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Psilophyton szaferi sp. nov. from the Lower Devonian of the Holy Cross Mountains, Poland

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Abstract

Philophyton szaferi sp. nov. belonging to the *Trimerophytina* was found in the Lower Devonian (Emsian) in the bore-hole Modrzewie 2A near Bostów in the Holy Cross Mountains (Góry Świętokrzyskie). The axes are sterile and fertile, their branching is dichotomous, unequally dichotomous and unequally dochotomous where the wider branch tends to form the main axis. The majority of axes branch in one plane, some in different planes; they show on their surface irregularly distributed enations in the form of rounded swellings. Some of them continue downwards as protruding ridges forming a characteristic longitudinal pattern. The apices of sterile axes are forking. Fertile axes end in clusters of fusiform, upright sporangia, arranged in pairs. The vascular strand shows protoxylem inside and metaxylem outside. Tracheids possess scalariform thickenings and what appear to be small pits between them. The systematic position of the plant and its position in the evolutionary sequence leading to megaphyllous leaves is discussed.

Key words: Lower Devonian, Psilophyton, morphology, anatomy, systematic position, megaphyllous leaf

INTRODUCTION

In the Holy Cross Mountains (Góry Świętokrzyskie) Devonian plants are known only from the western part of these mountains in Haliserites Beds (Czarnocki 1919).

The new species described in the present paper derives from the eastern part of the Holy Cross Mts., from beds recently discovered by Tymoteusz Wróblewski from the Geological Institute, Holy Cross Mountains Branch in Kielce. Those beds were found in the bore-hole Modrzewie 2A, near Bostów at a depth of 171.75 m (Wróblewski 1974).

Sandstones interspersed with grey claystones and siltstones with visible traces of sulphide mineralization and weathering occur in this profile.

On the basis of lithology and similarities with the Devonian beds of neighbouring areas, the age of the rocks in the bore-hole Modrzewie 2A has been determined as Lower Devonian — Emsian (Wróblewski 1974).

MATERIAL AND METHODS

Plant fragments represented by branching axes were found in grey claystone. Elliptical core fragments are about 15 cm long and 8 cm wide which limits the length of the plant fragments.

The axes are compressions or partly pyritized compressions. The flattened axes preserved as compressions are frequently crumbling and tend to fall off leaving on the rock impressions of axes, which are the most frequent type of material. Pyritized axes are slightly flattened and they show the cell structure on the broken surface. Such axes are brittle and easily disintegrate into single pyrite crystals.

As a result of such a type of fossilization it was not possible to use methods showing cell structure. Hydrofluoric acid and Schulze's solution destroyed compression fragments. Neither was it possible to make ground sections from pyritized axes because they crumbled during sectioning. To avoid crumbling of plant fragments they have to be kept in paraffin oil.

Nevertheless, certain details of plant structure were observed on impressions of axes, on the surface of fragments of compressions and on the broken surface of pyritized axes. On certain fragments of compressions outlines of epidermis cells were visible. The structure of pyritized axes was observed under paraffin oil on broken transverse and longitudinal surfaces of axes, because it was visible only under oil. For such observations a Carl-Zeiss, Jena reflected light microscope was used. It was not possible to use a scanning electron microscope, because during the coating process the plant material crumbled into very small pieces.

Photographs (Figs. 3-17) were taken with a reflected light microscope in the Department of Palaeobotany of the Institute of Botany of the Jagiellonian University.

SYSTEMATIC DESCRIPTION

Subdivision	*Trimerophytina* Banks 1968
Order	*Trimerophytales* Banks 1968
Family	*Trimerophytaceae* Banks 1968
Genus	*Psilophyton* Dawson 1859
Type species	*Psilophyton princeps* (Dawson) Hueber 1968

Psilophyton szaferi sp. nov.

Psilophyton szaferi occurs in the material as sterile and fertile axes. Their branching is dichotomous, unequally dichotomous and unequally dichotomous where the wider branch tends to form the main axis (Pl. I, 1-2, Pl. II, 3). The majority of axes branching in one plane, some in different planes. The distance between successive dichotomies is about 1.5-4.0 cm (Fig. 19). The width of the axes varies from 1.0 to 6.0 mm. The longest axis fragment is 12 cm, but the plant was certainly longer. The apices of sterile axes are forking, their ends form curved hooks (Pl. II, 6).

Typical for all types of axes are enations in the shape of small rounded swellings irregularly distributed on their surface, visible on the compression fragments (Pl. II, 3, 4; Pl. III, 7, 8). Their height is about 0.2-0.5 mm. They have acute or rounded apices. Certain swellings continue downwards forming a characteristic pattern of longitudinal discontinuous ribs on the surface of the axis (Pl. III, 7; Figs. 18, 19). Visible on the axes surface are bases of the rounded swellings remaining in the rock, in the form of circular or hocse-shoe like pits (Pl. III, 9, 10) and the ribs as delicate furrows.

In addition to the rounded swellings, the surface of the compressions shows outlines of epidermal cells (Pl. II, 4, 5), very distinct because of protruding anticlinal walls. The cells are narrow, elongated, their arrangement is parallel to the longitudinal axis of the branch, in dichotomies parallel to the angle of branching. The length of cells is from about 55 μm to 145 μm and their width from about 15 μm to 26 μm. It was not possible to observe stomata.

Two fragments of branching axes ending with sporangia (Pl. I, 2; Fig. 19) occur in the material. The lower parts of those axes are branched unequally dichotomously and those immediately below the sporangia appear to dichotonize in different planes. The sporangia are arranged in groups on the ends of the axes. They possess short stalks and appear to be standing in pairs (Pl. I, 2; Pl. III, 11, 12; Fig. 19). The sporangia are fusiform, with acute ends, 1.5-3.3 mm long and 0.8-1.1 mm wide (Pl. III, 11). The surface of the sporangium shows delicate, longitudinal ribs with small rounded swellings (Pl. III, 12). Unfortunately it was not possible to observe the dehiscence line of the sporangium, nor spores, either in the sporangia or near them on the rock.

Four of the flattened axes were pyritized and showed their internal structure, although the broken surface tends to crumble. On the transverse broken surface can be seen dark, coaly layer surrounding the axis. This layer is covered on the outside with epidermis showing rounded swellings. Below this dark layer are one or two layers of pyritized cells about 50-120 μm in diameter which can be interpreted as hypodermal cells, because on the longitudinal broken surface they are elongated and possess oblique transverse walls (Pl. IV, 14, 17). The vascular strand occurring inside the axis possesses a central protoxylem surrounded by the metaxylem (Pl. IV, 13). The tracheids are isodiametric in transverse section. The protoxylem tracheids are about 15-45 μm in diameter, the metaxylem tracheids about 55-76 μm in diameter. On the longitudinal broken surface of the axes scalariform thickenings of the tracheids are visible. It appears that small pits may be present between them, but this is not certain because pyrite crystals obscure the structure (Pl. IV, 15, 16).

RECONSTRUCTION OF *PSILOPHYTON SZAFERI*

The reconstruction of the plant was carried out by linking together the fragments of axes found separately. They all show the rounded swellings as the common character occurring on each fragment.

PSILOPHYTON SZAFERI SP. NOV.

Pl. I-IV, Figs. 18-20

Diagnosis. Axes 1.0-6.0 mm wide, their branching is dichotomous, unequally dichotomous and unequally dichotomous where the wider branch tends to form the main axis; branching in one plane or in different planes. Sterile branches forking, their ends form curved hooks. Surface

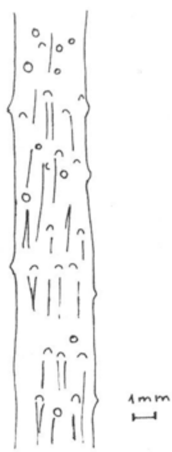

Fig. 18. Fragment of impression axis with bases of rounded swellings seen as small circles or horse-shoes continuing as ribs. S/99

of all axes showing irregularly distributed enations in the shape of small rounded swellings and ribs, 0.2-0.5 mm high. Bases of rounded swellings seen on impressions as small circles or horse-shoes. Surface of axes

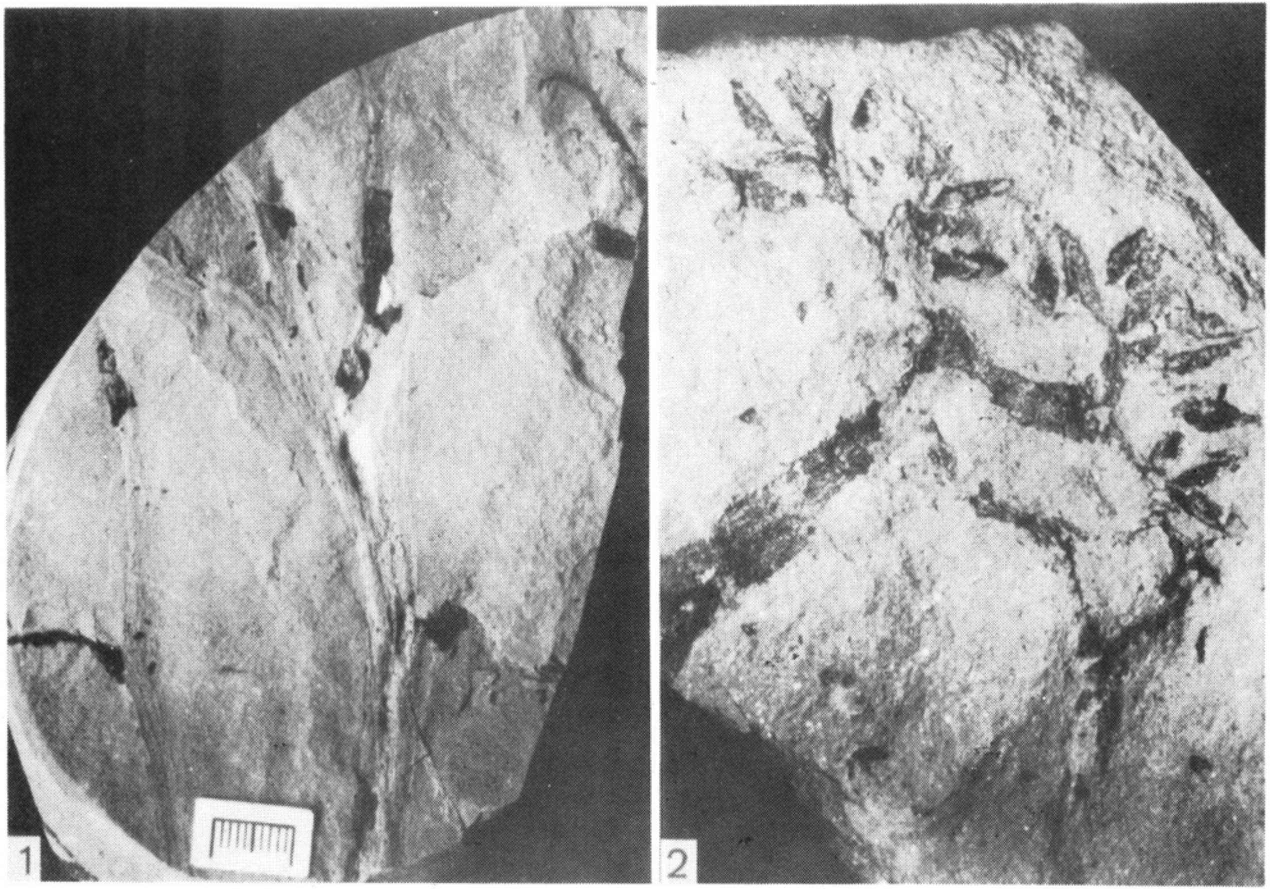

Fig. 1. Axes with branches. S/99/3, scale is 1 cm. Fig. 2. Holotype, axes with fusiform sporangia. S/99/1, ×6.5. (Photographs were taken by T. Wróblewski)

PLATE II

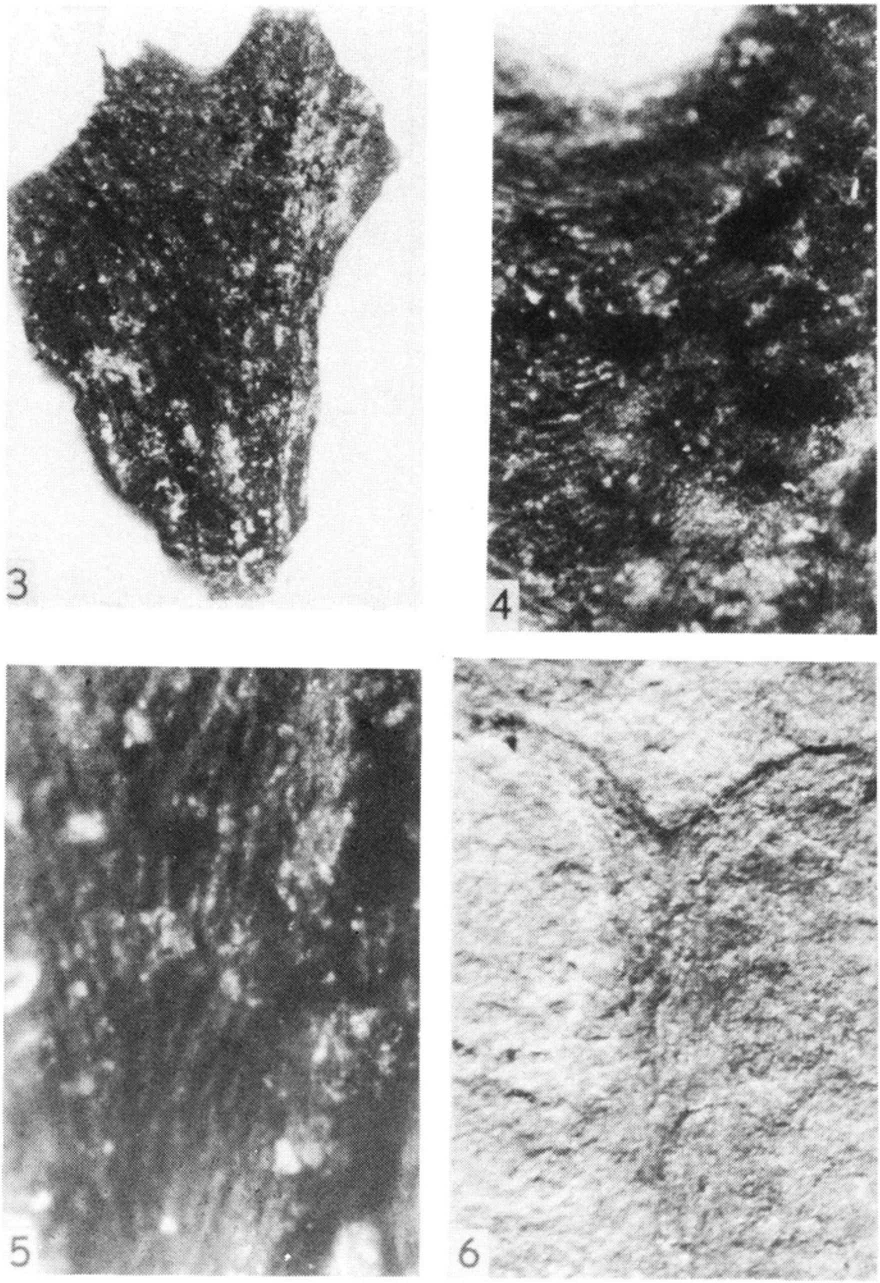

Fig. 3. Paratype, fragment of axis with branch. Surface showing rounded swellings and ribs. S/99/5, ×9.5. Fig. 4. Surface of axis from Fig. 3 (paratype) showing rounded swellings and cells of epidermis, ×40. Fig. 5. Surface of axis from Fig. 3 (paratype) showing elongated cells of epidermis, ×90. Fig. 6. Paratype, sterile branches forking on end. S/99/2, ×7

PLATE III

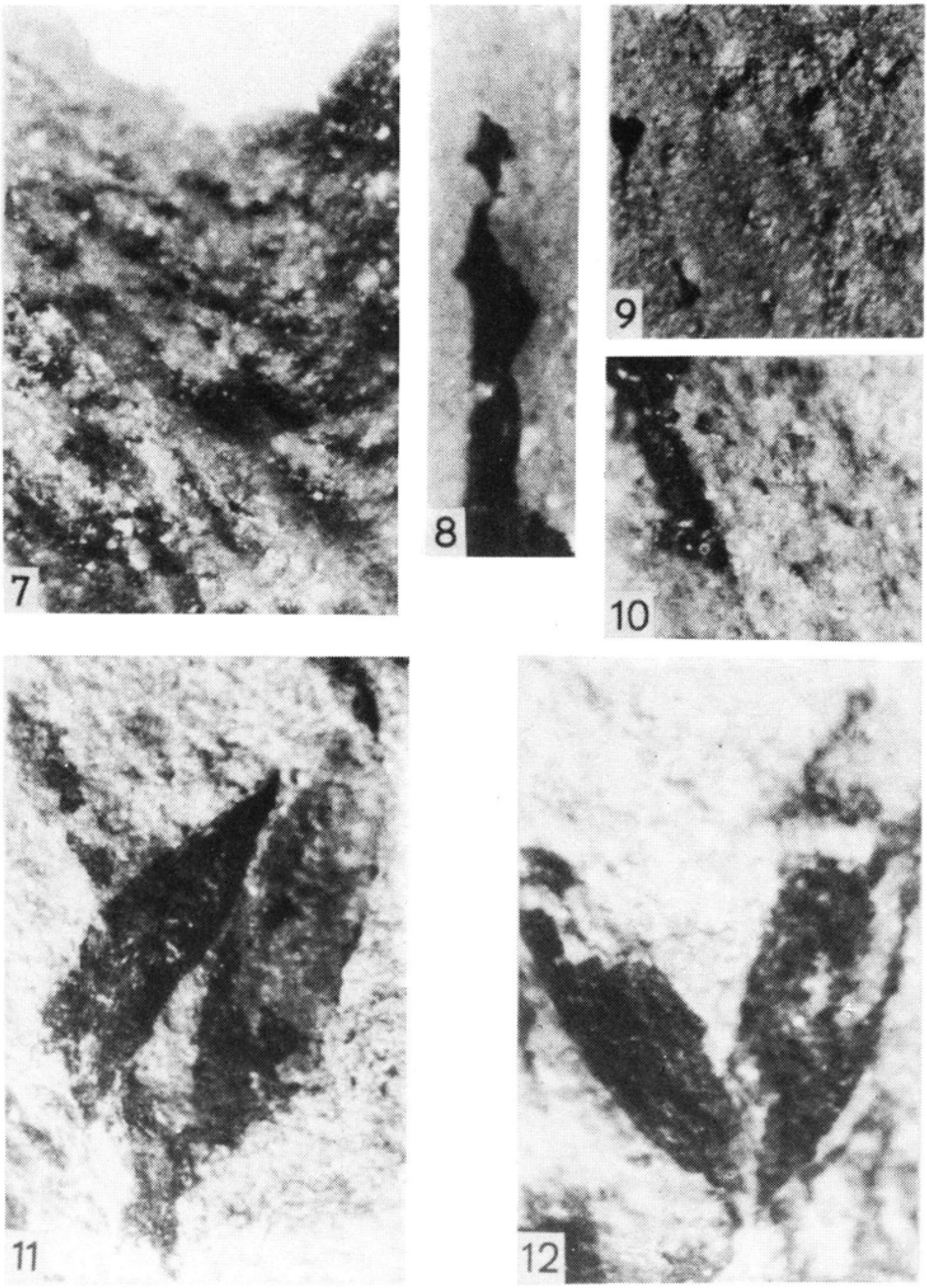

Fig. 7. Surface of axis showing rounded swellings with ribs. S/99/6, ×40. Fig. 8. Fragment of compression axis with two rounded swellings in marginal position. S/99, ×6. Fig. 9. Surface of impression axis showing bases of rounded swellings as small circles. S/99, ×10. Fig. 10. Fragment of surface of impression axis from Fig. 2 (holotype) showing bases of rounded swellings as horse-shoes, ×10. Fig. 11. Two sporangia with acute ends. S/99/1, ×15. Fig. 12. One pair of sporangia from Fig. 2 (holotype). Surface of sporangium (on left) showing delicate ribs and very small rounded swellings, ×15

PLATE IV

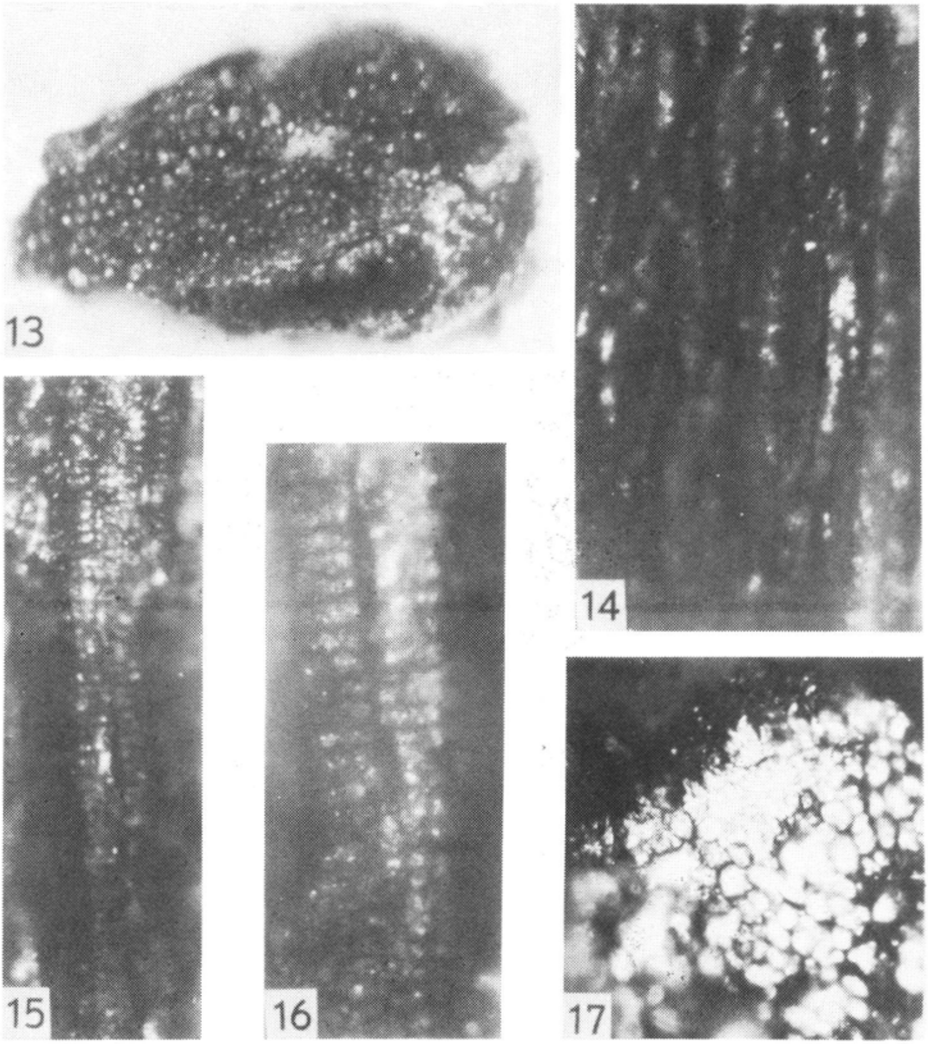

Fig. 13. Paratype, fragment of flattened transverse broken surface of axis showing vascular strand with protoxylem inside and metaxylem outside. S/99. × 30 Fig. 14. Cells of hypodermis in longitudinal broken surface of axis. S/99, × 140 Fig. 15. Metaxylem and protoxylem in longitudinal broken surface showing scalariform tracheids. S/99. × 150 Fig. 16. Metaxylem showing scalariform thickenings and? small pits between them in longitudinal broken surface. S/99, × 220 Fig. 17. Transverse broken surface of axis showing a black, coalified outer layer below the layer of cells which represent the hypodermis and inside the xylem strand with mataxylem outside and protoxylem inside. S/99. × 150

shows elongated cells about 15-26 μm wide. Xylem strand with protoxylem inside and metaxylem outside. Tracheids with scalariform thickenings and between them? small pits. Fertile unequally dichotomous branches terminating apparently in pairs of fusiform sporangia, details of their arrangement not known. Sporangia stalked 1.5-3.3 mm long, 0.8-1.1 mm wide. Surface of sporangium showing delicate ribs and very small rounded swellings. Spores unknown.

Horizon. Lower Devonian, Emsian

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

Holotype: S/99/1, Pl. I, 2, Pl. III, 10, 12. Paratype: S/99, Pl. IV, 13, S/99/2, Pl. II, 6, Fig. 19, S/99/3, Pl. II, 3, 4, 5. All specimens are deposited in the Palaeobotanical Museum of Institute of Botany, Jagiellonian University, Kraków, 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.

DISCUSSION

1. Comparison. In determining the systematic position of *Psilophyton szaferi* and attributing it to *Trimerophytina*, I followed the classification of Banks (1968, 1975). *P. szaferi* shows such characteristic features for the *Trimerophytina* as terminally borne groups of sporangia and the endarch strand. An important step in the understanding of the genus *Psilophyton* was the description of *P. dawsonii* by Banks et al. (1975), because this species possesses characters typical for the genus. The diagnosis of the genus *Psilophyton* emended by those authors was the basis for establishing the systematic position of *P. szaferi*. Generic characters shown by *P. szaferi* are unequal dichotomously and dichotomously branching axes, sporangia in groups born terminally and the endarch protostele.

Known in the genus *Psilophyton* are species with naked axes and species covered with enations. From the species with naked axes: *P. dawsonii* (Banks et al. 1975, Hartman and Banks 1980), *P. dapsile* (Kasper et al. 1974), *P. forbesii* (Andrews et al. 1968, Gensel 1979), *P. szaferi* differs in possessing enations in the form of rounded swellings. In addition, there are five other species of *Psilophyton* with axes covered with enations.

In 1859 Dawson described *P. princeps*, the diagnosis of which had been emended by Hueber (1968) and became the basis for descriptions of *P. princeps* from other localities. *P. princeps* is characterized by pseudo-monopodially branching axes covered with peg-like spines. Sporangia in terminal clusters are pendulous 7-8 mm long. *P. szaferi* differs from this species in having enations in the form of rounded swellings and upright sporangia 1.5-3.3 mm long.

P. szaferi is also different from *charientos* (Gensel 1979) which has pseudomonopodial axes, the main axis abudantly covered with delicate 2 mm long spines and pendulous sporangia 3.0-4.5 mm long.

P. szaferi is very different from *P. microspinosus* (Kasper et al. 1974, Andrews et al. 1977) which shows a distinct main axis with slender

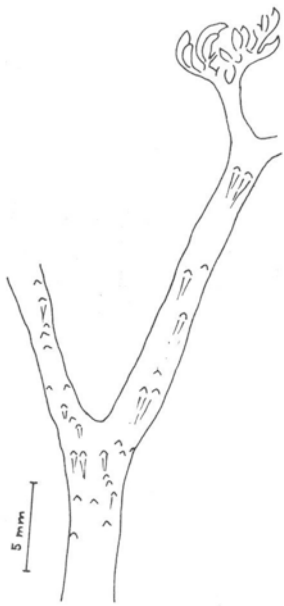

Fig. 19. Paratype, fragment of axis with sporangia. S/99/2

lateral sterile and fertile axes which are dichotomously branched. The axes show sparsely distributed needle-like enations, while *P. szaferi* is unequal dichotomously branched and covered with swellings.

The least known species is *P. kräuseli* (Obrhel 1959), characterized by hair-like enations and 2.0-2.2 mm long sporangia. *P. szaferi* is different in having sporangia 1.0-3.3 mm long and enations in the form of swellings.

The best preserved and therefore very well known species is *P. crenulatum* (Doran 1980). It shows pseudomonopodially or dichotomously branching axes covered with 6.0 mm long bifurcate or trifurcate spines and rounded 0.1 mm long crenulations. In *P. szaferi* the axes are covered only with 0.2-0.5 mm long swellings which are rounded or possess acute apices. In *P. crenulatum* the sporangia tips are pendulous while on *P. szaferi* they are facing upwards.

P. szaferi differs from all species of *Psilophyton* in possessing axes and sporangia covered only with rounded swellings. Some of them continue downwards forming a characteristic pattern on the impressions on the rock which in a way reminiscent of impressions of certain lycopod stems (Pl. III, 9, 10; Fig. 18).

2. Branching. The analysis of *P. szaferi* axes supplies data which may be entered into the discussion on the origin of megaphyllous leaves in plants. According to Kasper et al. (1974) and Banks (1980) the advanced type of branching in the genus *Psilophyton* is represented by species possessing a main axis and lateral branches. This type, as a result of evolutionary changes, might have led to the origin of leaves from lateral branches.

The primitive forms in the genus *Psilophyton* are represented by *P. dapsile* and *P. kräuseli* which mainly branch dichotomously. If so,

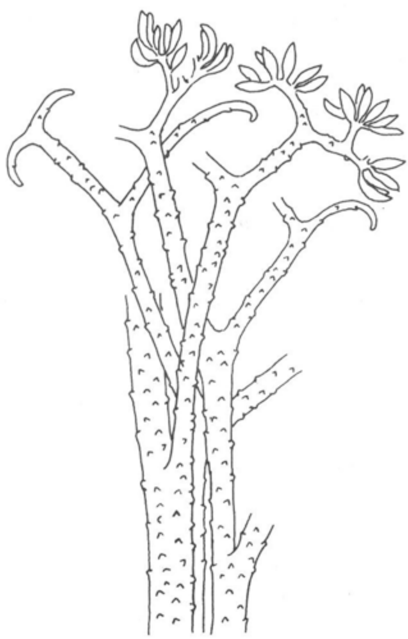

Fig. 20. Reconstruction of *Psilophyton szaferi*, about ×3

then *P. szaferi* is a more advanced form possessing dichotomous, unequally dichotomous and unequally dichotomous axes where the wider branch tends to form the main axis. *P. princeps*, *P. forbessii* and *P. microspinosum* are forms in which the main axis is already distinct but the lateral branches do not show such a variability as in the most advanced forms such as *P. dawsonii* and *P. crenulatum*. These two species possess a main axis systems of lateral branches. In particular the branches of *P. crenulatum* show that this type of branch could, as a result of evolution, lead to the origin of leaves of primitive ferns and progymnosperms. As a result, *P. szaferi* represents an intermediate form in this evolutionary sequence (Fig. 21).

3. Structure. The internal structure of axes is preserved in *P. szaferi*. Unfortunately, the small amount of material which easily disintegrates does not allow the role of the vascular strand of *Psilophyton* in evolution to be discussed. It is accepted that the representatives of the *Trimerophytina*

Fig. 21. Evolutionary sequence of the megaphyllous leaf. Based on Kasper et al. (1974) and expanded. A — *Psilophyton dapsile*. B — *P. szaferi*. C — *P. micropinosum*. D — *P. dawsonii*

were precursors in the evolutionary sequence leading to primitive ferns and *Progymnospermopsida* (Banks 1968, 1980, Doran 1980). The structure of tracheids in *P. szaferi* is not clear because it cannot be observed with certainty whether they possess scalariform bordered pits.

In general, the structure of the axis is similar to that of *P. dawsonii*. It will be possible to discuss it when more material is available.

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Psilophyton szaferi sp. nov. — nowy gatunek z dolnego dewonu Gór Świętokrzyskich

Streszczenie

Podgromada	*Trimerophytina* Banks 1968
Rząd	*Trimerophytales* Banks 1968
Rodzina	*Trimerophytaceae* Banks 1968
Rodzaj	*Psilophyton* Dawson 1859
Typ gatunku	*Psilophyton princeps* (Dawson) Hueber 1968

Psilophyton szaferi sp. nov.
Pl. I-IV, Figs. 18-20

Diagnoza. Pędy 1,0-6,0 mm szerokości rozgałęziające się w jednej lub różnych płaszczyznach. Rozgałęzienia o równej lub nierównej dichotomii wykazują tendencję do tworzenia pędu głównego (Pl. I, 1; Pl. II, 3; Fig. 20). Płonne pędy zakończone są hakowato (Pl. II, 6). Powierzchnia wszystkich pędów pokryta jest nieregularnie rozmieszczonymi emergencjami w postaci papilli, od 0,2 do 0,5 mm wysokimi (Pl. II, 3, 4; Pl. III, 7, 8). Nasady papilli są w zarysie okrągłe lub podkowiaste (Pl. III, 9, 10). Wiązka przewodząca jest typu endarchicznego, tzn. że protoxylem jest wewnątrz a metaxylem na zewnątrz wiązki (Pl. IV, 13, 17). Tracheidy mają drabinkowate zgrubienia, między którymi występują prawdopodobnie jamki (Pl. IV, 15, 16). Wrzecionowate zarodnie, 1.5-3.3 mm długie i 0.8-1.1 mm szerokie, występują na końcach dichotomicznie rozgałęzionych pędów (Pl. I, 2; Fig. 19). Powierzchnia zarodni jest delikatnie żeberkowana i pokryta papillami (Pl. III, 12).

Psilophyton szaferi został opisany z dolnego dwonu (ems) z wiercenia Modrzewie 2A koło Bostowa w Górach Świętokrzyskich. Roślina zachowała się w postaci uwęglonych i spirytyzowanych fragmentów rozgałęzionych pędów. Opisane cechy rośliny odpowiadają cechom rodzaju *Psilophyton*, w obrębie którego występuje szereg gatunków z emergencjami i bez emergencji. Od wszystkich opisanych gatunków *Psilophyton*, *P. szaferi* odróżnia się występowaniem emergencji w postaci papilli.

Analiza pędów *P. szaferi* pozwoliła nawiązać do dyskusji o powstaniu liści u roślin. Opiera się ona na analizie zróżnicowanych rozgałęzień w obrębie rodzaju *Psilophyton*, których bardziej zaawansowanym typem jest ten reprezentowany przez gatunki mające wyraźny pęd główny i boczne rozgałęzienia. Ten typ, w rezultacie zmian ewolucyjnych, mógł doprowadzić do powstania liści. *P. szaferi* reprezentuje formę pośrednią w szeregu ewolucyjnym doprowadzającym do powstawania liści prymitywnych paproci i roślin z podgromady *Progymnospermopsida* (Fig. 21). Można stwierdzić, że opisany nowy gatunek *P. szaferi* potwierdza słuszność wysuwanych koncepcji, które mówią, że *Trimerophytina* to grupa wyjściowa prymitywnych paproci i przedstawicieli podgromady *Progymnospermopsida* (Kasper et al. 1974, Banks 1980, Doran 1980).