THE TAXONOMIC POSITION OF THE PSILOTALES IN THE LIGHT OF OUR KNOWLEDGE OF DEVONIAN PLANT LIFE*

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ABSTRACT

The order Psilotales, containing the two recent genera *Psilotum* and *Tmesipteris* only, is usually classified by taxonomists and palaeobotanists in the phylum Psilophyta. This concept is, in spite of the synangia, based on the primitive general appearance reminding one of that of the Devonian Rhyniaceae. Numerous attempts have been made to derive both genera, including their synangia, from either the Rhyniaceae or from other Psilophyta. These attempts sometimes led to the acceptance of a series of missing links but this concept is, however, not supported by palaeobotanical data.

In the opinion of the present reporter the order has kept a primitive general appearance of its Devonian ancestors but in its synangia and in its monolete spores it is more advanced. In its anatomy, its microphyllous leaves, and in its gametophyte perhaps, it shows more affiinity to the phylum Lycopodiophyta. The present reporter clssifies the two genera as a separate order in the isosporous Lycopodiophyta. In his opinion the order is to be derived from the Protolepidodendraceae.

Available palaeobotanical data in the Devonian are in support of this concept. The present author has to admit, however, that between the Devonian and recent times no palaeobotanical or palynological data are known to support his concept.

INTRODUCTION

THE two recent genera *Psilotum* Sw. and *Tmesipteris* Bernh. have during a long time already, attracted the interests of plant taxonomists and phylogenists. Eames (1936) considered them the most primitive vascular plants. The primitive general appearance of, especially, *Psilotum* reminds of the Middle-Devonian Rhyniaceae: the genera *Rhynia* Kidst. et Lang and *Horneophyton* Bargh. et Darrah, by the green stiff, at first sight almost leafless, strictly dichotonous aerial shoots arising from a rootless creeping rhizome. The two genera, together forming the family Psilotaceae and the order Psilotales, have accordingly been classified by most authors in the Psilophyta, together with the exclusively Devonian Psilophytales and of the latter the Rhyniaceae are regarded usually as the closest relatives. Among those who take this stand I mention G. M. Smith (1955), Mägdefrau in Strasburger (1971) and Lemoigne (1968c). The concept of the last mentioned author will be discussed further on. Darrah (1960) states that the status of the putative primitive nature of the plant body in the Psilotaceae is controversial although there is a strong tendency to accept the family as a persistent remnant of the Psilopsida. Andrews (1961) states that *Psilotum* has been regarded by some botanists as a very simple land plant, possibly a very ancient type that has managed to survive for several hundreds of millions of years. Chadefaud (1950) even regarded them as ancestral to the Bryophytes. Others view its simple organization as a result of degeneration from a more complex ancestor. Thus the former viewpoint regards it as primitive and the latter as reduced. Nothing is known, however, of fossil records and there are no related modern plants which offer much aid in settling the problem.

There are, however, quite a number of objections, even scruples, to an attribution without more to the Psilophyta to which phylum further only Devonian fossils would belong. Of these objections I now mention already one, namely the leaves. *Psilotum* has very small, spinelike, microphyllous leaves without a midvein. The leaves of *Tmesipteris* are considerably larger and provided with a midvein. For this reason Lotsy (1909) regarded the *Psilotum* leaves as reduced, connected with its xerophytic and semisaprophytic life.

The upper parts of the shoots of both *Psilotum* and *Tmesipteris* are provided, moreover, with bifurcate leaves of the same size, supporting a very short stalk which bears a trilocular synangium in

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Psilotum and a bilocular synangium in *Tmesipteris*. This led, as no fossils are available, Professor Lam (1948) to his well-known ingenious, theoretical-phylogenetic, but highly hypothetical derivation from the Rhyniaceae with their terminal (stachyosporous) sporangia.

In this way he defended and tried to save the attribution to the Psilophyta without taking into account other features which contradict such an attribution as expounded below. Needless to say that Lam's concept lacks every palaeobotanical basis. Lam, consequently, rejects the term sporophylls for the bifurcate leaf-like organs supporting the synangia. Other features which might be objections to an attribution to Psilophyta we find, besides in the leaves and the sporangia, in the anatomy and, perhaps, in the gametophytes. Next to the general appearance the absence of roots is actually the only feature that is in favour of an attribution to the Psilophytes.

For these reasons a number of authors defend the attribution to a separate phylum of Pteridophytes or, if they prefer to consider the Pteridophytes a phylum altogether, to a separate classis. Such an isolated taxonomic position has been defended by a number of authors who, however, do not take account of fossil records. Palaeobotanists who defend an isolated position are, for instance, Gothan and Weyland (1964). A different position has been taken up by Lotsy (1909) who, on the basis of the presence of a vascular bundle in the sporangium stalk, decided to a relationship with the Sphenophyllales, a view shared more or less by Scott.

Sahni (1923a) regarded the sporangiophore of the Psilotaceae, on the basis of observed abnormalities, as consisting of axes bearing alternate whorls of sterile lobes and sporangia. This concept was shared by Bierhorst (1956) who interpreted the fertile appendage (i.e. the stalked synangium with its subtending bifid or trifid bract) of the Psilotaceae as bearing a verticil of sporangia (two or three remaining) fused to a central axis, and a verticil of sterile appendages (two or more remaining). In *P. nudum* and *P. complanatum* the vascular trace which enters the base of the sporangia-bearing portion of the fertile appendage, branches into three parts. Bierhorst, consequently, re-introduced the hypothesis that fertile appendages in the Psilotaceae are fundamentally verticillate in organization and this might point to a relationship with Equisetophyta, for instance Sphenophyllales.

As neither *Psilotum* nor *Tmesipteris* are articulate or show a verticillate organization in their aerial shoots, I reject this concept, the more as other conformities with Sphenophyllales are scarcely evident.

In later papers Sahni (1923b; 1925) brought forward anatomical evidence to bring the Psilotales nearer to the Devonian genus *Asteroxylon* which, in his opinion, supports the old view that the Psilotales are related to the Lycopods.

In 1930 Campbell defended an attribution to the Lycopodiophyta and the same concept was held by Zimmermann (1959). The possible relationship to Lycopodiophyta was discussed by a number of authors without taking a definite standpoint with respect to that. In this paper I am defending an attribution, as a separate order, to the isosporous Lycopodiophyta and in the following I will discuss my concept in comparison with arguments against a relationship to Psilophyta-Rhyniaceae.

ANATOMY

Psilophytes always have a haplostele in their rootstocks and aerial shoots. Primitive Lycopodiophytes have, in their aerial shoots, an actinostele of which in more advanced representatives the xylem either may divide into vertical plates (plectostele) as in certain *Lycopodium* species, or become tubular and filled with a central medula. Those siphonostelic conditions occur, for instance, in a number of Lepidodendrales. The complicate anatomy of Selaginellales and Isoetales is left out of consideration here. The roots often show in the above mentioned actinostelic, plectostelic, and siphonostelic groups a haplostelic anatomy.

The aerial shoots of *Psilotum* are actinostelic in principle. The hollow xylem body encloses initially a parenchymatous medulla which in the older parts becomes sclerenchymatous. According to Bierhorst (1954b) only rhizomes greater than 1 mm in diameter usually possess a complete stele. *Tmesipteris* also has a siphonostelic vascular cylinder with a central parenchymatous pith. These facts point into the direction of the Psilotales showing a rather primitive Lycopodiophytic anatomy which, however, presents a more advanced stage than the

most primitive Lycopodiophytic anatomy which is characterized by a massive actinostelic protostele without pith. There are no points of contact to the haplostele of the Rhyniaceae.

GAMETOPHYTE

The gametophyte of *Tmesipteris* has been studied extensively by Lawson (1917), by Holloway (1917, 1921), and by Bierhorst (1953, 1954a). The prothallus of the Psilotales is subterraneous, without chlorophyll, saprophytic, more or less cylindrical in shape and sometimes dichotomously branched. The gametophytes bear some resemblance to little rootstocks. In gametophytes of *Psilotum* annular and scalariform tracheids have been found, which may be regarded as a relic of a more isomorphic alternation of generations and, consequently, a primitive feature which is very rare among Pteridophytes.

In 1958 Merker surprised the palaeobotanists by his statement that he had discovered evidence of the occurrence of sunken archegonia in the rootstocks of the Rhynia's, i.e. he found embryos and only indications of archegonium remains. In another paper, the following year (1959), he again went into the consequences of his discovery namely that the *Rhynia* rhizome represents the prothallus. The Rhyniaceae have, consequently, a leafless sporophyte with terminal sporangia growing on the gametophyte in the way as the sporogones of the Bryophytes are attached to the gametophytes. When we combine this concept, which has not been proved however, with the work of Campbell (1925), of Chadefaud (1936), and especially with the work of Proskauer (1960) regarding corresponding structures in *Rhynia* and *Horneophyton* on the one side and in *Anthoceros* on the other side, we may conclude to a much closer affinity of the Rhyniaceae to the Bryophytes and especially to Anthocerotales. In that case there is no close relationship of the Rhyniaceae to the Psilotales as in *Psilotum* and *Tmesipteris* the rhizome is part of the sporophyte and the gametophyte is a separate prothallus not persistently bearing the sporophyte. In other words there is no justification any longer for an attribution of the Psilotales to the Psilophyta based on a similarity with regard to their general appearance.

A still more recent view was started by Lemoigne (1968a, b; 1969a) who found archegonia of the Pteridophyte type sunken in semiglobular tissue bodies on the stems of *Rhynia gwynne-vaughanii* and never on any part of *Rhynia major*.

He also published still vague indications for the presence of antheridia in small warts on the aerial shoots of *R. gwynne-vaughanii* (1969b). As he also states that the terminal sporangia are only known in *Rhynia major* and not in *R. gwynne-vaughanii*, he arrives at the conclusion that both species are gametophyte and sporophyte respectively of the same species. This possibility was already suggested six years before by Pant (1962). *Rhynia* consequently shows an almost isomorphic alternation of generations, quite unknown up till now in other Pteridophytes. I am astonished that this leads Lemoigne (1968c) to the conclusion that his discoveries have made it clear that both *Psilotum* and *Tmesipteris* belong together with *Rhynia* in the same order, Psilotales, of the Psilophyta. He argues this by pointing to the vasculiferous gametophytes. In his order Psilotales he classifies three families, viz. Rhyniaceae, Psilotaceae, and Tmesipteraceae. In my opinion considerable differences exist in the gametophytes of *Psilotum* and *Tmesipteris* on the one side and *Rhynia* on the other side if we accept that *Rhynia gwynne-vaughanii* is the gametophyte of *R. major*. *Psilotum* and *Tmesipteris* have subterraneous, though sometimes slightly vascularized prothallia and the gametophyte of *Rhynia* is in that case a dichotomously organized erect plant, provided with a haplostele, a cortex, an epidermis with stomata, and a subterraneous rhizome. Lemoigne also points to the probable early decay of the archegonium neck in *Rhynia*, a feature also present in *Psilotum* and in *Anthoceros* but generally rare in Pteridophyta though it is found in *Lycopodium*. As we have up till now only a vague idea of the structure of the *Rhynia* archegonium and the early decay of its neck cells is hardly more than surmise, one might use the feature as well to suggest a relationship between the recent Psilotales and the Lycopodiophytes.

LEAVES

Notwithstanding Lam's effort (1948) to deny the leaf nature of the *Psilotum and*

Tmesipteris leaves we may state that the two genera have microphyllous leaves whereas the Rhyniaceae are leafless.

In the probably monotypic genus *Tmesipteris* has *T. tannensis* Bernh. rather well-developed leaves with a midvein which communicates with the stele by a leaf trace in the cortex. This means that there is no impediment to regard them as real leaves. *Psilotum nudum* (L.) Griseb., on the other hand, has spinelike leaves without midvein or leaf trace in the cortex and it has been wondered, for instance by Manton (1950) and Tronchet (1954) whether they are to be regarded as leaves.

Lotsy (1909) assumed a reduction of the leaves of *Psilotum* in comparison to those of *Tmesipteris*, connected with the xerophytic and semisaprophytic life In *Psilotum complanatum* Sw. (=*P. flaccidum* Wall), however, a leaf trace in the cortex has been observed, terminating just below the leaf base This character is known also in the Middle-Devonian genus *Asteroxylon* Kidst. et Lang which was, on the basis of its presumed terminal sporangia, considered a member of the Psilophyta, notwithstanding its actinostele and its leaves which occur, densely crowded, along the aerial shoots like in *Lycopodium*. Lyon (1964), however, made clear that in all probability the observed sporangia-bearing, naked dichotomous branches did not belong to *Asteroxylon*. He found among masses of *Asteroxylon* in the Rhynie chert strobilus-like branches beset with both normal leaves and shortly stalked leaves supporting a sporangium. When accepting these organs as fertile parts of *Asteroxylon* there is no hindrance any more to classify *Asteroxylon* within the isosporous Lycopodiophyta. And, at the same time, this is a strong support to consider, the Psilotales Lycopodiophyta as well.

The leaves supporting the synangia of the Psilotales are bifurcate, however. It has been observed occasionally that in *Psilotum* there may occur a repeated bifurcation and in that case every bifurcation bears a synangium. Bifurcate leaves and sporophylls occur in the early Devonian genus *Protolepidodendron*, family Protolepidodendraceae. To this family also *Drepanophycus*, with spine-like leaves and sporophylls has been attributed, but in the opinion of some authors these differences made it necessary to base two families on this character, viz., Protolepidodendraceae with bifurcate leaves and Drepanophycaceae with spine-like leaves. Both are primitive Lycopodiophyta as the sporangia occur on the adaxial side of the sporophylls which have the same shape as the trophophylls. In these cases the sporophylls occur in the apical parts of the shoots but they are not arranged in distinct strobili. W. Schmidt (1955) described *Sugambrophyton pilgeri* from the West-German Lower-Devonian and this new genus was characterized by spine-like leaves in the lower parts and bifurcate leaves in the apical parts of the shoots. He even observed a repeated bifurcation occasionally. This makes it clear that the simple or bifurcate leaf is not a good character to distinguish two families on it as both leaf forms may occur in the same plant. But at the same time we may observe the same situation in *Psilotum* and *Tmesipteris* with the difference that in these two genera the bifurcate leaves always support a synangium. This is, in my opinion, the final reason to consider the Psilotales members of the Lycopodiophyta and not Psilophyta, In my concept the isosporous Lycopodiophyta are to be divided into two orders, viz. Lycopodiales consisting of three families: Protolepidodendraceae, Asteroxylaceae and Lycopodiaceae, and Psilotales with a single family Psilotaceae (genera *Psilotum* and *Tmesipteris*), Arguments against an attribution of the Psilotales to the Lycopodiophyta are the absence of roots (which in my opinion is a primitive character that does not turn of the scale) and the synangium which does not occur in other Lycopodiophytes but which does not occur in other Psilophyta either

PRIMITIVITY

The question arises, finally, whether the Psilotales are to be considered very primitive. In my opinion they show a mixture of primitive and more advanced characters. The general appearance is of course primitive and reminds to the primitive appearance of the shoots of Psilophyta, Protolepidodendraceae, and some Protopteridiales. The absence of roots is primitive and has not been observed, as far as known to me, in Lycopodiophytes whereas it is usual in Psilophyta though there is no proof that roots are always absent in Psilophyta.

The actinostele which is, at the same time, siphonostelic is more advanced than the most primitive steles known in Lycopodiophytes. The prothallus is, undoubtedly, primitive.

The synangium has to be considered advanced and so are, in my opinion, the monolete spores. The spores of Psilophyta are trilete as a rule and so are mostly Lycopodiophyte spores. The microspores of *Isoetes* are monolete, however, with occasionally some tendencies to a trilete condition. This character is apparently not in all cases settling the problem as in related ferns both conditions are possible. Kramer (1970) mentioned the occurrence of both monolete and trilete spores in the fern genera *Sphenomeris* and *Lindsaea*.

A combination of a primitive general appearance and advanced characters is not very rare. Good examples we find in the Devonian genus *Moresnetia* which in all probability produced seeds and in a number of aerial shoots of Devonian Protopteridiales, e.g. *Archaeopteris* (Beck, 1960) and *Svalbardia* (Carluccio, Hueber & Banks, 1966) which genera form secondary wood of a very advanced structure.

With regard to the Psilotales — which have quite a number of primitive characters in common with the early land plants, in combination with more advanced characters — the fact is left that no connecting fossil records are known between the occurrence of their far relatives, the Protolepidodendraceae in the Lower-Devonian, and the present.

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