

## Notes to the Morphogenetical Interpretation of the Fructifications of *Pentoxylon* SRIVASTAVA

Poznámky k morfogenetické interpretaci fruktiřakcí *Pentoxylon* SRIVASTAVA

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**Abstract** — The morphogenetical nature of the fructifications of the genus *Pentoxylon* SRIVASTAVA (i.e. *Sahnia nipaniensis* VISHNU-MITRE and *Carnoconites compactus* SRIVASTAVA) are discussed and a new theory of the morphogenetical origin of its cone like female fructifications is proposed. They are regarded as originally megaphyllous syntelomoid all round branched systems with terminal megasporangia, resp. ovules, the branchlets of which became shortened and finally utterly aborted; by this way the ovules were shifted as far as on the main rachis of the whole fertile systems, i.e. on the cone axis (— these fertile female systems never were subjected to any planation process sensu ZIMMERMANN, contrary to the respective megaphyllous sterile leaves, just as in the case of the male fructifications). They are therefore of the same nature (i.e. foliar) as the male fructifications, the morphogenetical nature of which is still evident. The *Pentoxyla* are just for that reason, as well as because of the polystelic character of their stems, regarded as the most primitive type of the *Cycadopsida*, exhibiting still some alliances with the Pteridosperms.

*Pentoxylon* SRIVASTAVA is the best known representant of the curious, utterly extinct and typically polystelic cycadaceous group (order) of *Pentoxylales*, which during the last years was discovered in the Jurassic of India. Besides silicified casts of stems also leaves (*Nipaniophyllum raoii* SAHNI i.e. *Taeniopteris spathulata* McCLELAND p. p.), clusters of male fructifications (*Sahnia nipaniensis* VISHNU-MITRE) as well as cone like female fructifications (*Strobilites pascaonii* SAHNI i.e. *Carnoconites compactus* SRIVASTAVA) have been described in detail. The structure of the stomata of their cuticles remained for a considerable time not well elucidated. Mostly they were regarded as syndetocheilic, wherefore the whole order has been generally placed nearest to the bennettitalean Cycadophyts (*Cycadeoideales*). But newly VISHNU-MITRE (1957) demonstrated their doubtless haplocheilic nature and by this way also nearer relations of this order to the more primitive evolutionary line of the class of *Cycadopsida* i.e. to the cycadaceous line in a strict sense. Their fructification clusters exhibit at first sight so many peculiar, strange and primitive features, that several botanists (e.g. CRONQUIST, TAKHTAJAN et ZIMMERMANN 1966) are at present regarding this curious type of plants as an independent group besides both already well known groups *Cycadeoideidae* (i.e. *Bennettitidae*) and *Cycadidae*. No doubt the order of *Pentoxylales* represents the most primitive type of the whole class of *Cycadopsida* (s. lat.) because of the still maintained polystely, which links them with the medullosan pteridospermous plants; in both more advanced cycadaceous groups (*Cycadidae* and *Cycadeoideidae*) the polystely was evidently suppressed in favour of a monostelic structure (see e.g. polystelic vascular

strands still in the seedling plants of several recent cycadaceous types). As to the morphogenetical interpretation of the fructification clusters of *Pentoxylon*, many tasks are not yet sufficiently elucidated, especially those concerning the female cone like clusters. But just a perfect knowledge of these features is no doubt of eminent importance if examining the mutual alliances (taxonomical relations) with the other cycadaceous plant types.

The male fructifications have form of rather small telomoid branches, bearing all round short side branchlets (ev. forklike divided) with terminal pollen sacks (microsporangia). These fertile organs are not subtended by any leaves or scales; they are arranged in a whorl at the top of rather big dwarf shoots (brachyblasts) and are mutually collar like connate at their bases. Below this fertile whorl, the dwarf shoots bear spirally arranged leaves (or protective leaflets?). The morphogenetical nature of the single ramified fructifications is according to their shape and their arrangement on the dwarf shoots quite evident: very primitive microsporophylls, which kept still their original syntelomoid and megaphyllous character (not yet modified by „planation“) and which passed from the original spiral arrangement on the dwarf shoot top to a cyclic one (one whorl). This whole complex of collar like at the base connate, ramified male fructifications, protected by spirally arranged sterile leaves may be most conveniently compared (as also admitted by many botanists at the present time) with the male „flowers“ of various bennettitalean plants, especially with those of the genus *Williamsonia* CARR. The only difference is that in the last named genus the microsporophylls are already modified by „planation“ i.e. either branched only in one plane or even provided with a flat lamina. Thus in *Pentoxylon* SRIVASTAVA the male fructifications are to be regarded as extremely primitive megaphyllous sporophylls (constituting simple “flower” complexes, quite homologous with the bennettitalean “flowers”), though at first sight they are very similar (as to their shape) to the axillary fertile (female) dwarf shoots of the genus *Trichopitys* SAP. (of which they differ essentially only in being not axillary!).

By far more puzzling are the clusters of the female fructifications. The single fructifications represent small stalked, oval till cylindrical, till 5 mm broad and 25 mm long, cone like bodies, arranged in a very low spiral (or nearly clustered) on very short side twigs (dwarf shoots), being not subtended by any leaflets or scales at all. Their stalks are naked (i.e. bearing no leaflets resp. scales) and their axis bear all round densely crowded and perhaps even partly mutually coalescent, sessile ovules; there are neither any leaflets nor any interseminal scales among the single ovules to be stated. At the first sight they are rather similar to the female “flowers” of the bennettitalean plants (especially with those of the genus *Westersheimia* KRASSER), but they differ essentially in having no stalked ovules and bearing no interseminal scales. All these facts admit, in my mind, two possible interpretations of the morphogenetical nature of the whole clusters of cone like female fructifications. At any rate we have to do with rather big axillary dwarf shoots, bearing the stalked strobili as side organs. It is then possible to consider the single stalked strobili either (1) as short side ramifications transformed into “flowers”, similar to those of the bennettitalean plants, or (2) as modified originally branched (like the male fructifications) sporophylls. In the first case we had to presume very strong reductions: shortening of the whole axillary branch system and an entire suppression of the leaflets subtending the single

fertile side twigs, as well as an at least similar strong reduction of the sporophylls born just on these side twigs as known in the bennettitalean plants (or still stronger, i.e. until to only one sessile ovule). In the second case there is not necessary to presume so many strong modifications: we have only to presume an entire suppression of the original telemoid stalks of the ovules (side branchlets) and a strong shortening of the main (syntelomoid) rhachis of the sporophylls born on the axillary dwarf shoots, by which way the ovules became (1) sessile and (2) densely crowded on the shortened sporophyll rhachis (i.e. the axis of the cone like fructification). The second of both just expressed alternatives seems to be much more probable, because it does not postulate so many hypothetical and rather strong modifications; it rather clearly interprets also the absence of any subtending leaflets or scales on the axillary dwarf shoots bearing the stalked cone like fructifications.

## Summary

According to all above mentioned morphological features which till present are known about the organisation of the fructification clusters of the genus *Pentoxylon* SRIVASTAVA, the following theoretical conclusions were made as to their morphogenetical origin, resp. the morphogenetical origin of their various parts:

1. Both kinds of these fructification clusters (male as well as the female ones) are principally of equal origin.

2. They represent big axillary unisexual dwarf shoots provided in their distal (i.e. end) portion with the respective sporophylls of megaphyllous nature and beneath eventually also with sterile leaves (or protective leaflets?).

3. The single sporophylls are derived from a very primitive type: an all round ramified syntelomoid system with terminal sporangia. In the male dwarf shoots their modifications are only very inconspicuous, their original organisation being still preserved. In the female dwarf shoots their modification is rather stronger: their main rhachis was transformed in a short axis, stalk like prolonged below and their side ramifications (fertile teloms) were wholly suppressed wherefore the originally terminal megasporangia — ovules — became sessile (and partly even connate) directly on the axis (main rhachis). The female sporophylls got by that way a non ramified, strobilar shape (at first sight similar to the female flowers of the bennettitalean genus of *Westersheimia* KRASSER).

4. The original spiral arrangement of the sporophylls on the dwarf shoot axis were transformed in the male fructification clusters into a whorl like (cyclic) one (at the same time the bases of the single sporophylls were mutually collar like connate), whereas in the female fructification clusters it was more or less preserved (or only slightly transformed into a densely cluster like one).

According to these facts and inferences we may regard the genus *Pentoxylon* SRIVASTAVA as a cycadaceous type, in which the sporophylls (especially the male ones) kept the most primitive imaginable construction: an all round ramified megaphyllous syntelomoid system with terminal sporangia. As mentioned also above, even the anatomical structure of the stems of *Pentoxylon* compared with other cycadaceous plants are of a rather primitive type, i.e. provided with a polystelic vascular system like in the medullosean Pteridosperms. Accordingly we have to regard the genus *Pentoxylon* SRIVASTAVA as well as its allied types as the most archaic types among the cycadaceous plants, perhaps as the direct descendants of the ancestors of both cycadaceous evolutionary lines, the *Cycadidae* and the *Cycadoideidae* (*Bennettitidae*), standing of course nearer to the first one because of the primitive (haplocheilic) structure of their stomatal apparatus.

## Soúhrn

Článek přináší rozbor morfogenetické podstaty fruktifikačních souborů cykasového rodu *Pentoxylon* SRIVASTAVA, a to se zřetelům k stavbě fruktifikací jiných, zejména megafylních gymnospermů. Vychází se ze základního stanoviska, že jako u všech ostatních cykasových rostlin, tak i u rodu *Pentoxylon*, samčí (*Sahnia nipaniensis* VISHNU-MITRE) i samičí (*Carnoconites compactus* SRIVASTAVA) fruktifikace jsou soubory sporofytlů megafylní povahy. Povaha samičích souborů je jasná; jsou (soulhasně s většinou dosavadních názorů) vykládány jako do kruhu (přesleny) sesunuté, nesmírně primitivní, telomoidně větvené a při spodu límečkovitě navzájem spolu srůstající mikrosporofyly na zkrácené větvi (brachyblastu), níže porostlé jalovými listeny (tj. ana-

logon samčího květu rodu *Williamsonia* CARR.). Stopkaté šištice samičí jsou, na rozdíl od dosavadních názorů, vykládány jako silně zjednodušené (redukované) megasporofyly, a to tak, že vajíčka přímo porůstají jejich zkrácené hlavní žebro (po potlačení teleomoidních postranních žebor, nesoucích původně vajíčka); jsou pak na zkrácené větvi (brachyblastu) sesunuty jen do husté šroubovice, čínící popřípadě dojem svazečku malých stopkatých šištice. Jednotlivé šišky nelze proto porovnávat se samičími květy (popř. květním lůžkem) bennettitových rostlin (ostatně jim chybí interseminální šupiny a jednotlivé šišky nevyrůstají z paždí listenů!). Samčí i samičí soubory fruktifikací mají stejný morfogenetický původ: zkrácené větévký (brachyblasty) porostlé sporofyly, z nichž samčí (nesmírně primitivní) jsou jen málo přeměněné a sesunuté do kruhu, samičí silně zjednodušené, ale v husté šroubovici. Z hlediska fylogenetického jde o neobyčejně primitivní typ cykasových rostlin, částečně konvergentní k bennettitovým rostlinám, s kterými však nejsou blíže příbuzné. Význačnou polystélií jsou ještě velmi blízké původním předkům (snad medullosní pteridospermy) cykasových rostlin.

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