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Evolution and Phylogeny of Vascular Plants based on the Principles of Growth Retardation. Part 3. Phylogeny of Macrophyllophyta in Devonian

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Classification of Devonian Land Plants

One of the most controversial problems is whether the main groups of plants evolved originally from a single ancestral plant (monophyletic), or whether they evolved separately from different ancestral plants (polyphyletic).

Until recent years, the psilophytes were considered to be the simplest and most primitive of all vascular plants, and to have been the ancestral plants from which the other groups of vascular plants evolved.

In ENGLER's Syllabus der Pflanzenfamilien (1954) the Psilophytales consist of five families, Rhyniaceae (*Rhynia*, *Horneophyton*, *Cooksonia*, *Yarravia*), Zosterophyllaceae (*Zosterophyllum*), Psilophytaceae (*Psilophyton*), Asteroxylaceae (*Asteroxylon*) and Pseudosporochnaceae (*Pseudosporochnus*). The range chart of the Pteridophyta in the book (p. 276, fig. 104) indicates that the Lycopsida, Psilotopsida, Articulatae and Filices were derived from a single order of the ancestral Psilophytales.

The Psilophytales of KRÄUSEL (1938) consist of eight families, Rhyniaceae, Horneaceae, Psilophytaceae, Zosterophyllaceae, Sciadophytaceae, Asteroxylaceae, Pseudosporochnaceae and Drepanophycaceae.

Now it is clear that *Drepanophycus spinaeformis* belongs to the Protolepidodendrales of the Lycopsida, *Pseudosporochnus* to the Cladoxylales of the Pteropsida, and *Protopteridium* (*Rellimia*) to the Progymnospermopsida. Therefore the Psilophytales are a highly unnatural polyphyletic group.

BANKS (1968, 1975) classified vascular plants into seven subdivisions.

Division Tracheophyta

Subdivision Rhyniophytina .....with terminal sporangia

Rhyniales

Rhyniaceae

Rhynia, *Horneophyton*, *Cooksonia*, *Steganotheca*, *Salopella*, *Dutoitea*, *Eogaspeciea*, *Taeniocrada*, *Hicklingia*, *Nothia*, *Yarravia* and *Hedeia*.

Subdivision Zosterophytina .....with lateral sporangia

Zosterophyllales

Zosterophyllaceae

Sawdonia, *Zosterophyllum*, *Gosslingia*, *Crenaticaulis*, *Rebuchia* and

Bathurstia.
Subdivision Trimerophytina
Trimerophytales
Trimerophytaceae
Psilophyton, *Trimerophyton*, *Pertica*, *Dawsonites*, *Hostinella*, *Psilodendrion* and *Psilophytites*.
Subdivision Psilophytina
Subdivision Lycophytina
Subdivision Sphenophytina
Subdivision Pterophytina

Class Cladoxylopsida	Class Progymnospermopsida	Class Cycadopsida
Class Coenopteridopsida		Class Coniferopsida
Class Filicopsida		Class Gnetopsida
		Class Angiospermopsida

Banks abandoned the name "Pteridophyta and Psilopsida" for the reason mentioned above, but Sporne (1959, p. 391) stated, "The name (Pteridophyta) is, however, so well established that it would seem worth while to retain it, so long as one realizes that it may imply merely a grade of evolution through which many phylogenetic lines have passed." The present writer used "Psilopsida" in this paper for the same reason and it contains Banks' Rhyniophytina, Zosterophytina and Trimerophytina.

Banks (1975) stated, "The newer grouping of psilophytes suggests some interesting evolutionary relationships. The Trimerophytina represent an evolutionary level clearly advanced over that shown by Rhyniophytina, the first vascular plants. Trimerophytes in turn show considerable variation at a level from which more recent groups such as progymnosperms, articulates, cladoxyleans and coenopterids might evolve." Again he stated, "Zosterophytina evolved soon after rhyniophytes and probably independently judging by their distinctive characteristics such as lateral sporangia and exarch protosteles." He considered two evolutionary lines, Rhyniophytina—Trimerophytina line (with terminal sporagia) and Zosterophytina—Lycophytina line (with lateral sporangia) and Trimerophytina were the ancestral plants of all vascular plants (ferns, progymnosperms, gymnosperms, angiosperms and articulates) except lycopods.

There are two theories on the origin of microphyll, Zimmermann's telome theory (Zimmermann, 1959) and Bower's enation thory (Bower, 1935). The former implied the evolution of all vascular plants (Lycopsida, Pteropsida and Sphenopsida) from a very simple leafless ancestral type, like *Rhynia*.

Adherents of the enation theory consider the evolutionary series of microphyll from *Rhynia* (naked axis) to *Psilophyton* (spine like enation), *Asteroxylon* (small trace of vascular tissue) and *Drepanophycus* (vascular tissue).

Banks' (1980) range chart of Devonian megafossils indicates that there were *Psilophyton*, *Drepanophycus*, *Baragwanathia*, *Rhynia* and *Asteroxylon* in Siegenian, of which the former two appeared slightly earlier than the latter three. *Rhynia* and

Psilophyton belong to the Psilopsida with naked axes and other three to the Lycopsida with microphylls.

Both *Drepanophycus* with microphylls and *Psilophyton* with spiny enations appeared at the same age as fossils. This means that the microphylls of *Drepanophycus* were not derived from the enation of such plant as *Psilophyton*.

There are great differences between the morphology of *Drepanophycus* of Lycopsida and *Psilophyton* of Psilopsida. Therefore the writer cannot agree with the enation theory that microphylls of the Lycopsida were derived from the enation of *Psilophyton*.

The present writer considers, on the basis of the principles of Growth Retardation, that the Pteropsida were derived from the plants with terminal sporangia (ZIMMERMANN's original type), but the Lycopsida and Sphenopsida were not derived from such plants as *Rhynia* with terminal sporangia. It is very difficult to consider that *Drepanophycus* or *Baragwanathia* with sporangia on the adaxial surface of leaves or in its axial might have been derived from the *Rhynia*-like plants with terminal sporangia within a very short period. Therefore the writer agrees with the telome theory on the evolution of the Pteropsida but does not agree on the origin of microphylls shown in the Lycopsida and Articulates.

Until recent years, it was considered that *Hyenia* and *Calamophyton* were the most primitive ancestral plants of the Articulates. However it was found that they do not belong to the Articulates but to ferns (LECLERCQ & SCHWEITZER, 1965; SCHWEITZER, 1972). Recently SCHWEITZER (1972) reported the very important discovery of Articulates, *Equisetophyton*, from the Lower Devonian of the Rhenish Schiefergebirge. *Equisetophyton praecox* SCHWEITZER has a well articulated stem with well developed sheaths at the nodes and is similar to the recent Equisetales.

SCHWEITZER (1972, p. 155) stated "with the change of *Hyenia* the Protoarticulatales loses its last claim. The oldest known Articulates for the time are *Sphenophyllum subtenerrimum*, *Eviostachya hoegi* and *Pseudobornia ursina*, all of which occur in the higher Upper Devonian. All of them are well developed, highly differentiated plants and cannot be the prototype of Articulates. Therefore it must be assumed that the oldest Articulates occurred earlier in the earth-history. Because the Articulates are the group of the Pteridophytes which has changed least and because the Upper Devonian Articulates show the same stage of differentiation as the Lycopsides and ferns of this time one can anticipate that their oldest members occurred in the Upper Devonian and that these members must have a stage of development comparable to the Lycopsides and the ferns of this time. In other words: the oldest members of the Articulates must have the characteristic articulation of their stems."

The present writer completely agrees with SCHWEITZER's opinion (1972). The writer had a great question, for a long time, whether *Hyenia* and *Calamophyton* must be the most primitive ancestors of the Articulates or not, because they had not clearly jointed stems and both *Calamophyton* and *Hyenia* had the main stem branched dichotomously.

The writer considers that the Articulates always have articulated stems and never branch dichotomously like *Calamites*. Therefore the first land plants of the Articulates must have had the jointed stems and whorled leaves.

Both the Lycophytes and Articulates have microphylls, which were arranged densely around the axis in the former and arranged in whorl around the nodes in the latter.

The Rhyniophytes have no true leaves, but have the naked dichotomous axes. This significant differences between vegetative organs of the Rhyniophytes, Lycophytes and Articulates are found in Siegenian age and it means that the plants of three lines had lived in parallel. So the writer considers that three lines of vascular plants, the Rhyniophytes (soon after changed to pterophytes and progymnosperms), Lycophytes and Articulates might have succeeded to come out of water to on land at about the same age. Therefore the writer classified the Devonian land plants as follows:

I. Microphyllophyta
  Microphyll-sporophytina (Lycopsida)
    Protolepidodendrales
      Drepanophycus, *Baragwanathia*, *Asteroxylon*, *Protolepidodendron*, *Colpodexylon*, *Leclercqia*, etc.

II. Macrophyllophyta
  Macrophyll-sporophytina
    Psilopsida
      Rhyniales
        Rhynia, *Horneophyton*, *Yarravia*, *Cooksonia*. etc.
      Trimerophytales
        Trimerophyton, *Psilophyton*, *Pertica*, etc.
      Zosterophyllales
        Zosterophyllum, *Gosslingia*, *Crenaticaulis*, *Sawdonia*, *Kaulangiphyton*, etc.
    Progymnospermopsida
      Aneurophytales
        Aneurophyton, *Rellimia*, *Tetraxylopteris*, *Triloboxylon*, *Proteokalon*, *Cairoa*.
      Protopityales
        Protopitys
      Archaeopteridales
        Archaeopteris, *Svalbardia*, *Actinoxylon*, *Siderella*, *Actinopodium*, *Archaeopitys*, *Eddya*.

III. Arthrophyta
  Articulate-sporophytina (Sphenopsida)
    Protocalamitales?
      Equisetophyton

All Devonian plants in three lines are characterized by the spore-producing re-

productive organs and they are classified into such subdivisions as the Microphyll-sporophytina with microphylls, Macrophyll-sporophytina with naked branches, and Articulate-sporophytina with articulate stems, respectively. Progymnosperms do not belong to gymnosperms, but to pteridophytes, because they have the spore-producing reproductive organs and do not have the naked seeds.

From the Dichotomous Naked Axis to the Pinnate Compound Leaf

Proposing the telome theory, ZIMMERMANN (1959) explained the origins of the Pteropsida, Lycopsida and Sphenopsida from the primitive dichotomous axes of *Rhynia*-like plants by the six possible modification processes such as overtopping, planation, reduction, fusion in leaf, fusion in stem, and recurvation. But there are many criticisms about the telome theory. SPORNE (1959) stated, "By judicious choice from the six possible modification processes, it is possible to derive (by mental processes) all the structures and shapes known to occur among the higher plants.——the whole thoery is 'too clever' and it is an over-simplification." Again he stated, "There are, roughly speaking, three attitudes that are now adopted towards the telome theory: (1) complete rejection by those who cling to the classical theory; (2) complete acceptance, by a large number of morphologists; and (3) qualified accepatance of parts of the theory by a growing number. Among this last group are those who accept ZIMMERMANN's derivation of megaphyllous plant organization, but who cannot accept this derivation of the microphyll and sporophyll of lycopods." The present writer belongs to SPORNE's third group.

Both *Drepanophycus* of the Protolepidodendrales and *Equisetophyton* of the Protocalamitales had already microphylls in Siegenian when they had succeeded to come out of water to on land. There we must recognize three evolutionary lines in Siegenian such as the Protolepidodendrales (ancestral type of the Microphyllophyta, with microphylls and without jointed stem), Protocalamitales? (ancestral type of the Arthrophyta, with microphylls and jointed stem) and the Rhyniales (ancestral type of the Macrophyllophyta with dichotomouns naked axes without jointed stem). The writer discussed the phylogeny of the Microphyllophyta in Part 2 (ASAMA, 1981b) and will discuss the phylogeny of the Arthrophyta in Part 5.

The dichotomous naked axes of early Devonian plants are the original type of all plants with macrophyllous leaves such as ferns, progymnosperms, macrophyllous gymnosperms and macrophyllous angiosperms without jointed stem. These plants have many kinds of macrophylls such as pinnate compound leaf, simple leaf, palmate leaf and etc., which might have been derived from the original dichotomous naked axes of the Rhyniales.

There is no doubt that all leaves of Carboniferous ferns and seed ferns which show the pinnate compound leaf in general might have been derived from the Dovenian naked axes of the Rhyniales, Trimerophytales, Aneurophytales and Archaeopteridales. First of all the origin of the pinnate compound leaf must be explained.

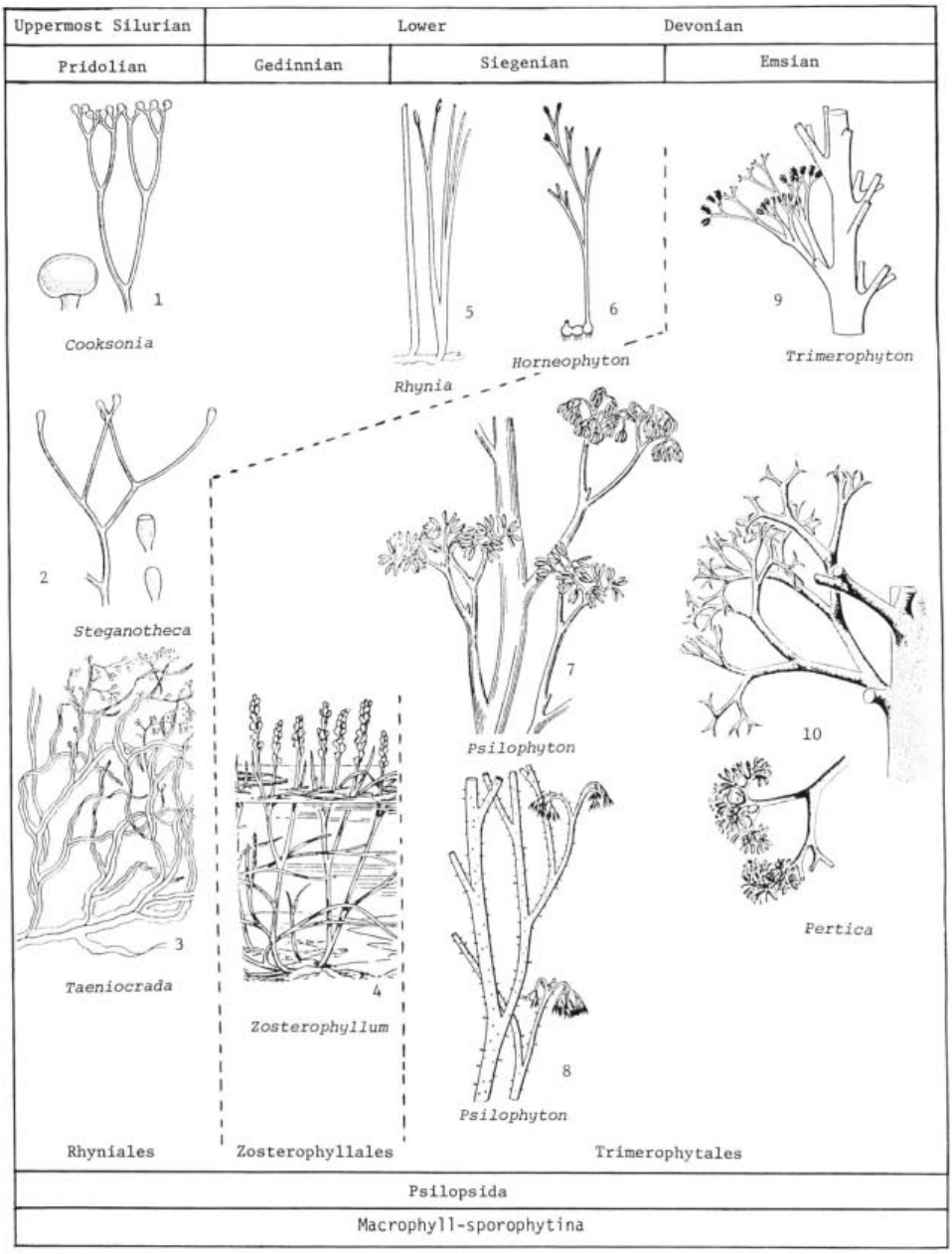
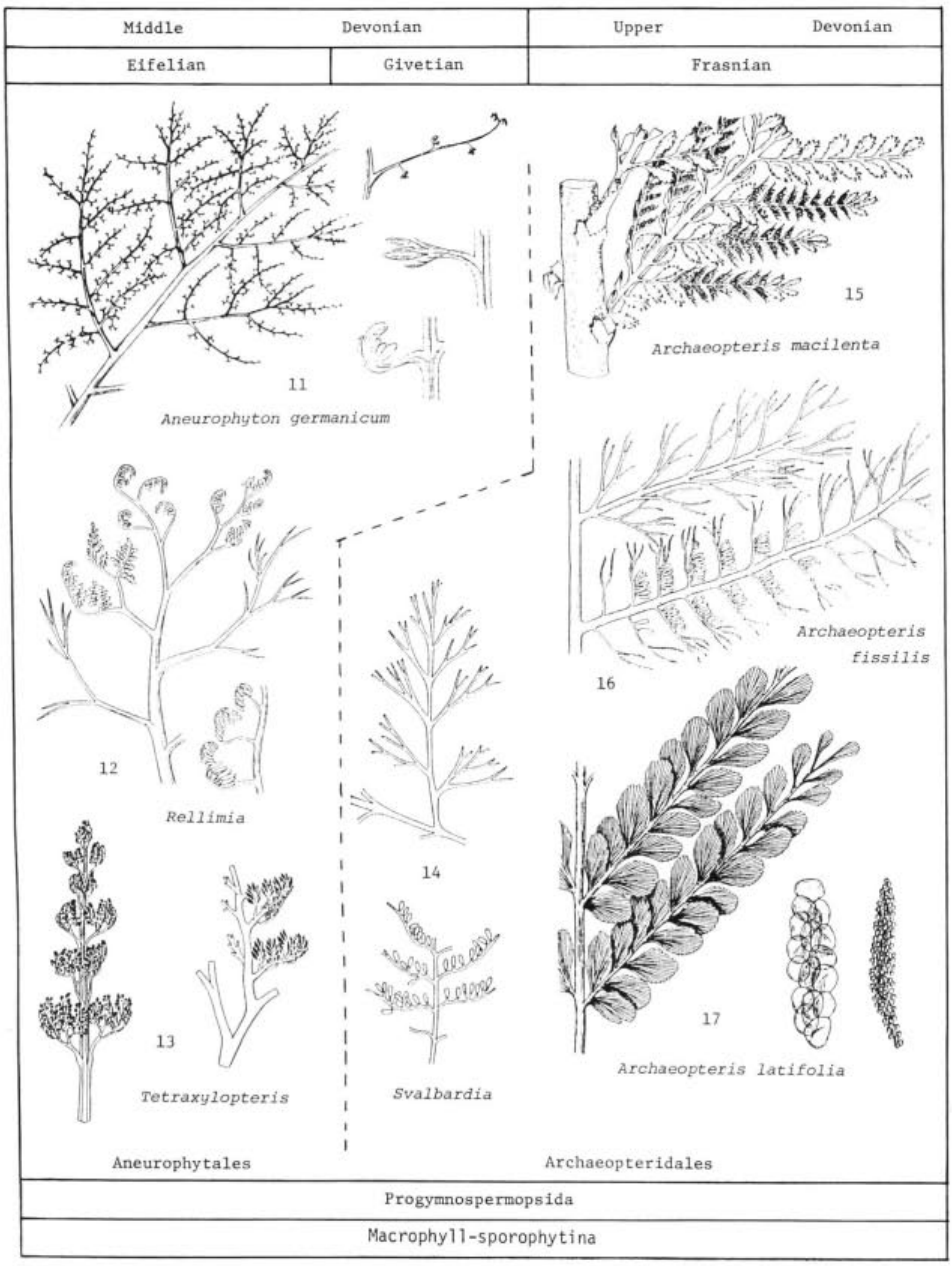


Fig. 1. Fossil evidences indicate that the dichotomous naked axes (1, 2, 5, 6) of Rhyniales had changed to the main stem with lateral dichotomous axes (7–10) of Trimerophytales, to the main stem with the first order of branches which have the lateral dichotomous axes (11–13) of Aneurophytales and to the bipinnate leaves (15, 17) or Archaeopteridales step by step successively. Adapted from BANKS (the first appearance of genus) 1980; EDWARDS (1, 2)↗



↘1970; KRÄUSEL & WEYLAND (3) 1930, (4) 1935, (11) 1926, (12) 1933; KIDSTONE & LANG (5, 6) 1920; BANKS, LECLERCQ & HUEBER (7) 1975; HUEBER (8) 1967; HOPPING (9) 1956; KASPER & ANDREWS (10) 1972; BONAMO & BANKS (13) 1967; HÖEG (14) 1942; BECK (15) 1962; ANDREWS, PHILLIPS & RADFORTH (16) 1965; ARNOLD (17) 1939.

The writer proposed the principles of Growth Retardation based on the evolution of Carboniferous and Permian plants in the continuous section of the Shihhotse valley, Shansi, China (ASAMA, 1959, 1960, 1962, 1981a). The principles of G. R. consist of eight principles; "Fusion", "Enlargement", "Enlargement & Fusion", "Reduction" (branching reduction and size reduction), "Shortening" (palmation, verticillation, leaf & axis shortening), "Ducurrency" (pinna decurrency and pinnule decurrency), "Vein aggregation" and "Enclosure" (ASAMA, 1960, 1981a, 1981b). These principles were found on the basis of the fossil evidences to explain the transformation of morphology of plants through ages. These principles show the manners of reaction of plants for environmental changes. The leaves of plants became smaller (reduction) with the change of climates from the favorable to the unfavorable for the growth of plants. Therefore the most important and common characteristic in all principles is "Reduction".

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

Fossil evidences support that the Rhyniales such as *Cooksonia*, *Steganotheca* and *Taeniocrada* were the first land plants, and they were characterized by the dichotomous naked axes with terminal sporangia (Fig. 1–1, 2, 3, 5, 6). They appeared as fossils in the uppermost Silurian, i.e., Pridolian. There is no doubt that the Rhyniales are simple and early vascular plants and the starting plants of the Macrophyllophyta. But some paleobotanists postulated that they were not the ancestral plants of the Microphyllophyta or Arthrophyta. The present writer considers that the starting plant of the Microphyllophyta might be *Drepanophycus* in Siegenian and that of the Arthrophyta *Protocalamites*? like young *Calamites* with microphylls in Siegenian, though it is not discovered at present (*Equisetophyton* with sheaths and jointed stem was found in Siegenian). In the next stages, Siegenian and Emsian, more advanced type of plants such as the Trimerophytales appeared. They are characterized by the main axis and the three dimensional dichotomizing naked branches with terminal sporangia, which are shown in *Psilophyton*, *Pertica* and *Trimerophyton* (Fig. 1–7, 8, 9, 10).

Psilophyton princeps had spine like or glandular enations (Fig. 1–8), but *P. forbesii* and *P. dawsonii* had smooth branches without enations. This may mean that the enations were glands. Therefore the writer does not agree to the enation theory about the origin of microphylls.

The Trimerophytales such as *Psilophyton*, *Pertica* and *Trimerophyton* are char-

acterized by the lateral branches (the first order of branches) similar to those of the Rhyniales with dichotomous axes and terminal sporangia.

In the next stages, Eiferian and Givetian, we find the plants of the Aneurophytales such as *Aneurophyton*, *Rellimia* and *Tetraxylopteris* (Fig. 1–11, 12, 13) which are characterized by the spiral arrangement of lateral branches. The lateral branches (the first order of branch) of *Aneurophyton* have the second order of branches with the dichotomous axes similar to the axes of the Rhyniales-stage.

The Archaeopteridales such as *Archaeopteris* and *Svalbardia* (Fig. 1–14, 15, 16, 17) are found in Givetian and Frasnian. *Archaeopteris* is a characteristic Upper Devonian plant which is represented by many species. They are characterized by the bipinnate compound leaves. The branch systems of the Trimerophytales and Aneurophytales are arranged in three dimensions and those of *Archaeopteris* are arranged in three dimensions in some case and in a plane in some case. In the latter case they show clearly the bipinnate compound leaf. It is concluded that the pinnate compound leaf, which is normal leaf form of ferns and seed ferns in Carboniferous, had been formed in the stage of the Archaeteridales through the stages of the Aneurophytales, Trimerophytales and Rhyniales.

Evolutionary Stages of the Devonian Land Plants

Fig. 2 shows the evolutionary stages of early land plants from the dichotomous axes as in *Rhynia* to the pinnate compound leaf as in *Archaeopteris*. The writer divided the transformation process of the pinnate compound leaf into four stages, *Rhynia*-stage, *Trimerophyton*-stage, *Aneurophyton*-stage and *Archaeopteris*-stage, respectively. The *Rhynia*-stage is characterized by the dichotomous axes without main stem, *Trimerophyton*-stage by the main stem with the lateral dichotomous branches, *Aneurophyton*-stage by the first order of branches with the lateral dichotomous branches (the second order of branches) without forming pinnules, and *Archaeopteris*-stage by the pinnate compound leaf as shown in Fig. 2.

The early land plants evolved through these stages step by step, forming the more advanced type of branches and acquiring the new character successively. The plants belonging to the Rhyniales were the starting plants of the Macrophyllophyta and they had acquired the new characters; main stem, in *Trimerophyton*-stage, secondary wood in *Aneurophyton*-stage and pinnules in *Archaeopteris* stage respectively. They could grow to larger plants by acquiring these new characteristic abilities to make main stem, secondary wood, and pinnules. These abilities were acqiured by reducing their vegettive organs successively as shown in the lower part of Fig. 2.

The *Trimerophyton*-stage contains *Rhynia*-stage; *Aneurophyton*-stage contains *Rhynia*-stage and *Trimerophyton*-stage; *Archaeopteris*-stage contains *Rhynia*-stage, *Trimerophyton*-stage and *Aneurophyton*-stage as shown in Fig. 2. and Fig. 3. This means that the plants belonging to the Rhyniales had become more complicated plants by adding more advanced forms stage by stage, successively. If we compare the

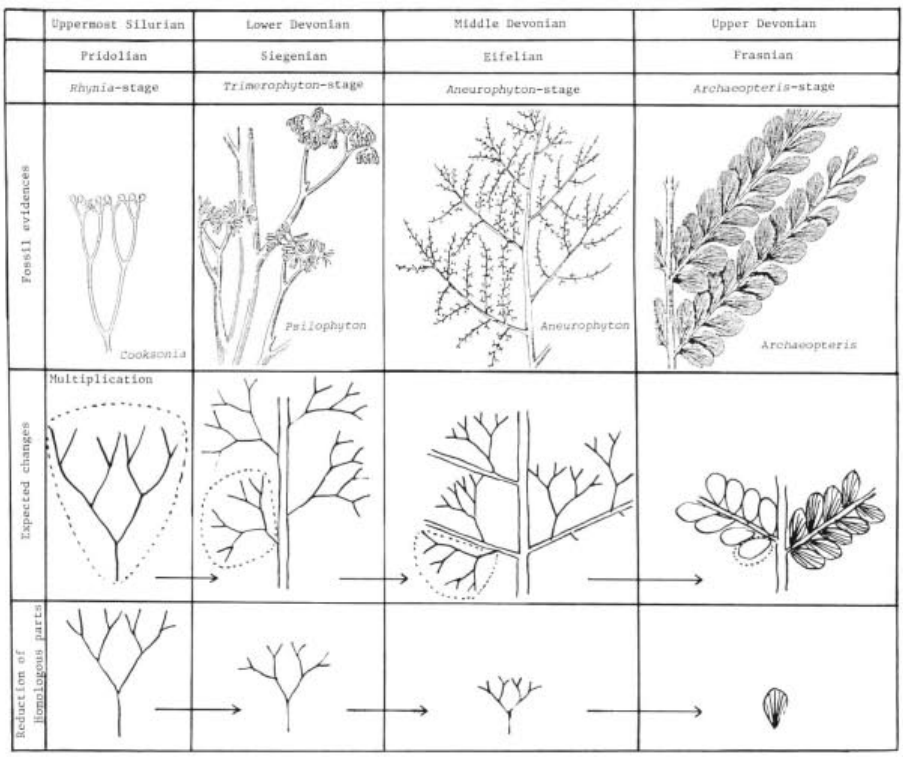


Fig. 2. Evolutionary stages of the early land plants and expected change of Devonian plants based on the principles of Growth Retardation.

homologous parts of plants at each stages, it will be found that they are reducing their size, step by step, successively (see the lowest part of Fig. 2).

Such Devonian fossil evidences as mentioned above indicate that we must recognize one more principle of Growth Retardation, "Multiplication."

Reduction is the Basic Principle in the Evolution of Vascular Plants

1) Reduction of the pinnate compound leaf of Carboniferous and Permian plants to form the simple leaf.

Besides eight principles, "Fusion", "Enlargement", "Enlargement & Fusion", "Reduction", "Shortening", "Decurrency", "Vein aggregation "and "Enclosure", deduced from transformation of leaf forms in Carboniferous and Permian plants (Asama, 1981a), ninth principle, "Multiplication", was observed in Devonian plants as mentioned above.

In Carboniferous the pinnate compound leaf had already been formed and the modification of the pinnate compound leaf since Carboniferous were explained by the principles of Growth Retardation (Asama, 1959, 1960, 1962, 1975, 1979). The leaf

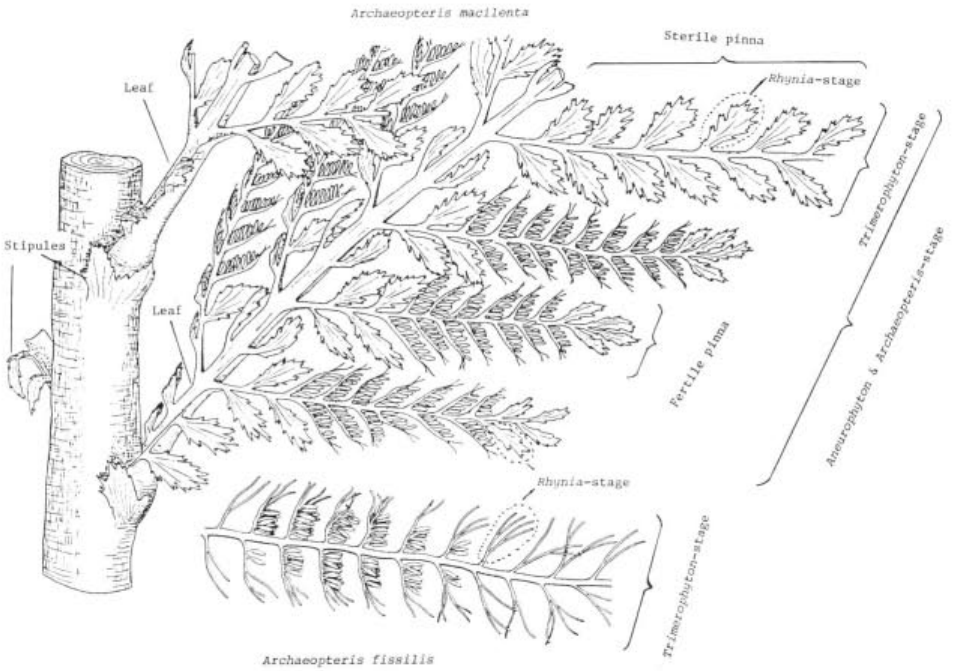


Fig. 3. Evolutionary stages in *Archaeopteris*, which contains the parts of *Rhynia*-stage, *Trimerophyton*-stage and *Aneurophyton*-stage. Adapted from BECK (1962).

form of the last stage of the pinnate compound leaf was simple as shown in the so-called *Gigantopteris* (with reticulate viens, by "Fusion"), *Taeniopteris* (with non-reticulate veins, by "Enlargement") *Glossopteris* (with reticulate veins, by "Enlargement") and *Schizoneura* (unipinnate, with parallel veins, by "Enlargement & Fusion") in Permian.

Fig. 4 (8–16) shows the simple leaf-forming processes observed in the Carboniferous and Permian plants of Cathaysia land, and the processes show that the homologous parts (circled by dotted lines) of plants at each stage had been reduced step by step successively, forming simple leaf (8, 12, 16) at the last stage of each series.

2) Reduction of the homologous parts of Devonian plants to form the pinnate compound leaf.

As stated above the dichotomous axes of the Rhyniales changed to the main stem with dichotomous lateral branches of the Trimerophyrales, to the main stem with the first order of branches having the dichotomous lateral branches without forming pinnules, and to the main stem with the first order of branches having pinnules on both sides of branches. The figures shown in the upper part of Fig. 4 indicate the process of the transformation from the dichotomous naked axes to the pinnate compound leaf. This process indicate that macrophylls might have been derived from the naked dichotomous axes by the principle of multiplication and that the plants belonging to the Psilopsida must have been the ancestral plants of macrophyllous

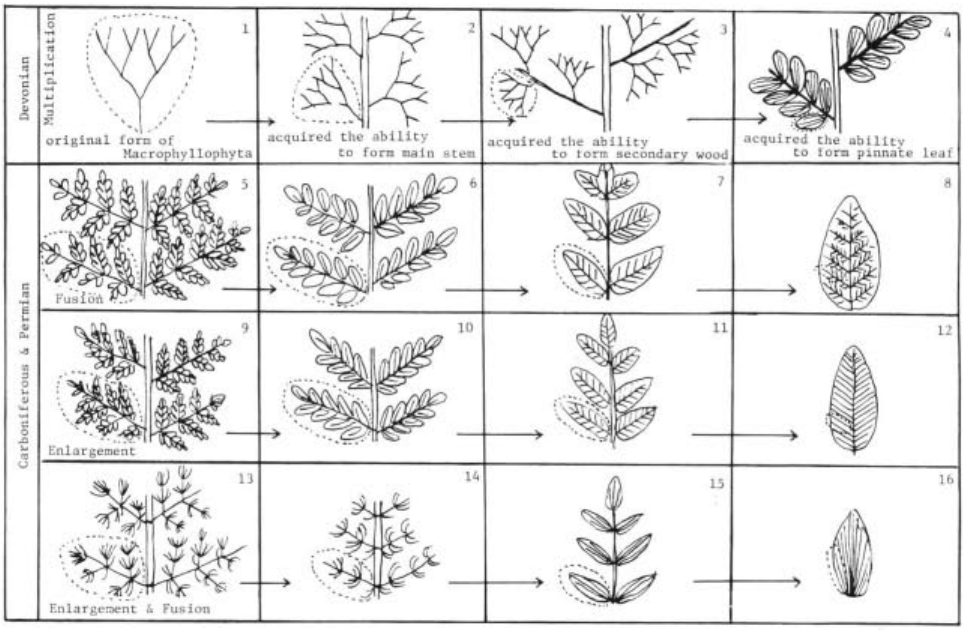


Fig. 4. Reduction of the homologous parts of Devonian plants to form the pinnate leaf (by principle of "Multiplication") and reduction of the pinnate leaf of Carboniferous and Permian plants to form the simple leaf. (Circling dotted lines show the homologous parts of plants in each stage)
1– 4, pinnate leaf-forming process
5– 8, simple leaf-forming process by "Fusion"
9–12, simple leaf-forming process by "Enlargement"
13–16, simple leaf-forming process by "Enlargement & fusion"

plants, ferns, progymnosperms and seed ferns in Devonian and Carboniferous. Therefore we must recognize three evolutionary lines in Devonian, the Macrophyllophyta, Microphyllophyta and Arthrophyta.

Devonian plants had become larger step by step, but if we compare the homologous parts at each stage of these plants (circled by dotted lines in Fig. 4), we will find the continuous reduction step by step.

Therefore "Reduction" is the basic principle in the evolution of vascular plants both in and after Devonian.

3) The meaning of the reduction

We found the reduction of homologous parts of plants both in Devonian (in the transformation process into the pinnate compound leaf) and post Devonian (in the transformation process into the simple leaf). In the former case the plants had become larger and larger, forming the pinnate compound leaf at the last stage, and in the latter case the plants had become smaller and smaller, forming the simple leaf at the last stage. Some author may say that the former process is an example of Growth

Acceleration, because the plants had become larger step by step. But this consideration is not correct, because we must compare the homologous parts of plants. It is apparent that the reduction of homologous parts had taken place. The plants are able to acquire the new character by reducing their vegetative organ, and they can grow larger by the activity of the new characters. Therefore both transformation processes of the pinnate compound leaf and the simple leaf are the example of Growth Retardation.

In general the angiospermous plants have the simple leaf which might have been derived from the pinnate leaf. The present writer considers that the simple leaves of plants forced tracheids to change to vessels in order to send much water from stem to leaves in a short time. Without these improvements of the tracheid-vessel system the angiospermous plants might not have become the dominant plants through Cretaceous and Tertiary.

The changes of plants by the Growth Retardation mean that the environment have changed to the unfavorable conditions for the growth of plants. The reduction of the homologous parts in Devonian and post Devonian plants indicates that the environment where plants evolved had changed to unfavorable conditions for the growth as shown in Part 1, fig. 9 (ASAMA, 1981a). This does not mean that the environment had changed to unfavorable condition for the growth of plants everywhere, but means that the region where plants evolved changed to unfavorable conditions. The place where plants evolved might have been the inland or upland of continents in middle or high latitude, but not on low latitude or islands. Because severe climate retards the growth of plants and mild climate accelerates the growth of plants, respectively, improvement of plants (evolution) had occurred not in mild climate, but in severe climate by reducing their vegetative organs, and the diversification of plants must have been accelerated in mild climate.

Archaeopteris is not the Ancestral Plants of Conifers

The generic name *Archaeopteris* was given to compressions of large fern-like pinnate leaves and it was considered to be the most widely distributed fern in the Upper Devonian. *Callixylon*, on the other hand, is a name originally applied to petrified wood of certain Devonian trees with gymnospermous secondary wood. It was considered that *Callixylon* was a seed plant and classified in the Pityeae of the Cordaitales. Therefore it was a great shock when BECK (1960a, 1960b) demonstrated organic connection between branches identified as *Callixylon zaleskyi* and large bipinnate leaves known as *Archaeopteris macilenta*.

Archaeopteris was characterized by spirally arranged bipinnate leaves and as far as known, all species were pteridophytic in reproduction. But *Callixylon*, trunk of *Archaeopteris*, was characterized by the secondary wood with tracheids similar to the modern conifers.

BECK (1960b, p. 363) stated, "Consideration of the classification of *Archaepteris*

in several established Upper Devonian taxa has emphasized not only differences but also characters shared in common with numbers of the Aneurophytales, Protopityales and Pityales. It seems especially significant that all genera of these three orders are characterized by secondary growth and an arborescent habit, secondary tracheids with gymnospermous, rounded-bordered pits, and large compound leaves or leaf-like branch system, and that all were pteridophytic in reproduction. The combination of these characters indicates that these orders form a natural group, and a new class, considered to be ancestral to gymnosperms, is here proposed to include them." So he proposed new class Progymnospermopsida.

Again he (Beck, 1960b, p. 366) stated, "Progymnospermopsida includes woody, pteridophytic plants bearing large compound leaves or leaf-like branch systems. In numerous characters of both external morphology and internal structure these plants are remarkably similar to two groups of gymnosperms, the Pteridospermales and Cordaitales, which are, respectively, the most primitive groups of the cycadophyte and coniferophyte lines of gymnosperm evolution. Because the Progymnospermopsida are pteridophytic, they cannot be logically classified with the ovule-bearing gymnosperms, but it is very likely that they comprise the ancestral complex from which the major groups of gymnosperms evolved. Certain primitive features, especially of the Aneurophytales, suggest that the Progymnospermopsida are descended directly from some psilophyte-like ancestors."

Carluccio *et al.* (1966), indicated that the pinnules of bipinnate leaves of *Archaeopteris* are not pinnules but leaves and that *Archaeopteris* is probably closely related to the primitive coniferophytes.

Beck (1966, 1970, 1971, 1776,) considers that the lyginopterid Pteridosperms probably evolved from the aneurophytes. And he (1976) stated, "The Archaeopteridales seem to be the most likely source of the coniferophytic gymnosperms, this view based largely on the remarkable resemblance between the secondary wood (*Callixylon*) and lateral branch systems of *Archaeopteris* and those of Coniferales."

As stated above, Beck considered that the lyginopterids were derived from the Aneurophytales and the conifers were derived from the Archaeopteridales. The present writer considers that the lyginopterids might have been derived from the Anurophytales and that the ancestral plants of conifers were not the Archaeopteridales but the Protplepidodendrales of Devonian (Asama, 1891b, Part 2).

The most important character of conifers is to form cones. Both *Cordaites* and Lebachiaceae form cones and they were regarded as the descendants of Archaeopteridales by the adherents of Archaeopteridales-Cordaitales-Lebachiaceae line. Progymnosperms do not have cones and have the fern-like or seed fern-like leaves. Cones might not be derived from these fern-like pinnate leaves or fern-like reproductive organs. Cone might have been derived from the strobilus (cone) of the Lycopsida as shown in Fig. 10 of Part 2 (Asama, 1981b). Similarities of reproductive organs must be more important factors than those of the secondary wood or the branching system for finding phylogenetic line.

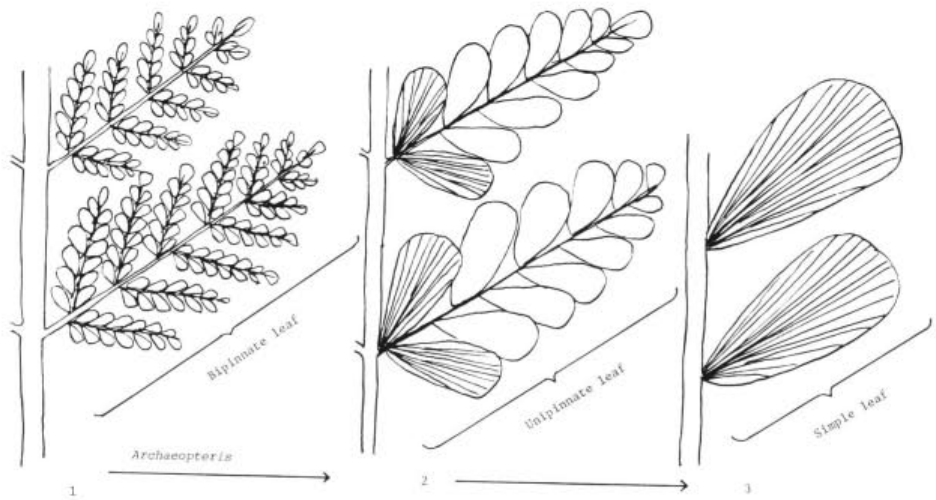


Fig. 5. Expected change of *Archaeopeteris* in next ages, Carboniferous and Permian. Bipinnate leaves (1) of *Archaeopteris* will change to the unipinnate leaves (2) and to the simple leaves (3) with fan-like veins as those of *Arhcaeopteris*. They will never change to the large long leaves with parallel veins like *Cordaites*, and never change to the microphylls of Lebachiaceae. *Archaeopteris* is not the ancestral plants of both *Cordaites* and Lebachiaceae.

Plants belonging to the Microphyllophyta and Arthrophyta with microphylls had formed cones in Carboniferous, but those belonging to Macrophyllophyta with macrophylls had never formed cones in Carboniferous.

Fig. 5 shows the expected changes of *Archaeopteris* based on the principles of Growth Retardation "Enlargement" in Carboniferous. All species of *Archaeopteris* have fan-like veins and they will change their leaves to the large fan-like form (like the leaves of Ginkgoales) reducing their branches step by step, which are never similar to the leaves of *Cordaites*.

Fig. 4. shows the evolution of branch system based on the principles of Growth Retardation, from the dichotomous axes to the pinnate compound leaf (1–4) and from the pinnate leaf to the simple leaf (5–8, 9–12, 13–16). This figure shows that the branch systems of the early Devonian plants will change to the pinnate leaf in the late Devonian and to the simple leaf in the Permian, and will never change to microphylls of conifers in Carboniferous or Permian. The change of branch systems indicate that the branch systems of the Aneurophytales and Archaeopteridales will change to the leaves of seed ferns in Carboniferous or Permian, i.e., Progymnospermopsida (Aneurophytales, Protopityales and Archaeopteridales) might have been the ancestral plants of seed ferns and not those of conifers.

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