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SAWDONIA ORNATA (= PSILOPHYTON PRINCEPS VAR. ORNATUM) FROM POLAND

Sawdonia ornata (= *Psilophyton princeps* var. *ornatum*) z Polski

ABSTRACT

Sawdonia ornata (Dawson) F. M. Hueber is described from a borehole at Opole Lubelskie. The material shows well preserved structure, but no sporangia. The structure of the plant agrees with that of *Psilophyton princeps* Dawson described by W. N. Edwards (1924) and Lang (1931) from Gaspé and with that of *Psilophyton* described by Lang (1932) from Scotland and *Psilophyton princeps* described by Hueber and Grierson (1961) from New York State and with that of *Sawdonia ornata* (Dawson) F. M. Hueber described by Hueber (1971).

The well preserved stomata are described in detail and a reconstruction of their transverse section is given. Above the guard cells there is a stomatal pit formed by raised projections of the anticlinal walls of the lateral subsidiary cells. The stoma is compared with those of other psilophytes and it appears to be very similar to that of *Zosterophyllum myretonianum* (Lele and Walton 1961) which suggests a closer affinity between these two plants.

CONTENTS

I. INTRODUCTION

The occurrence of psilophytes in Poland was known as early as 1919, when Czarnocki described the Devonian *Haliserites* Beds from the Holy Cross Mountains. Geological investigations during recent years, and that of deep boreholes in particular, showed that psilophytes occurred also in the Devonian of the Middle Sudetes, of the Radom-Lublin area and in the vicinity of Andrychów in the Carpathians. Short descriptions of these remains were given in the papers of Kuchciński (1964), Konior (1965), and Jakubowska (1968).

The material of *Sawdonia ornata* described in the present paper derives from a new locality near Opole Lubelskie (Lublin Upland, Eastern Poland). The plant remains are well preserved which enabled the description of the cuticle of the plant and the accurate establishment of its systematic position.

The work was carried out in the Palaeobotanical Department, Botanical Institute of the Polish Academy of Sciences, under the guidance of dr M. Reymanówna whom I would like to thank for advice and assistance. I am very grateful to prof. J. Dyakowska for her kind interest in my work and for helpful criticism, and to doc. R. Czapik for consultation. I wish to thank M. Sc. K. Mrozek for the material of *Sawdonia ornata*. To dr F. M. Hueber I am indebted for consultation concerning the name of the plant and to dr K. Alvin for the material of *Psilophyton princeps* var. *ornatum* from Gaspé.

The photographs were taken by eng. P. Nowak.

II. GEOLOGY OF THE LOWER DEVONIAN OF THE RADOM-LUBLIN AREA

During the last few years deep borings in the Radom-Lublin area revealed in some places the presence of Devonian strata reaching from the Frasnian to the Gedinian. According to Miłaczewski and Żelichowski (1970) the oldest Lower Devonian is represented by a loamy series with an abundant marine fauna which lead to the determination of this series as Gedinian. The Lower Siegenian is represented by a series of grey sandy siltstones in which Hajłasz (1968) determined the following *Tentaculites* which are index forms of the Siegenian: *Tentaculites gyrocanthus* Eaton., *T.* cfr. *attenuatus* Hall., *T.* cf. *antarcticus* Fischer *T. formosus* Hajłasz, *T. absimilis* Hajłasz, *T. mirabilis* Hajłasz.

In the whole area of the occurrence of the Devonian, the Upper Siegenian and Emsian are formed by the continental series of the Old Red which overlies marine sediments of the Lower Siegenian. This series contains no index fossils and its age can be determined only in an indirect

way. Organic remains rarely occur there: in the Ciepielów bore-hole they were found as well as casts of fin spines of *Macharocanthus* sp., bone plates of *Psammosteus* sp. which give evidence of its Emsian age. Ciepielów also yielded plant fragments of *Psilophyton goldschmidtii* Halle, *Dawsonites arcuatus* Halle, *Taeniocrada* sp., *Drepanophycus spinaeformis* Goeppert, *Sugambrophyton pilgeri Schmidt, Protolepidodendron* sp., *Sporogonites exuberans* Halle, *Hostinella* sp., *Aphyllopteris* sp. (Jakubowska 1968). According to Jakubowska (l.c.) these plant remains and the microspore analysis indicate the Lower Devonian age of this series.

The material described in this paper derives from the region of Opole Lubelskie, bore-hole OL-3, deph 1490,0—1493,0 m, from the Old Red facies of the Devonian. This age was established by M. Sc. K. Mrozek on the basis of the underlying Silurian strata dated by fauna.

III. MATERIAL AND METHODS

The plant material consisted of spiny axes preserved as compressions in dark-grey siltstone. In order to free the plants from the rock, the samples were placed in plastic containers with lids, and covered with hydrofluoric acid of commercial strength (38%) for 1—7 days, depending on the size of the sample. The free floating plant remains were frequently removed and washed on a plastic sieve, first with distilled water, then with tap water and finally with diluted ammonia, in orded to neutralize completely the acid. The so cleaned plant remains were kept for further inspection in Petri dishes in a mixture of water, alcohol and glycerine in proportion 1 : 1 : 1.

The material obtained in this way was of two kinds. Some plant fragments which had undergone natural maceration showed very clearly the cellular structure of the epidermis and hypodermis and in rare cases also of tracheids. Other plant fragments were dark and opaque and were therefore treated with macerating fluids. Of these the maceration with a commercial bleach „Bielinka" and maceration with nitric acid followed by ammonia gave no results. Only when Schulze's solution (concentrated nitric acid with potassium chlorate) followed by ammonia was used, cuticles with distinct cell walls were visible. However, in this macerated material the cuticles were much thinner and the cell outlines weaker than in the material from natural maceration. Therefore the description is based mainly on preparations from natural maceration. The entire comparative material from Gaspé had to be macerated in Schulze's solution and all these preparations also had a thin cuticle and weak cell outlines, as did the macerated material from Opole.

Larger fragments of axes were obtained when their surface was covered with a solution of cellulose nitrate in amyl acetate and left to dry before dissolving the rock in hydrofluoric acid.

The best plant fragments obtained in either way were embedded in glycerine jelly.

The Walton (1923) transfer method was used to obtain a preparation showing the surface of the axis with preserved protruding spines (Text-fig. 1, 1).

The material is deposited in the Palaeobotanical Department, Botanical Institute of the Polish Academy of Sciences, hand-specimens No 16, 18, slides No 15/1—15/12, 16/1—16/20, 17/1—17/39.

IV. SYSTEMATIC PART

SUBDIVISION ZOSTEROPHYLLOPHYTINA

Order **Zosterophyllales**

Family **Zosterophyllaceae**

Genus ***Sawdonia*** Hueber 1971

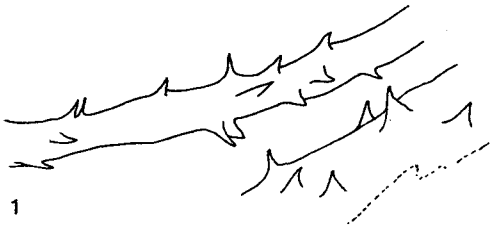
Sawdonia ornata (Dawson) F. M. Hueber 1971

Pl. I—VIII, Text-fig. 1—5

1871 *Psilophyton princeps* var. *ornatum* Dawson, P. 38; Pl. IX, fig. 101.
1924 *Psilophyton princeps* Dawson, W. N. Edwards, P. 377; Pl. 37, fig. 2, 3, 6, Text-fig. 1—5.
1931 *Psilophyton princeps* Dawson, Lang, P. 421; Pl. 27, fig. 2—8, 11.
1932 *Psilophyton*, Lang, P. 491; Pl. II, fig. 23, 32, Pl. III, fig. 43, 44, 46, 48, 60, Pl. IV, fig. 67—69; (but not Pl. II, fig. 17, 25—31).
1961 *Psilophyton princeps* Hueber and Grierson, P. 473; fig. 8—12.
1967 *Psilophyton princeps* Dawson, Höeg, P. 277; fig. 199 A, B, 201 B, D, E.
1967 *Psilophyton princeps* var. *ornatum* (non Dawson) Hueber and Banks, P. 81; fig. 8, 13.
1971 *Sawdonia ornata* (Dawson) F. M. Hueber, Hueber, P. 641.

Text-fig. 1. 1,2 — distribution of spines on axis; ×3, 1 — transfer 17/36, 2 — hand specimen 18, 3 — vascular strand in the form of a protruding band in the middle of axis; ×5,5 hand specimen 16, 4 — hair base; central cell with remains of periclinal walls; ×400, slide 17/7, 5 — papillae on surface of isodiametric epidermal cells; ×400, slide 16/1, 6 — epidermal cells without surface thickenings; ×400, slide 17/11, 7 — epidermal cells with cutinized ridges; ×800, slide 15/1

Ryc. 1. 1,2 — rozmieszczenie kolców na pędzie; ×3, 1 — preparat transfer 17/36, 2 — okaz 18, 3 — w środku pędu wiązka przewodząca w postaci wzniesionego pasemka; ×5,5 okaz 16, 4 — nasada włoska; centralna komórka z resztkami ściany peryklinalnej; ×400, preparat 17/7, 5 — papille na powierzchni izodiametrycznych komórek epidermy; ×400, preparat 16/1, 6 — komórki epidermy bez zgrubień na powierzchni; ×400, preparat 17/11, 7 — komórki epidermy z kutykularnymi grzebieniami; ×800, preparat 15/1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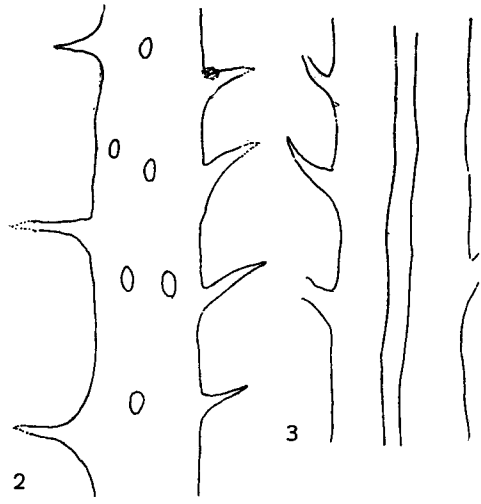
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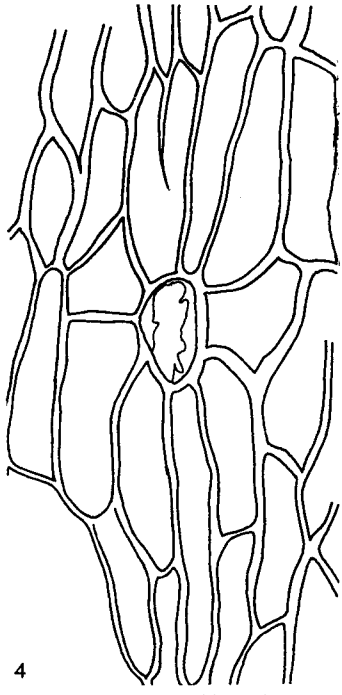
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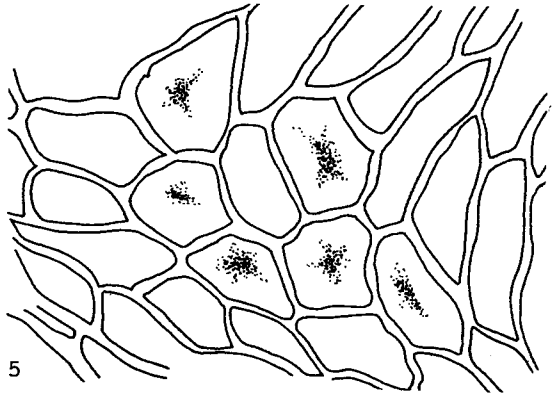
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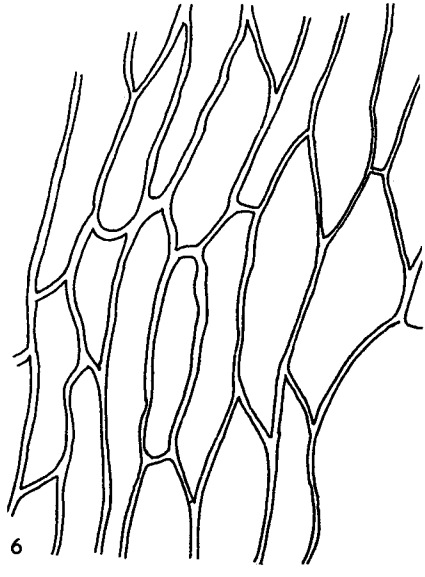
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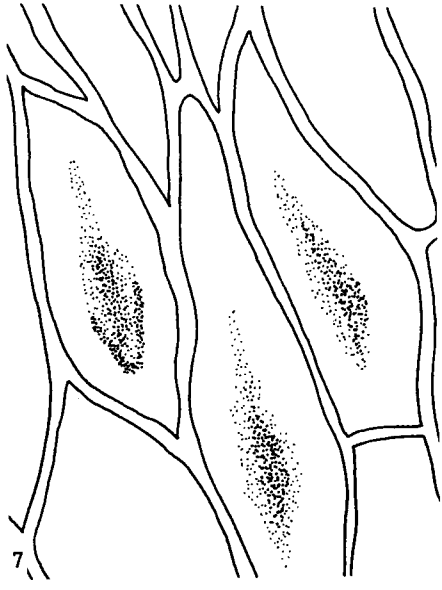
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DESCRIPTION

A x e s. Investigated fragments of axes up to 5 cm long, each of even width along the whole length. Width of axes from 1—3·3 mm. Only three branching axes present in material, all dichotomous and forming an acute angle between branches, width of branches almost equal. Spines on branches indistinct. Surface of certain axes showing delicate striation, possibly corresponding to cell walls of epidermis. In one axis the vascular strand visible in the middle as a slightly protruding band 0·6 mm wide (Text-fig. 1, 3).

Spines projecting from entire surface of axes, usually at an acute angle, rarely at a right angle. Spines arranged irregularly, often in groups (Pl. IV, fig. 3), exceptionally showing nearly spiral arrangement (Text-fig. 1, 2). On surface of hand-specimens only bases of broken spines visible in the form of little projections (of spines facing upwards, Pl. I), or in the form of small hollows with a dark dot in the middle (of spines facing inwards into the matrix). Spine bases oval or round in transverse section. Spines showing a considerable range of variation in length and width, their length being from 0·5 to 2·2 mm (3·4 mm) (Text-fig. 2, 1—14), the width of spine bases from 162 to 1200 μ. Spines showing also great variety of shape (Text-fig 2, 1—14). Most spines elongated and conical, tapering gradually from widened base towards apex which is never acute, or spines long and linear, or short and triangular, often constricted below apex. Apex (usually broken off) with a vesicular end (Pl. III, fig. 3, Pl. V, fig. 3), vesicle and part of spine below dark, as if filled with secretion, in damaged apices dark mass sticking out (Pl. III, fig. 2, Pl. IV, fig. 4). Spines without vascular strands and stomata, their epidermal cells lacking ridges and papillae. Epidermal cells of spines differing from those of axes in being elongated, narrower and in showing mainly oblique transverse end walls (Pl. V, fig. 2). Spine bases showing change from isodiametric cells into elongated ones where the epidermis of the axis merges into that of the spine.

E p i d e r m i s. Epidermal cells running parallel to axis, showing wide range of variation of shape and size over small areas. Most of them elongated, rectangular or with oblique end walls forming an acute angle with each other (Pl. IV, fig. 1). Usually near spine bases cells isodiametric (Pl. III, fig. 4). Length of cells form 42 to 228 μ, width from 15 to 66·6 μ. Anticlinal cell walls 1·2—6 μ thick, straight or slightly undulating, slightly

Text-fig. 2. 1—14 — spines showing variation in shape and size; regions filled with black substance indicated by solid black; ×50, slides: 15/2, 17/13, 17/3 16/2, 17/6, 17/5, 16/5, 17/4, 16/3, 17/1, 16/5, 16/4, 15/3, 15/4

Ryc. 2. 1—14 — zmienność kolców pod względem kształtu i wielkości; partie wypełnione ciemną substancją zaznaczone czarno; ×50, preparaty: 15/2, 17/13, 17/3, 16/2, 17/6, 17/5, 16/5, 17/4, 16/3, 17/1, 16/5, 16/4, 15/3, 15/4


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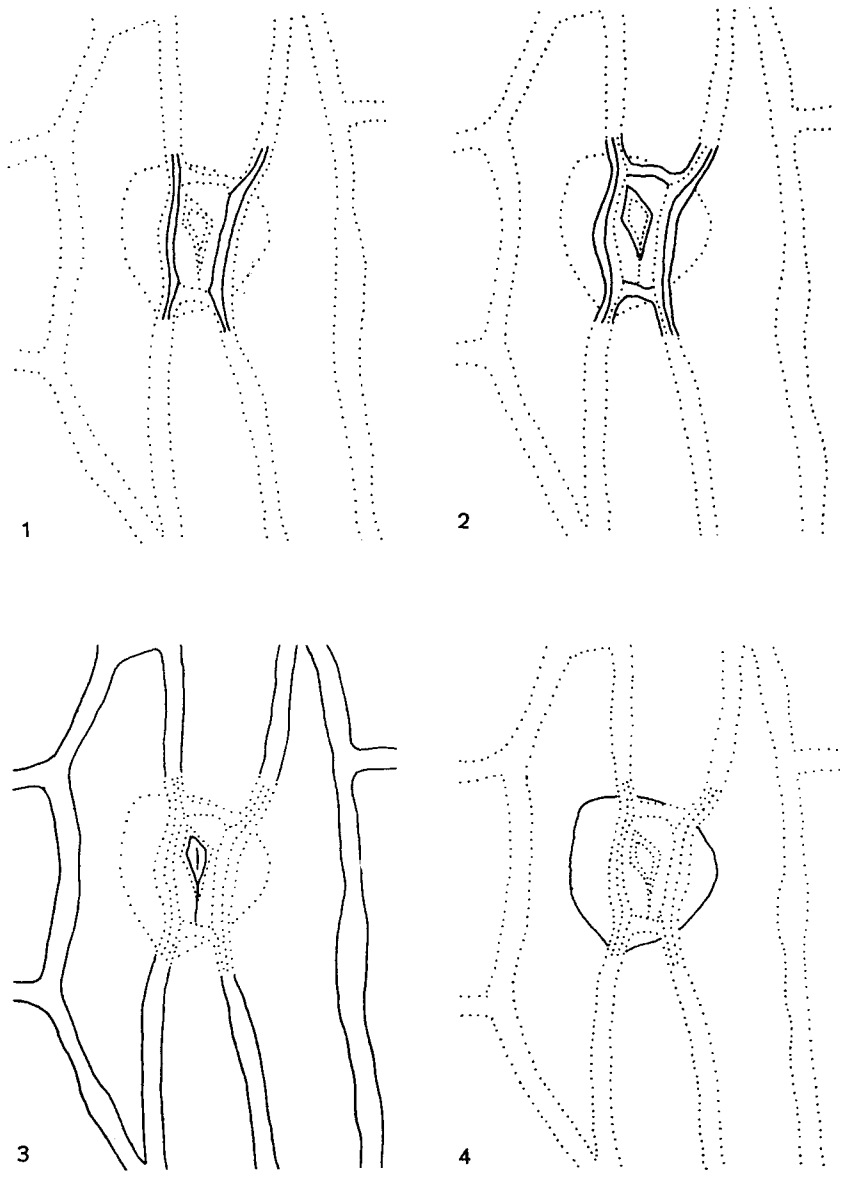


Text-fig. 3. 1—4 stoma viewed from the outside; the continuous line indicates parts in focus appearing at successive levels of the stoma; parts out of focus indicated with a dotted line; ×500, slide 17/7

Ryc. 3. 1—4 aparat szparkowy widziany od zewnątrz; linia ciągła oznacza zgrubienia nastawione na ostro na kolejnych poziomach aparatu szparkowego; części nieostre zaznaczone linią kropkowaną; ×500, preparat 17/7

projecting above surface of epidermis. In median part the periclinal walls bear characteristic thickenings in the form of ridges in elongated cells, and of papillae in isodiametric cells. In fragments of cuticle not showing

these thickenings in light microscope, they are visible in the phase contrast microscope.

Hair bases. In certain places on the epidermis a characteristic arrangement of 9—11 cells around a small rounded or oval cell (Pl. V, fig. 1—2) is visible. Periclinal wall of central cell thinner than in normal epidermal cells, without papilla and usually broken (Pl. V, fig. 1). Nature of these cells not known, supposed to be hair bases, but hairs never observed (cfr. W. Edwards 1924). Hair bases differing from spine bases in their much smaller diameter 28—126 μ, as compared with 162—1200 μ of spine bases, and in possessing a periclinal wall.

Hypodermis adhering to epidermis and contrasting with it by its dark brown colour. Hypodermal cells longitudinally orientated, their walls thick, showing an undulate outline, their transverse walls oblique. Length of cells from 197·4—527·6 μ, width from 36—87 μ.

Tracheid. One tracheid fragment found in connection with epidermis shows thickenings ranging from scalariform to reticulate (Pl. IV, fig. 2). The structure of the epidermis fragment and the fact that the entire plant material contains only remains of one single plant is evidence that this tracheid belongs also to the described *Sawdonia ornata*.

Stomata. The structure of the stomata is dealt with in detail in a separate chapter. It is sufficient to say here that the stoma of *Sawdonia* from Opole agrees with the descriptions of the stomata of the plants whose other features are also identical with this plant.

COMPARISONS

Sawdonia ornata from Opole is compared here only with those materials which show the same anatomical structure and with two species which certain authors regarded as identical with the species showing this structure. The relation of *Sawdonia* from Opole to species showing no structure is not known.

a. Comparison with the material from Gaspé

The material of *Psilophyton* with preserved structure from the Lower Devonian (Emsian) of Gaspé had been described by W. N. Edwards (1924) and Lang (1931) under the name *Psilophyton princeps* Dawson. Höeg (1967) based his interpretation of *Psilophyton princeps* mainly on their descriptions.

In his paper W. N. Edwards gave a detailed description of the structure of the epidermis and of the spines. Several features observed by him, such as the variable shape and size of the epidermal cells, the cuticular thickenings on their surfance in the from of ridges or papillae, the

characteristic arrangement of the hair bases and the variation of the shape of the spines agree with the material from Opole. Differences between the two occur in the size of the epidermal cells which are 75—300 μ long and 30—75 μ wide in W. N. Edward's material, while in the Polish material their length is 42—228 μ and the width in the middle of the cells 15—66·6 μ.

Lang gives a particularly detailed description of spines. The material from Opole is similar to that described by Lang in the width and striation of axes, possibly corresponding to cell walls of epidermis, in the size and shape of spines and their bases and in their probably secretory character (cfr. Pl. 27, fig. 3, 4, 6, 8, of Lang). The present material differs from that of Lang where the spines project at a right angle to the axis, while in mine they usually project at an acute angle. Nevertheless, in certain specimens shown by Lang (e.g. Pl. 27, fig. 5, 7) the spines also project at an acute angle.

I conclude from this comparison that the material from Gaspé described by W. N. Edwards and Lang and that from Opole show only minor differences and belong therefore to the same species.

I also had at my disposal some original material from Gaspé collected by dr K. L. Alvin and determined by him as *Psilophyton princeps* var. *ornatum*, but agreeing in structure with that of W. N. Edwards and Lang. This material agreed in the width of its axes, the delicate striation of their surface, the shape of the bases of the broken off spines, in the form of projections and hollows with the respective morphological features of the plant from Opole. Also such features as the shape and size of the epidermal cells, the cellular structure of the spines and their secretory character are common in both sets of material. In the material from Gaspé more spines with preserved ends are to be found, while there are only a few in my material. There is also the difference in the Gaspé material collected by dr Alvin that most of the spines project at a right angle, while in the Opole material they project at an acute angle, though in both sets of material there are some spines in a different position from the rest. To summarise, the differences are again of minor importance and comparison shows that the material from Opole represents the same species as that from Gaspé determined as *Psilophyton princeps* var. *ornatum* by dr Alvin.

b. Comparison with the material from Strathmore Beds in Scotland

In 1932 Lang described *Psilophyton* from the Strathmore Beds from Scotland which belong to the Lower Old Red Sandstone (now regarded as approximately Middle Siegenian). According to Lang there are two species present, *Psilophyton princeps* and *Psilophyton goldschmidtii* which Lang described jointly under the name *Psilophyton*.

Therefore I compared my preparations with particular photographs and used the text only as a supplement. An unquestionable similarity can be seen between the plant from Opole and fragments of axes on Pl. II, fig. 23, 32 of Lang, with spines on Pl. III, fig. 43, 44, 46, 48, 60, and with fragments of epidermis on PI. IV, fig. 67—69. The agreement in these features is confirmed in the text.

On the other hand, the plant from Opole is of a different habit from the specimen in Pl. II, fig. 17, 25—31 of Lang. The difference concerns mainly the branches which in the Scottish material are much thinner than the main axis and divide further into smaller branches, while in the material from Opole the width of branches differs only slightly from that of the main axis. In addition, there are marked differences in the width of the axes and of the epidermal cells. To conclude, I found that the specimens from Opole belong to the same species as those in the paper of Lang — Pl. II, fig. 23, 32; Pl. III, fig. 43, 44, 46, 48, 60; Pl. IV, fig. 67—69, but they are different from the species represented in his Pl. II, fig. 17, 25—31.

c. Comparison with the material from New York State

Psilophyton princeps with structure was also described by Hueber and Grierson (1961) from Schoharie County in New York State from the Upper Devonian (Frasnian) strata. This material agrees in the size of the axes, in the size and shape of the epidermal cells and the size and shape of the spines with the material from Opole. These authors also found scalariform and reticulate tracheids which is another common feature with the plant from Opole. The material from New York State is different in not showing any cutinized ridges or papillae on epidermal cells. However, in the material from Opole certain fragments of the epidermis also appear not to have ridges when observed in the light microscope, but when the phase contrast microscope is used, the ridges and papillae on epidermal cells are visible. As a result of the comparison, I regard the plant from Opole as identical with *Psilophyton princeps* described by Hueber and Grierson.

d. Comparison with *Psilophyton goldschmidtii* Halle

Höeg (1967) regarded the plant with the structure characteristic for *Sawdonia* from Opole as *Psilophyton princeps* Dawson. He assumed, however, that only the specimens from Gaspé and New York State represented this species, and regarded the material from Europe, i.e. that described by Lang (1932) from Scotland as probably belonging to *Psilophyton goldschmidtii*.

Psilophyton goldschmidtii, according to Höeg possesses a well developed branching system. Its main axis has a zig-zag habit and shows numerous lateral branches which dichotomize at a small distance from the main axis. These branches are much narrower than the main axis. The material from Opole, however, is characterized by straight axes, and lateral branches of almost the same width as the axes. As narrow branches were never found and as only three branching axes were found in the entire material, it may be inferred that the axes branch only at great distances. Another feature characteristic of *Psilophyton goldschmidtii* is the narrow light margin along the sides of the axes next to its dark inner part. In the material from Opole, however, the surface of the axis is alike throughout its entire width and does not show any margin. Also, in *Psilophyton goldschmidtii* the spines are sparse on the main axis and on the branches they occur only at their bases, frequently they are lacking. The shape of the spines ranges from narrow conical to subulate and their length reaches 4 mm. The plant from Opole is different in showing numerous spines which are elongated conical and only up to 0·5—2·2 (3·4) mm long. This comparison shows that the plant from Opole is different from *Psilophyton goldschmidtii.*

e. Comparison with *Psilophyton princeps* (Dawson) Hueber 1968

The characteristic features of this species are dichotomizing axes bearing terminal sporangia, axes up to 8 mm wide showing a ridged surface and bearing blunt spines irregularly arranged. The depressed in the middle, cup-like end of the spines is typical. The structure of the cuticle of this plant is not known because it dissolves in maceration. The plant from Opole differs from *Psilophyton princeps* sensu Hueber in the width of the axes, in their more delicate striation probably corresponding to cell walls of epidermis and in the shape of its spines. It is also known (Hueber and Banks 1967) that the species showing the structure characteristic of the plant of Opole bears lateral sporangia. Therefore the plant from Opole is different from *Psilophyton princeps* sensu Hueber.

f. Comparison with *Sawdonia ornata* (Dawson) F. M. Hueber 1971

In 1971 appeared the paper of Hueber on *Sawdonia ornata* which is the new name for *Psilophyton princeps* var. *ornatum Dawson* (1871). Hueber gives a detailed description of the morphology and structure of the plant. As a result of the comparison I found a similarity in morphological and anatomical structure of the plant from Opole with *Sawdonia ornata.* Differences are only in the size of certain parts of the plant which are given in the following table 1:

Table 1
Tabela 1

Comparison with *Sawdonia ornata*
Porównanie z Sawdonia ornata

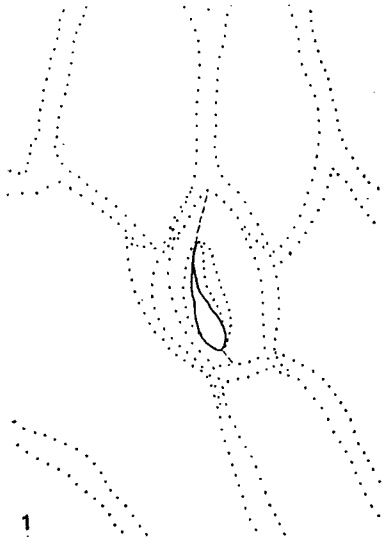
Part of plant *Część rośliny*	Material from Opole *Materiał z Opola*		*Sawdonia ornata* (Dawson) Hueber	
	length długość μ	width szerokość μ	length długość μ	width szerokość μ
Spine bases *Podstawy kolców*		162—1200		500—1800
Cells of epidermis *Komórki epidermy*	42—228	15—66·6	54—300	30—75
Stomata *Aparaty szparkowe*	42—60	18—30·6	39—72	17—34

As a result of the analysis of the compared characters of *Sawdonia ornata* (Hueber 1971) with those of the material from Opole, I found that both represent the same species.

ATTRIBUTION

I met with difficulties when trying to determine the specific name of the plant from Opole, because of the confusion which surrounds the name *Psilophyton princeps* (cfr. Hueber and Banks 1967). These two authors showed that Dawson described in 1859 *Psilophyton princeps* and in 1871 *Psilophyton princeps* var. *ornatum* which were afterwards regarded by certain authors as the same species and by others as two different species. Only recently when the material of Dawson was revised, did it become evident that *Psilophyton princeps* and *Psilophyton princeps* var. *ornatum* were two different plants, differing in such an important feature as the position of sporangia. *Psilophyton princeps* as described by Hueber (1968) bears sporangia at the ends of repeatedly dichotomizing branches, while in *Psilophyton princeps* var. *ornatum* (Hueber 1961, Hueber and Banks 1967) the sporangia are borne laterally along the axis.

Hueber and Banks (1967) and Hueber (1971) regard as *Psilophyton princeps* var. *ornatum* the plants with anatomical structure described from Gaspé by W. Edwards (1924) and Lang (1931) and from the USA, New State by Hueber and Grierson (1961). In the paper of 1967 Hueber and Banks announced that *Psilophyton princeps* var. *ornatum* should be transferred to a new genus. In 1971 Hueber instituted the new name *Sawdonia ornata* for *Psilophyton princeps* var. *ornatum* and described in detail its morphology and anatomical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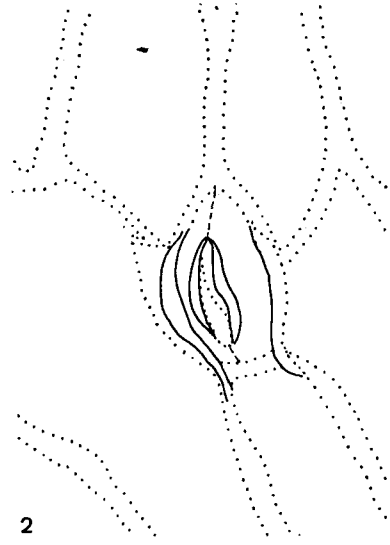
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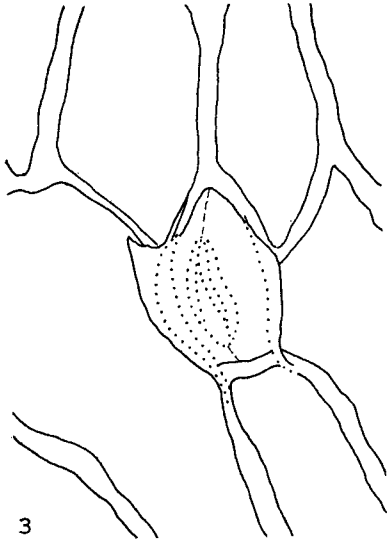
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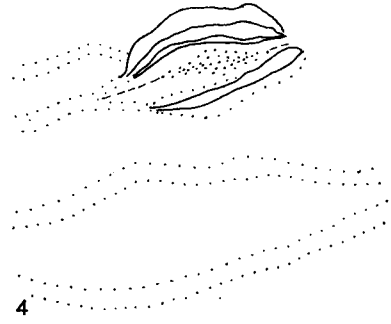
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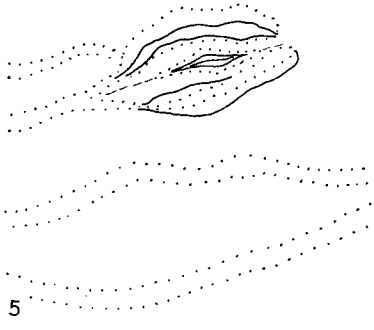
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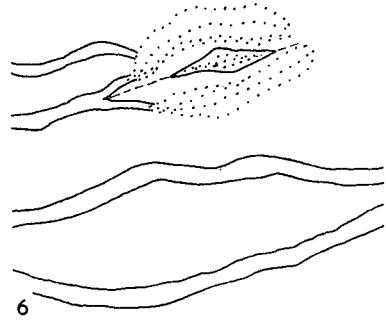
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structure. Also the systematic position of the plant is changed, because *Sawdonia* is placed not in the *Psilophytales* (H ö e g 1967), but in *Zosterophyllales.*

On the basis of the paper of H u e b e r (1971) and of the comparisons which show the similarity of the material from Opole to materials from other localities which were discussed in the preceding chapter, I came to the conclusion that the specimens from Opole belong to the species *Sawdonia ornata* (Dawson) F. M. H u e b e r.

V. STRUCTURE OF STOMA

The stomata were studied in detail because the Polish material from natural maceration showed a great deal more of the stomatal structure than had been described so far. I have studied the stomata under oil immersion and from the best preserved ones I made drawings and photographs at different planes of focus, from the outside or from the inside of the cuticle (Pl. VII, fig. 1, 2, Pl. VIII, fig. 1, 2, Text-fig. 3, 1—4, Text-fig. 4, 1—6). On these observations is based the description of the stoma and the reconstruction of its transverse section in Text-fig. 5.

DESCRIPTION

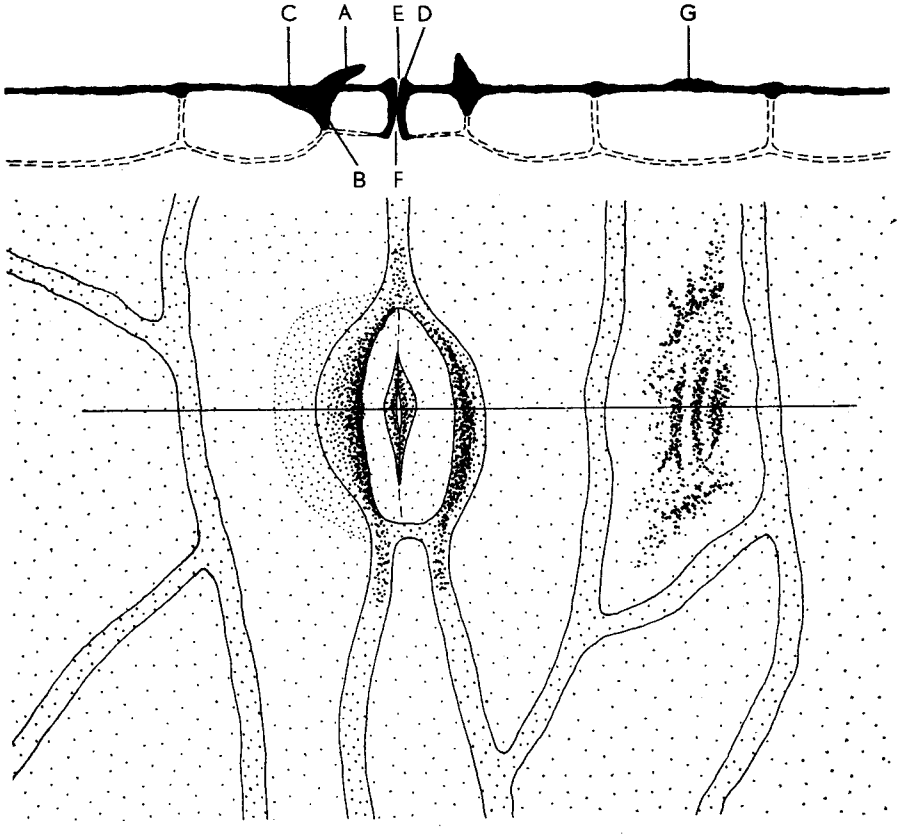
The stomata are arranged longitudinally along the axis, they are sparse, and their distribution is irregular. A stoma (probably) consists of two guard cells and 3—5 subsidiary cells, the anticlinal walls of which form projections which overhang the guard cells and form a shallow stomatal pit. The pit is elongated, its outline depends on the number of subsidiary cells, the end of the pit being rounded when two subsidiary cells meet and rectangular when three subsidiary cells meet. The length of the pit is 42—60 μ, its width 18—30·6 μ.

The outlines of the guard cells are only partially known. Their ventral walls are heavily cutinised forming around the aperture a tube which is narrowest at its median level and forms widenings facing outwards. (Text-fig. 5, E. F). The outer widening end of the aperture tube

Text-fig. 4. 1—3 stoma viewed from the inside; 4—6 stoma viewed from the outside; the continuous line indicates successively appearing cutinized thickenings of the stoma which are in focus; parts out of focus indicated with a dotted line; × 500, slides 16/1, 17/9

Ryc. 4. 1—3 aparat szparkowy widziany od wewnątrz; 4—6 aparat szparkowy widziany od zewnątrz; linia ciągła oznacza kolejno ukazujące się skutynizowane zgrubienia aparatu szparkowego, które są nastawione na ostro; części nieostre zaznaczono linią kropkowaną; ×500, preparaty 16/1, 17/9

ends in protruding thickened ridges (Text-fig. 5, Pl. VII, fig. 1). The polar ends of the guard cells are indistinct and so are the walls dividing the guard cell except for the region of the aperture. The outside of the guard cells is on the same level with the subsidiary and epidermal cells. (Pl. VII, fig. 1, 2).



Text-fig. 5. Reconstructed transverse section of a stoma, below same stoma in surface view (explanation in the text)

Ryc. 5. Rekonstrukcja aparatu szparkowego w przekroju poprzecznym, poniżej ten sam aparat szparkowy widziany z góry (objaśnienia w tekście)

The subsidiary cells agree with the ordinary epidermal cells in shape and size and differ from them only in the structure of the anticlinal walls bordering on the guard cells. These walls of the lateral subsidiary cells form along the dorsal walls of the guard cells raised cutinised projections which overhang the guard cells forming a shallow pit. The projections are highest in the median part of the stoma and become gradually lower towards its polar ends, merging finally into slight thickenings of the anticlinal walls of the subsidiary cells (Pl. VI, fig. 1, Text-fig. 3, 1—4). These

projections either stand upright and then the opening of the stomatal pit is wide, or else they lie more or less horizontally in which case the opening of the pit is narrow. Usually these cutinised projections cover up to 1/2 to 3/4 of the width of the pit though they never close the pit completely. The anticlinal walls of the subsidiary cells which form the projections are usually also cutinised below the epidermal surface for a varying distance (Text-fig. 5, B, Pl. VIII, fig. 1, 2, Pl. VI, fig. 3). Also a portion of the periclinal wall of these cells which lies next to the guard cells may be thickly cutinised from inside (Text-fig. 5, C, Pl. VIII, fig. 1, 2). In certain stomata the thickenings of the anticlinal or of the periclinal walls of subsidiary cells are lacking (Pl. VI, fig. 3), in others they are developed only on one side of the stoma (Pl. VIII, fig. 1, 2).

DISCUSSION

Explanation to Text-fig. 5.

In the reconstructed transverse section of the stoma the cell walls visible on preparations are indicated by a continuous line and the missing cell walls with a dashed line. The distances in the vertical direction are approximately proportional, and the horizontal distances are proportional to the real ones.

A — cuticle projections from the anticlinal walls of the subsidiary cells overhanging the surface of the guard cells and forming a shallow stomatal pit;

B — inward extension of cuticle of anticlinal walls of lateral subsidiary cells bordering on the guard cells. They may extend along the entire wall or only part of it;

C — thickening of the periclinal wall of the subsidiary cell;

D — projecting thickening of cuticle round the aperture;

E — outer widening end of aperture tube;

F — inner widening end of aperture tube;

G — cuticular ridge on the outer periclinal wall of the epidermal cell.

The reconstructed transverse section of the stoma in Text-fig. 5 shows some features which have been established and others about which there is less certainty. Such structures as the cuticle projections of the subsidiary cells which form the stomatal pit (A), the cutinization of the walls of the subsidiary cells bordering on the guard cells (B) and the thickenings of the periclinal walls of the lateral subsidiary cells (C) may be accepted with a fair amount of certainty. The position of the outer walls of the guard cells on a level with the rest of the epidermis appears certain as does the shape of the cutinized tube around the aperture. It is possible, however, that the guard cells in fact had the inner walls in an oblique position. This appears to follow from the position of the protruding dorsal and ventral walls of the guard cells when seen from inside.

Similarly as in *Zosterophyllum myretonianum* (cfr p. 17) it is not certain whether there were two quard cells, or only one with an aperture in the middle, and the division not continued in the polar ends. In fact, in none of the investigated stomata was the dividing wall observed with certainty in the polar ends, and this may be explained in two ways. It is possible that the guard cells were divided completely, only the walls being delicate were not preserved, as on the whole the outlines of the polar ends of the guard cells are indistinct. But it is also possible, that there was only one guard cell with a stomatal aperture, like in certain moss sporophytes (cfr. Lele and Walton 1961). This question could perhaps be solved by investigations on a larger material with well preserved stomata.

There also arises the question, whether there was a mechanism regulating the width of the opening of the stomatal pit. It was observed that its width varied in different stomata and it appears that this depended on whether the cuticle projections were in a vertical or more or less horizontal position. One can only guess that these projections could probably change their position and thus regulate the width of the opening of the stomatal pit. Sections of good stomata would probably help to understand this mechanism.

COMPARISON WITH STOMATA OF *SAWDONIA ORNATA* FROM OTHER LOCALITIES *

The descriptions of the stomata given by the previous authors give less details, but agree in the principal features with the structure of the stomata in *Sawdonia* from Opole. In particular, none of the authors mentions the raised cuticular projections forming the stomatal pit and probably the size of the stomata which they give, is in fact size of the stomatal pit.

The stomata in *Psilophyton* from Gaspé described by W. N. Edwards (1924) and Lang (1931), from Scotland by Lang (1932) and from New York State by Hueber and Grierson (1961) agree in their sparse distribution, longitudinal orientation, in outline, and in the position of the cutinised thickenings with the stomata in *Sawdonia ornata* from Opole. There are, however, minor differences in materials from particular localities.

The stoma differs slightly in size from the stomata described by W. N. Edwards, though it appears that he measured the size of the stomatal pit, not of the guard cells. The length of the stomata is according to Edwards 70 μ, its width 30 μ, while in the Polish material the

* cfr. synonyms p. 80 and Attribution p. 89.

length of the stomatal pit varies from 42 to 60 μ and its width from 18 to 30·6 μ. In addition, the stomata described by Edwards possess 4—7 subsidiary cells, while in the Polish material only 3—5 subsidiary cells were observed. In the material from Scotland described by Lang (1932) the stomata are slightly depressed below the level of the epidermis, while in that from Opole they are on a level with epidermal cells.

COMPARISON WITH STOMATA OF OTHER PSILOPHYTES

As far as I know, only the stomata of *Rhynia, Asteroxylon* and *Zosterophyllum myretonianum* have been described up to date. Zimmerman (1926) gave a description of the stomata of *Rhynia* and *Asteroxylon* both in surface view and in section. According to him, the stoma of *Rhynia* is simple, consisting only of two crescentic guard cells with almost no thickenings of their walls. Therefore they are different from the specialised stomata of the *Sawdonia* from Opole. The stoma of *Asteroxylon* is, according to Zimmermann, also specialised, in particular it shows heavy thickenings of the dorsal walls of the guard cells and raised cuticle projections above the surface of the stoma. These projections, however, rise from the surface of the guard cells, and not from the anticlinal walls of the subsidiary cells, as in the *Sawdonia* from Opole. The stomata of the two plants also differ in shape which is circular in *Asteroxylon* and elongated in *Sawdonia ornata*.

However, the stomata of *Sawdonia* from Opole appear to be similar in type to those described by Lele and Walton (1961) in *Zosterophyllum myretonianum*. They agree in their longitudinal orientation, in their elliptical or somewhat rectangular shape, though those of *Zosterophyllum* tend to be more elongated. They also agree in having cutinised thickenings around the aperture and guard cells (cfr. Pl. II, fig. 22—28 in Lele and Walton).

Moreover, the stoma of *Zosterophyllum myretonianum* does not show clear evidence that there were two guard cells, because no clear partition between the polar parts of the guard cells was ever observed. Whether this feature is due to the real absence of a dividing wall, or to its weakness and subsequent disappearance during fossilisation, it is nevertheless a common feature of the two plants. The stoma of *Zosterophyllum* appears to be different in not having subsidiary cells.

The similarity of the structure of stomata in *Sawdonia ornata* from Opole with those of *Zosterophyllum myretonianum* is particularly interesting. Banks (1968) presented new opinions on the evolutionary relationship between different psilophytes and proposed a new classification of these plants based on the position of sporangia. Banks proposed three subdivisions instead of the group *Psilophytales*, among them

Rhyniophytina which are characterized by terminal sporangia and *Zosterophyllophytina* with lateral sporangia. *Zosterophyllophytina* include among others *Zosterophyllum myretonianum* and *Sawdonia ornata*. The similarity of structure of the stomata between *Zosterophyllum myretonianum* and *Sawdonia ornata* from Opole is in agreement with this classification, and suggests, in addition, a closer affinity between these two plants.

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STRESZCZENIE

SAWDONIA ORNATA (= *PSILOPHYTON PRINCEPS* VAR. *ORNATUM*) Z POLSKI

W Polsce psylofity znane były do niedawna tylko z osadów dewońskich Gór Świętokrzyskich (Czarnocki 1919). Badania geologiczne ostatnich lat, a w szczególności głębokie wiercenia, wykazały obecność psylofitów w dewonie Sudetów Środkowych (Kuchciński 1964), okolic Andrychowa w Karpatach (Konior 1965) i na obszarze radomsko-lubelskim (Jakubowska 1968). Dotychczasowe opisy uwzględniały tylko budowę morfologiczną tych roślin.

Opisana w niniejszej pracy *Sawdonia ornata* pochodzi z głębokiego wiercenia w Opolu Lubelskim, z dolnego dewonu facji old-redowej. Dobrze zachowana budowa anatomiczna rośliny pozwoliła na jej dokładny opis, zawierający nowe szczegóły budowy i ustalenie pozycji systematycznej rośliny.

Pędy roślinne, zachowane w stanie uwęglonym, wydobyto ze skały za pomocą kwasu fluorowodorowego. Na skutek tzw. naturalnej maceracji otrzymano fragmenty pędów z dobrze widoczną budową komórkową. Ciemne fragmenty dla uwidocznienia budowy macerowano w mieszaninie Schulzego. Opis rośliny oparto przede wszystkim na preparatach sporządzonych z materiału pochodzącego z naturalnej maceracji.

Dichotomicznie rozgałęzione pędy *Sawdonia ornata* pokryte są nieregularnie rozmieszczonymi kolcami. Kolce charakteryzuje duża różnorodność pod względem kształtów i wielkości (tabl. 2, ryc. 1—14). Charakterystyczne ciemne zabarwienie zakończeń kolców, będące wynikiem zachowanych resztek substancji przez nie wydzielanej (por. Lang 1931), oraz ich pęcherzykowate zakończenia (tabl. III, fot. 3, tabl. V, fot. 3) wskazują na ich wydzielniczy charakter. Brak jest w nich wiązki przewodzącej i aparatów szparkowych.

Komórki epidermy, izodiametryczne do wydłużonych, posiadają na swej powierzchni charakterystyczne zgrubienia kutykuli w postaci grzebieni i papilli (tabl. V, fot. 1). W niektórych miejscach epidermy występują nasady prawdopodobnie po odpadłych włoskach (por. W. Edwards 1924) o charakterystycznym promienistym układzie komórek (tabl. V, fot. 1, 2). Pod epidermą zachowała się hypoderma o wydłużonych, grubościennych komórkach (tabl. III, fot. 1). Fragment tracheidy posiada zgrubienia drabinkowate, częściowo przechodzące w siatkowate (tabl. IV, fot. 2).

Opisana budowa morfologiczna i anatomiczna rośliny zgadza się z budową *Psilophyton princeps* z Gaspé (W. Edwards 1924, Lang 1931), ze stanu New York w USA (Hueber i Grierson 1961), z częścią materiału *Psilophyton* z warstw Strathmore ze Szkocji (Lang 1932) oraz z okazami *Sawdonia ornata* (Hueber 1971). Nie wykazuje natomiast podobieństwa z *Psilophyton goldschmidtii* Halle 1916 (Höeg 1967) i *Psilophyton princeps* Dawson (Hueber 1968).

Hueber i Banks (Hueber i Banks 1967, Hueber 1971) przeprowadzili analizę okazów *Psilophyton* opisanych przez Dawsona. W jej wyniku okazało się, że *Psilophyton princeps* i *Psilophyton princeps* var. *ornatum*, dotychczas opisywane pod wspólną nazwą *Psilophyton princeps*, to dwie odmienne rośliny, różniące się między sobą przede wszystkim ustawieniem sporangiów. W związku z tym Hueber (1968) dał dokładny opis *Psilophyton princeps* w nowym ujęciu; ze względu natomiast na charakterystyczne cechy *Psilophyton princeps* var. *ornatum* Hueber (1971) zaproponował dla tej rośliny nową nazwę *Sawdonia ornata* i umieścił ją w nowym rzędzie *Zosterophyllophytina*.

Najwięcej uwagi poświęcono budowie aparatów szparkowych, których dokładna obserwacja na materiale pochodzącym z naturalnej maceracji wykazała szereg dotychczas nie opisanych szczegółów budowy, jak i pozwoliła wykonać rekonstrukcję przekroju poprzecznego przez aparat szparkowy (tabl. 5).

Aparaty szparkowe rozmieszczone są nieregularnie w epidermie. Składają się — jak się wydaje — z dwóch komórek szparkowych, szparki i 2—5 komórek dodatkowych. Komórki dodatkowe kształtem i wielkością są podobne do pozostałych komórek epidermy. Odróżniają się jedynie skutynizowanymi antyklinalnymi ścianami, tworzącymi zgrubienia wystające ponad powierzchnię komórek szparkowych i sięgających w głąb wzdłuż ścian grzbietowych komórek szparkowych. Zgrubienia wystające ponad powierzchnię komórek szparkowych tworzą ściany płaskiej komory. Często również część peryklinalnej ściany komórek dodatkowych graniczącą z komórkami szparkowymi jest skutynizowana od wnętrza (tabl. VIII, fot. 1, 2). Liczba komórek dodatkowych warunkuje kształt komory. Zewnętrzna powierzchnia komórek szparkowych znajduje się na tym samym poziomie co powierzchnia komórek dodatkowych i epidermy. Otwartymi sprawami pozostają: liczba komórek szparkowych (gdyż nie stwierdzono ścian dzielących szparki w linii przedłużenia), kształt komórek szparkowych oraz zagadnienie, czy ściany komory były ruchome.

Przeprowadzono porównanie z aparatami szparkowymi innych psylofitów. Stwierdzono różnice w budowie z aparatami szparkowymi u *Rhynia*, pewne podobieństwo z aparatami szparkowymi *Asteroxylon* i *Zosterophyllum myretonianum* (Lele i Walton 1961), co mogłoby wskazywać na pokrewieństwo tych roślin.

Na podstawie pracy Huebera (1971) i przeprowadzonych porównań, stwierdzających podobieństwo materiału z Opola Lubelskiego do materiałów *Psilophyton princeps* z Gaspé (W. Edwards 1924, Lang 1931) i ze stanu New York w USA (Hueber i Grierson 1961), zaliczanych przez Huebera do *Sawdonia ornata*, uznano okazy z Opola Lubelskiego za *Sawdonia ornata* (Dawson) F. M. Hueber.

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Zakład Paleobotaniki

Plates

Tablice

Sawdonia ornata (Dawson) F. M. Hueber

Plate I

Fragments of axes; one branching and showing protruding bases of broken off spines; ×2·8, hand specimen 18

Tablica I

Fragmenty pędów; jeden rozgałęziający się z widocznymi sterczącymi nasadami po odpadłych kolcach; × 2·8 okaz nr 18

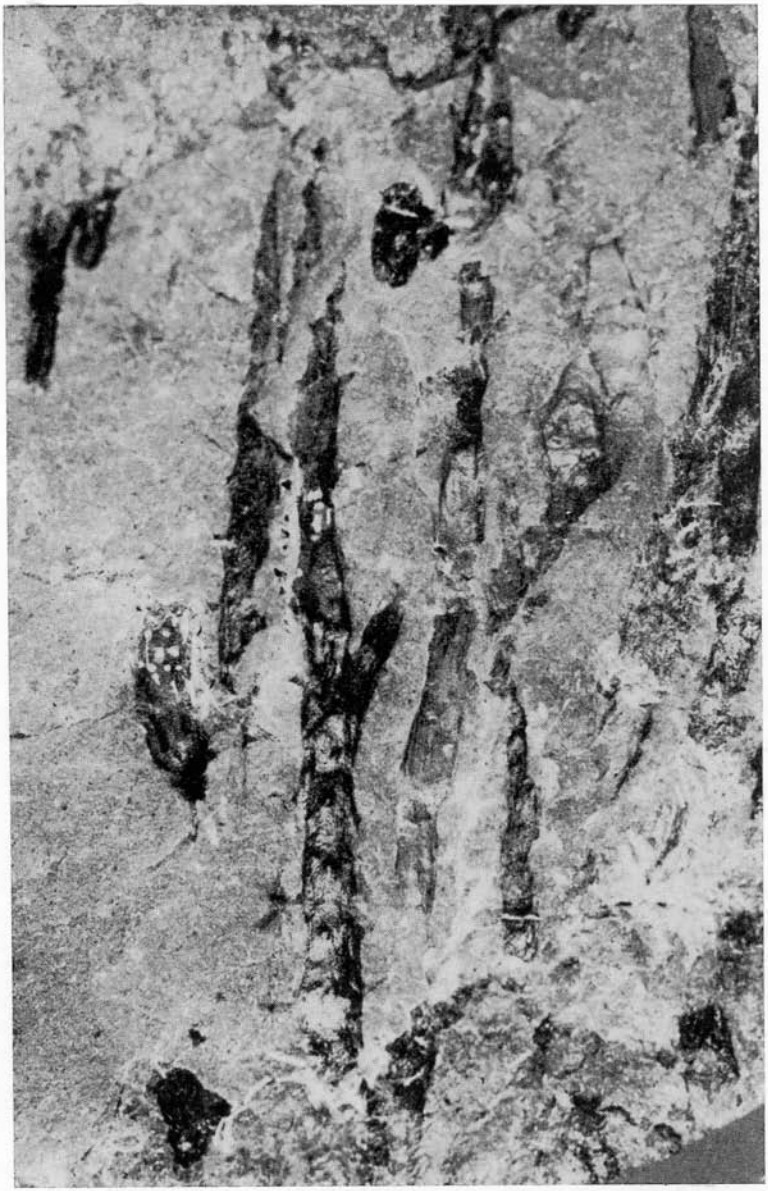

Plate II

1. Sample showing axes covered with spines; ×1·5, hand specimen 16
2. Fragment of branching axis; ×1·5, hand specimen 16
3. Spines; central showing vesicular end; ×50, slide 17/1

Tablica II

1. Powierzchnia próby z pędami pokrytymi kolcami; × 1·5, okaz nr 16
2. Fragment rozgałęzionego pędu; ×1·5, okaz nr 16
3. Kolce; środkowy kolec z widocznym pęcherzykowatym rozszerzeniem; ×50, preparat 17/1


1


2

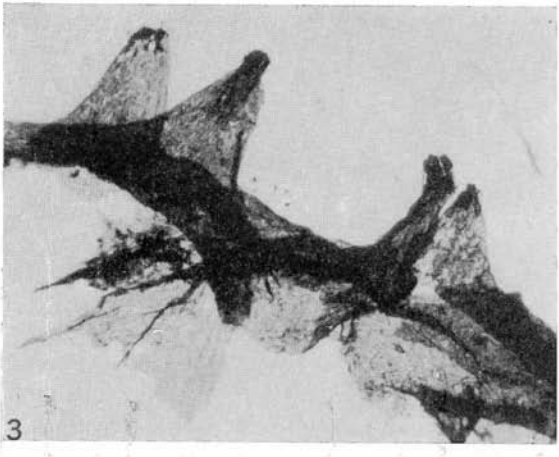
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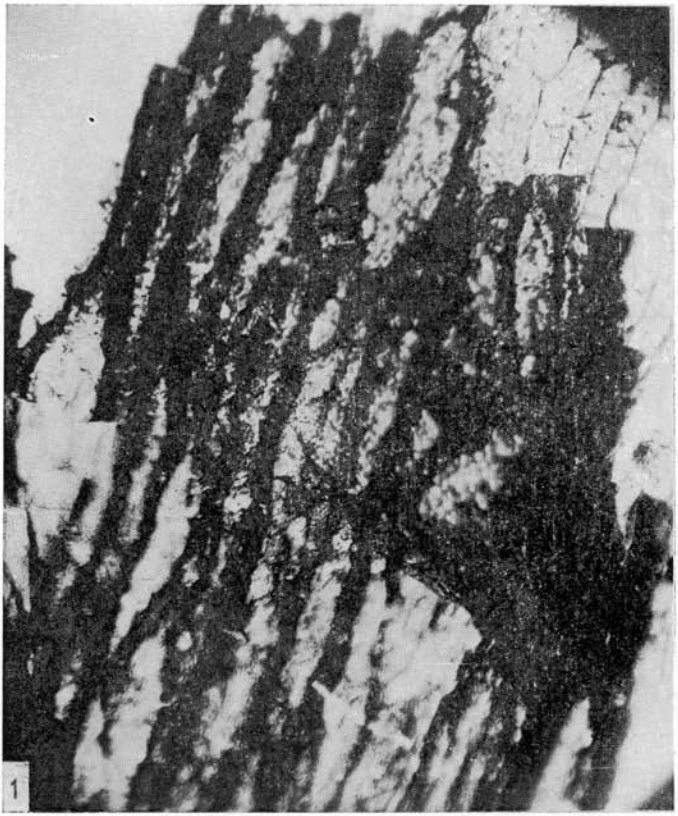
Plate III

1. Hypodermal cells adhering to epidermis; ×150, slide 17/12
2. Ummacerated spine showing open end with protruding dark mass; ×150, slide 15/5
3. Spine with widened vesicular end; ×40, slide 17/4
4. Spine with epidermis fragment showing elongated and isodiametric cells; ×40, slide 16/1

Tablica III

1. Komórki hypodermy przylegające do epidermy; ×150, preparat 17/12
2. Niemacerowany kolec z wystającą z otwartego szczytu ciemną substancją; ×150, preparat 15/5
3. Kolec z pęcherzykowato rozszerzonym szczytem; ×40, preparat 17/4
4. Kolec z fragmentem epidermy ukazującym długie i izodiametryczne komórki; ×40, preparat 16/1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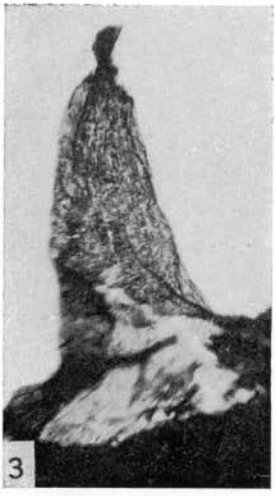
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4

Plate IV

1. Epidermal cells and stomata; ×150, slide 17/7
2. Fragment of tracheid with thickenings ranging from scalariform to reticulate; ×370, slide 17/10
3. Group of spines; ×40, slide 15/6
4. Unmacerated spine showing open end with protruding dark mass; ×150, slide 15/5

Tablica IV

1. Komórki epidermy z aparatami szparkowymi; ×150, preparat 17/7
2. Fragment tracheidy z drabinkowatymi zgrubieniami przechodzącymi w dolnej partii w siatkowate; ×370, preparat 17/10
3. Grupa kolców; ×40, preparat 15/6
4. Niemacerowany kolec z wystającą z otwartego szczytu ciemną substancją; ×150, preparat 15/5

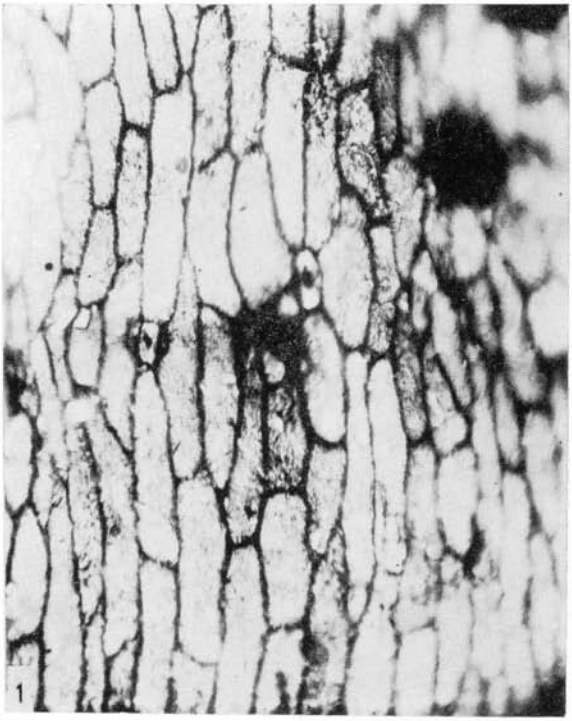
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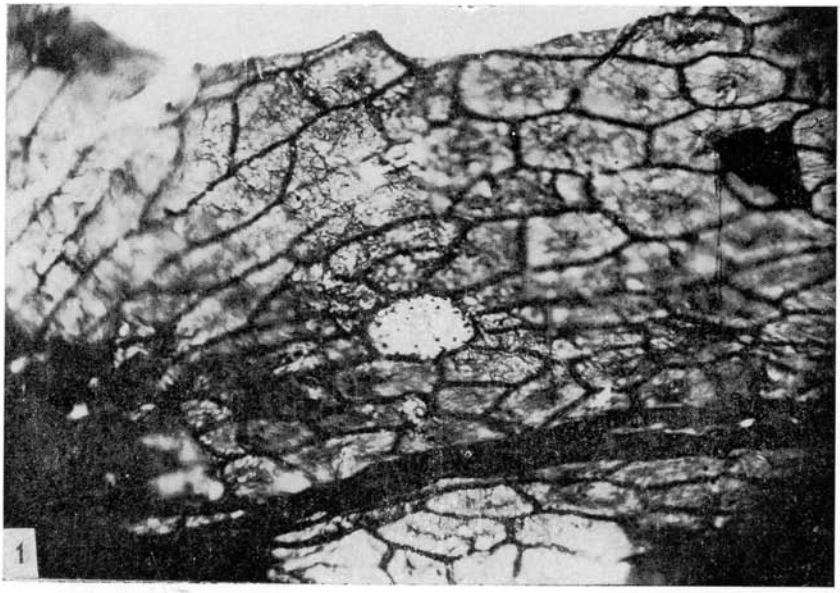
Plate V

1. Hair base showing central cell with preserved periclinal wall which is not thickened; surface of normal epidermal cells showing papillae and ridges; ×150, slide 17/8
2. Spines with fragment of epidermis showing hair base; ×40, slide 17/10
3. Spine with widened vesicular end which is open; ×180, slide 17/2

Tablica V

1. Nasada włoska z zachowaną błoną na centralnej komórce, pozbawioną zgrubień kutykuli; na powierzchni komórek epidermy widoczne papille i grzebienie; ×150, preparat 17/8
2. Kolce z fragmentem epidermy, na której widoczna nasada włoska; ×40, preparat 17/10
3. Pęcherzykowato rozszerzony, otwarty szczyt kolca; ×180, preparat 17/2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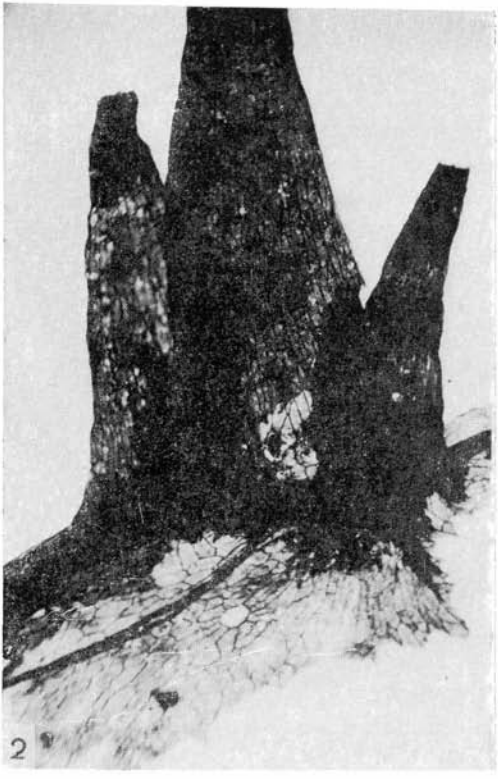
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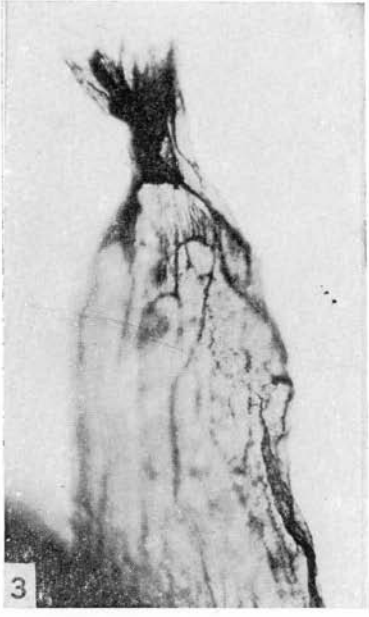
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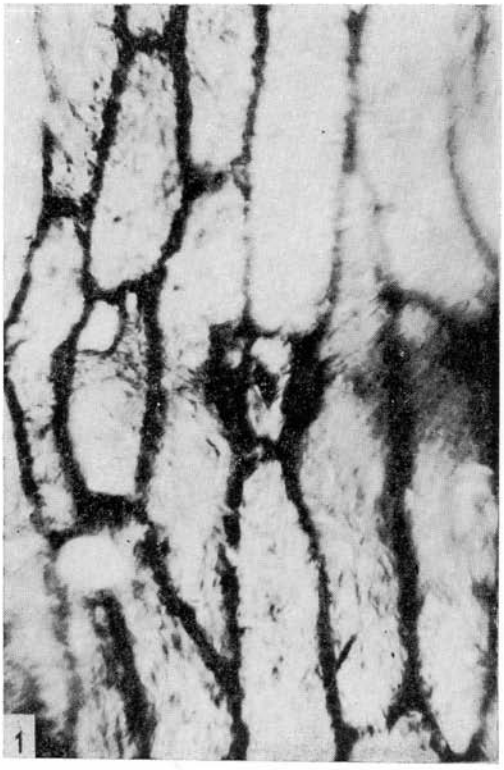
Plate VI

1. Stoma viewed from the outside, showing cutinized thickenings of the periclinal walls of the lateral subsidiary cells; ×370, slide 17/7
2. Epidermal cells and stoma; ×150, slide 17/7
3. Stoma viewed from the inside, periclinal thickenings of lateral subsidiary cells absent in this stoma; ×370, slide 16/1

Tablica VI

1. Aparat szparkowy widziany od zewnątrz; widoczne zgrubienia peryklinalnych ścian bocznych komórek dodatkowych; ×370, preparat 17/7
2. Komórki epidermy z aparatami szparkowymi; ×150, preparat 17/7
3. Aparat szparkowy widziany od wewnątrz; brak zgrubień peryklinalnych ścian bocznych komórek dodatkowych; ×370, preparat 16/1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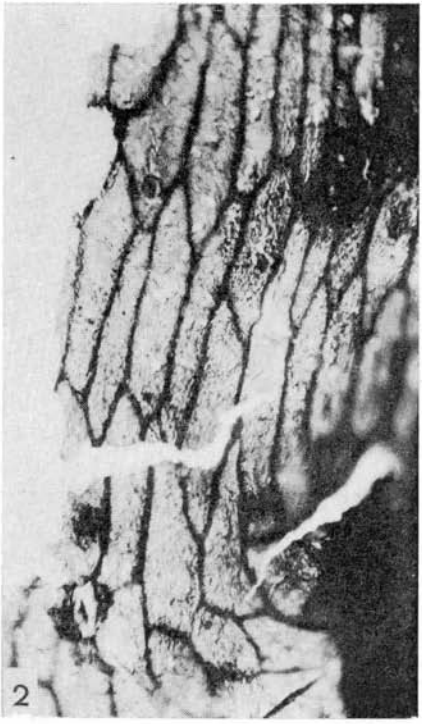
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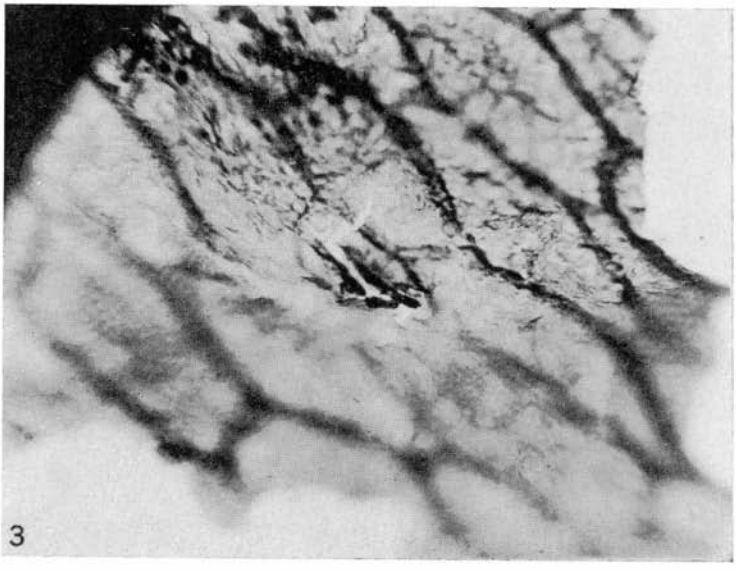
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Plate VII

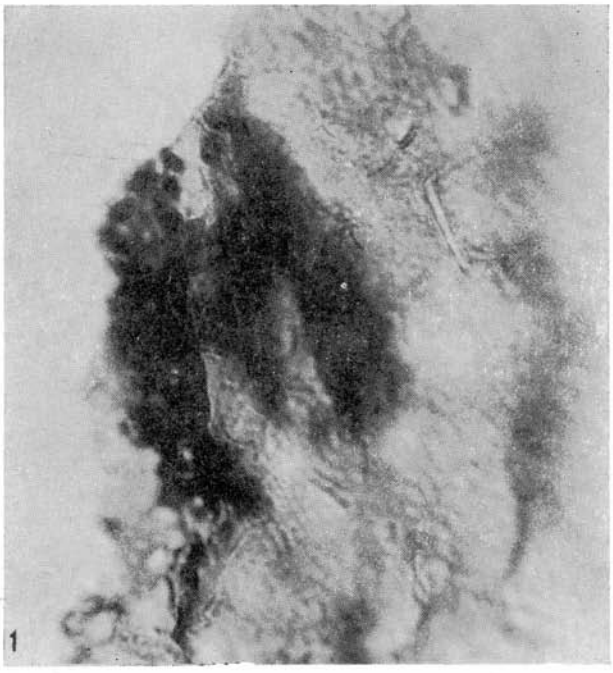
1—2. Stoma viewed from the outside; ×1000, slide 17/9

1. Higher plane of focus; in focus cuticle projections of anticlinal walls of lateral subsidiary cells and projecting thickenings of cuticle round the aperture
2. Lower plane of focus; in focus lower regions of cuticle projections of anticlinal walls belonging to lateral subsidiary cells, thickenings of cuticle round the aperture, surface of guard cells, of subsidiary cells, and of epidermal cells

Tablica VII

1—2. Aparat szparkowy widziany od zewnątrz; ×1000, preparat 17/9

1. Górny poziom ostrości; widoczne zgrubienia antyklinalnych ścian bocznych komórek dodatkowych i wąskie zgrubienia kutykuli wokół szparki
2. Dolny poziom ostrości; widoczne dolne partie zgrubień antyklinalnych ścian bocznych komórek dodatkowych, zgrubienia kutykuli wokół szparki, powierzchnie komórek szparkowych, dodatkowych i epidermy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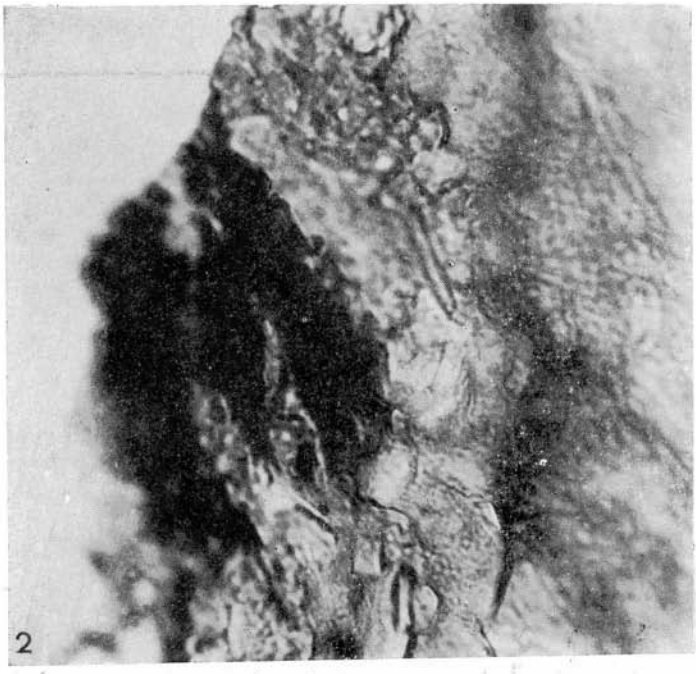
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Plate VIII

1—2. Stoma viewed from the inside; ×1000, slide 16/1
1. Higher plane of focus; in the focus the incurved thickenings of cuticle round the aperture
2. Lower plane of focus; visible thickenings of the periclinal wall of one lateral subsidiary cell, and surface of subsidiary cells

Tablica VIII

1—2. Aparat szparkowy widziany od wewnątrz; ×1000, preparat 16/1
1. Górny poziom ostrości; widoczne wywijające się na zewnątrz zgrubienia wokół szparki
2. Dolny poziom ostrości; widoczne zgrubienie peryklinalnej ściany jednej bocznej komórki dodatkowej oraz powierzchnia komórek dodatkowych