Evolution and Phylogeny of Vascular Plants based on the Principles of Growth Retardation.   Part 5.   Origin of Angiosperms inferred from the Evolution of Leaf Forms.

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As shown in Part 4, Fig. 1 (ASAMA, 1982), the writer divided the evolutionary stage of macrophylls into four stages: the pinnately compound leaf-forming stage (or the naked axes stage in Devonian), the simple leaf-forming stage (or the pinnately compound leaf stage in Carboniferous and Permian), the cycadophytic leaf stage in Mesozoic and the simple leaf stage in Cenozoic.

When we discuss about the origin and phylogeny of angiosperms, at first we must consider the ancestral sources of woody angiosperms, since the herbaceous angiosperms were derived from the woody angiosperms by reduction of secondary woods in the later stage of the angiosperm evolution, excepting aquatic angiosperms like Nymphaeaceae. The herbaceous angiosperms are the reduced type of woody angiosperms adapting to severer environments.

The characteristic leaf forms of woody dicotyledonous plants are the simple leaf with reticulate veins, whereas those of woody monocotyledonous plants are the simple leaf with parallel veins in Graminae and the pinnately or palmately compound leaf with parallel veins in Palmae.

Nobody discussed the origin of angiosperms on the basis of evolution of leaf forms and nobody have shown the process to form simple leaves, and the reason why the simple leaf was formed. The simple leaf is the representative leaf form of dicotyledonous angiosperms. Therefore the present writer concludes that it is meaningless to try to find the ancestral plants of dicotyledonous angiosperms without understanding the simple leaf forming process, and, hereby, he will try to discuss the origin of angiosperms on the basis of the evolution of leaf forms.

Origin of simple leaf with reticulate veins (Dicotyledons)

The simple leaf with pinnate secondary veins and reticulate veinlets is characteristic in dicotyledonous angiosperms which make a great part of angiosperms. Therefore we must make clear the process to form simple leaves to find the ancestral form of angiosperms. As shown in Fig. 1–6 and Part 4, Fig. 2–4, the simple leaf was probably derived from the pinnately compound leaf by "Fusion" of segments.

It appears to be logical to assume that tripinnate *Emplectopteris triangularis* (Fig. 1–3) had changed to bipinnate *Gigantonoclea lagrelii* (Fig. 1–4) by "Fusion" of segments, and changed to unipinnate *Bicoemplectopteris hallei* (Fig. 1–5), and then to simple leaf *Tricoemplectopteris taiyuanensis* (Fig. 1–6) successively. This means that the simple leaf was derived from the pinnately compound leaf, and also means that the simple leaf with reticulate veins could not be formed without repreating "Fusion" of segments of the pinnately compound leaf. Therefore the ancestral plants of angiosperms with simple leaf must be the plants with pinnately compound leaf.

Early and middle Devonian was the age of the naked axes or pinnately compound leaf-forming stage, (Part 4, Fig. 1, Asama, 1982) and the pinnately compound leaf appeared at first in the latest Devonian. Carboniferous and Permian were the ages of the pinnately compound leaf (or simple leaf-forming stage) and the simple leaf with reticulate veins appeared at first in the Early Permian. These simple leaf plants (so-called *Gigantopteris*) were described by Halle (1927) as *Gigantopteris nicotianaefolia* (=*Bicoemplectopteris hallei* Asama) and *G. lagrelii* Halle (=*Gigantonoclea lagrelii* Koidzumi); by Asama (1959) as *Gigantonoclea lagrelii* Koidzumi, *Bicoemplectopteris hallei* Asama, *Tricoemplectopteris taiyuanensis* Asama, and *Gigantopteris nicotianaefolia* Schenk; by Gu et Zhi (1974) as *Gigantonoclea rosulata* Gu et Zhi, *G. guizhouensis* Gu et Zhi, *G. hallei* (Asama), *G. mira* Gu et Zhi, *G. kaipingensis* Gu et Zhi, *G. acuminatiloba* (Schimakura), *G. taiyuanensis* (Asama), *G.* cf. *longifolia* (Koidzumi), *Gigantopteris nicotianaefolia* Schenk, *G. dictyophylloides* Gu et Zhi, *G. cordata* Yabe et Oishi: by Yabe & Oishi (1938) as *Gigantopteris fukienensis* Yabe et Oishi, *G. nicotianaefolia* Schenk and *G. cordata* Yabe et Oishi, all species mentioned above from China: by Kawasaki (1931, 1934) as *Gigantopteris nicotianaefolia* Schenk, *G. Lagrelii* Halle, *G. elongata* Kawasaki and *G. dentata* Yabe from Korea: by White (1912) as *Gigantopteris americana* White and by Read & Mamay (1964) as *Gigantopteris americana* White, *G.* sp. A, and *G.* sp. B from Texas, N. America. Jongmans & Gothan (1935) reported *Gigantopteris mengkarangensis* Jongmans et Gothan and *G. bosschana* Jongmans et Gothan from Djambi, Sumatra, and Wagner (1962) described *Gigantopteris nicotianaefolia* Schenk from Anatolia, Turkey. Asama (1968) reported *Bicoemplectopteridium longifolium* Asama, *Bicoemplectopteris hallei* Asama and *Gigantonoclea lagrelii* from Loei, Thailand, and he (1970) reported *Gigantopteris lagrelii* (*Gigantonoclea*) Halle, *Gigantopteris nicotianaefolia* Schenk, *Tricoemplectopteris taiyuanensis* Asama, from Linggiu, and *Bicoemplectopteris hallei* Asama from Jengka Pass, Malaysia respectively.

These so-called *Gigantopteris* mentioned above are all reported from Permian formations, and these fossil records mean that the simple leaf *Gigantopteris* was probably derived polyphyletically from various lineages with pinnately compound leaves (different ancestral species) by "Fusion" of segments. All pinnately compound leaves in the late Paleozoic had the possibility to become simple leaves to be adapted to changing environments by "Fusion" or "Enlargement" of segments. The simple leaf plants with reticulate veins, which appeared in the Permian, would be expected

to exist continuously in Mesozoic, but we do not find them untill the middle Cretaceous.

Why are we unable to find the descendants of Permian simple leaf plants till the middle Cretaceous? What does the blank of the Mesozoic 100 million years mean for simple leaf plants (proangiosperms)? Does this mean the extinction of the Permian simple leaf plants? If so, the middle Cretaceous simple leaf plants (the dicotyledonous plants in the middle Cretaceous) are considered to be derived from some plants with pinnately compound leaf in the late Jurassic or early Cretaceous, and we are to find the simple-leaf-forming process as those of Permian age in the late Jurassic or early Cretaceous again. However, no one had reported the process to form simple leaves, as the process found in the case of pinnately compound leaf plants in the late Jurassic or early Cretaceous. Therefore the present writer does not agree with the idea that the simple leaves of the Middle Cretaceous agiosperms were originated in the Lower Cretaceous (HUGHES, 1961; DOYLE, 1969), agree with the older predominant view of a possible Late Paleozoic or Early Mesozoic origin of angiosperms (AXELROD, 1952; CAMP, 1947; NEMEJEC, 1956, THOMAS 1957; EAMES, 1959,). The appearance of the simple-leaf plants like *Gigantopteris* in Permian suggest the idea that the dicotyledonous angiosperms were originated in the Late Permian or Early Triassic. If so, why are we unable to find the Late Paleozoic or Early Triassic angiosperms?

Origin of simple leaf with parallel veins (Palmales)

The so-called *Gigantopteris* (they should be collectively classified as Gigantopteridales) with reticulate veins were derived from the pinnately compound leaves by "Fusion" of segments, whereas the simple leaf (Fig. 1–16) with parallel secondary veins was possibly derived from the pinnately compound leaves with parallel secondary veins like *Alethopteris* by "Enlargement" of segments (Fig. 1–13~16 and ASAMA, 1981a, Part 1, Fig. 2). The Upper Paleozoic *Taeniopteris*, which is found mainly in Permian was probably formed by "Enlargement" of segments of *Alethopteris* or those of *Callipteris*, *Callipteridium*, *Pecopteris*, *Pecopteridium*, *Neuropteris*, *Neuropteridium* and so forth., all with parallel secondary veins.

Mesozoic is the cycadophytic leaf stage as shown in Part 4, Figs. 1 and 6 (ASAMA, 1982). These cycadophytes were possibly derived from the late Paleozoic *Taeniopteris* through the process of splitting their lamina as discussed in Part 4 (ASAMA, 1982), and we are able to find the successive change between the late Paleozoic *Taeniopteris* and the Mesozoic cycadophytes. However, we cannot find suitable plants among Mesozoic cycadophytes for the ancestor of Recent palms. There were 100 million years blank in Mesozoic between the Late Paleozoic cycadophytic *Taeniopteris* and the Late Mesozoic palms. What does Mesozoic 100 million years blank mean for propalms?
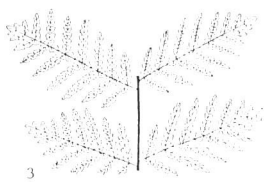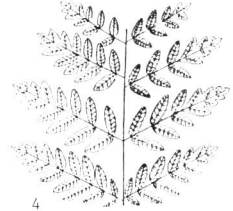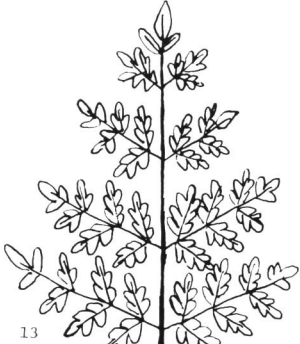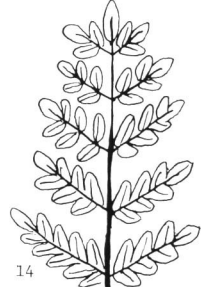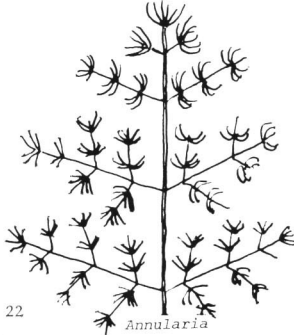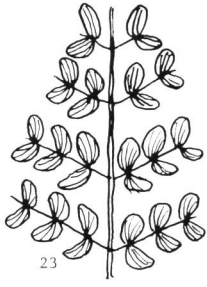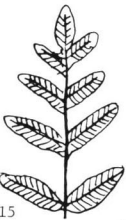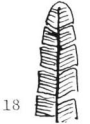
Fig. 1. Origin of simple leaves with reticulate veins, parallel veins and articulate stems. Pal-
eozoic floras were divided into two types of floras, upland type and lowland type, in the
earlier Mesozoic. Abundant plants of Upper Triassic floras are lowland type, which we

The figure is a three-by-two grid chart comparing Mesozoic and Cenozoic plant types.

	MESOZOIC	CENOZOIC
	7 Prodicotyledons (unknown) / UPLAND TYPE	
5 / 6 Gigantopteridales	8 Dipteridaceae	9 / 10 / 11 / 12 Magnoliales
	LOWLAND TYPE	Dicotyledons (Angiosperms)
	17 Propalmales (unknown) / UPLAND TYPE	
15 / 16 Taeniopterides	18 Cycadopsida (Gymnosperms)	19 / 20 / 21
	LOWLAND TYPE	Palmales (Angiosperms)
	25 Programinales (unknown) / UPLAND TYPE	
24 Schizoneura	26 Neocalamites / 27 / 28 Equisetites	29 / 30
	Equisetales	Graminales
	LOWLAND TYPE	LOWLAND TYPE

are easily able to find in many localities in the world.   But we cannot easily find the Triassic upland deposits, which contains the plants of upland type.

Origin of simple leaf with parallel primary veins (Graminales)

Recent angiosperms are classified into two major groups on the basis of the leaf forms: dicotyledons with reticulate veins and monocotyledons with parallel veins. No one had previously discussed on the origin of leaf-forms of angiosperms. As discussed above, the present writer considers that the representative simple leaf of dicotyledons was derived from the pinnately compound leaf of the Late Paleozoic by "Fusion" of segments. All leaf-forms of Recent macrophyllous plants were certainly derived from the leaf-forms of macrophyllous Paleozoic plants. The writer discussed the evolution of macrophylls in the previous chapter and Part 4 (Asama, 1982). The Early Devonian Rhyniales with naked axis changed to Archaeopteridales with the pinnately compound leaves of the Late Devonian (Part 4, Fig. 1), and changed to the simple leaves of Gigantopteridales, Glossopteridales and Taeniopterides in the Permian. But all plants did not change their leaf-forms to simple leaf, and some plants remained to have pinnately compound leaf. Some of Pteridosperms belong to the former type, and ferns to the latter type. These changes of leaf-forms strongly suggest that plants do not change their leaf-forms at random, but change by rules. The writer calls these rule as "Principles of Growth Retardation". The history of all leaf-forms of Recent plants is explained by "Principles of Growth Retardation".

There are three types of leaf forms in woody angiosperm: simple leaf with retitulate veins (dicotyledons), pinnately compound leaf or palmately compound leaf with parallel secondary veins (Palmales), and simple leaf with parallel primary veins (Graminales). As stated a bove, there was a blank of fossil records of simple leaves for Mesozoic 100 million years. Therefore we must search the ancestral plants with first type of leaf-forms of Recent angiosperms (dicotyledons) in the late Paleozoic. The "Principles of Growth Retardation" indicates that the representative simple leaf of dicotyledonous angiosperms was formed in the Permian from the pinnately compound leaves by "Fusion" of segments. Therefore we must search the origin of woody dicotyledons among the Permian plants with simple leaf; Gigantopteridales and Glossopteridales.

The second type of leaf forms of Recent angiosperms (Palmales) was probably derived from Permian Taeniopterides, which was seemingly derived from the Late Paleozoic plants with pinnately compound leaf. But we could not find propalms in the Early and Middle Mesozoic. The origin of the third type of leaf-forms of Recent angiosperms (woody Graminales) is the most questionable problem. Because we do not find the suitable simple leaf plants with jointed stems for woody Graminales in the Permian and in the Mesozoic.

Ancestral plants of Recent woody Graminales to be found among
Upper Paleozoic Calamitales

Morphological aspects of bamboos are very similar to those of the Upper Paleozoic *Calamites*. In general botanists consider that the resemblance (Fig. 2) between

Recent bamboos and Paleozoic *Calamites* is not homology but analogy. However, they have not explain the reason why they resemble so much each other and that which plants in Mesozoic and Paleozoic were the ancestral to Recent woody Graminales. The present writer considers that the similarity between bamboos and *Calamites* is homological. The reason is very simple. Both have the articulate stems, which characterize the line of Arthrophyta. The writer classified the vascular plants into three lines by the morphological characters: microphylls (Microphyllophyta), macrophylls (Macrophyllophyta), and articulate stems (Arthrophyta). The plants belonging to Arthrophyta always have articulated stems in Paleozoic, Mesoozic and Cenozoic. The articulated stems chatacterize the line of Arthrophyta, and this distinct character of Devonian articulates remained in the plants of Recent Graminales without losing its character through ages. The articulated stems are often found in Microphyllophyta and Macrophyllophyta, which are formed from the non-articulate primary stems by shortening of stems (Principle E, "Shortening-Verticillation", ASAMA, Part 1, 1981a). Of course they do not belong to Arthrophyta. Judgement of the lineage must be made on the basis of the original type of stems. It is not difficult to find whether such character as articulated stem is original or not. If the character is found in all plants belonging to an order, it is the original character, and if that is found only in some plants in the same order, it is the derived one. Articulated stems are found in all plants belonging to Graminales and found in some plants belonging to Palmales. Therefore the former's articulated stems are original character, and the latter's articulated stems are the secondary character derived from non-articulated stems. The former indicates linearge and the latter does not indicate lineage.

Therefore, if the idea is correct that the articulated stems characterize the line of Arthrophyta through ages, the Upper Paleozoic *Calamites* were the ancestral plants of Recent Graminales. This measn that taxa belonging to Graminales should be removed to Arthrophyta from Monocotyledoneae of Angiosperms.

In animals, if they have same habits, they will acquire similar morphological characters which are found in insects, birds, and bats as wings. These similarities are analogous. Plants are, however, unable to move their bodies as animals, therefore we do not find analogous similarities in plants. The writer considers that the articulate stems of jointed stems are the inherent character which was probably formed in algal stage before the vascular stage, and they are indicating the lineage of vascular plants.

Comparison between Palmales and Graminales

Palmales and Graminles are classified as monocotyledonous angiosperms but the writer considers that they were derived from different ancestral plants. The pinnately or palmately compound leaves of palms (Fig. 2–16, 18) were derived from the Upper Paleozoic pinnately compound leaves by "Enlargement" (Fig. 1–13 ~ 16), and by splitting of the lamina of the simple leaf (Fig. 1–17, 19, 20, 21). The simple leaf
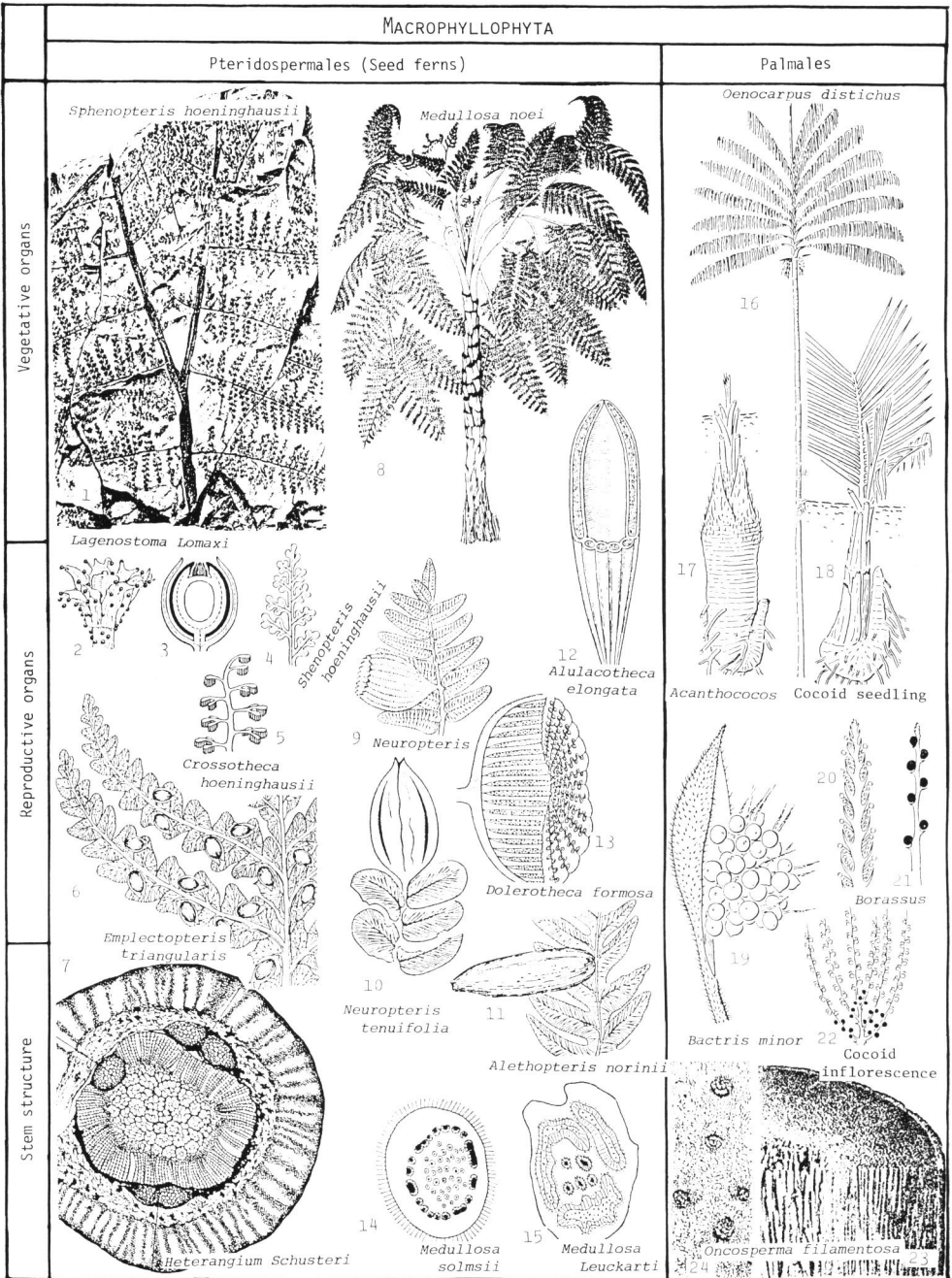
Fig. 2. Comparsion of morphological characters in seed ferns, calamites, palms and bamboos. Palms might have been derived from the Paleozoic seed ferns and bamboos from the Paleozoic calamites. Adapted from ANDREWS (1961), BAXTER (1963), CORNER (1966), HIRMER

ARTHROPHYTA

Calamitales | Graminales (Bamboos)

25 Calamites carinatus

26 Annularia Sphenophylloides

27 Schizoneura manchuriensis

28 Equisetites arenaceus

29 Palaeostachya andrewsii

30 Calamostachys casheana

31 Calamocarpon insignis

32 Calamites sp.

33 Calamites sp.

34 Phyllostachys viridi-glaucescens

35 Phyllostachys tanguillans

36 Shibataea Kumasasa

37 38 39 Dendrocalamus Latiflorus

40 Phyllostachys pubescens

41 42 43

(1927), KON'NO (1960), MCCLURE (1966), MUROI (1962), SCOTT (1962), SHIMAJI, SUDO & HARADA (1977) and ZIMMERMANN (1959).

with the primary parallel veins in bamboos was derived from the Upper Paleozoic calamitalean leaves by "Enlargement and Fusion" (Fig. 1–22 ~ 25, 29, 30).

Considering from the laef-forming processes of palms and bamboos, it appears that they had different ancestral lines of plants, *Alethopteris-Taeniopteris* line and *Annularia-Schizoneura*? line (Fig. 2–25 ~ 27) respectively.

As shown in Fig. 1–13 ~ 21 (*Alethopteris-Taeniopteris*-Palmales line) and Fig. 1–22 ~ 30 (*Annularia-Schizoneura*-Graminales line), the leaf-forming process of Palmales is different from that of Graminales. A leaf of palms corresponds to a fromd of the Upper Paleozoic tripinnate or bipinnate *Alethopteris* and a leaf of bamboos corresponds to the collected leaves or fused leaf of a whorl of *Annularia*. Therefore, the leaf of palms is very large and has long petiole but that of bamboos is small and has no petiole.

The root systems of bamboos (Fig. 2–34, 36) are very similar to those of the Upper Paleozoic Calamitales (Fig. 2–25, 28), and stems of both are characterized by the jointed stems. They are different from those of palms (Fig. 2–17, 18). Such similarities of root systems between Calamitales and Graminales may represent their homology. Jointed stems and rhizomes are found in all Calamitales and all Graminales, which indicate their homology.

Calamites have the secondary woods in their stems (Fig. 2–33) and bamboos do not have the secondary woods (Fig. 2–41, 43). We always find the reduction and improvement of vegetative organs in the evolution of plants. The best examples of the reduction of the secondary woods are found in changes from woody to hergaceous angiosperms. And for example, in Devonian plants they acquired new characters (their secondary walls developed from annular to spiral, scalariform and pitted elements) reducing their homologous parts (Part 3, Fig. 2, 4, Asama, 1981c). *Calamites* reduced their secondary woods for the adaptation to the changing environments in the Late Paleozoic or the Early Triassic. They acquired the new character, vessele, which are arranged at random in their stems.

Palms have the aractostelic stem (Fig. 2–24) as the stem of bamboos. The writer considers that the atactostelic stem of palms was derived from the polystelic stem of the Upper Paleozoic *Medullosa* (Fig. 2–14, 15) by the reduction of the secondary woods, and that of bamboos was derived from the Upper Paleozoic *Calamites* by the reduction of the secondary woods (Fig. 2–33).

Calamites have the cones of the spore-stage (Fig. 2–29, 30), and bamboos have those of the enclosed seed-stage (Fig. 2–37, 39). The reproductive organs of *Calamites* was developed from the homosporous (Fig. 2–29, *Palaeostachya*) to heterosporous (Fig. 2–30, *Calamostachys*) and to the megasporangium with a megaspore (Fig. 2–31, *Calamocarpon*). These successive imporvement of reproductive organ of *Calamites* suggests that *Claamites* acquired the enclosed seed in the later stage. The writer classified the vascular plants into three lines Microphyllophyta, Macrophyllophyta, and Arthrophyta. In both Microphyllophyta and Macrophyllophyta, the reproductive organs evolved from the spore stage of Devonian to the naked seed-

stage of the Upper Paleozoic (*Cordaites* and *Lebachia* in Microphyllophyta and the seed ferns in Macrophyllophyta,) and to the enclosed seed-stage (*Podocarpaceae*, *Taxaceae* and *Cephalotaxaceae* in the microphyllous conifers and in the macrophyllous dicotyledonous angiosperms).

Therefore it is expected that the reproductive organ of *Calamites* became improved from spores to the enclosed seeds in the late Paleozoic or Upper Triassic, because all vascular plants affected by the same environmental change from mild to severe climate. From the facts mentioned above, the writer concludes that the bamboos with distinct jointed stems were derived from the Upper Paleozioc *Calamites*, and they differ from plams in the origin. *Calamites* and bamboos should be classified to Arthrophyta and palms to Macrophyllophyta.

Why are we unable to find the Pre-Cretaceous angiosperms?

As discussed in the above chapter, there were the blank period of 100 million years for the simple leaf (proangiosperms?).

Theoretically the simple leaf (ancestral plants of angiosperms), which appeared in the Permian, should continue to live in the Triassic and Jurassic. But we do not find the angiosperms in the Early and Middle Mesozoic. Why are we unable to find the angiosperms in the Pre-Cretaceous? Fig. 3 shows the relation between the vascular plant evolution and the climatic change through ages. The first land plants (spore-stage) appeared in the latest Silurian, and evolved from plants with naked axes to plants with pinnately compound leaves in the latest Devonian, and some of them (seed ferns) changed to the simple leaf plants (angiosperm-like seed ferns) in the Permian, which disappeared in the Early Triassic. The simple leaf plants reappeared in the Middle Cretaceous as angiosperms, and continued to live as Recent dominant land plants. These evolutionary change from the spore-stage to the naked seed, and to the enclosed seed-stage were the adaptable change for the changing environment from mild (spore-stage) to severe (naked seed-stage) and to very severe (enclosed seed-stage) climate, as shown in Fig. 3. The great change of vascular plants occured in the period of eperogenetic movement: the first appearance of land plants in the latest Silurian or earliest Devonian of Caledonian movement (deposition of Old Red Sandstone); the appearance of smiple leaf (angiosperm-like seed ferns) in the Permian and Triassic after Hercynian movement (deposition of New Red Sandstone); and the reappearance of simple leaf (angiosperms) in the Middle Cretaceous of Yenshanian movement. The successive evolution of land plants resulted by the successive lowering of winter temperature from Devonian to Permian were interrupted by the mild climate in the Triassic as shown in Fig. 3. And when the winter temperature (in Fig. 3, the winter temperature means the lowest temperature in a year) lowered to the true winter, the simple leaf plants reappeared as angiosperms in the Middle Cretaceous. The appearance, disppearance and reappearance of simple leaf plants depended upon the climatic changes in ages from Permian to Cretaceous.
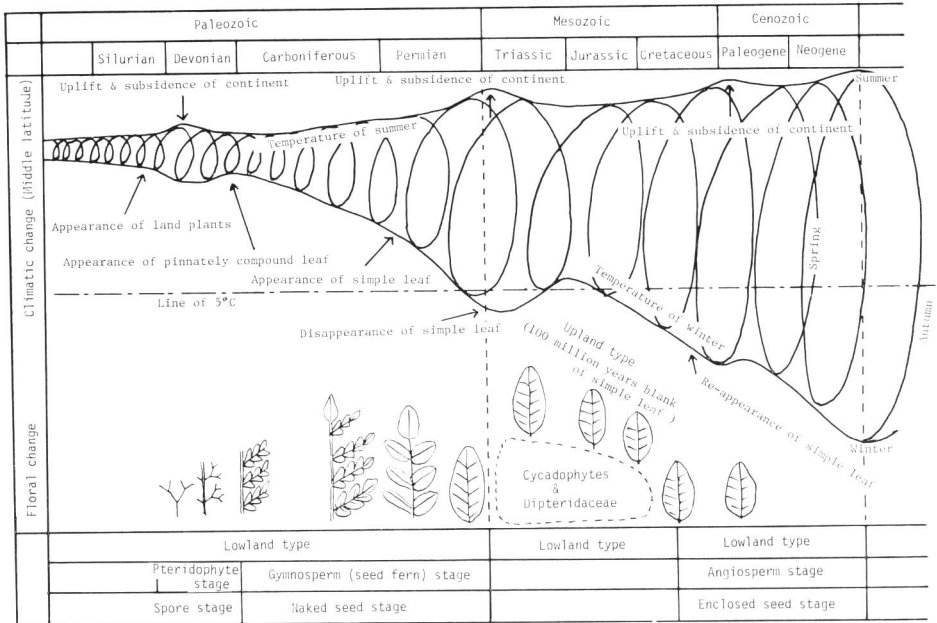
Fig. 3. Climatic change through ages inferred from the evolution of plants (in middle latitude). Gradual increasing of annual range might have been the main cause of plant evolution. We can reasonably explain the reason why occured the appearance of land plants, appearance of pinnately compound leaf, appearance of simple leaf, disappearane of simple leaf, appearane of upland type of plants in Mesozoic, re-appearane of simple leaf in the late Cretaceous, respectively.

We have observed the lowland type plants as fossils, which are more preservable in sediments of terrestrial deposits. The Upper Paleozoic luxuriant coal floras and the Upper Triassic floras are all found in the lowland terrestrial deposits, but almost no upland floras have been found, bacause the upland deposits containing fossil plants were probably eroded out through ages.

By lowering of the winter temperature through the late Carboniferous and the early Permian, the great ice age appeared in Gondwanaland, which occupied the southern hemisphere around the south pole. Gondwana flora which were mainly represented by Glossopteridales, distributed widely on the Gondwanaland. In the northern hemisphere Euramerian flora and Cathaysia flora were distributed near the equatorial zone, and Angara flora in the middle latitude. There were no continents around the north pole, so the continental glacier did not occur in the northern hemisphere.

There were no floral provinces in the world through Devonian and Lower Carboniferous, and a single floral province was divided into four floral provinces by the epeirogenetic movement through Carboniferous and Permian: Angara flora in the

north, Euramerian flora in the west, Cathaysia flora in the east and Gondwana flora in the south respectively.

This was the first greatest enviornmental change in the geological age and occured the greatest extinction in animal and plant kingdom in the latest Permian. The uplifting of continents by the epeirogenetic movement finished in the latest Permian, and the lowering of continents began in the Triassic. The severe climate of Permian changed to the mild climate in the late Triassic, and such tropical plants as Dipterid-aceae extended their distribution from tropical ot Greenland in the north and to Australia in the south. These world wide distribution of Dipteridaceae means the climatic change from the severe climate in Permian to the mild climate in the late Triassic. By these climatic changes the advanced Permian plants apparently migrated from the lowland of Permian to the upland of the late Triassic and the lowland was filled by the lowland floras.

Therefore we observe the world wide distribution of the Triassic lowland flora, which are characterized by Dipteridaceae and cycadophytes (Fig. 3) and we do not find the descendants of the advanced Permian plants which might have occupied the upland of Triassic age. It will be very strange, if we find descendants of the advanced Permian plants in the lowland. We cannot deny the relation between the climatic change and the migration of plants, which were well shown in the migration of Qua-ternary plants: northward migration in interglacial ages and southward migration in glacial age in northern hemisphere. It will be unreasonable to deny the plant migra-tion effected by the great climatic change through the Permian and Triassic age.

Evolutionary level of the Permian plants and the parallel evolution of plants and animals

Permian floras contain many kinds of seed ferns, and a great part of them dis-appeared in Triassic. Many paleobotanists have interpreted that the disappearance of seed ferns in Triassic was their extinction. But this interpretation is not reasonable, because the seed ferns are the gymnospermous plants with naked seeds, and they are more advanced type of plants than ferns with spores. Tropical Dipteridaceae with spores floulished in the late Triassic and this means that the climate in the late Triassic was mild and suitable for the life of ferns. Therefore it is unreasonable to consider that the seed ferns of the evolutionary higher level perished by the Triassic environment which was suitable for ferns of the evolutionary lower level. This may mean that the advanced seed ferns of Permian might have lived in the upland place in Triassic.

The writer showed the phylogeny of vascular plants and vertebrates in Part 2, Figs. 1 and 2 (ASAMA, 1981b), which suggest the parallel evolution of land plants and vertebrates. The level of evolution of pteridophytes, gymnosperms and ang-iosperms of land plants correspond with those of amphibians, reptiles and mammals of vertebrates. The evolution of land plants always proceeded a little earlier than those of vertebrates as shown in Part 2, Figs. 1 and 2, which mean that land plants

are more sensible for the environmental change than vertebrates.   When the environ-
ments changed to the unsuitable one, vertebrates can migrate to the suitable place,
but land plants cannot.

Mammal-like reptiles appeared in Gondwanaland through the late Permian and
Triassic are considered to be the ancestral reptiles of mammals.   Glossopteridales
and Gigantopteridales of seed ferns, which correspond to the mammal-like repriles in
vertebrates appeared in Permian.   Small Mesozoic mammals, which were derived
from the mammal-like reptiles, lived poorly with many kinds of dinosaurs in Mesozoic.
They expanded their distribution and diversity in the Early Cenozoic.   Small Mesozoic
mammals had widely developed in Cenozoic after 100 million years of poor living in
Mesozoic.

Mesozoic angiosperms have been described by many authors (Harris, 1932;
Lignier, 1908; Brown, 1956, etc.), but some authors (Richard, Scott, Barghoorn,
& Leopold, 1960) have denied their presence.   If we recognize the parallel evolution
between land plants and vertebrates, we should recognize the living of the angiosperm-
ous plants in Triassic and Jurassic.   We could not find the Mesozoic angiopserms, but
small Mesozoic mammals are found as teeth fossils.   The leaves of land plants are
softer than teeth of mammals and are difficult to remain as fossils.   From the view
point of parallel evolution between land plants and vertebrates, it is very reasonable to
consider the upland origin of angiosperms in the latest Permian or the earlier Triassic.

Site of origin of angiosperms

As discussed in the previcus chapter, the angiosperm-like seed ferns appeared as
Glossopteridales and Gigantopteridales in the Permian age, and the angiosperms
were probably derived from these angiosperm-like seed ferns in the latest Permian or
the earliest Triassic.   Glossopterides are found successively in Permian and Triassic
in the southern hemisphere, and Gigantopterides found in the Permian of the northern
hemisphere disappeared in the latest Permian.   The leaf characters of the former are
simple, and those of the latter are complicated which are very similar to those of
dicotyledonous angiosperms.   The morphological leaf characters of Gigantopterides
are more similar to dicotyledonous angiosperms than to those of Glossopterides.
This suggests the possibility that Gigantopterides were the ancestral plants of angio-
sperms.   Therefore, the writer considers that the site of origin of dicotyledonous angio-
sperms must be found within the distributional area of Permian Gigantopterides
which extend from Northeast China to Malaya and Sumatra through Central China
and Yunnan.

Shansi was the center of the evolution of Gigantopterides and was in the central
part of Cathaysia land in the Upper Permian, which was shown in the paleogeo-
graphical map of Liu (1955).   Liu's paleogeographical maps show that the Cathaysia
land and Angara land were connected by the disappearance of Monoglian geosyncline
in the Lower Triassic.

Judging from the facts mentioned above it was suggested that the proangiosperms were apparently evolving on the upland near Shansi, Kanssu and Monoglia. Therefore we must find the upland sediments, which was deposited in the Triassic, to search the site and origin of early angiosperms. Palynological studies of the Triassic upland sediments in Shansi, Kanssu and Mongolia might provide critical data for the origin of angiosperms.

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