

Evolution and Phylogeny of Vascular Plants based on the
Principles of Growth Retardation. Part 4.
Phylogeny of Macrophyllrophyta inferred
from the Evolution of Leaf Forms

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It is no doubt that the angiosperms show the most advanced morphological characters among vascular plants, i. e., simple leaf in the leaf form, vessel in the stem structure and the enclosed seed in reproductive organ. It is also no doubt that these characters of macrophyllous angiosperms were derived from the first land plants, Rhyniales, through Paleozoic, Mesozoic and Cenozoic. Therefore we cannot understand the phylogeny of vascular plants without pursuing the evolutionary processes from the naked branches of the Rhyniales to the simple leaf of angiosperms, from tracheid to vessel, and from spore to enclosed seed respectively.

We have abundant fossil evidences about the leaves of Paleozoic, Mesozoic and Cenozoic plants. Comparing the fossil leaves, we do not have much fossil evidences about the evolution of reproductive organs and stem structures which are sufficient to establish the phylogeny of vascular plants. Therefore at first we should establish the phylogeny of vascular plants on the basis of abundant fossil leaves, and then we should check the phylogeny of vascular plants by the fossil evidences of reproductive organs or stem structures.

Origins of land plants

There were three types of plants in the early Devonian: Protolpidodendrales (*Drepanophycus*, *Baragwanathia*, *Protolpidodendron*) with microphylls, Rhyniales (*Rhynia*, *Cooksonia*, *Steganotheca*) with naked branches, and Protoarticulatales (*Equisetophyton*) with articulate stems. Fossil evidences show that *Cooksonia* of Rhyniales was the first land plant which was found from the uppermost Silurian, but this does not mean that all other vascular plants were derived from *Cooksonia*. Soon after the appearance of *Cooksonia* we find *Drepanophycus* of Protolpidodendrales and *Equisetophyton* of Protoarticulatales (or Protocalamitales ?) in Siegenian (Early Devonian). It is very difficult to consider that *Drepanophycus* or *Baragwanathia* with sporangia on the adaxial surface of microphyllous leaves or in its axial was derived from the *Rhynia*-like plants with terminal sporangia in a very short period. And of course it is difficult to consider that *Equisetophyton* with articulate stem was derived from the *Rhynia*-like

plants without the articulate stem. The writer considers that these three types of plants succeeded to come out of water to on land in parallel. The branch system of Rhyniales had changed to the pinnately compound leaf of Archaeopteridales by the end of Devonian, which means that the Rhyniales were the ancestral plants of the post Devonian macrophyllous plants. Therefore we must recognize three lines of vascular plants; Microphyllphyta with microphylls, Macrophyllphyta with macrophylls, and Arthrophyta with articulate stems. These three lines of vascular plants must have evolved in parallel through Paleozoic, Mesozoic and Cenozoic by the influence of same environmental change.

Origins of gymnosperms

Fossil gymnospermous plants are classified into two main groups: Cycadopsida and Coniferopsida. The former contain Pteridospermales, Bennettitales, Cycadales and Pentoxylales and the latter contain Cordaitales, Coniferales and Ginkgoales. The present writer also classifies gymnospermous plants into two groups, Macrophyll-gymnospermophytina (Pteridospermales, Bennettitales, Cycadales, Pentoxylales and Ginkgoales) and Microphyll-gymnospermophytina (Cordaitales and Coniferales) by their characteristic leaf-forms, macrophylls, and microphylls. There were no fossil evidences that microphyll changed to macrophyll or macrophyll changed to microphyll. Therefore he considers that the microphylls of Lepidodendrales are homologous with the microphylls of Cordaitales and Coniferales, and that the macrophylls of Pteridospermales are homologous with the macrophylls of Bennettitales, Cycadales, Pentoxylales and Ginkgoales. In general plants with microphylls form cones, and plants with macrophylls do not form cones as reproductive organ at the early evolutionary stage in Carboniferous or Permian.

The writer recognized three lines in Devonian plants (pteridophytes), Microphyllphyta, Macrophyllphyta, and Arthrophyta, all of which are at the spore stage. These three lines of plants must have evolved in parallel by the influence of same environmental changes through ages. There were two kinds of evolution in vascular plants, the regressive evolution and the progressive evolution. Almost all Devonian plants were at the spore-stage, and these plants of three lines had evolved in parallel grading up their evolutionary stages from the spore stage to gymnosperm (naked seed) and angiosperm (enclosed seed) stage, step by step through ages. The writer calls these improvement of reproductive organ the progressive evolution. On the other hand some Devonian plants of three lines had remained at the spore stage without improving their reproductive organs. In this case they had remarkably reduced the size of their vegetative organs through ages. The writer calls them the regressive evolution.

In the case of regressive evolution the early leaf form (pinnately compound leaf) did not change so much and remained in the ancestral form (pinnately compound leaf), but in the case of progressive evolution the leaf form (naked branches and pinnately

compound leaf) had changed to simple leaf. The naked branches of Devonian plants (Rhyniales) changed to the pinnately compound leaf by the end of Devonian, and it was the first appearance of macrophyll in the history of vascular plants. Therefore the macrophylls of Macrophyllphyta are different from microphylls of Microphyllphyta in their origins. Neither had microphylls changed to macrophylls, nor macrophylls to microphylls. From the reason mentioned above the writer cannot agree with the idea that Archaeopteridales were the ancestral plants of Coniferales. The macrophylls of Archaeopteridales had not change to the microphylls of Coniferales. The writer considers that the cones and microphylls of Lepidodendrales are homologous with those of Coniferales. Therefore the ancestral plants of Coniferales must be Lepidodendrales and not Archaeopteridales, as discussed in Part 2 (ASAMA, 1981b). Archaeopteridales with macrophylls must be the ancestral plants of seed ferns with macrophylls.

Main Paleozoic gymnospermous plants are seed ferns and conifers. As mentined above the seed ferns with macrophylls must be derived from the Aneurophytales or Archaeopteridales with macrophylls, and the conifers with cones and microphylls must be derived from the Lepidodendrales with cones and microphylls. The Mesozoic gymnospermous plants are Bennettitales, Cycadales, Pentoxylales, Ginkgoales and conifers. The ancestral plants of the former three with macrophylls might be the Paleozoic seed ferns and that of Ginkgoales with macrophylls might be derived from progymnosperms.

Phylogeny of macrophylls

Fossil evidences show four evolutionary stages in the leaf history of vascular plants, the pinnately compound leaf-forming stage, the simple leaf-forming stage, the cycadophytic leaf stage and the simple leaf stage (Fig. 1). This means that the naked branch system of Devonian plants had changed to the simple leaf of angiosperms through time. Without the study of leaf form evolution of macrophylls we could not understand the phylogeny of Macrophyllphyta.

1) Pinnately compound leaf-forming stage (Origin of macrophylls)

The majority of angiosperms show the most advanced leaf form, simple leaf, in vascular plants. It is no doubt that the simple leaf of angiosperms was derived from the Devonian Rhyniales through Paleozoic, Mesozoic and Cenozoic. The evolution of leaf forms in Devonian plants are discussed in Part 3 (ASAMA, 1981 c).

The naked axes of Rhyniales (*Rhynia*-stage) had changed to the pinnately compound leaf of Archaeopteridales (*Archaeopteris*-stage) through *Trimerophyton*-stage and *Aneurophyton*-stage multiplying their axes step by step (Part 3, fig. 2). In the *Archaeopteris*-stage the pinnately compound leaf was formed. This was the first appearance of macrophyll in the leaf history of vascular plants, and this was the starting point of all macrophyllous plants; seed ferns in Upper Paleozoic, cycadophytic plants in Mesozoic and angiosperms in Cenozoic.

		Silurian	Devonian			Carboniferous	Permian	
		Uppermost	Lower	Middle	Upper			
Macrophyll-angiospermophytina	Monocotyledon							
	Dicotyledon							
Macrophyll-gymnospermophytina	Ginkgoales							
	Pentoxylales							
	Cycadales						 Nilssonia	
	Bennettitales						 Pterophyllum	
	ferns					 Sphenopteridium Mariopteris	 Glossopteris Gigantopt.	
		Seed					 Sphenopteris Neuropteris	 Callipteris Taeniopt.
	Macrophyll-sporophytina	Progymnospermis			 Aneurophyton Aneurophytales	 Archaeopteris Archaeopteridales	Simple leaf-forming stage	
		Pterophytes	 Cooksonia Rhyniales	 Psilophyton Trimerophytales	 Pseudosporocarpus Cladoxylales	 Rhacophyton Coenopteridales	 Adiantites Anisopteris	 Pecopteris
Pinnately compound leaf-forming stage						Pinnately compound leaf stage		

Fig. 1. Fossil evidences indicate that there were four leaf form stages in the leaf history of the cycadophytic leaf stage and the simple leaf stage.

Triassic	Jurassic	Cretaceous	Tertiary	Recent
		<i>Palmoxylon</i>	 Palmae	 Palmae
		 Magnoliales	 Acer	 Fagus
			 Platanus	
			Simple leaf stage	
 <i>Baiera</i>	 <i>Ginkgoites</i>	 <i>Ginkgoites</i>	 <i>Ginkgo</i>	 <i>Ginkgo</i>
	 <i>Pentoxylon</i>			
 <i>Palaeocycas</i>	 <i>Nilssonia</i>	 <i>Nilssonia</i>		 <i>Cycas</i>
 <i>Pterophyllum</i>	 <i>Ptilophyllum</i>	 <i>Anomozamites</i>	 <i>Otozamites</i>	 <i>Cycadeoidea</i>
Cycadophytic leaf stage				
 <i>Dictyophyllum</i>	 <i>Cladophlebis</i>	 <i>Gleichenites</i>	 <i>Woodwardia</i>	 <i>Phyllitis</i>

Macrophylophyta, the pinnately compound leaf-forming stage, the simple leaf-forming stage.

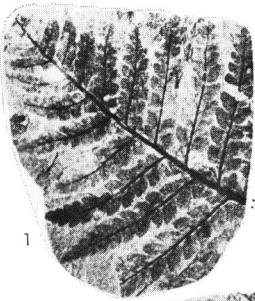
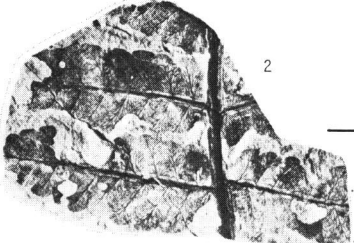
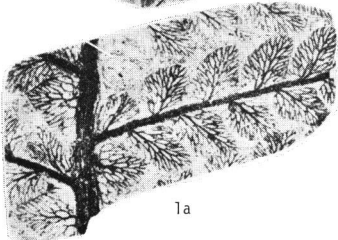
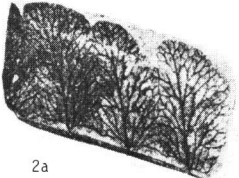
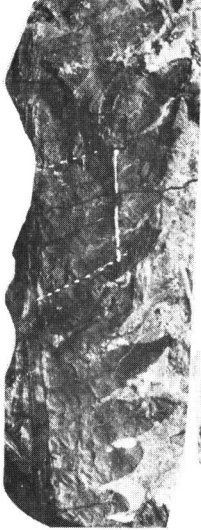
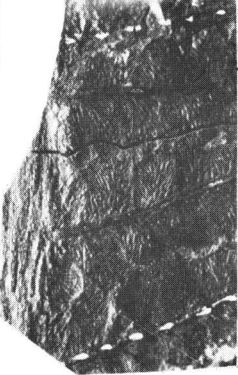
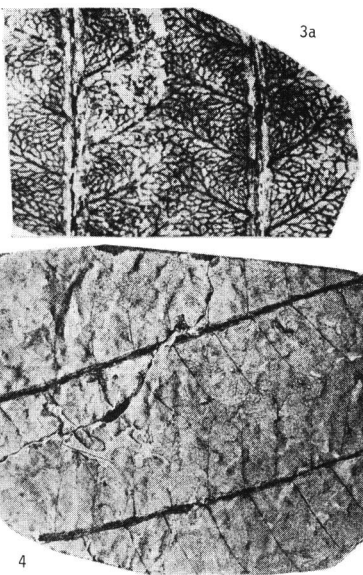
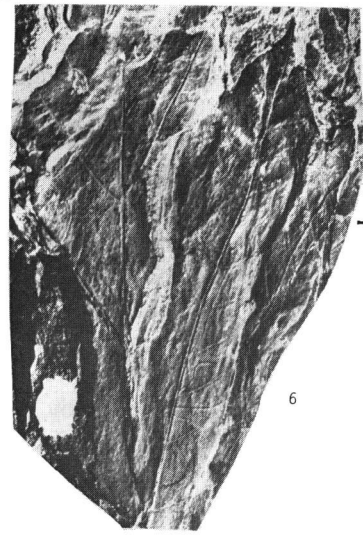
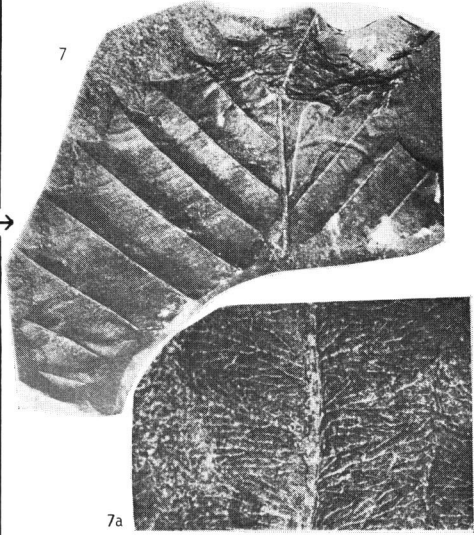
	LOWER			PERMIAN		
	Tripinnate	leaf	stage	Bipinnate	leaf	stage
Series <i>Emplectopteris</i>						
						
	<i>Emplectopteris triangularis</i>			<i>Gigantonoclea largrelii</i>		
Series <i>Emplectopteridium</i>						
						
				<i>Emplectopteridium alatum</i>		

Fig. 2. Simple leaf (4, 7) must have been derived from the pinnately compound leaf by “Fusion”

UPPER			PERMIAN		
Unipinnate	leaf	stage	Simple	leaf	stage
					
<i>Bicoempleopteris hallei</i>			<i>Tricoempleopteris taiyuanensis</i>		
					
<i>Bicoempleopteridium longifolium</i>			<i>Gigantopteris nicotianaefolia</i>		

of segments. Adapted from HALLE, 1927 (1-4); KAWASAKI, 1931 (6-7), ASAMA, 1959 (5).

2) Simple leaf-forming stage (Origin of simple leaf)

The most characteristic leaf form of angiosperms is the simple leaf. Therefore it is very important to find out the origin of angiosperms when the simple leaf was formed, where it appeared first and from which plants it was derived. Devonian was the pinnately compound leaf-forming stage; Carboniferous was the pinnately compound leaf stage; and Permian was the simple leaf-forming stage respectively. Almost all simple leaves were found in Upper Carboniferous and Permian as *Glossopteris* in Gondwana flora, so-called *Gigantopteris* in Cathaysia flora and Euramerican flora, and *Taeniopteris* in all floras. It was expected that the simple leaf would have been derived from the pinnately compound leaf because all Carboniferous macrophyllous plants were showing the pinnately compound leaf. But we could not find the simple leaf-forming process demonstrated by the fossil evidences except one locality, the Shihhotse valley of Taiyuan, Shansi, China.

In Shansi, fossil plant-bearing formations are divided into the following six series (HALLE, 1927):

- Shihchienfeng Series (Tartarian, upper part of Upper Permian)
- Upper Shihhotse Series (Kazanian, lower part of Upper Permian)
- Lower Shihhotse Series (Kungurian, upper part of Lower Permian)
- Shansi Series (Artinskian, lower part of Lower Permian)
- Taiyuan Series (Sakmarian, Lowest Permian)
- Penchi Series (Moscovian, Middle Carboniferous)

The Penchi and Taiyuan Series are marine formations. The Shansi and younger series are terrestrial formations. Up to the time of the Taiyuan Series, many of the plants are similar to the Euramerican flora, such as *Lepidodendron*, *Calamites suckowii*, *Annularia stellata*, *Sphenophyllum oblongifolium*, *Sph. emarginatum*, *Sphenopteris*, *Neuropteris*, *Linopteris*, and *Cordaitea*. In the Shansi Series the characteristic species of Cathaysia make their appearance. They are *Tingia*, *Lobatannularia*, *Protoblechnum*, *Emplectopteris*, *Emplectopteridium* and *Cathaysiopteris*. Starting with the Shansi Series the evolution of plants took place. These evolution of plants were adaptation of plants for the changing environment occurring by the uplift of Cathaysia land.

As indicated by the marine facies of the Penchi and Taiyuan Series, the Cathaysia region in those days was not a continent, but consisted of several islands. Later, the region gradually developed into a land mass which expanded farther, during the Shansi Series with Taiyuan at the center, covering Korea in the east and reaching as far west as Lanchow. Nevertheless, the land was still separated from the Angara land by the Mongolia geosyncline. As the upheaval continued, the Mongolia geosyncline disappeared during the Lower Triassic period, and the Cathaysia land was adjoined to the Angara land to form a vast continent. As a result, the region changed from a mild oceanic climate to a continental one. Doubtless, because of this climatic change, the Cathaysia flora became to have different characteristics from those of the Euramerican, Angara and Gondwana floras.

Plants must have attained their full growth in a mild climate. But as the climate

turned continental, their growth would be retarded, and their size was diminished. Consequently, various changes occurred in their leaf form, “Fusion” and “Enlargement” of segments were particularly significant changes.

The most important evolutionary changes were the appearance of simple leaf, and

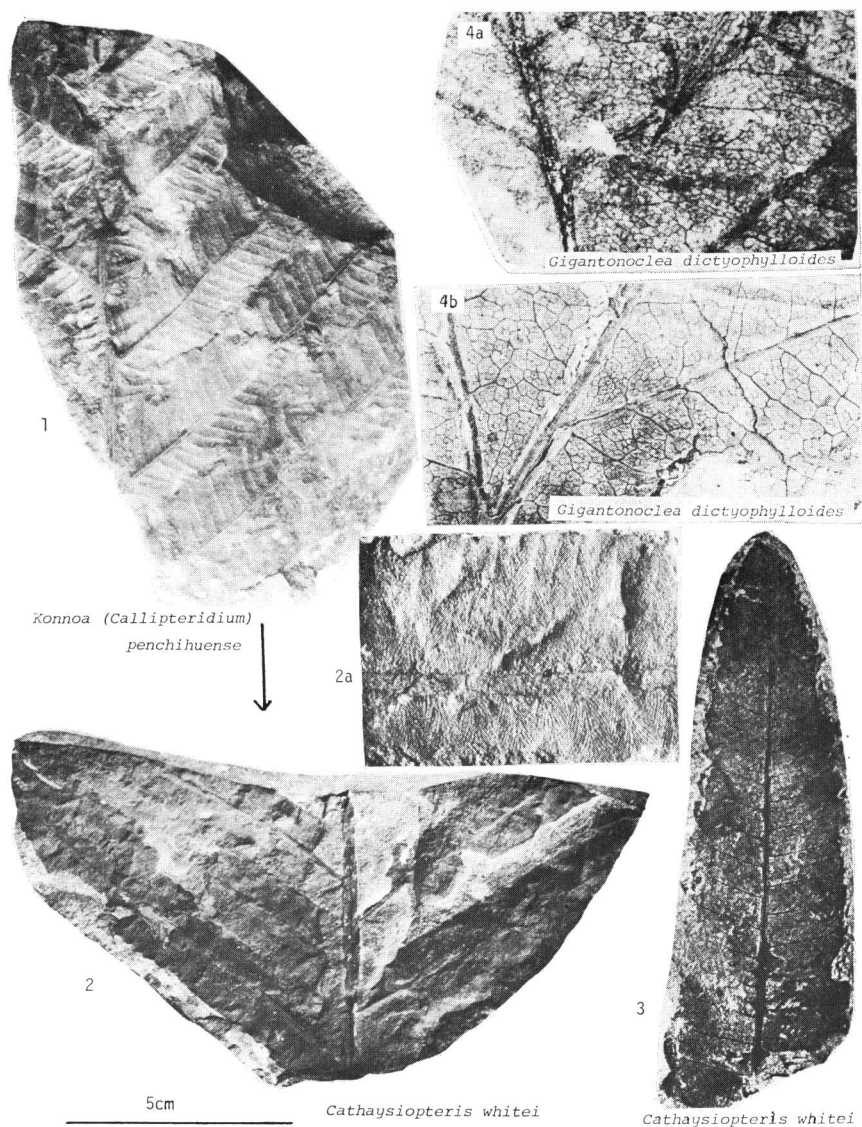


Fig. 3. Unipinnate *Cathaysiopteris whitei* must have been derived from the bipinnate *Konnoa (Callipteridium) penchihuensis* (1) by “Fusion” of segments. The venation of *Gigantonoclea dictyophylloides* is very similar to the venation of dicotyledonous plants. Adapted from ASAMA, 1959 (1, 2); GU & ZHI, 1974 (3, 4a, 4b).

it was found in the *Emplectopteris* Series of the Shihhotse valley, Taiyuan, Shansi. As the plant growth was retarded by the worsening climate, segments (pinnules) of *Emplectopteris triangularis* (Fig. 2-1) underwent fusion, and the tripinnate leaf became bipinnate, represented by *Gigantonoclea lagrelii* (Fig. 2-2). With continued deterioration of the climate, the bipinnate leaf of *G. lagrelii* underwent fusion and became unipinnate *Bicoemplectopteris hallei* (Fig. 2-3), and then evolved to the simple leaf of

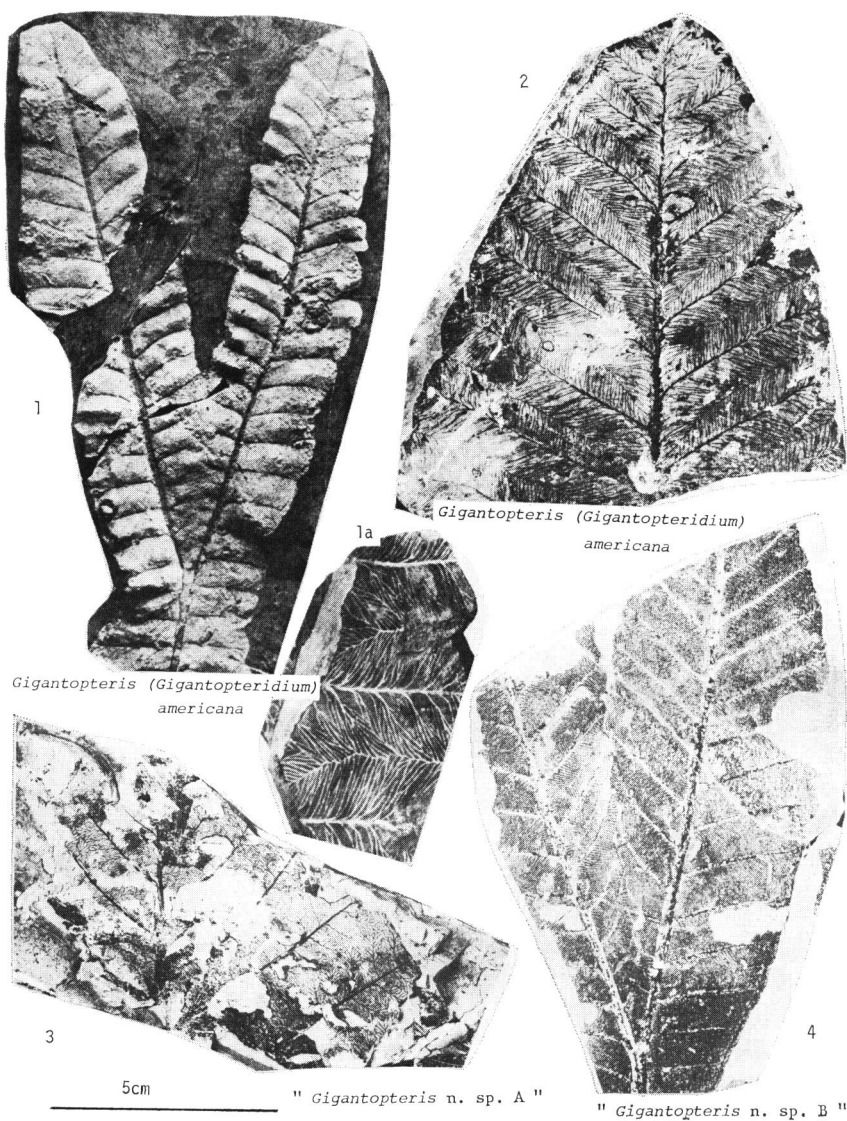


Fig. 4. So-called "*Gigantopteris*" reported from the Permian formation of Texas, N. America. Adapted from WHITE, 1912 (1); READ & MAMAY, 1964 (2-4).

Tricoemleptopteris taiyuanensis (Fig. 2-4).

Through similar process, *Emplectopteridium alatum* (Fig. 2-5) was transformed into *Bicoemleptopteridium longifolium* (Fig. 2-6) and later into *Gigantopteris nicotianaefolia* (Fig. 2-7).

Thus, tripinnate plants, when their growth is retarded, reduce the branching of leaf, so that the tripinnate leaf becomes bipinnate, then unipinnate, and, in the final stage, a simple leaf. If the growth is further retarded, the leaf becomes smaller without changing its form. The simple leaf remains the tripinnate venation, which reveals that the branching was tripinnate before the change occurred. The simple leaf also shows evidence of the preceding unipinnate and bipinnate forms.

Gigantopteris (*Carthaysiopteris*) *whitei* (Fig. 3) reported from the Lower Shihhotse Series (HALLE, 1927) shows the unipinnate leaf which might have been derived from the bipinnate *Konnoa* (*Callipteridium*) *penchiuensis* of Taiyuan Series.

WHITE (1912) reported a simple leaf plant under the name of *Gigantopteris americana* (*Gigantopteridium americanum* of KOIDZUMI, 1936) (Fig. 4-1) from the Wichita Formation of Texas, North America and the present writer considers that *G. americana* seems to be derived from *Alethopteris*-like plant by retardation. There is no connection between this species and the fused leaf plants (so-called *Gigantopteris*) of the Cathaysia flora (*Gigantopteris nicotianaefolia*, *Tricoemleptopteris taiyuanensis*, *Bicoemlepto-*

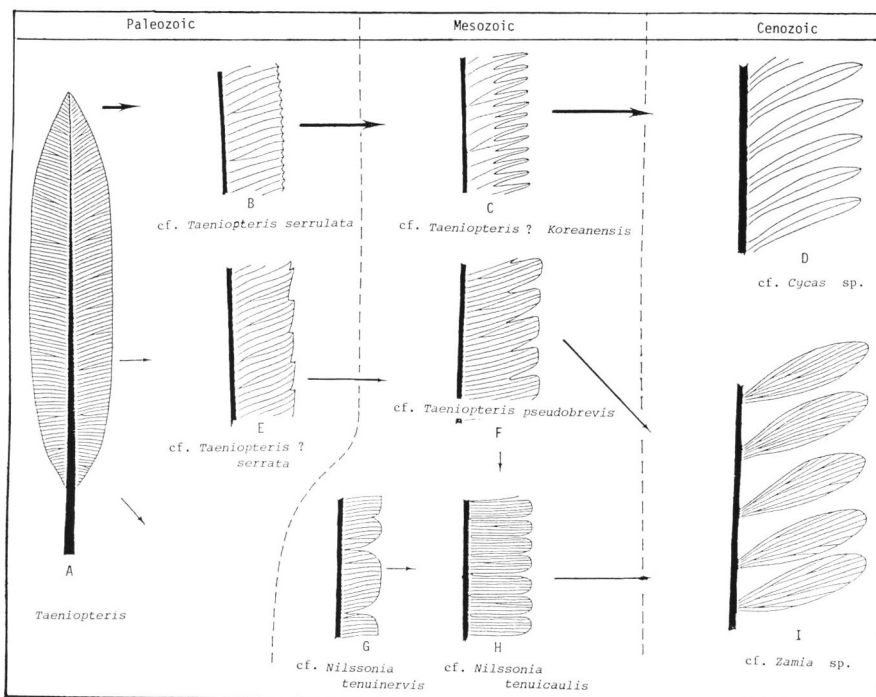


Fig. 5. The evolution of leaf-forms of Cycadales suggested by MAMAY (1976).

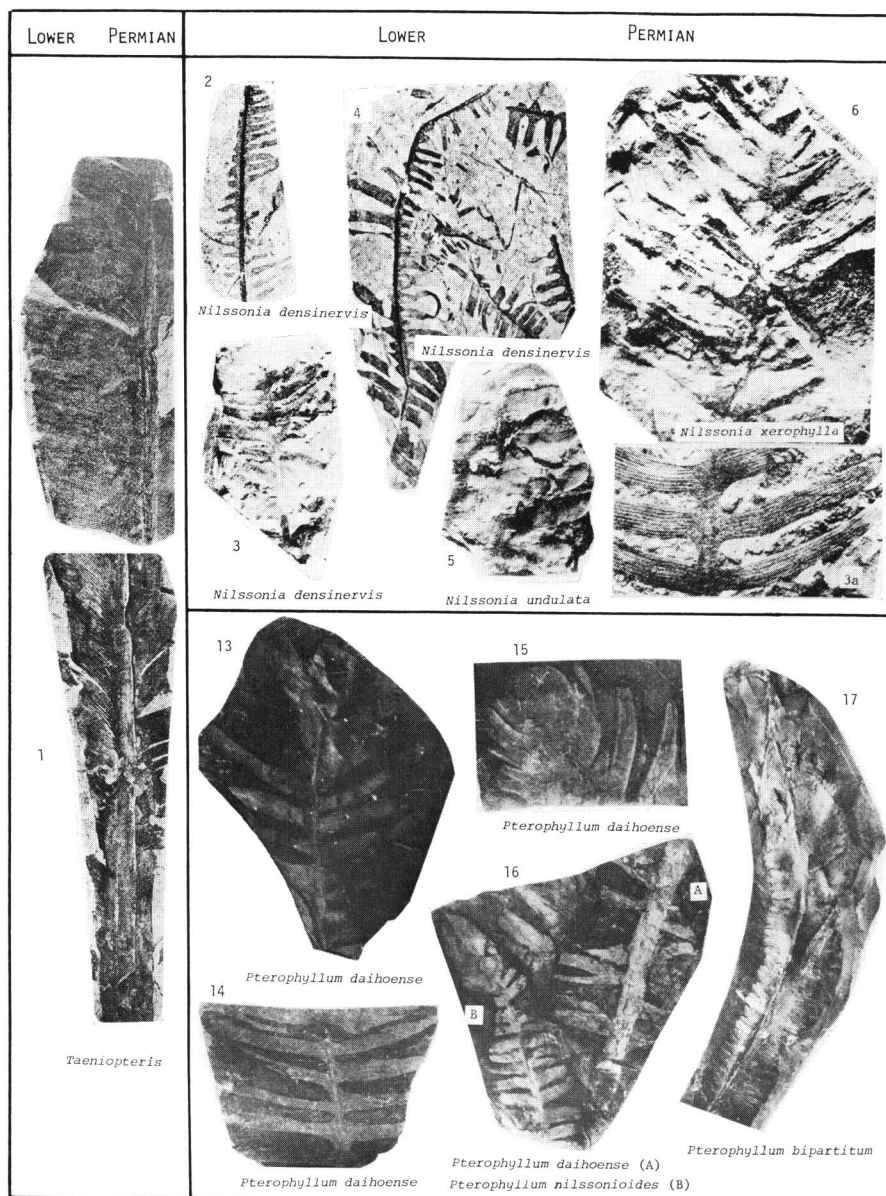
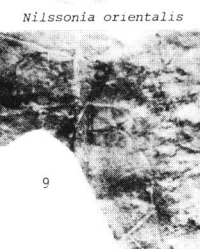
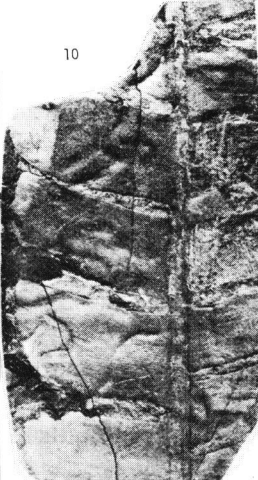
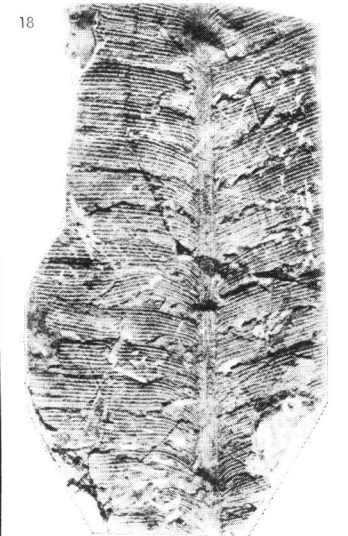
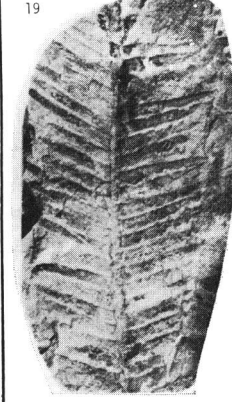
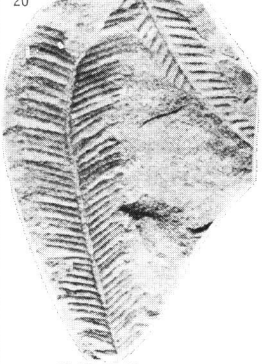
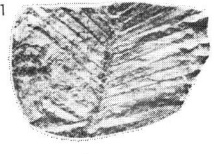


Fig. 6. Fossil evidences indicate that the cycadalean and bennettitalean leaves must have been pted from HALLE, 1927 (1-4): STOCKMANS & MATHIEU, 1939 (5, 6): KAWASAKI, 1931 (13-

pteris hallei, *Bicoemphleopteridium longifolium*, *Cathaysiopteris whitei*). The American species is also a fused leaf plant derived from *Alethopteris*-like plant by retardation. Fused leaf of these plants does not mean the same phylogenetic relation, but indicates

UPPER TRIASSIC		JURASSIC	CRETACEOUS	
7  <i>Nilssonia simplex</i>	8  <i>Nilssonia orientalis</i> 9  <i>Nilssonia orientalis</i>	10  <i>Nilssonia densinerve</i>	11  <i>Nilssonia schauburgensis</i> 12  <i>Nilssonia serotina</i>	CYCADES
18  <i>Pterophyllum ctenoides</i>	19  <i>Ptilophyllum pecten</i> 5cm	20  <i>Ptilophyllum pecten</i> 21  <i>Zamites tosanus</i>	BENNETTITALES	

derived from the entire leaves of *Taeniopteris* through splitting lamina into segments. Ada-17): OISHI 1932 (7-6, 18): OISHI, 1940 (10-12, 19-21).

severe environments in these regions. Therefore we need not consider that *G. americana* had migrated from Cathaysia to North America by the North Pacific (Alaskan) route as WHITE explained (1912, p. 513).

Later READ & MAMAY (1964) reported *Gigantopteris americana* (Fig. 4-2), *Gigantopteris* n. sp. A (Fig. 4-3) and *Gigantopteris* n. sp. B (Fig. 4-4) from the Permian of Texas. The original form of *G. americana* and *Gigantopteris* n. sp. B would be unipinnate *Alethopteris*. The original form of *Gigantopteris* n. sp. B seems to be bipinnate *Calopteridium* or *Alethopteris*. So, in origin they are entirely different from the Cathaysian *Gigantopteris* that originated in *Emplectopteris* and *Emplectopteridium*.

The plant previously reported from North America as *Tingia*, the characteristic Cathaysian genus, has been lately assigned to a newly created genus *Russellites* (MAMAY 1968), which is also quite different from any of the members of the *Gigantopteris* flora of Cathaysia. Thus, there is no relation between the Cathaysian *Gigantopteris* flora and the North American *Gigantopteris* flora (READ & MAMAY, 1964). However, in both regions the simple leaf was produced by "Fusion", which suggests similar environmental changes.

In Gondwanaland the representative simple leaf is *Glossopteris* which is different from *Gigantopteris* with pinnate secondary veins in having reticulate secondary veins. Pinnate secondary veins of *Gigantopteris* mean that they were derived from the pinnate plants by "Fusion", and reticulate secondary veins of *Glossopteris* mean that they were derived from the pinnate plants by "Enlargement" (see Part 1, fig. 2. Principles of Growth Retardation, ASAMA, 1981 a).

Almost all of macrophyllous Carboniferous and Permian plants had pinnate compound leaf from which the simple leaves of Gondwanaland and Cathaysia land must have been derived by "Enlargement" or "Fusion". Judging from the reproductive organs of *Glossopteris*, the form genus *Glossopteris* contains many different series of plants. It is natural that they must have been derived from many kinds of pinnate plants by "Enlargement". The venations of *Glossopteris* are very simple. Therefore it is impossible to distinguish some genera from other genus by their venation. However, the venation of so-called *Gigantopteris* formed by "Fusion" are very complicated showing the branching of pinnate plants before changes. The venations of plants formed by "Enlargement" show the venation of pinnule of pinnate leaf before changes, and those of plants formed by "Fusion" show the branching of pinnate plants before changes as shown in Part 1, fig. 2 (ASAMA, 1981 a).

The most common simple leaf in the Upper Paleozoic plants are found in *Taeniopteris* which is broadly distributed in the world, and it might have been derived from the pinnate plants by "Enlargement".

The fossil evidences of Devonian, Carboniferous and Permian plants indicate that the naked branch system changed to the pinnate compound leaf by the end of Devonian, and changed to the simple leaf in the Upper Carboniferous or Permian, i.e., the simple leaf appeared at the last stage of the pinnate compound leaf.

3) Cycadophytic leaf stage (Origin of cycadophytic leaves)

Fossil evidences show that the macrophyllous plants with pinnately compound leaf appeared in the late Devonian for the first time, and they flourished in the late Paleo-

zoic, Carboniferous and Permian, as ferns or seed ferns. Ferns continued to live through Mesozoic and Cenozoic but almost all of the seed ferns disappeared in the late Permian and the new types of macrophyllous plants, cycadophytes, appeared in the late Triassic (Fig. 1). Mesozoic was the age of the cycadophytic leaves in the macrophyllous plants. Therefore we must search the origin of cycadophytic leaves.

The writer agrees with Mamay's idea that *Taeniopteris* was the leaf of primitive cycads (MAMAY, 1976), from which the cycadalean plants were derived. The evolution of cycadalean leaves suggested by MAMAY is shown in Fig. 5 beginning with (A), an entire-margined ancestral taeniopterid leaf and, through progressively deeper incision of margins, resulting in two basic types of cycadalean leaves (D, cycadaceous type: I, zamiaceous type). The cycadaceous lineage, indicated by heavy arrows, consists of forms in which marginal teeth and ultimate foliar segments involve a single vein each (B, C, D).

The zamiaceous lineage, indicated by light arrows, consists of forms in which marginal incisions and ultimate foliar segments involve several veins each (E, F, G, H, I); forms such as E and G might have been derived independently from A, whereas H may have arisen from either F or G. Both cycadaceous and zamiaceous lineages evolved substantially concurrently (MAMAY, 1976).

Fossil evidences of the Lower Permian in Cathaysia land (Fig. 6) show that both cycadalean and bennettitalean leaves appeared in the lower Permian for the first time through splitting the lamina of *Taeniopteris* into segments.

Many types of *Taeniopteris* were abundantly found from the uppermost Carboniferous and Permian formations in Cathaysia land. As shown in the principles of Growth Retardation *Taeniopteris* is the simple leaf derived from many kinds of pinnately compound leaves by "Enlargement". Therefore it has many lineages of plants, large or small leaf type, long or short leaf type and coarse or dense venation type. In *Taeniopteris nystromei* described from the Lower Shihhotse Series (Lower Permian) of Shansi by HALLE (1927) the breadth of leaf attains 20 cm, in *Taeniopteris multineervis* from the same horizon 2.5 cm and in *Taeniopteris tingii* from the Upper Shihhotse Series (Upper Permian) only 1 cm. In general majority of *Taeniopteris* shows simple leaf but sometimes it shows unipinnate leaf as *Taeniopteris integra* reported from the Hung Ho Formation of Kaiping (Upper Permian), China (STOCKMANS & MATHIEU, 1957). This means that this species shows the intermediate stage between the pinnate compound leaf stage and the simple leaf stage, i.e., one stage before the simple leaf. This also means that *Taeniopteris* might have been derived from many kinds of pinnate plants of the different ages by "Enlargement" of segments. *Taeniopteris* has many lineages of plants and it will be expected that the polyphyletic descendants might have been derived from the polyphyletic *Taeniopteris* in parallel through Permian and Triassic. The leaves of cycadophytes might have been derived from the *Taeniopteris* by the splitting their lamina into segments forming the two lineages of plants, the bennettitalean and the cycadalean leaves respectively.

HALLE (1927) described *Nilssonia densinervis* (Fig. 6-2, 3, 4) from the Lower Shih-

hotse Series (Lower Permian) of Shansi, and STOCKMANS & MATHIEU (1939) reported three species of *Nilssonia* from the Chao Ko Chwang Formation (Lower Permian) of Kaiping, *Nilssonia densinervis*, *N. undulata* (Fig. 6-5) and *N. xerophylla* (Fig. 6-6). The breadth of leaf segments of these species are broad in some segment and narrow in some segment indicating that these leaf segments might have been derived from the entire *Taeniopteris* through splitting into segments.

KAWASAKI (1931, 1934) described four species of *Pterophyllum* from the Jido Series (Lower Permian) of South Korea, *Pterophyllum daihoense* (Fig. 6-14, 15, 16A). *P. samchokense*, *P. nilssonoides* (Fig. 6-16B) and *P. bipartitum* (Fig. 6-17). There were two types of leaves of *Pterophyllum* in Korea, larger leaf of *Pterophyllum samchokense* and small leaves of *Pterophyllum daihoense*, *P. nilssonoides* and *P. bipartitum*. The width of leaf of the former attained 18 cm and the latter 2-7 cm. The leaf apex of the latter three species were entire without splitting into segments, and segments were different in width indicating that the leaves of these species must have been derived from the entire leaves of *Taeniopteris* by dividing their lamina into segments.

From the fossil evidences stated above it is no doubt that the Mesozoic *Nilssonia* (Fig. 6-7, 8, 9, 10, 11, 12) must have been derived from the late Paleozoic *Taeniopteris* through Permian *Nilssonia* (Fig. 6-2, 3, 4, 5, 6). The Mesozoic *Pterophyllum* (Fig. 6-18), *Ptilophyllum* (Fig. 6-19, 20) and *Zamites* (Fig. 6-21) were also derived from the late Paleozoic *Taeniopteris* through the Permian *Pterophyllum* (Fig. 6-13, 14, 15, 16, 17) respectively. Therefore the ancestral plants of Cycadales and Bennettitales must have been the late Paleozoic *Taeniopteris* which were derived from many kinds of Carboniferous plants with pinnately compound leaves by "Enlargement" of segments.

4) Simple leaf stage (Origin of angiosperms)

There were two types of simple leaves in the late Paleozoic: reticulate vein and

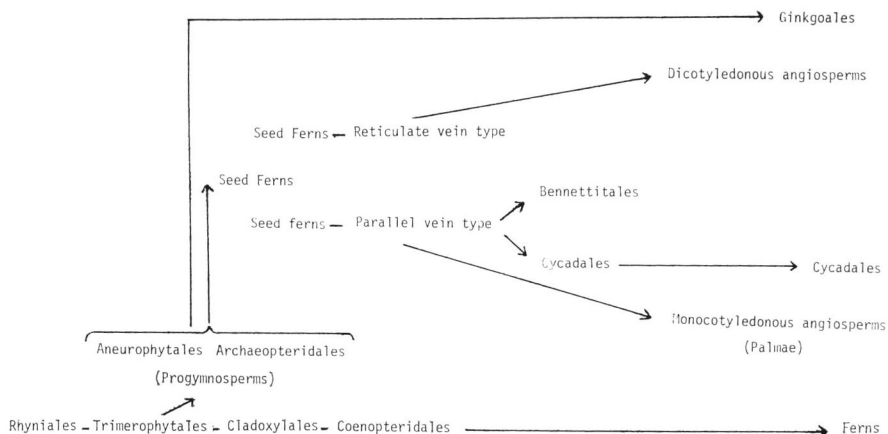


Fig. 7. The phylogeny of Macrophyllphyta inferred from the evolution of leaf forms through ages.

parallel vein types. The former type is the so-called "*Gigantopteris*" with reticulate veins of Cathaysia land and North America, and the so-called "*Glossopteris*" with reticulate veins of Gondwanaland. The latter type is *Taeniopteris* with parallel secondary veins. The descendants of the latter type are found in the Mesozoic as Cycadales and Bennettitales as mentioned above, but those of the former type are not found till middle Cretaceous as the simple leaves of dicotyledonous plants which are shown in Fig. 1. We cannot find the macrophyllous plants suitable for the ancestral plants of angiosperms in the pre-Cretaceous ages, which proposes a great problem on the origin of angiosperms. The writer will discuss about this important problem on the origin of angiosperms in Part 5.

From the facts stated above the writer considers the phylogeny of Macrophyllphyta as shown in Fig. 7.

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