

Notes on the Origin and the Past of the *Chlamydospermophyta*

Původ a minulost chlamydospermických rostlin

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Abstract — Various morphogenetical features, especially those of the fructifications ("flowers"), as well as the palaeontological documents of the occurrence in the past of the representatives of the *Chlamydospermophyta* (*Ephedra*, *Gnetum* and *Welwitschia*) are examined and a new conception of their past is suggested. They are considered as evolved nearly along with the *Angiosperms*, with which they have no nearer alliances, representing three quite independent, blind and very narrow evolutionary side lines (detached from different *gymnospermous* groups; polyphyletic origin), which never became more copiously split into diverse families and genera. From this point of view therefore they are not to be regarded as relic types of some hypothetical ancient, once rather more comprehensive taxons of which various missing links have become extinct. Their past is interpreted like that of several relict pteridospermous groups of the Mesozoic period (*Caytoniales*, *Corytospermales*, *Lepidospermales* [i.e. *Peltaspermales*] a.o.), which likewise have never represented any larger taxons.

The general meaning of the majority of various studies and considerations dealing at present with the chlamydospermic plants is that most probably they are related, partly (the genus *Ephedra* L.) with some stachyospermic *gymnosperms*, partly (the genera *Gnetum* L. and *Welwitschia* Hook.) with the *phyllospermic gymnosperms*, especially with the mesozoic bennettitalean plants, and that perhaps in the past they represented a much bigger and widely distributed plant group of which only a few rather rare types survived, in which way also the unusual taxonomic isolation of the three still living genera is generally interpreted. Most of such considerations are based on the structure of their vascular bundles, the character of their leaves (especially of their stomata), the features of their ovules, the peculiarities of the pollination act, their biochemical features (serodiagnostic reactions) and, not in the last, also on the construction of their fructification assemblages ("flowers"). They are however mostly formulated in rather too universal inferences, evidently on account of the deficiency of a larger documentary material (there are only three living genera, but no reliable fossils, except pollen grains ranging only from the Cretaceous) as well as owing to the unusually strong specialisations and reductions (or morphogenetical modifications) of the various organs of the still living representatives. Especially we need a clear elucidation of their past, and the causes of the taxonomical isolation of their three still living genera, which would not be in contradiction to the rather very scanty palaeontological discoveries.

I believe that most serious evidence of the natural alliances of the three living genera may be achieved by a very thorough morphogenetical analyses of their fructification assemblages ("flowers" or "inflorescences"). On account of some special features of their vascular bundles (especially the origin of

their vessels), we have to assume in the first place that they have no nearer relationships to the Angiosperms, and therefore any comparison of their "flowers" (resp. "inflorescences") with flowers of the Angiosperms is to be discarded on principle, and the various existing mutual similarities (e.g. the shape of the leaves, the stigmatal organs and others) are to be regarded only as the results of a convergent evolution of the respective plant groups. In my opinion the most trustworthy morphogenetic interpretation of the fructification assemblages ("flowers", "inflorescences") or other organs of the chlamydospermic plants may be reached only if compared with analogous organs of various gymnospermous plants.

In the genus *Ephedra* L. the small "flowers" are clustered into small axillary cone-like "inflorescences", mostly of separate sexes, the main axes of which bear several pairs (or whorls) of scale-like leaflets. The male cone-like clusters exhibit in the axils of their leaflets only one "flower", the very short axis of which bears beneath two laterally at their base connate protective scales which are followed by still one free scale, after which the end part of the "flower" axis is passing into a rather big terminal stamen (very often divided at least into two arms), bearing at the top several pollen sacks fused into a large synangium. The female cone-like clusters are of a similar type as the male ones. Their main axis also bears several pairs (or whorls) of scales; however, only some of them (those which are situated in the terminal part of the cone axis) bear in their axils single "flowers". The short axis of these flowers bears only one terminal ovule protected by one pair of laterally cup-like connate scales followed below by still another similar pair of connate leaflets.

The most probable explanation of the morphogenetical origin of these cone-like fructification assemblages is, I believe, one deduced by a comparison with the fructifications of the stachyospermic gymnosperms. Both types, the male as well as the female one, are evidently to be regarded as some compound cones like the spike-like "inflorescences" of the Cordaites or the whole fertile brachyblasts of the Ginkgos (in the Conifers only the female cones are compound!). The single axillary "flowers" are then equivalent to the small axillary bud-like small fertile dwarf shoots of the spike-like fructifications of the Cordaites or to the catkin-like "flowers" or stalk-like female "flowers" of the Ginkgos (or with the seed scales of the coniferous female cones). All that means that the single axillary "flowers" of the cone-like fructifications of *Ephedra* L. represent some very reduced and specially transformed axillary telomoid fertile dwarf shoots of the *Trichopitys* type. Their protective scales are to be regarded as sterilized side teloms (sterile scales of the fertile dwarf shoots in the spikes of the Cordaites or in female cones of the coniferous Walchiaceae), the single big and rather complicated terminal stamens of the male "flowers" as organs resulting through fusion of several still fertile teloms (like in the catkin-like male "flowers" of Ginkgos), and finally the single terminal ovules of the female flowers as the single remaining fertile teloms, the stalks of which were nearly completely suppressed, and which therefore assumed a terminal position (see similar reduction process in the female fructification of *Trichopitys vasilkovskii* SIXT. or in the *Taxaceae* family!). Thus in the genus *Ephedra* L. the male as well as the female fructifications are of an equal fundamental construction: compound cones resulting from a special reduction and transformation of some twigs bearing originally in their leaf axils fertile dwarf shoots (like in the genus *Trichopitys* SAP.). In the case of reductions or transformations leading to their final shape and construction, several similarities can be ascertained, especially regarding the evolution of fructifications ("flowers", "inflorescences") of the *Ginkgo*-trees.

In the genus *Welwitschia* Hook. the "flowers" appear singly in the axils of decussate scale-like leaflets closely on the axis of the stalked cones (of separate sexes) which are growing out of the axils of scale-like leaflets on some rather thin and dichasially branched twigs. The single "flowers" are of a radial symmetry and exhibit a very short axis. The male "flowers" are composed of two decussate pairs of protective leaflets, a ring of six stamens, bearing at the top a trilobulate synangium and fused at the base into a narrow collar, and finally of the rudiment of one ovule in the centre (i.e. at the top of the "flower" axis). In the female "flowers" there can be found only one pair of protective leaflets which are fused together into a sack-like cupule containing in the centre (i.e. terminally on the "flower" axis) a single ovule.

A comparison with the fructification assemblages of the stachyospermic Gymnosperms in this case seems to be very unjustifiable not only because of the construction of these "flowers" (especially of the male "flowers") but also with regard to the features of the leaves (a megaphyllous type!). In some respects they are slightly similar to the flowers of the Angiosperms, but true morphogenetic homologies between these both types of flowers are utterly out of question because of the facts mentioned above and especially because of the quite different type of the stamens. More acceptable seems to be the comparison with the "flowers" of several cycadaceous plants, especially with those of the *Cycadeoideales* (*Bennettitales*) group, or in several respects also with those of the *Pentoxylales* (only as to the male fructifications!). Their stamens may be regarded as much reduced microsporophylls of the *Pentaxylon* type (i.e. *Nipania* VISHNU MITTRE); they agree with them also in their cyclic arrangement as well as in the collar-like fusion of their bases. Similar features may be also observed in the male „flowers" of the *Williamsonia* CARR. genus, but the shape of the single stamens is quite different (mostly leaf-like, enlarged or pinnately divided). The existence of a rather reduced (rudimentary) ovule in the centre of the male "flowers" points out to our having to do here with very simplified (reduced) and originally bisexual flowers of the bennettitalean type. To the relationship with this group of mesozoic plants also points out the syndetocheilic nature of their stomata (which is admitted perhaps by the majority of the present-day botanists). The female "flowers", as mentioned before, are still more simplified; in contrast to the bennettitalean female (or bisexual) flowers their single ovule is not protected by any interseminal scales at all (— which perhaps aborted by reduction or have never been existing!). In *Welwitschia* Hook., as mostly assumed at present, we have really to do with "flowers" (i.e. simple cones) of phyllospermic nature, extremely reduced and indicating from the morphogenetical point of view to the relationship with the bisexual bennettitalean "flowers" and in certain features also with the "flowers" (only with the male "flowers") of the *Pentoxylales* (*Nipania* VISHNU MITTRE).

In the genus *Gnetum* L. the fructification assemblages are of a rather thin cone-like or spike-like shape. They are of separate sexes, arising out of axils of scale-like leaflets on some thin and sparsely branched side twigs (or even on unbranched ones and then assuming a terminal position). Their axes bear decussate pairs of in part laterally connate scales, in the axils of which are to be found either very numerous male or a small number of female "flowers"; among these "flowers" are present very numerous hairlike paraphyses of quite unknown morphogenetical significance (- perhaps mere trichomes?). No special subtending bract scales are to be met within the single "flowers". The male "flowers" are arranged densely in several whorls (i.e. collaterally and serially) and are composed of a bilobed cupshaped case (resulting in two protective fused scales) containing one terminal stamen with two synangia (in fact these are two longitudinally fused very simplified stamens or microsporophylls). The female "flowers", arranged only in one whorl, are composed of two cupshaped cases (representing two decussate pairs of connate leaflets) including one terminal ovule. Both types of "flowers" are radially symmetrical.

I believe that with regard to the megaphyllous character of this genus, we have to interpret the morphogenetical nature of its "flowers" in a similar sense like those of the genus *Welwitschia* Hook. i.e. as extremely reduced and simplified unisexual "flowers" (simple cones) of a bennettitalean type, which like some axillary buds are arranged collaterally or serially. Compared with the "flowers" of *Welwitschia* Hook. it was especially the male "flowers" that were affected by strong reduction: the number of stamens decreased to two, which then were fused into one terminal androphore like in the genus *Ephedra* L. (convergence!).

According to the just suggested interpretation the fructifications ("flowers", "inflorescences") of the *Chlamydospermophyta* are, from the morphogenetical point of view, of two quite different kinds as to their origin: [1] in the genus *Ephedra* L. we have to do with stachyospermic compound cones (bearing many common features especially with the fructifications of the *Ginkgoopsida*; further with those of the *Cordaitopsida* or with the female cones of the *Pinopsida*), whereas [2] in the genera of *Welwitschia* Hook. and *Gnetum* L. they are to be regarded as strongly simplified cyclic phyllospermic "flowers" bearing evident similarities to the bennettitalean *Cycadophyta* (as to the male flowers also to the *Pentoxylales*). All these experiences in connection with our knowledge of various features of their vegetative organs enable us to get a more accurate notion of the origin and taxonomical alliances of these three living chlamydospermic genera. The genus *Ephedra* L. may thus be regarded as a rather narrow and blind evolutionary side line arisen from some *Trichopitys* or *Dicranophyllum* like ancestral types along the *Ginkgoopsida*, which very soon achieved a considerably higher evolutionary stage (but not as high as the angiospermous plants!) than the just mentioned group, and which, at the same time, was affected by various reduction and specialisation processes correlative with their adaptation for special life conditions. In the same way may be explained the origin and alliances of the other two genera, *Welwitschia* Hook. and *Gnetum* L. We have only to look for their ancestors somewhere among the most archaic *Cycadophyta* (bearing most probably primarily bisexual "flowers"), and to assume a parallel evolution and perhaps even a remote alliance with the group of the *Cycadeoideales* (*Bennettitales*).

Our considerations on the taxonomic alliances of the chlamydospermic plants throw also some light upon the time at which these types developed. As mentioned already, the chlamydospermic genera have several very characteristic features in common with the Angiosperms because of the convergent morphogenetical evolution of certain structures or even whole organs. Such angiospermic features appear for the first time in the history of plants (but only in a minor degree) in the older mesozoic period (*Caytoniales*, *Corytospermales*, partly also *Cycadeoideales* [i.e. *Bennettitales*] and *Cheirolepidiaceae*). Besides, we know very well that in the history of plants essentially important progress from one more primitive evolutionary stage to another, a more advanced one (and at the same time usually also a more complicated one), or the development of various specifically new more progressive features leading to the development of new higher taxa of an equal evolutionary level (or stage), was always only a single phase event (e.g. the transition from the pteridophytic stage to the pteridospermic one at the end of the older Palaeozoic, the transition from the pteridospermic stage

to the completely gymnospermic one at the end of the Upper Palaeozoic [Permocarboniferous], and finally the transition from the gymnospermic stage to the angiospermic one during the end-phase of the older Mesozoic). Thus, because the chlamydospermic plants exhibit (due to their convergent evolution) in a high measure features characteristic (or at least very similar) just for the Angiosperms, we have to place the probable time of their arising approximately into the same period as that of the Angiosperms, at any rate later than that of the proangiospermic Pteridosperms (*Caytoniales*, *Corytospermales* and others, which have only very few features in common with the Angiosperms), i.e. somewhere into the later phase of the Mesozoic. Nevertheless many botanists (in agreement with SEWARD 1919) are of the opinion that these plants had a considerably much older origin than the Angiosperms, especially because of the strikingly strong taxonomic isolation of the single still living genera. Such an isolation is indeed usually believed to be a serious argument of a considerable antiquity of the respective plant group and also, at the same time, usually of the extinction of various missing links. So A. C. SEWARD assumed as rather probable that many of the older Cretaceous leaf impressions usually designed as angiospermous types (e.g. many forms described from the Potomac formation of USA) may in reality represent remains of various extinct chlamydospermic plants. By this way a hypothesis of a considerably ancient age and a much larger extent of this plant group in the past was formulated.

Up to the present palaeontology has offered only very scanty documents confirming the presence of chlamydospermic plants in the past. Very few and mostly utterly untrustworthy remains have been mentioned only from the Tertiary and Quaternary sediments, but a constant presence of indubitable pollen grains of these plants (mostly of the genus *Ephedra* L.) has well been known already from the middle periods of the Cretaceous. This fact does not seem to be in agreement with the just mentioned theory of a rather antique age, larger extent and distribution of the *Chlamydospermophyta* in the past. With regard to these and even other previously mentioned discrepancies, we have, I believe, to judge the whole past of this plant group from a quite different point of view than it has mostly been done till present. We especially have to consider the following facts: 1 The conspicuously unique many-sided convergency of the evolution of the three typically gymnospermous living genera with the evolution of the Angiosperms, 2 the entire lack of mutual taxonomic alliances between them, especially between the genus *Ephedra* L. (probable distant alliances with the *Ginkgoopsida*) and the other two genera (*Gnetum* L. and *Welwitschia* Hook.; distant alliances with the *Cycadeoideales* and *Pentoxylales*), 3 the unusual progressivity of various structures of their vegetative organs (compared with other gymnosperms) and various rather strong adaptive specialisations for some unusual life conditions, connected mostly with very strong reduction processes (fructifications!), and finally 4 the insufficiency of macropalaeontological documents and the rather late occurrence of their pollen grains in various sediments.

All these facts, just as the other inferences mentioned above make me to believe (contrary to the hitherto so often supported hypothesis of a considerable antiquity and a larger distribution of this group in the past) that this curious plant group is represented only by a very small number (two

or at least three) of rather specialised and utterly blind evolutionary side lines, which were split off of the above mentioned ancestral, already typically gymnospermic stocks (classes) at a very late period (at least not earlier than the Angiosperms; see the features of their vessels!), and most probably at a relatively more advanced stage (or organisation level) than was the stage of the mother stock of which the Angiosperms were derived. This is perhaps also the reason, why they acquired only partially the features characterising true Angiosperms (just as at a still minor scale the several pteridospermous evolutionary side lines which passed from the late Palaeozoic into the Mesozoic, e.g. *Corystospermaceae*, *Caytoniaceae* a.o.). And just as nearly all types representing only special evolutionary side lines which during the Mesozoic surpassed in certain directions the normal evolutionary trend of their ancestral stock and died rather soon without being split into a larger number of derived taxons, so even our three chlamydospermic types most probably never represented any more widely branched alliances. I believe that there is no reason to assume that their taxonomic isolation should be conditioned by the extinction of some unknown allied types (missing links). It seems to me much more probable that they evolved as already at the very beginning isolated trends from several, more or less distant ancestral stocks by a convergent evolution and that they never achieved a more complicated splitting, being rather soon stabilised or strongly specialised for some unusual life conditions, perhaps because of a rather progressive character of their direct ancestors.

Summary

Summarising all the mentioned facts and inferences, I suppose that the group of the *Chlamydospermophyta* represents an assemblage of several (at least three, still living) types which were at the very beginning of their evolution utterly isolated, because they were split off of some taxonomically rather distant or even quite independent ancestral evolutionary lines. The mutual similarity of many features in their organisation was no doubt conditioned by a convergent evolution, which on the other hand was also convergent with the evolution of the Angiosperms. The origin is to be placed somewhere in the Mesozoic period just as that of the Angiosperms (perhaps still later). Finally we must admit that their ancestors were much more advanced than those of the Angiosperms, which is no doubt also the reason, why the chlamydospermic types represent only rather narrow and quite blindly ending evolutionary side lines, which underwent no further splitting. In the genus *Ephedra* L. are to be most probably assumed some very remote relations to the stachyospermic class of the *Ginkgoopsida* and in the genera *Gnetum* L. and *Welwitschia* Hook. to the fyllospemic class of the *Cycadopsida*, especially to the orders of the *Pentoxylales* and *Cycadeoideales* (*Bennettitales*). The whole past of the chlamydospermic plants is no doubt comparable with that of the proangiospermic plants (*Caytoniaceae*, *Corystospermaceae* and others), which as some rather narrow convergent side lines were split off of the pteridospermic class of the *Lyginodendropsida* at the end of the Permocarboniferous, lived throughout the Triassic and Jurassic period without any essential changes and died out during the Cretaceous without leaving behind any new descendants.

Souhrn

Podrobným srovnáním význačných vlastností (zejména stavby fruktifikačních souborů) obalosemenných rostlin (*Chlamydospermophyta*) s vlastnostmi ostatních skupin nahosemenných rostlin, jakož i zhodnocením dosavadních našich zkušností s výskytem jejich fosilních zbytků, dospívá autor k zpřesnění názorů na jejich původ v tom smyslu, že rod *Ephedra* L., obvykle příbuzensky navazovaný velmi všeobecně na stachyospermické gymnospermy, má patrně bližší vztahy k vývojové řadě *Dicranophyllopsida* - *Ginkgoopsida* než k řadě *Dicranophyllopsida* - *Pinopsida*. Oba další dva rody, *Gnetum* L. a *Welwitschia* Hook., souhlasně s většinou současných botaniků, považuje za typy odštěpené od rostlin bennetitových, ovšem jen jako dvě slepé, navzájem blíže spolu příbuzensky nesouvisející vývojové linie. Vzhledem k dosavadním paleontologickým zkušenostem předpokládá, že tato skupina nikdy nebyla bohatě členěná a že osamocenost její tří

rodů je následek jejich vzniku a ne vymírání rozmanitých jejich zástupců. Pokládá se za pravděpodobnější, že vznikla (a to patrně skoro souběžně s rostlinami krytosemennými) jako soubor několika slepých vývojových linií, majících původ v několika různých skupinách nahosemenných rostlin a postoupivších na podstatně vyšší vývojový stupeň, čímž se ve mnohém přiblížily krytosemenným rostlinám, aniž k nim mají nějaké příbuzenské vztahy. V těchto ohledech, stejně tak jako v jejich osamoceném taxonomickém postavení i v celé jejich minulosti, mají obdobu v tzv. proangiospermických kapradosemenných rostlinách (*Corystospermales*, *Caytoniales* apod.) staršího mezozoika.

Literature

- APPEL J. (1937): Zur Phylogenie der Gnetaceen. — 7 p., Brno.
- BERRY E. W. (1911): The Lower Cretaceous of Maryland. — ed. Maryland geol. Survey, Baltimore.
- CONWENTZ H. (1886): Die Angiospermen des Bernsteins. — Danzig.
- ČIGURJAJEVA A. A. (1951): O nachodke mikroskop veličiji v eocenovych otloženijach zapadnogo Kazachstana. — Bot. Ž., Moskva—Leningrad, 36 : 515—516.
- (1956): Atlas mikroskop iz tretičnyh otloženij SSSR. — 136 p. — ed. Sarat. gos. univ. Izd., Univ. Charkov.
- EAMS A. J. (1952): Relationship of the Ephedrales. — Phytomorphology 2 : 79—100.
- EMBERGER L. (1944): Les plantes fossiles dans leur rapports avec les végétaux vivants. — 492 p., Paris.
- ENGELHARDT H. (1891): Über Tertiärpflanzen von Chile. — Abh. Senckenb. naturforsch. Ges., Frankfurt a. M., 16.
- FLORIN R. (1931): Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. — K. svensk. vet. Akad. Handl., Stockholm, ser. 3, 10/1 : 1—588.
- (1934): Die Spaltöffnungsapparate von Welwitschia mirabilis Hook. — Svensk bot. Tidskr., Uppsala, 28/2 : 264—289.
- HALLIER H. (1905): Provisional scheme of the natural (phylogenetic) system of flowering plants. — New Phytol., London, 4 : 151—162.
- HEER O. (1877): Beiträge zur Juraflora Ostsibiriens und des Amurlandes. — Flora fossilis arctica, Zürich, 4 : 1—121.
- HENDRYCH R. (1952): K otázce fylogenetického významu třídy Gnetineae. — Preslia 24 : 111—134 (— see in this paper also the detailed bibliography dealing with the organisation of the recent types!).
- JANSONIUS J. (1961): Palynology of Permian and Triassic sediments, Peace river area, Western Canada. — Imp. Oil Limited, Prod. Dep., Western Canada, Exploration Research Dep., Calgary, Alberta, 165 p.
- KIRCHHEIMER F. (1950): Mikrofossilien aus Salzablagerungen des Tertiärs. — Palaeontographica, Stuttgart, sect. B, 91/4—6 : 127—160.
- KRUTZSCH W. (1961): Über Funde von ephedroidem Pollen im deutschen Tertiär. — Geologie, Berlin, 10/32 : 15—53.
- LIGNIER O. et TISON A. (1911): Les Gnetales sont des angiospermes apétales. — C.R. Acad. Sci. Paris, Jan. 23.
- MAHESHWARI P. et VASIL G. (1961): Gnetum. — Botanical Monograph, New Delhi, no. 1. (See also: Fortschr. Bot. 25 (1963) : 88 (Merxmüller); Bot. Jb., Stuttgart, 81 : 43).
- NÉMEJC F. (1950): Přirozená systematika rostlin ve světle dosavadních paleontologických dokladů. — Sborn. nár. Mus. Praha, sect. B, 6 (1950) : 3—83.
- PACLOVÁ B. (1961): On some plant microfossils from the fresh water sediments of the Upper Cretaceous (Senonian) in the South Bohemian basin. — Sborn. ústř. Úst. geol. Praha, sect. paleont., 25 : 47—102.
- REID C. et REID E. M. (1915): The Pliocene Flora of the Dutch-Prussian Border. — Meded. rijks. onsp. Delft., The Hague, 6.
- SAMOJLOVIČ S. P. (1953): Pylea i spory iz permskich otloženij čerdinskogo i aktjubinskogo Priuralja. — Paleobot. Sborn. (Trudy neft. geol.-razv. Inst. VNIGRI Moskva, ser. n. 75 : 5—57.
- SEWARD A. C. (1919): Fossil plants 4. — 543 p., Cambridge.
- SYKES M. G. (1910): The anatomy of Welwitschia mirabilis Hook. in the seedling and adult stages. — Trans. Linn. Soc., London, 7/2.
- TACHTADŽJAN A. L. (1956): Vyššije rastenija 1. — 488 p., Moskva—Leningrad.
- VELENOVSKÝ J. (1910): Srovnávací morfologie 3. — p. 613—1012, Praha.
- ZIMMERMANN W. (1959): Die Phylogenie der Pflanzen. 2. Aufl. — 777 p., Jena.