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Notes on the evolution and taxonomy of the stachyospermic gymnosperms

Introduction

Examining the origin, phylogenetical evolution as well the taxonomy of the Gymnosperms, though most of the representants of this plant group belong at present to the rather remote geological past, we stand on a much safer and more concrete soil than in the case of the Angiosperms. The reason of that is no doubt the fact that this plant group left from its past much more numerous fossils of such kind, which permits not only mere morphological studies of their external appearance but also studies of their finer anatomical structures. After the very numerous palaenotological researches and discoveries of the last 25 years, it would seem at the first sight, that the Gymnosperms represent indeed one of the best recognized plant types as to its origin and evolution. But at a more detailed and thorough analysis of all our present knowledges we must however objectively admit, that by far this is not yet a true reality. Perhaps such problems and relations are much more evident in their phyllospermic branch (i. e. Pteridosperms and Cycads). Contrary in their stachyospermic branch (Cordaits, Ginkgos, Conifers) nearly all such principal relations disappear in the far past of the geological times, just as if we set to examine similar problems concerning the Angiosperms. And just several of these principal tasks concerning the origin and evolution of the stachyospermic branch of the Gymnosperms are subject of the following account.

The stachyospermic branch of the Gymnosperms passed in the course of its evolution no doubt quite analogical stages like the phyllospermic branch, which even as to the stratigraphical occurrence is rather parallel with it. This means, that it produced quite analogical arrangements of certain organs from the morphological as well as anatomical point of view, by which its representants were gradually better and more conveniently adapted to the essential conditions of their terrestrial environments. In other words, we have to trace in the organisation of both these gymnospermic branches a whole series of quite convergent features from the point of view of the adaptation to the life under terrestrial conditions. The essential difference between both these branches consists of the principal architecture of the respective plants, which points also in a certain measure to the phylogenetic origin of both these branches. The representants of the phyllospermic branch are characterised by simple or only sparely branched axis and by leaves of rather very large dimensions and mostly of a form of abundantly and decoratively divided fronds. Contrary in the stachyospermic branch types are prevailing, which exhibit mostly abundantly branched axis and leaves of smaller size, very often simple or fork-like divided, which in many cases are reduced only to linear or needlel-ike, uninerved leaflets. This means that the first of both groups possesses leaves of the macrophyllous type, whereas the second group bears leaves of the microphyllous, resp. sphenopsid type. This fact attests, that both these branches since their utter rise are mutually quite strange, without any true kindred relations. Therefore if we find on both sides, as already told, in the principal features several evident agreements or striking similarities, we cannot speak about results of some mutual relationships, but only about results of a parallel evolution, i. e. about mere convergences.

Innumerable palaeontological discoveries point rather indisputably that the phyllosporous types by their most primitive group of the Pteridosperms are rather clearly related with the Ferns and by the mediation of these last (especially by several representants of their most primitive group of the Profilicineae) also rather clearly with some psilophytoid types of the siluro-devonian floras. Incomparably less clear are these relations within our stachyospermic branch of Gymnosperms. It is no doubt possible to point out even among these types several groups, which as to their general organisation correspond to the group of the Cycads or to that of the Pteridosperms. The first one is represented by the Ginkgopsida, which just as the Cycadopsida are producing seeds preserved by embryos as well as actively mobile ciliate spermatozoids. The second, still more primitive type is represented by the permocarboniferous Cordaitopsida, within the seeds of which till now no embryos were ever found at all, just like in the goup of the Pteridosperms. We may divide therefore our stachyospermic branch quite analogically into 3 gradually more and more suitably or perfectly organised groups like the phyllospermic evolutionary branch, perhaps with the only difference that the stachyospermic (i. e. microphyllous) group never reached a distinctly angiospermic state, though in its last descendents (the group of the Conifers) are produced as male gametes instead of actively mobile spermatozoids mere generative nuclei which are passively transported by way of the pollen-tubes like in the true Angiosperms. Accordingly we have to trace in our stachyospermic branch successively one after other a pteridospermic stage in the form of the Cordaitopsida, occurring during the Permocarboniferous, a cycadoid stage in the form of the Ginkgopsida, which attained the maximum of their distribution during the older Mesozoic (Triassic, Jurassic) and finally an intermediate stage, occupying from the point of view of the organization of its reproductive organs a position between both previous gymnospermic stages and between the Angiosperms, the Conifers, the stratigraphical distribution of which is to be followed up from the end of the Permocarboniferous untill to the present days with a maximum perhaps at the end of the Jurassic and in the Cretaceous. The special peculiarity and nature of this whole series is by that mean very clear and we have therefore if discussing the origin and evolution of the various groups of the Conifers much more advantage than in the case of the Angiosperms. By no means the Angiosperms can be traced back just as directly and with such a facility untill to the series Ferns-Pteridosperms-Cycads as we have indicated it here between the Conifers and the other more primitive stachyospermic Gymnosperms. Some equally direct relations to the series Ferns-Pteridosperms-Cycads may be perhaps more likely supposed in the case of the Gnetopsida. As to the Conifers, we are even able to point out direct morphogenetical relations of the very modified coniferoid leaves and fertile organs to those (less modified or utterly "primitive") of the other members of our stachyospermic series, which in the case of the Angiosperms without speculations is on account of a total lack of palaentological documents inconceivable.

On some morphological and anatomical features of the stachyospermic Gymnosperms important from the point of view of the evolution of this plant group

The leaves of the Conifers as well as of the other stachyospermic Gymnosperms exhibit indeed many features in common with the leaves of the psilotopsid (psigmophyllopsid) and sphenopsid Pteridophyts and that especially with regard to their external shape and morphological arrangement. They represent principally palmately dichotomousely divided organs which on the one side followed an evolutionary tendency to the formation of rather broad and simple plurinerved leaf blades (condensation), on the other side in contrary an evolution with remarkably reductional tendencies leading untill to the formation of simple lineal or needle-like and uninerved leaflets. The first case is realized in the permocarboniferous Cordaits and in the mesozoic Podozamites as well as in the youngest derivatives of the ginkgoalean evolutionary trend. The second aim was achieved especially clearly by the Conifers. This two-sided evolution of the leaves of the stachyospermic Gymnosperms is especially well evident in the fossil records from the ginkgoid and coniferoid groups. Here on both sides among the oldest types forms with dichotomousely divided leaves are well known (among the Conifers especially the genera *Buriadia* Sew.-Sahni, *Carpantieria* Njc. and partly in several species of the genus *Lebachia* Florin). Moreover it seems that the permocarboniferous genera *Dicranophyllum* Gr. Eury and *Trichopitys* Sap. occupy an intermediate position between both just named groups. They will be of great interest for us also from the point of view of their fertile organs. Unfortunately we do not know, whether they were already of a typically gymnospermous character, or still of an only pteridospermous one like the Cordaits.

Especially of great importance at the evaluation of the mutual relations between the various stachyospermic Gymnosperms are morphological deductions derived from a very careful analysis of their fertile cones or "flowers". This was well known to all older taxonomists and morphologists and became especially obvious after the new careful examinations by O. Hagerup and R. Florin. As to the male cones, it was already long ago rather clearly stated by most of the morphologists, that they represent mostly simple cones resp. flowers. But as to the nature of the female cones, many discussions and polemics were carried on for a long time, whether they are to be regarded as simple cones (flowers) or some compound formations (i. e. inflorescences), and eventually in which genera or families they are of the first or of the second named nature. In several Conifers (especially in the family *Pinaceae*) already some teratological monstrosities clearly proved (see J. Velenovský) the compound feature (inflorescence) of their female cones, but in other cases these conditions were for a long time rather obscure (e. g. in the families *Araucariaceae* or *Cupressaceae*) and many botanists favoured in such cases rather the presumption of a simple nature (a cone-like flower). To the solution of this task, which is of a fundamental importance also to the taxonomy of the Conifers and of the other stachyospermic Gymnosperms, the main contributions were brought during the last years in many palaeobotanical studies by R. Florin as well as in several ontogenetical works by O. Hagerup. In the light of these discoveries, the female cones nearly in all Conifers and also in several allied groups (e. g. in the Podozamites) appeared as compound bodies (inflorescences). But simultaneously even several different theories were expressed, which compared such cones with various rather complicated fertile cones of several Pteridophyta, especially with those of the genus *Sphenophyllum*; the evident compound nature of many coniferous female cones (e. g. in the family of *Pinaceae*) was then explained (e. g. M. Hirmer) by various serial and collateral splittings of the originally simple sporophylls. But till present no palaeobotanical evidences have ever confirmed such speculations. Most of the coniferous female cones are therefore to be regarded as variously reduced and transformed inflorescences.

At present we know already an immense number of various types of coniferous female cones showing the most manifold kinds of reductions of their fertile elements as well as fusions of such variously reduced fertile elements with the supporting cone scales or bracts. Their morphological features became now clear in most of the fossil as well as living types. Of course it is but rather probable, that the point of view of various botanists as to the evaluation of such reductional stages for the phylogenetical or taxonomical researches will not be always equal. The degree of probality or veracity of our deductions of that kind will certainly depend also of a simultaneous and harmonious evaluation of a whole series of other fundamental peculiarities, like the form of the male flowers, the shape of the leaves, anatomy of the wood a. o.

The most original or primitive female cones, i. e. least of all attacked by reductions and fusions, within the group of the Conifers, which are at present the chief representants of the stachyospermic Gymnosperms, were stated in the permocarboniferous Walchiae, especially in the genera *Lebachia* and *Ernestiodendron*. We have to do here with rather large cones, in which in the axils of each bract is sitting one very small lateral shoot bearing either only stalk like (telomoid) uniovulate sporophylls, or simultaneously stalk like sporophylls and several sterile narrow lanceolate scales. In several species these axillary evidently strongly reduced shoots are nearly radially symmetrical, but mostly they are dorsiventrally altered, with scales more or less displaced in a plane parallel with the supporting bract. In several geologically slightly younger genera (Permian, Triassic), like *Pseudovoltzia*, *Voltzia*, *Glyptolepis*, *Voltziopsis*, *Swedenborgia*, it is possible to observe how the small sterile scales of the dwarf shoots are fusing together, which is accompanied by a strong reduction of the dwarf shoot axis as well as of the telomoid stalks of the ovules, which then slowly become sessil (adaxially) at the base of the fused complex of the sterile scales. The fertile axillary dwarf shoots were transformed by that way into more or less lobed simple ovuliferous scales (at present realized in several genera of the family *Taxodiaceae*), which at the base bears a larger number of ovules. In a considerable number of Conifers by a further reduction scales with entirely whole margins were achieved (e. g. already in the permocarboniferous *Ullmannia*, in the family of *Pinaceae*). In various types further reductional processi led to a successive fusion of such ovuliferous scales with the respective supporting bracts (e. g. *Taxodiaceae*, *Araucariaceae*). Their last remnants appear then as the well known ligules (e. g. in the *Araucariaceae*, *Cheirolepidaceae*), or they contribute to the formation of the fleshy epimatia or arilli (*Podocarpaceae*), or they disappear even utterly being either totally fused with the supporting bracts or aborted (*Cupressaceae*, *Cephalotaxaceae*). There are known also cases, where in such lateral dwarf shoots never any sterile scales existed at all or where such scales on account of reductional processi very soon disappeared. More progressive types of that kind bear therefore no ovuliferous scales or these appear very irregularly. After reduction or even fusion of such dwarf shoots with the supporting bracts types result the cones of which seem to represent simple cones (cone like flowers). The first case, where the dwarf shoots perhaps never contained any sterile scales and where they were fused with the supporting bracts, is realized in the mesozoic *Stachyotaxaceae* (*Palyssia*, *Stachyotaxus*). The type, the dwarf shoots of which due to the reductional processi left only very irregularly small remainders of the ovuliferous scales and where no fusion of the dwarf shoots with the supporting bracts were accomplished, is realized in the family *Cephalotaxaceae*.

Paralelly with these reductional processi affecting the axis and the sterile leaflets of the fertile dwarf shoots proceeded also by its own way the reduction of the number of the ovules to 2 (e. g. *Pinaceae*, *Cheiropelidaceae*) or even only 1 (*Ullmanniaceae*, *Araucariaceae*).

Beside these interesting reductional processi we have to observe in certain Conifers also realization of certain features, which may be termed best perhaps as angiospermid characters. As such especially concealing of the ovules from direct influences of the whole environment is to be pointed out. It was achieved in several families by different ways: by plunging of the ovules into the tissue of the fused scales (*Araucaria*), by forming of special pockets of fleshy tissue of the ovuliferous scales concealing all respective ovules (in the mesozoic family *Cheirolepidaceae*), or finally by forming of some drupe or berry like fruits of the whole rather reduced cones the bracts of which became rather fleshy and partly mutually fused (*Juniperus*). As an incomplete or imperfect kind of such phenomena the various types of arilli or receptacula of the families *Taxaceae* and *Podocarpaceae* may be regarded.

Another feature, which at the comparative studies of various coniferous female cones seems to be also of great importance, is their size depending of the number of the dwarf shoots crowded together on the cone axis i. e. on a more or less reduced and modified fertile branch. In several families it is evident, that originally very large cones underwent during long geological times a considerable reduction, the number of their dwarf shoots was strongly restricted and the cone axis strikingly shortened (see especially in the families of *Taxodiaceae* and *Cupressaceae*). On the other hand it is but very probable, that in several cases the cones were just at their origin very poor in dwarf shoots, which by the following reductional processi became still more emphasized. Perhaps most representants of the family *Podocarpaceae* belong to such a type. An utterly extreme case of that kind according to all at present known data is represented by the family *Taxaceae*, which therefore is regarded by R. Florin as a special independent order *(Taxales)* aside from all other Conifers (Florin's order *Coniferales*). Here as already stated by J. Velenovský, the small uniovulate female flowers are in fact simple cone like flowers (no inflorescences). Florin's studies on fossil material showed, that such conditions existed already in very old representants of this group, e. g. in the jurassic *Taxus jurassica* Flor. or in the triassic *Palaeotaxus rediviva* Nath. Florin justly regards these flowers as some miniature uniovular strongly reduced simple lateral fertile shoots, quite homological to the dwarf shoots of the female cones of the other Conifers. But contrary to all other Conifers he ascribes here to the ovules an axial origin with regard to their terminal position. But I think that there is still another explanation possible, which with regard to all hitherto known stachyospermic Gymnosperms seems to me much more probable. I believe that the origin of the ovules in the *Taxaceae* cannot be specifically different from that of the other stachyospermic types. We have to suppose that they were originally also born at the top of some telomoid sporohylls of similar lateral shoots. But these shoots never were crowded into any special inflorescenses, they kept their independence and by that way also their radial symmetry. Further reductions led to the shifting of the only one remaining ovule into its present terminal position, where also its radial symmetry was well preserved. The last phenomenon, i. e. the preservation of a radial symmetry of organs, which in the course of the evolution became terminal in position, is in the plant kingdom rather frequent; even whole flowers of many Angiosperms normally of zygomorphous shape, if situated terminally at the top of an inflorescence, acquire a radial construction (peloric flowers). The main feature by which the female fructifications of the *Taxaceae* differ from the other Conifers, consists therefore only in the fact that the lateral fertile shoots, due to their independence, kept their radial symmetry, and that before their reduction leading to the formation of the small bud-like uniovular flowers they never were crowded into any cone-like inflorescences. Till afterwards in their final state, they were eventually approached loosely in a small number on certain twigs (e. g. *Torreya*, also in *Taxus*), but always without forming any specialized cone-like inflorescences.

In the mesozoic Podozamites conditions very similar to those of the Conifers were stated: at the base of the large leafy supporting bracts two ovules are sitting, which in many cases are provided by two small scales (i. e. 2 unfused ovuliferous scales). We have to do here therefore just as in the most of the Conifers with a cone-like inflorescence (*Cycadocarpidium*).

The conditions in the Ginkgoales, at least in the group of forms related to the recent *Ginkgo*, are also well known. The single female stalk like flowers provided at the end with 2 (or even more) ovules represent single lateral fertile shoots homologous to the dwarf shoots of the coniferous cones, where the axis was strongly reduced and the telomoid ovuliferous sporophyll stalks were fused (in teratological cases sometimes partly free). The male flowers are here of a catkin like shape, the axis of which is constructed of fused basal parts of the single telomoid sporophylls (stamens); they represent quite similar lateral fertile shoots, the original axis of which was suppressed by reductions. Just as in the coniferous family *Taxaceae* no cone like inflorescences were created here.

Entirely the reverse is to be seen in the permocarboniferous Cordaits. The female as well as the male fructificating organs are represented by some loose spike-like inflorescences, bearing on rather thin axis linear supporting bracts. In the axils of these bracts we find the single radially symmetrical and in different degree reduced lateral fertile shoots provided by several sterile scales and fertile telomoid sporophylls (stamens or ovuliferous stalks).

A key position as to the explanation of the morphological nature of all these flowers or inflorescences of the stachyospermic Gymnosperms is at present mostly and certainly with full right ascribed to two permocarboniferous unfortunately not perfectly known types: to the genera *Trichopitys* and *Dicranophyllum*. Mostly they are regarded as representants of some very archaic Ginkgopsida. Better are known only their female fertile orgas, but even here we do not know at present whether these are already of a typical gymnospermic character or whether we have to do still with some pteridospermous types like in the group of the Cordaits.

In the genus of Trichopitys, which from the point of view of the very curious type of sterile leaves (more times fork-like divided organs with unflattened nearly cylindrical linear liciniae) seems to represent a very archaic type, the fertile ovuliferous organs represent some lateral branched shoots sitting in the axils of leaves on normal twigs; their telomoid branchlets are terminally provided by one ovule. They are quite similar to the fertile dwarf shoots of such *Lebachia* or *Ernestiodendron* species, where no sterile scales are developed, they are only much larger in size. It is very probable (and this is also the opinion of most of the palaeobotanists of today) that these fertile *Trichopitys* axillary organs kept their original archaic psilophytalean telomoid shape, i. e. that in the far past they never assumed the form of leafy twigs. Such conditions are in good agreement with those in various stachyosporic Pteridophyta. Here too sterile leaflets and fertile organs (sporophylls or sporangiophores) evolved each by their own way of some lateral telomoid branch systems; the formation of leaflets or of various sterile protecting lobes or scales within the fertile organs must be then explained by a successive sterilization and foliarization of originally fertile telomoid branchlets (R. Florin explains by that way also the origin of the integuments of the ovules). Comparing the ovuliferous lateral branched telomoid short twigs of *Trichopitys* with the fertile dwarf shoots of the Cordiats or of the various archaic Conifers, we come quite unconstrained to the conclusion, that the fertile dwar shoots of the cordaitean or coniferous fructificating organs (flowers or inflorescences) in the far past never had the shape of normal leafy twigs (just as the cones of the sphenopsid or psilotopsid [psygmophyllopsid] Pteridophyta) and that therefore also the origin of the sterile scales in the fertile dwarf shoots of these plant types cannot be explained by reduction of some originally normal leaves but in contrary by sterilization and foliarization of originally fertile (ovuliferous) telomoid branchlets. These last represent thus true stegophylls in the sense of the "new morphology" of Thomas or Lam. The formation of sterile leaves and the formation of sterile scales in the fertile dwarf shoots represent thus two independent and with respect to the date of their origination never synchronous, but morphogenetically quite parallel and homologous processi.

In the genus *Dicranophyllum*, which has normal flattened and fork-like divided leaves, female fructifications are better known than the male ones. Female fructificating branches are rather similar to sterile specimens. They bear spirally disposed leaves, which are slightly shorter than the leaves of sterile branches and which in their basal undivided portion are provided by a series of ovules along the midrib. These conditions are quite analogical to those of the cone scales in the mesozoic genera of *Stachyotaxus* and *Palissya*. I suppose therefore that, just as in both these mesozoic genera, also here in *Dicranophyllum* we have full right to explain these ovuliferous leaves by a fusion of some axillary fertile branches of the type known in the genus *Trichopitys* with the bases of the supporting leaves. R. Zeiller described here also some male fructifications (in *D. robustum* Zeil.). They represent some small cones similar in a certain measure to the male cones of the genus *Taxus*. The state of preservation of Zeiller's specimens is unfortunately very indistinct. The mentioned conelets are situated in the axils of normal leaves, by which (just as by their general shape) they point to some relations to the true Conifers. The Dicranophylla on the basis of all these principal features are manifesting themselves as derived directly from the type of *Trichopitys.*

Along with the morphogenetical changes of the leaves and fructification organs also various changes of the anatomical structure of the stems proceeded successively. Principally all hitherto known stachyospermic Gymnosperms are provided with an eustelic vascular system (collateral vascular bundles). Changes, which are to be observed within this system up from the Palaezoic untill to the Kainozoic period, refer in the first range to the successive straitening of the pith space as well as to the replacement of the old archaic ,,araucarioid'' type of tracheids (with densely crowded bordered pits) by a modern "abietinean" one (with loosely arranged bordered pits). This evolutionary events, just as all others, proceeded not equally fast in various evolutionary lines; some of them maintained the archaic structures very long, several ones untill to the present days (*Araucariaceae*). Very voluminous pith and at the same time araucarioid type of pitting are commonly spread among the palaeozoic Cordaits and several related still more primitive types (*Pityae*). "Araucarioid" pitting combined also with rather wide pith is known also in all palaeozoic Conifers of the families *Walchiaceae* and *Ullmanniaceae*; we find it also in the permotriassic family *Voltziaceae.* During later times still further complications especially as to the wood structure are to be observed (arrangement of the medullary rays, formation of resin reservoirs or canals). During the older Mesozoic many wood casts appear, which show the most diverse combinations of various archaic and more modern features as to the anatomy.

The older history of the vascular system of the stems is here but rather uncompletely known. We know nothing about the anatomy of the carboniferous genera of *Trichopitys* and *Dicranophyllum.* As to the Ginkgopsida we are informed only about the stem anatomy of the last member of this whole series, i. e. of the recent *Ginkgo.* Similarly we have till now no data about the stem anatomy of the mesozoic *Podozamites.* As to the Conifers, the oldest data refer to the permocarboniferous *Walchiaceae.* But this family seems to be already a very advanced type. It exhibits a very large woody cylinder and a rather thin cortex. There is still a rather large pith, but the formation of centripetal metaxylem is already utterly suppressed. Considerably much more archaic types of stem anatomy are known only in the group of Cordaits, which of course also from the point of view of various morphological features represent a much more primitive stage among the hitherto known stachyospermic Gymnosperms, i. e. a pteridospermic one. Their most progressive family, the *Cordaitaceae,* in this respect represents an equivalent stage with the coniferous *Walchiaceae* in having a rather voluminous pith, pycnoxylic wood without centripetal metaxylem and tracheids exhibiting an araucarioid pitting. Similar wood and pith is also in the family of *Mesoxylaceae.* But this family exhibits still the centripetal metaxylem. Still more archaic conditions are realized in the family *Poroxylaceae*: voluminous pith, centripetal metaxylem and wood of manoxylic character, like in the most palaeozoic Pteridosperms. Thus this last family exhibits the most archaic stem anatomy among all hitherto known stachyospermic Gymnosperms. Very similar anatomical conditions are known also in the so called *Pityae* and *Calamopityae* of which we know mostly only petrified stem casts, but not the shape of the leaves and fructificating organs. On account of the stem anatomy they are often regarded as gymnospermous plants or at least as some Pteridosperms. But most of these types come from still older strata than the Cordaitopsida, mostly from the Devonian or the transition beds between the Upper Devonian and Lower Carboniferous, where from no true seeds are yet known. It is therefore not quite improbable, that just among such types (*Pityae*, *Calamopityae*) are at least several ones, which represent pteridophytic ancestors of the whole stachyospermic gymnospermous evolutionary line.

The probable origin of the stachyospermic Gymnosperms

All the just discussed morphological as well as anatomical pecularities, which were stated in the various groups of the fossil as well as recent types of the stachyospermic Gymnosperms, lead us to the conclusion, that we have to look for the origin of this plant type somewhere in the neighbourhood of such pteridophytic plants, which had axis provided in a spiral arrangement by sphenopsid leaves, in which the assimilating leaves and the sporophylls underwent a mutually independent morphogenetic evolution and finally where the evolution of the stelar conditions of the stems tended towards a typical eustely i. e. to a cylindrical system of vascular bundles arranged in a ring. This means that we have to look for it in a special evolutionary line of the pteridophytic *Psygmophyllopsida**) (*Psygmophyllineae*, *Psilotopsida* or *Tmesopsida*). But just here the history of this whole stachyospermic plant group begins to disappear in the darkness of the far past. Till present we have absolutely no knowledge of the external shape of plants represented by the stem casts known as Pityae or Calamopytiae, within which ancestors of the Cordaits are so often presumed. We have also no direct palaeontological evidences as to the shape of the organs which in the course of the evolution preceded true leaves and the small fertile shoots of the Cordaits, Dicranophylla, Trichopitys and of the *Wachlchiae.* Only with a slight probability we have to suppose, that they might exhibit some similarities with the respective organs of several primitive devonian psygmophyllous Pteridophyta like *Barrandeina*, *Duisburgia*, *Cladoxylon* a. o., which all are but perhaps of plectostelic nature. Finally we are hitherto utterly in want of any fossils, which would exhibit some still more primitive structures than the mentioned Pityae and which at the same time would belong to the evolutionary line Pityae-Cordaitinae resp. Pityae-Ginkgoinae and Coniferinae. We stand here before a similar very difficult question as in the case of the origin of the Angiosperms. With regard to the curious still slightly telomoid character of the leaves and of the fertile shoots of the premocarboniferous *Trichopitys*, I believe that the ancestors of the whole stachyospermic gymnospermous group evolved from some very primitive forms at the passage from the psilophytoid stage to the psygmophylloid (psilotoid or tmesopsid) pteridophytic one, but not from any already well defined psygmophylloid types of the devonian or older carboniferous era. The Sphenopsida (i. e. Articulatineae) represent a parallel partly eustelic and partly actinostelic line, with special tendencies to a whorl like arrangement of leaves. Genera, like *Barrandeina*, *Duisburgia*, *Cladoxylon* a. o. are then representants of an actinostelic counterpart line just to our unknown psygmophylloid ancestors of the stachyospermic Gymnosperms.

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*) With a morphogenetic splitting into two from the point of view of the stem anatomy principally different evolutionary lines, one tending to actinostely (resp. plectostely), the other to the eustely, we meet in all main taxonomical divisions of the Pteridophyta.

The evolutionary lines and the taxonomy of the stachyospermic Gymnosperms

As to the ecological point of view, we may among the stachyospermic Gymnosperms distingnish at one side several groups, which in general had rather high claims of humidity; we meet their remains very often in large quantity directly in the coal seams or in coaly shales. The main part of the carboniferous Cordaits or of the mesozoic Podozamites may be named as typical examples. At the other side evidently much more numerous are types of rather mesophytic chracter or even such with humble claims of humidity, like a great part of Ginkgopsida and of Coniferopsida. Also here the distribution of fossil remains offered already a large number of evidences and several more hygrophylous types of these groups are rather to be regarded as secondary adaptations. In full agreement with these conditions is before all the shape of the leaves of the respective types: rather broad leaves prevailing among the Cordaits and Podozamites (partly also among the Ginkgopsids), on the contrary a striking tendency to the formation of leaves divided into rather narrow laciniae or of quite simple lineal (or needle like) uninerved leaves in the groups of Ginkgopsida and Conifers. No doubt dryer or more arid terrestrial conditions played a principal part at all the successive reductional events which are to be observed here in the female flowers or cone like inflorescences especially in the Conifers, and which in several extreme cases led finally to the elaboration of the mentioned nearly angiospermid structures (*Cheirolepidaceae*, *Araucaria*, *Juniperus*). Conditions stimulating the whole evolution of the stachyospermic Gymnosperms, especially of the Conifers, were thus the same which were acting at the evolution of the Angiosperms. A very conspicuous difference exists here in the fact that the most progressive evolutionary line of this large group, the Conifers, never attained a typical angiospermy. This certainly depends of a much more restricted general plasticity of all representants of the stachyospermic gymnospermous plants, which (compared with the conditions in the angiospermous evolutionary lines) is especially evident in a complete lack of any herbaceous types in this whole group. Perhaps just in these events are hidden also the principal causes of a more rapid specialization but at the same time also of a more rapid extinguishing of the various stachyospermic groups, compared with the corresponding phyllospermic groups (e. g. Cordaitopsida and Pteridospermae, Ginkgopsida and Cycadineae).

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All facts as well as various circumstances mentioned in the previous lines indicate that only a very harmonious and critical examination of the progressivity of the various organs in different fossil as well as recent representants of the stachyospermic gymnospermous group affords a successful limitation and definition of the single evolutionary lines, which during the past were successively splitted off from the common ancestral stock of this large group or of its main evolutionary branches. Every overestimation of only one quality (e. g. the anatomy of wood, the organization of female flowers a. o.) without respecting the whole complex of all other features inevitably must lead us to some rather one-sided, partial or even more or less erroneous, deceptive conclusions.

We have already stated that the ancestral type of all stachyospermic Gymnosperms exhibited most probably branched axis provided by dichotomously divided sphenopsid leaves and axial fertile more or less telomoid shoots, which during the later evolutionary processi were transformed into simple small (mostly cone like) flowers or owing to some more extensive reductions became as small axillary dwarf shoots the main components of complicated cone like inflorescences. To this conception does not correspond the group of the Cordaitopsida, though this palaeozoic group represent evidently the most primitive evolutionary stage hitherto discovered within the whole series of stachyospermic Gymnosperms; they have already too strongly altered leaves and their fertile branches are reduced to spike-like inflorescences. Much nearer to our conception of the ancestral stachyospermic gymnospermous type no doubt stands the carboniferous genera *Trichopitys* and *Dicranophyllum*, which as mentioned are often regarded as the most archaic types of the Ginkgopsida; but as evident from the foregoing, they might be regarded by the same right as an utterly primitive type of the Conifers. Their occurrence at the end of the Carboniferous is of a clearly relic character. Especially the genus *Trichopitys* is a very rare type. Obviously they are the last remainders of a very archaic old plant group, which in the far past gave rise not only to the Ginkgopsida and to the Conifers but most probably also to the Cordaits. The Cordaits represent than a special evolutionary side line exhibiting very harmoniously and simultaneously proceeding condensation and reduction tendencies in all main organs (leaves, male as well as female inflorescences). Contrary various fossil as well as recent types of Ginkgopsida, Podozamites as well as of Conifers show that in these groups the various reduction and condensation processi were not manifested by such a harmoniously parallel way; several of their organs were usually retarded in their morphogenetic evolution behind the other ones.

As we have already indicated, in the Cordaits the leaves tended to the formation of large, mostly broad elongated whole blades, the male as well as female organs to the formation of principally equal spike like inflorescences. In the Dicranophylla the shape of the leaves remained principally unchanged (dichotomously divided), the male axillary shoots (according Zeiller's discoveries) were altered into small axillary simple cone like flowers, but the female organs remained principally unchanged, they were only fused longitudinally with the basal undivided part of the supporting leaves. In the Gingkopsida a rather slight tendency to the formation of broad leaf blades is to be remarked, especially at the end of their evolution (*Gingko*). Besides there is an evident tendency to the formation of brachyblasts which are rather big in forms related with the recent genus *Gingko* (*Bayera*, *Ginkgoites*), very small (and falling off together with the leaves) in the mesozoic genus *Czekanowskia* and several related forms (*Sphenobayera*, *Hartzia*, *Windwardia*, *Arctobayera* a. o.). In the first series of forms (*Ginkgo*-series) the fertile axillary shoots (situated in the brachyblasts) have lost by reductional processi their main axis and were altered by fusion of their telomoid fertile branchelets into the well known simple catkin like male flowers or stalk like female flowers. In the second series of forms (*Czekanowskia*-series) loose cone or raceme like complicated inflorescences were discovered (the morphology of which is not yet well elucidated). Still another combination of morphogenetic tendencies may be found in the Podozamites and Conifers. The first of both are characterised by large whole leaf blades (not unlike in the Cordaits). In the Conifers very reduced, linear till needle like leaves are prevailing. As to the female fructifications, cone like inflorescences quite homologous with the spike like inflorescences of the Cordaits are prevailing (only in the family Taxaceae no inflorescences were ever built up), which in the course of evolution were strongly altered by various reductional processi. Contrary to the Cordaits, the male flowers (at least in all Conifers; in the Podozamites we are not yet informed about them) are represented here by solitary fertile dwarf shoots cone-like altered. According to the conditions known in some very old Conifers (e. g. the palaeozoic *Walchiae*) it seems, that the reduction of leaves proceeded at a much slower pace than in fertile organs (— leaves and especially the supporting bracts of the cones are here very often still fork like divided, whereas the flower resp. conelike inflorescences are already well established).

Taking into consideration all these facts and respecting also the gradual modifications of the spermatozoids and seeds, we have to sketch the main evolutionary lines of the stachyospermic Gymnosperms in the following way (fig. 1.).

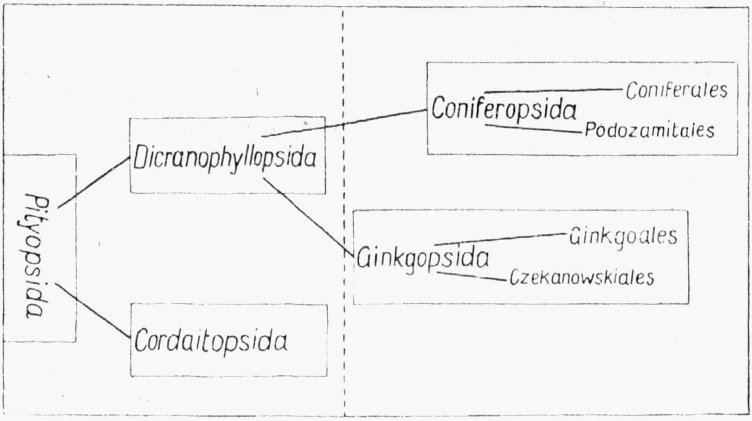

Fig. 1

The evolution within the single stachyospermic main groups

The Cordaitopsida seem to exhibit a relatively considerable uniformity of the principle organization of their male as well female spike-like inflorescences just as of the shape of their leaves. Various evolutionary tendencies are marked here perhaps much clearer in the anatomy of the stems. As evident from various fossil permocarboniferous specimens, the most archaic types (*Poroxylaceae*) had still a manoxylic wood and also the centripetal metaxylem was well developed here. In the more progressive types (*Mesoxylaceae*, *Cordaitaceae* and *Noeggerathiopsidaceae*) the very archaic type of wood was replaced by a pycnoxylic one. Several forms kept still the centripetal metaxylem (*Mesoxylaceae*), but in other ones such structures disappeared utterly (*Cordaitaceae*, *Noeggerathiopsidaceae*). Also the pith underwent some successive changes; in adult stems or branches it became transversaly ruptured, septate (already in several Mesoxyla, in all Cordiats and Noeggerathiopsids). At the end of the evolutionary process (uppermost Carboniferous, Lower Permian) forms were splitted off, which exhibited well marked annual rings (Noeggerathiopsids), evidently owing to the formation of some strongly differenciated moderate climatical zones (Angara and Gondwana). The Noeggerathiopsids may be thus regarded as an arcto- resp. antarcto-carboniferous evolutionary branch of the rather thermophilous Cordaits. Fig. 2 demonstrates schematically this evolutionary splitting proces:

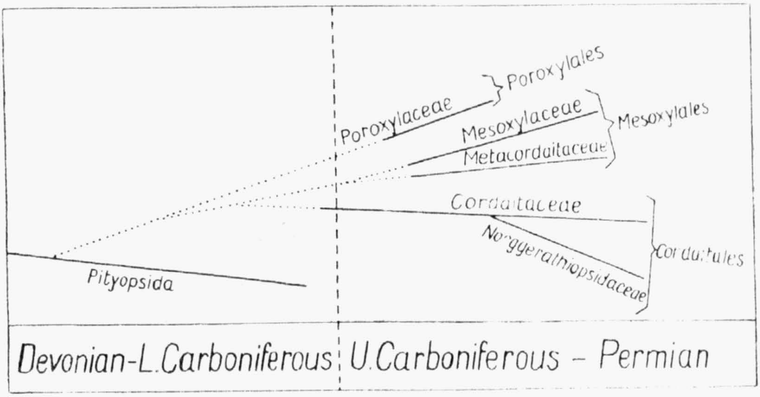

Fig. 2

The palaeozoic group of Dicranophylla is represented only by 2 better known types, the genera *Trichopitys* and *Dicranophyllum*. Both are no doubt representants of two very distinct families. As mentioned, they exhibit relations equally to the Ginkgopsida as well as to the Conifers. An extreme reduction of leaves, like in the Conifers has been achieved here perhaps only in some very rare and till present not yet enough well known forms (e. g. "*Pinites*" *permiensis*). Otherwise all better known species have leaves several times fork-like divided. Nevertheless, as already told, in the genus *Dicranophyllum* the fusion of the axillary female fertile shoots with the respective supporting leaves was realized at a stage, when either the whole fertile branches or their leaves exhibited still a normal unreduced appearence. The male fructifications according to Zeiller's discoveries (in *Dicr. robustum* Zeil.) are of the form of small axillary cones (similar to the male flower of *Taxus*); the respective supporting leaves are of a nearly normal shape. The shape of these male flowers points slightly to some nearer relations to the Conifers rather than to Ginkgopsida. These relations as well as the derivation of Dicranophylla from the *Trichopitys* type are illustrated by the scheme in Fig. 3.

In the group of Ginkgopsida, as mentioned, two distinct types have been discovered. The first one, i. e. the genera relating to the recent *Ginkgo*, stands according to all mentioned facts much nearer to some ancestral *Trichopitys* like forms than the second group containing types allied with the mesozoic *Czekanowskia*. Its flowers consist of the single fertile dwarf shoots altered by reduction and fusion of their telomoid stalks or branchlets and as such are situated separately in the axils of the leaves or scales on the brachyblasts; they retained their original radial symmetry and never were crowded in any specialized inflorescence. Contrary in the extinct *Czekanowskia* and several other allied fossil genera, where the brachyblasts attained a similar strong reduction like in the pine-trees of the present days, fertile organs (at least female organs; male flowers are not yet known with utter certainty) in the form of large ovuliferous scales are arranged loosely on rather slender axis, which remind some large catkin- or raceme like inflorescences (perhaps whole fertile brachyblasts transformed by reductions and eventual organ-fusions in a different manner than the sterile brachyblasts: *Microcheiris*, *Staphidiophora*, *Leptostrobus* [T. Harris 1935, 1951]). This bipartition of the whole ginkgoalean evolutionary line is no doubt of a very ancient date, as the representants of both these series are already well developed in the Triassic and several types of the second, more progressive series, were discovered even in the Permian (*Sphenobayera*). Certainly both these evolutionary series have to be regarded as two well defined orders (Ginkgoales sensu stricto and Czekanowskiales). Their mutual relation as well as their relations to some more ancient types are indicated in Fig. 3.

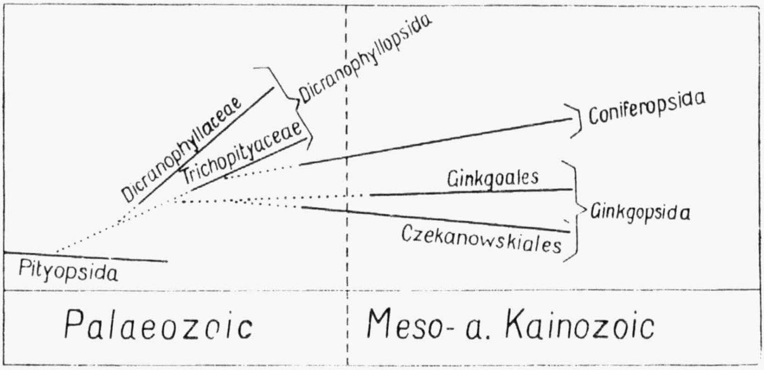

Fig. 3

In the evolution of the Coniferopsida a very strong and nearly general tendency (with the exception of the family *Taxaceae*) to the formation of rather complicated female cone-like inflorescences was attested by numerous studies on fossil as well as recent material. At the other side the morphogenetic development of leaves points to a distinctly biparted evolution: the group of the Podozamites at one side with normal large leaf blades and the Conifers at the other side with leaves tending to a linear till needle like shape.

The morphological as well as anatomical features of the Podozamites group are not yet well elucidated. Their stem anatomy is quite obscure; their epidermis is provided by coniferoid haplocheil stomata. Unsufficiently clear are also their male flowers. Some palaeobotanists (T. Harris 1935) are assigning hereto several rather big loose catkin or raceme like fructifications (*Sphaerostrobus*, *Ixostrobus*) of which we do not yet know, whether they represent only simple flowers, like the male catkins of *Ginkgo*, or whether they are to be regarded as whole inflorescences (the last opinion seems to be more probable). Their rather large female cones (*Cycadocarpidium*) were recognised

(R. Florin) as inflorescences quite homologous with the fertile spikes of the Cordaits; basal parts of their supporting bracts are fused with the base of the axillary fertile shoots of which owing to the reductional processi only two ovules (resp. seeds) and eventually in several species also two sterile scales remained. This whole group seems to be very homogenous. It represents a very conspicuous element nearly of all mesozoic floras and disappears at the end of the Cretaceous. We may regard it as a very archaic evolutionary side line, which was separated most probably very early from the common stock of the Coniferopsida owing to similar morphogenetical tendencies like the Cordaitopsida from the common stock of all stachyospermic Gymnosperms.

The group of the Conifers in a more restricted sense exhibits an unusualy great diversity in the detailed morphological structures of the female cone like inflorescences, in consequence of which it is possible to distinguish here a rather large number of special evolutionary lines.

As to the stem anatomy, the most ancient types (the groups of *Walchiae* and *Voltziae*) are provided still by rather large pith and an archaic ("araucarioid") pitting of the tracheids, which in a high measure in the family *Araucariaceae* persisted untill to day. In other families these features were slowly replaced by more modern structures, the pith cavity was strongly reduced, a rather loose pitting ("abietoid") of the tracheids was established and even some other new structures (resin reservoirs or canals, complications in the medullary rays a. o.) came into existence.

The leaves retained their original dichotomously divided shape only for a rather short era: we find such leaves only in some paleozoic types (*Buriadia*, *Carpentieria*, several species of the genus *Lebachia*). From the Upper Permian up only simple mostly linear, needle-like event. scale-like reduced leaves are to be observed; larger and plurinervous leaves are rather rare (in several species of the families *Araucariaceae* and *Podocarpaceae*).

Male flowers as mentioned correspond to the single fertile axillary dwarf shoots, which retained their radial symmetry and were cone-like altered. Only in a second rate, i. e. probably very late these cone like flowers were crowded in some loose more or less spike like (*Podocarpaceae:* several species of *Podocarpus*) or globular (*Cephalotaxaceae*) inflorescences, but without any stronger reduction of the single flowers.

As to the female fructifications, it was already indicated, that rather complicated cone like inflorescences composed of a rather variable number of the original fertile telomoid dwarf shoots came into existence, whereby the extreme cases are represented by the family *Taxaceae*, in which the dwarf shoots remained solitary and retained, being not crowded in any special inflorescence, the original radial symmetry. As to the morphogenetic development of these cone like inflorescences, we have to observe at least 8 principal events, which in various combinations participated at the elaboration of such coniferoid female cones:

1) Unequal number of the original axillary dwarf shoots on shortened axis, by which already originally very large cones (*Walchiaceae*, *Voltziaceae*, *Ullmanniaceae*, *Araucariaceae*, *Cheirolepidaceae*, *Abietaceae*, *Stachyotaxaceae*, *Sciadopityaceae*, *Taxodiaceae*, *Cupressaceae*) or only small ones (probably most of the *Podocarpaceae* and the *Cephalotaxaceae*) resulted; in extreme cases the dwarf shoots remained solitary (*Taxaceae*).

2) Secondary reduction of the size of the cones resp. of the number of their fertile elements. (*Taxodiaceae, Cupressaceae,* partly also in the *Abietaceae* and *Podocarpaceae*).

3) The plagiotropic, dorsiventral adaptation of the fertile dwarf shoots (excepting the *Taxaceae* nearly in all Conifers; only in several species of the lower permian genus *Ernestiodendron* radial symmetry is still at least partly retained).

4) Sterilization of several originally ovuliferous telomoid sporophylls of the dwarf shoots by which sterile scales came into existence (true stegophylls in the sence of the "new morphology").

5) Reduction of the syntelomoid axis of the axillary shoots and the fusion of its sterile scales (stegophylls) into a simple ovuliferous scale (excepting the palaeozoic *Walchiaceae* and the *Taxaceae* in all other Conifers).

6) Fusion of the dwarf shoots (resp. ovuliferous scales) with the supporting bracts (*Araucariaceae, Cheiroleplidaceae, Taxodiaceae, Cupressaceae, Stachyotaxaceae, Podocarpaceae*) which may be often combined with the reduction of the already elaborated ovuliferous scales.

7) Diminution of the number of the ovules produced by each dwarf shoot (resp. ovuliferous scale) and the stabilization of this number at 2 or even only 1.

8) Formation of various types of protecting arilli, epimatia, pocket like excrescences round the ovules (*Podocarpaceae, Taxaceae, Stachyotaxaceae, Cheirolepidaceae*).

A type, which no doubt relates rather directly to the palaeozoic series *Trichopitys-Dicranophyllum,* is no doubt the family Taxaceae (in the most restricted sense), where both, male as well as female dwarf shoots remained sessile solitary in the axils of normal leaves (resp. scale like reduced leaves). As already told, the number of ovules in every female flower was fixed at 1, which then was pushed into a terminal position and provided by the well known protecting arillus. Only very late such miniature bud-like flowers were arranged in a small number into some loose groups (*Torreya,* partly also *Taxus*) indicating a slight tendency to the formation of a kind of inflorescences, but true specialized cone or raceme like inflorescences were never elaborated here. The whole family is of a very high age, because types provided with female flowers differing by nothing of the recent *Taxus* were discovered already in the Triassic (*Palaeotaxus rediviva* Nath.)

In all other families of the Conifers the original female dwarf shoots were arranged in variousely voluminous cone like inflorescences as definitively and undoubtedly stated by R. Florin and O. Hagerup. But evaluating thoroughly all principal features of their male as well as female organs, it is very difficult to agree with the so often expressed opinion that the ancestral type of all them is to be seen in the permocarboniferous group of the *Walchiae.* In contrary it seems to me much more probable that just this palaeozoic group, which no doubt represents a common ancestral stock of several rather modern types (*Araucariaceae, Abietaceae* (= *Pinaceae*), *Taxodiaceae, Cupressaceae* and *Cheirolepidaceae*) is one of several more or less parallel evolutionary lines (like the *Taxaceae*), into which the ancient *Trichopitys-Dicranophyllum* series was once perhaps rather suddenly split.

I regard as such rather independent evolutionary lines i. e. not directly related to the palaeozoic *Walchiae*-group, especially the families *Podocarpaceae*, *Stachyotaxaceae* and *Cephalotaxaceae*.

The history of the Podocarpaceae is unfortunately very incompletely known. Representants of this group appear still in the older Mesozoic, without offering any kind of indication of at least several qualities of their ancestors. The morphology and anatomy of their female cones indicates, that originally mostly small inflorescences were perhaps prevailing here, which was later still reinforced by reductions (in several species untill to cones containing only 3, 2 or only 1 flower). The reduction of the ovuliferous scale and its fusion with the supporting bract attained in many species a very progressive stage, even the fusion of the vascular traces of both was realised (several species of the genus *Dacrydium*, in the genera *Saxegothea*, *Microcachrys* and *Phaerosphaera*). The very reduced cones were then in many cases arranged secondarily into inflorescences of a still higher rank (especially in the genus *Podocarpus*). The number of ovules in each ovuliferous scale was reduced to only one. In most of the genera fleshy protecting epimatia are developed, which by several botanists is regarded as an indication of some relations to the *Taxaceae*. Interesting is also here a slight tendency to the formation of rather broad leaf blades (especially in the genus *Podocarpus*).

The mesozoic family Stachyotaxaceae (genera *Stachyotaxus* and *Palissya*) is distinguished by fertile dwarf shoots completely fused with the supporting bracts; no sterile scales were ever developed here. From this point of view a strong similarity is to be found here with the palaeozoic *Dicranophylla*, the chief difference being here in the formation of specialised cones, which at the first view look like simple cones with multiovulate scales. The single ovules are provided by similar arilli like in *Taxus*, wherefore many botanists have also here pointed to some possible relations to the *Taxaceae*.

In the family Cephalotaxaceae very specialized male inflorescences (rather small and oval in shape) sessile in the axils of normal leaves were formed, a feature which in the family *Podocarpaceae* is only slightly indicated. Very interesting is here also the structure of the female cones. All analysis hitherto executed (R. Florin, O. Hagerup) showed, that we have to do here with a type, where the development of sterile scales in the original fertile dwarf shoots was rather irregular; often even no such scales were formed (it is also possible that these scales often underwent at the reduction of the dwarf shoots a total abortion). The number of ovules in the small cones mostly do not correspond with the number of the reduced remainders of the ovuliferous scales. No fusion of the reduced dwarf shoots (resp. of the ovuliferous scales) was ever realized here. Evidently the reduction processi led in this family to nearly isolated ovules sitting directly in the axils of the supporting bracts. Unfortunately the history of this family is very poorly known, wherefore we have no idea of its eventual archaic nature.

All the rest of the Conifers, as mentioned, shows incontestable morphological relations to the palaeozoic family *Walchiaceae*. Their female cones points to an origin of rather big cone like inflorescences, very rich in fertile dwarf shoots. The single geologically younger or even recent groups (or families) represent various evolutionary side lines, which are characterized best by different special reductional features concerning chiefly the female cones.

Several of them are even mutually related as some successive evolutionary stages (*Voltziaceae*, *Taxodiaceae* and *Cupressaceae*, *Abietaceae* and *Cheirolepidaceae*, most probably also *Ullmanniaceae* and *Araucariaceae*).

In the Walchiaceae (*Lebachia*, *Ernestiodendron*, *Carpentieria* a. o.), occuring at the end of the Carboniferous and in the Lower Permian, the supporting bracts are mostly of a bifid shape and the fertile axillary dwarf shoots are still well developed, bearing a variable number of ovuliferous telomoid sporophylls (sporangiophors) as well as some sterile scales (stegophylls, which eventually in several species are quite missing). These dwarf shoots exhibits already a clear tendency to plagiotropical adaptation having mostly their scales spread nearly in one plane parallel to the plane of the respective supporting bract.

In the permostriassic family Voltziaceae fusion of the basal parts of the sterile scales of the fertile dwarf shoots into a lobate ovuliferous scale is realized successively in several genera. In the permian Ullmanniaceae is already the whole sterile part of the dwarf shoots fused into a disclike body and the number of the ovules is reduced to only one, which in an inverse position is adnate to the disc-like scale. In both these families the resulting ovuliferous scales are quite free.

In the family Auracariaceae the conditions are very like as in the palaeozoic *Ullmanniaceae*, the number of the ovules being here too reduced till to only one. A further evolutionary progress (compared with *Ullmannia*) consists here in the fusion of the ovuliferous scale with the supporting bract.

In the family Taxodiaceae the conditions are principally rather similar to those of the *Voltziaceae*, the difference being only the successively more and more intimate coalescence of the originally multilobate ovuliferous scale (still visible e. g. in the genus *Cryptomeria*) with the supporting bract. The number of the ovules pro each scale remained unchanged. Similar conditions are to be met also in the family Cupressaceae, where the fusion of the ovuliferous scales with the supporting bracts is so complete, that the resulting bract organ appears as a quite simple cone scale (of course with two kinds of vascular strands, which at the base are also often fused). Further complications were caused here by the verticillate arrangement of the leaves, which is also maintained in the arrangement of the cone bracts; also a strong tendency to the gradual diminution of the cones is here evident. In extreme cases (*Juniperus*) some small drupe- or berry-like fruits were formed. A transition between both these last families (Taxodiaceae and Cupressaceae) may be found in the genera *Sequoiadendron*, *Sequoia*, and *Metasequoia*, the last of which has also whorled leaves. It is then evident that the three families *Voltziaceae*, *Taxodiaceae* and *Cupressaceae* represent a rather successive evolutionary line with three stages, which is also more or less documented by their stratigraphical distribution: the maximum of the occurrence of the *Voltziaceae* falls on Permian and Triassic, that of the *Taxodiaceae* on Jurassic and Cretaceous and finally that of the *Cupressaceae* on younger Cretaceous and Tertiary.

The family Abietaceae (or Pinaceae) in contradiction to the *Taxodiaceae* represent a type, where no fusion of the dwarf shoots (resp. ovuliferous scales) with the bracts was ever achieved, only the number of ovules was diminished (to 2) by the reductional processi. Further progressive changes may be observed in the extinct mesozoic family Cheirolepidaceae, where in different genera a successive fusion of the ovuliferous scales with the bracts is to be observed, and where special protecting pockets of epinatium character were formed round the ovules (2 in each scale like in the *Abietaceae*). Accordingly we have to regard both these families as a parallel line to the foregoing *Taxodiaceae* and *Cupressaceae* having its origin somewhere very near to the permotriassic *Voltziaceae*.

The whole evolution of the Conifers according to all hitherto known facts, as briefely refered, may be then illustrated by the scheme of Fig. 4.

As to the phylogenetical splitting of the common ancestral stock of the Coniferopsida into the single lines leading to the various orders or families also some facts concerning the palaeogeographical distribution of the various types or genera are of rather great importance. We meet a very interesting event just at the very beginning of the emersion of the Conifers in the late palaeozoic (stephano-permian) strata. The various elements of the *Walchia*-group were already at that time not spread throughout the whole world uniformly or quite cosmopolitically. We meet for instance the genera *Lebachia*, *Carpentieria*, *Ernestiodendron*, *Voltzia*, *Ullmannia* a. o. only in the Euramerian zone. But in the Gondwana regions they are totally missing being here replaced by the genera *Buriadia*, *Moranocladus*, *Paranocladus*, *Voltziopsis*, *Walcomiella* a. o. We have therefore to suppose that the rather unquiet climatical conditions of the late Carboniferous restricted the geographical distribution of various rather well fixed and specialized types to certain regions according to the climatical conditions. Accordingly we have but also to suppose that the evolving of the several main evolutionary lines have taken place already before the Stephanian, and it is then not surprising to find already in the Triassic many such types (e. g. the *Taxaceae*) fixed in a form which absolutely by nothing differs from their present shape.

During the mesozoic time, when a considerable appeasement of the rather extreme climatical contrasts was accomplished and when anew a quiet and undisturbed development of the whole flora took place on very large areas of

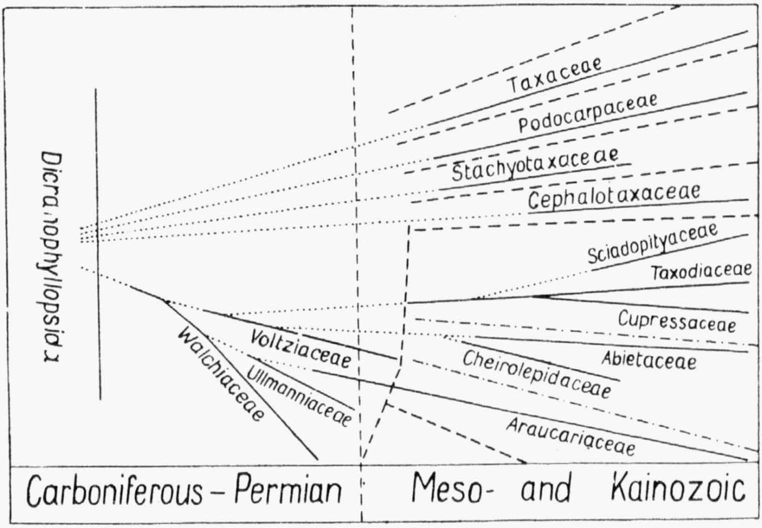

Fig. 4

the world, many later separated types (e. g. *Taxodiaceae*, *Araucariaceae*), were very widely spread on both hemispheres. But the kaenozoic orogenetical as well as climatical disturbances have again, similarly like at the end of the Palaeozoic, straitened these large areas of their geographical distribution, as we can see to day following the present natural habitats of such types. (e. g. *Taxodiaceae* on the northern hemisphere, *Araucariaceae* on the southern hemisphere, *Abietaceae* mostly also on the northern hemisphere; even many genera of the most modern family *Cupressaceae* were confined to certain more or less restricted areas).

These conditions clearly apparent in the geographical distribution of various coniferoid types in the past as well as at the present days correspond rather well with the two or even three main phases, which are indicated in our scheme Fig. 4.

Rough outline of a phylogenetically founded system of the stachyospermic Gymnosperms* (incl. their pteridophytic ancestors)

- I. Class *Pityopsida* (pteridophytic stage)
  - Orders: *Pityales*
    - Families: *Pityaceae*, *Calamopityaceae* a. o.
- II. Class *Cordaitopsida* (pteridospermic stage)
  - Orders: *Poroxylales*
    - Families: *Poroxylaceae*
  - *Mesoxylales*
    - Families: *Metacordaitaceae*, *Mesoxylaceae*
  - *Cordaitales*
    - Families: *Cordaitaceae*, *Noeggerathiopsidaceae*
- III. Class *Dicranophyllopsida* (pteridospermic or already cycadoid stage ?)
  - *Orders: Dicranophyllales*
    - Families: *Trichopityaceae*, *Dicranophyllaceae*
- IV. Class *Ginkgopsida* (cycadoid stage)
  - Orders: *Ginkgoales*
    - Families: *Ginkgoaceae*, *Erethmophyllaceae*
  - *Czekanowskiales*
    - Families: *Sphenobayeraceae (Sphenobayera)*, *Czekanowskiaceae (Czekanowskia, Hartzia)*, *Arctobayeraceae (Arctobayera)*, *Windwardiaceae (Windwardia, Culgoveria)*, *Torelliaceae (Torellia, Pseudotorellia, Stephenophyllum)*
- V. Class *Coniferopsida*
  - Orders: *Podozamitales* (or *Wielandiales* Emb.)
    - Families: *Podozamitaceae*
  - *Coniferales*
    - Suborders: *Taxineae*
      - Families: *Taxaceae*
    - *Podocarpineae*
      - Families: *Podocarpaceae*
    - *Cephalotaxineae*
      - Families: *Cephalotaxaceae*
    - *Stachyotaxineae*
      - Families: *Stachyotaxaceae* (i. e. *Palyssia*, *Stachyotaxus*)

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*) On account of various not yet clearly elucidated problems the fam. *Ephedraceae* is not included in this systematical conspectus.

Abietineae:
Voltzioidae: fam. *Walchiaceae*, *Voltziaceae*, *Ullmanniaceae*
Auracarioidae: fam. *Araucariaceae*
Abietoidae: fam. *Abietaceae* (= *Pinaceae*), *Cheirolepidaceae*
Taxodioideae: fam. *Taxodiaceae*, *Sciadopityaceae*, *Cupressaceae*

F. Němejc:

Poznámky o evoluci a taxonomii stachyospermických nahosemenných

Naše znalosti morfologických a anatomických vlastností tzv. stachyospermických gymnospermů a z nich zejména konifér pokročily během posledního čtvrt století i v oboru palentologie (obzvláště zásluhou švédského badatele R. Florina) tou měrou, že si dnes již můžeme o jejich původu a rozvoji učinit dosti dobrou představu i když některé zcela zásadní otázky z jejich nejstarší fáze vývojové (devon—spodní karbon) nám přece jen zůstávají stále tajemstvím. Ve stati, anglicky sepsané, pokouším se k některým z těchto problémů, které byly poslední dobou vícekráte v literatuře projednávány, zaujmout jakési souborné stanovisko. Vycházím z celé řady morfologických a anatomických znaků, hodnotím jejich progresívnost a přihlížím i k důsledkům plynoucím z geologicko-stratigrafického a paleogeografického výskytu různých vymřelých i dosud žijících typů. Tím získávám obraz o určitých směrech, jimiž se dál vývoj v celé této skupině, tj. dospívám k stále užším taxonomickým jednotkám, ve které se celý tento okruh postupně štěpil a získávám též pojem o geologických fázích, během nichž se pravděpodobně toto štěpení odehrálo. V nejstarší fázi (patrně pozdní devon—sp. karbon) z pravděpodobně ještě pteridofytních Pityopsid se vyštěpily typy cordaitové a dicranophyllové. Typ dicranophyllový (patrně během karbonu) dal dále vznik větvi rostlin ginkgovitých a koniferových, z nichž poslední se velmi záhy (patrně již v pozdním karbonu) rozestoupila ve dva okruhy: Podozamity a vlastní Conifery. Typ tisovitý na rozdíl od běžného dnešního názoru považuji pouze za extrémní stav (nedošlo zde ke združení samičích „sporofylů" a jejich podpůrných braktei v šišky) v postupné řadě typů (podřádů nebo čeledí), ve které se konifery posléze rozčlenily (patrně koncem permu, některé ještě během staršího mesozoika). Na základě takových úvah vyplynula pak i celá soustava stachyospermických gymnospermů, kterou jako výsledek studie uvádím na konci anglického textu.

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