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# ANATOMICAL STRUCTURE OF *PSILOPHYTON SZAFERI* ZDEBSKA AXES FROM THE LOWER DEVONIAN OF THE HOLY CROSS MOUNTAINS IN POLAND AND RELATED PHYLOGENETIC CONSIDERATIONS

Budowa anatomiczna pędów *Psilophyton szaferi* Zdebska z dolnego dewonu Gór Świętokrzyskich i łączące się z nią rozważania filogenetyczne

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ABSTRACT. The new species *Psilophyton szaferi* was described from the Lower Devonian (Emsian) of the borehole Modrzewie near Bostów in the Holy Cross Mountains (Zdebska 1986). It is for the first time in the Polish palaeobotanical literature that it is possible to describe a representative of the genus *Psilophyton* using both its morphological (Zdebska 1986) and anatomical structure (the present paper). This is also the first description of a species of *Psilophyton* with preserved anatomical structure from a locality in Europe. It is visible in pyritized axes which show the structure of the vascular strand and accompanying secretory cells, cells up to now not described in the genus *Psilophyton*. The vascular strand is an endarch protostele. The tracheids possess scalariform thickenings and probably also pits between them. The tracheids are isodiametric in transverse section, 15–45 μm in diameter in the protoxylem and 55–75 μm in diameter in the metaxylem. The structure of the vascular strand was investigated in the part of the axis below branching level showing the structure of the strand on six successive ground sections. The vascular strand in the process of branching is accompanied by secretory cells which form around it a discontinuous ring 2–4 cells wide. The diameter of the secretory cells ranges from 38–69 μm. Those cells resemble in their character and distribution in the axes the secretory cells in the axes of the primitive ferns of the order *Coenopteridales*. In connection with the similarity of the anatomical structure of axes of *P. szaferi* and of axes of these primitive ferns the question of phylogenetic connections between the trimerophytes and ferns of the order *Coenopteridales* is discussed.

KEY WORDS: Lower Devonian, *Psilophyton*, anatomical structure, secretory cells, phylogenesis, megaphyllous leaf

## INTRODUCTION

The knowledge of the anatomical structure of early Palaeozoic plants is essential from the evolutionary point of view. The establishing of the proper phylogenetic con-

nections is possible when we are able to investigate in addition to morphology, also the changing anatomical structure of the plants.

During the last three decades the progress in better understanding of the anatomical structure of the first land plants allowed to look in a different manner at the subdivision *Psilophytina* (division *Telomophyta*), regarded hitherto as a homogeneous unit. The distinction inside it of the subdivisions *Rhyniophytina*, *Trimerophytina* and *Zosterophyllophytina* on the base of the structure of the vascular strand and the position of sporangia was made by Banks (Banks 1968, 1975). This made possible more detailed considerations concerning the phylogenetic development of vascular plants.

The genus *Psilophyton* of which were described the most species (more than ten) belongs to the subdivision *Trimerophytina*.

The anatomical structure, however, of its axes is known to a different degree of accuracy only in a few species. It had been described up to now in *Psilophyton princeps* originating from the Lower Devonian of Gaspé, Canada (Dawson 1859, Hueber & Banks 1967 – anatomical structure of the vascular strand badly preserved), *P. forbesii* from the Lower Devonian of Maine, Canada (Andrews et al. 1968, Gensel 1979), *P. charientos* from the Lower Devonian of New Brunswick, Canada (Gensel 1979), *P. dawsonii* from the Lower Devonian of Quebec and Ontario, Canada (Banks et al. 1975, Hartman & Banks 1980), *P. crenulatum* from the Lower Devonian of New Brunswick, Canada (Doran 1980) and *P. coniculum* from the Lower Devonian of New Brunswick, Canada (Trant & Gensel 1985).

The describing by Banks et al. (1975) of *P. dawsonii* lead to major progress in our knowledge of the genus *Psilophyton*. The considerable diversification of morphology of *P. dawsonii* and the in detail described anatomical structure of its axis, as well as the detailed descriptions of other species created the possibility of discussion of the role of the genus *Psilophyton* in the evolution of vascular plants. The trimerophytes are considered by many authors as ancestors of the primitive ferns of the order *Coenopteridales* (Phillips 1974, Holmes 1977, 1989, Banks et al. 1975, Banks 1980, Stewart 1983).

*P. szaferi* is another species which can be included into this discussion, taking into account the anatomical structure of its axis.

*P. szaferi* originating from the Lower Devonian of the borehole Modrzewie in the Holy Cross Mountains was described for the first time in my paper "*Psilophyton szaferi* sp. nov. from the Lower Devonian of the Holy Cross Mountains, Poland" (Zdebska 1986). There were described the morphology of the vegetative and generative axes and their anatomical structure, basing only on broken surfaces of pyritized axes. Therefore this description could not include all the details, because not all were visible.

An additional material of pyritized axes and the adaptation of a method of preparing microscopic slides allowed to make detailed investigations of the anatomical structure and to add new information concerning the genus *Psilophyton*.

# MATERIAL AND METHODS

The anatomical structure of *Psilophyton szaferi* axes is preserved in compressed and pyritized axes. The axes preserved as compressions showed the morphology as well as the structure of epidermis (Zdebska 1986) and the pyritized axes the anatomical structure. The axes were only loosely connected with the rock and it was easy to separate them without the use of chemicals.

Repeated attempts of maceration of plant fragments preserved as compressions gave no results. The material fell into pieces when treated with substances such as nitric accid, Schulzes's solution or commercial bleach ("Bielinka"). The description of the plant is therefore based on unmacerated material.

Additional fragments of axes preserved as compressions obtained from deeper layers of the rock showed more accurately the morphology of the plant (Pl. 1 figs 2–4).

The main subject of the investigations were, however, pyritized axes. I have obtained in addition 8 fragments of axes 3–6 mm long and 1–3 mm in diameter. One fragment was 15 mm long but was divided into four shorter fragments. From them was prepared a series of four transverse (ground) sections which showed successive stages of division and structure of the vascular strand of *P. szaferi* (Pls 5–7).

All the axes were unfortunately not very well preserved. They showed deformations and cracks where the mineral substance (pyrite) was lacking. This is illustrated on Pl. 2.

The axes fell apart particularly in contact with water, therefore they were kept in paraffin oil and not in a mixture of water and glycerine.

It has to be stressed that the obtained fragments were taken from single not branching axes. Their length was limited by the diameter of the borehole sample, therefore it is difficult to decide of what type was the branching above the analyzed pyritized fragments.

The most problems arose during the preparation of ground sections for reflected light from these axes in order to investigate more accurately their anatomical structure. Earlier it was observed only on the transversally and longitudinally broken surface of the axes (Zdebska 1986).

I have used a modified methods of preparing ground sections from pyritized material, described by Stein et al. (1982) and Zdebska (1982). It was not possible to use the single method of Stein et al. (1982) because the plastic masses proposed by the authors for embedding of the specimens were not available in our country. Also the method I used earlier (Zdebska 1982) for embedding of fragile material did not prove useful, because immediate embedding of the axes in dental plaster of Paris which had to protect them from crumbling, proved impossible. Under the influence of the fresh dental plaster mass the axes dissolved into respective crystals of pyrite and coal particles. In connection with this, in order to cement the brittle mineral material forming the axes and to protect them from crumbling, I have boiled the axes in Canada balsam diluted with xylene. The diluting of balsam was necessery in order not to destroy the axes, because balsam of normal density caused their crumbling during embedding. The degree of dilution depended from the degree of brittleness of the axes. The axes impregnated by balsam and hardened by boiling were finally embedded in dental plaster of Paris in order to protect them additionally and make grinding easier (axes are avery small diameter). I have ground them by hand using corundum grinding powder of various granulations, obtaining finally sections about 0.5 mm thick. Also the protection of the surface of the ground section demanded special caution. The fixing of the section to the object glass with Canada balsam and covering with cover glass demanded heating of the preparation and this had to be done with great caution. In connection with those difficulties in preparing ground sections and the necessity of making experiments, a few fragments of axes were destroyed.

The pyritized axes showed on the ground sections their anatomical structure with new details which before were difficult to distinguish on their broken surface.

For investigation were used a Technival and Vertival microscope (Carl Zeiss, Jena).

Unfortunately the use of the scanning electron microscope for the observation of the anatomical structure was not possible, because the axes fell into pieces during the coating process for this microscope.

I took the photographs in the reflected light on a Vertival microscope (Carl Zeiss, Jena) in the Department of Paleobotany of the Botanical Institute of the Jagiellonian University.

The microscopic preparations are kept in the Palaeobotanical Museum of the Botanical Institute, Jagiellonian University under the collection number S/99.

## DESCRIPTION

### Compression axes

Axes of *Psilophyton szaferi* 1–6 mm wide are branching dichotomously (Pl. 1 fig. 1) and monopodially (Fig. 1,1, Fig. 3,3, Zdebska 1986). Most axes are branching in one plane but there occur also branchings in two planes. A characteristic feature of the sterile axes (Pl. 1, figs 2–4) and of the fertile ones (Pl. 1 fig. 1) are emergencies in the shape of small (0.2–0.5 mm long) swellings which are arranged irregularly on their surface (Pl. 1 figs 2, 4). On the surface on the split rock lost emergencies leave horse-shoe like pits (Pl. 1, figs 2, 3). They may in some regions of the axis show a more regular arrangement (Pl. 1 fig. 3), which reminds of leaf scars in certain Devonian lycopods e.g. *Cyclostigma kiltorkense* (Nathorst 1902, Chaloner 1968, Gensel & Andrews 1984).

This is a morphological character distinguishing best this species of *Psilophyton* from other species of this genus. It has to be stressed that this is also a character which could have as a result an erroneous classification of this plant, if only fragments of compressions of axes were preserved (Pl. 1 fig. 3).

The sporangia arranged in groups on the ends of the axes (Pl. 1 fig. 1) do not contain spores (Zdebska 1986). Repeated attempts of maceration of the sporangia in order to show their anatomical structure and spores gave no results. The material crumbled unter the influence of chemicals.

### Pyritized axes

The fragments of pyritized axes are in general badly preserved. Not all elements of the anatomical structure were observed. Cells of the cortex and phloem are not preserved. The ground sections show distinctly only the structure of the vascular strands and the described here for the first time secretory cells. On the broken surfaces the secretory cells were difficult to distinguish from the dark, cracked parts and therefore in the first description of this plant they were not mentioned and were not included in the diagnosis of the species.

Single flattened fragments of axes show a structure of the vascular strands indicating that they represent fragments of axes below branching (Pl. 2 and compare Text-fig. 5a–k, Text-fig. 6c, d, Banks et al. 1975). Before branching of the axis the vascular strand divides earlier announcing this process (Esau 1973, Banks et al. 1975, Hejnowicz 1980, Trant & Gensel 1985). All the ground sections show this moment (Pls 2, 3, 5–7).

The vascular strand of *P. szaferi* is an endarch protostele i.e. it has a protoxylem in the middle which is surrounded by a metaxylem (Pl. 3 fig. 2, Pl. 8 fig. 2).

The protoxylem tracheids which are isodiametric in transverse section, are 15–45 μm in diameter and the metaxylem tracheids 55–75 μm in diameter. In longitudinal section the tracheids are elongated with oblique transverse walls and scalariform thickenings

which are visible both in the protoxylem and metaxylem tracheids (Pl. 8 fig. 2). It is not possible to measure their length because of their not best preservation.

Unfortunately the longitudinal ground sections gave no definite answer whether between the scalariform thickenings occur pits, described in *P. dawsonii* (Banks et al. 1975), *P. coniculum* (Trant & Gensel 1985), *P. charientos, P. forbesii* (Gensel 1979) and *P. crenulatum* (Doran 1980).

Observations of the longitudinal ground sections of the fractures of pyritized axes (Fig. 15 and 16, Zdebska 1986, cp. Pl. 17 fig. 7, Banks et al. 1975) suggest the presence of such pits in *P. szaferi*. Their absence in the ground sections is probably connected with the fragility of axes, which might cause destruction of the delicate pits structures during grounding.

The vascular strand in a single axis, below the branchings, is rounded, about 0.7 mm in diameter. It becomes lobar, however, when its division starts (Pl. 3, Pl. 3–5).

Plates 3–8 illustrate the structure of vascular strands during their division, in the transverse and longitudinal sections.

Plate 3 fig. 1 shows the transverse section of the fragment of a single axis, with a visible, lobar, arch bent vascular strand. The cylindrical protoxylem in the central part of the strand becomes longitudinal during the division, which is clearly visible in the left part of the strand. The protoxylem is less visible in the right part, because the terminal part of the strand is destroyed. Might be that there was an increase in the amount of metaxylem in this part. A similar phenomenon has been observed in *P. dawsonii* (Banks et al. 1975). This picture of the strand suggests that there will occur a branching to axes of unequal width. It is illustrated in Fig. 1. One may also presume that the strand bending is not a result of the changes caused by fossilization but it shows that the branching will occur in the plane different from the branching located below this fragment of the axis. Similar branchings have been observed in *P. dawsonii* (Text-fig. 6, Banks et al. 1975). The branchings in two planes occur in *P. szaferi*.

The sequence of dividing strands may be observed in the following plates: Pl. 5 fig. 1, Pl. 6 figs 1, 2 and Pl. 7 figs 1 and 2. The subsequent sections were carried out of the single, 15 mm long axis, cracked randomly into four smaller fragments.

Pl. 5 fig. 1 shows the lowest level of this axis. The cylindrical protoxylem, visible on the left side, elongates during division and the whole strand becomes lobar. This is even more visible in Pl. 6 fig. 1 and 2, where a narrowing in the lobar strand may be observed. In this part the strand will divide, which is illustrated in the next sections, above the preceding (Pl. 7 fig. 1 and 2). The highest level of the section is shown in Pl. 7 fig. 2. A significant narrowing of the strand is here visible and its right part is more rectangular. It is a sign of the strand division. From the comparison of the right part of the strand of this photo with the left part (which is here destroyed) of the lower level of the section (Pl. 7 fig. 1), basing on the almost equal mass of the xylem, it may be concluded that the axis branching which has to occur will be dichotomous. The dichotomous branchings in *P. szaferi* are characteristic both for the hook ends of axes (Fig. 6, Zdebska 1986) and for the axes with sporangia (Pl. 1 fig. 1). It is illustrated in Fig. 2.

The interesting section is shown in Pl. 8 fig. 1. The single axis has the trifurcating

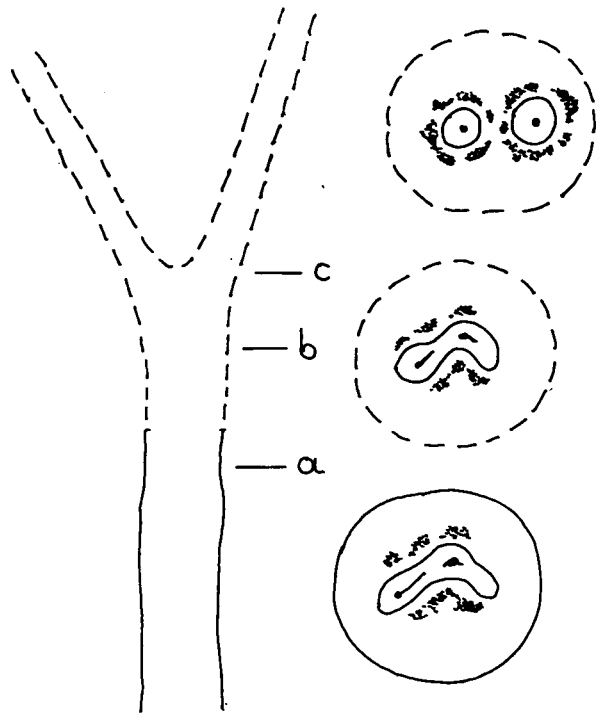


**Fig. 1.** Diagrams of successive series of transverse sections of axis with dividing protostele inside. a – section level seen on Pl. 3 fig. 1; b, c – supposed division of vascular strand and axis leading to monopodial branching. Explanations: inside vascular strand dark protoxylem, autside vascular strand secretory cells shows as dark dots

strand. This fragment of the axis suggests that the transverse section is taken below the trifurcation, which is not visible because of the dimensions of the borehole. Trifurcations occur in *P. dawsonii* and the behaviour of its strands below these branchings is similar (Pl. 24 figs 62–65, Banks et al. 1975). This fragment of *P. szaferi* axis is interesting also because the observations of the morphological structure of the axes preserved on the rock in the compressed form have not lead to the conclusion that *P. szaferi* axes may trifurcate too. It seems that they could appear occasionally. The interpretation of this division of the vascular strand is shown in Fig. 3.

New, interesting point of the anatomical structure of this plant are secretory cells, (Pl. 3–8) which have not been described yet either in *Psilophyton*, or in other earliest land plants. This is the first report on their presence.

The secretory cells are isodiametric, of a diameter varying between 38 and 69 μm (Pl. 3 fig. 2, Pl. 4 fig. 2, Pl. 8 fig. 3). Their walls are thinner than the tracheid ones. They are filled with a dark secretion, which does not fill the whole interior of the cell. The space between the secretion and the cell wall is filled with pyrite. The secretion is also visible in cells, in the longitudinal sections (Pl. 4 fig. 1, Pl. 5 fig. 2). In the longitudinal section the cells are elongated, roughly from 60 to 85 μm in length, and have the rounded terminal walls. The secretion does not fill the whole cell either, but it is apparently contracted, while the space between the cell wall and the secretion is filled with pyrite.

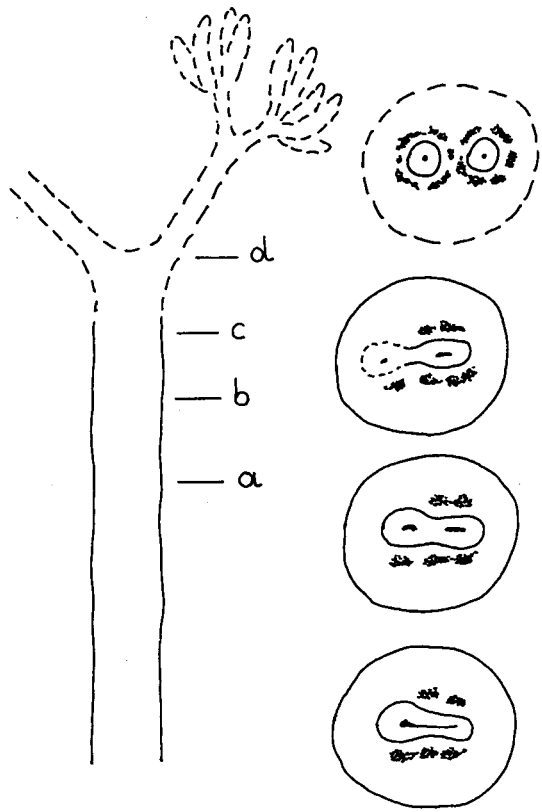


**Fig. 2.** Diagrams of successive transverse sections of axis with dividing protostele inside. a – section level seen on Pl. 5 fig. 1; b – section level seen on Pl. 7 fig. 1; c – section level seen on Pl. 7 fig. 2; d – supposed division of vascular strand and axis leading to dichotomous branching. Explanations on Fig. 1

The secretory cells accompany the vascular strands, surrounding them. They form around the vascular strands a discontinuous ring, consisting of groups of several to a dozen or so cells (Pl. 3 fig. 1, Pl. 5 fig. 1, Pl. 6, 7). The width of the ring changes from 2 to 4 cells. The secretory cells are in the close neighbourhood to the vascular strand. There are places, where this direct neighbourhood of these cells and the strand is visible (Pl. 3 fig. 2, Pl. 4 fig. 2, Pl. 8 fig. 3). It seems that in this case they could adhere closely to phloem, whose elements have not been preserved, but which was located peripherally in respect to the xylem. Its location is determined by the cell-free zone, visible between the xylem and the secretory cells (Pl. 3 figs 1, 2, Pl. 4 fig. 2, Pl. 5 fig. 1, Pls 6–7, Pl. 8 figs 1, 3). The occurrence of the phloem in the cell-free zone may be concluded from its presence in the axes of *P. dawsonii*, in which species it has been preserved. Phloem in *P. dawsonii* formed a layer of 2–6 thin-walled cells around the xylem (Pl. 19 fig. 19, Banks et al. 1975).

Thus the secretory cells in *P. szaferi* were accompanying the vascular strand, being present also in its divisions, in the axes, which were branching.

The presence of the secretory cells has not been reported in the diagnosis of *P. szafe-*

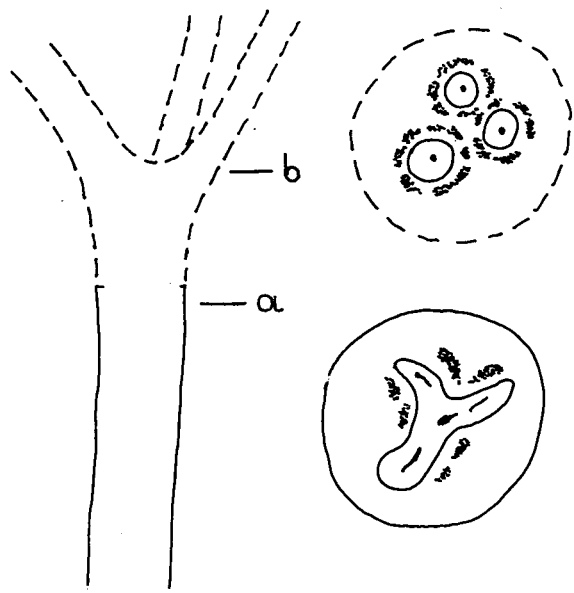


**Fig. 3.** Diagrams of successive transverse sections of axis with dividing protostele inside. a – section level seen on Pl. 8 fig. 1; b – supposed division of vascular strand and axis leading to trifurcating branching. Exlanations on Fig. 1

*ri* (Zdebska 1986). Therefore there is a necessity of adding this fact as the feature, characteristic for these species, and reported in Psilophyton for the first time.

**Emended specific diagnosis to *Psilophyton szaferi*.** Axes 1–6 mm wide, branching dichotomously or monopodially, sporadically trifurcating in one or two planes, ends of axes in the form of hooks. the surface of axes covered with irregularly distributed emergencies in the shape of small rounded swellings 0.2–0.5 mm high betweem them visible short ridges. On impressions visible circular or horse-shoe shaped bases of emergencies. The vascular strand circular, with central protoxylem surrounded by metaxylem. Tracheids with scalariform thickenings, between them probably pits. Vascular strands surrounded by discontinuous ring of secretory cells, 2–4 cells wide. Fertile axes bearing terminally groups of fusiform sporangia, 1–3 mm long and 0.8–1.1 mm wide. Surface of sporangium showing delicate ridges and small swellings. Spores unknown.

Horizon. Lower Devonian, Emsian

Locality. Bore-hole Modrzewie 2 A near Bostów in the Holy Cross Mountains, Poland

Holotype: S/99/1, Pl. I fig. 2, Pl. III figs 10, 12 (Zdebska 1986). Paratype: S/99, Pl. IV fig. 13, S/99/2, Pl. II fig. 6, S/99/3, Pl. II figs 3–5, Fig. 19 (Zdebska 1986), S/99/2, Pl. 1 fig. 1 (the present paper). All specimens are deposited in the Palaeobotanical Museum of Institute of Botany, Jagiellonian University, Kraków, coll. no. S/99.

Derivation of name. The specific name is in honour of the late Professor Władysław Szafer, the Polish botanist and palaeobotanist, professor of the Jagiellonian University and founder of the Botanical Institute of the Polish Academy of Sciences.

The comparison with other trimerophytes, with the preserved anatomical structure

There is some similarity in the anatomical structure between *P. szaferi* and several species of the genera *Psilophyton*, of a known anatomical structure of axes. These are *P. princeps*, *P. crenulatum*, *P. charientos*, *P. forbessi*, *P. coniculum* and *P. dawsonii*. The anatomical structures of axis in these plants are preserved to a different extent, except for the vascular strand, which is well visible in all species, similarly as in *P. szaferi*. It is a rounded or elliptical endarch protostele, with a single, cylindrical protoxylem, surrounded by metaxylem. This character is common for the above mentioned species of *Psilophyton*. The second characteristic feature of the strand structure are tracheids, with the scalariform thickenings and pitting between them, found in *P. charientos*, *P. forbessi*, *P. crenulatum*, *P. coniculum* and *P. dawsonii*. The pitting between scalariform thickenings in *P. szaferi* is less visible, but it may be presumed that it has also occurred.

When the strand is being divided, the protoxylem behaves similarly in all strands, elongating during the division, while the strand becomes lobar. Pl. 5 fig. 1, Pl. 6 figs 1, 2 and Pl. 7 fig. 1 show the dividing strands in *P. szaferi*, which look similar to the dividing strands found in *P. forbessi* (Pl. 8 figs 5, 6, Gensel 1979), *P. coniculum* (Fig. 16, Fig. 21 B, Fig. 31 Eb, Trant & Gensel 1985) and in *P. dawsonii* (Pl. 17 fig. 9, Fig. 6c, Banks et al. 1975).

The similarity between *P. szaferi* and *P. dawsonii* may be also noted in the occurance of the hypodermal tissue. A hypodermal tissue occurs in *P. dawsonii* under the epidermis, in the outer part of cortex, which is described by the author as a colenchimatic (Pl. 18 fig. 17, Banks et al. 1975). In *P. szaferi* occurs also the hypodermal tissue, with the thick-walled, elongated cells, visible in the longitudinal section (Fig. 14 and 17, Zdebska 1986). Because of the behaviour this tissue could be described with the general term – hypodermis.

The above characters are common for *P. szaferi* and the species of the genus *Psilophyton* with the preserved anatomical structure.

The character of the anatomical structure, which distinguishes *P. szaferi* from the other species of the genus *Psilophyton*, is the presence of the secretory cells, accompanying the vascular strand in the axis.

Apart from the genus *Psilophyton* the following genera belong to trimerophytes: *Trimerophyton* described from the Lower Devonian of Canada (Hopping 1956), *Pertica* from the Lower Devonian of Maine, Canada (Kasper & Andrews 1972) and *Yunia* from the province Yunnan in China (Shou-Gang & Beck 1991).

The anatomical structure of axes is known for *Yunia* only. The axes of this plant are characterized by the endarch protostele, similarly as in the genus *Psilophyton*. The character definitely distinguishing this genus from the genus *Psilophyton*, and this way also from *P. szaferi*, is the occurance of the parenchimatic cells within the centrally located protoxylem (Pl. 4 fig. 24, Shou-Gang & Beck 1991).

The occurance of the secretory cells in the axes of *P. szaferi* leans towards making comparisons of this plant with the representatives of other groups of plants, in which the secretory cells occur and which are filogenetically bound to trimerophytes. The rep-

resentatives of the oldest ferns of the group *Coenopteridales* form such a group of plants.

### The comparison of the anatomical structure of axes in *P. szaferi* and in the representatives of the primitive ferns of the order *Coenopteridales*

The characteristic feature in the anatomical structure of these ferns is the protostelic strand, which makes them similar to trimerophytes. Another character is the occurrance of secretory cells in the anatomical structure of axes and leaves. These cells are also present nowadays in several ferns (Ogura 1972).

The secretory cells are present in the oldest representative of *Coenopteridales*, which is *Botryopteris antiqua* from the family *Botryopteridaceae*, from the Culm (Lower Carbon) of France (Kidston 1908, Boureau 1972). They are located loosely, form a several cells wide periphery around the protostele and do not adhere closely to the strand, but they form a layer in the internal part of the cortex. The characteristic feature of the cells is a dark secretion, sometimes filling the whole interior of the cell. An interesting species is *B. trisecta* from the Carboniferous period, Illinois, USA (Mamay & Andrews 1950). The secretory cells form a layer, several cell wide, on the border between the inner and outer cortex. These cells are filled with a secretion. When the strand is dividing, these cells accompany these divisions, too (Pl. 4 fig. 13, loc. cit.), but they do not adhere closely to the strand. Worth mentioning is however the occurance of the thin strip around the strands (the authors do not report the number of cells) of endoderm, the whose cells are filled with a secretion, similarly as the secretory cells. In this position in *P. szaferi* there are the secretory cells.

Similar endodermal cells, filled with a secretion, around protostele are in *B. dichotoma* from Westfal (Upper Carbon), of Belgium (Holmes & Galtier 1983). It seems, basing on Pl. 2 fig. 123 (loc. cit), that the endoderm consists of 1–3 layers of cells. The secretory cells have formed however a wider strip in the inner part of the cortex. Pl. 3 fig. 4 (loc. cit.) is interesting, showing the secretory cells in the neighbourhood of xylem, similarly as in *P. szaferi*.

The filled with secretion endodermal cells are also present in *Psalixochlaena cylindrica* from Westfal (Upper Carboniferous period) of England (Holmes 1977). This single layer endoderm is filled up with secretion in older axes (Pl. 2 figs 3, 9, loc. cit.).

The secretory cells in inner layers of the cortex have been also found in the representative of the paleozoic family *Zygopteridaceae Grammatopteris* (Sahni 1932).

The occurance of the filled with secretion endoderm around the strands will allow to discuss its role in the anatomical structure.

## DISCUSSION

Although the anatomical data obtained for the vascular strand in *P. szaferi* are incomplete, because of the lack of more sections on the different levels of branchings of the

axes, they are still comparable with other mentioned species of the genus *Psilophyton* and convince that the anatomy of the strand, being an endarch protostele, is relatively uniform in this genus. The endarch, protostelic strand have also rhyniophytes, and their representative *Rhynia gwynne-vaughani* (Kidston & Lang 1920, Edwards 1986), but its strand is of relatively small diameter, in comparison to the strand in *P. szaferi* and other species of this genus. In the genus *Psilophyton* this strand is more massive and fills up a considerable part of the axis (1/3 of the plant axis). The further anatomical specialization in the genus *Psilophyton*, in relation to *Rhynia*, is visible in the structure of tracheids. Tracheids in *Rhynia* have the more primitive with annular thickenings, cristall-like walls, while in *P. szaferi*, *P. dawsonii*, *P. crenulatum* and *P. coniculum* they are scalariform, with pitting between the thickenings.

Observing the structure of vascular strands on various levels of branchings of the axes in the genus *Psilophyton* and their changing structure, we have found the morphological variety of branchings. The evolution of the vegetative and fertile branching systems towards increasing variety is visible in comparison to *Rhynia*. In this series of variability *P. szaferi* is an intermediate, less advanced form (Fig. 21, Zdebska 1986) in respect to the one represented by the multiple branchings of axes in *P. dawsonii* and *P. crenulatum*.

The genus *Psilophyton* is a good basis for comparison with other plants, namely with the primitive ferns of the order *Coenopteridales*, which may be derived from trimerophytes. This derivation is drawn from the fact that the leaves of these ferns are weakly distinguishable from the axis, which resembles the branchings in trimerophytes (Holmes 1989). There is a large regularity in repeating the branchings in several ferns, like for instance in *Botryopteris dichotoma* (Holmes & Gultier 1983), or *Psalixochlaena cylindrica* (Holmes 1977, Doran 1980). This is another character of trimerophytes.

The analysis of the vascular strands structure allowed for concluding which branchings could develop in the fern leaves. The most numerous data were found in *P. dawsonii* (Banks et al. 1975) and *P. crenulatum* (Doran 1980), which have multiple systems of lateral branchings. The analysis showed that the terminal systems of branchings could be the precursors of the leaves of primitive ferns, and further of the leaves of modern ferns. *P. szaferi*, with its dichotomic, monopodial and infrequently trifurcated branchings of axes confirms this evolutionary line, being an intermediate form in this evolutionary series.

Another interesting fact, which allows to discuss whether trimerophytes are ferns precursors basing on *P. szaferi*, is the similarity between the anatomical structure of its axis with the anatomical structure of axes in ferns of the order *Coenopteridales*. The characteristic feature of these ferns is the protostelic strand, around which there are secretory cells in many species (Ogura 1977, Fahn 1979), similarly as in *P. szaferi*. This element of the ferns axis structure is characteristic for them and draws attention.

The modern investigations on plants, which have secretory cells, show that the occurance of secretory cells is a results of the plant adaptation to the surrounding environment. They indicate that the plant is adapted to the edaphic and climate conditions (Fahn 1979). In the evolutionary development of the secretory cells, their primitive type make single secretory cells or their groups occurring between the tissues of mesophyll, in the

contact with the vascular strands. Their evolutionary development was further directed to formation of the more specialized structures, like secretory ducts, secretory cavities (Fahn 1979). Therefore, the occurance of secretory cells in *P. szaferi* would suggest that this plant was living in the environmental conditions different from that, which were on the places, from which have been derived the species described with the anatomical structure: *P. forbessi*, *P. charientos*, *P. crenulatum*, *P. dawsonii* and *P. coniculum*. They were described from the different, but closely located places from Lower Devonian of the Gospé Peninsula in Canada, while *P. szaferi* comes from the Lower Devonian in the middle Europe.

The secretory cells in *P. szaferi* surround closely the vascular strand and are located in the place where there is endoderm in some ferns. This fact is worth stressing and emphasizing in view of new look at the character of endoderm (van Feet 1961).

Endoderm (according to the older definition) is a layer of single cells, distinguishing in the structure of cell wall, often with thickenings, so called Caspary strips, or it may take a form of so called starch sheath (Esau 1973).

New investigations showed that endoderm has no morphological importance and its presence is a result of reactions, proceeding at the border between the vascular system and cortex. That means it is a results of reactions proceedings between substances present in the vascular system and in cortex cells (van Feet 1961). Van Feet (1961) proposed another, extended definition of endoderm. He has defined it as a layer or layers of cells between the vascular strand and the basic tissue (cortex), in which various chemical reactions proceed. These reactions reflect the environmental conditions and their activity may lead to morphological differentiation of the cells.

This statement seems to find its reflection in the anatomical structure of ferns axes, in the species in which the endoderm, filled with secretion substances is present (*Botryopteris trisecta* – Mamay & Andrews 1950, *B. dichotoma* – Holmes & Galtier 1983, *Psalixochlaena cylindrica* – Holmes 1977) and in the axes of *Psilophyton szaferi*, where the secretory cells occur in the position taken by endoderm in ferns. It may be assumed that the strip of secretory cells around the vascular strands in *P. szaferi* may have played a role of endoderm (according to the van Feet suggestion), separating the protostele from the remaining cells of the axis, as it occurs in the above mentioned primitive ferns. Thus, it would be a reaction to the environmental conditions, under which the plant was living.

Summarizing one may state that *P. szaferi*, together with other species of the genus *Psilophyton*, shows for great ductility of the representatives of trimerophytes. Significant evolutionary changes shown by these species in respect to rhyniophytes as well as the characters common with the primitive ferns of the order *Coenopteridales* indicate that it was a type of changes, which could have lead to development of ferns and their macrophyll leaves, as the result of further evolution.

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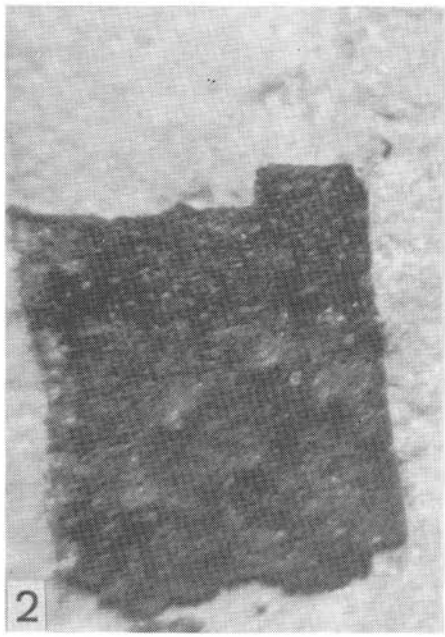
# PLATES

## Plate 1

*Psilophyton szaferi* Zdebska

1. Paratype. Fragment of axis with sporangia. S/99/2, × 0.63
2. Fragment of compression axis covered with rounded swellings. S/99/4, × 1.6
3. Fragment of impression axis showing horse-shoe like bases of rounnded swellings. S/99/4a, × 1.6
4. Fragment of comprepression axis with rounded swellings in marginal position. S/99/4, × 1.6


1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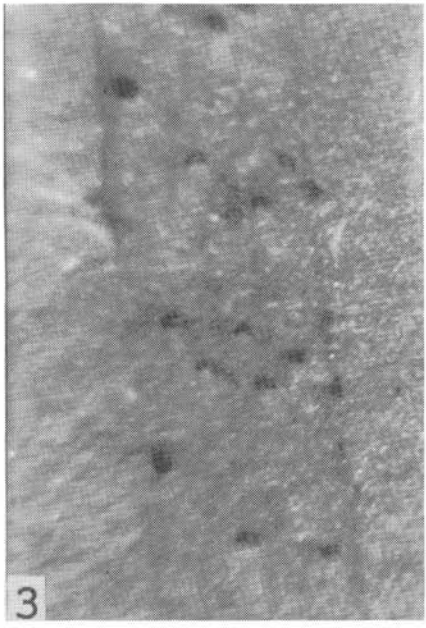
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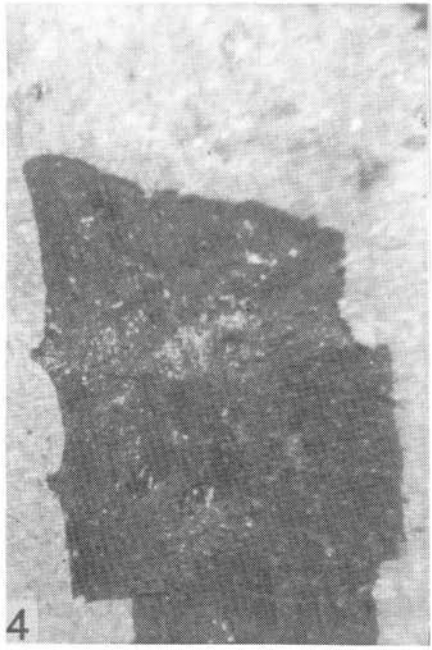
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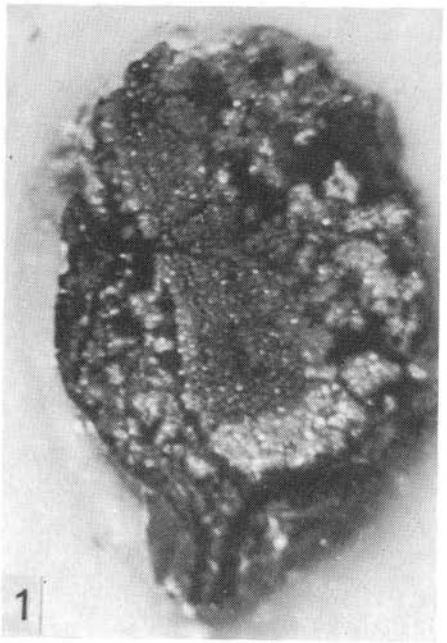
Plate 2

*Psilophyton szaferi* Zdebska

Transverse sections of pyritized axes showing stages of division of vascular strand below branching. × 1.6

1. specimen S/99/5a from Pl. 5 fig. 1
2. specimen S/99/5b from Pl. 6 fig. 1
3. specimen S/99/8 from Pl. 3 fig. 1
4. specimen S/99/11 from Pl. 8 fig. 1

Explanations: sc – secretory cells, px – protoxylem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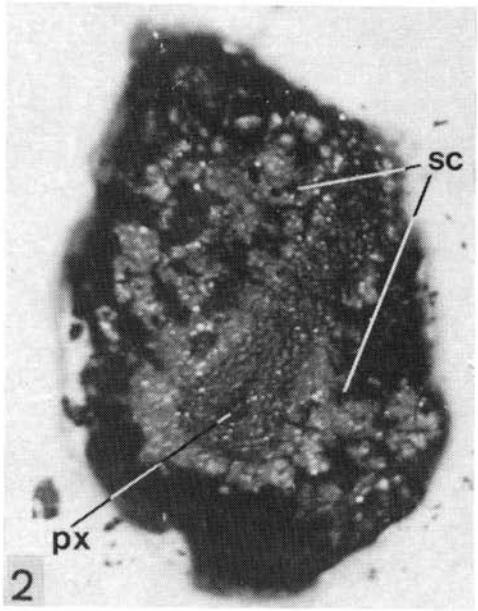
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px
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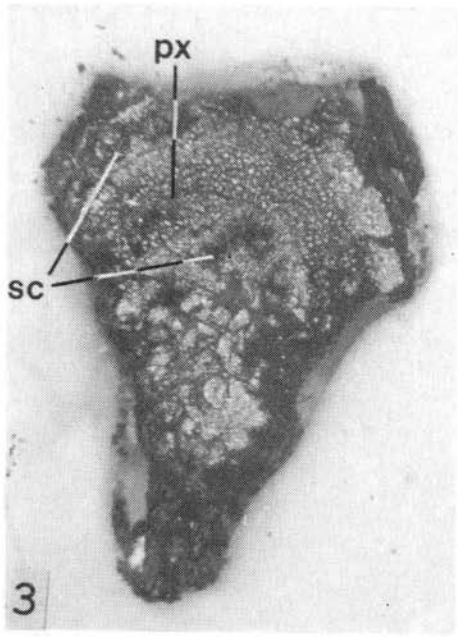
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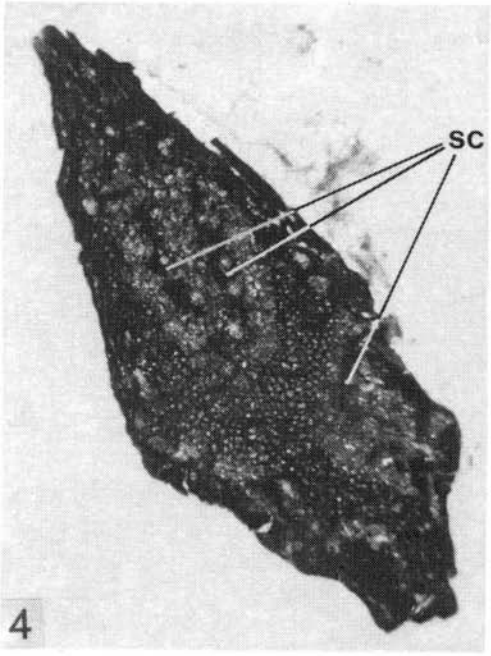
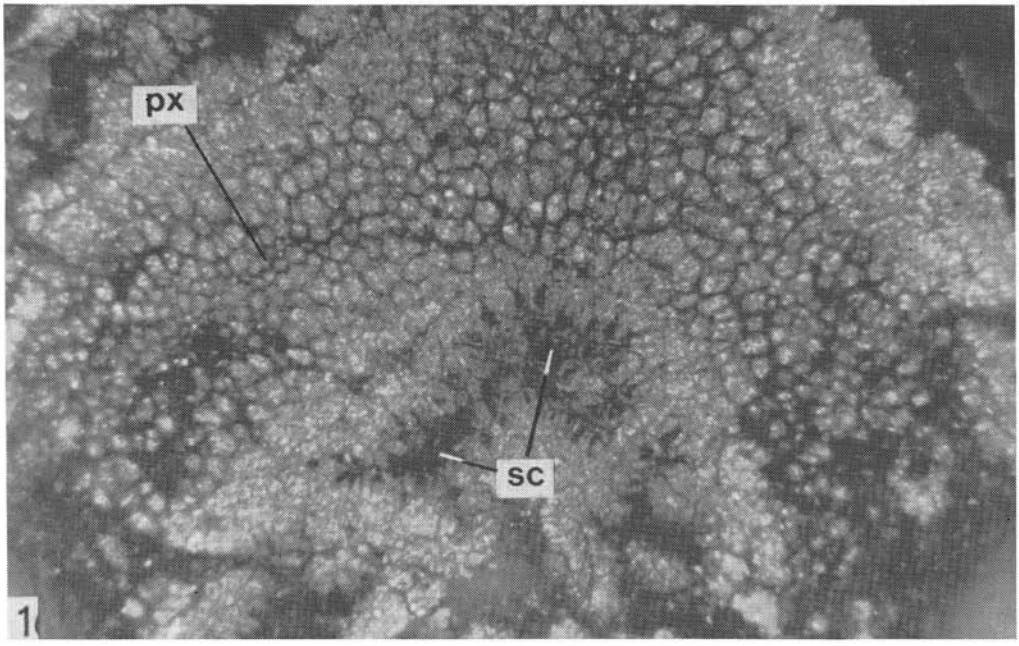

sc
4

Plate 3

*Psilophyton szaferi* Zdebska

1. Transverse section of axis showing a dividing vascular strand below branching and secretory cells. S/99/8, × 6.5
2. Fragment of vascular strand from fig. 1 showing secretory cells. × 12.5

Explanation on Pl. 2



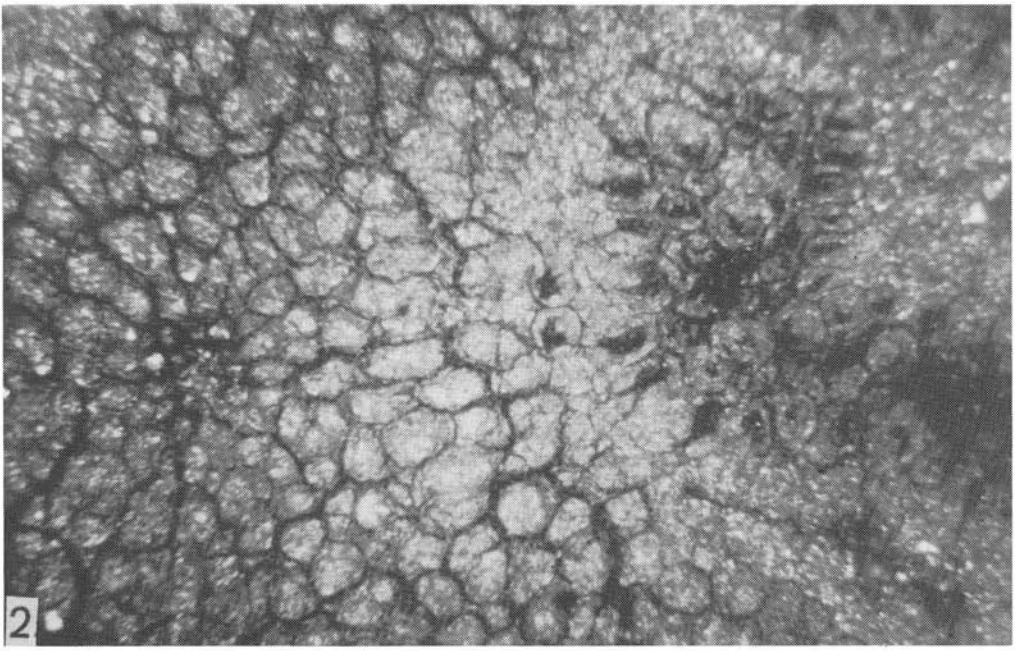




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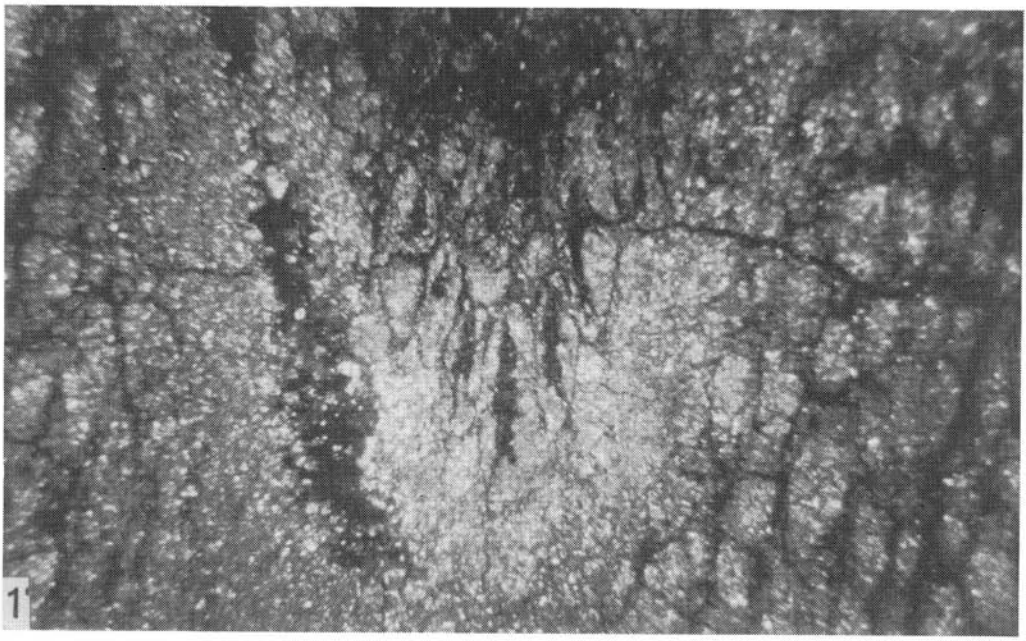
Plate 4

*Psilophyton szaferi* Zdebska

1. Longitudinal section of axis from Pl. 3 showing secretory cells with dark secretion inside and tracheids. S/99/8a, × 12.5
2. Transverse section of axis. Outside the metaxylem present a group of secretory cells. S/99/9, × 12.5



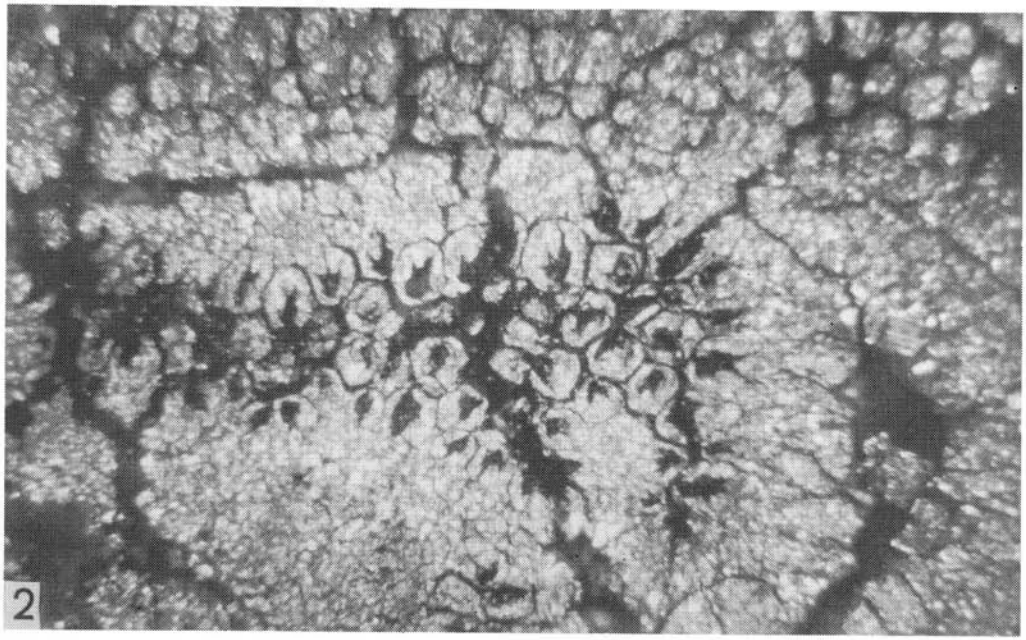




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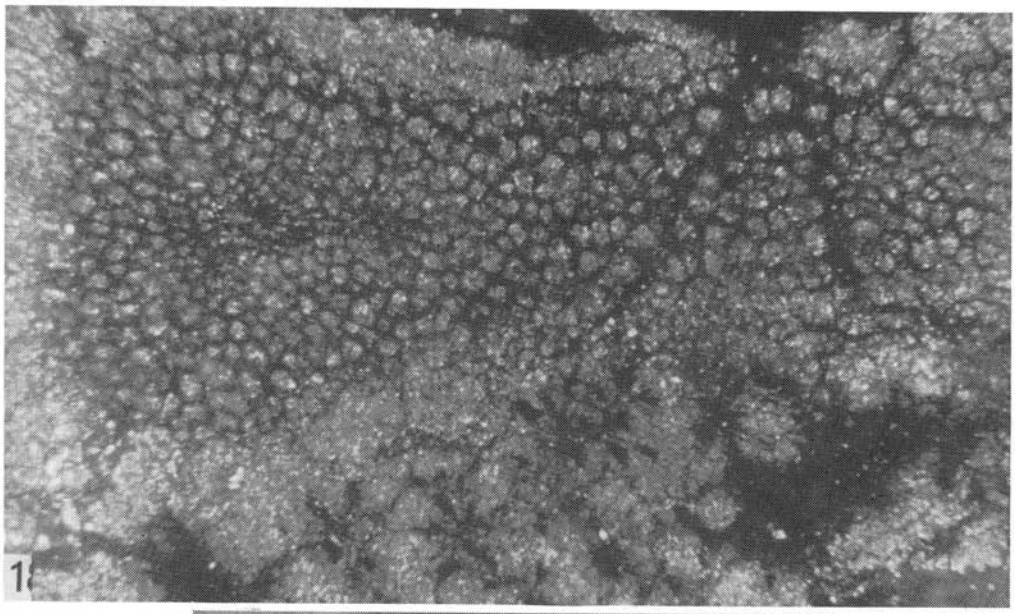
Plate 5

*Psilophyton szaferi* Zdebska

1. Transverse section of a dividing vascular strand below branching. Outside vascular strand present fragment of broken ring of secretory cells. S/99/5a, × 6.5
2. Longitudinal section of vascular strand from fig. 1 showing secretory cells and tracheids. × 12.5



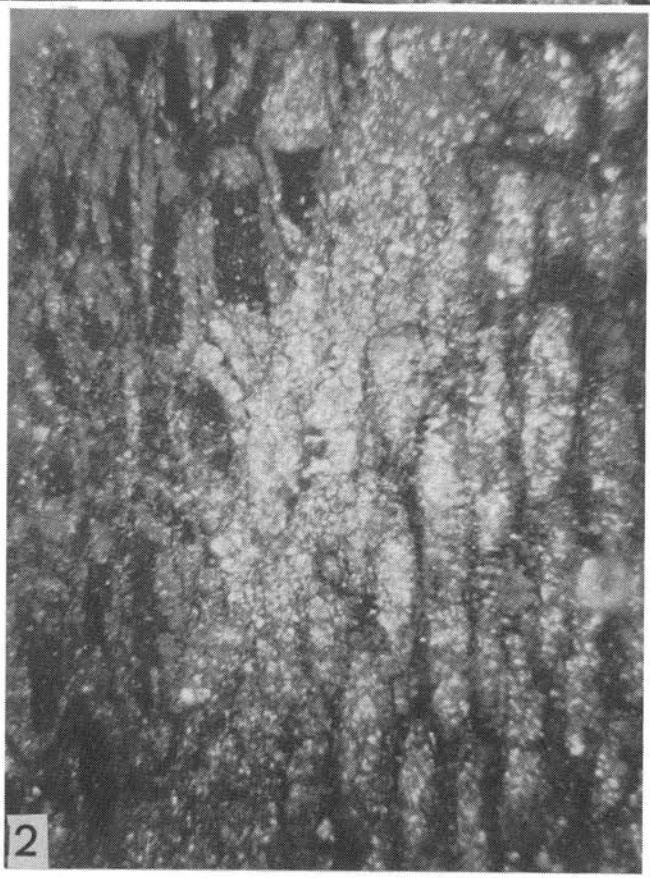


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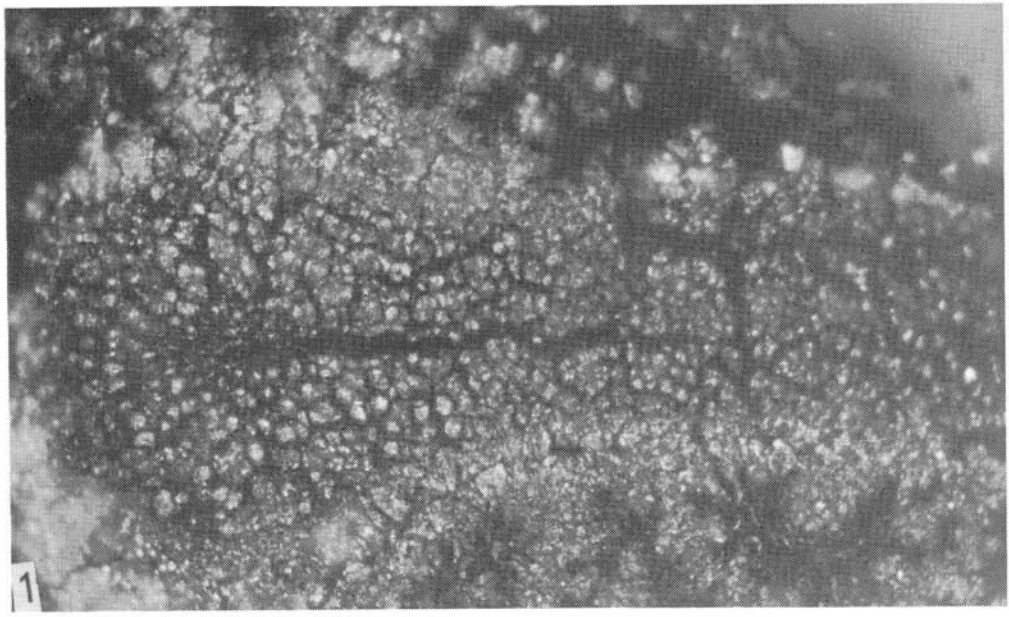
Plate 6

*Psilophyton szaferi* Zdebska

Transverse section of a dividing strand below branching at a higher level than the section visible on Pl. 5 fig. 1. S/99/5b, × 6.5

1. Seen from the side of the object glass of the preparation
2. Seen from the side of the cover glass of the preparation (section 0.5 mm thich)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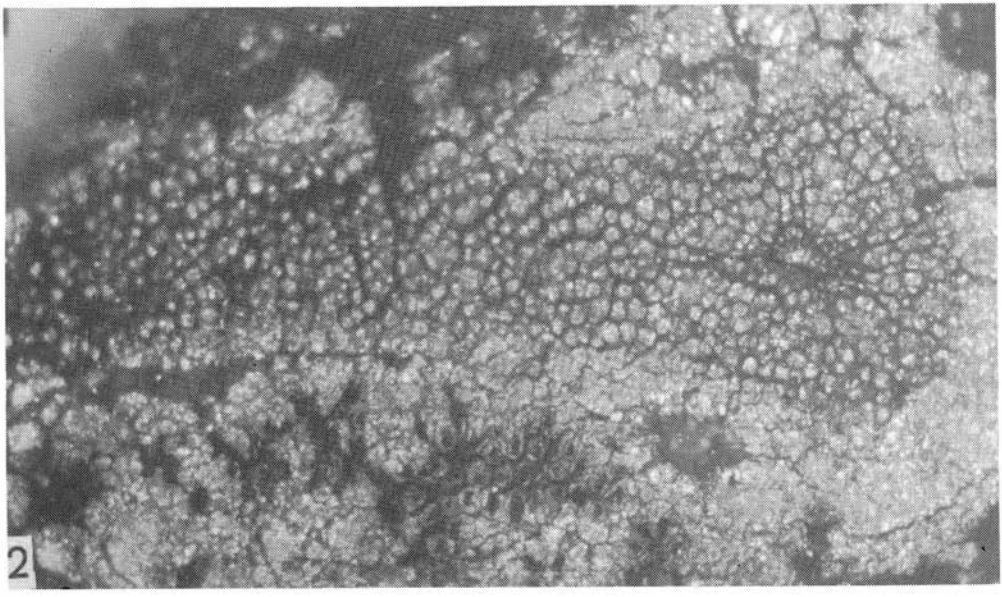
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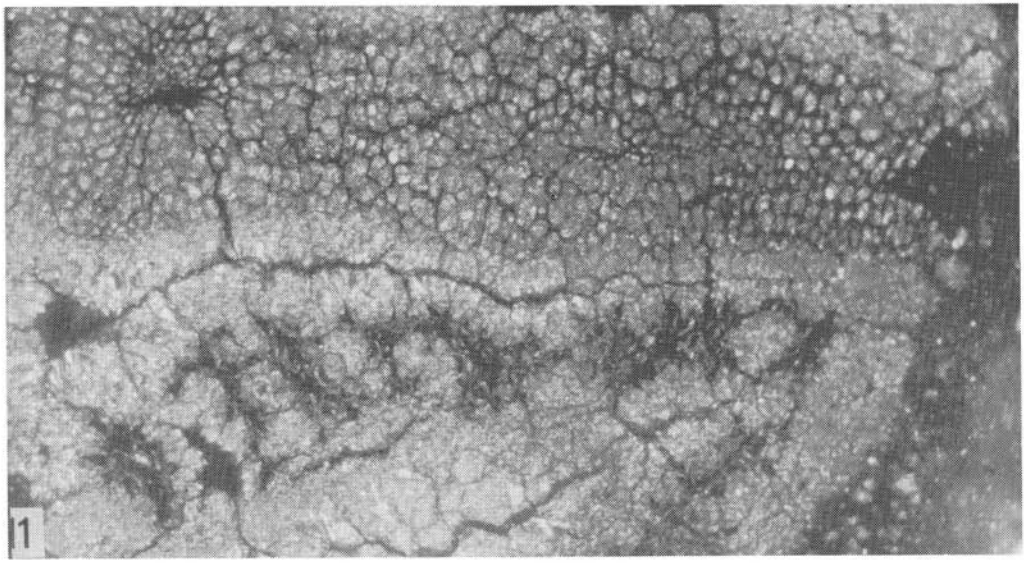
Plate 7

*Psilophyton szaferi* Zdebska

Transverse section of a dividing vascular strand below branching:

1. at a higher level than the section visible on Pl. 6. S/99/7, × 6.5
2. at a higher level than section visible on fig. 1. S/99/10, × 6.5



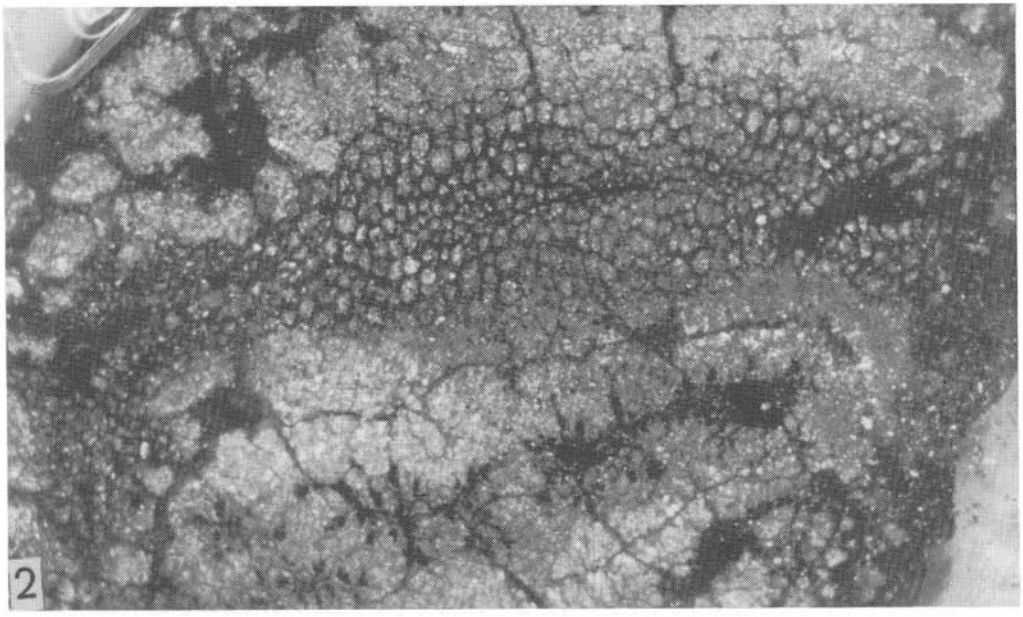




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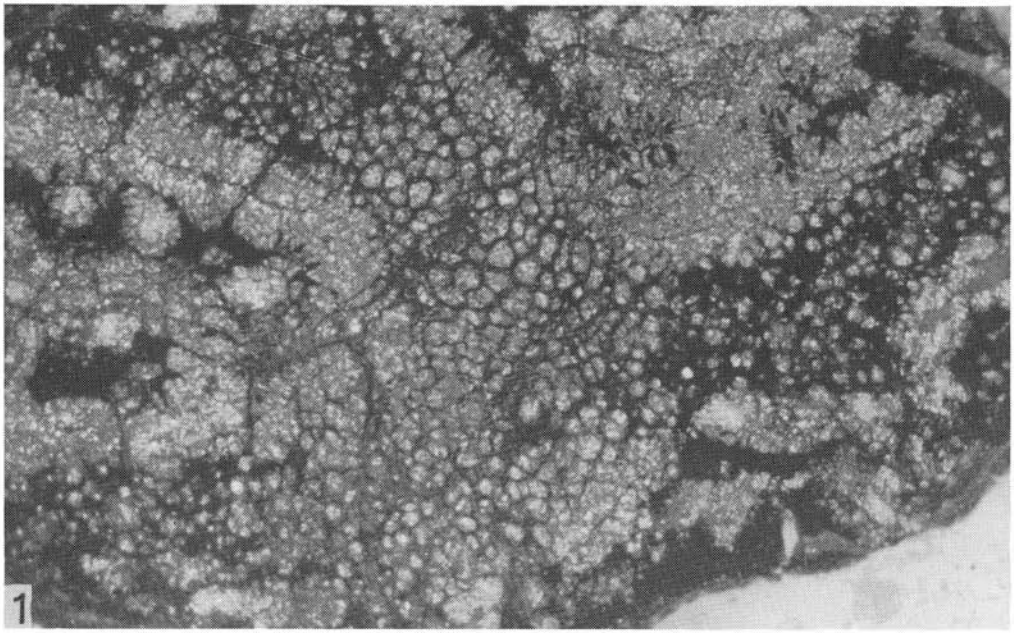
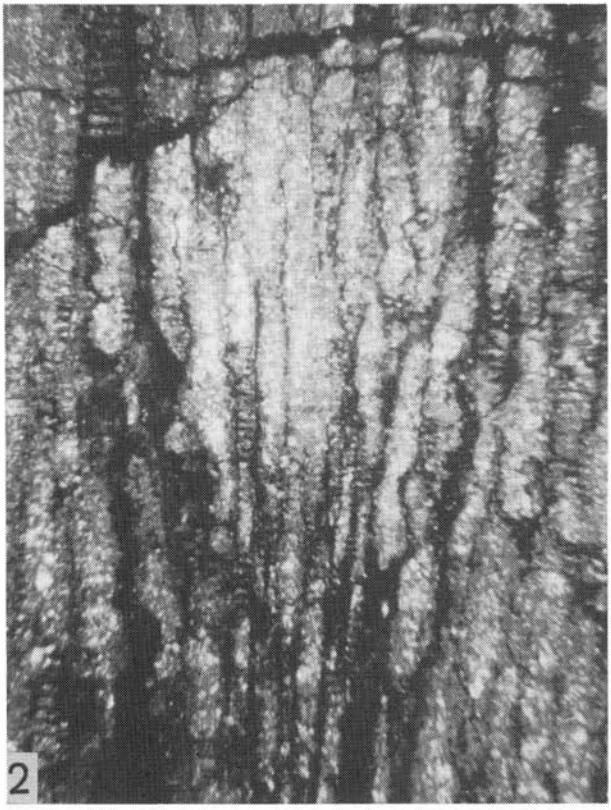
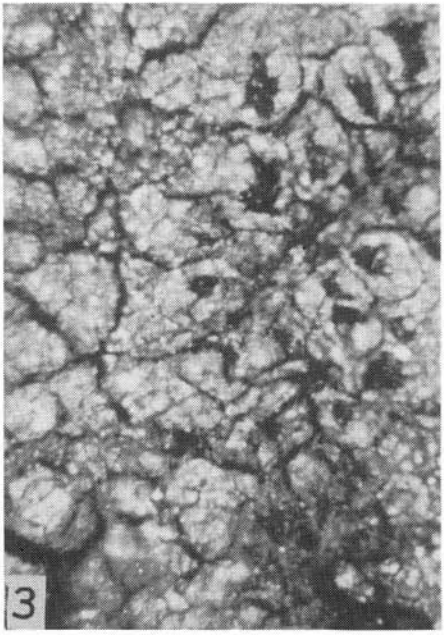
Plate 8

*Psilophyton szaferi* Zdebska

1. Transverse section of a dividing vascular strand below trifurcating branching. Vascular strand is surrounded by secretory cells. S/99/11, × 6.5
2. Longitudinal section of vascular strand showing protoxylem and metaxylem tracheids. Tracheids showing scalariform thickenings. S/99/12, × 12.5
3. Transverse section. Fragment from fig. 1 with secretory cells. × 12.5

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