F. NĚMEJC:

PŘIROZENÁ SYSTEMATIKA ROSTLIN VE SVĚTLE DOSAVADNÍCH

PALEONTOLOGICKÝCH DOKLADŮ.

THE NATURAL SYSTEMATIC OF PLANTS IN THE LIGHT OF THE PRESENT

PALAEONTOLOGICAL DOCUMENTS.

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Během posledních 30 let se stále více ukazuje, že přirozená soustava hlavních rostlinných skupin tak, jak jsme ji uvykli začátkem tohoto století ve většině větších kompendií užívati, není s hlediska fylogenetického vývoje rostlin zcela v pořádku. Již z dřívějších dob datuje se na př. nejasnost v systematickém postavení skupiny Psilotineí, přistupují tu různé problémy s ohledem na vzájemný poměr různých skupin gymnospermických a posléze i celá řada neujasněných otázek u angiospermů. Velmi jasně všechny takové otázky se projevují přihlížíme-li k některým nověji objeveným resp. nověji studovaným nálezům rostlin fosilních, jmenovitě z období palaeozoických nebo ranně mesozoických. Tu dokonce jsme často na rozpacích, kam některé z nich vlastně máme v soustavě rostlinné zařaditi; — vzpomínám jen namátkou na př. devonské Aneurophyton, Protopteridium, Barrandeina, Svalbardia, Cladoxylon, Archaeopteris nebo karbonské Rhacopteris, Noeggerathia, Palaeopteridium a j. Právě tady se stále více a jasněji ukazuje, že zejména při studiu palaezoických květen nelze vystačiti s roztříděním pteridophyt pouze na 4 základní skupiny (t. j. Psilophytineae, Lycopodineae, Articulatineae a Filicineae), nýbrž že tu třeba uvažovati ještě o alespoň jedné další skupině, blízké patrně k Articulatineím, mající však lodyžky nečlánkované. To ovšem musí nezbytně mít pak patřičné následky na posouzení fylogenetických vztahů vyšších t. j. gymnospermických ev. i angiospermických rostlinných typů. Vyslovil jsem tuto myšlenku již u příležitosti studia karbonských Noeggerathií; později obíral se jí též R. Kräusel při studiu devonských Barrandein. Tím ovšem nebyly zcela rozřešeny vztahy různých jiných podivných devonských resp. ranně karbonských rostlin (Svalbardia, Archaeopteris, Aneurophyton, Protopteridium, Stauropteris, Rhacopteris a j.).

Takové a jiné nejasnosti vedly mne k hlubším úvahám o vzájemných poměrech dosud známých základních řádů resp. čeledí rostlinných zejména v oboru Pteridophyt a Gymnospermů, kde paleontologická dokumentace jak po stránce morfologické, tak i anatomické jest zatím nejbohatší. Výsledky svých úvah jsem sestavil do následujících statí sepsaných anglicky. Zabývám se v nich v prvé řadě přirozenou systematikou Pteridophyt a Gymnospermů a jen jaksi doplňkem letmo též rostlin nižších; angiospermů, kde obdobná dokumentace zatím jest značně kusá, dotýkám se jen s ohledem na jejich celkové hrubé fylogenetické odvození, aniž se dotýkám vzájemných vztahů jednotlivých jejich řádů a čeledí.

Své úvahy jsem založil v prvé řadě na morfologické povaze sterilních i fertilních lodyžek resp. u výše organisovaných suchozemských rostlin na povaze listů a plodolistů, na vztazích mezi lodyžkami a listy a na změnách, které tyto orgány prokazatelně (t. j. podle skutečně nalezených fosilních zbytků) prodělaly během fylogenetického vývoje v různých příbuzenských řadách. Při tom se velmi často opírám o anatomii os, případně i řapíků listových neb i jiných orgánů, neboť data tohoto druhu nám nejednou dovolují rozeznati, zda máme co činiti s více méně jednotným příbuzenským okruhem resp. vývojovou řadou rostlinnou či s více paralelními řadami jen vnějškem si podobnými (konvergence). Při tom všem nemohl jsem se ubrániti jednomu nadmíru obdivnému úkazu: sledujeme-li totiž nezaujatě fylogenetický vývoj různých takových vývojových linií či příbuzenských řad, neubráníme se dojmu, jako by výchozí organismy byly vždy poměrně velmi členité, vzezření značně rozkladitého, kdežto jejich potomstvo jako by spělo za vytvářením stále hustěji stavěných, jakoby kondensovaných útvarů (zkracování os, vřeten listových, splývání lístků v souvislejší čepele, zkracování stopek fruktifikací a jejich srůstání atd.), což vede často k orgánům v zásadě velmi komplikovaným ač zdánlivě vnějšího vzezření poměrně jednoduchého (list angiospermů, šistice konifer, samčí fruktifikace mnohých pteridospermů a j.) ; snad tu jde o následek ustavičného přizpůsobování rostlin na suchozemské prostředí.

Na konci anglicky sepsaných úvah, v nichž jsem se snažil i o jakési grafické znázornění příbuzenských vztahů jednotlivých skupin, připojil jsem přehled rostlinné soustavy, jak se mi dnes jeví po zevrubném přezkoumání všech dosavadních dat o povaze různých fosilních zbytků (zejména listů, lodyžek, plodních útvarů a p.). Tato úprava přirozené soustavy rostlin liší se v podstatě od dosavadních systémů ve 2 hlavních bodech: 1. Vedle dosavadních čtyř nám běžných skupin pteridophyt zavádím ještě skupinu pátou pod názvem Psygmophyllineae (v podstatě můj dřívější bohužel tehdy příliš úzce definovaný pojem Noeggerathineí), která shrnuje veškeré neartikulované typy pteridophyt se vztahem k articulatineím a případně Lycopodineím (sem řadím právě též zmíněnou spornou skupinu Psilotineí) 2. V oboru gymnospermických rostlin rozlišuji 2 základní řady resp. vývojové okruhy: A. Cycadophyta (obsahující pteridospermy, cycasovité a gnetineie), jež odvozuji od macrofylního typu pteridophyt t. j. v podstatě od typu kapradinovitého, a B. Coniferophyta (obsahující konifery, gingkovité, cordaity, podozamity a p.), jež odvozuji od microfylního typu pteridophyt t. j. v podstatě od Psygmophyllineí (od

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kterých na druhé straně odvozuji pteridophytní řady Lycopodineí a Articulatineí).

Ostatní detaily a patřičná odůvodnění různých dedukcí nalezne laskavý čtenář v následujících anglicky sepsaných statích.

<p style="text-align:center">*</p>

Introduction.

Since the times when the theory of a progressive and gradual evolution of all living beings has been commonly aknowleged and accepted as a leading principle of all biological sciences, the taxonomists and systematists of plants kept on seeing more and more a double aim in the systematic of plants. They endevoured to build up not only a system of the whole plant kingdom, which would enable us to get an easy and clear information about various plant groups resp. plant species for more or less practical uses, but which at the same time would through some light on the mutual true relationship of the various plants i. e. which at the same time would represent a picture of mutually really related plant groups as well as of their genealogy. Generally and mostly also quite justly the degree of this relationship was always seen in the degree of the mutual similarity of various functionally homonymous plant organs i. e. according to the similarities or differences of their morphological features. The whole problem was certainly regarded also quite correctly as much more easy in the case of the higher organised plants, where the whole abundantly differenciated plant body exhibits far more numerous possibilities for speculations, than if we have to do with various rather primitive plant types as e. g. the various primitive algae or even bacteria, which exhibit often only a very restricted number of well observable morphological features. Besides the external shape of the various plant organs, rather serious stress has also always been laid on the inner organization (i. e. anatomical features) of the respective plant organs. Both these criteria the morphological as well as the anatomical one were in the older epoch of the natural systematic and taxonomy of plants the chief basis of all studies. Very soon still a third point of view were added, the study of the young, germinating plants, where students were looking for quite analogical possibilities as if studying in the animal kingdom the various larval stadia reminding so often the ancestors of the respective adult animals. We know well that all conceptions as to the real relationship of plants constructed on the basis of these three cardinal categories of features led nearly always to more or less different conclusions according to the stress laid by various students to various special qualities and according to that, which of them (or even whole organs) have been regarded as primitive or in various degree derived. Just this idea of the primitiveness or derivativeness (simplicty or complexity) of various plant organs became one of the most serious tasks in the natural taxonomy and systematic of plants, though it is undiscutable that just these criteria admit a very large field of subjectivity, because it is not always easy to state with absolute certainty if a special organ is originally primitive or reduced on account of some special environmental conditions. But untill

present already so numerous and laborious studies from the point of view of these three methods (comparative morphology, anatomy and embryology) relating to the natural systematic and taxonomy of plants has been done, that at least the chief lines of this branch of science can be considered as roughly well settled.

During the last time also several physiological and biochemical methods (especially the serodiagnostical ones) helped us to clarify several difficult tasks especially as to the more primitive plant types, where the morphological and anatomical methods are of relatively problematical use (Bacteria a. o.). But without any doubt the most reliable corrective for all our speculations and deductions concerning the natural systematic and taxonomy of plants became during the last century the palaeobotany. All facts stated in these field of scientific researches are able either to attest or modify with utter objectivity many of our speculations deduced by means of the above mentioned ways, or to deny all their validity. To remember at least only one example of the influence of the palaeobotanical researches on our imagination arisen from the study of the plant body of higher plants (Trachaeophyta) on the basis of the comparative morphology and anatomy I would like to point out at least the pericaulom theory or the anaphyton theory. Both these theories became at once only mere fantastical speculations without any concrete basis, when at Rhynie in Scotland several of the most primitive landplants (*Rhynia, Hornea, Asteroxylon*) hitherto quite unknown have been discovered in the devonian quarzitic rocks and published in the famous reports by Kidston. In fact we must aknowledge that palaeobotanical researches have modified already many of our systematical as well as taxonomical conceptions and it is to be expected that this will be also in future the fate of this branch of botanical science, because every more important discovery in the field of the palaeobotany will cause inevitably always a corresponding influence on our imaginations deduced from the study of the respective living plants. We have not to forget, that we due just to palaeobotanical researches the discovery of an immense number of plants already long ago extinct, among which many are completing the various groups of still living forms, other represent more or less clearly the missing links between several still living plant groups.

But nevertheless even at present, though the results of the palaeobotany are already in many respects considerably advanced, there remains a very large field for speculations, especially as to the solution of the mutual relation as well as of the origin of several main groups of the plant kingdom, where we always are in want of the knowledge of true missing links.

As to the palaeobotany, our conceptions of the true relationship as well as of the evolution and origin of various plants and plant groups may be deduced chiefly from two categories of features. To the first category belong the geological and stratigraphical distribution of various plant types, which enables us to get a rough idea of their occurrence within the time space and therefore to recognize at least with a certain measure of probability, which of the found forms have more claim to be considered as an ancestral or eventually only as a derived type. Very

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often, looking backward in the history of plants, we are also able to evaluate, which forms apparently of very primitive features, are really primitive or only secondarily reduced by means of adaptation to various special conditions of their environments. The second category of features supporting our studies consists in certain morphological and anatomical features of the found plant remains. Here we must of course look always for such features, the variability or changes of which are not in direct relation with the environmental conditions (edaphic, atmospheric a. o.), e. g. the various finer structures of the radicells, of the last divisions of the leaflets a. o., but for those, which are depending rather from more general changes (climatic a. o.) evoked by various stronger and rather permanent geological events, or even from such changes, the causes of which are to be searched with more or less probability in the inner of the plant body, in a permanent and slow change of the constitution of the own living plant substance on account of the life processes of a whole long series of succeeding generations (popularly speaking by its wearing out during rather long geological eras).

Thus before I shall deal with a phylogenetically based plant system which would be in accordance with our present knowledges of the palaeo-botanical science, I have to point out at least several of the most important facts concerning both just mentioned categories of features leading us to the knowlege of the evolutionary problems of the plant kingdom.

I. The history of plants (resp. stratigraphical palaeontology) as a corrective of our phylogenetical speculations.

If we overlook the whole history of the plant kingdom as far as it was discovered untill present in the hardly enumerable series of various palaeobotanical papers and handbooks, than at least six large and unusually complicated pictures arise before our eyes as six miraculous progressive stages of the evolution of plants.

The first of them belonging to the hardly imaginably old times of the algonkian period (even to its oldest known strata, e. g. within the boulders of coarse conglomerates of the basal algonkian horizons) brings to our eyes on many spots of our earth [especially in N. America*)] large masses of limestones, many beds of quarzitic cherts or iron ore rocks, which after very thorough microscopical studies have been re-cognized as the remnants of the life processes of several most primitive and often also smallest plant organisms, chiefly of bacteria and blue green algae (*Schizophyta* and *Cyanophyta*), perhaps already besides some first and rare traces of more advanced algae. Both just named chief plant types were found in the respective deposits in the same morphological appearence as we find them in the nature of to day; there is absolutely no difference in the shape of their cells resp. cell colonies with regard to the still living species. The greatest part of plants found here represent

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*) Gruner's discoveries in the iron ore formation of Michigan as well as Wall-cott's and Mann's discoveries in the limestones of Montana.

types, the cells of which are deprived of any normally developed nuclei. Without any doubt we stand here before the end of an immensely long time space, during which the whole evolutionary activity was directed toward the creation of living highly organized cells containing nuclei as centres of their all life activity, which than became the basis for all living organisms, plants as well as animals.

Both named types of plant organisms known from the earliest algonkian series, *Schizophyta* and *Cyanophyta,* may be therefore justly regarded as forerunners of all other living beings and at the same time their organisation mostly as originally (not by means of secondary reduction) primitive. They are the only two types of plant organisms, which are safely known from the earliest palaeozoic rocks, but of which many lasted untill to our present days in an utterly unaltered state. Their previous history is unfortunately covered by the mistery of the oldest (archaic) rock series, which untill present have nothing revealed of the life, which once was burried into themselves. Only "per analogiam" we are justified to believe that both these plant groups must have had also a great deal of ancestral types, among which also various evolutionary tendencies were manifested, tendencies leading to the stabilisation of numerous forms, which partly kept their original primitive character of cells without any specialised nuclei and incapable of a further morphological evolution leading to "higher types", partly gave rise to more complicated cells with more or less differenciated nuclei, which, as told, became the evolutionary bases for all "higher" organized living beings. The whole evolutionary tendency during that dark time consisted without any doubt chiefly in the genesis of "higher" or "more complicated" inner organization of the cells i. e. in an improvement of the cytological features. It is also quite sure, — analogically as during all other geological periods —, that the greatest part of such arising forms disappeared without leaving any trace in the respective sediments. We must only suppose that they had one very prominent common character—the absence of a typical cell nucleus. Otherwise it is also to be presumed with great probability that among them existed forms which partly exhibited various outer features characterising at present animals, partly such characterizing plants. And indeed if we pay attention to the various groups of the *Bacteria* and *Cyanophyta,* which from this whole hypothetical assamblage of akaryontal living beings survived (of course in a rather strongly modified and specialized state) of the dark geological past untill to the algonkian period and than till to our present time, we must admit that especially the type of the *Cyanophyta* is in all respects of a "plant nature". In the group of Bacteria a variety on a far larger scale seems to exist still at present. We find among them types of typically "plant character", autotrophous, with more or less stiff cell walls, just as other types reminding by their rather inconstant and fine pellicle as well as by their heterotrophous kind of nutrion (e. g. *Spirochaeta, Leptospira* a. o.) rather more some very primitive animals than plants. Of both these akaryontal groups, the group of *Cyanophyta* seems to be already since the oldest algonkian times much more stabilised than the group of *Bacteria.* This last assamblage kept evidently a far greater variability and much more evolutionary vitality as well as capability for

adaptation; its representants performed also always a much more important role in the whole living nature. In the whole the group of the *Cyanophyta* exhibits since the time of the oldest palaeozoic era untill to the present days a rather relic-like character, being incapable of any further evolution, whereas the *Bacteria* are representing an assamblage of very heterogenous types, of which many seems to be still at present full of life energy. I would say, that the whole evolutionary tendency of the *Bacteria* was always otherwise directed, than that of the*Cyanophyta* resp. also of other "higher" living beings, i. e. not in the direction towards an effort to build up cytologically or eventually also morphologically "perfect" or "complicated" bodies, but in contrary toward an anusually high improvement of their biochemical activities without any special complication of the construction of their bodies. In this light the group of *Bacteria* appears still at present as a very large assamblage of akaryontal beings exhibiting perhaps more plant like features, which cannot be considered as a relic-type from the dark past, but in contrary as a special very large and old evolutionary line besides all plants and animals, having its own phylogenetical tendencies and rules and exhibiting its own phylogenetically stabilised and perhaps relic-types as well as other ones being still at present highly active and capable of further evolution as well as adaptation in accordance with the evolution of all other living beings animals as well as plants, which (be it in a living or dead form) very often became the basis for their life.

Both groups, *Cyanophyta* and *Bacteria,* seem to represent therefore two rather remote evolutionary lines. The term of *"Akaryonta"* comprizing at once *Bacteria* and *Cyanophyta* as a systematical plant unit, as used also by several modern authors, seeems to me at least somewhat unconvenient with regard to the construction or delimitation of other systematical higher units. The *Cyanophyta* may be characterized as of algal like nature, whereas the *Bacteria* appear as a special (third) type of living beings besides all plants and animals, which kept their original akaryontal feature loosing not their evolutionary vitality. The name of *Akaryonta* seems to represent rather a more suitable term for the whole vegetation assamblage theoretically assumed for the dark time space before the early algonkian (as found still at least partly at the beginning of that period), thus as a merely eocological term (analogically as we are using e. g. for the vegetation of the carboniferous period the term of pteridophytic vegetation) or finally as a term indicating the general evolutionary stage achieved during that remote time by the living substance in general, but without regard to the true relationship of the various components of this whole assamblage (resp. vegetation).

During the periods of the later Algonkian, Cambrian and partly even during the early times of the Silurian the picture of the world vegetation was essentially enriched by a large ammount of new types of an essentially "higher" and more complicated organization and provided by well developed cell nuclei. But till present we have from this era no reports of the existence of any land plants. All that we know are various types of algae, which in many spots grew along with the large calcarous masses or reefs built up of *Cyanophyta* and *Schizophyta.* It is interesting to note

that even such "highly" organised forms as the red algae (*Rhodophyta*) were found within the sediments of that period (the group of the *Solenoporaceae*). With certainty only one algal group is utterly missing at this time i. e. the *Bacillariophyta (Diatomaceae)*, and the existence of true *Charophyta* is not yet safely stated (we do not yet know with utter certainty if the so called *Sycidia* and *Trochilisci* are of true characeous affinity). These facts attest, that the origin of the great algal groups *Rhodophyta, Chrysophyta (Chrysomonadina, Heterocontae), Phaeophyta* and *Chlorophyta* may be dated much backward if compared with that of the *Bacillariophyta* and perhaps also of the true *Charophyta*, which both are to be met not early than in the older mesozoic periode and which must be therefore regarded as derived much later than the other above mentioned algal groups. Though we meet just in the early periods of this epoch algae, which represent already large and rather complicated multicellular thalli (of course besides many small till unicellular types as various *Flagellates* or *Protophyta*), nevertheless the whole evolution of the above named algal groups was not finished during these older phase of the Palaeozoic. During later times, especially during the later palaeozoic periods as well as during the mesozoic era we see to emerge one after the other various new and new forms, especially in the evolutionary lines of the *Rhodophyta (Melobesiaceae, Corallinaceae)* and *Chlorophyta (Coodiaceae, Dasycladaceae)*. Very meagre are unfortunately our knowledges about the conditions in the group of the *Phaeophyta*, but this fact depends perhaps only of the great difficulty as to the fossilization of their bodies, which are of a very ephemeral consistence bearing no resistent mineral skeletons. Even otherwise our knowledges in this branch of palaeobotanical science are somewhat restricted, because also among the other algal groups only such forms, which contain harder calcareous or quartzitic skeletons, were preserved in the rocks in a state convenient for our detailed studies. Therefore we must suppose that the far greatest part of the algal vegetation of the past remains quite unknown to us, and that also the stratigraphical records unfortunately cannot tell us anything more precise about the succession, in which the named great algal divisions emerged one after the other or eventually aside. Taking in mind the rather ephemeral substance of the algal bodies we must admit that we perhaps never shall be informed about this processus. The mutual relations and the origin of these great algal groups remain thus without any precise answer and equally we do not know absolutely any missing links between this whole rather very advanced algal flora of the cambro-silurian period and between the early algonkian (or even older) akaryontal beings.

The first apparition of a land flora may be stated in the third picture, yielded by the discoveries of the geological stratigraphy dealing with the problems of the late silurian and early devonian period. I think that till present in the various discussions and textbooks dealing with the first land flora it never was laid enough stress or importance to the principal characters of the plants, which achieved the ability of living on dry land and which were of two fundamental kinds. On the one hand there are forms, which are constructed of branched filaments mutually densely

interwoven like a plectenchymateous tissue of the fungi; we know them under Kräusel's name of *Algomycetes* (*Parka, Foerstia, Protosalvinia, Nematothallus* a. o.) On the other hand there are plants, the bodies of which are constructed of normal cellular compact tissues (parenchyma a. o.) and which contain typically developed vascular strands, but which are not yet well differenciated into leaves, roots and stems as in the land plants of all later periods. This second type seems to have been much more frequent; we know it under the name of the *Psisophytineae* (or *Psilopsida*), a group representing the most primitive vascular plants.

All fossil remains of both just mentioned oldest types of land plants represent the sporophytic generation. The first type of both, the *Algomycetes*, never achieved a distribution of larger scale and died out during the earliest times o fthe devonian period, without any true descendents. Perhaps only the great cap fungi, which are built up also of a mere plectenchyma represent an analogical younger but exclusively heterotrophous evolutionary line of land plants derived directly from certain algal ancestors. The plectenchymatical tissues are no doubt to be regarded as representing a lower stage of plant tissues than the various coherent textures of all later "higher" or "more perfect" plant types (parenchyma a. o.)

Very soon (perhaps already at the end of the silurian period) also several rare land plants appeared along with the group of the *Psylophytineae*, the body of which (also of sporophytic nature) was distinctly differenciated into stalks and leaves. First of them are several forms of the *Lycopodineae* (*Barragwanathia, Drepanophycus, Protolepidodendron, Lycopodites* a. o.), several non articulated plants with more or less wedgelike or fan shaped leaflets (I propose for them the term of *Psygmophyllineae:* — *Barrandeina, Duisburgia, Cladoxylon* a. o.) and finally also several traces of true *Articulatineae* (*Calamophyton, Hyenia* a. o.) as well as the first traces of some fern-like plants (*Protopteridium, Aneurophyton, Swalbardia* a. o.) But untill present we do not know absolutely any record of a form, which could be safely regarded as an intermediate plant form between the true algal water forms and the mentioned earliest types of vascular land plants.

The following three pictures, which the stratigraphical geology reveals before our eyes, are perhaps much more easy to be comprehended than the previous ones. They contain a far greater number of various plant forms on account of a more resistent character of the bodies of the vascular land plants, which since the Middle Devonian performed the main role in the composition of the land vegetation. These three pictures represent the gradual evolution of this vascular type of plants toward a state, which with respect to the propagation requires the possibly minimal quantity of water in their environments. The distribution of the representants of the main systematical plant groups within the time space from the end of the palaeozoic era untill to our present days is indicated by the general composition of the vegetation of the three main geological time sectors: in the later palaeozoic era (end of the devonian period and the carboniferous as well as the early permian periods) pteridophytic till pteridospermic, in the mesozoic era (more precisely: late permian, triassic,

jurassic as well as early cretaceous periods) gymnospermic and finally in the kaenozoic era (more precisely: later cretaceous, tertiary and quaternary periods) angiospermic. There are several facts of great interest as to the occurrence of the various subordinate systematical plant units. The extinction of the most primitive group of the *Psilophytineae* took place during the Middle Devonian; at the end of the Devonian already no traces of these plants are to be found. The group of the *Articulatineae* is represented at the end of the Devonian and in the earliest times of the Carboniferous by two types: first by several representants of the family of the *Sphenophyllaceae* (as well as some of their allied forms), which then occur numerously untill to the end of the Permian, and second by the group of the *Asterocalamitaceae* (and several allied forms), which disappear at the end of the Lower Carboniferous (Kulmian) being for a short time (chiefly in the Namurian) replaced by another equisetalean type, the *Mesocalamites,* and still later (during the whole Westphalian, Stephanian and Permian) by the most common palaeozoic horsetail type of the *Calamites.* True *Calamites* are disappearing at the end of the Permian, where they are relieved by the *Neocalamites,* which disappear during the middle times of the mesozoic era. During the Middle Carboniferous still another horsetail types emerge: the first traces of the *Equisetites,* which played a remarcable role during the early mesozoic era and which at the end of the Cretaceous were replaced by our common herbaceous genus of *Equisetum,* further in the Middle Carboniferous several other equisetalean genera with more or less dichotomously divided leaflets (like *Sphenasterophyllites, Autophyllites* a. o.; I propose for such forms the family name of the *Sphenasiterophyllitaceae)* and simultaneously with the type of the *Equisetites* up from the later Permian untill to the Lower Cretaceous the genera of *Phyllotheca* and *Schizoneura.* As to the group of the *Lycopodineae* the herbaceous types of *Lycopodium* and *Selaginella* are stated perhaps during all the three last periods but always only as a subordinate component (the type of *Lycopodium* already up from the Upper Devonian, the type of *Selaginella* from the Westphalian). The late palaeozoic era was especially characterized by the enormous development of the large treelike clubmosses of the group of the *Lepidophyta.* First traces of them were stated already in the later devonian period; they are disappearing with the end of the Permian and the beginning of the Lower Triassic; during the early mesozoic era far smaller forms emerge before our eyes (in the Triassic the genera *Pleuromeia* and *Bedheimia,* in the Lower Cretaceous the *Nathorstiana*) and finally during the later Cretaceous and the Tertiary only various herbaceous species of the genus of *Isoetes* are known, which remained as an old relic type from this formerly so important group untill to our present days.

A very interesting sequence may be stated also as to the stratigraphical occurrence of the chief families of the large group of the ferns (sensu latissimo). The artificial group of the *Archaeopterides* and the various *Coenopteroid* ferns are characteristic for the earlier times of the later palaeozoic era (first traces already at the end of the Devonian, last traces in the Permian). The *Marattiaceae* (sensu latissimo i. e. incl. the *Pecopteridaceae)* are most frequent during the Carboniferous and

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Permian, later and untill to the present days only in a very restricted quantity. First traces of the family of the *Osmundaceae* were stated in the later phase of the Permocarboniferous, culmination of their development in the older and middle Mesozoic, later and untill to our present days they occur also only in a rather restricted number. The families of the *Gleicheniaceae* and of the *Schizaeaceae* are must abundant in the later mesozoic times, but there are already in the Middle Carboniferous several forms exhibiting many common features with both these groups; both are at present just as the *Osmundaceae* in a considerable retreat. In the later mesozoic period appear very abundantly also representants of the *Dicksoniaceae,* which now are also on a strong retreat, whereas the related family of the *Cyatheaceae* left only very rare traces in the mesozoic rocks being first at the present days in a very busy development. Nearly the same as for the *Cyatheaceae* holds also for the family of the *Polypodiaceae,* which no doubt represents the most recent type among the true ferns. Unfortunately the geological history revealed absolutely nothing essential about the past of the family of the *Hymenophyllaceae;* several rather uncertain records are reported *(Hymenophyllites)* already from the later Carboniferous. Very interesting is also the history of the groups of the *Matoniaceae* and *Dipteridaceae.* Unknown in the palaeozoic era they emerge as a very important component of the fern flora during the older Mesozoic; during the Upper Cretaceous they became more and more rarer and at present they belong to typical relic plants. An especially mysterious problem are the heterosporous water ferns *(Hydropteridineae);* the stratigraphical geology discovered till present absolutely nothing as to their older past.

The so called *pteridospermic* plants, which exhibit similarities partly with the Lycopodineae, but chiefly with the ferns, are most common during the latest palaeozoic period (Carboniferous, Permian). Untill present we do not know any certain traces of this group from the later Devonian; they occur in a very restricted quantity nearly throughout the whole mesozoic period except perhaps the latest times of the Upper Cretaceous *(Caytoniaceae, Lepidopteris, Corystospermaceae,* a great part of the so called *Thinnfeldia* series a. o.); their last traces were stated in the older sediments of the Upper Cretaceous (Cenomanian: *Sagenopteris).*

The group of the *Cycades* is a predominately mesozoic type. Its first traces are known from the end of the Middle Carboniferous, where also several more or less intermediary types between these group and the *Pteridosperms* are to be found *(Pteridozamites, Emplemopteris).* With the end of the Cretaceous their occurrence became extremely restricted.

The *Cordaitales,* which mostly are regarded as one of the most primitive types of the *Coniferophyta* though they exhibit many features peculiar to the *Pteridosperms* (especially the character of the seeds and pollen grains), occur chiefly only during the Permocarboniferous; no safe traces of them have hitherto been found earlier than in the Lower Carboniferous, just as in the early Mesozoic. The first typical Coniferous plants *(Walchiae* a. o.) are known not earlier than in the stephanian division of the late Carboniferous; they are especially numerous during

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the later Mesozoic as well as during the early Kaenozoic. They relieve in the forest vegetation in the just sense of this word the palaeozoic lycopodiaceous group of the *Lepidophyta* at the limits of the palaeozoic and mesozoic era having in common with them the whole outer appearence of their stems, leaves as well as the cone like fructifications.

Rather obscure seems to be the history of the *Ginkgophyta;* they appear most numerously during the early and middle Mesozoic. First safe traces of the *Ginkgophyta* were stated in the Permian. But there are known already up from the later devonian times rather numerous leaf impressions, which strongly remember leaves of this family. Quite obscure is meanwhile also the past of the three *Gnetalean* genera *Gnetum, Ephedra* and *Welwitschia;* the geological stratigraphy tell us absolutely nothing about them.

A very mysterious chapter from the point of view of the stratigraphy represent the flowering plants *(Angiospermae)* of to day. They appear rather suddenly during the later stratigraphical divisions of the Lower Cretaceous; very rare but at the same time very uncertain traces of them were observed already since the end of the Triassic *(Furcula* in the Rhaetic of Greenland, several silicified woods as well as very rare leaf impressions in the Jurassic of England and France). But there has not yet been discovered absolutely any plant remain, which could be proclaimed as "intermediary" between this large group of plants and one of the older more primitive plant types. Several botanists (e. g. P. Bertrand) suggested that perhaps several of the late palaeozic *Pteridosperms* with very compound leaves and complicated nervation as e. g. the *Gigantopterides* of the stephano-permian strata of the Cathaysian regions might be perhaps with great probability looked on as one of such forms (or at least standing very near to them). It is only sure that even in the earliest times of their existence on the world scene (just among the obscure jurassic impressions) both types of the angiospermic groups, the monocotyledonous as well as the dicotyledonous forms occured side by side. But the further stratigraphical distribution of the various families of he flowering plants seems to be very often of only a very restricted value for phylogenetical speculations or taxonomy because the herbaceous plants compared with the woody ones had always much less chance to be preserved as fossils and thus our whole picture of the distribution of the various angiospermic families is and will remain even in future rather distorted; the woody plants will always emerge in the foreground of all our imaginations. It is also very important to state just here that many types, which on account of the very simply constructed flowers have been mostly regarded as rather reduced and derived forms from some more "complicated types" (e. g. many forms of the "Apetalae": Salicaceae, Betulaceae, Fagaceae, Myricaceae etc.), occur already among the oldest angiospermic associations. Also the sympetaleous type seems to emerge very soon within the angiospermic flora (e. g. the genus Viburnum in the earliest cretaceous vegetations). It is therefore to be expected that even in future further more detailed stratigraphical researches in this field of palaeobotany will reveal many precious facts completing our conception of the early past of the various angiospermic plant families.

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Finally I have to mention at least briefly also the group of the *Bryophyta*. Newer records have shown, that this type of plants is of a rather very old origin. On account of a special chemical feature of their tissues their preservation as fossils depends on especially favourable conditions and therefore our knowledges are very restricted. The oldest known specimens are to be dated as middle and upper carboniferous. These exhibit absolutely nothing specially differing from the organization of forms living still at present *(Musci, Hepaticae)*. Till now no traces of their eventual relations to some algal types or at the other hand to the vascular plants were ever discovered.

As seen from the above mentioned 6 pictures presented us by the stratigraphical geology, our cardinal conception of the taxonomical and systematical value, of the mutual relations as well as of the sequence of the chief plant groups as defined hitherto by means of various morpho-logical and anatomical studies on recent plant material, was already long ago rather well established at least in their most coarse lines. But already during the last 30 years it was often necessary to modify many more detailed problems just with regard to the newer palaeobotanical discoveries and there remain still many others, which expect a convenient confronta-tion with the results of this branch of botanical science (e. g. the relations of the genera of Psilotum and Tmesipteris, the problem of the heterspo-rous water ferns, the mutual relations of the various gymnospermic plant groups a. o.). But nevertheless we must confess, that the palaeobotanical researches did not yet reveal in spite of all efforts the most desirable "missing links" i. e. some transitional forms between the akaryontal beings and those provided by well differenciated nuclei, between the algae and the kormophyta as well as between the gymnosperms (resp. vascular cryptogams) and the angiosperms.

II. Several fundamental principles of the comparative morphology in the light of the palaeontological evidences.

Most of the palaeobotanical records, which are dealing more with the problems of the comparative morphology, refer mainly to the various types of the Pteridophyta and Gymnosperms. Therefore also the most important changes caused on the bases of palaeobotanical records in the systematic and taxonomy of plants are concerning mostly these two groups. In other parts of the plant system all such changes are coming rather from the side of the above discussed stratigraphical evidences or even from a detailed collecting work, discovering of new hitherto unknown species and genera a. o. As to the morphological problems concerning these last named groups *(Thallophyta, Bryophyta, Angio-sperms)* we have to refer chiefly to the still living plant material: in the "lower" plants because only exceptional specimens are to be found in fossil state, in flowering plants because most of their fossil specimens are represented mostly by mere leaf impressions, whereas flowers and fruits in fossil state are rather rare.

One of the most important problems from the just mentioned point of view is without any doubt the differenciation of the vascular plant body into leaves, stalks (stems) and roots. The study of early devonian resp. late silurian plants revealed several very primitive vascular types, the bodies of which are composed merely of dichotomously ("homo-brachially hemiblastic" according to Domin's classification) branched stalks *(Rhynia, Hornea, Hicklingia, Loganella, Scyadophyton* a. o.), which eventually are altered at the tops into oval or elliptical spore bearing capsules *!Rhynia, Hornea);* the stalks are smooth and without any special assimilating appendages. But at the same time we know from the early Devonian also forms, which are differenciated into special systems of ramified twigs bearing the spore procucing organs and other utterly sterile branches *(Gosslingia, Zoosterophyllum, Bucheria* a. o.) which are very often flattened (in some cases also the main stalks) and slightly enlarged. In certain special cases *(Pseudosporochnus, Swalbardia)* only the last short branchlets are transformed into short, flattened, nar-row, wedgelike and often furcated assimilating organs. Finally there are also forms the twigs of which are provided by special hairlike or spinelike enations ressembling very strongly the linear leaflets of many *Lycopodineae.* In several species *(Psilophyton)* they represent true trichomes having no vascular strands nor any stomatal organs, in other more advanced types they are at least in their basal parts provided by a well developed vascular strand and their cuticle bears typical stomata *(Asteroxylon).*

All these conditions seem at first sight to be quite in agreement with the most commonly admitted t h e o r y (Lignier, Schoute, Darrah a. o.) o f a t w o - w a y o r i g i n o f l e a v e s of all vascular plants: t h e m i c r o p h y l l o u s l e a v e s derived from mere enations (like in Asteroxylon) and t h e m a c r o p h y l l o u s l e a v e s derived from small lateral and eventually branched twigs. The first of both are gene-rally ascribed to the group of the *Lycopodineae,* and by several authors also to that of the *Articulatineae.* Other plant groups are generally supposed as macrophyllous. But all further palaeontological records con-cerning the oldest known plant types of the groups of the *Lycopodineae* as well as of the *Articulatineae* show that just among the silurodevonian forms species with more compeund, dichotomously divided leaf appen-dages are rather frequent *(Calamophyton, Hyenia; Protolepidodendron,* a. o.), which means that the simple linear leaflets of the "younger" resp. "higher organised" forms represent rather an already reduced leaf form. It is true of course that there are already in the Silurian among the *Lycopodineae* types with utterly simple linear leaves *(Barragwanathia),* but just such forms exhibit at the other hand an enough complicated inner anatomical structure (plectostelic vascular strands) wherefore we must regard such types as strongly transformed by a rather long evolu-tionary processus and not primitive at all. Unfortunately we do not know untill present absolutely any plant type, which could be regarded as an intermediate form between true *Lycopodineae* and the above mentioned most primitive vascular plants *(Psilophytineae)* or which would approach at least slightly to such a theoretical intermediate stage. But nevertheless

on account of the above mentioned dichotomously divided leaflets in several devonian *Lycopodineae (Protolepidodendron)* I suppose that the leaves of the *Lycopodinee* are of the same morphological nature as those of the *Articulatineae* i. e. conveniently transformed and highly reduced small side twigs of limited growth. Such a form of assimilating leaves developed in a typical state may be observed also in several devonian plants, which according to our present definition of the cardinal pteridophytic plant division cannot be joined to any of them (i. e. *Psilophytineae, Articulatineae, Lycopodineae* and *Filicineae*), for instance the devenian *Bröggeria, Barrandeina, Duisburgia, Cladoxylon* (further also the carboniferous *Noeggerathiae, Tingiae, Palaeopteridia, Saaropterides* and finally also the living *Psilota* and *Tmesipterids*), which bear on unraticulated branches mostly wedgelike leaflets often dichotomously divided (or at least with dichotomously divided nervation) as in the more primitive types of the group of the Articulatineae. An example of the most primitive form in this respect, showing still a transition stage between the branch character of such assimilating side appendages and between well differenciated sphenopsid leaflets, is represented perhaps by the devonian *Bröggeria*. This type exhibits somewhat irregularly dichotomously ramified main branches bearing in an (? irregular) spiral arrangement numerous very short simple or irregularly and poorly divided branchlets, which are notyet of a leafy appearence (in contrary to this primitive state of "leaves" the fructifications of *Bröggeria* are already of a rather advaced conelike shape!). And just this kind of leaf appendages (termed often alse as pseudomacrophyllous) must be therefore regarded as the ancestral form of all so called microphyllous laeflets of the various higher Pteridophyta (especially of the *Lycopodineae* and *Articulatineae*). To avoid any possible mistakes I shall name it as the "sphenopsid" type. True "microphyllous" leaflets in the original sense of Lignier (Schoute a. o.), i. e. leaflets derived phylogenetically from simple trichomelike enations, seem to me according to all hitherto known palaeontological evidences to be extremely rare and to be present only in several very old psilophytalean types like the named *Asteroxyla*.

The "sphenopsid" leaves in the above mentioned sense represent thus from the point of view of the comparative phylogenetical morphology organs derived very early in the history of plants from dichotomously (hemiblastic and homobrachial at the same time) divided small side branches adapted for assimilating purposes (i. e. conveniently flattened, with limited grouth, provided with stomata a. o.) Palaeontological documents attest that they are capable not only of a strong reduction into organs quite equal (as to the shape) with Lignier's "microphyllous" leaves (of trichome nature), but also of a further evolution into large coherent wedge like till oval flat and rather large leaves with dichoto-

mously divided vascular strands (see for instance the genera *Archaeopteris, Sphenophyllum, Noeggerathia* a. o. with the "pseudomacrophyllous" leaves or leaflets). But we have till now no documents of an eventual possibility of their transformation into pinnate leaf organs. On account of an utterly equal attitude of the leaves of the gymnospermic plant groups of the *Coniferae, Ginkgoaceae* and without any doubt also of the *Cordaitaceae* as well as of the small group of the *Podozamites,* I regard also these groups as bearing also "sphenopsid" leaves. The dichotomously divided leaflets of several of the oldest known *Coniferae* (the palaeozoic genera *Buriadia* with twice divided leaflets, *Carpentieria* with once divided leaflets and the once divided leaves on thicker branches of several species of the *Walchiae),* which strongly remind leaves of the devonian lycopodiaceous *Protolepidodendron,* seem to be a sufficient palaeontological proof of this theory. We have therefore to suppose that plant types bearing typical linear one nerved leaflets, "microphyllous" in the common large sense, arose chiefly three times in the history of plants: first during the oldest period of the evolution of the vescular plants, perhaps at the end of the Silurian (Lycopodineae), second during the early Carboniferous (in the group of the *Articulatineae)* and for the third time at the end of the later Palaeozoic (in the coniferophytic evolutionary line of the gymnosperms).

An essentially different kind of leaves are the m a c r o p h y l l o u s l e a v e s as found in the ferns. If otherwise not reduced they are mostly very compound and of a very large size, variously pinnate with dichopodial or dichotomous last divisions resp. nervation. In a young state they are very often spirally rolled up. They are growing with apical cells of the growing points at the tops and we know even species *(Lygodium* a. o.) where the growth in length is in a certain measure unlimited. If we go back into the history of plants we find even forms, the leaves of which show an intermediate shape between the true dorsiventral compound fronds and between large systems of branches. Just such plants show quite clearly that the large compound fernlike fronds originated by two ways: either by a plagiotropic arrangement of the branches in only one plane (e. g. the various *Protopteridia* show excellent examples from types nearly Rhynia like [*P. minutum*] untill to wholly fernlike species [*P. hostimense, piedbeufi* a. o.] ; another examples are the early devonian *Swalbardia* and the late devonian genus of *Archaeopteris),* or by a progressive reduction of the number of the planes of symmetry from a radially symmetrical branch system untill to a dorsiventral frond with only one plane of symmetry (e. g. 4 planes of symmetry in *Stauropteris,* 3 in *Aneurophyton,* 2 in *Rhacophyton* as well as in the *Zygopteroid* ferns a. o.). It is evident that these facts are leading us backward untill to several types of the devonian *Psilophytineae* where also circinately enrolled tops of branches and stalks are well known (Asteroxylon, Psilophyton a. o.) and where, as already mentioned, very often also certain systems of twigs are slightly transformed to special assimilation purposes *(Taeniocrada* a. o.). As to the transformation of larger systems of branches into fernlike fronds, palaeobotanical records yielded already many concrete examples. At this transformation one processus is very remar-

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cable: the transitien from a dichotomous branching to a dichopodium and finally to a pinnate dorsiventral system. In such systems the eventual original assimilating appendages i. e. the small sphenopsid leaflets represent the aphlebiae or the last pinnules (leaflets) on the rhachises (many examples in the group of the coenopteroid ferns of the *Phyllophorales*). There are known among the early devonian plants even such forms, which kept their most primitive leaflet-like enations (i. e. "microphyllous" leaves in Ligniers's or Schoute's sense) and which at the same time achieved the stage of compound fronds like the genus of *Dowsonites*. All these facts attest that the macrophyllous fronds of the ferns are really of another, "higher" rank, than the first mentioned sphenopsid leaves.

We have therefore to state among the Pteridophyta 3 kinds of leaves from the point of view of the comparative morphology: microphyllous leaves in the original Lignier's sense (i. e. enations), sphenopsid leaves (microphyllous leaves of the most of the authors resp. pseudomacrophyllous leaves, i. e. theloms of Zimmermann, transformed short side branches) and finally the macrophyllous leaves (i. e. transformed whole systems of branched twigs bearing eventually microphyllous or sphenopsid leaflets).

Now it is still a serious task: are we just if regarding the *Psilophyta* like *Rhynia* or *Hornea*, constructed only of smooth cylindrical leafless branches, as originally the most primitive land plants? I do not believe that at any rate. On account of the conditions under which they have been discovered (quarzitic cherts containing an innumerable quantity of individuals densely associated in the same manner like many aquatic or swampy plants), they remember too much several specially adapted forms of higher aquatic or swampy plants (Juncus a. o.). But it seems that their secondary simplification on account of the special adaptations was not a very strong one (perhaps we might think of the loss of various enation like leaf appendages or only hairs [like in the *Asteroxyla* or *Psilophytons*], of the change of the shape of the assimilating branchiets from more or less flat ones into only cylindrical organs a. o.). The character of the sporangia (especially in *Hornea*) as well as of their position on the branchlets (i. e. at the very ends of the last twigs) are without any doubt a sufficient testimony of a certain original simplicity. I regard therefore these plants as a very soon stabilized phylogenetic side line adapted for special environmental conditions (and therefore without any further evolution), which cannot be therefore looked on as a direct ancestral type of the other Pteridophyta.

We have still to answer the question, which plantgroups besides the ferns are provided with true macrophyllous leaves. I believe that we have here two rather safe guides: the pinnate character either of the larger parts of the leaves or at least of their main nervation and eventually also the circinately erolled ends in the young stage of the leaves. These characters are more or less distinctly exhibited in the representants of the great groups of the Pteridospermae as well as of the Cycadeae. Among the older forms, — especially pteridospermous plant types —, we find very often leaf fronds with dichotomously forked main rhachises (e. g. the *Lygi-*

nopterides and *Heterangia* of the later Palaeozoic or several types of the *Thinnfeldia* series of the older mesozoic era), which evidently points to a very early departure of the pteridospermous evolutionary line from some primitive pteridophytic forms perhaps still of psilophytalean affinities, where the assimilating branch systems were still stristly dichotomously divided. There are also many forms among the Pteridosperms, where various transition stages between a dichotomy and a pinnate system are stabilised (i. e. various stages of a dichopodium like in the "genera" Mariopteris, Diplotmema, Callipteris a. o.). At first sight essentially different conditions are to be found in the leaves of the *Gnetophyta* and *Angiospermae*. But even here (of course if we have not to do with leaves too strongly reduced) several of the just mentioned main features are to be clearly stated: the pinnate character of their nervation and very often also of their whole outline. Figuratively speaking, their lamina is on account of a special phylogenetical evolution extremely "reduced" and "condenced" loosing nearly all possible ancestral characters of a branch system (which has its chief expression in the highly complicated areolate nervation), their ontogenetical development is essentially accelerated being not executed as in the ferns or cycades by an apical progressive growth, but by their whole margine (or independently by all its lobes and pinnules) and also more or less intercalarly, and finally they never are circinately enrolled during their young stages. They evidently achieved the character of quite independent organs with a special kind of growth entirely dissimilar to any normal branch system. They represent an essentially much more advanced leaf form if compared with typical macrophyllous fronds of the ferns, pteridosperms or cycades. There is but one very interesting circumstance, which attests that also here the leaves arose from originally dichotomously divided branch systems, just as in the above discussed pteridospermic till cycadophytic evolutionary lines. Many of the oldest angiospermic leaves are provided by forklike divided main rhachis (resp. nerve), like in the curious rhaetic *Forcula* or in several older cretaceous leaf impressions. It seems therefore that here *(Angiosperms)* we have also to suppose a very early departure from more primitive types at least from such *Pteridosperms*, where the dichotomy of the main rhachises was not yet quite lost or transformed in a purely pinnate stage.

The second moment from the point of view of the comparative morphology which has an equally decisive importance as to the critical examination of the mutual relations of the main groups of the vascular plants, is t h e p r o b l e m o f t h e o r i g i n o f t h e s p o r o p h y l l s with their variously dislocated sporangia. Before all we have to answer the task, in which way and by which organs the spores were produced in the most primitive landplants and which were the ways of the transformation of such spore or sporangia bearing organs during the later phylogenetical evolution. No doubt nearly all still living plants are too much changed by this evolutionary processus; they are yielding us only very inaccurate and incomplete indications. But even the palaeobotanical records, though these are already in many respects rather very satisfactory, they nevertheless did not reveal any definitive answer as to the cardinal task: Are all sporangia and sporangiferous organs (vulgo "sporo-

phylls") of the vascular plants of the same morphological value? Till present there have been discovered already a sufficiently large quantity of various extinct types, which nearly all are in favour of the theory, that originally the sporangia were placed terminally at the tops of some vascular thalloid branches or at the ends of the last twigs in special branch systems. *Rhynia, Hornea, Taeniocrada* a. o. old devonian plants attest clearly that the sporangia represented originally mere tops of such branches, the whole tissue of which between the central vascular strand (which in Hornea is still preserved as a columella) and the outer cortical (resp. epidermal) tissue served as a sporogenous parenchyma. More often we may observe among the old devonian fossils various types where the sporogenous ends of the twigs are more or less transformed into rather well differenciated oval capsules, which in several cases exhibit also a differenciation of their superficial texture, without any doubt with the aim of the opening in the maturity. At the same time changes as to the size and the complexity of tissues (towards simplification) are evident. The most important fact is the specialization of several branch systems for sporogenous function. We find among the old psilophytalean plants types showing large dichotomously divided branch systems wholly fertile (*Asteroxylon, Taeniocrada, Himanthaliopsis* a. o.). In other ones, like *Hedeia*, the single twigs of such fertile dichotomously divided systems are strongly abbreviated yielding thus a corymbose appearance, or in extreme cases (*Yarravia*) we find a considerable number of very shortly stalked sporangia clusterlike arranged at the end of simple side branches. Other types like *Gosslingia, Zoosterophyllum* a. o. exhibit spike like arranged very shortly stalked sporangia on simple straight branches (evidently of dichopodial nature). In several more advanced plant types with branch systems more or less transformed into primitive leaf fronds we find such very abbreviated fertile branch systems sitting irregularly on the "rhachises" of such fronds as larger or smaller side organs (*Protopteridium, Aneurophyton, Rhacophyton, Archaeopteris, Stauropteris* a. o.). In still "perfectly" organized types with already well differenciated leaf fronds (*Zygopterides*) these small fertile branch systems are transformed by an extreme reduction into rounded clusters of shortly stalked sporangia (*Etapteris*) arranged into two rows along the rhachises of last degree or in extreme cases the sporangia are sessile forming rounded groups — "sori" — pushed on the lower (abaxial) side of the last pinnules (*Corynepteris* a. o.).

Further evolution of the whole sporogenous apparatus of the macrophyllous types (ferns, pteridosperms, cycades) is well demonstrated by numerous discoveries in the late palaeozoic as well as mesozoic flora. It consists in a progressive migration of the sporangial groups (as seen in the genera *Etapteris, Corynepteris* a. o.) on the lower (resp. abaxial) side of the more or less coherent lamina formed by the transformation and fusion of the single original leaflets (of microphyllous or sphenopsid character) and at the same time in a gradual abbreviation or utter reduction of the sporangial stalks as well as the simplification of the sporangia, which led finally to the formation of small groups of either pedicillate or sessile free sporangia (sori of the most part of the true

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ferns and Cycades). In many cases the sporangia exhibit an evident tendency to coalescence, which is especially well demonstrated in the palaeozoic group of the *Pecopterides* as well as the later *Marrattiales* and which led to the origin of the well known large multilocular synangia.

There are among the palaeozoic macrophyllous plants also several types, where we must suppose a similar but slightly different origin of groups of sporangia, consisting in gradual reduction of such dichotomously divided and sporangia bearing branch systems as found newly in the Silurian of Australia and described under the name of *Hedeia*. The reduction of the single sporangia stalks led evidently to the origin of stalked clusters of sporangia as seen in another equally Silurian (Australia) type called *Yarrawia* and also in the carboniferous *Telangium, Crossotheca, Potoniea* a. o. By similar coalescens of the single sporangia just like in the foregoing case various often very complicated synangia were formed *(Aulacotheca, Boulaya, Whitelesseya)* and we know also cases where more such synangia grew together (after a reduction of the stalks of the whole fertile branch resp. rhachis system) producing by that way large and massive, bellshaped and very complicated male organs *(Dolerothaca)*. This slightly differing kind of origin of spore bearing organs is especially characteristic for certain palaeozoic groups of the *Pteridospermae*.

An essentially different processus must be assumed in this respect in the case of the microphyllous evolutionary lines. Here everywhere an evident tendency to the formation of special cone or spike-like fertile branches bearing spirally (event. in whorls) arranged sporangiferous side branchlets may be observed. As from the foregoing evident, these fertile appendages are to be considered as morphologically homologous with the equally arranged leaflets of the sterile branches; just as these last they represent only small branch systems pushed aside in consequence of the dichopodial construction of the whole plantbody and adapted resp. specialized for sporogenous function instead of an assimilatory one (e. g. *Barrandeina, Cladoxylon, Hyenia* a. o.). Typical representants of such cone-like fructifications are to be seen among the *Articulatineae* and the *Lycopodineae*. They are here of three fundamental types: 1. The cone axis is provided by sporophylls bearing in their basal, part and on their adaxial side only one sessile or rarer shortly pedicillate sporangium. 2. The cone axis is provided by sporophylls to the bases of which (also on their adaxial side) are attached special sporangia bearing stalk-like sporangiophores, the vascular strands of which are in direct contact with the vascular strands of the sporophylls (as their side branches). These sporangiophores may be eventually partly or wholly fused with the lamina of the sporophylls, wherefore finally the sporangia are then placed upon the adaxial side of the respective sporophylls. 3. The cone axis bears independent sporangiophores either without any accompanying protective sterile bracts or intermingled more or less regularly with sterile leaflets, the leaf traces of which are but not in direct connection with the vascular strands of the sporangiophores. The first of these three types is best known in the group of the *Lycopodineae*, the second one in the palaeozoic *Sphenophylla* and several rarer allied forms as *Cheirostrobus*, in the carboniferous *Tingiae* and *Noeggerathiineae* as well as in the recent

Psilotum and *Tmesipteris,* finally the third type is to be found in the *Equisetales.*

The morphelogical nature of the two last named cone types is now after many very detailed studies (especially as to the cones of *Sphenophylla* and those of the *Calamariaceae)* rather clear and beyond any discussion: In the second type *(Spehnophylla* a. o.) the sporangiophores (resp. sessile sporangia) with the sterile protective appendages ("sporophyll") represent sporebearing lateral branch systems of which several abaxially declined branchlets were transformed into sterile protective leaf like organs, other ones adaxially declined into fertile sporangiophores; in the third type *(Equisetales)* the sporangiophores represent independent reduced lateral wholly fertile branch systems and the eventually present sterile bracts whole sterile also quite independent reduced lateral branchsystems. As to this last cone type, we know among the devonian land plants many examples showing very well their origin, like the fertile shoots of the genera of *Hyenia, Calamophyton, Cladoxylon, Barrandeina, Protocalamostachys, Asterocalamites* a. o.

More difficulties seems to offer the explanation of the morphological nature of the mentioned first type of our conelike fructifications i. e. those of the *Lycopodineae.* Their utterly constant constitution of one nerved sporophylls bearing everywhere only one sporangium more or less sessile (rarer shortly stalked) at their base on the adaxial side, is well established already in the oldest known types (the silurian *Barragwanathia,* the early devonian *Drepanophycus, Protolepidodendron* a. o.). We do not yet know among the early devonian or silurian plants any forms, which as to the organisation of their fructifications may indicate at least slightly the way of the origin of such extremely simple sporophylls; till present no "intermediary" type between the psilophytalean group and that of the *Lycopodineae* was ever discovered. At present there exist two main theories interpreting the origin of such sporophylls. Both are based on the morphological nature of the sterile leaves of the Lycopodineae. Those botanists who see in the lycopodiaceous microphylleus leaflets mere enatinos (like in *Psilophyton* or *Asteroxylon)* regard the respective sporangia also as mere enations, which by an evolutionary processus were finally conveniently placed behind the protective leaflets or eventually on their adaxial side. They tell that it is not necessary to assume that all ancestral forms of our vascular plants bore their fructificating organs exclusively terminally on the twigs, but that analogically as in the large thalli of the various algal seaweeds *(Phaeophyta, Rhodophyta)* the sporogenous bodies were produced everywhere on the surface of the whole thalloid vascular plantbody as considerably large enations and that first during the further evolution it happened, that their production was more or less stabilised on certain special places, in the *Lycopodineae* otherwise than in all other known vascular cryptogams. According to this theory (Schoute a. o.) the *Lycopodineae* are supposed to have only a very problematical and very remote affinity with all other vascular plants. The second theory (strongly defended by the german author Zimmermann), which seems to me to be also much more verisimilar, is based on the assumption, that the lycopodiaceous leaves are of the same nature as in all other vascular

plants (especially as in the *Articulatineae)* i. e. short systems of branches transformed into leaf appendages, and assumes that therefore also the sporophylls of all *Lycopodineae* must be regarded too as specially adapted fertile systems of branched twigs. I do not see therefore in the lyco-podinean sporophylls anything else than the same phenomenon as in the sporophylls of the *Sphenophylla* or of several similar types, where the single branchlets of the sporangiferous side systems were originally only partly fertile and differenciated later into sterile protective abaxially declined lobes and the fertile sporangiophores adaxially declined. But just as the sterile assimilating leaf appendages of the *Lycopodineae* were extremely strongly reduced into only undivided linear uninerved (or very rarely forklike divided) typically "microphyllous" leaflets, also their sporo-genous organs were finally simplified in the same way. The *Lycopodineae* according to this second theory do not represent thus essentially remote type of the vascular cryptogams, but only a rather very soon achieved specially adapted and simplified evolutionary stage of *Pteridophyta*, standing evidently much nearer to the ancestors of the *Articulatineae*, than commonly accepted by various botanists.

The study of the morphology of the pteridophytic cone like fructifi-cations in connection with the knowledge of the evolution resp. reduction of the sphenopsid leaves (resp. leaf appendages) as well as with the know-ledge of the evolution of the articulated stems lead us to the distinction of 3 more or less parallel evolutionary lines, which all had common an-cestors presumably provided with unarticulated dichotomously divided stems bearing dichotomously divided leaf like side appendages (the "sphe-nopsid leaves", the last divisions of which bore eventually terminal spo-rangia. Fertile side appendages of these theoretically assumed ancestral types had certainly an evident tendency to the formation of spike or cone like fructifications, being arranged in a considerable number on special fertile branches. These three cardinal evolutionary lines are as follows:

1. The direct unarticulated descendents of the just mentioned hypo-thetical ancestral forms with sphenopsid leaves like *Barrandeina, Duis-burgia, Cladoxylon, Tingia, Noeggerathia, Psilotum, Tmesipteris* a. o. On account of the often *Psygmophyllum* like appearence of their leaves I shall term this whole evolutionary assamblage as the **Psygmophyllineae** (instead of my previous term of the Noeggerathiales, which has a too narrow sense).

2. The very reduced typically microphyllous type of the **Lycopodineae**, mostly unarticulated (articulated forms are extremely rare, e. g. *Eleuthe-rophyllum, Zimmermannia).*

3. The assamblage of typically articulated and sphenopsid (till micro-phyllous) Pteridophytes, the **Articulatineae,** which according to the arran-gement of their fructifications represent in fact at least two rather independant parallel groups with special relations to several types of the 1. line*) (i. e. the *Psygmophyllineae)* : the *Sphenophyllales* (with several allied genera like *Cheirostrobus* a. o.) and the *Equisetales.*

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*) For instance there are evident relations between the *Sphenophylla* and the carboniferous *Tingiae* and *Noeggerathiae.*

The heterospory and the production of seeds are also without any doubt two very remarkable degrees in the evolution of land plants towards more "perfect" types and we know among extinct plants even various transition stages. For instance in the group of the palaeozoic *Calamariaceae* or *Lepidophyta* homosporous as well as heterosporous species are known and besides also such forms, where the difference in size between both spore types is indeed very insignificant. Further among the *Lepidophyta* we know species, where the macrosporangia contain only one well developed large spore *(Lepidostrobus major Bgt, L. bohdanowiczi Tad.)*, which eventually were not shed out. In this last case the megasporangia remind than some very primitive nucelli free from any integuments. But in the same plant group still another forms were discovered, like the genera *Lepidocarpon* and *Miadesmia*, where such large unisporic megasporangia are enclosed in a kind of cupular outgrouth of the respective sporophyll lamina as in a very primitive integumental organ. We have here to do with an example of a most simple gymnospermic seed or better to say with a transition stage between a macrosporangium and a true seed. Both named groups, but especially that of the palaeozoic *Lepidophyta*, exhibit excellent examples showing very distinctly the origin of the seeds from pteridophytic sporangia, organs which became later the common form of reproductive bodies in all "higher" plant groups.

There are then in the further evolution of seeds 2 well known main steps: the gymnospermic type, where the ovules are freely expesed on convenietly adapted fronds resp. sporophylls *(Pteridosperms, Cordaitales, Cinkgoales, Coniferales, Gnetineae)* and the angiospermic type, where the ovules are enclosed within special receptacles formed by the fusion of one or more sporophylls. The tendency to conceal the young seeds (resp. ovules) in special capsules appears in a "less perfect" development already in several special cases among the gymnospermic plants. So the pteridospermic family of the triassic *Corystospermaceae* exhibits ovary like capsules round the single ovules made up of the lamina of the respective fertile last pinnules. Another at present also already well known pteridospermic family, the mesozoic *Caytoniaceae*, shows capsules of the same morphological kind containing a larger number of ovules. Another case may be pointed out in the family of the *Cheirolepidaceae* of the group of the Coniferales. Here the seeds are enclosed in a large pocket like outgrouth of the fruit scale (a slight tendency to covering the seeds may be seen also in other types of the Coniferales e. g. *Araucaria, Juniperus, Taxus* a. o.).

Further "improvement" of the seeds were carried out by the gradual reduction of the gametophytic plantule contained within the mocrospore by the gradual complication of the pollination act as well as by the elaboration of the embryo. The degree of the improvement of these circumstances is a very convenient moment pointing to the still primitive or rather advanced stage of various discussed plant groups.

As to the presence or absence of an embryo within the ripe seeds, I regard as highly important that in the seeds of the *Pteri-*

dosperms as well as in those of the *Cordaitales* no embrya have ever been detected. The *Ginkgoales* seem to represent in this respect a transition type, as the embryo in the seeds of the recent *G. biloba* is developing very late after the maturity, often even long after the seeds have fallen down from the tree. Well "advanced" seeds with rather well developed embrya (except several special cases e. g. plants with exceptionally small, i. e. reduced seeds like the Pirolaceae, Orchideaceae a. o.) are a common feature nearly of all "higher" plants *(Cycadeae, Coniferineae, Gnetineae, Angiospermae).*

As to the pollination act, we have to consider two factors, one concerning the morphological and anatomical features of the microspores, the other refering to the adaptation of the female organs to catching the microspores. Both exhibit also several degrees of improvement resp. of adaptation to the land conditions. As to the first problem, we have to distinguish here two stages: one "more primitive", where ciliate spermatozeids are produced *(Cycadeae* and *Ginkgoales* as well as according to the organisation of the inner content of the microspores also most probably all *Pteridosperms* and *Cordaitales),* and an "advanced" one, where no mobile spermatezoids are produced at all, but where the passive male nuclei-gamets are transported by the pollen tube into the female nucellus (all other "higher" seedbearing plants).

The first "lower stage" of the microspores exhibits during the plant evolution two very striking morphologically rather well characterised degrees. In the first degree the content of the ripe microspores is clearly multicellular (last remnant of the male gametophytic plantule). Their outer appearence is in several cases still of essentially pteridophytic features (small sized, rounded, tetrahedral and provided with a polar three radiate scar; known in several more primitive *Pteridosperms),* but mostly they are differing from the spores of the Pteridophyts by their larger size and elliptical elongated shape (often winged), by the very often obliterated or absent three radiate scar and by the presence of a longitudinal ridge (many of the palaeozoic as well as mesozoic *Pteridosperms,* specially the group of the *Medullosae* and the *Cordaitales).* In the second more advanced degree the content of the ripe microspores do not exhibit the segmentation into a well defined multicellular tissue. Their size and shape is in the whole similar to the more advanced stage of the just foregoing organization degree (rather large and elliptical in shape). At the germination they are sending off shert pollentubes containing still well developed ciliate mobile spermatozoids (Cycadeae, Ginkgoales).

As to the catching of the microspores (resp. pollengrains) by the female organs, we have to distinguish 3 successive stages. In the most of the gymnospermic plants these bodies are caught by a drop of mucilaginous liquid, which is secreted by the nucellus into the pollen chamber or the micropylar room. A higher stage may be observed in the group of the *Gnetineae* where the integument of the ovules is extended into a tubular organ with a glandular and funnel like enlarged end reminding strongly the style with the stigma of the Angiosperms. This special

stylelike integumental organ is here evidently taking up from the nucellus the original function of catching off the male spores. The third and final stage is the formation of the gynoecia or pistils as observed in the true angiospermous plants. Here the last mentioned function is transfered to the sporophylls enclosing the seeds, which fused together and are extended at the top into the well known stalklike style with the viscous glandular stigma adapted for retention of pollengrains. A very similar organ is also present in the group of the pteridospermic families of the *Corystospermaceae* and *Caytoniaceae*. But here the pistils are not built up of the whole sporophylls (only of the single fertile last leaflets of the rather large pinnate macrophyllous fronds) and the process of the polination is utterly identical with that of the "lower stages" of the Gymnospermae: the pollengrains are to be found within the small sac like ovaries often just upon the ovules and no pollentubes have been ever stated.

All the just mentioned facts concerning the gradual adaptation of the reproductive organs for the life on rather dry land are in favour of the following conception demonstrating the steps of the further evolution resp. differenciation of the cardinal evolutionary lines stated above:

In the macrophyllous line:					
Filicineae	Pteridospermae	Cycadeae		Gnetineae	Angiospermae
In the microphyllous resp. sphenopsid lines:					
Articulatineae Lycopodineae Psigmophyllineae	Lepidospermae Cordaitales	Ginkgoales	Coniferineae		
Cryptogamic (No seeds developed)	Seeds without embrya Pollengrains with multicellular content	No style and stigma developed		Style and stigma formed of the integuments	Style and stigma formed of the sporophylls
		Pollengrains without any well developed inner texture			
	Ciliate spermatozoids present		Pollen tubes transfering the immobile male gamets developed		
	Seeds containing well developed embrya				
Silurian, Devonian Carboniferous	Carboniferous a. Permian	Triassic, Jurassic and Cretaceous			Kaenozoic

This scheme in connection with our knowledges of the stratigraphical distribution of plants shows many interesting moments concerning the evolution of the "higher" vascular plants. The group of the *Cordaitales* appears here as a pteridospermic stage of the microphyllous resp. sphenopsid line. The same relation is evidently between the *Cycadeae* and the *Ginkgoales;* this last plant ordre appears as a cycadophytic stage of the sphenopsid evolutionary line. T h e c u l m i n a t i o n o f t h e p t e r i d o - e p e r m i c s t a g e o f p l a n t s e f b o t h m e n t i o n e d e v o l u - t i o n o r a y l i n e s m a y b e s t a t e d a t t h e e n d o f t h e p a l a e o - z o i c e r a i. e. d u r i n g t h e p e r m o c a r b o n i f e r o u s p e r i o d, t h a t o f t h e c y c a d o p h y t i c s t a g e d u r i n g t h e o l d e r a n d m i d d l e m e s o z o i c e r a (Triassic and Jurassic). The culmination of the Coniferineae is to be dated nearly between the era of the cycadophytic plant stage and between the period of the angiospermous plants i. e. during the Cretaceous. As evident there exists a rather pronounced regularity in the sequence of the organisation stages of the reproduction organs in the evolution of the "higher" vascular plants.

T h e p r o b l e m o f t h e o r i g i n a n d m o r p h o l o g i c a l n a t u r e o f t h e f l o w e r s. — As evident from an enormous number of fossil records from the late palaeozoic as well as from the mesozoic periods, simultaneously with the above described adaptation processus of the seeds and pollengrains still another morphologically very important processus concerning also the fructificating plant organs took place: t h e f o r m a t i o n o f t h e f l o w e r s. This consists in a very far reaching reduction of the sporophylls or even of the whole fertile branch systems and at the same time in a strong "condensation" of all participating members. The reduction of the sporophylls even in the macrophyllous evolutionary lines reached very often untill to the formation of only small simple leaflets or stalked small discs bearing several microsporangia or ovules and differing finally nearly by no essential features from a similarly reduced fertile members of the sphenopsid (microphyllous) evolutionary plant lines. It is highly interesting, that the flowers, which were developed within the sphenopsid (microphyllous) plant lines are mostly only of a strobiloid shape with rather elongated axis, reminding as to their outer appearence very strongly the fructifications of the cryptogamic *Lyco-podineae* and *Articulatineae,* whereas in the macrophyllous plant lines the far predominating type of flowers are more or less dislike bodies with a short and thick axis, like a kind of a compact dwarf shoot with a more or less cyclic arrangement of their members. *(Bennettitales, Gnetineae* and most part of the angiospermous plants), an outer zone of protective sterile leaves, the zone of the male sporophylls (resp. stamens) and in the centre of the disc (i. e. at the top of the axis) the female sporophylls.

The morphological problem of the often very large dislike flowers of the macrophyllous plant types is a rather simple one. That the single elements of such flowers do represent from the morphological comparative point of view enormousely reduced whole and originally rather complicated pinnate fronds (sterile or fertile) is best attested by the various transition forms of the male as well as female sporyphylls in various groups of the

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Cycadophyta. These flowers are thus of a very simple construction: a more or less shortened, undivided branch bearing spirally arranged protective sterile leaflets and in its upper part sporophylls.

More complicated conditions may be met within the sphenopsid ("microphyllous") evolutionary plant line. In the most primitive types, like in the group of the *Cordaitales,* we may state only simply organized strobiloid fructifications (flowers) consisting of a thin axis bearing spirally arranged fertile leaflets. They are grouped generally in greater number on certain more er less specialized branchlets of rather limited growth, which are provided by some scale like reduced leaves within the axils of which the single mentioned strobiloid flowers are placed. The male flowers (cones) kept this simply strobiloid constructien throughout the whole evolutionary processus untill to the most "modern" Coniferineae. But as especially evident on several late palaeozoic coniferoid types *(Walchia, Voltzia, Ulmannia)* the female flowers (cones) underwent various reductive processus during the later evolution. These oldest conifers bore rather large female conelike fructifications, the axis of which were provided by spirally arranged large sterile bracts with small budlike dwarf shoots in their axils. These last in several species of the genus of *Walchia* were bearing at the base some sterile leaflets and at the top 1—5 sporophylls, each provided by one ovule. In the genus of *Ernestiodendron* the number of the leaflets of these dwarf shoots is reduced mostly till to 3—5 and the dwarf shoots are at the same time plagiotropically flattened. In the permotriassic genus of *Voltzia* we see in the axils of the narrow lanceolate bracts a 5 lobed fructificating organ derived evidently from such plagiotropically flattened dwarf shoot by reduction resp. utter abortion of its axis and fusion of its sporophylls and in the group of the *Abietineae* we have finally to do only with a simple ovuliferous scale in the axils of the protective bracts. We see thus in the whole series of the Coniferineae a gradual reduction and condensation process leading from small budlike female flowers to only scale like ovuliferous organs sitting in the axils of the bracts. Another process, which took place more or less simmlutaneously with the just mentioned reduction of the female flowers in several genera of the Ceniferineae, consisted in the coalescence of the mentioned ovuliferous scales (originally simple flowers) with the protective bracts *(Ulmannia, Araucarineae, Taxodineae),* in the reduction or utter abortion of the ovuliferous scale (Cupressineae) and besides also in a gradual decreasing of the number of the bracts leading often to the formation of very small female cones. By these ways female strobiloid organs were formed, which though apparently very simple, cannot be compared morphologically with the male coniferous flowers, but which represent enormously reduced whole spike like inflorescences. Of a similar morphological nature as the just discussed female cones of the Coniferineae seems to be also the female conelike fructifications of the curious mesozoic *Podozamites* (joined unjustly by many botanists often to the *Cycadophyta*) called *Cycadocarpidium.*

Evidently slightly different processus took place in the evolution of the flowers of the *Ginkgoales* and of the coniferoid family of the *Taxineae.*

In the group of the *Taxineae* the reduction attained a special and extreme stage. Perhaps the "inflorescences" were already originally rather poor in "flowers" compared with the large cone like "inflorescences" of the ancestors of all above mentioned other Coniferineae. In all living (see in Velenovský) as well as fossil (Florin) *Taxineae* they are very small, budlike; their main axis bears several scalelike leaflets and in the axils of the leaflets sitting just at the aborted top of the axis are placed 1 (Taxus) or 2 (Torreya) extremely short fertile side branchlets corresponding morphologically to the fertile scales of the other Coniferinae i. e. to the small budlike "flowers" of the *Walchiae*. The ovules are deprived entirely of their sporophylls, are pushed terminally on the top of the respective "flower" brachlet (perhaps the fleshy arillus of *Taxus* represents the last remnant of the sporophyll). Thus in contrary to all other Coniferae, the radial symmetry of the single "flowers" and their budlike form is here well conserved; they are only extremely simplified, just as the whole "inflorescence".

In the *Ginkgoales* we are better infermed only about the floral conditions of the recent *Ginkgo biloba*. The single flowers are placed within the axils of scalelike reduced leaves of the brachyblasts, which bear generally at their ends normal leaves. As shown by very detailed anatomical studies, both, the male as well as the female fructifications, are simple flowers (no inflorescences). But their true axis is generally aborted and the apparent axis of the male "catkins" just as the long stalks bearing at the end one or 2 ovules are in fact organs arisen by fusion of the stalklike transformed sporophylls; only in exceptional teratological cases the original axis is prolonged and its vascular strand may be then followed within the centre of the mentioned false stalks. According to that in the *Ginkgoales* we have to compare from the point of view of the morphology the whole fertile brachyblasts with the spikelike inflorescence fructifications of the *Cordaitales* or with the inflorescence cones of the *Coniferineae*.

As evident from the above the female fructifications of the sphenopsid (resp. microphyllous) gymnosperms represent from the point of view of the comparative morphology whole branches bearing in the axils of leaves short fertile side twigs (cones). These whole inflorescences are in various manner and degree reduced, in extreme cases untill only a budlike and uniovular organ *(Taxus)*. These is an essential difference if compared with the flowers as met with among the macrophyllous gymnospermic groups. Both phylogenetical gymnospermic lines exhibit therefore also in the formation of flowers two quite different tendencies.

As to the flowers of the angiospermic plants, we know after all detailed analyses (Velenovský a. o.), that here we have to do with organs of the same simple morphological construction as we have seen in the macrophyllous gymnospermic evolutionary line (Bennettitales a. o.). It is highly interesting that the more complicated second type of "flowers" achieved by the*Coniferineae* is unknown among the angiespermic flowering plants. I see in this fact still one proof more as to my opinion that the *Coniferineae* represent the highest stage of the sphenopsid gymnospermic phylogenetical plant line which did not produce any further more "advanced" resp. more "complicated" flowering plant type. The type

of the *Cordaitales, Ginkgoales* as well as the *Coniferineae* cannot be therefore regarded at any rate as probable ancestors of any angiospermic group. For these last we have to look only somewhere to the macrophyllous evolutionary line ferns-pteridosperms-cycadophyta.

The evolutionary history of the typical angiospermic flowers, of which the first steps are slightly indicated in the Bennettitalean branch of the Cycadeae, is till present covered with a veil of mystery; we know only more or less the present final stage represented by the enormous variety of the flowers of the dicotyledonous and monocotyledonous plant families. Even among the oldest known angiospermic plant remains (lower and middle cretaceous) no transitional types between the well organised angiospermic flowers and some hypothetical ancestral primitive forms have ever been discovered. Just as in the Bennettitales even here the flowers may be variously complicated organs, just as rather simple ones. Their eventual simplicity can be no doubt either of an original feature or of a secondary character, gained by a more or less deep reduction. These problems, which certainly are of a cardinal importance as to the correct arrangement of the system of higher plants (see for instance the problem of the systematic relations of the apetalean families of the angiosperms Salicaceae, Juglandaceae, Cupuliferae a. o.) represent one of the most delicate and most difficult task of the whole phylogenetical systematic of plants, because in spite of our very advanced knowledges in palaeobotany our knowledge of true ancestral types of the angiosperms is nearly null; between the pteridospermous and cycadophytic types, which without any doubt must be regarded as the nearest allies of the ancestors of the angiosperms, and the true angiospermous plant type exists a very large gap, which till present did not succeed to be overarched. A considerable obstacle in this respect represents also the extreme rarity of fossilised angiospermic flowers, especially from the late mesozoic times. The palaeobotany does not tell us therefore nearly nothing concrete about the origin of the various cardinal types of the angiospermic flowers, and all our opinions there about generally are mere speculations gained only by thorough comparing of the flowers of various still existing plant types. From a quite general point of view we may point out in the evolution of the fertile organs of the angiospermous plants a processus utterly parallel with the origin of the very complicated female cone like fructifications of many of the Coniferae, which as already mentioned were formed from a whole branched system bearing numerous small simple cones after an enormous reduction and condensation into an apparently rather simple cone like body. Just here in the angiosperms the single flowers are very often placed on slender twigs of special branched fertile systems (the inflorescences) and in many cases we see that these systems on account of the reduction of the flower stalks and eventually also of the gradual reduction of the flowers themselves were transformed into special individualised fertile bodies reminding in a certain measure simple flowers (just as the mentioned female "cones" of the conifers) e. g. cylindrical cone like catkins of the *Amentiferales*, capitula of the *Compositae*, the various oval till cylindrical strobiloid inflorescences of the *Moraceae*, *Platanaceae* a. o. In this respect we may observe an utter analogy between

the organisation of the highest sphenopsid (microphyllous) plant types (Coniferineae) and the highest macrophyllous plant types (Angiospermae). But this whole problem of the evolution of the angiospermic flowers on account of lack of sufficient palaeontological evidences, is beyond the sphere of palaeobotany and connot be further discussed in this paper.

The morphological problem of the roots represents one of the most obscure tasks of the phylogeny of vascular plants. The palaeobotany presents only very stigny stories about. The chief reson may be that these organs are, — as justly suggested by Zimmermann a. o. — without any doubt underground organs, which were formed and specialized very soon, perhaps still before the perfect differenciation of the leaves. There are several facts, which seem to admit the possibility that just as the leaves also the roots of various plant types are not always of an equal morphological significance resp. origin.

In many of the most primitive landplants, the siluro-devonian *Psilophytineae*, we see that the function of the roots was performed by large rhizomelike systems of underground branches, which in several cases were quite smooth *(Asteroxylon* a. o.) in others *(Rhyniaceae,* several *Coenopteroid* ferns) provided by numerous hairs (like true roots). A similar state may be met with still in the recent species of the family of the *Psilotaceae.* Lignier termed this very primitive state of underground absorbing branch organs as "rhizome primordiale". — Another conditions may be seen in the palaeozoic Lepidophyta, where an evident bipolarity of the stems is developed and where the lower end of the stems is equally branched as its upper end but instead of leaves these underground branches (called *Stigmaria)* bear in a similar arrangement dichetomously divided rootlike organs *(appendices)*. A certain reduction of this whole underground absorbing apparatus may be observed in the mesozoic *Pleuromeia* and *Nathorstiana* as well as in the recent *Isoëtes*. The very regular distribution of the appendices on the surface of the stigmarian branches points evidently to a close relation to the leaflets of the overground normal assimilating branches. Without any doubt the rootlike appendages of the *Lepidophyta* — *Isoëtes* series are derived from conveniently adapted and reduced small lateral branches, just as the microphyllous leaflets on their over ground branches, of course already in a very old ancestral stage of these whole evolutionary series, when perhaps also their assimilating leaves were still in a state of developing. Another similar but semewhat less regularly constructed underground absorbing organs were discovered in the devonian *Aneurophyton germanicum*. I regard therefore these appendices organs as original lateral branches with rhizome primordial features, which on account of special environmental conditions became more and more endogenous (in the palaeozoic *Lepidophyta* not yet perfectly, in the recent *Isoëtes* already completely as normal roots) receiving thus at the same time the character of more or less adventious organs. The most primitive stage of such *Stigmaria* branches with the named "appendices" rootlike absorbing organs may be seen in the middle devonian *Barrandeina*. Here several stem cast were discovered which bear partly (i. e. on their above ground parts) normal

leaflets provided by stalklike decurrent petioles and flat wedge shaped lamina, partly (on their basal i. e. underground parts) similar stalklike petioles, which bear no lamina, but which are divided at their ends rather irregularly forklike into several long rootlike strands. I believe therefore that just in *Barrandeina* we have a typical case of underground branches representing an intermediate stage between normal leafy branch systems and between the underground Stigmaria organs. — A slightly different kind of root organs is developed in the devonian *Pseudosporochnus*. Here the lower end of the whole plant body is tuber like swollen and is provided by a large number of rather irregularly disposed long and dichotomously divided rootorgans similar to some long "appendices" of the palaeozoic *Lepidophyta*. Here no *Stigmaria* branches were formed but all large branches of the lower end of the stem are immediately transformed into "large appendices" — roots, without any doubt by a similar way as the small appendices of the *Aneurophyton, Lepidophyta* and *Barrandeina*. I believe that just this case of *Pseudosporochnus* may be regarded as an example of the origin of roots of the most part of plants, which in contrary to the *Lepidophyta* have lost their bipolarity in a very early ancestral stage. Their roots from the purely comparative morphological point of view may be compared thus with whole large branch systems adapted for absorbing function still better than the original rhizome primordiale (their adventitious character, formation of root caps a. o.), which must be regarded as their older stage. Such roots as to the kind of origin are comparable with the macrophyllous leaves.

According to all above, we may point out 2 d i f f e r e n t s t a g e s in the evolutionary history of the absorbing underground plant organs: r h i z o m e p r i m o r d i a l e a n d t r u e r o o t s. The second of both exhibit just like the leaves t w o d i f f e r e n t c a t e g o r i e s as to their origin: a p p e n d i c e s (of "sphenopsid" nature) a n d n o r m a l r o o t s (of macrophyllous nature). W e h a v e b u t t o p o i n t o u t t h a t t h e s e d i f f e r e n t k i n d s of r o o t o r g a n s a r e i n n o d i r e c t r e l a t i o n s w i t h t h e k i n d o f a s s i m i l a t i n g l e a f o r g a n s of the respective plants. So for instance the rhizome primordiale are to be found in the leaf less *Rhyniaceae* just as well as in the sphenopsid (resp. "microphyllous") *Psilotaceae,* the appendices are known in the microphyllous *Lepidophyta,* but not in the equally microphyllous *Lycopodiaceae* or *Selaginellaceae;* we know them in the *Aneurophyton,* which as to its assimilating organs represents a transition to a macrophyllous type. True normal roots are to be met among sphenopsid (resp. "microphyllous") plant types *(Lycopodiaceae, Selaginellaceae, Articulatineae),* just as nearly in all various macrophyllous forms.

The notion of the morphological nature of the root organs is evidently of less importance for the systematic and taxonomy of plants than that of the assimilating leaves. Neverthelless it help us to comprehend more clearly the relations of several "difficult" types of vascular cryptogams *(Isoëtes, Psilotum, Tmesipteris a. o.).*

III. The role of the comparative anatomy and embryology as a guide in the systematic of the great plant divisions.

In the historical (stratigraphical) chapter we have already mentioned that in the silurian and in the devonian times also land plants existed, the body of which was built up of nonparenchymatous tissues i. e. of a mere plectenchyma (*Algomycetes* of R. Kräusel) like in the present non green fungi or in several larger types of algae, and we have deduced that t h i s plectenchymatous kind of tissue represents an essentially lower stage in the evolution of plant tissues than the parenchymatous resp. other derived coherent tissues as found in the most of the present green land plants. The bodies of these higher plants are differenciated internally into several cardinal unities as the ground tissues, the conducting tissues, cortical tissues a. o., which all in the course of the development of the plant body were gradually differenciated from the parenchymatous tissue of the meristematic regions according to the function of the respective developing plant organs or members. The chief affair of the comparative anatomy from the point of view of the phylogenetical systematic of the great plant divisions may be seen in two purposes: 1. To state within which organs of the higher plants the inner structures of the tissues undergo to rather immediate changes evoked by direct influences of the environments, and 2. in which places of the plant body the inner structures are the less in contact with the environmental conditions or this contact is only indirect. — In the first case we have only very minimal chance to find out characters reminding anatomical features of the ancestors of the studied plants and therefore also relations to some allied contemporaneous forms (as such organs may be regarded e. g. the last divisions of the leaves, finer branches of the roots a. o.). In the second case we have to do with structures the changes of which may be regarded as highly dependent of the gradual evolution of the respective plant species and less attacked by the local or momentary influences from outward. It was already sufficiently attested by many botanists as well as palaeobotanists (see especially the excellent work by P. Bertrand « Les végétaux vasculaires ». Paris 1947), t h a t s u c h p l a c e s a r e t o b e f o u n d e s p e c i a l l y w i t h i n t h e s t e m s (stalks) a n d w i t h i n t h e l e a f r h a c h i s e s [there are of course also other organs, which on account of various protective arrangements are not exposed to direct influences of the environmental conditions as e. g. the reproductive organs, the reproductive bodies (spores, gamets, seeds, fruits a. o.)]. Otherwise it seems according to many detailed studies (Florin, Harris, Thomas) that also the main features of the stomata in the cuticles are not directly influenced by the environments (I remember at least the importance of the haplocheilic or syndetocheilic form of the stomata for the natural systematic of the gymnospermous plant groups as stated by Florin, Thomas, Harris a. o.).

Most of the anatomical studies are especially attesting t h e g r e a t i m p o r t a n c e o f t h e c o n d u c t i n g v a s c u l a r t i s s u e s

within the stems or leaf rhachises and here not only of the character of their cellular elements, but also of the mutual relations of the various tissues of which they are built up. It was also already emphasized that we have to study such structures not only in their adult stage, but also analogically to the conditions in the animal kingdom, in various stages of the development of the respective plants, i. e. from the embryological point of view. In this last respect the botanists have still another advantage. It is a well known fact that nearly all organisms do repeat more or less in their ontogeny at least several of the chief stages, which they passed during their phylogenetical evolution (the principle of Serres-Müller). And just here as to the anatomical structures of the higher plants we must add still another well known experience attested by the works of all palaeobotanists of the newer time, that even on adult plants various inner textures of the developing organs (especially leaves and their rhachises) pass at first several more primitive stages than as seen in their distal well developed main parts. Thanks to the numerous studies by D. H. Scott, Worsdell, Ch. and P. Bertrand, R. Corsin, Sahni a. o. we know, that just these more primitive structures represented once the adult stage, which were attained by the ancestors of the respective studied plants. It is especially within the lowest (basal) parts of the lateral twigs or of the leaf rhachises or at the branching places of these organs, where such ancestral anatomical structures are often to be observed. Therefore the conditions of the vascular strands became an excellent expedient for phylogenetical and systematical deductions.

As to the single elements of the vascular strands it was stated that especially the character of the tracheids and the eventual presence or absence of true vessels is of great importance. For instance true well and typically developed vessels are present first in the angiospermous plants except of several very archaic forms (Drymis a. o.). The tracheids of the more primitive pteridophytic types exhibit mostly only spiral, annular or scalariform sculptures (*Psilophytineae, Lycopodineae* incl. the palaeozoic *Lapidophyta*, ferns a. o.). Bordered pits are characterising the tracheids of rather more derivated plant groups (several Articulatineae, Pteridosperms, Gymnosperms a. o.) and we have here to distinguish two evidently progressive stages: tracheids with densely crowded and generally multiseriate bordered pits as a more primitive type (*Articulatineae, Pteridosperms, Cycadeae, Cordaitales* and several older conifers: *Walchiae, Voltziae, Araucariae* a. o.), and tracheids with developed Sanio's rims and therefore remote pits as a rather derivated type (*Ginkgoales,* most part of the *Coniferineae*).

As to the arrangement of the fundamental tissues within the vascular strands (stele) of the stems or branches, the conditions have been recognized already in so many fossils (even in those of the oldest periods wherefrom any landplant remains were ever discovered) that it was possible to establish not only various types characteristical for different larger systematical groups, but also to deduce the more complicated types from several more primitive ones. It was for instance possible to recognize 2 divergent evolutionary lines in the group of the *Lycopodineae*, which cor-

respond well with the morphological character of the spermatzooids as well as with that of the roots: 1. the series of *Lepidophyta* with the successive stelar evolution from protostelic to siphonostelic or even untill imperfectly eustelic (several *Sigillariae*) types with cylindrical shape of the whole vescular strands, and 2. another series of forms with actinostelic till plectostelic type of the vascular strands, which evidently are very remote from the first series (eg. *Lycopodium, Selaginella,* the silurian *Barragwanathia*). Also in the *Articulatineae* we have to do evidently with more evolutionary lines of which especially 2 are very distinct: 1. the actinostelic *Sphenophylla* and 2. the siphono-till typically eustelic equisetalean type. The group of the ferns exhibits, — with the exception of several actinostelic Coenopterides — , an evolution from protostely through the syphonostely untill to dictyostely and eventually even untill to polystely *(Marrattiales, Ophioglossales)*. There are among the Pteridophyta still many other types showing various variants of actinostely till plectostely and attaining even a kind of polystely (*Asteroxylon, Cladoxylon, Stauropteris, Psilotum, Tmesipteris* a. o.). Evidently such types cannot be put into relations with any of the mentioned proto-siphono-eustelic or proto-siphono-dictyopolystelic evolutionary lines. Very complicated stelar arrangements resp. evolutionary lines were found in the Pteridospermic plant groups. We may state here for instance tendencies of an evolution from nearly protostelic types to siphonostely *(Heterangium, Lyginopteris)* or even to an imperfect eustely (several species of *Heterangium*), further we have recognised here typically protostelic types with tendencies to actinostely *(Tetrastichia)* as well as variously complicated polystelic forms *(Medullosae)* attaining often very similar stelar conditions as known from the group of Cycadeae. Far simpler conditions are among the *Coniferophyta:* here is to be observed a successive improvement of an eustely arisen without any doubt from a siphonostelic ancestral type with cylindrical vascular strand. The same conditions are to be met with in the most part of the dicotyledonous angiosperms. In several groups of the Dicotyledons (like *Casuarina, Piper, Nymphaea, Thalictrum, Papaver* a. o.) a further change in the arrangement of the single strands of the cylindrical vascular system took place, which led to the dislocation of the single eusteles in 2 or even more concentric rings i. e. to a vascular system known under the term of atactostely. This last arrangement became the most common and well established vascular system of the *Monocotyledons,* which must be therefore regarded from the anatomical point of view as a still further derivated plant type.

These just mentioned several examples may suffice to show the great importance of the comparative anatomy, if justly applied, for the construction of the natural evolutionary lines resp. for the correct definition of the various plant groups in a natural system. We have here a very sensible corrective of our eventual purely morphological considerations. We have seen for instance that just for anatomical reasons the great phylum of the *Lycopodineae* must be regarded as containing at least 2 rather independent evolutionary lines.. Something similar was stated in the *Articulatineae*. Also the palaeozoic *Pteridosperms* contain at

least 2 very distinct and considerably independent lines (the *Heteran-gium-Lyginodendron* series and the *Medullosae*. For similar reasons we cannot join phylogenetically the *Coniferophyta (Ginkgoales, Cordaitales* and *Coniferineae)* to any hitherto known pteridospermic type and it seems according to several other features (seeds, pollengrains a. o.) that just the coniferoid group of the *Cordaitales* represents the pteridospermic stage of the whole phylum of the *Coniferophyta* and that the next ancestral still more primitive conipherophytic type must be pursued everywhere among the so called Pityae*) from the end of the older palaeozoic era.

Another extremely important task concerns t h e c o n d i t i o n s o f t h e v a s c u l a r s t r a n d s i n t h e l e a f p e t i o l e s o r t h e l e a f r h a c h i s e s. This problem has been discussed in the palaeobotanical lite-rature especially in detail with regard to the conditions in the macrophyl-lous groups of the ferns, pteridosperms and cycads; very valuable deduc-tions have been gained in the first of them i .e. in the ferns. On many examples of palaeozoic ferns and several fernlike plants (*Cladoxylon, Stauropteris*, the group of the *Phyllophorales* a. o.) the gradual trans-formation of large branch systems with radial symmetry into systems with a simpler symmetry (along only 4 or 2 planes) untill to the for-mation of dirsiventrally symmetrical branches representing then the rhachises of large dorsiventrally symmetrical fronds, was rather clearly shown. We must add that this inner processus was more or less parallel with the gradual evolution of the outer appearence of such fronds i. e., with their morphological differenciation resp. stabilization as leaforgans. This transformation of large branch systems into dorsiventral leaf organs ("fronds") are known already in many devonian plants like the genera *Protopteridium, Aneurophyton, Rhacophyton, Archaeopteris* a. o. but unfortunately we are notyet well informed about the features of the vascu-lar strand resp. of their relations to the stelar conditions of the suppor-ting stems. Better knowledges were already gained as to the plecto- resp. polystelic *Cladoxylon*. Here the frondlike lateral branches exhibit simpler stelar conditions than the supporting main stems, the single steles being at the same time orientated symmetrically only to one plane *(Hiero-gramma, Arctopodium)* and the steles of the still thinner side twigs of the last ones exhibit a still simpler and essentially dorsiventral arrange-

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*) We have notyet any reliable documents about the nature (—whether crypto-gamic or gymnospermic?—) of these plants, of which mostly only casts of stems have been discovered. But it is very interesting to note that in so old strata as most of the Pityae occur, no true seeds have been stated with utter certainty. This group of incompletely known plants seems therefore to represent true cryptogamic resp. pteridophytic ancestors of the whole assamblage of the *Coniferophyta*. We must therefore suppose in the case of the *Coniferophyta* an utterly independent origin, an evolutionary line without any relations either to the palaeozoic Pterido-sperms or to any group of the ferms, which is well in agreement with our pre-viousely presented opinion about the rather direct relations of the *Coniferophyta* with some sphenopsid (resp. microphyllous) types of the oldest land flora of the silu-rodevonian era derived on the bases of a thorough morphological comparing of their leaves and sporophylls with those of the various archaic types of the same era (—our group of the *"Psygomophyllineae"*—). That means, that the *Coniferophyta* have evidently nearer relations to the *Lycopodineae* and *Articulatineae*, than to any macrophyllous group (ferns, Pteridosperms, Cycadeae).

ment *(Syncardia)*. Within the monostelic group of the *Phyllophorales* the lateral branches (so called "phyllophores") exhibit in many more primitive genera *(Clepsidropsis, Dineuron, Metaclepsidropsis, Zygopteris, Etapteris* a. o.) a strictly bilateral symmetry according to 2 planes, their vascular strands being of a biscuit, H or X shape and first the pinnae born upon them show a dirsiventral organization. But in several more advanced forms *(Ankyropteris, Asterochlaena, Tubicaulis)* we have to observe a more or less horseshoe like curvation of the cross section of the vascular strand i. e. a gradual transformation into a dorsiventraly symmetrical organ is here quite evident. Still more transformed and simplified types are to be stated in the groups of the *Inversicatenales* and *Osmundales*. Both exhibit in adult stages of their petiols already well elaborated horseshoe shaped (in cross section) vascular strands (the first of both abaxially opened, the other one adaxially opened). But at their very base we easily recognise that this form of vascular strands was derived from a radially symmetrical tubular (or even protostelic) strand which passes through several at first bilateral than more and more dorsiventral stages.

Following very thoroughly these and various other stelar conditions of the frond rhachises and paying of course also attention to the stelar conditions of the stems, it was (as shown especially by the excellent works by P. Bertrand and R. Corsin) possible to divide the various ferns and fernlike plants into several evolutionary lines, which have perhaps only very problematical or at least very remote mutual relationship, as for instance the *Aneurophyton* and *Rhacophyton* series, the *Stauropteridales, Cladoxylales, Phyllophorales, Inversicatenales, Osmundales, Marattiales, Ophioglossales, Leptosporangiales* a. o.

In the higher plant groups (Pteridosperms, Cycadeae or even in the Angiosperms) the ancestral stages of the vascular strands of the leaf petioles are only very undistictly or even no more visible. They are like completely effaced on account of a very long and farreaching phylogenetical evolutionary processes. We cannot expect that the plant organs in so complicated cases would recapitulate in their ontogeny, which represents only an enormousely shortened picture of the whole phylogenetical evolution, all main stages, which they have passed once in their ancestral forms. The extreme case is represented no doubt just by the ontogeny of the leaves of the angiospermic plants, where we are in vain looking to find out such clear pictures of ancestral stages as fond in the basal parts of the petiols or their ramifications in the ferns.

IV. Outlines of the phylogenetic relationship of the great plantdivisions based on palaeontological evidences.

A. The relations of the lower i. e. thallophytic plants.

As evident from the foregoing lines, the palaeontological documents of this great division of plant kingdom are very unsufficient for some far reaching speculations about the evolutionary history of the single
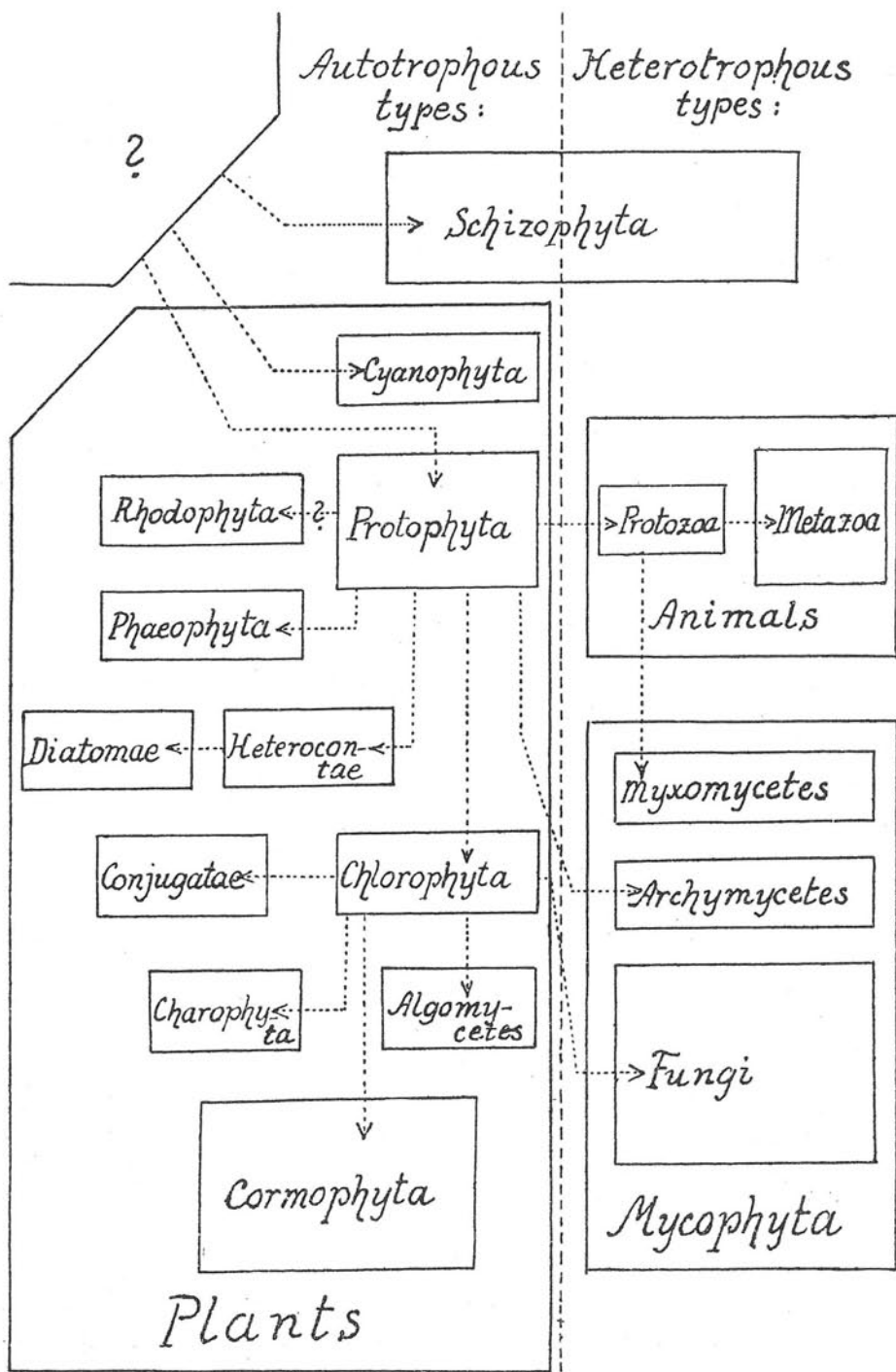
Fig. 1.

groups in consideration. Our opinions there about will evidently always depend in the first range on the morphological, anatomical and cytological conditions as stated by a very thorough study of the recent plants. We have only to rectify our deductions according to the evidences yielded mostly by the stratigraphical branch of the palaeobotany. By this wey an enormous age of the *Schizophyta* as well as of the *Cyanophyta* was stated. It was also demonstrated an unexpected relatively high age of the red algae *(Rhodophyta)*, which show so many strange features (not in the last range also their non motile reproduction cellules) compared with all other algal types. And finally such investigations have demontrated at least partly an equally high age of the *Fungi* with the age of the most of the *Algae*, which both groups seem to represent two in all essential features parallel but polyphyletic lines. They have shown also the rather derivated character of the algal group of the *Bacillariophyta (Diatomaceae)* as assumed already on account of their cytological and biochemical pecularities by many algologues (Pascher); their occurrence is to be traced back only untill to the jurassic period. Something similar seems to hold also for the group of the Charophyta, though here several discoveries seem to attest a much higher age (the mentioned palaeozoic *Sycidum* and *Trochiliscus*).

Taking all these facts into consideration we may trace the evolution and relations of all great divisions of lower plants in the following way: Fig. 1.

The chief aim of this scheme is to demonstrate first the relative independence of the *Schizophyta, Cyanophyta* and the assamblage of all other organisms with well developed cell nuclei and producing ciliate zoospores resp. gamets (resp. those derived from such types as forms with non motile gamets or spores), second to show the derivation of the three main types resp. kingdoms of heterotrophous non green living beings the Schizophyta (vulgo Bacteria), the animals and the Mycophyta (vulgo Fungi), and finally the relations of several plant types, which during their evolution (and no doubt on account of special environmental conditions) have lost the motility of their reproductive cellules *(Rhodophyta, Conjugatae, Diatomaceae, most part of the higher Fungi)*.

The problems concerning the relatively independent position of the *Schyzophyta* and the *Cyanophyta* was already sufficiently discussed at the beginning of this paper and needs no further notes. We may perhaps only add that several types of Bacteria seem to represent mere derivatives of Cyanophyta after the loss of their green pigments, which problem waits still for further investigations.

An open question seems to be the phylogenetical problem of the red algae, the *Rhodophyta*, which have well developed cell nuclei, but which differ essentially from all other "caryonta" by an utter absence of ciliate motile propagation cellules; in any of the hitherto known type neither zoospores nor cilitate gamets were ever observed. The *Rhodophyta* as known at present exhibit a rather advanced

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organizations as well as a very regular kind of sexual reproduction. As to the first particularity I may note that the lowest type of organization here observed are branched filaments. Otherwise their more complicated thalli are the result only of a more or less regular close interweaving of such branched filaments. We do not know any unicellular red algal type which would yield us at least a slight picture of some ancestral forms from which the filamentous red algae were derived. And finally we must take into consideration, that even in very old periods of the Palaeozoic era already very complicated forms with massive tuber like thalli occur (the family of the *Solenoporaceae*). This high age of the *Rhodophyta* agree without any doubt with their high specialization of the whole reproduction act and with the rather complicated form of their thalli reminding even in many cases strongly the higher leaf bearing plants. It was already several times suggested that this group has perhaps no relations with the other "caryontal" plant or animal types and that it is to be derived as a further higher descendent directly from the Cyanophyta, just on account of its non ciliate and non motile reproduction cells. It was also pointed out that just several types of this last named group (e. g. the marine blue green alga *Trichodesmium erythraeum* living in an enormous quantity in the Red Sea) are provided by similar red pigments as known in the *Rhodophyta*. I believe that this hypothesis is lacking absolutely any more concrete basis; the differences not only as to the cytological features, but also as to the morphology of the thalli as well as of the reproduction acts are too strong. Indeed we do not yet know any true intermediary types. But it seems to be also probable that the red algae stand much nearer to other "caryontal beings" than generally accepted in the last time. It is very probable that they were specialized for quite special and unusual living conditions (adaptation for the life under much diminished light radiation, in much deeper levels of the sea waters a. o.) in a very early period before the elaboration of all other algal groups. The eventual loss of ciliae of their reproduction bodies (if such ever have been developed) may be then regarded as a similar reductive processus as observed also in other algal groups e. g. *Diatomaceae, Conjugatae* or as normally stated in the large group of the *Fungi*. Only by this way, which is in agreement with the surprisingly early occurrence of already very high organised types of the *Rhodophyta*, this curious isolation in the plant system is to be understood.

All other thallophytic evolutionary lines are rather easy to be understood, especially on account of their cytological and morphological pecularities. We meet some difficulties only in the cases of the most advanced forms of the *Charophyta* and of the fossil *Algomycetes* on account of an absolute lack of any types showing at least slightly several ancestral features leading to some very "low" unicellular organisms. Without any doubt we stand here before a somewhat similar fact as in the just discussed problem of the red algae. Both named groups according to their stratigraphical distribution exhibit also a considerably high age though perhaps not quite as enormous as the red algae. — The *Algomycetes* represent a typical kind of siluro-devonian plectenchymatous

highly "derived" land plants, which at present are still too fragmentary known. We do not yet know at present any fossil, which might be considered as a transition form to some of the other algal types. It was often assumed that several forms of the *Algomycetes* (e. g. the *Prototaxites*) should be considered as brown sea weeds. But in the most recent time many pecularities were stated, which seem to attest their appurtenance to some green forms, mostly landplants (cuticularised epidermal textures [*Foerstia, Protosalvinia, Nematothallus*] anular thickenings of certain filaments [*Nematothallus*] a. o.) and the discovered tetraspores of certain species attest, that the known algomycetal thalloid bodies represent a sporophytic generation. I am therefore inclined to see in the *Aygomycetes* a special very advanced type of green algae, specially more or less adapted to the life on land, which very soon retreated, giving way to the still more advanced and still better for land life adapted primitive forms of the *Cormophyta*, the *Psilophytineae*. — In the *Charophyta* the ciliate spermatozoids and the purely green chloroplasts indicate without any doubt also to a relationship to the *Chlorophyta*. Their very advanced kind of reproduction reminding so much all "higher" plants (especially *Bryophyta)* and the rather very stabilised morphology of their thalli (the verticillate arrangement of the branches, which are built up of specially enlarged cells containing eventually more nuclei arisen by amitotic division) point to a rather derived, highly specialized and relatively old plant type. And as already told, we may indeed trace undiscutable *Charophyta* deep back into the mesozoic strata and besides several Chara-resembling spores are well known already from the siluro-devonian periods *(Sycidium, Trochiliscus)*. All these facts seem to me to attest the view, that the *Charophyta* are a rather old evolutionary line derived from the green algae and more or less parallel to the groups of the *Siphonocladiales* and *Siphonales*.

The other remaining great algal divisions *(Phacophyta, Heterocontae, Bacillariophyta, Chlorophyta* and *Conjugatae)* indicate very clearly by several of their primitive types to an origin from the group of the chlorophyll bearing and therefore autotrophous flagelloid protists (termed generally as *Phytomastigina, Flagellata* or *Protophyta)*, which exhibit at the other side an undeniable relationship to the heterotrophous and often very similar but animal like protists, the *Zoomastigina*. We stand here before an assamblage of living beings, of which it is often very difficult to tell, whether we have to consider them as plants or as animals. Many scientists regard them justly therefore as an ancestral type, which gave rise to the most of the plants just as to all animals and they unite them all under a common term of the *Mastigophora* (Doflein a. o.).

Among the plantlike still living *Mastigophora* i. e. the *Protophyta* (resp. *Flagellata* or *Phytomastigina)* generally the following divisions are distinguished (Doflein a. o.):

1. *Chrysomonadina*

2. *Cryptomonadina*

3. *Dinophlagellata*

4. *Euglenoidina*

5. *Phytomonadina (Volvocales)*

6. *Chloromonadina.*

The green groups 3, 4 and 6 represent partly rather very fixed flagelloid types, partly forms highly specialized for special kind of life conditions (especially many forms of the gr. 3 and 6), which underwent no far reaching evolution. Only within the group of the *Dinophlagellata* (3) are known several rare species which attained a sessile, alga-like stage (the family of the *Phytodinideae: Gloeodinium*).

The *Chrysomonadina* (1) exhibit rather clear cytological as well as morphological relations to the algal groups of the *Heterocontae* and *Bacillariophyta*. They are provided by special yellow till yellow brown pigments (karotene, phycoxanthene a. o.), by which also the *Heterocontae* and *Bacillariophyta* are distinguished. Many algologues unite therefore these three groups under a common term of the *Chrysophyta*. Otherwise there are several other pecularities concerning especially the character of the gamets and zoospores as well as of the resting zygotes. Especially in the morphology of the resting zygotes of the *Chrysomonadina* are visible certain common features with the morphology of the cells of the *Heterocontae* and of the *Bacillariophyta:* their cell walls are composed of two mostly unequal pieces and are often slightly silicified. Also the shape of the zygotes in these three groups exhibit often certain strong similarities The incrustation of cell walls by quartz is strongest developed in the *Bacillariophyta*, whereas in the *Heterocontae* it is only very slight and in many species utterly missing (strongest in their zygotes). The production of motile zoospores and gamets is in the *Baccillariophyta* mostly utterly suppressed (we meet it only in several rare cases in the group of the marine *Centricae*). None of these three groups achieved a higher more "complex" shape of thalli than mere cell colonies or filaments composed of rather independent cells. Palaeobotanical records are of course rather very scarce except the quartz-encrusted diatoms. These last are known as mentioned up from the triassic and jurassic periods. Several silicius or calcareous shells bearing *Chrysomonadina* are to be traced back untill into the cambro-silurian times *(Coccolithophoridae, Discoasteridae, Silicoflagellidae* and *Ebriidae)*. Several species related to the genus of *Botryococcus* of the group of the *Heterocontae* were discovered first in the Carboniferous *(Pila);* it was also suggested that the ordovician alga *Gloeocapsomorpha prisca* of the bituminous shales from Estonia known as kuckersit may represent also a botryococcalean alga, but others believe it to be of cyanophytic nature related perhaps to the genus of *Gloeocapsa*. According to all these dates the whole evolution in this chrysophytalean assamblage may be sketched in the following way: fig. 2.
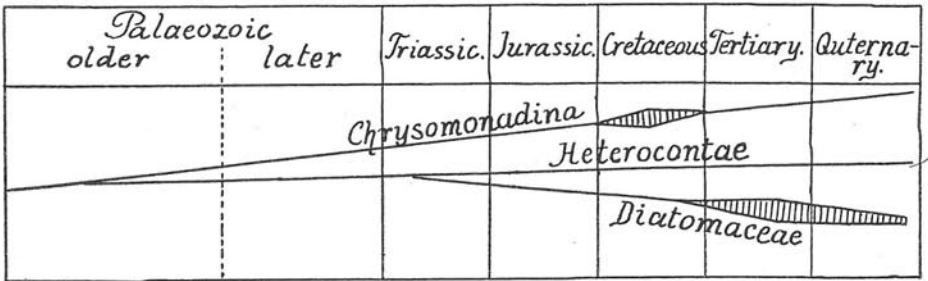
| Palaeozoic | | Triassic. | Jurassic. | Cretaceous | Tertiary. | Quaterna- |
older	later					ry.
		Chrysomonadina				
			Heterocontae			
			Diatomaceae			

Fig. 2.

Very unsufficient are our records as to the history of the brown algae, the *Phaeophyta*. The various sea weed like imprints, which are known already very early in the sediments of the older palaeozoic times, cannot be taken more seriously into consideration; they attest only very imperfectly the rather very high age of the more advanced and morphologically highly defferenciated phaeophytic types. A certain picture of the ancestral forms of the *Phaeophyta* was gained only by a very thorough study of several very primitive forms of this group (the family of the *Phaeocapsideae*). Such forms lead us evidently by the way of the filamentous *Phaeothamnion* and some genera representing only mere cell colonies like *Phaeocystis, Naegeliella* a. o. untill to the group of the *Phytomastigina* in general, perhaps also to the *Chrysomonadina* or to the *Cryptomonadina,* a group of the flagelloid *Protophyta* with laterally placed flagellae just as in the zoospores or gamets of the *Phaeophyta,* and provided by similar brown or yellow brown pigments as found in this last algal group. No doubt on account of a very high geological age of this whole phaeophytic evolutionary line, though perhaps not as enormous as in the case of the *Rhodophyta,* the relations to the flagellatean types were already long ago strongly effaced, much more than in the following case of the *Chlorophyta*.

Still more evident is the ancestral stage of the *Chlorophyta:* the *Phytomonadina*. They are mostly regarded as directly the most primitive division of the *Chlorophyta* and then termed as the ordre of the *Volvocales*. As the first steps of the derivation of more advanced chlorophytic algal types may be regarded the sessile stages, the so called Palmella-stadium, which are leading to the colonial forms of the *Tetrasporales* and *Chroococcales*. Further evolution is evident from the study of various filamentous types of the group of the *Ulotrichales,* which contains even several types forming large foliaceous thalli *(Ulvaceae)* built up of parenchymatous tissues. A special tendency in the evolution of the *Chlorophyta* may be seen also in the formation of large multinuclear cells *(Hydrodyction, Protosiphon,* several rare species of the *Chaetophoraceae* and *Trentepohliaceae),* which tendency no doubt led to the *Siphonocladiales* and *Siphonales* (with the highly specialised calcarous *Dasicla-*

daceae and *Codiaceae*) and in another direction perhaps also to the already mentioned *Charophyta*. A special problem are the *Conjugatae*, unicellular *(Desmidiaceae)* or filamentous *(Zygnemaceae)* green algae the cellules of which are very independent even if connected into filaments. Their special peculiar kind of reproduction without ciliate gamts or zoospores remember lively the conditions of the *Bacillariophyta*. Also the shape of the cellules (especially in the family of the *Desmidiaceae)* exhibits many common features with the *Bacillariophyta*. We have to do here with very similar evolutionary tendencies and the *Conjugatae* are therefore to be regarded as a green parallel line to the chrysophytalean line of the *Bacillariophyta*, arisen very soon from the green *Phytomonadina* and developed parallelly to the normally organized unicellular *Tetrasporales* resp. *Protococcales* and several more advanced filamentous types (of the group of the *Ulotrichales)*.

The phylogenetical evolution of the various great divisions of the true *Algae* from the flagelloid *Protophyta*, exhibits several interesting main tendencies. The first step in all above mentioned lines is represented by the stabilization of a non motile, sessile stage ("Palmella-stadium"). Than comes the arrangement of such sessile cells into variously shaped colonies or the arrangement into filaments, in which all cells are functionally rather independent. As a still later stage are to be regarded such filamentous forms (eventually branched), where the cells are in many mutual relations and eventually specialized for various functions. From such filamentous types may be derived forms where the filaments being more or less regularly interwoven and closely adpressed compose large, rather compact and often even very ornamental thalli (thalli composed of rather irregularly interwoven filaments are very common in the groups of the large brown sea weeds like the *Laminariaceae* and the *Fucaceae*, in the green *Codiaceae*, in the fossil *Algomycetes;* thalli composed of rather regularly mutually adpressed filaments are very characteristical for the red *Rhodophyta)*. We may regard this kind of texture of the algal thalli as a lower stage of forming of larger massive plant bodies. Another kind of evidently higher rank is the formation of parenchymatous tissues. Examples are known among the *Phaeophyta (Sphacelariales, Dictyotales)* as well as among several higher green algae *(Ulvaceae)*.

The evolutionary history of the whole green algae assemblage or the Chlorophyta may be sketched according to the above discussed facts in the following way: fig. 3.

Another tendency, which is especially well expressed among several green algae, led to the formation of large multinuclear cells and finally to thalli composed of only 1 "gigantic cell" without any transverse walls (Siphonocladiales, Siphonales). No doubt the *Charophyta* exhibit this tendency also in a slight measure.

As to the ramification of the algal thalli, we may observe also a tendency to the verticillate arrangement of the side branches. An interesting example are the *Dasycladaceae*, which as stated in an excellent manner by Pia, are to be derived from old palaeozoic non verticallate forms. The same phenomenon is stabilized in a very regular manner in the *Charophyta*.

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Palaeozoic older · later	Triassic	Jurassic	Cretaceous	Tertiary	Quater-nary

Phytomonadina (Volvocales)
Tetrasporales a. Protococcales
Conjugatae
Ulotrichales
Cormophyta
Algomycetes
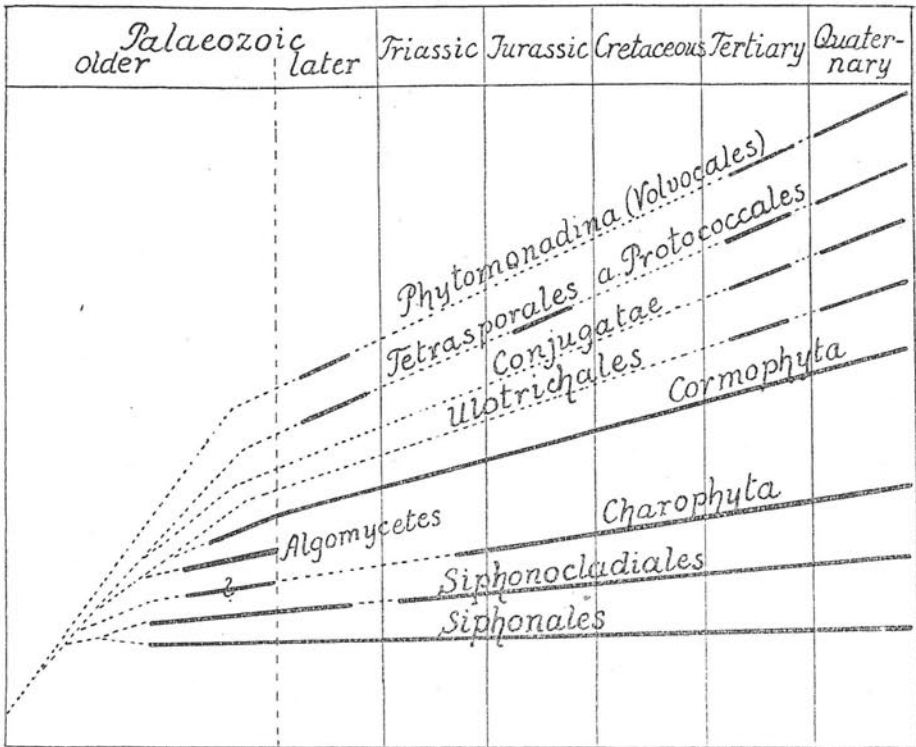*Charophyta*
Siphonocladiales
Siphonales

Fig. 3.

We have further observed here also several reductive processes concerning especially the motility of the reproduction cells. We have stated it in the *Bacillariophyta* and in a still more stabilized anr perfect manner in the *Conjugatae*. Perhaps, as already mentioned, the non motile reproduction cells of the *Rhodophyta* are also to be regarded as a very early stabilised event of the same kind, but more advanced one, to which we do not know at present already any ancestral motile stage.

Finally we have still to point out one interesting oecological event in the kingdom of the algae: the ability of several species to persist on relatively dry places outside of the water environment. This is known especially among the green algae in the divisions of the *Tetrasporales*, *Protococcales* and *Ulotrichales*.

If we overlook briefly all these various facts concerning the evolutionary lines of the *Algae* and if we examine well the various stages of perfectness achieved, we must state without any doubt, that in many of them are in fact incorporated various presumptions leading to the origin of the simplest multicellular higher i. e. land plants of the type of the *Cormophyta*. It seems to me most likely, that just the *Ulotrichales* of the green algae represent also an evolutionary algal line, which stand the

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nearest by all its essential particularities (the ability of living on dry places, the tendency to forming thalli of parenchymatous tissues etc.) to the hypothetical ancestral type of all *Cormophyta*. I am not inclined to look for such ancestors in the division of the brown sea weeds, as also often suggested by various botanists; these plants are more likely a side line specialised already very strongly perhaps on account of their brown pigments for quite limited life conditions, i. e. a side line which achieved already very soon a rather stabilized and very perfect (similar to all higher plants) kind of sexual reproduction alternating quite regularly with an asexual (sporohytic) one under water conditions (just as in the red algae). There is something similar in this problem of the origin of the Cormophyta, as we shall see later in the case of the problem of the origin of the *Angiosperms*. Both these groups comprise a large number of particularities, which in the foregoing eras were distributed singly in a large number of various plant types (e. g. circular cyclic flowers in the Bennettitaceae, enclosed ovules in the Cyatoniales a. o.).

A second task related to the phylogenetical evolution of the *Algae* is also the origin of the *Fungi* or *Mycophyta* in general. Among the lower types of the Fungi an enormously large quantity of examples is known, which as to their organization as well as to their kind of reproduction point unfailingly to an origin from the green algal groups in the largest sense, several very primitive fungi *(Archimycetes: Olpidiaceae, Synchytriaceae, Woroninaceae* a. o.) directly to that from some *Flagellata*, and the *Myxomycetes* even to some very primitive types of the animal group of Protists, the Amoebina (e. g. the genus of *Wahlcampia* a. o.). There is very doubtful if also other algal groups *(Rhodophyta, Phaeophyta, "Chrysophyta")* gave ever rise to some *Fungi*. The small mycophytalean group of the *Laboulbeniales* as well as several more primitive types of the *Ascomycetes* exhibit in their exual reproduction acts indeed several features reminding strongly the conditions in the group of the red algae (the loss of the motility of the gamets as well as of the asexual spores, the presence of a trichogyne organ a. o.), which led several botanists to the idea of a probable relationship between the red algae and several types of Fungi. Newer more precise studies (see in Gäuman's Vergleichende Morphologie der Pilze, 1926) seem to attest that many of such common features are mere convergencies (the trichogyne of the *Laboulbeniales* or *Ascomycestes* represents e. g. an organ utterly homologue with the fertilising tube of the *Oomycetes)*, i. e. similar or equal organs or events arisen under special conditions independently in far remote evolutionary lines and emphasizing only several similar evolutionary tendencies especially as to the features of the reproductive organs. In the water inhabiting Rhodophyta these tendencies are only partly realised (non motile reproductive cellules, the presence of a trichogyne fertilizing tube, but the sexual act as well as the morphological expression of the sexuality of the reprodutive cellules is well kept). In the more advanced Fungi (higher groups of the *Ascomycetes* and especially in the most part of the *Basidiomycetes)* these tendencies, no doubt on account of their life on rather dry land lead in the course of their evolution to far stronger changes consisting not only in the loss of the motility of their reproductive cellules,

but also in a strong supperssion of the various morphological particula-
rities conditioned generally by the sexuality. It is not the aim of this paper
to deal more in detail with this task; we have to examine here mainly the
evolution of the autotrophous green plants, which left in the sedimentary
rocks a large amount of fossil remains, whereas the Fungi represent as
evident a mere, though enormously large, side line (or assamblage of more
side lines), the fossil traces of which are extremely rare.

Summarising all above, I may state that the further evolution of
the most part of plants, be it the heterotrophous mycophytalean branch
or all the higher organized green autotrophous land plants, was pre-
vailingly due to the green algae, the *Chlorophyta*.

The resulting system of the *Thallophyta* may be according to the
above discussions traced as follows:

   I. Schyzophyta.
  II. Cyanophyta.
 III. Protophyta:
     Chrysomonadina
     Cryptomonadina
     Dinoflagellata
     Euglenoidina
     Chloromonadina
     Phytomonadina
 IV. Algae:
     Rhodophyta
     Phaeophyta
     Chrysophyta:
         Heterocontae
         Bacillariae
     Chlorophyta:
         Chlorophyceae
         Conjugatae
         Charae
         Algomycetes
  V. Mycophyta:
     Myxomycetes
     Archymycetes
     Fungi:
         Phycomycetes
         Ascomycetes
         Basidiomycetes.

B. The evolution of the higher land plants
(Cormophyta).

It is very difficult to imagine the relations of both cormophytalean
plant division known as *Bryophyta* and *Trachaeophyta*. Their common
ancestors, if such ever have existed, shall perhaps remain hidden for ever
to our inquisitive eyes. According to all facts mentioned in the previous

chapters, we have probably to assume the existence of rather large common starting group in the assamblage of the green algae with affinities of the *Ulotrichales,* which during the later evolution was split into more lines leading partly to types with prevailing gametophytic generation, partly with prevailing sporophytic generation. An intermediary stage between both just mentioned tendencies is at least partly realized in the small liver worts group of the *Anthocerotales.* An evidently polyphyletic origin on larger scale of this enormously large plant division seems to me rather improbable on account of the uniformity of the fundamental morphological as well as anatomical elements of which the bodies of all *Cormophyta* are built up.

The history of the 1. division i. e. of the *B r y o p h y t a* is utterly mysterious. The palaeobotany did not reveal till present the smallest bit of it. It was stated (especially by Walton) that the oldest known *Bryophyta* coming from the carboniferous era were already well divided into two distinct and highly specialised plant types: the mosses *(Musci)* and the liver worts *(Hepaticeae),* and further that all untill now discovered fossil species are morphologically as well as anatomically utterly identical with species or at least genera of the present days. This whole plant group underwent thus up from the Carboniferous absolutely any essential changes in their organisation. As to the evolutionary tendencies, which are to be assumed as incarnated within this plant division, we may characterise them as the concentration of the vegetative life manifestations or functions within the gametophytic generation*) of a highly stabilized life cycle (to which rather remote analogues are to be found in the highly organized red or brown algae resp. especially in the green *Charophyta),* in contrary to the second great cormophytalean division the *Trachaeophyta,* where all vegetative life functions are concentrated in the sporophytic generation.

For an absolute lack of palaeontological evidences we shall renounce to further mere speculations about the evolutionary problems concerning the *Bryophyta* and we shall rather pay attention to the second main division of the land plants, the *T r a c h a e o p h y t a,* which in the course of the history up from their first appearence during the siluro-devonian era underwent unnumbered morphological as well as internal anatomical changes till to the creation of the wonderful flowering phenomens of the present vegetation. The palaeobotany, as already told above, revealed already such a large number of fossilised remains of various intermediary stages between the imaginably most primitive forms untill to the most complicated angiospermous plants of to day, that we find here a much more effective field for reflection, than in the case of the *Thallophyta.* We have only to take into consideration one cardinal

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*) There are of course among the Bryophyta also several types, which are slightly approaching the trachaeophytalean type either by a strong reduction of the gametophytic plantule and an unusually mighty development of the sporogons *(-Buxbaumia* a. o.), by a special adaptation of the sporogons, which are long stalklike and growing up for a considerable time simultaneously with the spore production *(-Anthoceros);* this last type especially reminds (—though rather remotely—) several devonian psilophytalean plants like Hornea, Sporogonites a. o.

tendency: the gradual better and better adaptation of all organs, but especially those producing the reproduction cells or organula, for the life on dry land. And we may note already here at the beginning of our following reflexions, that the chief problem leading to this aim consisted just as in the *Algomycetes* (or partly also in the kingdom of the heterotrophous non green *Fungi)* in the formation of more or less massive bodies containing special textures for transporting of mineral or organic nutritive solutions as well as in the loss of the motility of the reproduction cells, which were then transported in a rather more and more passive way.

1. The most primitive trachaeophytic landplants.

The problem of the *Psilophytineae.*

Among the plant remains found in the silurian and early (lower and middle) devonian rocks, we find many forms *(Rhynia, Hornea* a. o.), which by their primitive external shape as well as internal anatomical pecularities stand very near to our present conception of the most primitive ancestral type of all *Trachaeophyta:* a thalloid, dichotomously ramified system of leafless branches, of which a part is creeping under the surface of the earth, absorbing here mineral solutions, another part is growing more or less upright into the atmosphere or creeping upon the surface of the substratum, being determined for the assimilation processes. All branches are built up of parenchymatous ground tissues and provided inside by a rather primitive water solution conducting strand of tracheids, the underground branches eventually by absorbing hairs on their surface; the assimilating branch systems are green and their cuticle is provided by scattered stomata. The production of spores is more or less restricted to the very tops of many of the last branch divisions which are than slightly swelled and their parenchymatous ground tissue is altered into sporogenou cells. In several forms these sporiferous twig ends exhibit in their centre still the continuation of the vascular strand *(Hornea, Sporogonites)*, reminding very lively the columella of *Anthoceros* or of many of the sporogons of the mosses; otherwise the whole content of the sporiferous branch tops is transformed into sporogenous tissue and then the vascular strand ends immediately below this tissue *(Rhynia* a. o.).

These most primitive trachaeophytalean land plants with regard to the organisation of the sporogons of the *Bryophyta* points in a certain measure to the probable features of their ancestors as well as to the possible derivation of the moss sporogoniums on the one side and the sporophytic plantule of the *Trachaeophyta* on the other side, from some primitive types with still predominating gametophytic (prothallium) generation. In both groups we see an evident tendency to the "sterilization" of the sporogonium tissues (resp. to a mighty development of the sterile vegetative and more or less auxiliary tissue) and than a gradual elaboration of the proper spore capsule or of the vegetative tissues. In the mosses we see how the chief stress in the evolution is laid on the elaboration of a relatively large and often very complicated sporecapsule, whereas the vegetative part of the moss sporogoniums remained much

behind, representing always only a simple stalklike organ. The Trachaeophyta in contrary exhibit an enormous developement of the vegetative stalks exceeding the development of the organization of the propre spore capsules, which exhibit rather a reduction, at least as to their size. The type of the *Anthoceros* sporogoniums occupies evidently an intermediate position and it is nothing curious that it was very often considered by many prominent morphologists (Velenovský a. o.) as an image showing us the probable or possible shape of the ancestors of all higher (vascular) plants.

We have to believe that the further elaboration of the trachaeophytalean plantules during the early stages of their evolution, their ramification, the adaptation of several branches for assimilating porpuses a. o. were simultaneous with their flattening, which promises the best chance as to the photosynthesis. Therefore I think that we have to suppose that the thalloid branches of the first land plants with developed independent sporophytic generation were mostly flattened and not cylindrical in shape (e. g. like in Scyadophyton a. o.). The cylindrical shape of the branched bodies of several oldest *Trachaeophyta,* like the *Rhyniae, Horneae* a. o. seem to represent more probably a derived later stage adapted for some special conditions of the environment (like in several higher plants, Juncus a. o.), even if the fructification type of such forms exhibits many very primitive characters (e. g. the often dichotomously divided sporangia, the presence of a columella in the *Hornea* sporangium a. o.). These most primitive vascular land plants exhibit mostly a rather regular dichotomous (dibrachial) branching (the silurian *Cooksonia,* the devonian *Scyadophyton, Rhynia, Hicklingia* a. o.), but we know from the same oldest times also several forms with a modified kind of branching, a slightly advanced i. e. dichopodial one (the devonian *Loganella*), which evidently lead to the formation of a stronger main axis and a series of thinner side branches. There appear also many irregularities in the branching leading to nearly polybrachially divided plant bodies (*Pseudosporochnus* a. o.).

A further step in the evolution of the *Trachaeophyta* was the spesialisation of certain branchsystems for fructification purposes: their ramification becomes generally much denser ,the branchlets being shorter and much thinner than in the other normal sterile parts of the same plants (eg. *Taeniocrada, Hymanthaliopsis* a. o.). We know also species where simultaneously the side twigs of such fertile branchsystems become simplified and shortened, or finally the sporangia are nearly sessile laterally on the original main branches giving by this way rise to spikelike fructifications bearing numerous short stalked or sessile sporangia (*Gosslingia, Zoosterophyllum, Bucheria* a. o.). Similar evolutionary processes are also known among fossils, where the surface of the branches are provided by hair like enations *(Psilophyton),* which in extreme cases bear also stomata, like some very primitive leaflets *(Asteroxylon)* ; here such fertile dichotomously divided branch systems are mostly smooth.

All these primitive forms, which are not yet differenciated into any special assimilating leaf organs and special stems, are now generally summarised under the term of *Psilophytineae.* But as already partly

evident from the foregoing lines, simultaneously with them were collected also several more complicated plant remains. Just in the upper silurian beds of Australia aside of several typical *Rhynia* like forms *(Cooksonia)* a highly organised typical lycopodinean type, the *Barragwanathia*, was found. Further we know from the early devonian strata of various countries forms, which by a fargoing transition from a dichotomous to a dichopodial branching and by the transformation of their side branchlets into leafy appendages remember very strongly some equisetalean or fernlike plants *(Bröggeria, Pseudosporochnus, Swalbardia*, several species of the genus of *Hyenia, Protopteridium, Aneurophyton, Hedeia, Yarrawia* a. o.). We may observe here a further "condensation" and at the same time diminishing (a typical gradual reduction) of the fertile branch systems untill into a form of small stalked often bifurcating sporangia groups, sitting more or less regularly on larger branch systems, which at once eventually are pushed into a lateral position on still thicker branches or stems. More or less simulatneously the sterile endparts of such large branch systems become often enlarged and leaf like *(Protopteridium, Swalbardia, Rhacophyton* a. o.).

All these discoveries within the sphere of the oldest known land vegetation revealed in fact a large number of plant forms, which represent undeniable transition types between the primitive *Rhynia* like types and between the ferns (see especially several rather simple types of the genus of the *Protopteridium*, like *P. minutum* a. o.). And we may already state hre very clearly several evolutionary directions or tendencies, by which this fern like habitus was attained: by the plagiotropic orientation of larger branchsystems and a simultaneous enlargement and flattening of their branchlets (e. g. in the series of the known *Protopteridium* species), by the formation of leaflet like more or less wedge shaped flattened appendages out of the ends of the dichotomously or dichopodially divided branchlets and than a following plagiotropical orientation of the whole branch systems *(Pseudosporochnus, Swalbardia, Archaeopteris)* and finally also by a gradual diminishing of the number of the symmetry planes of the respective branches, which underwent the transformation into frond like large leaves. By this last way also various intermediary stages between the radially symmetrical stems or branches and between the dorsiventrally symmetrical leaf — or frond — rhachises arose, the so called phyllophores of P. Bertrand *(Rhacophyton, Stauropteris,* ferns of the groups of the *Asteropterideae* and *Zygopterideae).*

Similar evolutionary tendencies are to be pointed out also in such psilophytalean groups, the branches of which are provided by hairlike (eventually assimilating ?) enation appendages *(Psilophyton- Asteroxylon* series). Even here we may state several fernlike descendents like the devonian *Dawsonites ellenae*, which remembers in all features the hairless smooth *Protopteridia*. Unfortunately this group of plants is much less known than the previous one.

The whole group of the Psilophytineae in the most restricted sense as defined above, was evidently very much participating in the origin of the ferns; as evident from the above, we can easely point out directly within

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the known siluro-devonian vegetaiton many extinct plant types, which indicates more or less precisely the elaboration processes leading to the creation of fernlike leaves.

More difficult seems to be this problem as to the articulatinean plant type, which on account of their articulated axis as well as the whorl like arranged leaflets point to a very deep transformation of their original bodies. We know at present without any doubt several very primitive forms like the devonian genus of *Calamophyton* or *Hyenia,* where the branching of the whole plant body is still a rather purely dichotomous one and where even the articulation of the stems and branches is rather imperfectly developed; but otherwise the differenciation of the body into special stem and leaf like appendages is here already rather well fixed. Perhaps only several more primitive species of the genus of *Hyenia* show still a slight indication, that even here the leaf like appendages are nothing else than reduced and laterally pushed small side branches [for instance in the subgenus of *Hyeniopsis (H. vogti)* it happens often that instead of a leaf (not in the axil of this leaf!) a side branch is given off, which attest sufficiently the morphological indentity of both these organs, evidently not yet well stabilized]. But so clear transition types to some utterly primitive psylophytalean forms as we have seen in the series leading from the *Psilophytineae* to the ferns, were not yet revealed here with utter certainty. Perhaps the devonian *Bröggeria**) with its dichotomously till irregularly dichopodially branched stems, which bear more or less spirally arranged short branched and rather twig like than leaf like side appendages, may be regarded as a still more primitive stage leading to the mentioned most primitive devonian *Articulatineae* (known under Hirmer's term of Protoarticulatales).

The just mentioned *Bröggeria* points still to another possible evolutionary line. We know from older devonian as well as later times a considerable number of non articulated plants bearing small dichotomousely divided leaflets not much dissimilar from the leaflets of the last mentioned *Articulatineae,* though often of larger size (eg. *Barrandeina, Duisburgia, Cladoxylon* a. o.; the late palaeozoic *Tingiae, Noeggerathiae* a. o.). And it is very interesting to state that many of these higher organized forms, which in a high measure exhibit several similar features (especially as to the fructifications) with the *Articulatineae,* show at the other side even very clearly some tendencies common with the evolution of the ferns: in the *Cladoxyla* whole large branch systems provided with more or less spirally arranged leaflets become bilaterally till dorsiventrally symmetrical (by means of more simplified branchlets called *Hierogramma, Arctopodium* or finally *Syncardia*), in the late palaeozoic *Noeggerathiae* or *Tingiae* by a plagiotropic arrangement of the leaflets (not unlike the upper devonian *Archaeopterides*), in the carboniferous *Palaeopteridia* by a plagiotropic arrangement not only of the leaflets but also of a whole system of branches.

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*) May be that the devonian *Haspia* represents another similarly simply organized transitional form.

All just mentioned discoveries attest that we have not yet revealed with certainty any true ancestral type of the Articulatineae; untill present we know only a considerably large series of non articulated but rather highly organised and enough specialised forms, which may be regarded rather as a parallel evolutionary side line to the *Articulineae* (— in 1931 I have applied to them the term of the *Noeggerathiales;* but as this term was too much restricted comprising only several late palaeozoic plant types characterised at once also by special kind of fructifications, I propose now a larger term comprising also the various above mentioned devonian forms and derived in the first range from the main characters of the stems and leaves, the term of the *P s y g m o p h y l l i n e a e*). Both these lines, the *Articulatineae* as well as the *Psygmophyllineae,* are as evident well fixed already much earlier during the siluro-devonian time than the foregoing evolutionary line of the ferns (the *Filicineae*). They are evidently of a relatively much older origin than the ferns, which is perheps also the chief reason, why we have not discovered any of their true ancestors among the siluro-devonian plant remains (except such plant remains like *Bröggeria* and *Haspia,* which stand perhaps rather near to them).

At the mean time an utterly mysterious origin must be ascribed to the group of the Lycopodineae, which as told above are met already in the Silurian and that anatomically as well as morphologically quite perfectly organised (*Barragwanathia* with a very complicated plectostelic vascular strand). I mentioned already in the chapter dealing with the morphological principles of the evolution of the main plant organs all reasons which led me to the opinion (in accord with Zimmermann's point of view) that even here we must assume for the origin of the leaflets a reduction processus quite identical with the origin of the leaflets of the *Articulatineae* or of the *Psygmophyllineae*. In the previous lines I have emphasized that the *Asteroxyla* belong much more probably to the evolutionary line leading from the *Rhyniales* directly to fernlike plants, especially on account of the specialisation of large branchsystems for sporeproducing function, and that therefore their leaf bearing branches cannot be regarded as homologous to the leaf bearing branches of the Lycopodineae. Otherwise the more or less adaxial position of the lycopodinean sporangia at the base of the leaflets would be quite incomprehensible. I believe that the palaeobotany has not yet revealed any evidence about the ancestors of this group. We may only suggest that these were rather similar to the ancestors of both just previousely mentioned groups of the *Articulatineae* and *Psygmophyllineae,* but that the *Lycopodineae* were derived still much earlier than the *Articulatineae* and that all devonian lycopodinean plants are already representants of a highly specialized plant group with enormously reduced leaves (originally of a sphenopsid shape like in the *Psygmophyllineae*) as well as sporophylls.

All these problems concerning the oldest known siluro-devonian land flora which were discussed here above from the morphological point of view, become still more complicated, if we pay attention also to the anatomical structures of the stems or frond rhachises. Unfortunately we do not know these conditions in all till now discovered siluro-devonian plant remains. But nevertheless several rare discoveries point often to a certain

polyphyletism of the mentioned great systematical divisions of the *Pteridophyta*.

Most of the true *Psilophytineae* are provided with cylindrical protostelic strands *(Rhyniales)*. In the genus of *Psilophyton* the same kind of stele may be found and in the rather very advanced *Asteroxylon* we see in the thinner ramifications also protostelic and cylindrical strands but in thicker branches they assume an actinostelic shape.

More or less irregularly lobed protostelic vascular strands may be found also in the transitional fernlike plants of the groups of the *Iridopteridaceae* as well as in the *Protopteridia*, which cannot therefore be brought into a direct relation to other ferns of the later geological times (late palaeozoic or meso- and kaenozoic), which in their most primitive and oldest types exhibit anew protostelic and cylindrical vascular strands, partly with a tendency to actinostely (various coenopteroid ferns) but mostly with an evident tendency to soleno- till dictyostely (most part of the true ferns).

The curious devonian *Aneurophyton* and *Rhacophyton* exhibit also already strongly specialized stelar conditions: the first one a more or less triangular type reminding slightly the conditions in several stems of an-known affinity termed as *Stenomyelae, Palaeopityae* a. o. as well as those of several *Articulatineae (Calamophyton, Sphenophyllum)*, the second one a bipolar (biscuit shaped) form reminding rather strongly the shape of the vacular strands of the phyllophores of many of the coenopteroid ferns *(Phyllophorales)*.

Rather complicated conditions were stated in several more advanced devonian types of the group of the *Psygmophyllineae: Duisburgia, Barrandeina, Cladoxylon* a. o. Many of them exhibit a very complicated plectostely or even nearly a plectostelic polystely. Such forms must be undoubtedly regarded as already highly specialized and rather fixed types without any further phylogenetic relations to some later eventual descendents.

The early devonian *Articulatineae* as far as known exhibit solid vascular strands (without any medullary cavity in the centre). Their shape is meanwhile unfortunately better known only in the genus of *Calamophyton*, **where** they are triangular in cross section just as in the late palaeozoic *Sphenophylla*.

The siluro-devonian Lycopodineae contain already two distinctly differenciated anatomical types: one exhibiting rather primitive cylindrical and protostelic vascular strands *(Protolepidodendron,*) Drepanophycus)* and the other provided by an actino- resp. plectostelic strand *(Barragwanathia)*.

As already pointed out, we know from these early periods also several other stem structures, but without any knowledge of the outer morphological features of the respective mother plants, to which the various stem casts (mostly silicified) belonged. We know them under various "family" terms like the *Calamopityae, Protopityae* a. o. Several of them

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*) According to several newer statements the stele of the Protolepidodendra seem to be slightly triangular in crosssection.

contain in the centre of their vascular strands already a rather large cylinder of parenchymatous modullary tissue, in others this pith contains still many scattered tracheids. We have here to do evidently with transition types from protostelic to siphonostelic types. These and other similar stem casts on account of still many other particularities point to some relations with the early carboniferous and late devonian group of the *Pityae,* which generally are consider (and perhaps quite justly) as more or less allied with the group of the carboniferous *Cordaitales.*

On account of all briefly above mentioned as well as still of many other similar morphological and anatomical pecularities and taking also into consideration the stratigraphical conditions of the various discovered plant remains, I propose to assume the following scheme, expressing the phylogenetical relations of the various at present better known plant types of the oldest vascular land flora: Fig. 4.

Fig. 4.

By this scheme may be emphasized:

1. The utterly identical fundamental morphological architecture of all *Trachaeophyta* yet known from the oldest past: the differenciation of leaves by means of reduction and condensation of branch systems pushed laterally by a gradual transition from a dichotomous (dibrachial) or event. also polybrachial branching to a monopodial one.

2. In a very early period (without any doubt already long before the Devonian) in a part of the primitive land plants rather small strictly dichotomously divided lateral appendages were fixed as small "sphenopsid" leaflets by the way mentioned sub 1, which afterwards underwent eventually a strong reduction yielding only simple lineal uninerved (event. binerved) leaves (typical "microphylls": *Lycopodineae, Calamariaceae, Equisetaceae* a. o.). This processus led to the non articulated "sphenopsid" group of the *Psygmophyllineae* and to the "microphyllous" *Lycopodineae*.

3. A second similar later processus of pushing laterally certain branch systems but on larger scale than that mentioned sub 2, to which underwent the vascular land flora anew in a stage when eventually the sphenopsid (resp. "microphyllous") leaflets were already rather fixed (or even simultaneously with this processus), led to the creation of the various fernlike plants or finally to the true ferns. As attested by various well known fossils, this third evolutionary processus took place evidently during the latest silurian and early devonian times. We know therefore from this era also several types combining ferncharacters with those of the other mentioned great plant divisions: *Aneurophyton* combining some evident fern features (fructification, fronds) with those of some primitive Hyenia species (vascular strand, last "leaflets"), *Cladoxylon* combining the dorsiventrally frondlike adapted side branches with spikelike fructifications known in the groups of *Psygmophyllineae* or *Articulatineae* a. o.

4. During the same siluro-devonian period still another very curious processus take place: the grouping of leaves in a certain number into whorls and a more or less simultaneous regular articulation of the stems and branches i. e. the creation of the plant type known as the *Articulatineae*. This processus was observed very rarely in the group of the *Lycopodineae (Zimmermannia, Eleutherophyllum)*. The chief part of this whole articulatinean assemblage is no doubt to be derived directly from the primitive non articulated sphenopsid forms, i. e. in general from our division of the *Psygmophyllineae*. Within the group of the later ferns we may observe anew slight indications of this tendency (but without articulation of the stems) f. inst. in several *Psaroniae* or in the group of the *Cyatheaceae* and *Dicksoniaceae* just as well as in the water ferns of the gen. of *Salvinia*.

5. The *Filicineae* (incl. the true ferns as well as various ancient fernlike plants) from the stratigraphical point of view appear therefore as a more or less parallel group to the Articulatineae, both being of a much later origin than the *Lycopodineae*. The devonian Psilophytineae must be than regarded as a side line, which never reached a higher organisation, but in contrary remained on a rather low evolutionary stage perhaps very similar to the ancestral forms of all *Trachaeophyta*.

6. These 5 mentioned great plant division of the siluro-devonian vascular land flora *(Psilophytineae, Psygmophyllineae, Lycopodineae, Articulatineae, Filicineae)* are of the anatomical point of view certainly of more or less polyphyletic character. As will be emphasized in the following chapters they contain ancestral types of all later higher plant forms.

7. Untill present we do not know from the silurian and early devonian land floras any true safely prooved seeds. It is highly probable that all land plants of this period were of pteridophytic nature (vascular cryptogams).

The evolution of the *Psilophytineae.* — All what the palaeobotany has revealed us from the history of this once certainly large group of vascular but still thalloid plants, is merely its end phase. Last traces of them are to be found in the later Devonian; their early history is unknown. But nevertheless several main features of their evolution are to a certain measure evident from the above chapter discussing in general several of their chief morphological and anatomical particularities. I doubt very much, whether we are really in possession of any fossil remains of true ancestral, primitive psilophytic types. As already emphazised, I cannot agree with the opinion that *Hornea* or *Rhynia* are to be regarded as such types, which gave rise to other higher forms. I regard them as highly adapted for semiaquatic or swampy life, therefore perhaps even slightly reduced, but keeping at the same time well a very archaic kind of spore producing organs. Both are thus representants of a very soon derived side line without any direct connections with higher forms. Besides this very characteristical and primitive plant group we find at the same period still two further but a little more advanced (specialization of certain fructificating branch systems) and no doubt rather parallel plant groups: one more frequent, containing forms like *Taeniocrada, Zoosterophyllum* a. o. with smooth twigs, and the other rarer exhibiting branches provided with hairlike enations till small spiny leaflet like appendages as *Psilophyton* and *Asteroxylon.* The further evolution of these both types exhibit evidently in the first stages very similar tendencies: rather regular dichopodial transformation of the stronger axis and further reduction of the sporangiferous branch systems leading already to fernlike plants: *Protopteridium* a. o. in the first case, *Dawsonites* in the second one. Meanwhile we do not know any further descendants arisen from the evolutionary line *Psilophyton-Asteroxylon-Dawsonites* On the other hand it seems that the first named plant assamblage (with smooth branches) gave rise to a large series of further evolutionary lines diverging in several directions: by a rather irregular and more or less polybrachial transformation to *Pseudosporochnus* and further to several "higher" more or less fern like plants as *Swalbardia* or even to *Archaeopteris,* by an early "condensation" of the dichopodially constructed body *(Protopteridium* a. o.) and its plagiotropic orientation to *Rhacopteris,* by a rather very early formation of bilaterally symmetrical axis (phyllophores) to *Rhacophyton,* by the formation of a thick and dichopodially constructed and radially symmetrical main axis to the groups of *Lyco-*

podineae as well as *Psygmophyllineae* and therefore also to the *Articulatineae, Aneurophyton* a. o. Just similar forms are to be assumed as ancestral stages of all ferns and therefore also of all other macrophyllous plants, perhaps through intermediary stages not unlike *Protopteridia, Rhacophyta* a. o. by means of a still stronger "condensation" of whole very large branch systems provided mostly already by smaller leaflike side appendages, which finally as already told led to the formation of large fronds.

The probable evolution of the Psilophytineae and their relations to the various higher plant types may be sketched in the following way: Fig. 5.
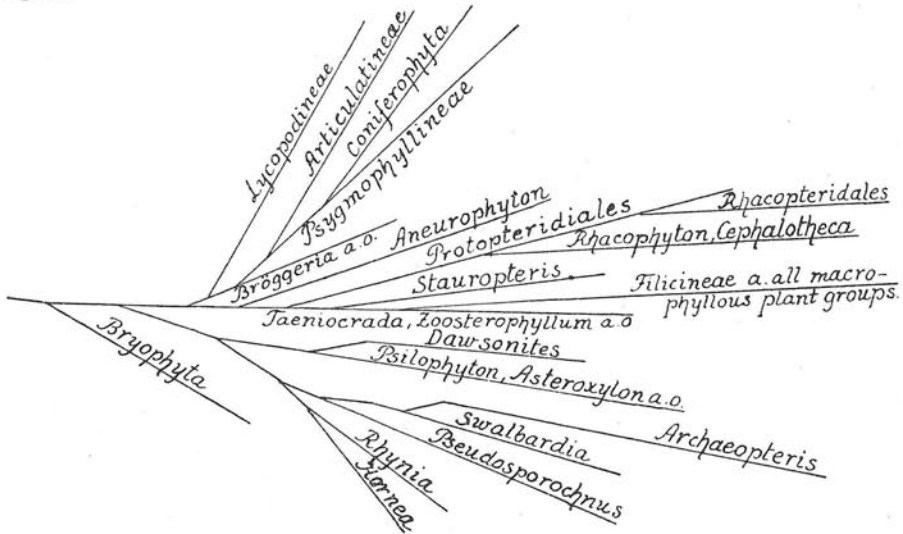
Fig. 5.

2. The evolution of the *Lycopodineae*.
and *Articulatineae.*

The phylogenetical evolution of the *Lycopodineae* as documentated by fossil plant discoveries appears as rather simple one. As mentioned above already in the silurodevonian periods we have to state at least two parallel lines of plant forms side by side, which both are well characterized anatomically as well as morphologically. And it is also a well known and interesting fact that both these lines divides anew evidently also very soon equally into two well defined series: non ligulate genera and those with leaves provided by small ligular outgrowth at the base on their ventral side. Stratigraphically the ligulate forms appear somewhat later.

The first lycopodineae evolutionary line comprises various rather low herbaceous plants with well developed normal roots. We know them already

from the upper Devonian in a stage differing nearly by nothing from the recent *Lycopodium (Lycopodites oozensis)* and in the Carboniferous both recent genera *Lycopodium* and *Selaginella* are well known under the terms of *Lycopodites* and *Selaginellites*. Anatomically they are characterised by a tendency to actino- resp. plectostely and differ by this particularity essentially from the following second evolutionary line. They occured always only as a subordinate element within the various plant associations just as at present. Their spermatozoids, at least of their recent representants, are bciliate. It is not excluded that the silurian actino- till plectostelic *Barragwanathia* may be ranged also as an ancestral more robust type into this line.

The second evolutionary line comprises many treelike club mosses which plaied in the later Palaeozoic an excellent role in the swampy coal producing forests. As told, they are characteristically bipolar and their rootlets, the "appendices" of the underground *Stigmaria* branches are of a more primitive kind, than the normal roots of nearly all other higher plants. Their vascular strands are cylindrical in shape and we have to follow here a very instructive phylogenetical series from a nearly proto- stelic or at least siphonostelic stage untill to the most primitive eustelic forms (several younger species of the genus of *Sigillaria*). Just as the members of the first mentioned evolutionary line, they are to be stated also already in the Upper Devonian. After an unsually luxuriant occur- rence in the Carboniferous, they became suddenly very rare and during the mesozoic times we meet only several not numerous dwarf descendents *(Pleuromeia, Betheimia, Nathostiana)*. During the Tertiary (resp. also at present) only one genus, *Isoëtes*, survived as a low herbaceous very reduced type with polyciliate spermatozoids.

As also already pointed out the palaeobotany yielded till present absolutely no safe evidences of any form which might be regarded as an intermediary type between both these lines. The possible ancestors of both these main groups of the *Lycopodineae* are hidden by the mysterious cover of the oldest past. Their evolution from the siluro-devonian times untill to day may be sketched in the following way: Fig. 6.
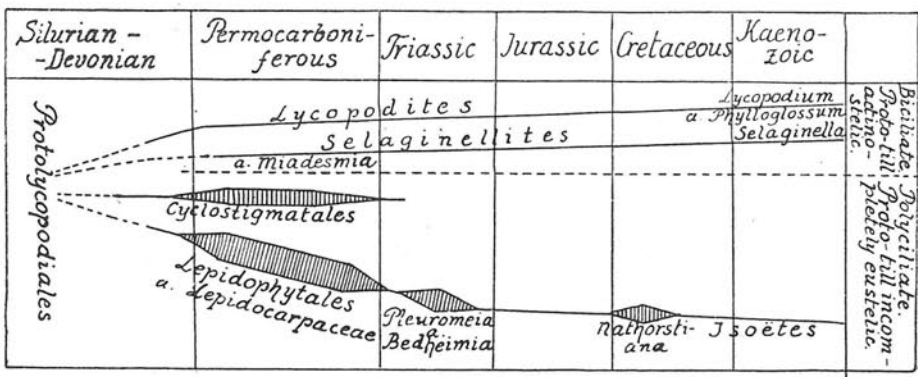

Fig. 6.

The evolution of the division of the *Articulatineae* is already partly well evident from the above chapters. From the anatomical point of view we have to distinguish here two rather remote lines: One provided with solid vascular strands exhibiting a well marked tendency to actinostely and a second one provided by cylindrical strands with generally well developed central pith and achieving in advanced forms typically eustelic features. The first of both may be pursued back untill into the Lower and· Middle Devonian (the genera *Calamophyton* and *Hyenia* of the order of the *Protoarticulatales)* and it comprises the orders of the *Pseudoborniales Sphenophyllales* as well as the *Tristachyales*. The cross sections of their vascular strands, as far as known, are mostly of a three radiate shape (or at least a multiple of the number of 3). The mutual relations of these just mentioned orders are not yet well cleared up on account of lack of more detailed knowledges of the anatomy and morphology of several of their members (especially of *Pseudobornia* and *Tristachya)*. The second mentioned evolutionary line is represented by only one well defined order — the *Equisetales*. Oldest types of these last are better known first from the Lower Carboniferous — the well known *Asterocalamites*. The relations of this family to the devonian *Protoarticulatales* are not yet precisely stated. The whole order differs from all the members of the first named evolutionary line not only by the anatomy of their stems, but also by many features concerning the morphology of their leaves and sporophylls as already pointed out in the above chapters. All at present known fossil as well as living genera according to their anatomical (the arrangement of the primary vascular strands and their detailed construction in the stems) as well as morphological (the shape of their leaves, the construction of their fructifications) features may be divided into 5 families: *Asterocalamitaceae, Sphenasterophyllitaceae, Phyllothecaceae, Calamitaceae* and *Equisetaceae*. The mutual relations of the various types contained within these families, as traced in the following figure 6. b.), point at least to three more or less parallel evolutionary lines: 1. a line leading most probably more or less directly from the old *Asterocalamites* to the mesozoic genera of *Phyllotheca* and *Schizoneura*, 2.another line leading from the *Asterocalamites* by the way of the genus of *Mesocalamites* to a large tree horse tail assamblage of the late Palaeozoic i. e. the carboniferous genus of *Calamites* and several rarer types (our family of the *Sphenasterophyllitaceae: Bornia, Autophyllites, Sphenasterophyllites)*, which with the beginning of the mesozoic era became extinct (their last descendents were the permo-triassic *Neocalamites)*, and finally 3. a line leading most probably also by way of the *Mesocalamites* to the big (but not woody) mesozoic (during the carboniferous period extremely rare) *Equisetites* and by a strong reduction finally to the herbaceous genus of *Equisetum,* the single genus which from this whole once enormously rich articulatinean plant division remained till to our present days as a mere relic type. (See fig. 7.)
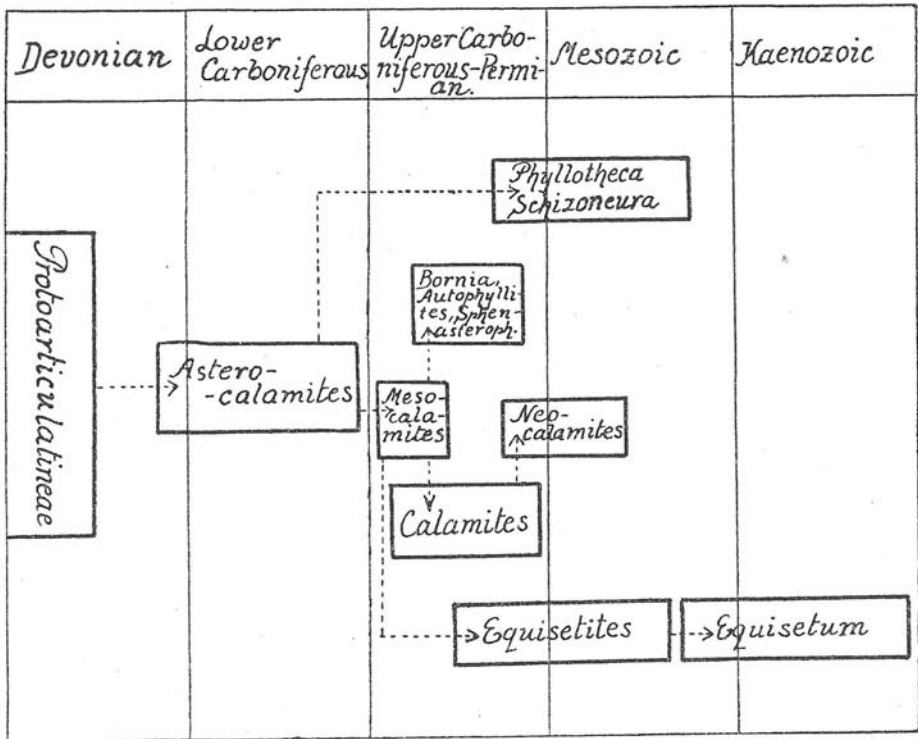
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Devonian	Lower Carboniferous	Upper Carboniferous-Permian	Mesozoic	Kaenozoic
Protoarticulatineae	Astero-calamites	Phyllotheca Schizoneura; Bornia, Autophyllites, Sphen-asteroph.; Meso-calamites; Neo-calamites; Calamites	Equisetites	Equisetum

Fig. 7.

3. The problem of the *Psygmophyllineae*.

In the previous chapters I have established a new term for a large division of rather archaic pteridophytic plants, which achieved an evolutionary stage, where already well defined stems are developed. These are more or less dichotomously till dichopodially branched and bear rather regularly disposed lateral leaflike appendages arisen originaly by adaptation of smaller branch systems for assimilating function; they in fact represent therefore sympodially constructed organs covered by sphenopsid (resp. pseudomacrophyllous) leaflets. In 1931 I have already comprised a part of these plants (the carboniferous *Noeggerathiae, Plagiozamites, Tingiae, Palaeopteridia* a. o.) under the name of the *Noeggerathiales* as a special pteridophytic plant type, which may be best characterized as "non articulated Articulatineae" and I. Brown in 1933 pointed out their relatively very near relations to the carboniferous *Sphenophylla*. Later R. Kräusel after a detailed study of several devonian fossils *(Barrandeina, Duisburgia* a. o.) expressed the view, that perhaps many of the devonian forms bearing more or less wedgelike and often even dichotomously divided leaflets are to be joined just to the carboniferous *Noegge-*

rathiales as their very old allied. On account of their characteristical leaf form I proposed here the name of the *Psygmophyllineae.**)

The evolutionary processus leading to the creation of this plant type is perhaps slightly indicated in several devonian plants, which are generally regarded also as a transitional stage leading to the most primitive ferns, like the *Protopteridia, Pseudosporochnus* a. o., where the transition from a very primitive nearly Rhynia-like dichotomously branched plant body to a dichopodially constructed stem bearing dichotomously divided leaf organs is well evident (compare e. g. *Protopteridium minutum* and several higher organized species like *P. hostimense*). The outer appearence of such "intermediary" plant types is on account of the rather large "leaves" mostly fernlike. But in fact we are missing here typically developed macrophyllous fronds i. e. plagiotropically transformed large branch systems bearing eventually simultaneously sterile assimilating appendages as well as many groups of sporangia (i. e. reduced sphenopsid leaflets as well as reduced sporangia bearing branchlets). The derivation of a leafy shoot of the psygmophyllinean character from such plants may be immagined only by a simple reduction of smaller side branch systems, whereas the derivation of true fern fronds requires a much far reaching reduction and transformation of whole large dichopodially constructed branches bearing more of such smaller side branch systems. With this morphological character agrees rather well also the stratigraphical distribution of both these plant types: the more primitive psygmophyllinean type appears already very early in the Devonian, whereas typically developed true ferns resp. fernlike plants are known first in the later phase of the Devonian. As examples of plants which have already well differenciated straight main axis, but in which the side appendages (small reduced branch systems pushed aside) did not yet achieved a typical leaf character, I may point out the already cited devonian *Bröggeria, Haspia* and perhaps also several very primitive species of the genus of *Hyenia*.

There is now a task, which plants resp. plant groups are to be brought to this pteridophytic division and especially if there are also several forms still among the living plants.

Among the various devonian fossils we have to point out two cardinal different plant types bearing sphenopsid leaflets and non articulated stems or twigs: 1. Plants reminding in a high measure some (especially large leafy) *Articulineae*, provided by straight rather big and dichotomously till dichopodially branched stems or branches bearing more or less spirally and densely arranged leaves or (very often at the ends of several twigs in a conelike or spikelike arrangement) sporophylls (*Barrandeina, Duisburgia* a. o.). 2. Forms with rather irregularly dichotomously till dichopodially or polybrachially divided twigs with the ends of the last ramifica-

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*) Many of them are no doubt members of Arber's or Hoeg's proposed group of the *Palaeophyllales* or of Darrah's group of the *Sphenopsida*. But the first name was established as only a mere artificial group comprising all forms of unknown systematical affinity and exhibiting leaves like the palaeozoic *Psygmophylla*, the second term comprises especially the typical *Articulatineae* with several archaic nearly allied types (*Calamophyton, Hyenia*). Therefore it is very difficult to apply any of them to our non articulated sphenopsid plant types.

tions flattened and enlarged more or less wedgelike and often deeply incised; in this case we are missing the spiral arrangement of leaflets on well differenciated axis, which holds also for the sporophylls (the sporangia are sitting terminally on the last twigs of special branchlet systems). An excellent example of this second group is Hoeg's *Swalbardia* from the norwegian Devonian. Perhaps the middle devonian *Pseudosporochnus* may be regarded as an intermediary stage leading to such curious plants from the still more ancient Psilophytineae.

The whole appearence of the just named second type is rather fernlike; though there are not yet any well differenciated large fronds. Also the kind of fructification organs reminds very much several primitive fernlike plants as *Protopteridium, Rhacophyton, Aneurophyton,* but especially the upper devonian *Archaeopteris.* Several species of the genus of the *Archaeopteris* reminds the devonian *Swalbardia* also by the shape of their leaflets *(A. fissilis* a. o.). There are thus serious reasons to believe (as done by Hoeg) that *Swalbardia* and similar plants led in the evolutionary history directly to several ferns or fernlike plants bearing no conelike or spikelike fructifications. I believe therefore, that this second type of primitive devonian leaf bearing plants is not to be regarded as members of typical *Psygmophyllineae,* but already os representants of the most primitive fernlike plants.

I regard therefore only the first of both just mentioned devonian plant types as the representants of the pteridophytic division of the *Psygmophyllineae.* This division as to the morphology of the leaves and fructifications is wholly parallel to the *Articulatineae.* Besides several already mentioned devonian genera we may range hereto also many fossils from the later Carboniferous as the genera *Noeggerathia, Plagiozamites, Tingia, Palaeopteridium, Saaropteris,* the upper carboniferous *Rhacopterides;* also the devonian till lower Carboniferous *Cladoxyla* (according to Kräusel's reconstruction) are to be joined hereto. Finally in the devonian and lower carboniferous strata of various countries a large number of silicified stem fragments are known, which as to their anatomical features absolutely do not remember any type of the ferns, or any lycopodinean or even articulatinean plant. They are known, as already told, under the family names of *Protopityae, Calamopityae,* a. o. By several anatomical features, concerning especially the vascular cylindres, some of them remind several very primitive members of the group of the *Cordaitales* and especially of the *Pityae,* which often are joined to the *Cordaitales* as their ancestors. Instead of the various actionstelic till plectostelic vascular strands as stated in the greatest part of the previously enumerated devonian psygmophyllinean types, these stem casts exhibit mostly cylindrical strands of protostelic, siphonostelic or even eustelic type. Without any doubt all these discoveries represent also a special branch of the psygmophyllinean evolutionary line and there are serious reasons to consider them as the ancestral type which led to the creation of the Coniferophyta.

As to the recent flora, I have to point out two genera, the systematical position of which never was satisfactorily defined: *Psilotum* and *Tmesi-*

pteris. Several botanists pointed out here features common with the *Lycopodineae,* other ones laid more stress to particulatities common with the *Articulatineae.* Their whole organisation agrees best with the conditions of our division of the *Psygmophyllineae* (proto-or actinostelic vascular strands, very primitive "microphyllous" leaflets, spike like fructifications with sporophylls bearing sporangia resp. synangia upon their adaxial side, rhyzome primordial instead of true roots, straight unarticulated stems a. o.) Both represent evidently last relics of this mainly palaeozoic pteridophytic plant division.

In several more advanced members of this division an undeniable tendency to the formation of larger dorsiventrally orientated, flat branch systems reminding very strongly some fern fronds is evident. We may point out the devonian or lower carboniferous *Cladoxyla,* the carboniferous *Plagiozamites, Noeggerathiae, Tingiae, Palaeopteridia, Saaropteris* a. o. as well as not in the last range also the recent genus of *Tmesipteris.* In the first of them *(Cladoxylon)* whole large systems of branches assume a more or less dorsiventral character visible also in the arrangement of their vascular strands *(Arctopodium, Hierogramma, Syncardium),* in the carboniferous *Tingiae, Noeggerathiae, Plagiozamites* or *Saaropterids* only single undivided shoots are transformed into plagiotropic "fronds", in the *Palaeopteridia* we see "fronds" constructed of plagiotropically orientated and regularly once pinnately divided shoots. All such curious rather fern similar types (the devonian *Cladyxyla,* the carboniferous *Noeggerathiales,* in a certain measure also the recent *Tmesipteris)* differ essentially from true ferns by the spike or cone like arrangement of their sporophylls. We have to imagine that this difference lay in the succession of events concerning their phylogeny. In the evolution of the ferns the transformation of whole large branch systems into plagiotropical and dorsiventral fronds took place still before any regular arrangement of the small fertile side branchlets (the later sporophylls) into spike or cone like organs were achieved, wherefore such fertile ramified twigs were more *(Swalbardia, Archaeopteris, Protopteridium,* the kulmian *Rhacopterides)* or less (all other ferns) regularly scattered on the ramifications of the originating fronds (being afterwords reduced and transformed into the well known sori). In contrary in the evolution of the mentioned fernlike *Psygmophyllinae* the fertile appendages were arranged into well defined cones or spikes long before the shoots resp. systems of shoots achieved their dorsiventrality, by which they resemble so much to the ferns.

Summarising all, what is possible to read out of the history, morphology and anatomy of this psygmophyllinean pteridophyts, we have to point out especially that there are 2 parallel lines or assamblages just as in the *Lycopodineae:* one showing an evident tendency to actino-till plectostelic vascular strands, the other bearing typically cylindrical strands. Both groups led in the further evolution to certain articulatinean forms *(Sphenophylla* and several allied genera on one side, *Equisetales* on the other side), the second of them during a later time also to the *Coniferophyta.* On account of the lack of any nearer knowledge of the anatomical conditions of the later palaeozoic forms, we are at the mean time unable to state more precisely the mutual relations of many of the discovered

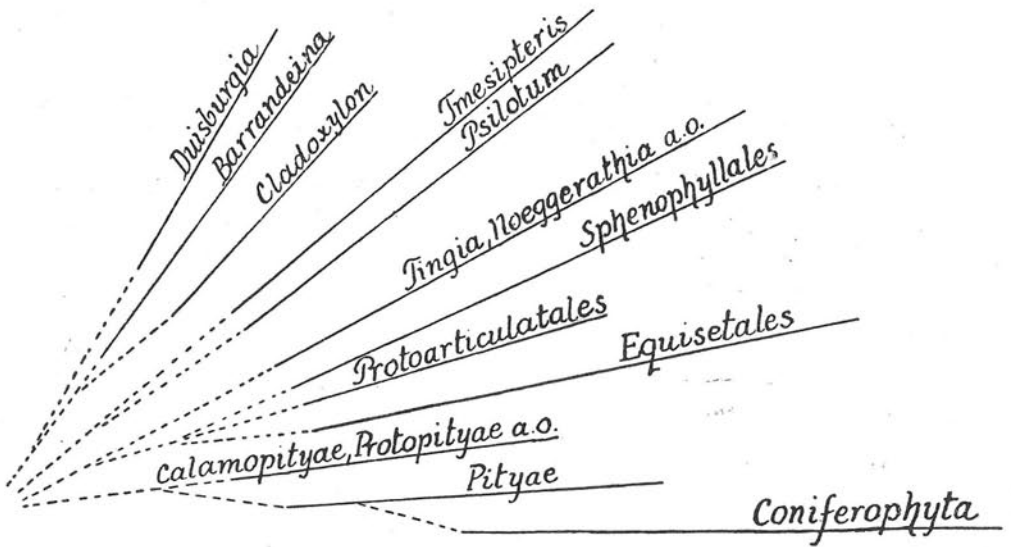fossils. The following scheme shows only very roughly all supposed relations: Fig. 8.

Fig. 8.

4. The group of the *Pteropsidineae*.

[True ferns *(Filicineae)* and several old fern like plants.]

In the foregoing chapters dealing with the *Psilophytineae* and with the *Psygmophyllineae* we often met fossils, which by many features (especially by the tendency to built up of larger branch systems some greater assimilanting frond like organs) of their outer appearence ressemble strongly true ferns as known from the present living vegetation. As told above, the term of true ferns is connected with two very characteristical morphological features: typical macrophyllous leaves and sporangia situated in more or less regular groups along the margin or on the adaxial side (resp. on mere rhachises deprived of the lamina) of such leaves; no special spike or cone like fructifications are to be stated here. On account of that we have already excluded from this group several palaeozoic fernlike plants as the *Noeggerathiae, Palaeopteridia, Tingiae, Cladoxyla* a. o. joining them to the *Psygmophyllineae*. But even now our term of ferns is considerably large, comprising many types of rather different kind of phylogenetical origin as already partly evident from the above discussion on the evolution of the *Psilophytineae* and *Psygmo-phyllineae*. In the morphological chapter I pointed out that the formation of large fronds was achieved not always in the same way. Especially in the older phase of the history of the evolution of the ferns (Devonian

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and Lower Carboniferous) we met a considerable diversity as to this problem. Later, up from the Upper Carboniferous, a peculiar uniformity appears. It seems that during the Carboniferous and Permian existed only two types of the ferns, which are characterised by certain anatomical features and which both are rather nearly allied: the coenopteroid ferns and the true ferns. The first group of both exhibits in the stems vascular strands with a tendency leading to actinostely, whereas the second one that leading to the formation of cylinlrical strands with solenostelic, dyctiostelic or even polystelic architecture. The first group exhibits distinctly developed phyllophores, whereas in the second one typical dorsiventrally symmetrical fronds are present. But there are serious reasons, that even the rhachises of the second group represent only dorsiventrally transformed phyllophores (the dorsiventral adaptation of the phyllophores in several coenopteroid ferns like *Ankyropteris, Tubicaulis* a. o., the ontogenetical evolution of the frond rhachises of certain older types of the *Osmundaceae)* and that we are just, when regarding also the fronds of all more modern ferns *(Marratiales, Leptosporangiales)* as plagiotropically as well as dorsiventrally transformed and reduced phyllophores as believed by several botanists (Emberger). Of course the fronds of the most modern ferns *(Leptosporangiales)* are morphologically so well fixed and stabilised organs, that they do not exhibit in their ontogenetical development absolutely any ancestral traces, which would definitively answer this task. According to all that true ferns appear as a special side line of the late palaeozoic coenopteroid ferns, a line especially full of vital energy representing up from the end of the Permocarboniferous the only type of fernlike plants.

As to the further evolution of these group of true ferns i. e. during the end phase of the Palaeozoic as well as during the Meso- and Kaenozoic especially the particularities of the sori and sporangia are very important. Their evident tendency to a more and more far reaching simplification (from eusporangial to leptosporangial character; decreasing in size and transformation into mere trichomelike organs) of the sporangia and sori ("simplices", "gradatae", "mixtae" untill to the loss of well defined sori and a dispersion of the sporangia upon the surface of the leaf lamina) is without any doubt the best diagnostic character for the various fern families and we have to state a very regular stratigrafical occurrence of these families, parallel to the just mentioned simplification processus. If justly taking into consideration all these various evolutionary tendencies, we easily can sketch the following evolutionary lines within the group of the true ferns, which appears then as rather monophyletic: Fig. 9.

A great and rather difficult problem represent the possible relations of the so called *Hydropteridineae* (the heterosporous ferns) to this group of the true ferns, which all are without any exception isosporous. There are some features in the arrangement and form of the sporangia, which led several authors to the opinion, that the family of the *Marsiliaceae (Marsilia, Regnelidium, Pilularia)* is related to the *Schizaeaceae*, the families of the *Salviniaceae* and *Azollaceae* on the other hand to the gradatae-simpleces fern type. Unfortunately the palaeobotany gives us not the least information about the older past of this curious aquatic fern
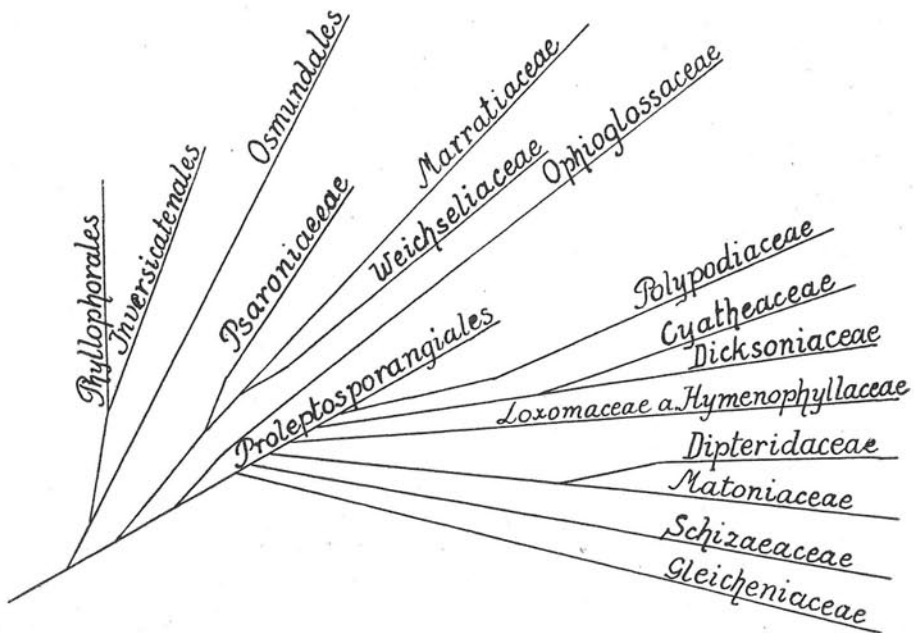
Fig. 9.

group; all fossil species known till now are geologically too young (chiefly only tertiary). The recent genera represent no doubt only a very small relic, only three very isolated and highly specialized types, strongly adapted to the water life, with extremely reduced fronds and stems, with rather primitive (no doubt also reduced) vascular strands. In the family of the *Marsiliaceae* we find still a kind of spirally coiling of the fronds in the youth, but not so in the genera of *Salvinia* and *Azolla*. In the genus of *Salvinia* a whorl-like arrangement of the leaves (by 3) and a kind of articulation of the stems was achieved, by which this genus reminds slightly the conditions of the palaeozoic *Sphenophylla*. All these features attest a farreaching transformation of their original shape and architecture, due to the special living coditions. No doubt the Hydropteri-dineae are of a very polyphyletic origin representing last relics of some evolutionary side lines from the stock of the leptosporangiate ferns, which achieved a heterosporous character. But their enormously reduced orga-nization and the isolated position of the single genera does not allow to recognize their precise systematical and phylogenetical relations.

The prae- and partly also the lower carboniferous ferns resp. fernlike plants are from the morphological as well as anatomical point of view much more diverse, pointing thus to the possibility of still other kinds of origin and evolutionary stages, than as seen in the just discussed coeno-pteroid and true ferns. The most part of them have not yet well or "per-fectly" specialized leaves as the later ferns and in many cases *(Proto-*

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pteridia, Swalbardia a. o.) we may see typical transition stages between mere ramifications and well developed fern fronds. In the foregoing chapters I have also pointed out that the shape of such not yet "perfectly" specialized fronds exhibits many features indicating very much their origin: we have pointed examples where the fronds represent transition stages from a dichopodially arranged branch system *(Protopteridia* and several allied of the devonian genera, *Dawsonites)* or from a polybrachial system *(Archaeopteris, Aphlebiopteris; Swalbardia)* or even from various more or less phyllophoralean stages *(Rhacophyton, Cephalotheca, Stauropteris, Aneurophyton)*, of which several remember strongly the coenopteroid ferns (e. g. *Stauropteris)* and are in fact often by various palaeobotanists also joined to them. Nearly none of these old primitive fernlike plants have well specialized sori. Their sporangia as mentioned in the above morphological chapter are born at the tops of the last twigs of the often very reduced small fertile branch systems, which are more *(Protopteridia* and several allied forms, the culmian *Rhacopterids)* or less *(Aneurophyton, Rhacophyton)* regularly placed within the system of the frond rhachises. From this point of view they represent typical transitional stages between psilophytalean plants of the type of *Taeniocrada, Zoosterophyllum* a. o. and between the later true ferns. The anatomical conditions of the various known fossils are of very different features and suggest a rather polyphyletic origin of this whole assamblage of old fern like plants if compared with the simple conditions met with in the previous group of the post devonian fern families. I propose for this whole curious fern-like plant assamblage the term of the *Profilicineae*. They are to be regarded evidently as the direct ancestral stage of the true ferns as known from the post devonian periods and untill to day. The mutual relation of the various known chief groups resp. genera belonging to this evolutionary stage as well as their relation to the true ferns is illustrated by our schemes fig. 4, 5.

5. The origin and evolution of the *Gymnosperms*.

The *Gymnosperms* represent an intermediate stage in the plant evolution between the pteridophytic and the angiospermic stage. It is just the stage during which the plant evolution achieved the creation of true seeds. Simultaneously with this processus also a further elaboration, specialisation and improvement of the leaf organs as well as of the vascular strands in the stems passed forward. The evolutionary tendencies, which are to be observed here, are certainly only a continuation of several phenomena indicated here and there already among the *Pteridophyta*, phenomena, which consisted mainly in various processes of reduction and "condensation" of formerly larger and more abundantly divided organs or in the abbreviation and simplification of their ontogenetical evolution. Having the intention to comprehend the evolutionary lines contained in the enormously rich material of fossil as well as recent gymnospermic plants hitherto discovered, we have to take attention especially to the following cardinal principles mentioned already partly in the previous chapter dealing with the morphological factors of the plant evolution.

1. The architecture of the sterile leaves and their gradual simplification connected no doubt with the further adaptation to the life on rather dry land. From this point of view we have defined among the gymnosperms two main evolutionary lines: the macrophyllous line of the *Pteridospermae* and *Cycadeae* and the line of microphyllous plants, the *Coniferophyta* comprising the orders of the *Cordaitales, Ginkgoales, Podozamites* and *Coniferales*.

2. Gradual changes concerning the pollen grains (microspores) and the mail gamets (spermatozoids). In the macrophyllous line *Pteridospermae-Cycadeae* (or the *Cycadophyta*) we have stated at a lower stage (most part of the pteridosperms) pollengrains with multicellular content. The highest stage here achieved (Cycads) exhibits unicellular pollengrains, the content of which very soon (already before they are set free from the microsporangia) is segmented into three cells (extremely reduced prothallium) and which at the germination are producing a short pollentube containing two ciliate spermatozoids. In the second line, the *Coniferophyta*, three gradual steps are to be stated: considerably large pollengrains with multicellular content and no pollentubes in the order of the *Cordaitales*, pollengrains with degenerative prothallia and rather well developed pollen-tubes containing ciliate and very small spermatozoids in the *Ginkgoales* and finally pollen grains producing extremely reduced prothallia (only several cell nuclei) and large pollentubes with non ciliate and passive antherozoids instead of motile spermatozoids in the *Coniferales* (the conditions in the small group of the mesozoic *Podozamites* are meanwhile unknown). The stage achieved in the Cordaits corresponds wholly with the Pteridosperms, that achieved in the Ginkgos with the Cycads. The stage of the Conifers has no analogon in the line Pteridosperms-Cycads and must be regarded as still more advanced; it has its analogon first in the *Gnetineae* and than in the *Angiospermae*, but both these groups are in other views much more advanced and cannot be therefore regarded as equivalent macrophyllous analoga of the microphyllous Conifers.

3. The creation of typical seeds and their gradual improvement. — In the large series of the gymnospermous plant remains we have stated ovular organs of several types, which are characteristic for certain main divisions and which appear as some general stages achieved by the phylogenetical evolution. They are of two chief kinds:

A. Changes concerning the inner structures of the nucellus. Especially interesting is here the presence or absence of an embryo. Seeds without developed embrya were stated (besides the *Lepidospermae*) in all *Pteridospermae* (even in the most "perfectly" organized and stratigraphically youngest of them, the *Caytoniaceae*) and in the *Cordaitales*. Seeds with well developed embrya are known in all other gymnospermous groups (in the Ginkgos the embryo is often developing a considerable time after the seeds have fallen off).

B. The improvement of the protective arrangements and of the pollination processus. — a) As to the protective arrangements round the ovules, we have stated in the whole three possibilities, of which only two

are realized in the Gymnosperms: ovules free or provided only by special cupshaped but opened receptacles, not wholly enclosed in any special gynoecia (in the most part of the Gymnosperms), or ovules enclosed in a very imperfect kind of gynoecia without a typical style and stigma and formed only of a small portion of the fertile leaves *(Caytoniaceae, Corystospermaceae* and in a certain measure also in several Conifers like in the family of the *Cheirolepidaceae)*. — b) As to the pollination act we have seen that nearly in all Gymnosperms the pollen grains are caught by mucilaginous liquids secreted directly by the nucellus. Only in the group of the *Gnetineae* a further step forwards was attained: a tubular style- and stigma-like apparatus effected of the top of the integument, which received this function.

4. The arrangement of the sporangia resp. ovules in larger units resp. the arrangement of the whole sporophylls into flowers (ev. cones). As evident from our chapter on the principles of the comparative morphology, various specialized flowers resp. flower-cones are known in all groups of the Gymnosperms except the Pteridosperms; also in the small lycopodinean seed bearing group of the *Lepidospermae* the sporophylls are grouped on special axis into definite cone-like flowers. The Pteridosperms in contrary appear as an utterly flowerless type. But even here the sporogenous organs achieved in certain cases special kinds of grouping into larger and often even very massive and complicated organs placed on the rhachsises or on the lamina of their large and ramified fronds.

The morphological significance and the phylogenetical meaning of the various conelike fructifications resp. flowers of the Coniferophyta as well as of the conelike or more or less disclike flowers of the Cycadeae were already sufficiently discussed above. I mentioned there also all important as to the processus of their eventual "condensation" into rather complicated inflorescences-cones or reduction untill to uniovulate and very small sized strobiloid flowers.

Of special and very serious interest seem to be the pteridospermous fructifications, which were not yet discussed in the above chapters. They throw some light on the relations of this plant group to its eventual ancestors as well to its more advanced descendents, the *Cycadeae*.

As to the female fructifications of the Pteridosperms, we know from the numerous fossils of the late palaeozoic times two eventualities: the ovules (seeds) are situated singly along the margin of the lamina of the often more or less reduced leaflets (resp. they are pushed upon its upper or lower side), eventually they are sessile on leafless frond rhachises of higher order, or the ovules (seeds) are enclosed within special opened cupshaped organs. As to this last type, we know Pteridosperms bearing only 1 seed within each cupule, which is the most frequent type among such cupule bearing Pteridosperms, but there have been discovered also forms exhibiting a larger number of ovules in each cupule *(Calathiops, Calathospermum, Gnetopsis* a. o.) As especially clearly stated in the *Calathospermum,* the cupshaped organs are built up of several mutually fused leaflets. The uniovular cupule bearing Pteridosperms must be then regarded as more advanced and specialized types by means of reduction

of the number of the enclosed ovules, as well as by the pushing of the single ovule into a terminal (resp. central) position at the end of the vescular strand of the resp. rhachis twig.

The microsporangia resp. pollen sacs of the most of the palaeozoic Pteridosperms are in contrary to the greatest part of the ferns of an elongated shape, but are also associated in variously arranged groups *(Telangium* a. o.). They often exhibit the same tendency to mutual coalescence, by means of which rather large synangia arise *(Conodotheca, Goldenbergia, Aulacotheca, Boulaya; Potoniea* a. o.). Such simple synangia are mostly born on special ramifications of frond rhachises deprived wholly of lamina. In several extreme cases still more complicated fructifications were produced by mutual coalescence of a considerable number of such simple synangia, no doubt due to an extreme reduction of their stalks *(Dolerotheca)*.

In the later i. e. mesozoic Pteridospermic plants we have to state a curious tendency to the formation of special small gynoecea like capsules enclosing wholly one or even more ovules *(Corystospermaceae, Caytoniaceae)*, an analogical phenomenon to the very perfectly organized gynoecea of the Angiosperms, the first traces of which appear more or less simulatneously just with these most advanced mesozoic Pteridosperms. The formation of both kinds of gynoecea (the primitive ones of the last survivals of the Pteridosperms as well as the more advanced ones of the Angiosperms) are thus two quite contamporaneous phenomena in the history of the plant evolution. As to the male fructifications of the mesozoic Pteridosperms, we may only briefly note, that they are principally similar to some palaeozoic *Telangia* or *Crossothecae* composing considerably large ramified fructification systems deprived utterly of sterile lamina. Many of them *(Caytonia* a. o.) show an evident tendency to coalescence and formation of small quadriloculate synangia, a tendency reminding in some measure the conditions of the stamina of higher, flowering angiospermic plants.

As to the anatomy of the Pteridosperms we may point out at least two main types indicating two great evolutionary lines: 1. Proto-till syphonostelic forms leading eventually untill to some transitional stages to eustely *(Tetrastichia, Lyginopteris,* the various *Heterangia)*. The most primitive discoveries show even a tendency to actinostely *(Tetrastichia)* which seems to be wholly parallel to the conditions among the most primitive discoveries show even a tendency to actinostely *(Tetrastichia)* which seems to be wholly parallel to the conditions among the anatomical conditions known in the Cycads.

It is very interesting to note that the first anatomical type of the palaeozoic Pteridosperms is provided mostly with cupulate female fructifications and rather simple *(Telangia)* male fructifications, whereas the polystelic i. e. anatomically more advanced types *(Medulloseae)* exhibit a very simple kind of female fructifications (naked ovules at the margin of the leaflets or on frond rhachises, not unlike as in the Cycads) but very complicated male fructifications, massive synangia. But besides these two rather specialized types of paleozoic Pteridosperms we know also a whole series of more or less intermediary forms, know unfortunately

mostly only as impressions, showing very simple Telangia as the male fructifications and at the same time quite naked ovules sitting singly at the margin of the leaf lamina (*Dicksonites, Pteridozamites, Eremopteris, Wardia*) resp. secondarily pushed on the ventral side of the leaf lamina (*Pecopteris wongi*). Just such primitive forms exhibit the strongest similarity with the conditions known among the primitive Cycads. We have therefore serious reasons to regard such intermediary primitive Pteridosperms as the more or less direct ancestral type of the *Cycadeae*.

As already mentioned, several very advanced types of pteridospermic plants are known from the mesozoic period: *Peltaspermaceae, Corystospermaceae* and *Caytoniaceae*. We have just discussed briefly their morphological pecularities; unfortunately we are not yet informer about their anatomy. But nevertheless still their morphological features suggest that we have to regard them as a further younger evolutionary line of macrophyllous types with "non cycadean" tendencies, a line more or less parallel to the evolutionary line of the Angiosperms. The character of their male as well as female fructifications indicate that we have here to do with very advanced descendents (or allied) of the more primitive palaeozoic pteridospermic forms (the mentioned "intermediary types") and not of the rather advanced types as the *Lyginodendrae* or *Medullosae*. Their relations to the palaeozoic Pteridosperms is in a certain sense very similar to that of the Cycads. Both appear as two parallel evolutionary lines.

Among fossils known from the early mesozoic or already from the latest phase of the palaeozoic times a large series of still other pteridospermic forms than as mentioned above were discovered; but their morphology and anatomy is till present only very fragmentary known or even quite unknown. I remember at least the names of *Glossopterideae, Gigantopterideae, Thinnfeldiae, Scoresbya* etc. Many of them show a curious kind of "condensation" of the leaf lamina with its nervation, which is the reason that several authors (P. Bertrand a. o.) regard many of them as forms standing perhaps very near to the real ancestors of the Angiospermae.

5. The anatomical features of the vascular strands and especially the conditions of the secondary xylem. — We have already emphasized the importance of the occurrence of pitted (bordered pits) tracheids of the secondary xylem in the most part of the gymnosperms in contrary to the majority of the pteridophytic (especially filicinean or lycopodinean) groups. I stated also that the pteridospermic and Cycadean groups are distinguished by rather manoxylic wood, whereas the other gymnospermic types (mainly the Coniferophyta) achieved a much higher stage being provided by picnoxylic wood (though even here several very old genera [e. g. the *Poroxylae* of the group of the Cordaits] are also manoxylic). Another anatomical particularity, which enables us to evaluate the mutual relations of the various gymnospermic types is the arrangement of the bordered pits on the walls of the xylem tracheids. In genera regarded generally as more archaic (or really in stratigraphically rather old wood fragments) we find generally the mentioned "araucarioid" kind of pitting without Sanio's rims, whereas in geologically younger fossils and therefore more

	Palaeozoic			Triassic, Jurassic	Cretaceous, Kaenozoic
Cryptogamic.	Ovules imperfectly developed.	Ovules without embrya. Spermatozoids ciliate, motile.		Ovules with developed embrya. Spermatozoids ciliate, motile.	Ovules with developed embrya. Non ciliate and non motile antherozoids.

Fig. 10.

advanced types tracheids with slightly remote pits separated mutually by well developed Sanio's rims are to be stated. To the first type belong besides all Pteridosperms and Cycads (many of them exhibit of course also only spiral, annular or scalariform structures) the Cordaits, the primitive Conifers of the Palaeozoic *(Voltziineae)* as well as the still living family of the *Araucariaceae*. The Ginkgos (at least the recent type) as well as all other Conifers exhibit a rather advanced character. This is especially singnificant for the Ginkgos, which otherwise from the geological point of view appears as a considerably old group, though from the point of view of the organization of the seeds a rather advanced group if compared with tho Cordaits or Pteridosperms, The archaic stage of the xylem tracheids of the family of the *Araucariaceae* is evidently to be regarded as an indication of its very close relations to the ancestral stock of the palaeozoic Conifers *(Voltziineae)*. In this light all other recent families of the Conifers appear as various highly advanced evolutionary side lines.

Summarising all above stated morphological as well as anatomical principles and taking into consideration also the stratigraphical distribution of the various gymnospermic plant groups, we come to the following evolutionary fundamental scheme: Fig. 10.

The parallel above discussed evolutionary processes in both lines are in this scheme well indicated. I regard as e s p e c i a l l y i m p o r t a n t the notion of the pteridospermic feature of the *C o r d a i t e s* and the most probably cryptogamic character of the cordaitalean ancestors, the *P y t i a e* (resp. also of the *Calamopityae, Protopityae* a. o.).

As to the further splitting of the just defined fundamental gymnospermic groups, especially the conditions in the larger groups of the *Pteridospermae* and *Coniferales* are of special interest. I may suggest in agreement with the previous discussions the following derivation of the various types in these groups:

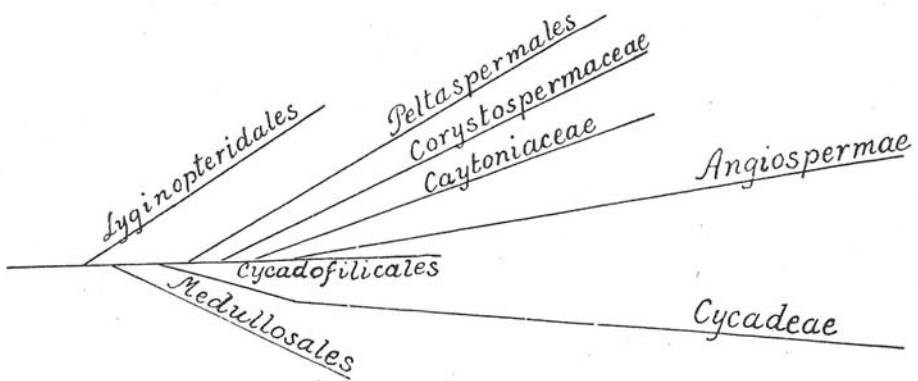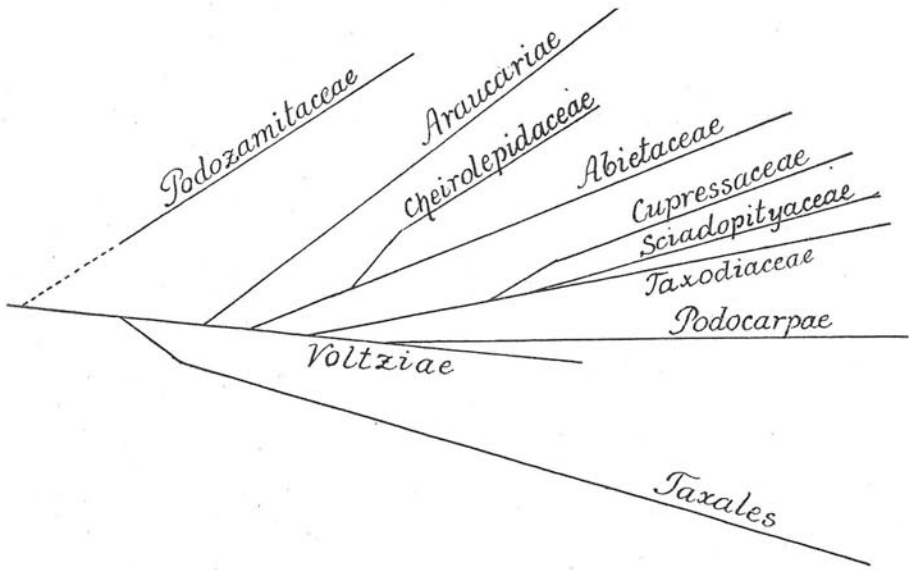In the Pteridospermae: Fig. 11.

In the Coniferales: Fig. 12.

Fig. 11.

Fig. 12.

6. The origin of the *Gnetineae* and the *Angiospermae*.

We must admit that the problem of the origin of the *Gnetineae* and of the *Angiospermae* belongs to the most difficult tasks of the palaeobotany, though both these groups are of rather recent geological age. I may tell that this problem is as to the available palaeontological evidences in a high measure similar to the already discussed problems of the origin or derivation of the primitive siluro-devonian green land flora (i. e. *Trachaeophyta* in general) from the thallophytic water flora, especially from the green algae. We know indeed various morphological as well as anatomical features characteristic for the angiospermic plants realized singly already in various groups of the older gymnospermic plants (e. g. the closed gynoecea like female capsules of the *Corystospermaceae* and *Caytoniaceae*, the more or less disclike circular flowers of the *Bennettitineae* a. o.), we know also rare fossil leaves with an angiospermic nervation already from the triassic beds (*Furcula* from the Rhätic of Greenland). But the chief difficulty seems to lay in the fact, that we do not know any intermediary forms between well differenciated angiospermic plants and several of the known extinct gymnospermic groups (or perhaps still directly cryptogamic forms). The Gnetineae, which very often are regarded as such intermediary types, are according to the previous notes rather a parallel and perhaps even a relatively older side line, but certainly no intermediary or ancestral type at all.

Both, the *Gnetineae* as well as the *Angiospermae*, exhibit as to the anatomical particularities, well developed vessels (tracheae), though in the first group somewhat more primitive. In both groups we find mostly circular flowers of only one common plan, no typical cone like fructifications. They exhibit the same enormous reduction and "condensation" of formerly macrophyllous fronds and thus also an utterly similar nervation of the leaf lamina. There is also an analogical kind of style and stygma apparatus in the female fructifications, but as already told only an analogical one. The style and stigma of the *Gnetineae* are built up of the prolongated tubular upper end of the ovule integument, whereas in the *Angiospermae* this organ is made of the reduced lamina of the sporophylls. The *Gnetineae* represent thus a lower stage in the evolution of the macrophyllous plant type toward the angiospermy.

The chief difficulty in the derivation of the Angiosperms consists in the present absolute lack of any fossil type which would show us the way of transformation of the sporophylls into the pistil prolonged into the style and stigma organ (perhaps several recent plants with more or less opened pistils like in the group of the Resedaceae a. o. may serve us as of course only a very incomplete analogon of this processus). Without a perfect knowledge of this processus we in wain are endeavouring to find out the true ancestral type to this most recent plant type among the enormous quantity of fossil plant remains. As partly already mentioned, perhaps some slight indications are also visible in the architecture of several leaves of some supposed Pteridosperms of the late Palaeozoic and early Mesozoic, in which a tendency to a "condensation" of the leaf lamina is undeniably realized. We know this particularity in the fronds of the late palaeozoic *Gygantopterides* of Eastern Asia and North America, in the rhätic *Scorsbya* of Greenland as well as in several alethopteris like fronds from the upper triassic (Keuper) period of central Europe, like *Scythophyllum* a. o.

All these and similar facts seem to attest that the angiospermous plants represent a continuation in the evolution of the macrophyllous line of the gymnospermous plants. But unfortunately the palaeobotany did not yet reveal anything more concrete of the kind and ways of their respective morphological and anatomical transformations.

As to the second i. e. microphyllous resp. sphenopsid line of the gymnospermic plants, we find at the present state of our knowledges no reason to suppose a further evolution of this plant type. The rather large number of relic species or genera (often even whole families) are also a certain proof that this second group shows absolutely no tendency to any further evolution.

The further evolution and splitting of the angiospermous type into the various orders and families cannot be the subject of this paper. This is rather a problem of the study of recent plants. The palaeontology can offer here at present perhaps only some additional material dealing with their stratigraphical and palaeogeographical distribution in various sections of their history or several scattered details as to some seeds and more resistent fruits especially from the later (tertiary) periods besides an enormously large mass of various leaf impressions, which are generally

very difficult to be precisely and reliably determined. But this branch of botanical science has not yet revealed us anything more complete about the constitution of the angiospermic flowers and fruits of the plants from the older cretaceous or even jurassic times, which perhaps would throw more light on this youngest sector of the plant evolution. The derivation of the single groups of the Angiosperms is, I believe, just for that reason covered by a veil of mystery or at least of much uncertainty. And I believe it will remain so for a still considerably long time, till the beds of the earth will once give out several of these secrets.

7. A rough outline of a natural system of the Cormophyta based on palaeontological evidences.

A. Bryophyta:
      1. Anthocerotales.
      2. Hepaticae.
      3. Musci.
B. Trachaeophyta:
    α) Pteridophyta:
        I. Psilophytineae.
           1. Rhyniales:
               Horneaceae.
               Rhyniceae.
           2. Pseudosporochnales:
               Pseudosporochnaceae.
           3. Taeniocradales:
               Taeniocradaceae.
               Zosterophyllaceae.
           4. Asteroxylales:
               Psilophytaceae.
               Asteroxylaceae.
        II. Psygmophyllineae.
           1. Bröggeriales:
               Bröggeriaceae.
           2. Barrandeinales:
               Barrandeinaceae.
           3. Duisburgiales:
               Duisburgiaceae.
           4. Psilotales:
               Psilotaceae.
           5. Noeggerathiales:
               Tingiaceae.
               Noeggerathiaceae.[1]
               Eurhacopteridaceae.[2]

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[1] Includes besides *Noeggerathia* also the genera of *Palaeopteridium* und *Saaropteris* as well as the formgenus of *Plagiozamites*.
[2] Includes most of the later carboniferous *Rhacopterides* of the subgenus of *Eurhacopteris* Oberste-Brink.

6. Cladoxylales:
   Cladoxylaceae.
   Voelkeliaceae.

7. Pityales:
   Calamopityae, Protopityae and several other imperfectly
       known families.
   Pityaceae.

III. Lycopodineae.

   1. Protolycopodiales:
      Protolepidodendraceae.
      Arthrostigmataceae.

   2. Eleutherophyllales:
      Eleutherophyllaceae.[1])

   3. Lycopodiales:
      Barragwanathiaceae.
      Lycopodiaceae.

   4. Selaginellales:
      Selaginellaceae.
      Miadesmiaceae.[2])

   5. Cyclostigmatales:
      (the various natural families are not yet well defined.
          This order includes eligulate palaeozoic tree club
          mosses like the genera Cyclostigma, Pinacodendron,
          Ulodendron, Asolanus a. o.).

   6. Lepidophytales:
      Archaeosigillariaceae.
      Lepidodendraceae.
      Bothrodendraceae.
      Sigillariaceae.
      Pleuromeiaceae.
      Nathorstianaceae.[3])
      Isoetaceae.
      Lepidocarpaceae.[2])

IV. Articulatineae.

   1. Protoarticulatales:[4])
      Hyeniaceae.
      Calamophytaceae.

   2. Pseudoborniales:
      Pseudoborniaceae.

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[1]) Includes the genera *Zimmermannia* Goth. and *Eleutherophyllum* Zimm.
[2]) Both these genera *(Lepidocarpon and Miadesmia)* are incompletely "Le-
pidospermic".
[3]) Includes the genera *Nathorstiana* and *Bedheimia*.
[4]) Besides the two mentioned families still other (very primitive) genera are
known from the early Devonian: *Spondilophyton, Climaciophyton, Boegendorfia*
a. o. but they are very incompletely known and do not allow any more precise
systematical taxation.

3. Sphenophyllales:
   Sphenophyllaceae.
   Cheirostrobaceae.
4. Tristachyales:
   Tristachyaceae.
5. Equisetales:
   Asterocalamitaceae.
   Sphenosterophyllitaceae.[1]
   Phyllothecaceae.[2]
   Calamitaceae.
   Equisetaceae.
V. Pteropsidineae.
 A. Profilicineae:
  1. Aneurophytales:
   Aneurophytaceae.
  2. Rhacophytales:
   Rhacophytaceae.
   Cephalothecaceae.
  3. Stauropteridales:
   Stauropteridaceae.
  4. Swalbardiales:
   Swalbardiaceae.
  5. Archaeopteridales:
   Archaeopteridaceae.
  6. Protopteridiales:
   Protopteridiaceae.[3]
   Dawsonitaceae.
   Iridopteridaceae.[4]
  7. Rhacopteridiales:
   Anisopteridaceae.[5]
 B. Filicineae:
  1. Phyllophorales:
   a) Asteropteridae:
    Asteropteridaceae.
   b) Zygopteridae:
    Etapteridaceae.
    Ankyropteridaceae.
    Tubicaulidaceae.
    Grammatopteridaceae.
  2. Inversicatenales:
   Botryopteridaceae.
   Anachropteridaceae.

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[1]) Sphenasterophyllites, Autophyllites a. o.
[2]) Phyllotheca and Schizoneura.
[3]) I am joining hereto also the genera Pectinophyton, Barynophyton a. o. from the early Devonian.
[4]) At present not yet well defined and somewhat artificial "anatomical" family.
[5]) Including chiefly the kulmian species of the form genus of *Rhacopteris* (*"Anisopteris* Oberste-Brink") as well as the upper devonian Archaeopteris sphenophylloides.

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3. Osmundales:
 Osmundaceae.
4. Eusporangiales:
 Psaroniaceae.
 Marratiaceae.
 Weichseliaceae.
 Ophioglossaceae.
5. Filicales[1]) (i. e. Leptosporangiales):
 a) Simplices
  isosporic:
   Schizaeaceae.
   Gleicheniaceae.
   Matoniaceae.
   Dipteridaceae.
  heterosporic:
   Marsiliaceae.
 b) Complicatae
  isosporic:
   Loxomaceae.
   Hymenophyllaceae.
   Dicksoniaceae.
   Cyatheaceae.
   Polypodiaceae.
   Parkeriaceae.
  heterosporic:
   Azollaceae.
   Salviniaceae.

β) Gymnospermae:

 A. Cycadophyta.

  I. Pteridospermae.[2])

   1. Cycadofilicales.[3])

   2. Lyginopteridales:
    a) polyspermae
     Mariopteridaceae.[4])

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[1]) Most of the upper carboniferous genera of this order cannot yet be well joined hereto on account of our present imperfect knowledges (*Crossotheca, Zeilleria*, the whole group of the *Proleptosporangiales* a. o.).

[2]) The systematical position of many discovered species (especially of many mesozoic types eg. *Gigantopteris, Chiropteris, Scoresbya* a. o.) on account of quite unknown fructifications cannot be defined.

[3]) This order is meanwhile not quite clear. I unite under this term several species bearing the ovules at the margin (—or on the surface) of the often more or less reduced leaflets (*Dicksonites, Eremopteris, Pteridozamites, Wardia, Emplectopteris, Pecopteris wongi, Nyströmia* a. o.) and provided mostly by rather simple Telangia like male fructifications, types which are to be regarded as relatively most primitive Pteridosperms. At present I am unable to define here the various natural families.

[4]) Besides this family still other polyspermic types are known (*Calathospermum, Gnetopsis* a. o.). But at present it is impossible to define the respective natural families.

b) monospermae
Tetrastichiaceae.
Heterangiaceae.[1])
Lyginopteridaceae.
3. Medullosales:
Whittleseyaceae.
Potonieaceae.
Dolerothecaceae.
4. Glossopteridales:
Glossopteridaceae.
5. Peltaspermales:
Peltaspermaceae.
6. Ptilozamitales:
Ptilozamitaceae.
7. Proangiospermales:
Corystospermaceae.[2])
Caytoniaceae.[3])

II. Cycadeae.
a) Cycadineae.
1. Nilssoniales:
Nilssoniaceae.
2. Cycadales:
Cycadaceae
Zamiaceae[4])
b) Bennettitineae.
1. Bennettitales:
Cycadeoideaceae
Williamsoniaceae
Wielandiellaceae
Sturiellaceae
2. Pentoxylales:
Pentoxylaceae

III. Gnetineae.
a) Haplocheilae.
1. Ephedrales:
Ephedraceae.
b) Syndetocheilae.
1. Gnetales:
Gnetaceae.
2. Welwitschiales:
Welwitschiaceae.

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[1]) This family comprises most probably also the group of the *Euspheno-pterides*.

[2]) Includes most probably many species of the *Thinnfeldia* series.

[3]) Includes the genera of *Sagenopteris* and *Drepanozamites*.

[4]) This term containing all species provided with cone like female frucitfications seems to be too large. Perhaps it will be more natural to split it into more natural families.

B. Coniferophyta.
  I. Cordaitineae.
      1. Cordaitales:[1])
          Poroxylaceae.
          Mesoxylaceae.
          Cordaitaceae.
          Noeggerathiopsidaceae.
  II. Ginkgoineae.
      2. Ginkgoales.[2])
  III. Coniferineae.
      1. Wielandiales:
        Podozamitaceae.
      2. Coniferales:
        a) Voltziae:
            Walchiaceae.
            Voltziaceae.
            Ullmanniaceae.
        b) Araucariae:
            Araucariaceae.
        c) Abietae:
            Abietaceae (Pinaceae)
            Cheirolepidaceae.
        d) Cupressae:
            Taxodiaceae.
            Sciadopityaceae.
            Cupressaceae.
        e) Podocarpae:
            1. Podocarpaceae.
      3. Taxales:[3])
        Taxaceae.
        Cephalotaxaceae.
        (Stachyotaxaceae).
        (Diplostrobaceae).
γ. Angiospermae.

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[1]) The group of *Pityae* generally united by many systematists with the Cordaits is joined here to the pteridophytic group of the *Psygmophyllineae* on account of its probably pteridophytic features.

[2]) A more detailed systematic of the fossil *Ginkgoales* is at present not possible, as we know only numerous remains of sterile shoots or leaves but only very little on the respective fructifications and on the anatomy.

[3]) The morphological conditions of the genera *Pallisya, Stachyotaxus (-Stachyotaxaceae)* as well as of the genus of *Diplostrobus (-Diplostrobaceae)* are not yet well cleared up. Therefore their place within the order of the *Taxales* is only a provisory one.