PSYGMOPHYLLOPSIDA, ONE OF THE FUNDAMENTAL PTERIDOPHYTIC DIVISIONS (PHYLA)

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ABSTRACT

In this article the establishment of a fourth pteridophytic phylum the *Psygmophyllopsida* is explained. The Devonian *Barrandeina* Pot. et Bern., *Duisbergia* Kr. et W., *Jenisseiphyton* Anan., *Haspia* Kr. et W. and similar types are attributed hereto. The Devonian *Cladoxylineae*, the Carboniferous *Noeggerathiineae* as well as the recent *Psilotineae* are regarded as special pteridophytic evolutionary trends, arisen directly out of this group. The pteridophytic phylum *Sphenopsida* (Articulatineae) as well as the gymnospermic phyla *Cordaitopsida*, *Ginkgopsida* and *Coniferopsida* are regarded as major evolutionary lines arisen too of this phylum.

INTRODUCTION

AT the present time it seems that the taxonomic significance of the fundamental phylum *Psilopsida* (or Psilophytineae) including the most primitive vascular plants ever found is very far from being clear enough. In the Devonian and Upper Silurian floras we meet many primitive types reminding some lycopodioid or equisetoid plants and there are especially many primitive fern-like plants, which according to many palaeontologists are often regarded as psilophytic or at least of psilophytic nature. Indeed no sharp boundary seems to have been yet established in this respect between the Psilopsida and the other more progressive pteridophytic phyla. We meet the same taxonomic problem full of uncertainties if we study the more primitive or archaic types belonging already to the single pteridophytic phyla; only the lycopodioid type seems utterly isolated without any relations either to the Psilopsida or to any of the pteridophytic types (articulatinean or filicinean). The relations to the group of the Devonian asteroxyla seems to be only fictitious. There are in the Palaeozoic flora, types which remind the Sphenopsida but exhibiting normal dichotomous kind of branching, unarticulated stems and often even leaflets not quite regularly whorld, as well as loose spike-like fructifications recalling some equisetalean spikes, e.g. in the genus *Hyenia*. Or, there are types with spirally disposed leaflets like the leaves of some sphenophylla, spike-like arranged sporophylls, unarticulated stems and branches with plagiotropic orientation and arrangement like some fern leaf fronds, e.g. in the genus *Cladoxylon*. The types with spirally arranged petiolate leaves with wedge-like enlarged blade as in various sphenophylla, and spike-like arranged sporophylls bearing perhaps terminally at the tops of the laciniae a larger number of sporangia, remind thus partly the conditions in the Lycopsida and partly those in the Sphenopsida, e.g. the genus *Barrandeina*. Some types exhibit fructifications of a shape very characteristic in several typical ferns, but axis not yet differentiated into normal stems and leaves or fronds, having only the tops of their last ramifications enlarged into some deeply incised wedge-shaped blades, e.g. the genus *Svalbardia* with fructifications like *Archaeopteris*. Last but not the least, even the representatives of the recent order *Psilotales* (the genera *Psilotum* and *Tmesipteris*) have also to be mentioned here as a type in which lycopodioid characters, such as unarticulated stem and leaflets, are combined with some articulatinean ones such as sporophylls, sporangia and their position. It is indeed very difficult to define exactly the true taxonomical position of such strange plant types.

In my various studies of the Carboniferous floras of Bohemia, I met this taxonomical problem in the case of the genera *Noeggerathia*, *Palaeopteridium*, *Saaropteris* and *Eurhacopteris*, as well as in that of the fructifications called *Discinites*. At present I am especially occupied with it being entrusted with the compilation of a larger textbook of systematic palaeobotany for our Czech students or experts in geology or botany.

EXPERIENCE ACHIEVED BY THE STUDY OF THE GENUS *NOEGGERATHIA* AND SOME ALLIED UPPER CARBONIFEROUS PLANT TYPES

In my monograph on the Noeggerathiae and Archaeopterides from the coal districts

of Central Bohemia (NEMEJC, 1928), being affected by the opinions of my precursors, I tried to explain the morphology and taxonomic position of the genus *Noeggerathia* from the point of view of the morphological features peculiar to the ferns or cycads. But later (NEMEJC, 1931) comparing this curious type with several other Carboniferous types like *Tingia, Palaeopteridium* and its probable cones called *Discinites, Saaropteris* as well as *Eurhacopteris,* I recognized that such point of view was not in accord with many peculiarities possessed by these plants. It became obvious that (1) the once pinnate "fronds" of Noeggerathiae are no real leaf fronds, but leafy shoots with limited growth and plagiotropic orientation of their simple leaflets, e.g. in the genus *Tingia* they are disposed in four rows; (2) in the genus *Noeggerathia,* similarly as in *Tingia* or in the fructification called *Discinites* (which belongs most probably partly to *Palaeopteridium,* partly also to *Saaropteris* and *Eurhacopteris*) the sporophylls are arranged in mighty cone-like organs like those in various representatives of the Lycopsida or Sphenopsida; (3) the axis on which sterile as well as fertile leaflets are joined, just as all other branches or stems (recognized by me in several *Discinites* and *Palaeopteridium* remains, newly by J. Setlik also in *Noeggerathia foliosa* Stbg.), exhibits absolutely no indication of any articulation; (4) they are of pteridophytic nature, mostly heterosporic, e.g. *Noeggerathia, Discinites*; (5) The sporangia are situated in a large number on the adaxial side of the sporophylls; and finally (6) the spores as far as known exhibit great similarities with the spores of several Sphenopsida, especially with those of the Carboniferous Calamariales.

Conformably with all these data, in a short study (NEMEJC, 1931) I stated that the Noeggerathiae cannot be regarded as fern-like plants but that even within the pteridophytic phyla of Lycopsida or Sphenopsida we meet absolutely no perfectly comparable plant type, though many characteristic features such as cone-like fructifications, sporophylls provided by a larger number of sporangia, the type of leaflets, the shape and character of spores, are no doubt common with the Sphenopsida and attest, at least some, for mutual relations (*see* also BROWNE, 1933). I expressed, therefore, the opinion that we have to do here with representatives of a further pteridophytic phylum hitherto not yet well known or even defined, besides the three hitherto approved phyla, *Lycopsida, Sphenopsida* and *Pteropsida.* As a special group (or class) of this new phylum I designated this assemblage of curious Carboniferous plants by the name of *Noeggerathiineae.*

MORPHOLOGICAL RESEMBLANCES IN SOME DEVONIAN PLANT TYPES

At first sight it is doubtless that all the members of the Carboniferous *Noeggerathiineae* are considerably transformed by some secondary adaptations for special life conditions. Their twigs are in all these genera very strongly altered by plagiotropic orientation, by which they attain a fern-like or cycadeoid appearance. Also the position of their sporangia on the adaxial side of the sporophylls must be regarded as of secondary character, derived from a terminal one. In an unaltered type of that kind we have certainly to expect radially symmetrical leafy twigs of unlimited growth and sporangia terminal on some telomoid sporophyll laciniae (e.g. like in the Sphenophylla or some other articulatinean plants). For such plant types we have no doubt to look for in the Siluro-Devonian or Lower Carboniferous floras. One of the best examples of plants of that kind is no doubt the middle Devonian *Barrandeina.* Some species of the Devonian genus *Hyenia* stand also very near to such theoretical conception, but here several morphogenetical tendencies, e.g. the more or less pronounced shifting of the leaflets into a whorled position show already incontestable relations to the most primitive Sphenopsida. Similar features are exhibited also by the genus *Duisbergia,* which by the presence of only one sporangium per sporophyll reminds to some extent the lycopodiaceous type. Very near to such type stands also the Upper Devonian genus *Cladoxylon* with its small, nearly *Sphenophyllum* or *Hyenia*-like leaflets, spirally arranged on bifid and unarticulated branches, and wedge-like deeply incised sporophylls, arranged into loose spikes and bearing terminally at the tops of their laciniate single sporangium. They exhibit only by the plagiotropic arrangement of whole branch systems, which is also evident in the anatomical structure of their vascular strands, a slight resemblance with the ferns, like our Carboniferous Noeggerathiae or Palaeopteridia.

In all these very archaic plants, relations as to fundamental morphological features to

the Carboniferous *Noeggerathiineae* are well manifested. But at the same time we also see here rather clear relations with the Sphenopsida. Several rare similarities with the *Lycopsida* or *Pteropsida*, e.g. one-sporangiate sporophylls in *Duisbergia*, plagiotropic arrangement of the whole branch systems in Cladoxyla, seem to be only mere morphogenetical convergences. Of utterly different kinds are the morphogenetic relations of such archaic Silurian-Devonian plants like the genera *Protopteridium*, *Barinophyton*, *Pectinophyton*, *Aneurophyton*. These genera also show unarticulated type of branches, the plagiotropic orientation of rather large branch systems is realized here equally well as in the Cladoxyla, but small fertile synteloms are not arranged here on special straight axes like some special sporophylls in some cone or spike-like fructifications, but are included within the large plagiotropic branch systems like some telomoid branchlets or pinnae within large leaf fronds. Here the fern-like features are evidently prevailing, wherefore such archaic types must be, and indeed even by most of the botanists are regarded as, the most primitive representatives of the ferns.

We see thus very clearly that between the group of our *Noeggerathiineae* and the normal ferns there is a fundamental morphogenetic difference, but that on the other hand the relations of this group to the phylum of the Sphenopsida are of very important nature.

ESTABLISHMENT OF THE NEW PTERIDOPHYTIC PHYLUM *PSYGMOPHYLLOPSIDA* AND ITS TAXONOMIC RELATIONS

Just these and similar considerations led me in 1950 to the creation of a new taxonomic term, that of Psygmophyllineae, just for the phylum including all plant types agreeing in all fundamental morphological features with the presumed ancestors of the Carboniferous *Noeggerathiineae* as well as all of its direct pteridophytic descendants, the *Noeggerathiineae* including. According to our present nomenclatorial rules we have now to assign this phylum by the name of *Psygmophyllopsida*.

From the geological point of view, this pteridophytic phylum is no doubt a very old one. We have to include herein several Devonian types, the taxonomical position of which were hitherto rather uncertain, like the genera *Barrandeina* Pot. et Bern., *Duisbergia* Kr. et W., *Jenisseiphyton* Anan., *Haspia* Kr. et W. Accordingly, as plant types only slightly altered by secondary adaptations, i.e. as direct descendants, we have to regard the groups of *Cladoxilineae* and *Noeggerathiineae* which in many textbooks are regarded often as ferns.

As evident in the case of the Devonian genus *Hyenia* Nath. we have to assume that in this archaic phylum the Sphenopsida took their origin, by shifting down of the leaflets into definite whorls and by a simultaneous articulation of the stems. Whether the Lycopsida are to be regarded as reduced descendants (with special type of leaflets, number of sporangia reduced up to one, special position of the sporangia) of this phylum too, is not at present clear; there is at present no certainty as to the morphogenetical nature of the lycopodiaceous leaves and sporangia. Several new discoveries in the Siberian Cambrian, e.g. *Aldanophyton* Kryst., seem to attest an enormously high age of this phylum and consequently the possibility of a special independent origin.

Among living plants all the fundamental features characterizing the phylum Psygmophyllopsida are to be found in the small pteridophytic family of the Psilotaceae, the taxonomical position of which always caused considerable difficulties to the botanists. On account of their small uninerved leaflets and unarticulated twigs they have been mostly regarded as a curious evolutionary side line of the Lycopsida. Recently on account of several very primitive features such as rather primitive vascular strands, no roots, etc., they are also often regarded as more or less direct descendants of the Silurian-Devonian Psilopsida. I regard them too as direct descendants of our phylum Psygmophyllopsida, and that as a special reduced type on account of its saprophytic or epiphytic kind of life, which at the same time kept several original very primitive features, e.g. primordial rhizomes instead of roots. This small plant group agrees with the other Psygmophyllopsida in having the same morphogenetic type of leaves (even dichotomously divided sporophylls), spirally arranged on unarticulated stems and plurisporangiate sporophylls, bearing the sporangia on their adaxial side. Their short linear and incompletely uninerved small leaflets must be regarded as some very reduced

organs. Finally, in the genus *Tmesipteris* Bernh., we may see even a tendency to a special plagiotropic orientation of the whole shoots, not unlike in *Cladoxylineae* or *Noeggerathiineae*. The family of the *Psilotaceae* represents in this light the last, of course rather reduced, remnant of this once very large pteridophytic phylum; it stands in the present flora quite isolated. This isolated position was recently expressed especially by A. L. Tachtadzjan by the creation of the phylum *Tmesopsida* specially for this family.

As to the relations of this new phylum to some more progressive, that is, gymnospermous plants, I pointed out already in a paper (NEMEJC, 1950) that many common fundamental morphological features are to be ascertained in the gymnospermous phyla Cordiatopsida, Ginkgopsida as well as Coniferopsida (incl. the genera *Trichopitys* and *Dicranophyllum*). In the most ancient types we find a similar, wedge-like and dichotomously divided type of leaves, arranged spirally on non-articulated twigs (*Buriadia, Lebachia, Carpentiera, Dicranophyllum, Trichopitys*) as well as nearly all Ginkgopsida as well as syntelomoid, often even fork-like divided sporophylls bearing terminal sporangia (pollen sacs or ovules; *Cordaites, Walchia*) and arranged in some miniature strobili. The group of Pitiae, the pteridophytic character of which is very probable, is perhaps to be regarded as an intermediary type between our ancient *Psygmophyllopsida* and the three mentioned gymnospermous phyla. The group of Pitiae, which from the point of view of the stem anatomy stands very near to some more primitive genera of the Cordaitopsida, represents thus also a direct descendant, a special evolutionary trend of the Psygmophyllopsida, like the Cladoxylineae, Noeggerathiineae or the recent Psilotineae (*Psilotaceae*).

With regard to the very early occurrence (Carboniferous and Permian) of the Cordaitopsida, Ginkgopsida and Coniferopsida as well as to the enormous quantity and variety of the plant types included within these gymnospermous phyla, we have to suppose that a considerably large part of our phylum of the Psygmophyllopsida very soon started on an evolution leading rather quickly to the gymnospermy. Another also very large part, as evident from the foregoing, was no doubt absorbed at the rise of the pteridophytic phylum Sphenopsida (*Articulatineae*). Perhaps it is just because of these two mighty evolutionary events, that indeed unaltered types of the Psygmophyllopsida phylum are rather rare already at the end of the older Palaeozoic (Silurian and Devonian), as compared with the considerably large quantity of types of the other pteridophytic phyla (Lycopsida, Sphenopsida and Pteropsida). I believe that even at future researches we cannot expect that such plant types should ever be discovered in a considerably larger quantity.

CONCLUSION

Summarizing the chief opinions expressed in the foregoing lines we have to state :

1. Besides the three commonly approved pteridophytic phyla (Lycopsida, Sphenopsida and Pteropsida), one more phylum, to which the name of Psygmophyllopsida was given, has been established.

2. The new phylum includes pteridophytic types with spirally arranged microphyllous (of the type of the articulatinean plants) leaves on non-articulated stems, with sporophylls arranged in some spike or cone-like " inflorescences " and with sporangia situated terminally, marginally or on the adaxial side of the sporophylls.

3. Various Silurian-Devonian plants, the taxonomical position of which cause various difficulties like *Barrandeina* Pot. et Bern, *Jenisseiphyton* Anan., *Haspia* Kr. et W., *Duisbergia* Kr. et W. are to be included here in.

4. The fossil plant groups (classes) of Cladoxylineae and Noeggerathiineae, the group of the *Pityae* as well as the recent family of the Psilotaceae (Tachtadzjan's Tmesopsida) represent slightly specialized evolutionary trends arisen directly of that new phylum by means of only less important alterations.

5. The pteridophytic phylum of the Sphenopsida must be regarded as a large evolutionary line related rather nearly with our new phylum (as indicated also by IS. BROWNE, 1933, in the case of *Tingia* Halle).

6. The gymnospermous phyla Cordaitopsida, Ginkgopsida and Coniferopsida (incl. *Trichopitys* and *Dicranophyllum*) are also to be regarded as some major evolutionary trends related with this phylum by mediation of the curious pteridophytic group *Pityae* (and allied types), which itself, as mentioned, must be regarded as a derived psygmophyllopsid type.

REFERENCES

BERTRAND, P. (1947). Les végétaux vasculaires. *Paris.*

BROWNE, Is. (1933). The Noeggerathiae and Tingiae. *The New Phytologist.* **32**(5).

Idem (1935). Some views on the morphology and phylogeny of the leafy vascular sporophyte. *Bot. Rev.* **1**: 383-404, 427-447.

EMBERGER, L. (1944). Les plantes fossiles dans leur rapports avec les végétaux vivantes. *Paris.*

GOTHAN, W. & WEYLAND, H. (1954). Lehrbuch der Paläobotanik. *Berlin.*

HIRMER, M. (1927). Handbuch der Paläobotanik. *Berlin.*

Idem (1941). *Noeggerathia* und neuentdeckte verwandte Formen und ihre Stellung im System der Farne. *Biol. Gen.* **15**: 134.

HIRMER, M. & GUTHÖRL, P. (1940). Die Karbonflora des Saargebietes: Abt. 3. Filicales u. Verwandte, Lief. 1. Noeggerathiineae *Rhacopteris. Palaeontographica.* **B. 9.**

KON'NO, E. (1929). On genera *Tingia* and *Tingiostachya* from the Lower Permian and the Permo-Triassic beds in Northern Korea. *Japanese Jour. Geol. and Geog.* **6**(3, 4).

KRISTOFOVIC, A. N. (1957). Paleobotanika (4th ed.). *Leningrad.*

NEMEJC, F. (1928). A revision of the Carboniferous and Permian Flora of the Coal Districts in Central Bohemia, I. (Introduction, *Noeggerathia* and *Archaeopterides*). *Palaeontographica.* **12**.

Idem (1931). The morphology and systematic relations of the carboniferous Noeggerathiae with regard to the genera *Tingia* and *Plagizamites* of Eastern Asia. *Preslia* (*Journal of the Czechoslovakian Botanical Society*). **9**.

Idem (1950). The natural systematic of plants in the light of the present palaeontological documents. *Acta Mus. Nat. Pragae.* **6B** (3): Praha.

Idem (1937). On *Discinites* K.F. *Bull. Internat. de l'Acad. des Sci.* Praha.

Idem (1942). Weitere Fruktifikationen vom Typus *Discinites* nebst einigen Bemerkungen über die Archaeopteriden der mittelböhmischen Kohlenbecken. *Mitteilungen der Tschechischen Akademie der Wissenschaften.* Praha

Idem (1942). Dalsí príspevky k poznání stredocesky'ch svrchnokarbonsky'ch Noeggerathií a Archaeopteridu. *Rozpravy České Akad. ved.* c. 28. Praha.

SCOTT, D. H. (1920/1923). Studies in Fossil Botany. **1, 2**: *London.*

SETLÍ'K JAR (1956). Contribution a l'étude de *Noeggerathia foliosa* Stbg. *Rozpravy Ústredního ústavu Geol.* **21**: Praha.

SEWARD, A. C. (1898, 1910, 1917, 1919). Fossil Plants. **1, 2, 3, 4**: *Cambridge.*

Idem (1933). Plant Life through the Ages. *Cambridge.*

TACHTADZJAN, A. L. (1956). Vyssie rastenija I. *Moskva-Leningrad.*

VERDOORN, FR. (1938). Manual of Pteridology. *The Hague.*

WALTON, J. (1957). On *Protopitys* (Geoppert): with a Description of a Fertile Specimen "*Protopitys scotica*" sp. nov. from the Calciferous Sandstone Series of Dunbartonshire. *Trans. Roy. Soc. Edinburgh.* **63**(15): Part II.

ZIMMERMANN, W. (1930). Die Phylogenie der Pflanzen. *Jena.*