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Evolution and Phylogeny of Vascular Plants based on the Principles of Growth Retardation Part 6. Triphyletic Evolution of Vascular Plants

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Criticisms for existing phylogenetic trees of vascular plants

Many authors have proposed various charts to show phylogeny of vascular plants. Plants have changed their leaves, reproductive organs and stem structures to adapt to changing environments through ages. If so, we should present charts showing both the phylogenetic and environmental changes through ages, which forced plants to change their leaves, reproductive organs and stem structures to adaptable forms.

Many authors present only the phylogenetic charts and do not present the idea of the environmental change. Therefore we could not understand the reason why plants changed their vegetative and reproductive organs. There must have been reasons which graded plants up from the spore stage to the enclosed seed stage through the intermediate naked seed stage step by step. The present writer considers that we should present both the phylogenetic chart and the environmental change through ages. The environmental changes mostly means climatic changes.

Macroclimatic changes through ages

Whereas Recent plants are indicator of Recent climate, fossil plants are the indicator of paleoclimates. We can deduce paleoclimates on the basis of fossil plants. Recent plants show zonal distributions from the equator to high latitudes, evergreen broadleaf forest, deciduous broad leaf forest, evergreen needle leaf forest and deciduous needle leaf forest rcspectively, if the influence of dry climate is excluded.

Axelrod (1952) discussed the angiosperm evolution and proposed a theory that angiosperms originated in upland regions, in areas sufficiently removed from usual lowland basins of deposition to have precluded their occurrence as contemporaries in fossil records. As stated in Part 5 (Asama, 1982b) the present writer agrees with Axelrod's idea of upland origin of angiosperms. He considers the tropical upland origin of angiosperms, and the present writer proposed the upland origin in middle latitude, where the environments are more severe than tropical upland.

The distribution charts of plants or climate show that the zonal distribution of plants or climate had become more distinct through ages as shown in the following table (adapted from Axelrod, 1952, Fig. 11 and Fig. 14: excluded the inflcuence of dry climate).

Permo-Triassic
Subpolar
Temperate to cool temperate
Tropical to warm temperate
Temperate to cool temperate
Subpolar

L. Triassic-Jurassic
Temperate to cool temperate
Tropical to warm temperate
Temperate to cool temperate

Early Cretaceous
Temperate to cool temperate
Tropical to warm temperate
Temperate to cool temperate

Mid-Cretaceous
Arcto-Cretaceous flora
Tropic-Cretaceous flora
Antarcto-Cretaceous flora

Early Tertiary
Temperate forest
Warm temperate forest
Rain forest & Subtropic forest
Warm temperate forest
Temperate forest

Mid-Tertiary
Tundra to Polar
Temperate forest
Warm temperate forest
Rain forest & Subtropic forest
Warm temperate forest
Temperate forest
Tundra to Polar

Late Tertiary
Tundra to Polar
Temperate forest
Warm temperate forest
Rain forest & Subtropic forest
Warm temperate forest
Temperate forest
Tundra to Polar

Ouaternary
Tundra to Polar
Temperate forest
Warm temperate forest
Rain forest & Subtropic forest
Warm temperate forest
Temperate forest
Tundra to Polar

There were four distinct floras in the Late Paleozoic (Late Carboniferous to Permian), Angara flora, Euramerican flora, Cathaysia flora and Gondwana flora. The floral composition of the Euramerican and Cathaysia floras indicates that they might have lived in the tropical climate. The major group of Gondwana flora is Glossopteridales which occupy about 90% of the flora. Therefore, *Glossopteris* flora is very similar to the recent duriherbosa, which indicates the flora under the special environment. The Gondwana flora would be formed under the influence of glaciation.

Permo-Carboniferous floras

Angara flora (Temperate)

Euramerican flora Cathaysia flora (Tropical to warm temperate)

Gondwana flora (Cool temperate)

Glossopteris and *Gangamopteris* had simple leaves, so about 90% of Gondwana flora had simple leaves. There had been no known simple leaves in the pteridophylls of Angara flora. This means that Angara flora lived in the warmer climate than Gondwana flora. Simple leaves would be derived from the pinnate compond leaves by the Growth Retardation as stated in Parts 1, 2 and 4 (Asama, 1981a, b, 1982a).

According to Chaloner and Meyen (1973) the two floral provinces are recognized in the Lower Carboniferous, *Lepidodendropsis* flora and Angara flora. The former covers the Gondwana and Euramerican areas and is characterized by the presence of *Lepidodendropsis*, *Sublepidodendron*, *Lepidodendron*, *Archaeosigillaria*, *Stigmaria*, *Archaeocalamites*, *Sphenopteridium*, *Rhodeopteridium*, *Fryopsis*, *Cardiopteridium* and *Anisopteris*. The flora of the Angara area is characterized by (?) *Lepidodendropsis*, (?) *Sublepidodendron*, *Lophiodendron*, *Archaeocalamites*, *Chacassopteris* and *Angaropteridium*.

The Lower Devonian floras are characterized by such primitive plant as *Zosterophyllum*, *Cooksonia*, *Drepanophycus*, *Psilophyton*, *Sporogonites*, *Sciadophyton*, etc. in the Northern Hemisphere and by *Baragwanathia*, *Haplostigma*, *Palaeostigma*, *Archaeosigillaria*, *Protolepidodendron*, *Dutoitia*, etc. in the Southern Hemisphere. There were two contrasting floras in the Lower Devonian, one was found in the Northern Hemisphere and in Austlaria, while the other was restricted to the Southern Hemisphere (Edwards, 1973). *Drepanophycus spinaeformis* is common in the Northern and Southern Hemispheres.

The distinction between Southern and Northern Hemisphere floras was still present in the Middle Devonian, but *Protolepidodendron scharianum*, *Leptophloeum australe* were common in both Hemispheres.

In the Upper Devonian there were many common genera in both Hemispheres such as *Barinophyton obscurum*, *Leptophloeum australe*, *Archaeopteris howettii*, ? *Cyclostigma australe*, *Sphenopteris iguanensis*, *Kalymma* sp. and *Protolepidodendron lineare*. Thus, in the Upper Devonian the earlier distinction between Northern and Southern Hemisphere floras had disappeared (Edwards, 1973),

There are two contrasting floras in the Lower and Middle Devonian, one in the Northern Hemisphere and the other in the Sortheun Hemisphere, but the distinction between both Hemispheres disappeared in the Upper Devonian.

From the facts mentioned above the change of floral zones from Devonian to Quaternary are summarized in Fig. 1. One floral zone in the Devonian had been changed into four floral zones in the Quaternary of Northern Hemisphere. This means that the zoning of plant distribution gradually intensified through ages excepting the

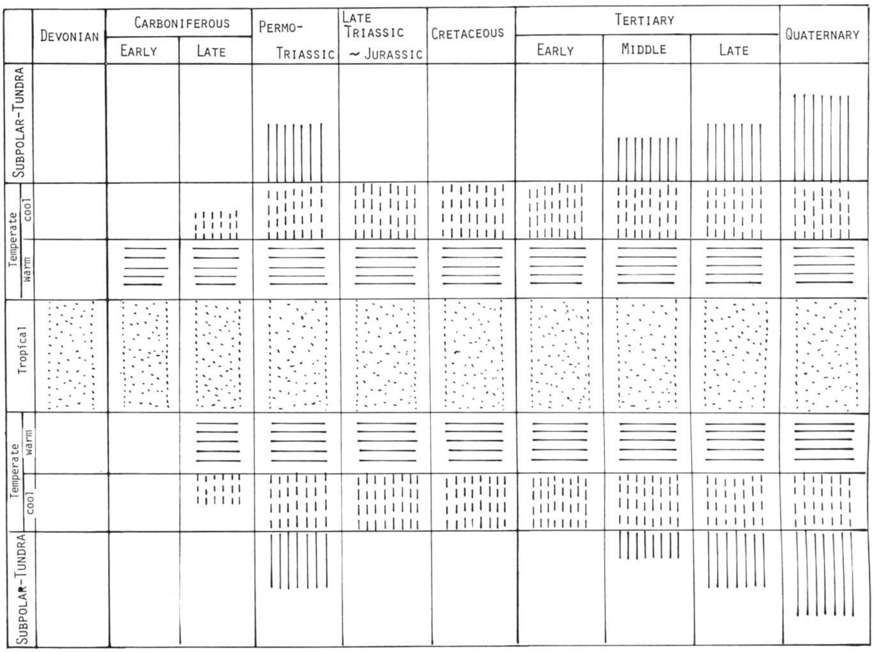


Fig. 1. The change of zonal distribution of vascular plants through ages. Adapted from AXELROD (1952) and EDWARDS (1973).

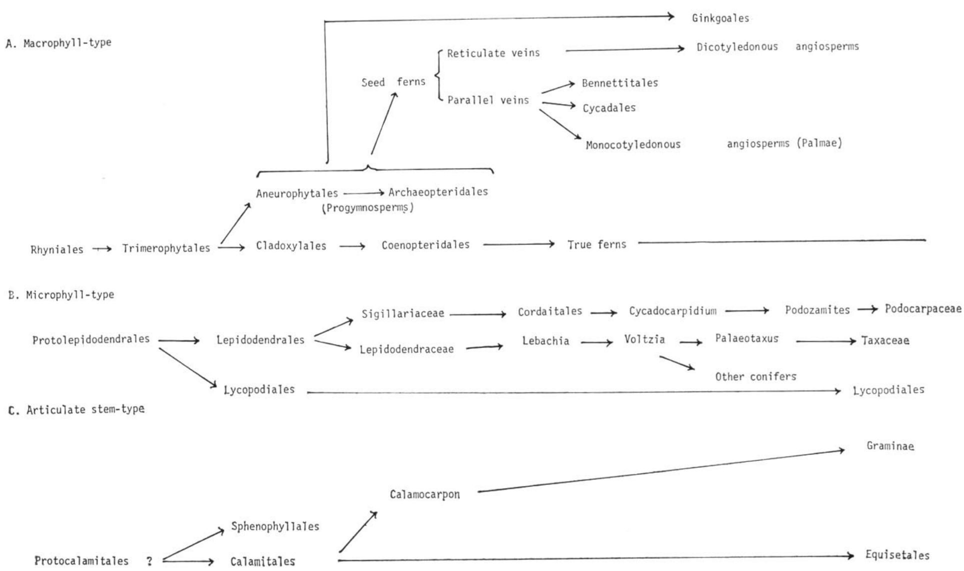


Fig. 2. Three lines of vascular plants based on the leaf forms.

Permo-Triassic zoning, which would have been accelerated by the Hercynian orogenic movement. This also means that the seasonal change seemed to become more and more distinct through ages as shown in Fig. 3 of Part 5 (ASAMA, 1982b).

There was one floral zone in the Devonian, which does not mean that the tropical climate distributed all over the world, but it means no great seasonal change had existed in the Devonian. It is natural that the climate in high latitude was colder than that of equatorial zone, but the difference of temperature between high and low latitude would not be so great as at present.

First land plants in the Latest Silurian or Early Devonian are all small primitive plants, and evolved into tall arborescent trees by the Late Paleozoic as shown by *Lepidodendron* and *Sigillaria* in Lycopsida, *Psaronius* in Pteropsida and *Calamites* in Sphenopsida. They were all very tall trees attaining 20–30 m in height. But their descendants are all small herbaceous plants as shown in Lycopodiales in Lycopsida, ferns in Pteropsida and Equisetales in Sphenopsida. The Late Paleozoic plants were able to grow to become tall trees as seen in *Lepidodendron*, *Psaronius* and *Calamites*, but Recent *Lycopodium*, ferns and *Equisetum* cannot grow to become tall trees and remained in the state of small herbaceous plants. This means that the climate of the Late Paleozoic was very mild and that of present is very severe.

These size reductions seen in Lycopsida, Pteropsida and Sphenopsida, all in the spore stage, support the paleoclimatic changes shown in Fig. 3 of Part 5 (ASAMA, 1982b).

Macroclimatic change is fundamental cause of the vascular plant evolution

As the Recent plants are the indicator of the Recent climate, the Paleozoic, Mesozoic and Cenozoic plants are the indicators of paleoclimate of each geological age. There is intimate connection between plants and climate. Therefore, if the climate of a certain area in a certain age changes, the plants, in where they live, must change their vegetative and reproductive organs into the adaptable forms. If they are able to change their organs into the adaptable forms for the changed environments, they will evolve into the next adaptated plants, and if not, they will be extinct.

As stated above we know the macro-paleoclimatic change through ages deduced by the zonal floral distribution of each age and the macrochange of size reduction in Lycopsida, Pteropsida and Sphenopsida, which were shown in Fig. 3 of Part 5. Therefore, the plants of Paleozoic, Mesozoic and Cenozoic must have changed their vegetative and reproductive organs to the adaptable forms.

Macro-climatic change through ages and the Principles of Growth Retardation are the basic concept of plant evolution. Paleoclimatic change is the cause and the Principles of Growth Retardation is the results derived from the cause.

Three lines of vascular plants based on the leaves

Recent plants are mainly classified on the basis of reproductive organs, and the vascular plants (Division Tracheophyta) are classified into three Subdivision, Pteridophytina, Gymnospermophytina and Angiospermophytina. Pteridophytina are characterized by the reproductive organ of the spore, Gymnospermophytina by the naked seed and Angiospermophytina by the enclosed seed, respectively. The reproductive organs had changed from the spore to the naked seed and then to the enclosed seed through ages. If so, the reproductive organs indicate the level of evolution and do not indicate the lines of vascular plants. It is necessary to find the indicator of lines to establish the phylogeny of vascular plants. Many botanists and paleobotanists consider that the reproductive organs are the main characters to search the phylogeny of vascular plants but they are the main characters indicating the level of evolution and do not indicate the lines of vascular plants.

Paleozoic vascular plants in the spore-stage are classified into three lines, Lycopsida, Pteropsida and Sphenopsida, by such leaf characters and stem structures as microphylls, macrophylls and articulate stems. Both microphylls and macrophylls had changed through ages, but they did not lose the characters of microphyll and macrophyll in any age, which indicate the lines of vascular plants. It is unquestionable that microphylls changed into large leaves, and macrophylls changed into small leaves in some cases, but they changed into large type or small type by rule. Therefore, if we understand the rule, Principles of Growth Retardation, we are easily able to find the lines in the plants of any age.

The reproductive organs teach us the level of evolution of vascular palnts and we can search their lines by such characters of vegetative organs as microphylls, macrophylls and articulate stems. Therefore, we should indicate the grade (level of evolution) and line of vascular plants in the phylogenetic chart. And it should be indicated that the environmental change through ages, which would be the main cause of evolution of vascular plants.

The writer classified the vascular plants into three Divisions, Microphyllophyta, Macrophyllophyta and Arthrophyta by the characters of vegetative organs, microphylls, macrophylls and articurate stems. Plants of each Division had evolved into two directions, regressive and progressive.

The former adapted to the changing environments, which are stated above, by reducing their size and the latter by improving their reproductive organs. The writer calls these changes the regressive evolution (or change) and the progressive evolution (or change).

The writer discussed the macro-climatic change through ages by the change of zonal distribution of plants and the size reduction of plants of three lines in the spore stage. All plants had to change their size or reproductive organs to the adaptable froms.

1) Change of leaf forms in regressive groups of macrophyll series

Fig. 3 shows the representative plants of each age indicaing the change of leaf forms through ages. There are great differences in the changed forms of leaves and reproductive organs in the progressive groups of vascular plants. Therefore it is very difficult to find the lines of vascular plants and many authors consider that such characters as microphylls, macrophylls and articulate stems are the characteristics only in pteridophytes and not characteristics in gymnosperms and angiosperms. Both leaves and reproductive organs had changed by the changes of environment, which were stated above, in the progressive groups. There is small difference in the regressive groups, and it is easy to find lines.

The naked branch systems of the Early Devonian plants (Fig. 3–1 ~ 4), orginal leaf form of Macrophyllophyta, had changed into the pinnately compound leaves (Fig. 3–5) in the Carboniferous, which remained in the great part of Recent ferns and sometimes show the simple leaves (Fig. 3–12), which were derived from the pinnately compound leaves. Therefore, the pinnately compound leaves are the main leaf form through ages (Fig. 3–5 ~ 11) in the regressive group with macrophylls (ferns).

The microphylls of the Devonian Protolepidodendrales (Fig. 3–37 ~ 39), orginal leaf form of Microphyllophyta, had remained in the leaf form of the Recent Lycopodiales (Fig. 3–45), without changing their leaf form.

The original leaf form of Arthrophyta (*Equisetophyton*) is not known, and it is considered that the dichotomous leaves of the Lower Carboniferous *Archaeocalamites* (Fig. 3–60) are indicating the original leaf form, which changed into the small simple leaves shown in the leaves of *Annularia* of Carboniferous and Permian (Fig. 3–61). They changed into three directions, the first is shown in the very small leaves of *Equisetites* (Fig. 3–65 ~ 67) or *Equisetum* (Fig. 3–68), which were derived from the size reduction of leaves of *Calamites*, the second is shown in the long leaves of *Neocalamites* (Fig. 3–64) derived from the short leaves of *Calamites* by Enlargement of segments (leaves) (ASAMA, 1981a, Part 1, Principles of Growth Retardation) and the third is shown in the large leaves of *Schizoneura* (Fig. 3–63) derived from the leaves of *Calamites* by Enlargement and Fusion of segments (ASAMA, 1981a, Part 1, fig. 2 and ASAMA, 1982b, Part 5, fig. 1).

2) Change of leaf forms in progressive groups of macrophyll series

The naked branch systems of the Early and Middle Devonian (Fig. 3–1, 2, 13), original leaf form of Macrophyllophyta, had changed into the pinnately compound leaves of Archaeopteridales (Fig. 3–14) by the Late Devonian. Therefore, the Devonian is the naked leaf stage or the compound leaf forming stge in the progressive group of macrophyll series. The pinnately compound leaves (Fig. 3–15 ~ 17, 25, 26), which were formed in the Latest Devonian, had changed into the simple leaves seen in *Taeniopteris* (Fig. 3–18), *Glossopteris* of Gondwanaland (Fig. 3–27) and *Gigantopteris* of Cathaysia land (Fig. 3–28) in the Latest Carboniferous or Early Permian. Therefore the Carboniferous and Permian are the pinnately compound leaf stage or the simple leaf forming stage in the progressive group of macrophyll series. The simple leaves seen in *Glossopteris* and *Gigantopteris* with reticulate veins are the latest stage in the evolution of leaf forms and it would be expected from the view point of climatic change that these simple leaves will change into the smaller type by the next "Growth Retardation" in Mesozoic and Cenozoic. In the regressive group of macrophyll series the

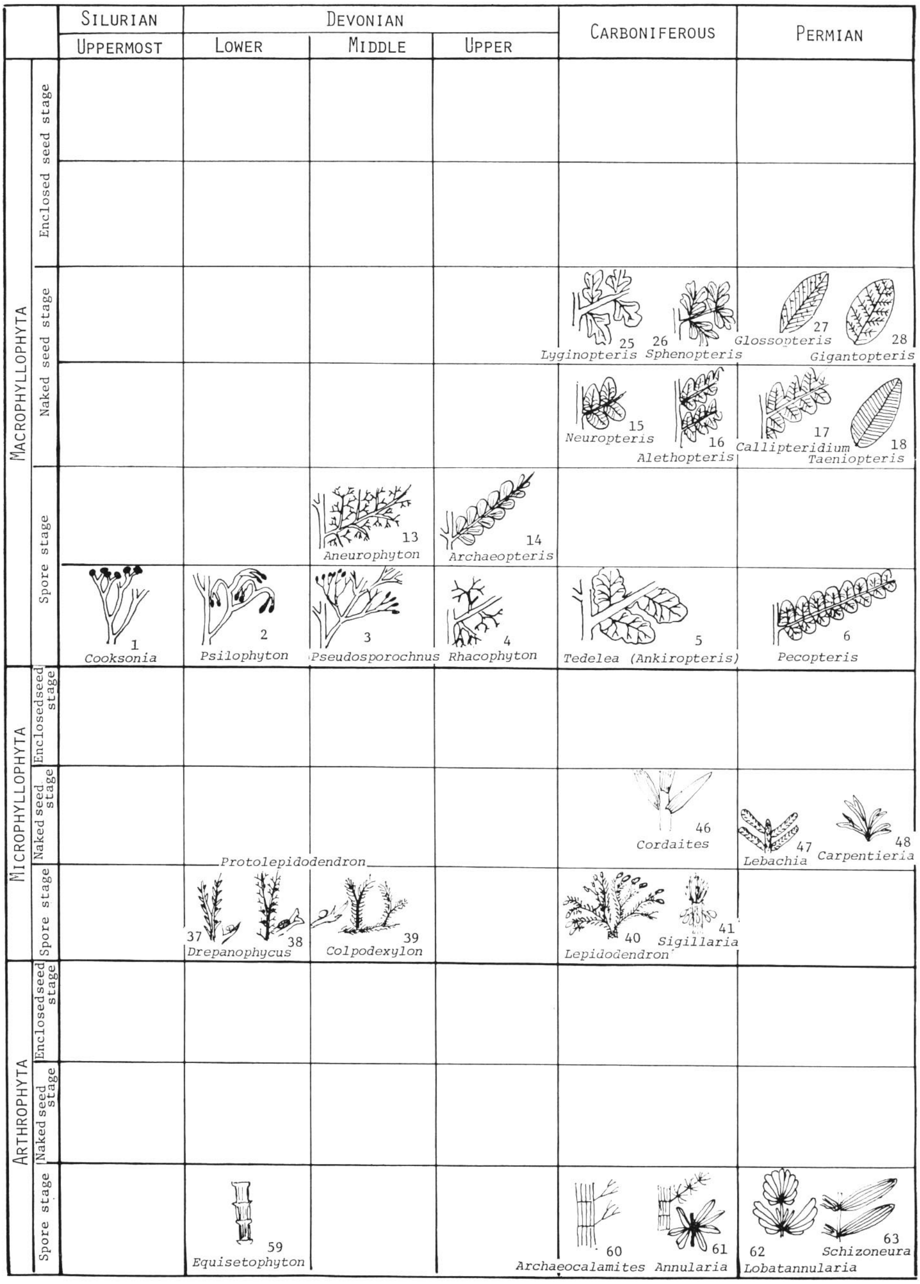
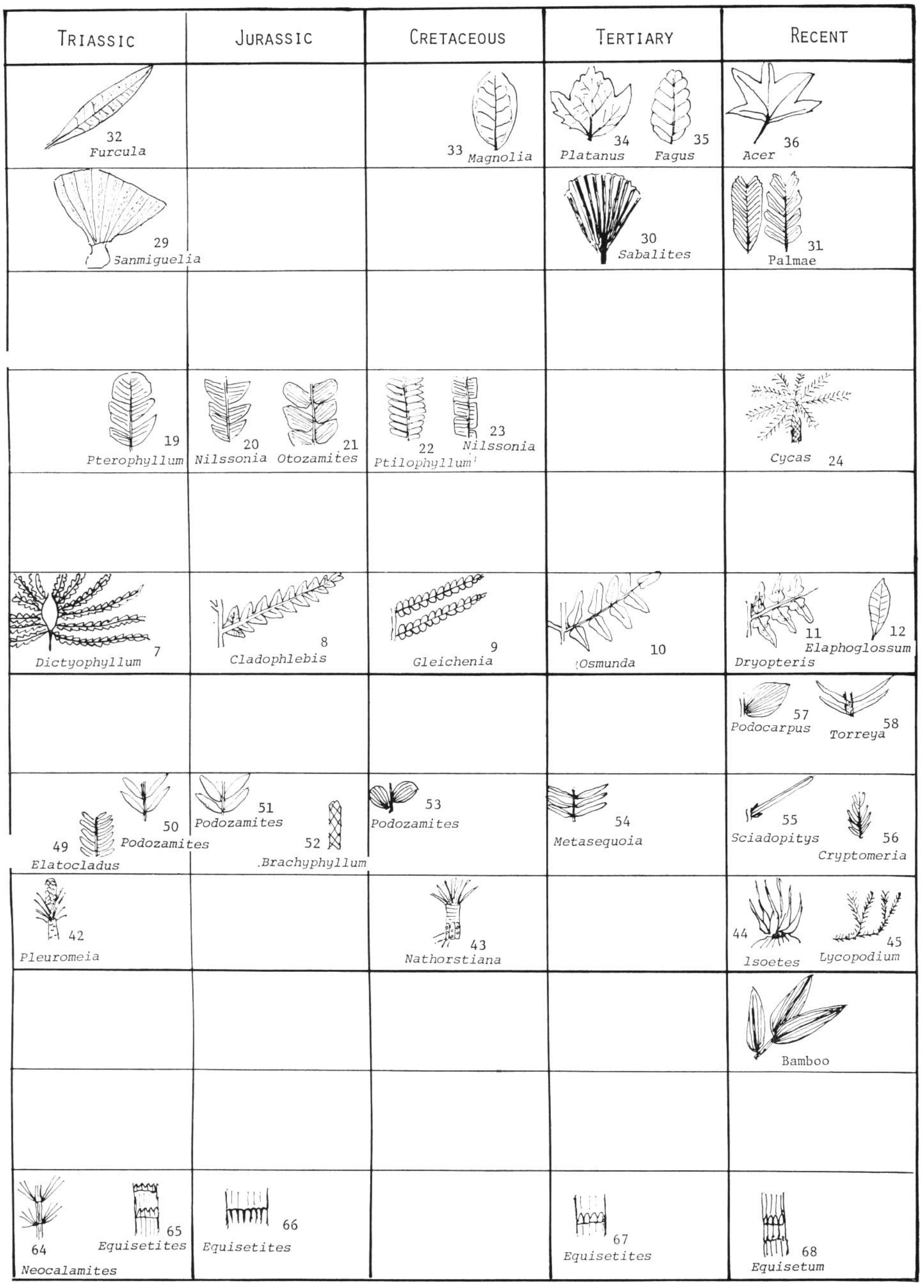


Fig. 3. Comparison of leaves between macrophyll series, microphyll series and articulate stem (1951), Brown (1956), Edwards (1970), Florin (1951), Harris (1932), Hirmer (1927), (1968), Schweitzer (1972), Sporne (1965, 1975).



series. Adapted from ARNOLD (1939), ANDREWS & PHILLIPS (1968), BANKS (1968), BAXTER HUEBER (1967), KRÄUSEL & WEYLAND (1926, 1935), LECLERCQ & BANKS (1962), MÄGDEFRAU pinnately compound leaves are dominant through the Carboniferous to Recent and the simple leaves are found only in several genera of Recent ferns. But in the progressive group of macrophyll series the simple leaves are the general leaf forms from the Permian to Recent except the leaves of Bennettitales and Cycadales. The progressive group could change their pinnately compound leaves into the simple leaves by the improvement of reproductive organs, the naked seed.

The simple leaves with parallel secondary veins, Taeniopterides, had changed into the leaves of Cycadales and Bennettitales in Mesozoic as staged in Part 4 (ASAMA, 1982a) and into the leaves of Palmae ? in Cenozoic, respectively.

3) Phylogeny of macrophyll series

From the facts stated above the original plants of macrophyll series (Rhyniales and Trimerophytales) had changed into two evolutionary directions in the Middle Devonian, the one proceeded to the regressive direction without improving their reproductive organs, from Trimerophytales (*Psilophyton*) to Cladoxylales (*Pseudosporochnus*), Coenopteridales (*Rhacophyton*) and to true ferns. The other proceeded to the progressive direction improving their reproductive organs, from Trimerophytales to Progymnosperms (Aneurophytales and Archaeopteridales) and to seed ferns. The seed ferns have two types of plants, parallel veins type (Taeniopterides) and reticulate veins type (Glossopteridales and Gigantopteridales). The former evolved to the direction of Bennettitales, Cycadales and into the monocotyledonous angiosperms (Palmae), and the latter into the dicotyledonous angiosperms. These evolutionary lines are shown in Fig. 2.

4) Change of leaf form form in progressive groups and phylogeny of microphyll series

In the progressive groups of macrophyll series the naked branch systems had changed into the pinnately compound leaves (consists of many segments, pinnules and pinnae) and into the simple leaves (one segment) reducing the number of their segments by "Fusion" or "Enlargement" of segments (ASAMA, 1981a, Part 1, Fig. 2). The plants of macrophyll series could evolve into the naked seed stage and into the enclosed seed stage by the enlargement of segment-size reducing the number of segments. The largest leaf is simple leaf which consists of one segment.

Microphylls correspond to the segments (pinnules or pinnae) of macrophyllous plants in the evolutionary stage. The enlargement of segment-size had occurred in the progressive groups of microphyll series, which are seen in the *Cordaites* line, *Cordaites* in Paleozoic, *Podozamites* in Mesozoic and *Podocarpus* in Cenozoic. In the other lines of conifers the leaf forms did not change so much, but the reduction of branches also occurred in them like those of *Cordaites* line, which are seen in *Pinus*, *Larix* and *Sciadopitys* (ASAMA, 1981b, Part 2, fig. 9). Phylogeny of microphyll series is shown in Fig. 2.

5) Change of leaf forms in progressive groups and phylogeny of articlate stem series

The enlargement of segment-size had occurred in the articulate stem series like those shown in the macrophyll series and microphyll series. The leaves of *Schizoneura* reported from Gondwanaland and Cathaysia land correspond to the unipinnate fronds in macrophyll series. which is indicating the penultimate stage of leaf form evolution. The ultimate stage of leaf form evolution in macrophyll series is shown in such simple leaf as *Glossopteris* and *Gigantoptetis* and shown in the simple leaf of bamboos in articulate stem series. The simple leaf forming process of Gigantopteridales is shown in the Late Paleozoic fossil records of Cathaysia land (ASAMA, 1981a, Part 1, Fig. 1; 1982a, Part 4, Fig. 2) but we could not find the simple leaf-forming process of woody Graminae (Bamboos). The fact that the fossil records of the progressive group of articulate stem series are very few may be indicating the upland life of those plants during the great part of Mesozoic and Cenozoic. The lowland types of the articulate stem series are seen in *Neocalamites* and *Equisetites* through Mesozoic and Cenozoic, both of which belong to the plants of regressive group of articulate stem series.

6) Three lines of vascular plants based on the leaves and stem structures

Fig. 3 shows the comparison of leaves and stem structures between the three lines of vascular plants, macrophyll series, microphyll series and articulate stem series.

As shown in Fig. 3 the vascular plants are divided into three lines by the characteristics of vegetative organs, macrophylls, microphylls and articulate stems. Many authors consider these characters as the effective characters to classify only pteridophytes. But the present writer believes that these characters are effective not only for the classification of pteridophytes but also for the classification of gymnosperms and angiosperms, namely for all vascular plants. These characters are already shown in the early land plants, Rhyniales, Protolepidodendrales and Protoarticulates. Therefore the writer cannot agree with the telome theory of ZIMMERMANN (1959; ASAMA, 1981b, fig. 5), which explains that all vascular plants are derived monophyletically from the original dichotomous plants like *Rhynia*. The writer believes that plants had already possessed such characters as macrophylls (ancestral naked branches), microphylls and articulate stems before they landed on the continents, and that these characters had been remained without losing their characters as line.

The leaf forms had been changed through ages but if we understand the "Principles of Growth Retardation", we are able to trace the lines of macrophylls, microphylls and articulate stems. It should be considered that the plants of each line proceeded into two directions, regressive (without improving reproductive organs) and progressive (improvement of reproductive organs; grading up of reproductive organs, from spore to naked seed and to enclosed seed). The former did not change too much their leaf forms. The latter changed their leaf forms to the direction of enlargement of segment-size and formed the simple leaves in their latest stage of leaf form evolution such as *Glossopteris*, *Gigantopteris* and *Taeniopteris* in macrophyll series, *Cordaites*, *Podozamites* and *Podocarpus* in microphyll series and woody Graminae in articulate stem series.

The enlargement of segment-size means the reduction of branches to form simple leaf in the latest stage of leaf form evolution, and the reduction was always the basic principle of leaf form evolution, which was indicating the unfavorable climatic change for the growth of plants. The leaf form changes seen in three lines of vascular plants were all adaptable change for the changing environments. The writer calls these three lines of vascular plants, Macrophyllophyta, Microphyllophyta and Arthrophyta.

Three lines of vascular plants based on the reproductive organs

There were two directions in the evolution of reproductive organs, regressive and progressive. In the regressive groups the reproductive rogans did not change too much and they were remained in the spore stage, but in the progressive groups they had changed so much grading them up from spore stage to naked seed stage and to enclosed seed stage.

1) Three types of reproductive organs

There were three types of arrangement of reproductive organs in the Early Devonian plants. The first type (Fig. 4, Terminal-type) was shown in Rhyniales (Fig. 5–1, 2), which have sporangium at the terminal part of dichotomous branches. The second type (Fig. 4, Spiral-type) was shown in Protolepidodendrales (Fig. 5–37, 38), which have sporangium on the sporophylls arranged spirally around axis. The third type (Fig. 4, Whorl-type) should be shown in *Equisetophyton* but we have no fossil record. The deduced arrangement of sporangium in the third type was shown in Fig. 5 of Part 2, (ASAMA, 1981b). The sporophylls of the second type, Protolepidodendrales, were arranged spirally around axis and those of the third type might be arranged in whorl. The writer calls these types of reproductive rogans, terminal-type, spiral-type and whorl-type, respectively (Fig. 4). These plants of three types of reproductive organs, which were shwon in Rhyniales, Protolepidodendrales and Protocalamitales, might have been the starting points of three lines of vascular plants, macrophyll series, microphyll series and articulate stem series.

Rhyniales with terminal sporangia changed into Trimerophytales in Siegenian of Early Devonian (Fig. 5–1 ~2), and there are no difference in the arrangement of sporangium, both have terminal sporangia. This is the reason why the present writer did not agree with the telome theory of ZIMMERMANN (ASAMA, 1981b, Part 2, p. 103). Judging from the principles of Growth Retardation it is very difficult or impossible to change their arrangement of sporangium in a short period from the terminal sporophylls of dichotomous branches (Rhyniales) to spiral (Lycopsida) or whorled (Sphenopsida) sporophylls around axis. Therefore, the telome theory is availabe in the early evolution of macrophyll series and is not in both microphyll series and articulate stem series. These fossil records indicate the three lines of vasculat plants, Macrophyllophyta, Microphyllophyta and Arthrophyta.

2) Multiplication stage and Reduction stage

Before the discussion of the reproductive organs, it is necessary to state the multiplication stage and the reduction stage of vascular plants. As stated in Part 3 (ASAMA, 1981c, p. 138) the Early Devonian plants such as *Cooksonia* and *Rhynia* had been grown up to such large trees as *Archaeopteris* and *Rhacophyton* by "Multiplication" step by step (Part 3, Fig. 2). And these multiplication of plant bodies continued into

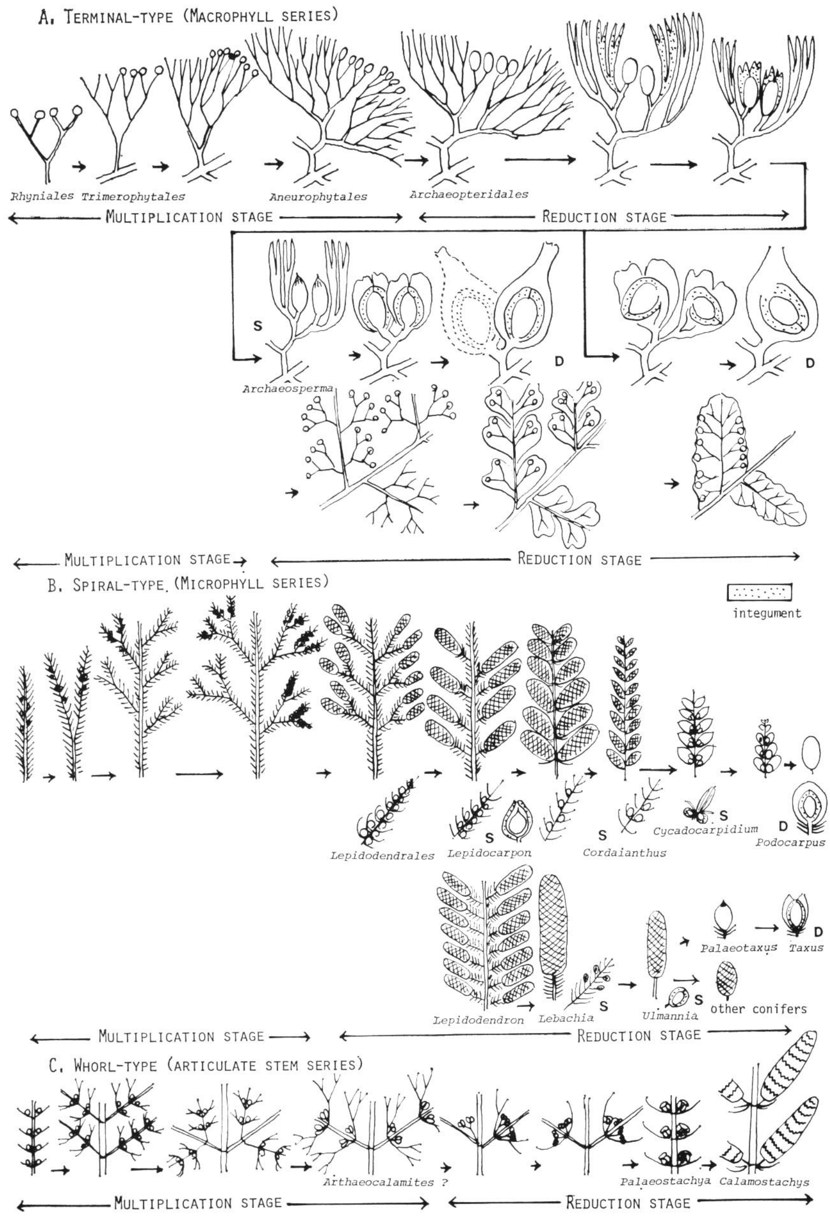


Fig. 4. Three types of reproductive organs and their evolution based on the Growth Retardation. Sporangium were enclosed by lateral segments forming the single protected ovules (S) and again enclosed by lateral segments foring the double protected ovules (D). These changes were adaptable change for the changing environment through ages.

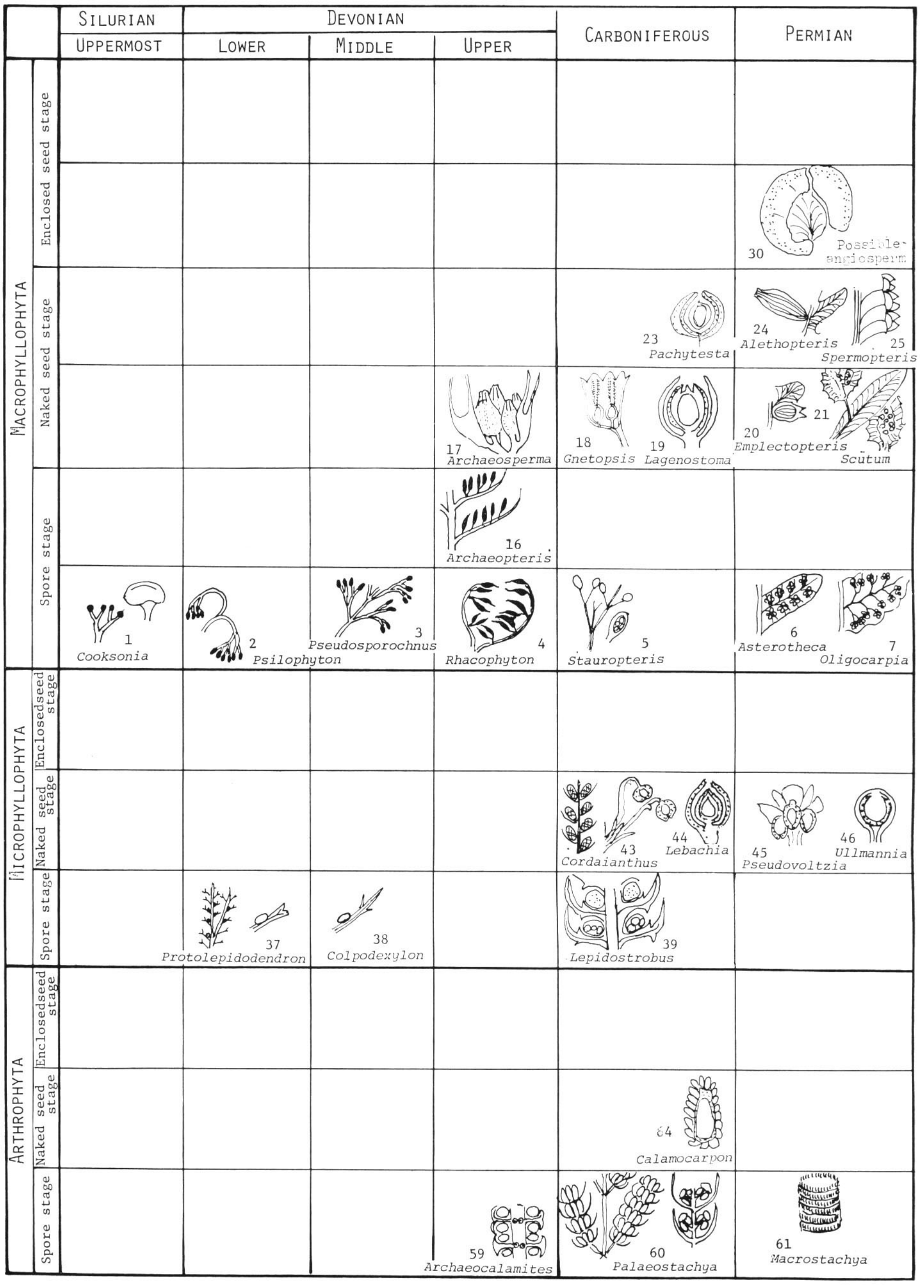
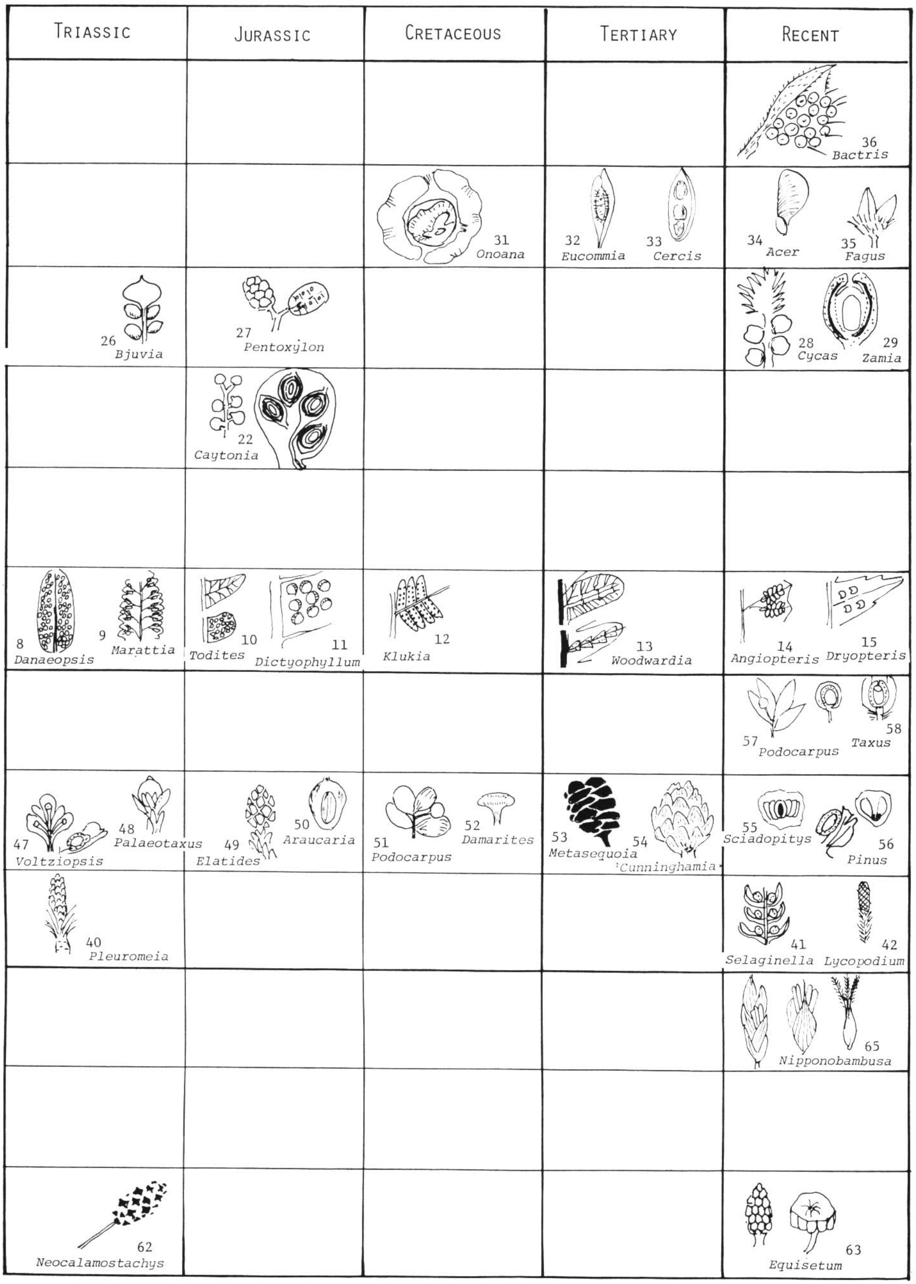


Fig. 5. Comparison of reproductive organs between macrophyll series, microphyll series and AXELROD (1961), BAXTER (1955, 1963), EDWARDS (1970), FLORIN (1951), HALLE (1927), MAMAY (1976), PETTITT & BECK (1968), PLUMSTEAD (1956, 1962), SAHNI (1948), STEWART



articulate stem series. Adapted from ANDREWS (1961), ANDREWS & PHILLIPS (1968), HIEMER (1927), HUEBER (1967), KRÄUSEL & WEYLAND (1935), LECLERCQ & BANKS (1962), (1954), THOMAS (1925).

the latest Devonian or the Carboniferous Period. The Early Devonian plants became able to grow to large trees through ages step by step by the improvement of stem structures, from annular thicknings of xylem tracheids to spiral, scalariform and bordered pits, to be able to conduct water more easily. Therefore plants could grow to large trees forming large leaves.

Leaves of macrophyll series had changed into simple leaves during the period from the Late Carboniferous to Permian (ASAMA, 1981c, fig. 4), and the reduction of leaves had continued to the Quaternay. The writer calls these periods of multiplication and reduction, as the multiplication stage (Early Devonian to Late Devonian or Early Carboniferous) and the reduction stage (Latest Devonian or Late Carboniferous to Quaternary) respectively.

3) Change of reproductive organs in the regressive groups

In the macrophyll series Rhyniales (*Cooksonia*, Fig. 5–1) changed into Trimerophytales (*Psilophyton*, Fig. 5–2) Cladoxylales (*Pseudosporochnus*, Fig. 5–3), Coenopteridales (*Rhacophyton*, Fig. 5–4) and into true ferns successively, from the Early Devonian to Carboniferous, multiplying their bodies and leaves from the naked branches to the pinnately compound leaves (Fig. 4). And the reproductive organs were aggregated to the special branches, namely the fertile branches or fertile pinnae. The terminal sporongium of naked branches (Rhyniales) changed their position to the lower side of pinnately compound leaves by "Fusion" of segments and never formed cones like those of microphyll series (Lycopsida) and articulate stem series (Sphenopsida) in Paleozoic. The fertile pinnae, which were formed in the multiplication stage, did not change their basic form in the reduction stage from the Carboniferous to Recent (Fig. 5–6 ~ 15).

In the microphyll series the sporangium, which were on the sporophylls arranged spirally around axis, was aggregated to the special branches, namely the cones (Fig. 5–37 ~ 39). And these cones, which were formed in the multiplication stage, remained in the reduction stage through Carboniferous to Recent without changing their basic form (Fig. 5–39 ~ 42 and Fig. 4).

We do not have the fossil records on the cone-forming process of articulate stem series, but we are able to deduce the process by the cone-forming process of microphyll serirs. The cones of the Carboniferous Calamitales (Fig. 5–59 ~ 60) might have been formed in the multiplication stage, which were shown in Fig. 4. And they were remained through ages to Recent without changing their basic form (Fig. 5–60 ~ 63).

4) Change of reproductive organs in the progressive groups

Archaeosperma arnoldii, described from the Upper Devonian of North America by PETTITT and BECK (1968), was the first gymonspermous plant. Recently GILLESPIE, ROTHWELL and SCHECKLER (1981) reported the earliest seeds from the late Devonian Hampshire Formation of Randolph County, West Virginia (Famennian in age). In both cases the sporangium were covered by integument and have cupules.

The ovule forming process (naked seed forming process) deduced by the principles of Growth Retardation was shown in Fig. 4. The writer discussed the Principle, "Enclosure" in Part 2 (ASAMA, 1981b, p. 107), when he stated the cone forming process, and the process from spore to naked seed and to enclosed seed of Microphyllophyta. If the growth of plants is retarded by some environmental change, the growth of central part of stem will be more retarded than those of lateral part sometimes. Thereforee, the central part will be enclosed by the lateral part. The writer calls this process "Enclosure".

The naked seed forming process of *Archaeosperma arnoldii* by "Enclosure" was shown in Fig. 4. Rhyniales changed into Trimerophytales and Aneurophytales multiplying their dichotomous branches, and in the next stage the terminal sporangia had become larger reducing their branches and had been enclosed by lateral segments in the final stage as shown in Fig. 4. The enclosure means the protection of sporangia. We call the protected sporangia ovule or ovary, the former of which is protected by a single appendage (integument) and the latter by double appendages (integument and carpel). Protection indicates the three evolutionary stages, the spore stage (with naked sporangium), naked seed stage (with sporania enclosed by a single appendage) and enclosed seed stage (with sporangia enclosed by double appendages). In general the spores are weak in dry or cold environment, the naked seeds are tolerant of dryness but weak in cold environment, and the enclosed seeds are tolerant of both dry and cold environment.

In the macrophyll series the terminal sporangium of Rhyniales (Fig. 5–1, 2) changed to those of Aneurophytales in Eifelian (Middle Devonia) and probably to the naked seed of *Archaeosperma* (Fig. 5–17) in the Latest Devonian and to the seed ferns in Carboniferous.

The writer do not know when the naked seeds of these Carboniferous seed ferns had been enclosed by the protective cover. If the possible angiosperms (Fig. 5–30) reported from the Lower Permian coal of the Transvaal of South Africa by PLUMSTEAD (1962) were true angiosperms, it may be able to say that the angiosperms might have orginated in the Permian at least. The earliest angiosperm fruit *Onoana* (Fig. 5–31) had been described from the Ono Formation of northern California (Hauterivian of the early Cretaceous) by AXELROD (1961).

The evolutionary change of the reproductive organs in progressive group of microphyll series was discussed in Part 2 (ASAMA, 1981b, p. 107) and shown in Fig. 4.

The fossil records are very few to discuss the evolutionary change of reproductive organs of articulate stem series, but we can deduce the naked seed forming process from the ovule forming process of microphyll series. Both in microphyll series and articulate stem series the spiral and worled sporophylls had been aggregated into cones and they might have evolved in parallel from the spore stage to the naked seed stage and then to the enclose seed stage respectively as shown in Fig. 4.

Three lines of vascular plants based on the stem structure

Vascular plants are clearly divided into three lines by the characters of the vegeta-

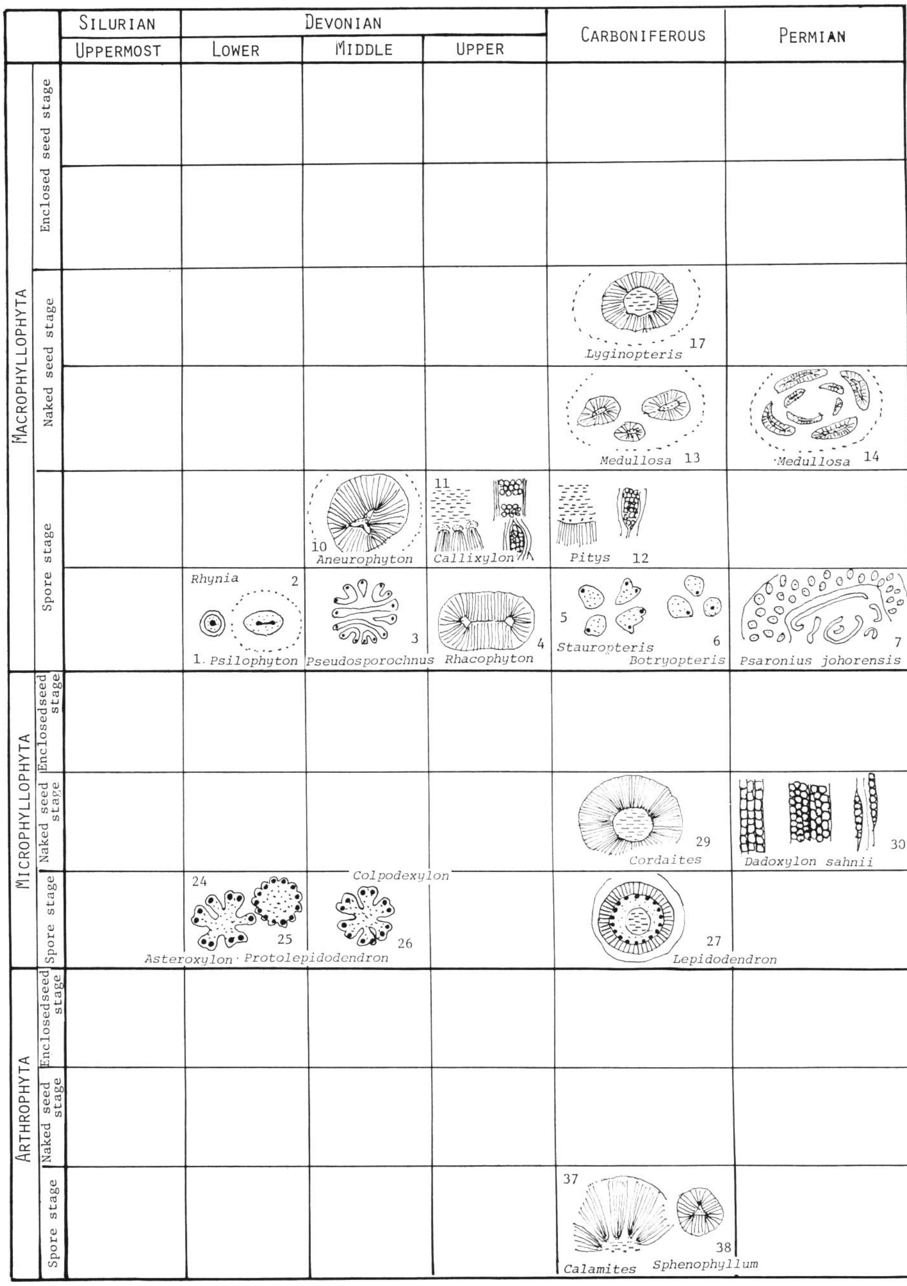
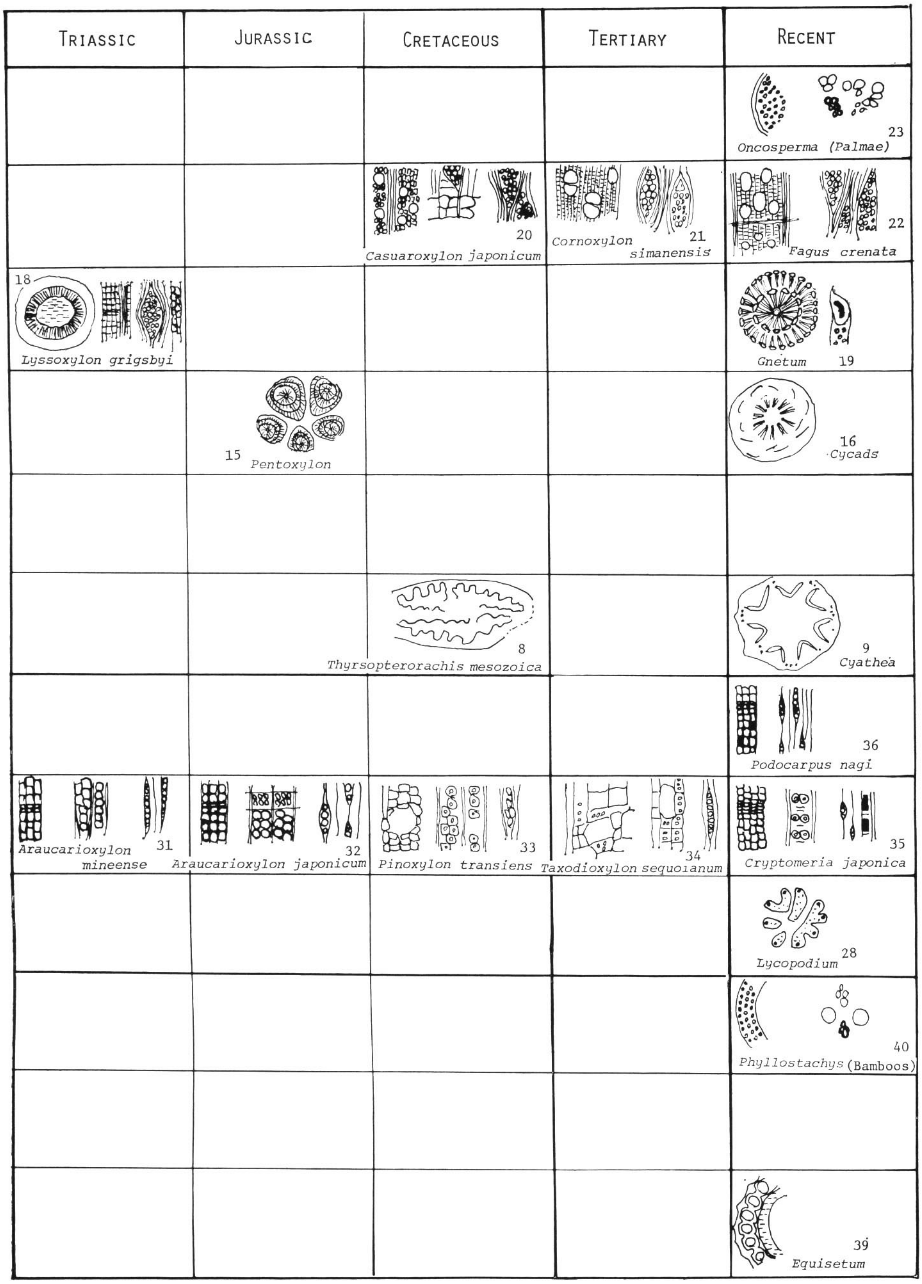


Fig. 6. Comparison of stem structures between macrophyll series, microphyll series and arti-
(1982c), BANKS (1968), GU & ZHI (1974), NISHIDA (1979), OGURA (1944, 1960, 1972), SHI-



culate stem series. Adapted from ANDREWS & PHILLIPS (1968), ARNOLD (1931), ASAMA MAKURA (1936, 1937), SPORNE (1965, 1975), WATARI (1948).

tive organs, macrophylls, microphylls and articulate stems. And they are also clearly divided into three lines by the characters of the reproductive organs, terminal-type, spiral-type and whorl-type. There are no distinctive character to identify three lines of vascular plants in the stem structure, which reflect the leaf forms and the environmental change through ages.

1) Stem structures of the regressive groups

The stems of the primitive plants such as Rhyniales (Fig. 6–1 ~ 2) and Protolepidodendrales (Fig. 6–24 ~ 26) are protostelic and as they evolve by the additoin of new characters, from annual to spiral, scalariform and bordered pitted tracheids, their stem structures had become polysteric multiplying their vegetative parts. Some of them had the secondary xylem becoming the large trees such as *Rhacophyton* (Fig. 6–4), Lepidodendrales (Fig. 6–27) and Calamitales (Fig. 6–37). Their descendants are all small herbaceous plants now by the reduction of secondary xylem (Fig. 6–9, 28, 39) as climate has changed from mild to severe through ages.

2) Stem structures of the progressive groups

In the macrophyll series Rhyniales had changed into Trimerophytales, Aneurophytales (Fig. 6–10) and into Archaeopteridales (*Callixylon*, Fig. 6–11) becoming large trees by the improvement of conductive tissues. It is noted that *Archaeopteris* had already the multiseriate ray which characterizes the ray of angiosperms.

There were two types of stem structure in Paleozoic seed ferns, *Lyginopteris* type (Fig. 6–17) and *Medullosa* type (Fig. 6–13, 14). The former had the monosteric stems, which means the possibility of secondary growth more and more, and the latter had the polysteric stems, which means limit of secondary growth. The writer considers that the former had evolved into angiosperms and the latter into Cycadales and Bennettitales (Fig. 4).

Angiosperms had diversified through the Tertiary since the Late Cretaceous and they are characrerized by the secondary woods with vessels and multiseriate rays which reflect the environmental change through ages. The writer believes the phylogeny of angiosperms from Archaeopteridales to Lyginopteridaceae and to angiosperms based on the characters of leaf forms and reproductive organs.

In the progressive group of microphyll series the secondary woods are characterized by the uniseriate rays in general (Fig. 6–30 ~ 36) and have not vessels in any age. Tracheids were the starting points of the secondary woods of the macrophyll series and microphyll series. Some tracheids of the macrophyll series had evolved into vessels but they did not evolve into vessels in the microphyll series. The differences of xylem structure between the macrophyll series and microphyll series are depending on the difference of leaf forms. The former have the leaves of latge type, and the latter have those of small type. In the macrophyll series the segments of pinnately compound leaves had evolved into larger segments step by step and into one segment in the final stage. Simple leaf forming process, from pinnately compound leaf to simple leaf, had occured in the unfavorable environment for the growth of plants. The plants must had stopped their growth during a cold or dry season. When a warm or wet season came, a large amount of water was required for the growth of large segments. Repeat of this process forced tracheids to change into vessels to conduct a large amount of water. The occurrence of vessels and multiseriate rays for storage reflect the change of climate.

The small leaves of the microphyll series did not require a large amount of water and multiseriate rays for storage. In the macrophyll series the angiosperms could survive cold winter losing their leaves. In the microphyll series the conifers could survive the cold winter by having resin canals and resin cells.

Three lines of vasecular plants

As stated above the vascular plants are divided into three lines on the basis of three types of vegetative organs: macrophylls, microphylls and articulate stems; and three types of reproductive organs: terminal-type, spiral-type and whorl-type. These types of vegetative organs and types of reproductive organs indicate respective line.

These three lines of vascular plants have changed their leaf forms and reprocuctive organs in parallel adapting to the changing environments which changed from mild to severe climate as shown in Fig. 3. of Part 5 ASAMA, 1982b, p. 54). Therefore there are strong reasons to consider that the changed forms of reproductive organs, spores, naked seeds and enclosed seeds, are indicative of the level of evolution of vascular plants.

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