THE TAXONOMIC SIGNIFICANCE OF THE TERM PSILOPSIDA AND THE EVOLUTIONARY TRENDS OF THIS PLANT PHYLUM

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ABSTRACT

The taxonomical significance of the term Psilopsida is discussed in this article. As a special plant phylum the Silurian-Devonian Psilopsida *sensu stricto* are regarded as an independent intermediary cryptogamic vascular type standing between the Bryophyta and all true pteridophytic plant phyla and exhibiting its own peculiar evolutionary trends. The opinion is suggested that we have to investigate these special evolutionary trends quite independently and irrespectively of the evolution of the single pteridophytic phyla. Several of these trends are indicated.

THE existence of still more archaic or primitive vascular plants than the pteridophytic phyla Lycopsida, Pteropsida, Sphenopsida and Psygmophyllopsida* was recognized about the year 1915 by R. Kidston and W. H. Lang. As a special group, which is most abundantly distributed in the Silurian-Devonian beds, they were later called Psilophitineae or Psilopsida and as plant types not yet differentiated into the well-known fundamental morphological units, viz. leaves, axis and roots, they caused considerable revolution in our morphological conceptions as regards the nature of the bodies of all vascular plants and even of the Bryophyta. Most of the botanists have regarded them, on account of their very primitive morphology, as the direct starting point of the evolution of all main types of true Pteridophyta, and lately also as the starting point of the reducing processes which presumably led to the origin of the Bryophyta. No doubt just for these reasons the whole term of Psilopsida up to the present day is not yet as clearly defined from the taxonomical point of view as are the four named pteridophytic plant phyla (LYCOPSIDA, PTEROPSIDA, SPHENOPSIDA and PSYGMOPHYLLOPSIDA). But in the very ancient floras of the Lower and Middle Devonian there are forms, which by their very primitively developed axis and leaves can be considered either as of psilophytic nature or as some of the most primitive pteridophytic types as the ancestors of the last ones. The boundary between the Psilopsida and the four named pteridophytic plant phyla seems, therefore, very vague and indefinite. The respective chapters in various text books dealing with the Psilopsida and with other very archaic Silurian-Devonian plants are the best proof of this state of our present taxonomical conceptions (*see* e.g. in the new edition of Potonié-Gothan's "Lehrbuch der Paläobotanik" by H. Weyland, 1953). But I believe that there are many circumstances, which are already suggesting to us some quite different opinions or an utterly different attitude to this whole taxonomical problem.

First of all we know at present not only spores of a type commonly spread in the pteridophytic vascular plants already up from the Cambrian, but we became newly acquainted also with the impressions of twigs of a typical pteridophytic plant of the Middle Cambrian, i.e. *Aldanophyton antiquissimum* Kryst., found in East Siberia, which reminds very strongly several Devonian primitive lycopodioid types, especially the well known *Drepanophycus*. We must, therefore, assume that rather archaic or primitive pteridophytic types with more or less developed leaves must have existed much earlier than ever expected before, and that they existed perhaps in subordinate position along with the primitive undifferentiated vascular types, the psilophytic types, already long ago before the Upper Silurian or Lower Devonian period, where their origin mostly was assumed. That means, of course, that vascular types, exhibiting bodies not yet well differentiated into axis, leaves and roots, must have been of still earlier origin, and that such primitive undifferentiated (i.e. psilophytic) types, which we know from the Lower and Middle Devonian where already many representatives of the pteridophytic phyla are to be found, must be regarded as mere survivors of

*The phylum of *Psygmophyllopsida* was defined by me (originally under the name of Psygmophyllineae) in 1950 for vascular cryptogamic plants related morphogenetically most nearly with the Sphenopsida but having non-articulated stems and spirally arranged leaves.

a rather large phylum, which had its period of maximum development already accomplished long ago before the Devonian period. It is then also very probable that many pteridophytic types showing differentiated leaves, evolved from rather similar ancestors quite parallelly along with other such primitive types, which never succeeded in producing any typical leaf or root organs. Accordingly true ancestors of both these types, i.e. psilophytic types as well as the pteridophytic ones, are at present perhaps quite unknown. Hence it is clear enough that the Silurian-Devonian psilophytic or psilophytoid types cannot be regarded as true ancestral types of any recognized pteridophytic type. Most likely the same may be presumed also as regards the origin of the moss plants, because the oldest ever discovered representatives of this evolutionary branch, the carboniferous liverworts and mosses, exhibit specifically no strange features from either morphological or anatomical point of view, if compared with the living forms.

Taking into consideration all these circumstances, I presume that we have to pick out of the whole Silurian-Devonian plant assemblage a whole series of very primitive plants, which as a parallel group to the true Pteridophytes as well as to the Bryophytes evolved long before the Devonian time quite independently and more or less simultaneously, perhaps even from the very starting point when some alga-like plants began their invasion of the dry land, penetrating from their original acquatic environment. According to my mind only such types of the Silurian-Devonian floras, i.e. intermediary in habit between the mosses and true pteridophytes, are to be classified as true Psilopsida. All the other ones showing undoubted relations, be it from the morphological or anatomical point of view, with the lycopodioid, sphenopsid or filicinean types, must be regarded as true representatives, even though very primitive, of some of these pteridophytic types. Their eventual relations to the true psilophytic Silurian-Devonian types must really be regarded as unusually remote.

The second logical consequence of these examinations is that in resolving various taxonomical and phylogenetical problems concerning the representatives of this most primitive and most archaic vascular plant phylum, we have to investigate the morphogenetic evolution of their organs from a quite different point of view and on quite different principles than as we are accustomed to do in the consideration of the well known pteridophytic phyla. We have to take into consideration that the representatives of this psilophytic phylum, which kept their primitive organization, had to attain the same objectives as regards the adaptation for life conditions under terrestrial environments by quite different arrangement or equipment of their bodies, than the morphologically very much differentiated representatives of the pteridophytic phyla, for surviving in the life competition for longer geological periods. We have thus to investigate within this phylum some special evolutionary trends, which are in no relations with the elaboration of the true pteridophytic types.

In this light many of the Silurian-Devonian psilophytic primitive plants appear indisputably as plant types, which underwent, on account of special life conditions, a kind of evolution by reduction. It is especially in the genera like *Thallomia* and *Sciadophyton* where we have to observe an analogous tendency as in various thalloid liverworts, the formation of flat, creeping thalli, rather broad in *Thallomia* with sporangia submerged into the thalloid tissue and narrow in *Sciadophyton*. Special adaptation for life on wet and muddy coastal soils by means of reduction is here evident. Even such plants like *Rhynia, Hicklingia, Cooksonia* which on the one hand exhibit some certain original archaic and primitive features (e.g. sporangia terminal on most of their twigs, without being arranged in some special inflorescences), show on the other hand several features which point to special adaptations for some peculiar life conditions, viz. only rounded cylindrical undifferentiated telomoid twigs without any indication of some special arrangement for making the best use of the solar radiation, and fastened together into dense tufts. Such type of twigs or leaves are to be found at present especially in several swamp or water plants, e.g. our common rushes — *Juncus*.

Psilophytic plant types, which exhibit a more or less normal mesophytic appearance or at least not directly a swampy or aquatic one, are no doubt represented by such types like *Taeniocrada, Zosterophyllum, Gosslingia, Bucheria, Hedeia, Yarravia, Psilophyton* and finally also by *Pseudosporochnus* and *Asteroxylon*, of which the last two genera, compared with the other named types, are in many respects of a much more progressive character. In the first named plant types we see a clear

differentiation of branches into sterile syntelomic systems with often flattened ultimate telomoid twigs, or with twigs preserved by a dense cover of hairs which are often glandulous, and into syntelomoid fertile systems with thin cylindrical and always naked twigs, bearing terminal sporangia. In several genera these fertile systems look like some more or less panicle-like inflorescences, e.g. *Taeniocrada, Psilophyton*; in other ones a clear tendency to the formation of some spike-like or corymboid fructifications by means of a very regular reduction or even abortion of the telomoid stalks of the single sporangia is evident, e.g. spike-like in *Zosterophyllum, Gosslingia* and *Bucheria*, corymboid in *Hedeia*. This in extreme cases, where the syntelomic main axis has been extremely reduced or even abortive, led finally to such fructifications as found in *Yarravia* : sporangia crowded round the top of a telomoid twig into a globular body; in *Psilophyton pubescens* Kr. et W., we find finally, fork-like, once divided corymboid clusters of very shortly stalked sporangia, as in several species of the genera *Aneurophyton* or *Protopteridium*. In the genus *Pseudosporochnus* we see another special tendency : the formation of a big stem and the crowding together of the thin telomoid branchlets into several large but still rather irregularly branched frond systems. A still more progressive type is no doubt the genus *Asteroxylon*, which otherwise is provided by equally primitive fructification and root (mere primordial rhizomes) systems as in *Taeniocrada* and allied genera. In *Asteroxylon* we see already small leaflets reminding the short linear leaves of the club mosses, with distinct stomata, which evidently are not of telomoid provenance, but representing most likely only assimilating excrescences, not unlike the leaflets in the moss plants. A quite special type of the psilophytoid plants are *Horneophyton* and the imperfectly recognized genus *Sporogonites*, which (at least *Horneophyton*) exhibit the same primitive external appearance as *Rhynia* and several allied types. Here we may observe at the same time several features common with the moss plants, especially the columella within their sporangia, in *Sporogonites*, also the neck-like sterile portion at the base of the sporangia.

All such data undoubtedly indicate that the group or phylum of Psilopsida, in the narrow sense as recognized, exhibits besides some distinctly visible reduction features a large number of progressive characters, which from the morphological point of view are relative chiefly to the assimilating telomes (resp. synteloms), or to the sporangia bearing synteloms and in several rather rare cases also to the sporangia. The reduction features, as far as mentioned, are no doubt related to special adaptations to some unusual life conditions. Most of the above-mentioned peculiarities represent no doubt features indicating the trends of evolution in various directions of this highly primitive vascular phylum. If observed in detail, they very often remind of the several features characterizing different pteridophytic phyla and where we find them always in various rather characteristic and stable combinations, characteristic of each pteridophytic phylum. On the contrary, in various psilophytic genera, families or orders, mostly only one such fundamental progressive feature was realized, without being combined with some other ones. None of the hitherto recognized true psilophytic plant types could therefore lead, in the evolutionary sense, to any of the representatives of the higher pteridophytic phyla. Moreover, we have also seen in several genera of the Psilopsida organs exhibiting moss-like characters. The Psilopsida thus appears as an intermediary plant phylum between the Bryophyta and all the pteridophytic phyla. All features, which the Psilopsida have in common either with the mosses or with the pteridophytic types, cannot be morphogenetically brought in direct connection with the same or similar features in these two phyla. They only represent mere morphological convergences, i.e. features gained quite independently, without any real kindred relations either to the moss plants or to any pteridophytic type.

Accordingly we have to divide our Psilopsida phylum, as far as known from the Silurian and Devonian, into the following systematic groups :

PSILOPHYTA

Phylum : Psilopsida

1. Class : Horneophytineae
   - (i) Order : Horneophytales
     - Horneophytaceae (*Horneophyton* Bargh.)
     - Sporogonitaceae (*Sporogonites* Halle)
2. Class : Psilophytineae
   - (i) Order : Thallomiales
     - Thallomiaceae (*Thallomia* Heard et Jones)

(ii) Order : Sciadophytales
Sciadophytaceae (*Sciadophyton* Kr. et W.)
(iii) Order : Rhyniales
Rhyniaceae (*Rhynia* Kidst. et Lang, *Hicklingia* Kidst. et Lang *Cooksonia* Lang.
(iv) Order : Taeniocradales
Taeniocradaceae (*Taeniocrada* Goepp., *Himanthaliopsis* Zal.)
Zosterophyllaceae (*Gosslingia* Heard, *Zosterophyllum* Lang, *Bucheria* Hoeg.)
Hedeiaceae (*Hedeia* Cooks.)
Yarraviaceae (*Yarravia* Lang et Cooks.)
(v) Order : Scougophytales
Scougophytaceae (*Scougophyton* H. et G. Termier)
(vi) Order : Loganellales
Loganellaceae (*Loganella* Stolley)
(vii) Order : Pseudosporochnales
Pseudosporochnaceae (*Pseudosporochnus* Pot. et Bern)
(viii) Order : Psilophytales
Psilophytaceae (*Psilophyton* Dawson)

3. Class : Asteroxylineae
(i) Order : Asteroxylales
Asteroxylaceae (*Asteroxylon* Kidst. et Lang)

All these systematic groups must be regarded from the point of view of the phylogeny as rather parallel to all, even the most primitive, pteridophytic types, e.g. *Aldanophyton*, *Drepanophycus*, *Hyenia*, *Barradeina*, *Swalbardia*, *Protopteridium*). Accordingly, there exists absolutely no direct relationship between these two kinds of plant types.

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