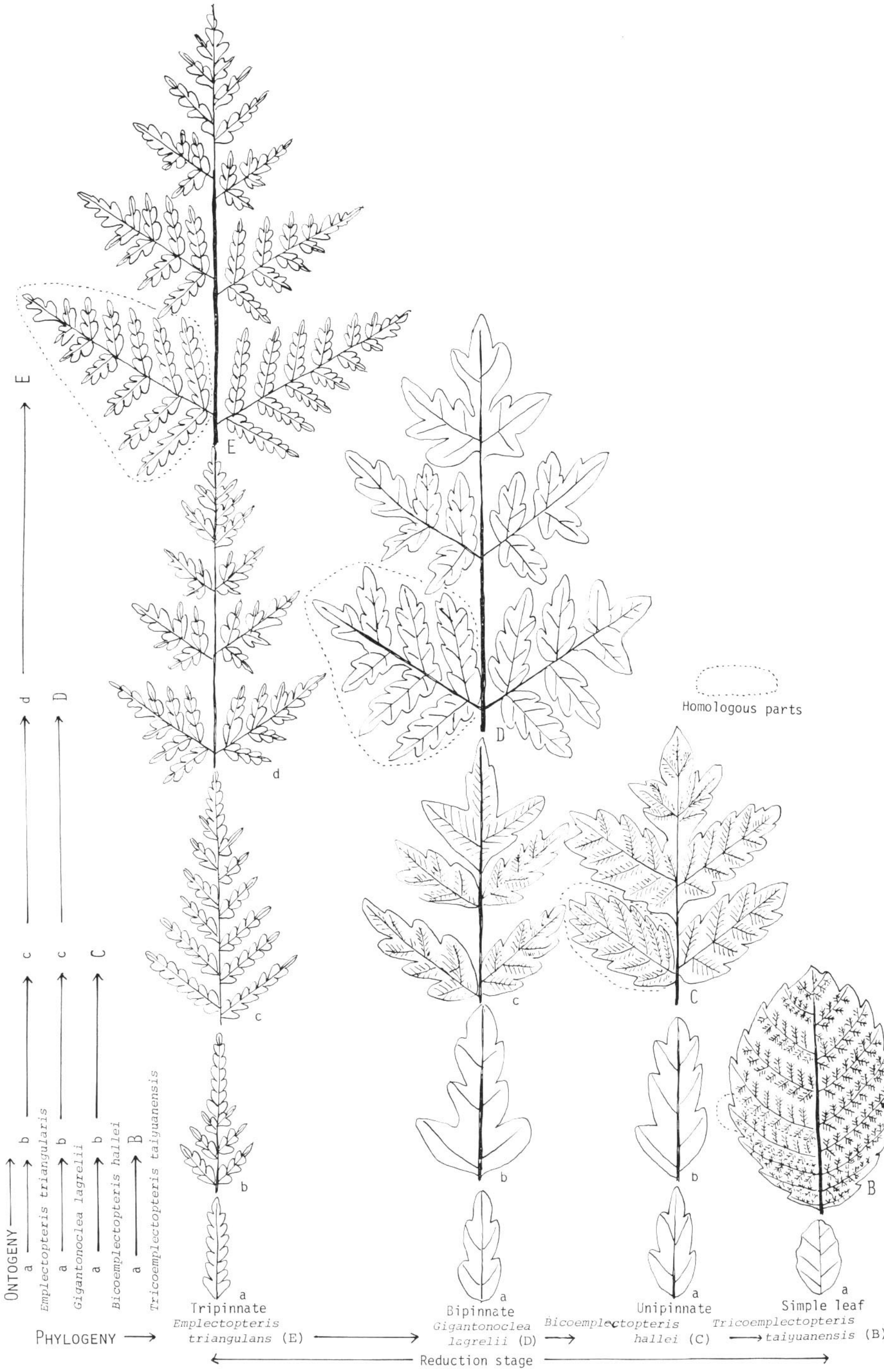


Fig. 1. Phylogeny and supposed ontogeny of macrophyll series in the multiplication stage. Naked branches became larger step by step elongating their ontogeny and formed pinnate leaf at final stage.

Fig. 2. Phylogeny and supposed ontogeny of macrophyll series in the reduction stage. Pinnate leaf became smaller step by step reducing their ontogeny and formed simple leaf at final stage.


ONTOGENY →
a → b → c → d → E
Emplectopteris triangularis
a → b → c → D
Gigantonoclea lagrelii
a → b → C
Bicoemplectopteris hallei
a → B
Tricoemplectopteris taiyuanensis
Homologous parts
Tripinnate
Emplectopteris triangulans (E)
Bipinnate
Gigantonoclea lagrelii (D)
Unipinnate
Bicoemplectopteris hallei (C)
Simple leaf
Tricoemplectopteris taiyuanensis (B)
PHYLOGENY →
Reduction stage

shown in the following table and Fig. 1:

	Ontogeny
Rhyniales:	a →b →C (dichotomous branches)
Trimerophytales:	a →b →c →D (main stem+lateral dichotomous branches)
Aneurophytales:	a →b →c →d →E (main stem+primary branches+lateral dichotomous branches)
Archaeopteridales:	a →b →c →d →e →F (bipinnate compound leaf)
Phylogeny:	C →D →E →F

small letters: plants of young stage

capital letters: plants of mature stage

Plants belonging to Rhyniales had been changed to those of Trimerophytales, Aneurophytales and Archaeopteridales elongating their ontogeny step by step. The small naked branches of Rhyniales changed to very large trees with bipinnate compound leaves such as *Archaeopteris* by the elongation of their ontogeny step by step.

2) Phylogeny and supposed ontogeny of macrophyll series in the reduction stage

As stated in Part 1 (ASAMA, 1981a, p. 65) the tripinnate *Emplectopteris triangularis* had changed to the bipinnate *Gigantonoclea lagrelii,* unipinnate *Bicoemplectopteris hallei* and to the simple leaf *Tricoemplectopteris taiyuanensis* reducing their branches step by step. Their phylogeny and supposed ontogeny are shown in the following table and Fig. 2.

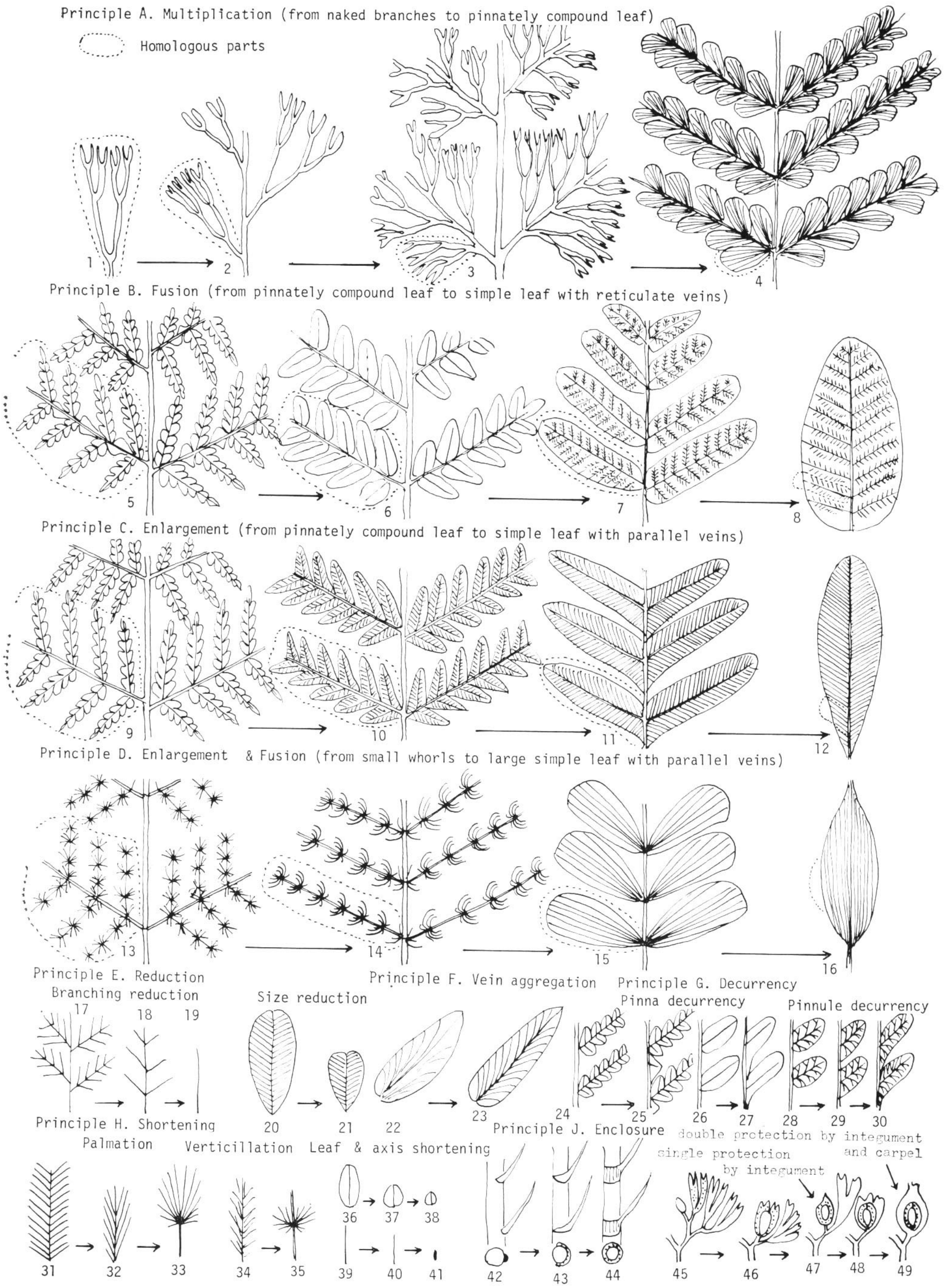
	Ontogeny	
Emplectopteris triangularis:	a →b →c →d →E	(Tripinnate)
Gigantonoclea lagrelii:	a →b →c →D	(Bipinnate)
Bicoemplectopteris hallei:	a →b →C	(Unipinnate)
Tricoemplectopteris taiyuanensis:	a →B	(Simple leaf)
Phylogeny:	B ←C ←D ←E	

The tripinnate *Emplectopteris triangularis* had been changed to the simple leaf *Tricoemplectopteris taiyuanensis* reducing their ontogeny step by step and very large leaf of *Emplectopteris triangularis* changed to small simple leaf of *Tricoemplectopteris taiyuanensis* reducing their leaf size step by step.

3) Elongation and reduction of ontogeny in the macrophyll series

There were two different stages in the evolution of leaf forms in macrophyll series, the multiplication stage and the reduction stage. The former indicates the pinnately compound leaf-forming stage and the latter indicates the simple leaf-forming stage respectively (ASAMA, 1982a, Fig. 1; 1982c, Fig. 4). We can observe the former process of evolution in the Devonian plants and the latter process in the Carboniferous and

Fig. 3. Principles of Growth Retardation. These principles except Multiplication may be called the principles of neoteny in the evolution of vascular plants.


Principle A. Multiplication (from naked branches to pinnately compound leaf)
Homologous parts
1
2
3
4
Principle B. Fusion (from pinnately compound leaf to simple leaf with reticulate veins)
5
6
7
8
Principle C. Enlargement (from pinnately compound leaf to simple leaf with parallel veins)
9
10
11
12
Principle D. Enlargement & Fusion (from small whorls to large simple leaf with parallel veins)
13
14
15
16
Principle E. Reduction
Branching reduction
17
18
19
Size reduction
20
21
22
Principle F. Vein aggregation
23
Principle G. Decurrency
Pinna decurrency
24
25
26
27
Pinnule decurrency
28
29
30
Principle H. Shortening
Palmation
31
32
33
Verticillation
34
35
Leaf & axis shortening
36
37
38
39
40
41
Principle J. Enclosure
42
43
44
double protection by integument and carpel
single protection by integument
45
46
47
48
49

Permian plants.

The plants belonging to Rhyniales, Trimerophytales and Aneurophytales had no leaves and had only dichotomous branch systems which changed to bipinnate compound leaf of Archaeopteridales by fusion of dichotomous branches and by reducing the secondary xylem of rachis, namely, the bipinnately compound leaves were formed in Archaeopteridales at first. These bipinnately compound leaves indicate the intermediate leaves between the branch systems and true leaves. Because the bipinnately compound leaves of *Archaeopteris* had the secondary xylems in their rachis, which does not mean the true leaves of Recent macrophyllous plants.

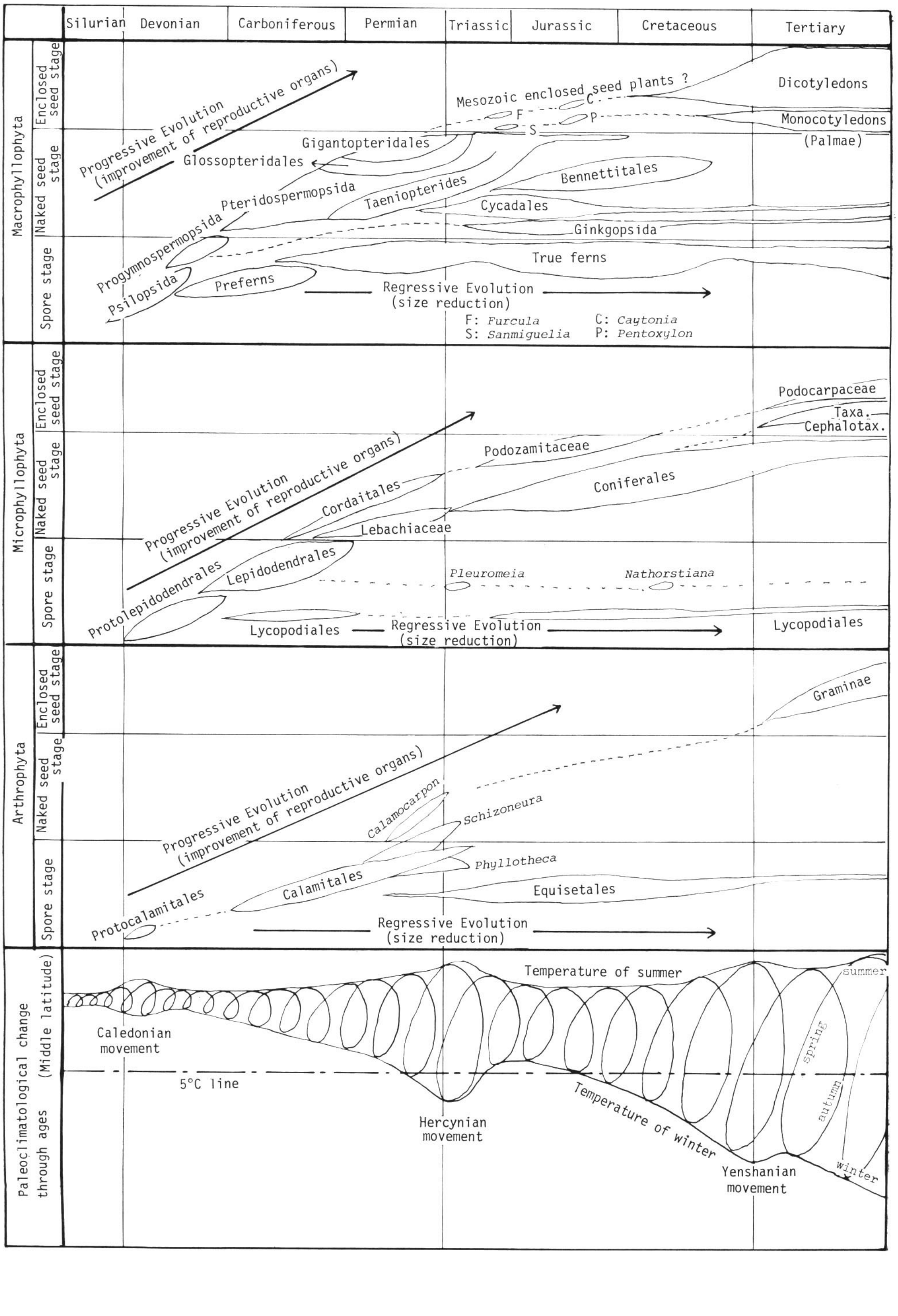
The leaves had become larger by the elongation of ontogeny in the pinnately compound leaf-forming stage and had become smaller by the reduction of ontogeny in the simple leaf-forming stage. The plants had acquired the new characters in the stem-structure step by step in the former case and had not acquired the new characters in the petiole-structure step by step in the latter case. Therefore the plants had increased their size in the former case and had decreased their size in the latter case. But the plants in the latter case could improve their reproductive organs from spores to naked seeds and to enclosed seeds, and their conductive tissues from tracheids to vessels by reduction of their leaves. The elongation of ontogeny means acquirement of new characters and the reduction of ontogeny means no acquirement of new characters in the inner structute of rachis.

4) Principles of Growth Retardation

Principles of Growth Retardation and macroclimatic change, which are derived from the continuous Growth Retardation and the increasing zoning of plant distribution through ages, are the fundamental conception to explain the evolution of vascular plants. Principles of Growth Retardation shown in Part 1, Fig. 2 (Asama, 1981a, Fig. 63) are revised and two new principles (Multiplication and Enclosure) are added to the Principles (Fig. 3). The writer believes that all evolutionary changes of vascular plants are explainable by these principles, that is the continuous increase of unfavorable climatic changes to controling the growth of plants (Fig. 4). One of the principles, Multiplication, indicates the change in the multiplication stage, and other 8 principles indicate those of the reduction stage. Plants changed by reduction resemble the plants of young stage before change reducing the process of their ontogeny step by step in the reduction stage, which means the neotenic change. Therefore the principles of Growth Retardation except Multiplication may indicating the principles of neoteny in the evolution of plants.

There were two types of stages in the evolution of macrophyll series, the one is the multiplication stage and the other is the reduction stage. Plants had become larger elongating their ontogeny in the case of the former and in the case of the latter they had become smaller reducing their ontogenetic process. In both cases the homolog-

Fig. 4. Three lines of phylogenetic trees and macroclimatic change of increasing annual range deduced by the continuous Growth Retardation of plants and zonig of floral distribution.



Silurian
Devonian
Carboniferous
Permian
Triassic
Jurassic
Cretaceous
Tertiary
Macrophyllophyta
Enclosed seed stage
Naked seed stage
Spore stage
Progressive Evolution
(improvement of reproductive organs)
Mesozoic enclosed seed plants ?
F
C
S
P
Dicotyledons
Monocotyledons
(Palmae)
Gigantopteridales
Glossopteridales
Bennettitales
Pteridospermopsida
Taeniopterides
Cycadales
Ginkgopsida
Progymnospermopsida
True ferns
Psilopsida
Preferns
Regressive Evolution
(size reduction)
F: Furcula
S: Sanmiguelia
C: Caytonia
P: Pentoxylon
Microphyllophyta
Podocarpaceae
Taxa.
Cephalotax.
Podozamitaceae
Coniferales
Cordaitales
Lebachiaceae
Lepidodendrales
Protolepidodendrales
Pleuromeia
Nathorstiana
Lycopodiales
Arthrophyta
Graminae
Calamocarpon
Schizoneura
Phyllotheca
Calamitales
Equisetales
Protocalamitales
Paleoclimatological change through ages (Middle latitude)
Temperature of summer
summer
spring
autumn
winter
Caledonian movement
5°C line
Hercynian movement
Temperature of winter
Yenshanian movement

ous parts were reduced as shown in Fig. 3, namely, the evolution of marcrophyll series are totally explainable by the continuous Growth Retardation.

5) Three phylogenetic trees of vascular plants based on the principles of Growth Retardation

There were three lines of characteristic plants in the Early Devonian; *Cooksonia, Steganotheca* and *Rhynia* characterized by the dichotomous naked branches; *Drepanophycus, Baragwanathia* and *Protolepidodendron* characterized by the microphylls; and *Equisetophyton* characterized by the articulate stems. There are great morphological differences between the naked branches of Rhyniales, the microphylls of Protolepidodendrales and the articulate stems of Protocalamitales. And these three lines of plants have been found in Siegenian, which means that the morphological differences between these three lines of plants are too large to admit ZIMMERMANN's telome theory. Therefore present writer considered that ZIMMERMANN's theory can only explain the evolution of macrophyll series (Fig. 1 and Fig. 4, Macrophyllophyta), but not the evolution of microphyll series and articulate stem series (ASAMA, 1981b, p. 103). Silurian *Baragwanathia* (GARRATT, 1978) supports this interpretation.

These three lines of plants had been affected by the same environmental changes through ages. The environmental changes means the climatic change which shown in Fig. 4, from the Paleozoic mild to the Recent severe climate. If these climatic changes are correct, it will be expected that three lines of vascular plants would change their vegetative and reproductive organs to adaptable forms to the changed environments. The writer believes that these three lines of plants had been changed their reproductive organs in parallel, namely from spores to naked seeds and to enclosed seeds. In the macrophyll series the spores of Psilopsida changed to the naked seeds of seed ferns and to the enclosed seeds of angiosperms through ages. In the microphyll series the spores of Protolepidodendrales changed to the naked seeds of Cordaitales and Lebachiaceae and to the enclosed seeds of Podocarpaceae, Taxaceae and Cephalotaxaceae.

In the articulate stem series the most cones of *Calamostachys* were homosporous and some species were heterosporous. *Calamocarpon* was the cone with heterospores and their megasporangium had only one megaspore like that of *Lepidocarpon* of microphyll series. *Lepidocarpon* might have been evolved to the cones of conifers but we could not find the fossil records of articulate plants with naked seeds in the Late Paleozoic and Mesozoic. Recent bamboos distribute widely in the northern and southern hemisphere but we cannot find the fossil bamboos with seeds even in Tertiary and their fossil leaves are also very rare in Tertiary sediments. The writer do not know the reason why the ancestral fossil plants of bamboos are not found in the Mesozoic and Tertiray Periods. This may be the reason that they might have lived in the upland (ASAMA, 1982b, fig. 1).

There were two types of evolution in each phyletic line, microphyll series (Microphyllophyta), macrophyll series (Macrophyllophyta) and articulate stem series (Arthrophyta) respectively. The one is the progressive evolution, which means the changes of grading up of their evolutionary level, from spore to naked seed and to enclosed seed stage in the reproductive organs, and from tracheid with annual thickning to spiral, scalariform and bordered pits, and to vessel to conduct much water in the vegetative organs.

The other evolutionary type is regressive evolution, which means the size reduction, from the giant Carboniferous lycopods to the small Recent herbaceous lycopods, from giant Carboniferous tree ferns to the small Recent herbaceous ferns and from giant Carboniferous horse tails to the small Recent herbaceous horse tails. These size reduction indicate the climatic change, from the Carboniferous mild to Recent serve climate through the ages as shown in Fig. 4 and Part 1, Figs. 6–9 (ASAMA, 1981a).

The writer's conclusion discussed in Part 1 — Part 6 was shown in Fig. 4, which indicates the three phylogenetic trees of vascular plants based on the Principles of Growth Retardation and the macroclimatic change through ages.

6) Comparison with the other author's phylogenetic trees

The present writer's phylogenetic trees shown in Fig. 4 are characterized by the three lines of vascular plants (Macrophyllophyta, Microphyllophyta and Arthrophyta), parallel grading up of reproductive organs of each line (from spore–stage to naked seed-stage and to enclosed seed-stage) and parallel size reduction in each line. Progressive evolution means the change of gradin up of reproductive organs and regressive evolution means the change without improvement of reproductive organs through ages. Macroclimatic changes are showed with three phylogenetic trees to explain reasonably the change of vascular plants, progressive and regressive evolution.

If we accept these macroclimatic change through ages, which were deduced based on the zonal floral distribution of each age and the macrochange of size reduction in Lycopsida, Pteropsida and Sphenopsida, the progressive and regressive evolution of vascular plants shown in Fig. 4 are reasonably explainable as the adapted change to the changed climate. Therefore these macroclimatic changes through ages were the fundamental cause of plants evolution and the three phylogenetic trees were the effects showing the relation between plants and environment through ages.

There are many phylogenetic trees proposed by many authors and most of them are monophyletic trees (ZIMMERMANN, 1959; DOYLE, 1977: EHRENDORFER, 1971: etc.), which are indicating one origin of pteriodophytes (spore-stage), one origin of gymnosperms (naked seed-stage) and one origin of angiosperms (enclosed seed-stage) respectively.

BANKS (1968, 1970) considers two lines of pteridophytes, Rhyniophytina with terminal sporangia and Zosterophytina with lateral sporangia, and he considers one origin of gymnosperms, progymnosperms, from which cyacdophytes and coniferophytes were derived.

GREGUSS (1964) classified land plants into three lines by such branching as monopodial, dichotomous and verticillate. But the present writer thought that such leaf or stem as microphyll, macrophyll and articulate stem are more essential characters than branching system recognizable through pteridophytes, gymnosperms and angiosperms.

Many authors (BECK, 1976; MEEUSE, 1965; DOYLE, 1977; EHRENDORFER, 1971; etc.) believe that such gymnosperms as seed ferns, Glossopteridales, Cordaitales and Ginkgoales seemed to be derived monophyletically from Progymnospermopsida. But the present writer cannot agree this idea.

Gymnosperms are classified into three types of plants in the Upper Paleozoic, Coniferophytes, Cycadophytes and Ginkgophytes by their vegetative and reprocudtive organs. The most important characters of Coniferophytes is to form cones. *Archaeopteris,* which is the representative plants of Progymnospermopsida, do not have cones and have the fern-like or seed fern-like pinnate leaves. Cones might not be derived from these fern-like pinnate leaves in Carboniferous. The present writer considers that the cones of coniferophytes (Cordaitales and Lebachiaceae) might have been derived from the strobilus (cones) of the Lycopsida in Carboniferous as shown in Fig. 4 (Microphyllophyta). And Archaeopteridales (Progymnospermopsida) might have been only the ancestral plants of seed ferns (Pteridospermopsida) as shown in Fig. 4 (Macrophyllophyta). In general it is considered that Ginkgoales belong to Coniferophytes. The stem structure of Ginkgoales is very similar to those of conifers but the leaves of them are macrophyllous and do not form cones. Therefore the writer considers that Ginkgoales belong to Macrophyllophyta and seemed to be derived from Progymnospermopsida.

The most complicated problem is the origin and phylogeny of angiosperms (ASAMA, 1982b). The reproductive organs changed from the spore-stage to the naked seed-stage (single protection) and to the enclosed seed-stage (double protection) through Paleozoic and Mesozoic. The writer considers that these transformation of reproductive organs occurred in three lines, macrophyll series, microphyll series and articulate stem series in parallel. Therefore the vascular plants have three origins of pteridophytes (spore-stage), three origins of gymnosperms (naked seed-stage) and three origins of angiosperms (enclosed seed-stage). If we call gymnosperms the plants with single protected reproductive organs and call angiosperms the plants with double protected reproductive organs, we will find angiospermous plants in the microphyll series (Podocarpaceae, Taxaceae and Cephalotaxaceae) and in the articulate stem series (Graminae).

Considerations on the continuous Growth Retardation and evolutionary thoughts

The writer discussed the evolution of vascular plants and proposed the Principles of Growth Retardation to explain the adaptable change of vascular plants through ages and found the facts that all adaptable change of vascular plants in Paleozoic, Mesozoic and Cenozoic periods are only explainable by the Principles of Growth Retardation and not by the Growth Acceleration. Therefore we must theoretically explain the reason and process of Growth Retardation. Which evolutionary theory can explain the continuous Growth Retardation?

Many evolutionary theories have been proposed by various authors to explain the evolution of plants and animals. Main evolutionary theories are Lamarkism, Neo–Lamarkism, Darwinism and Neo-Darwinism (or synthesis theory), of which the synthesis theory is the most popular and supported by many scientists, mainly by the geneticists.

The writer thinks that the evolution was the events in geological ages and that therefore the processes and patterns of evolution affected by the environmental changes through geological ages was the most important evidences for the evolution. Previous evolutionary theories, even the synthesis theory proposed by the geneticists, are based on the changes of Recent plants and animals and not based on the fossil evidences and the environmental changes through geological ages. Therefore the most important evolutionary processes showed in fossil records through ages were neglected. We will be unable to find the true evolutionary theory without the correct interpretation of fossil records of Paleozoic, Mesoeic and Cenozoic. Therefore we must study the fossil records of each periods to find the the patterns of evolution at first. To change does not always mean the progressive evolution as shown in fossil record (Fig. 4).

1) Similarities in the patterns of macroevolution of vascular plants and vertebrates

We must fully recognize the process and pattern of evolution through geological ages to explain the evolutionary changes, which is shown in the phylogenetic trees of plants and animals.

General phylogenetic trees of vascular plants and vertebrates were shown in Part 2, Figs. 1, 2 (ASAMA, 1981b). The patterns of macroevolution of vascular plants and vertebrates are very similar as shown in the phylogenetic trees of both. The first land plants, Rhyniales which succeeded out of water on to land, are found in the Latest Silurian or the Eary Devonian and such pteridophytes as Pteropsida, Lycopsida and Sphenopsida had flourishied in the next Carboniferous. The most flourishing plants in the Late Paleozoic were such pteridophytes as tree ferns, Lepidodendrales and Calamitales and therefore we may call the Late Paleozoic the pteridophyte stage or spore-stage. Judging from the Recent pteridophytes, it seems very strange that the plants in spore stage could grow to be giant trees. This may mean that the environments in the Late Paleozoic were very different from those of the present. Therefore we are unable to find the correct evolutionary theory without consideration of the past environments based on the fossil records. It is very strange that no evolutionist had discussed about the macro-environmental change through Paleozoic, Mesozoic and Cenozoic.

There were such Paleozoic gymnosperms as seed ferns and Cordaitales in the Late Plaeozoic but they disappeared in the end of Permian, and such gymnosperms as Bennettitales, Cycadales, Ginkgoales and Coniferales reached their greatest development in Mesozoic. Nevertheless it can be said that Bennettitales was the representative of Mesozoic gymnosperms, and it diversified into many forms of plants such as Williamsoniaceae, Wielandiellaceae and Cycadeoideaceae which were disappearing in the Late Cretaceous. Generally speaking, the stage of the greatest developments of pteridophytes, gymnosperms and angiosperms were in the Late Paleozoic, Mesozoic and Cenozoic respectively.

The patterns of macro-evolution of vascular plants mentioned above are very similar to those of land vertebrates. Many similar patterns will be found by comparing the macro-evolutionary patterns of land plants with those of land vertebrates. Evolutionary stages of such land plants as pteridophytes, gymnosperms and angiosperms are coresponding with those of amphibians, reptiles and mammales in land vertebrates respectively.

Pteridophytes and amphibians succeeded come out of water on to the land but they could not live away from water. Gymnosperms and reptiles are adapted to the life of the dry land but they could not live in the low temperature. Angiosperms and mammals are adapted to live in both dry and cold environments.

Angiosperms must have been derived from the Late Paleozoic angiosperm-like seed ferns (Part 2, Fig. 1) and there was very long interval, about 100 million years, by the age of great diversification of angiosperms in the Late Cretaceous. Mammals must have been derived from the Triassic mammal-like reptiles (Therapsida) (Part 2, Fig. 2) and there was very long interval too, about 100 million years, by the age of great diversification of mammals in the Early Tertiary.

Why the angiosperms-like seed ferns could not evolve to become angiosperms in Mesozoic? They disappeared in Triassic and it was such other gymnosperms as Bennettitales, Cycadales, Ginkgoales and Coniferales that had been floulished in Mesozoic. It is very strange from the theoretical view point that the advanced type of gymnosperms (angiosperm-like seed ferns) disappeared and that the less advanced type of gymnosperms (Bennettitales, Cycadales, Ginkgoales, etc.) fluolished in Mesozoic.

Same patterns are found in the vertebrate evolution.

The advanced type of reptiles (Therapsida) disappeared in Jurassic and the less advanced reptiles (dinosaurs, etc.) floulished in Jurassic and Cretaceous.

The writer discussed about this question in Part 5, p. 53 (ASAMA, 1982b) and considered that such gymnosperms as Bennettitales and Cycadales which were found abundantly in Mesozoic are the lowland plants, but the upland plants, in which the angiosperms seemed to be contained, are not found.

2) Three types of evolutionary pattern of land plants and land vertebrates

Generally speaking, land plants evolved from pteridophytes of Paleozoic to gymnosperms of Mesozoic and to angiosperms of Cenozoic grading up their reproductive organs through ages.

The reproductive organ changed from the spore of pteridophytes to the naked seed of Gymnosperms and the naked seed changed to the enclosed seed of Angiosperms through ages. This means that the reproductive method had become steady age by age protecting spore and seed by the changed leaves (integuments or carpels). The plants of spore stage (pteridophytes) in Paleozoic must have been lived under the warm and wet climate as the adaptive environment, the naked seed plants (gymnosperms) in Mesozoic under the warm and sometimes dry climate, and the enclosed seed plants (angiosperms) in Cenozoic could have lived under even drier and colder climates. That is to say, the reproductive organ had changed to be capable of more and more severe environments.

With the advancement of paleontological researches, fossil evidences of evolution have been accumulated in great quantitities. Evolution of mammals such as horse and elephant is particularly well known. In land vertebrates a great evolution started with fish, and passing through the stages of amphibians of Paleozoic and reptiles of Mesozoic, it attained to mammals of Cenozoic.

These evidences of evolution of animals and plants have some common points. The first of the points is that the evolution has advanced in a certain direction. That is to say, the evolution is the directional changes through ages (not orthogenesis). The second point is that the structure changed from simple to complex stepping up their grades, namely, a progressive evolution. However, a reverse trend, that is, the structure became simple reducing their size, is also found. This is a regressive evolution. When the directional change advances upwards it becomes a progressive evolution, and when it advances downwards it becomes a regressive evolution. The third common point is the change in size, by which the animals became larger and plants became smaller. We can find many examples of size-increase in animals, namely, the size-increase of fusulinids in the Late Paleozoic, ammonites in Mesozoic, reptiles in Mesozoic, mammals in Cenozoic, etc, Not all animals became larger, but the size-increase was normal phenomena in the animal kingdom in any geological ages. Contraty to size-increase of animals the size reduction was the normal phenomena in the plant kingdom as discussed in Part 1, Figs. 6–8 (ASAMA, 1981a). The forth common point is the diversification which will typically be found in the adaptive radiation of reptiles and gymnosperms in Mesozoic, mammals and angiosperms in Cenozoic, fusulinids in Late Paleozoic, ammonites in Mesozoic. etc.

As stated above we find three types of evolutionary pattern, progressive evolution, regressove evolution and diversification in the successive changes of land plants and land vertebrates. Of which the most important pattern of evolution is the progressive evolution, which means the grading up of evolutionary level in both land plants and land vertebrates. The fossil records mentioned above are the characteristics of the evolutionary processes of land plants and land vertebrates.

The vascular plants progressively evolved from algae to pteridophytes, gymnosperms and angiosperms increasing their adaptability to environmental changes through ages. The vertebrates progressively evolved from fishes to amphibians, reptiles and mammals increasing their adaptability for environments age by age.

The evolutionary stages of vascular plants shown as algae, pteridophyte, gymnosperm and angiosperm stage are corresponding with those of vertebrates indicating fish, amphibian, reptile and mammal stage in both their adaptability to environments and geological ages of their climax. That is to say, vascular plants and vertebrates evolved in parallel.

This is the most important similarity in the patterns of macroevolution of vascular plants and vertebrates. We can explain the reason why they had to evolve parallel by postulating the paleoclimatic change through ages (Fig. 4).

Any of the numerous theories of evolution should be able to elucidate satisfactorily these patterns of evolution, progressive evolution, regressive evolution, diversification and parallel evolution between plants and animals. First of all, it must explain the cause of progressive evolution theoretically. It seemed that all evolutionary theories proposed by various authors have not been successful to explain the cause of progressive evolution logically. It is natural, because they did not base on the fossil evidences and climatic changes through ages. We cannot discuss the cause of evolution without considering the fossil evidences, because the evolution is the past facts occured in geological ages.

From the reason mentioned above we must research the relation between the fossil evidences and the environmental change through ages to clarify the cause of progrsesive evolution. Telling us more about relation between environment and life is plants rather than animals. So the writer thinks that it is the first step to know the environmental changes through ages by studies of successive fossil plants, the second step is to test them whether we can explain the evolution of animals through ages by the environmental change postulated by plant evolution or not.

Similarities in the pattern of evolution of plants and animals are explained by the environmental change postulated by fossil plants. Because plants and animals were affected by the same environmental changes through Paleozoic, Mesozoic and Cenozoic.

3) Fundamental factor and individual factor as the causes of evolution

There were three types of evolutionary pattern, progressive evolution, regressive evolution and diversification through geological ages. The most important pattern of evolution is the progressive evolution, which is shown in the macro-change from pteridophytes to gymnosperms and to angiosperms in vascular plants and from amphibians to reptiles and to mammals in land vertebrates respectively. The progressive evolution means the directional evolution which shows the grading up of evolutional level during the long periods. The writer calls the cause controlling these directional evolution the fundamental facotr. Therefore the fundamental factor, which had drived vascular plants from pteridophytes to angiosperms and land vertebrates from amphibians to mammals, was the macro-climatic change of increasing annual range shown in Fig. 4.

The regressive evolution means the directional evolution, which was shown in the size reduction of vascular plants from the Paleozoic giant woody pteridophytes

(Lepidodendrales, tree ferns and Calamitales) to Recent small herbaceous pteridophytes (Lycopodiales, ferns and Equisetales). The progressive evolution means the grading up of reproductive organs from spore-stage to nakes seed stage and to enclosed seed stage, but the regressive evolution means no grading up of reproductive organs indicating the evolution in same level. The progressive evolution and regressive evolution of vascular plants had the evolutionary trend, the former had upwards trend (improvement of reproductive organs) and the latter had downwards trend (size reduction without improvement of reproductive organs). The forces controlling the evolutionary trends shown in progressive and regressive evolution was the fundamental factor and the macro-climatic change of increasing annual range.

The most important evolutionary trend through ages was the size reduction in vascular plants and the size increase in animals (Vertebrates and invertebrates). This general evolutionary trend was found in both plants and animals in any geological age and everywhere in the world. Both the size reduction of vascular plants and size increase of animals were the adaptation to the coldness or the annual range of temperature between summer and winter. To increase the body size of animals is effective to avoid the coldness of winter but not effective to avoid the heat of summer.

Vascular plants could survive by decreasing leaf or stem size adapting severer environment successively through ages. Most of animals had been increased their size to be adaptable to the lowering temperature successively through ages, too.

The cause of these evolutionary trend, size reduction of vascular palnts and size increase of animals, was the macroclimatic change of increasing of annual range and this is the fundamental factor of evolution.

The causes of diversification were many kinds of environment, many kinds of habitats and many kinds of habits, which had drived plants and animals to many trends diversifying their morphological and physical characters. Therefore the causes of diversification are different in each phyllum, order, family, genus and even each species. The writer calls these causes the individual factor. Land plants and land vertebrates had evolved accepting the affection of both fundamental factor and individual factor through ages.

4) Progressive evolution are not explainable by synthesis theory

The most important pattern of evolution is progressive evolution. If the evolutionary theory proposed above is correct, three evolutional patterns, which are found in fossil records, must be explained reasonably by that theory. Therefore at first the progressive evolution must be explained by the theory. The progressive evolution menas the continuous leveling up of plants and animals through ages.

We cannot explain the progressive evolution without considering the environmental change through ages. Any of evolutionary theories proposed by eminent authors till now did not discuss the environmental change through ages and even synthesis theory did not consider about the continuous environmental changes through long periods. Changes explainable by these evolutionary theories are not progressive evolution but only changes during a certain short time.

Evolutionary changes are always the continuous progressive change indicating some evolutionary trend.

The synthesis theory is mainly based on mutation and natural selection, which are unfavourable to explain progressive evolution. Mutation is considered as mistakes of gene duplication and appearance of mutation is rare and appearance of favourable mutation is more rare. Progressive evolution means directional changes through ages, which indicate the long period of successive change of grading up of plants and animals. Mutations appear at random and have no trend. Progressive evolution means the long period of evolutionary trend and mutations have no trend. The possibility of continuous appearance of same trend of mutation during long periods would not be considered. Therefore progressive evolution will not be explained by synthesis theory. Evolutionists, who support synthesis theory, may say that evolutionary trends are formed by natural selection. How nature can select successively the favorable mutations which are no possibility of appearance? If we accept the continuous appearance of favourable mutation during long periods, from Paleozoic to Recent, as shown in the size reduction of regressive group of plants, it is not scientific.

Evolutionary theory based on mutation has fatal fault. Many organs of plants and animals are working cooperatively. Therefore the progressive evolution means that many organs of plants and animals had simultaneously changed to the adaptable forms for the changed environments. Mutations are the mistake of gene duplication. Therefore it is natural that there are many fatal mutations as shown those induced by X-ray.

The industrial melanism of moths found in England is said that this change of coloration of moths, from light to dark colour, indicates the good example of natural selection but these changes of coloration are not progressive evolution and it indicates only a part of diversification caused by protective coloration. Therefore a part of diversification will be explained by natural selection but the progressive and regressive evolution, which were found in fossil records as the main evolutionary pattern, will not be explained by natural selection.

5) The cause of mass extinction of dinosaurs at the end of Cretaceous was not the extraterrestrial events

The writer would like to discuss about the massive extinction of dinosaurs at the end of Mesozoic based on the paleoclimatic change deduced by continuous Growth Retardation. Many theories were proposed by various authors about the cause of the massive extinction (Bakker, 1977, etc.). Recently the new ideas of the cause of the mass extinction of dinosaurs by the extraterrestrial events were proposed and they are becoming the general interpretation as reported by Science (Alvarez and others, 1980). They are the supernova explosion theory and the impact theory of a large earth-crossing asteroid. The present writer cannot agree with these extraterrestrial cause. The massive extinction of dinosaurs may be explained by these extraterrestrial events but the appearance of mammals after the extinction of dinosaurs in Cenozoic would not be explained by these extraterrestrial events. The cause of massive extinction of dinosaurs was the same as the cause of appearance of mammals as shown in the latter chapter. The present writer would not like to deny the supernova explosion and the impact of a large earth-crossing asteroid. The writer would like to say that if it happened these extraterrestrial events, the evolution of plants and animals would not be affected so much by these events.

The evolution of biotas had proceeded constantly accepting the influence of fundamental factor and individual factor through ages, and they are indicating progressive evolution, regressive evolution and diversification.

The paleoclimatic change of the increasing annual range tells us about the cause of massive extinction that dinosaurs could not endure the temperature range between summer and winter. They increased their body size to the limit to be able to endure the coldness of winter but their body size were too large to endure the heat of summer. The mammals of small size could endure the coldness of winter because they were warm blooded, and they could endure the heat of summer. Because their bodies were small and they could easily avoid heat going into shades.

Through Cenozoic the temperature of winter decreased, and mammals had to increase their body size to endure the coldness of winter successively. Therefore many mammals have acquired large bodies through Tertiary radiating to a various habitats.

It is well known facts that large type of mammals become extinct after Quaternary glaciation (AXELROD, 1967). The writer thinks that these large types of mammals could not endure the heat of summer after glaciation because of their size which were too large to avoid the summer heat.

The progressive and regressive evolution, appearance, disappearance and extinction of plants and animals simultaneously occurred in the world wide scale. Therefore the cause of these processes must have been climatic change in the world wide scale. The writer postulated that the progressive and regressive evolution, appearance and extinction of organisms were caused by the paleoclimatic change of increasing annual range which were deduced by the continuous Growth Retardation of vascular plants.

6) Relation between phenotype and genotype

It is impossible to search the function of gene from fossil records, but we can speculate the process of gene transformation by the progressive and regressive evolution found in vascular plants and land vertebrates. The size reduction of plants and size increase of animals were the most important evolutionary patterns. These change of plants and animals were adaptation to the paleoclimatic changes of increasing range of the annual temperature. As shown in Fig. 4 the temperature of winter might have been successively lowered through geological ages except the effects of epeirogenetic movement. Plants had to reduce their leaf size to endure the cold climate and animals had to increase body size to endure the cold climate of winter successively. The size reduction of plants and size increase of animals were the adaptation to the cold climate.

The size reduction of plants and size increase of animals were the most important evolutionary patterns through geological ages, from the Carboniferous to Recent (size reduction of pteridophytes), from the Early Mesozoic to the Late Mesozoic (size increase of reptile) and from the Early Cenozoic to the Late Cenozoic (size increase of mammals).

The size reduction of plants and size increase of animals through long period indicate that phenotypes of plants and animals had changed successively over the norm of reaction of genotype. These successive changes of phenotypes suggest that genotypes of plants and animals had changed successively also. The successive change of phenotype over the norm of reaction might have forced genotype to change successively to adaptable type of genotype. It is important to note that a change in the genotype may produce a change in the norm of reaction, and a change in the norm of reaction of phenotype does not induce a change in the genotype. But if the phenotype change over the norm of reaction by the excessive change of environment, what will happen in genotype then?

Fossil records in plants indicate that such phenotypes of three lines of giant pteridophytes (20–30 m tall) as shown in the regressive evolution from Carboniferous to Recent (Asama, 1981a, Part 1, Figs. 6–8) had changed to the very small adaptable forms (about 1 m tall or more small) to the changed environments. This means that both phenotypes and genotypes of pteridophytes had changed to the adaptable types to the changed environments in parallel. Therefore we may say that the excessive environmental change will induce the change of genotype. All progressive and regressive evolution shown in plants and animals through ages are indicating the successive changes induced by the changing environments. No one doubt that plants and animals will change their phenotypes and genotypes by the change of environments. But the mechanism acquiring the inheritable changes are interpreted by different authors in different ways. Neo-Darwinists explain the mechanism of inheritable change by natural selection and predaptation, Neo-Lamarkists (GORCZYNSKI and STEELE, 1980) by the inheritance of acquired characters, and WADDINGTON (1953, 1956) and others (MATSUDA, 1982) by the genetic assimilation.

The progressive and regressive evolutionary changes shown in the three lines of pteridophytes (Fig. 4), the size reduction of plants (Fig. 3) and the size increase of mammals in Cenozoic indicate the same trend of change of phenotypes during the long periods, which mean the successive same trend of change of genotypes. If the inheritance of acquired characters is correct mechanism acquiring the inheritable change as indicated by Lamarck, Darwin, Gorczynski and Steel, and ect., the progressive and regressive evolutionary changes of plants and animals would be reasonably explained.

If we try to explain the progressive and regressive evolutionary changes of plants and animals by natural selection, we have to assume the continuous appearance of adaptable mutational genes through very long periods (about 300 m.y. of regressive evolution of pteridophytes and 60 m.y. of mammal radiation in Cenozoic, etc.). Mutation is considered as mistakes of gene duplication and appearance of mutation is rare and no trend. Therefore it is very diffiuclt and not reasonable to explain the progressive or regressive evolutionary changes through ages by natural selection. Genetic assimilation may mean the inheritance of acquired characters.

The following experiments by USUBUCHI, SATO and KUDO (1982) seem to show the mechanism of the inheritance of acquired characters:

Non-inbred rats of both sexes of Gifu strain, weighing 150–180 g, were used in all experiments. Tumor cells employed were those of Hirosaki sarcoma which had developed in the cervical lymphnode of a non-inbred rat and has been serially transplanted i.p. in non-inbred rats for 30 years in this department. The minimum effective dose of mitomycin C (MMC) to Hirosaki sarcoma *in vivo* is 50 μg/kg/day.

A clonal cell line of Hirosaki sarcoma was established in rats. Forty-eight hr after the i.p. transplantation of 1×10^7 cells of the clonal cell line, the tumor was treated daily with i.p. administration of 1 μg/kg of MMC. Tumor cells treated were serially transplanted to the next passage before the host dies and the similar treatment was repeated in the new host. Although a complete resistance of the tumor to 5 daily administrations of 100 μg/kg of MMC was not recognized after 63 intermittent administrations of 1 μg/kg of MMC in 111 days, the resistance was recognized after 25 continuous administrations in 25 days in the subline of this tumor treated additionally with daily doses of 1 μg/kg of MMC immediately after the i.p. transplantation of tumor cells. Similarly, although a complete resistance of the original line was not recognized after 88 intermittent administrations in 160 days, it was recognized after 9 continuous administrations in 9 days in the subline of this tumor treated additionally with daily doses of 1 μg/kg of MMC immediately after i.p. transplantation of tumor cells. Finally, after 109 intermittent administrations in 190 days, the original line showed a complete resistance to MMC. Thus, the process of the development of resistance to MMC seems to be a gradual one.

The intermittent administration of 1 μg/kg of MMC to the original line was stopped when 120 administrations were done in 208 days. In the examination after 6 months, the tumor showed a complete resistance to 100 μg/kg of MMC. Moreover, each of 20 clonal cell lines derived from this MMC resistant Hirosaki sarcoma was also resistant to 100 μg/kg of MMC.

These results seem to show that most of Hirosaki sarcoma cells may have gradually acquired a hereditary resistance to MMC in the course of the contact with the ineffective dose of MMC, which did not make the selection.

These experiments seem to indicate the mechanism acquiring the inheritable characters without mutation and selection, and mean that the environmental change induce the somatic inheritable characters. If these experiments show the general process acquiring the inheritable characters, the progressive and regressive evolution of plants and animals will be reasonably explained.

The discovery of "reverse transcriptase" (RNA-directed DNA polymerase) by TEMIN (1971, 1976) may suggest the possibility of the inheritance of acquired characters. Acquired characters do not inherit in normal condition as shown in the molecular biology's central dogma but under the special condition (when the phenotype changed over the norm of reaction) we have to accept the inheritance of acquired characters as shown in the progressive and regressive evolution of plants and animals. The present writer wishes earnestly to be proved in molecular biology that the acquired character would be inherited in special case when the phenotype changed over the norm of reaction. Fossil records show that the environments changed successively through ages and these environmental changes forced plants and animals to change successively their phenotype over the norm of reaction. If we accept the inheritance of acquired characters, the progressive and regressive evolution, and diversification caused by habits or habitats would be reasonably explained.

7) Growth Retardation theory

There were three types of evolutionary patterns, progressive evolution, regressive evolution and diversification (Fig. 4). A part of diversification as shown in the industrial melanism by protective coloration can be explained by Neo-Darwinism and a great part of diversification by Neo-Lamackism. Any of proposed evolutionary theories could not reasonably explain the progressive and regressive evolution. Progressive and regressive evolution mean the directional evolutionary change through long periods. Therefore we cannot reasonably explain the progressive and regressive evolution without considering the environmental change through ages.

The writer proposed the Growth Retardation theory to explain the progressive and regressive evolution and diversification. The continuous Growth Retardation through ages suggests the macroclimatic change as shown in Fig. 4. These climatic change of increasing annual range had formed diversified and layered (spring to winter) environments through ages. The progressive evolution had been caused by the increasing layered environments, and diversification had been caused by diversified environments respectively. The climatic change of increasing annual range through ages is the fundamental factor of macroevolution, and the progressive and regressive evolution are the effects derived from the relation between biotas and environments through ages.

Acknowledgements

The writer wishes to express my sincere gratitude to Drs. Ikuwo OBATA, Teruya UYENO and Mr. Yukimitsu TOMIDA of National Science Museum, Tokyo for their criticism and suggestions during the course of the present work.

References

ALVAREZ, L. W., W. ALVAREZ, F. ASARO & H. V. M CHEL, 1980. Extraterestrial cause for the Cretaceous-Tertiary extinction. *Science*, **208** (4448): 1095–1108.

ASAMA, K., 1981a. Evolution and phylogeny of vascular plants based on the Growth Retardation. Part 1. Principles of Growth Retardation and climatic change through ages. *Bull. Natn. Sci. Mus., Tokyo. Ser C.*, **7** (2): 61–79.

——— 1981b. Evolution and phylogeny of vascular plants based on the Growth Retardation. Part 2. Phylogeny of Microphyllophyta. *Ibid.*, **7** (3): 79–113.

——— 1981c. Evolution and phylogeny of vascular plants based on the Growth Retardation. Part 3. Phylogeny of Macrophyllophyta in Devonian. *Ibid.*, **7** (4): 129–145.

——— 1982a. Evolution and phylogeny of vascular plants based on the Growth Retardation. Part 4. Phylogeny of Macrophyllophyta inferred from the evolution of leaf forms. *Ibid.*, **8** (1): 1–17.

ASAMA, K., 1982b. Evolution and phylogeny of vascular plants based on the Growth Retardation. Part 5. Origin of angiosperms inferred from the evolution of leaf forms. *Ibid.*, **8** (2): 43–58.

——— 1982c. Evolution and phylogeny of vascular plants based on the Growth Retardation. Part 6. Triphyletic evolution of vascular plants. *Ibid.*, **8** (3): 93–115.

AXELROD, D. I., 1967. Quaternary extinctions of large mammals. *Univ. Calif. Pub. Geol. Sci.*, **74**: 1–42.

BAKKER, R. T., 1977. Tetrapod mass extinctions —— A model of the regulation of speciation rates and imigration by cycle of topographic diversity. In A. HALLAM (ed.), Patterns of evolution as illustrated by the fossil record: 439–468. Elsevier Sci. Pub. Co., Amsterdam, London, New York.

BANKS, H. P., 1968. The early history of land plants. In E. T. DRAKE (ed.), Evolution and environment, New Heaven, Yale Univ.

——— 1970. Evolution and plants of the past. Fundamentals of botany series. 1–170 pp. Belmont, California, Wadsworth Pub. Co.

——— 1975. Reclassification of Psilophyta. *Taxon,* **24** (4): 401–413.

BECK, C. B., 1976. Current status of the Progymnospermopsida. *Rev. Palaeont. Paly.*, **21**: 5–23.

DOYLE, J. A., 1977. Patterns of evolution in early angiosperms. In A. HALLAM (ed.), Patterns of evolution as illustrated by the fossil record: 501–546.

EHRENDORFER, F., 1971. Systematik und Evolution: Apermatophyta, Samenpflanzen. In Lehrbuch der Botanik für Hochschulen ("Strasburger"), G. Fischer, Stuttgart.

GARRAT, M. J., 1978. New evidence for a Silurian (Ludlow) age for the earliest *Baragwanathia* flora. *Alcheringa*, **2** (3–4): 217–224.

GORCZYNSKI, R. M. & E. J. STEELE, 1980. Inheritance of acquired immunological tolerance to foreign histocompatibility antigens in mice. *Proc. Natl. Acad. Sci. USA*, **77**: 2871–2875.

GREGUSS, P., 1964. The phylogeny of sexuality and triphyletic evolution of the land plants. *Acta Biol. N.S.*, **10**: 3–50.

MATSUDA, R., 1982. The evolutionary process in tailitrid amphipods and salamanders in changing environments, with a discussion of "genetic assimilation" and some other evolutionary concepts. *Nat. Res. Council Canada*, **60** (5): 733–749.

MEEUSE, A. D. J., 1965. Angiosperms — Past and present — Phylogenetic botany and interpretative floral morphology of the flowering plants. *Advancing frontiers of plant science*, **2**: 1–228, New Delhi.

TEMIN, H. M., 1971. The protovirus hypothesis; speculation on the significance of RNA-directed DNA synthesis for normal development and for carcinogenesis. *J. Natl. Cancer Inst.*, **46** (2): 3–8.

——— 1976. The DNA provirus hypothesis. *Science*, **192**: 1075–1080.

USUBUCHI, I., T. SATO & H. KUBO, 1982. Mechanism of the development of resistance to mitomycin C in Hirosaki sarcoma. *Chemotherapy*, **30** (7): 719–723.

WADDINGTON, C. H., 1953. Genetic assimilation of an acquired character. *Evolution*, **7**: 118–126.

—— 1956. Genetic assimilation of the bithorax phenotype. *Ibid.*, 10: 1–13.

ZIMMERMANN, W., 1959. Die Phylogenie der Pflanzen. 777 pp., 2 Aufl. G. Fisher, Stuttgart.