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ON *WEICHSELIA RETICULATA* AND *FRENELOPSIS HOHENEGGERI* FROM THE WESTERN CARPATHIANS

Weichselia reticulata i Frenelopsis Hoheneggeri z Karpat Zachodnich

INTRODUCTION

The best known Mesozoic plants from the Carpathians are the silicified *Cycadeoidea* stems. Though none of them was found *in situ*, they derive most probably from the Lower Cretaceous Grodziszcze beds (cf. Reymanówna 1960). However the first descriptions of Lower Cretaceous plants from the Carpathians are found in Ettingshausen's "Beitrag zur Flora der Wealden Periode" (1852), where among others are described plant remains from localities in the Moravian Gate (Brama Morawska) and the Silesian Foreland (Pogórze Śląskie) in the vicinity of Cieszyn. The localities lie on both sides of the border between Poland and Czechoslovakia. Schenk (1869) concentrated especially on this area and described in his paper ("Die fossilen Pflanzen der Wernsdorfer Schichten in den Nordkarpathen") 22 plant species from 7 localities.

In 1960 I found shales containing small plant fragments farther to the east, in Przenosza near Skrzydlna in the Middle Beskid (Beskid Średni). The shales occur in a natural outcrop in a stream bed, about 100 m. from the place where a *Cycadeoidea* stem had previously been found.

Later this year Dr. W. Nowak of the Geological Institute in Cracow showed me shales containing the same plants in Lipnik near Bielsko in the Silesian Foreland. We believe that this is the same Lipnik or Leipnik where Schenk found *Frenelopsis Hoheneggeri*.

In Przenosza and Lipnik the shales contain abundant though small plant fragments with strongly prevailing *Frenelopsis Hoheneggeri* and *Weichselia reticulata*. The shales are dark grey and contain $CaCO_3$ and occasionally pyrites. According to Geroch and Nowak (1963, pp. 247, 261, 262) the strata with plants found in Lipnik belong to the Grodziszcze shales and are of Lower Cretaceous (Hauterivian-Lower Berremian? age).

SYSTEMATIC DESCRIPTION

Filicinae incertae sedis

Weichselia reticulata Stokes et Webb

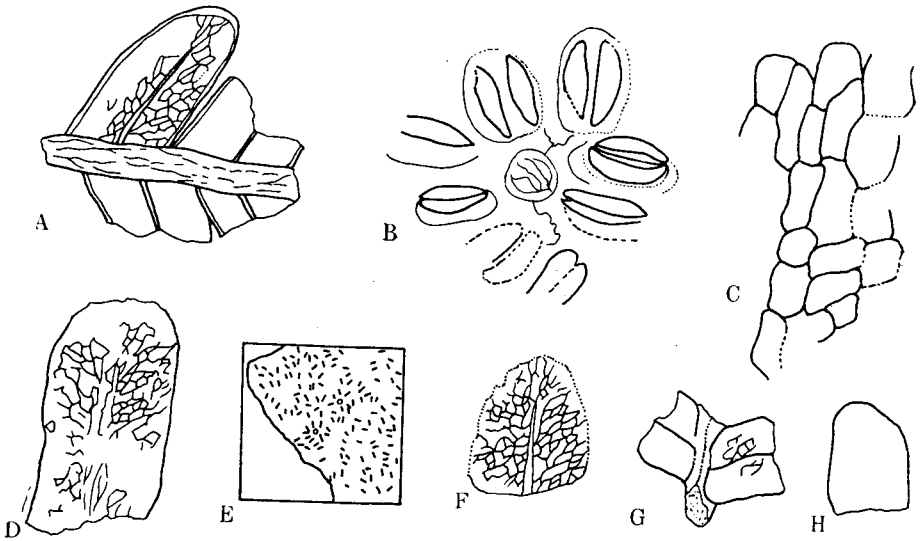
Pl. I, figs. 7—11; Text-fig. 1A—H

1889 *Lonchopteris recentior* Ettingshausen, Schenk, P. 4; Pl. I, figs. 2—6.
1910 *Weichselia reticulata* Stokes et Webb, Bommer, P. 297; one Plate.
1932 *Weichselia reticulata* Stokes et Webb, Lipps, P. 241; Pl. 26, 27.
1952 *Weichselia reticulata* Stokes et Webb, Vakhrameev, P. 163; Pl. 6, figs. 10, 11.

Description. Pinna rachis 1 mm. wide, oval in section, upper surface bearing a narrow groove; no hairs nor ramenta present. Pinnae arising from upper side of the rachis at an angle of 50—60° to it, subopposite, attached with the whole base; margins of adjacent pinnae in touch or separated by a narrow gap. Pinnae either extending flatly in the same plane or standing more or less upright, occasionally opposite pinnae in contact with their upper surfaces ("butterfly position" of Lipps).

Pinnae straight and symmetrical or occasionally with a falcate apex, their length typically 5 mm., their width typically 2·5 mm. Pinnae margins parallel or slightly converging towards a broad, rounded apex. Some pinnae (probably near the leaf base) shorter, rounded and usually standing upright. Lamina convex, margin entire, thick, recurved. Lamina substance very thick, up to 80 μ measured at margin.

Midrib sunken above, 150 μ broad and very prominent below, dissolving near the apex into a net of veins. Veins marked above, distinct and prominent below. Lateral veins arising from the midrib at intervals of about 0·4 mm. and anastomosing to form angular, elongated meshes about 0·5 mm. long; about 5 rows of meshes present on either side of the midrib. Outermost branches of veins not anastomosing but running straight towards the margin.



Text-fig. 1. *Weichselia reticulata*. A, rachis with pinnae seen from below, × 5, S 220. B, lower cuticle showing stomata and a papilla (drawn from a peel), × 400, S 204. C, upper cuticle (drawn from a peel), × 400, S 204. D, venation of pinna, × 8, S 206. E, distribution of stomata and papillae in one sq. mm. of cuticle, S 204. F, venation of pinna, × 5, S 219. G, rachis and two pinnae bases seen from above, × 5, S 218. H, falcate apex of pinna, × 5, S 221.

Ryc. 1. *Weichselia reticulata*. A, fragment liścia widziany od dołu, × 5, S 220. B, dolna kutykula z widocznymi szparkami i papillą (rysowane z preparatu na błonce), × 400, S 204. C, górna kutykula (rysowana z preparatu na błonce), × 400, S 204. D, unerwienie odcinka liściowego, × 8, S 206. E, rozmieszczenie szparek i papilli na 1 mm², S 204. F, unerwienie odcinka liściowego, × 5, S 219. G, oś liścia i nasady dwóch odcinków liściowych widziane od góry. H, szczyt odcinka liściowego × 5, S 221.

Cells of midrib and pinna margin narrow and elongated. Parts of lamina inside meshes sunken and bearing crowded stomata, about 50 μ long, orientated in all directions. Upper epidermis of pinna built of small quadrangular cells with straight or slightly sinuous walls.

Indusia in form of pentagonal discs with a stalk attached in the middle. Disc about 1 mm. in diameter, with an incurved margin. Distal side of disc smooth and shiny, in the middle a cavity with a central knob. Proximal side of disc showing protruding veins radiating from the stalk towards the disc margin.

Occurrence. I. Lipnik near Bielsko, rocks in the stream near the Forestry building. 2. Przenosza near Skrzydlna, outcrop in the stream bed near the bridge.

Material and techniques. In order to obtain plants remains, the shale was broken down with dilute H_2O_2 and the plant fragments

picked out under a binocular. Then they were cleaned first with dilute, then with concentrated HCl, then washed and treated with diluted HF. The shale reacts violently to H_2O_2, HCl and HF, so it was necessary to start with a weak solution of the reagent. If the reaction was too violent, water had to be added to prevent the plant remains from being damaged.

Weichselia fragments show very well preserved structure. In reflected light the epidermal cells are clearly visible and also the cells of the internal tissues in broken leaves. But it is very difficult to make preparations. The material resists long maceration in concentrated $HNO_3 + KClO_3$ and heating in this reagent. Only one pinna gave small fragments of lower cuticle after maceration. It was possible, however, to make small peel preparations of both the upper and the lower cuticle.

Preservation of cell structure and resistance to maceration are characteristic for plant material preserved in form of charcoal. *Weichselia* fragments show also further properties of charcoal: they are black, shiny, and brittle, and they smear the fingers. I think therefore that they became charred during a fire and then were washed by rain into a river or immediately into the sea (Comp. Harris 1958).

The material of *Weichselia reticulata* consists mainly of separate pinnae, but also fragments of rachis bearing 2—3 pinnae occur, though they usually break up during treatment with HF. Apart from this there were found a few small discs with stalks, resembling *Weichselia* indusia. They occur separately in the matrix.

Discussion and comparison. Usually such small fern fragments as are described here cannot be determined. I think, however, that the determination of *Weichselia* fragments is safe, because they possess a very characteristic reticulate venation. In Mesozoic ferns reticulate venation occurs in certain species of the genus *Phlebopteris,* such as *P. polypodioides, P. Woodwardi,* and *P. Dunkeri.* But judging from the descriptions and figures in the monograph of Harris (1961), in the *Phlebopteris* species the lateral veins never form a regular net of uniform meshes over the whole lamina, which is characteristic of *Weichselia reticulata.*

The separate small discs, figured on Pl. I, figs. 7, 10 are similar in their polygonal shape and the presence of a small knob in the middle, to the discs of which consist the fructifications of *Weichselia* as described and figured by Bommer (1910) and Lipps (1932). I have seen *Weichselia* fructifications from the Bommer Collection. The stalked discs of which these fructifications consist and which are presumably the indusia, are very similar in shape and size to discs in my material.

Harris (1961) figured indusia of *Matonidium Goepperti* which are similar, but smaller, as they are only about 0·25 mm. wide while in my material they are about 1 mm. wide. The discs were found in the shale

from the outcrop in the locality Przenosza where *Weichselia* leaves often occur. I think therefore that these discs are in fact indusia of *Weichselia reticulata,* though I have never found them connected with other organs of that plant.

Age and distribution. According to Gothan (1910) *W. reticulata* is an important leading fossil of the Neocomian occurring only seldom in the Gault. According to Vakhrameev (1952) *W. reticulata* is a widespread Lower Cretaceous species, connected with the Wealden of Western Europe. In the Moscow region and in the Far East it was found in the Aptian, in the Western Kazakhstan in the Albian, and possibly in the Cenomanian of Egypt. It is also known from India, China and North America.

Coniferae

Cupressaceae

Frenelopsis Hoheneggeri Schenk

Pl. I, figs. 1—6; Text-fig. 2A—M.

1869 *Frenelopsis Hoheneggeri,* Schenk, P. 13; Pl. IV, figs. 5—7, Pl. V, 1—2, Pl. VI, figs. 1—6, Pl. VII, fig. 1.
1946 *Frenelopsis Hoheneggeri* Schenk, Romariz, P. 135; Pl. I, figs. 1—3, Pl. II, figs. 1—2, Pl. III, figs. 1, Text-fig. 1.
1948 *Frenelopsis Hoheneggeri* Schenk, Teixeira, P. 59, 65; Pl. 24, figs. 1—4.

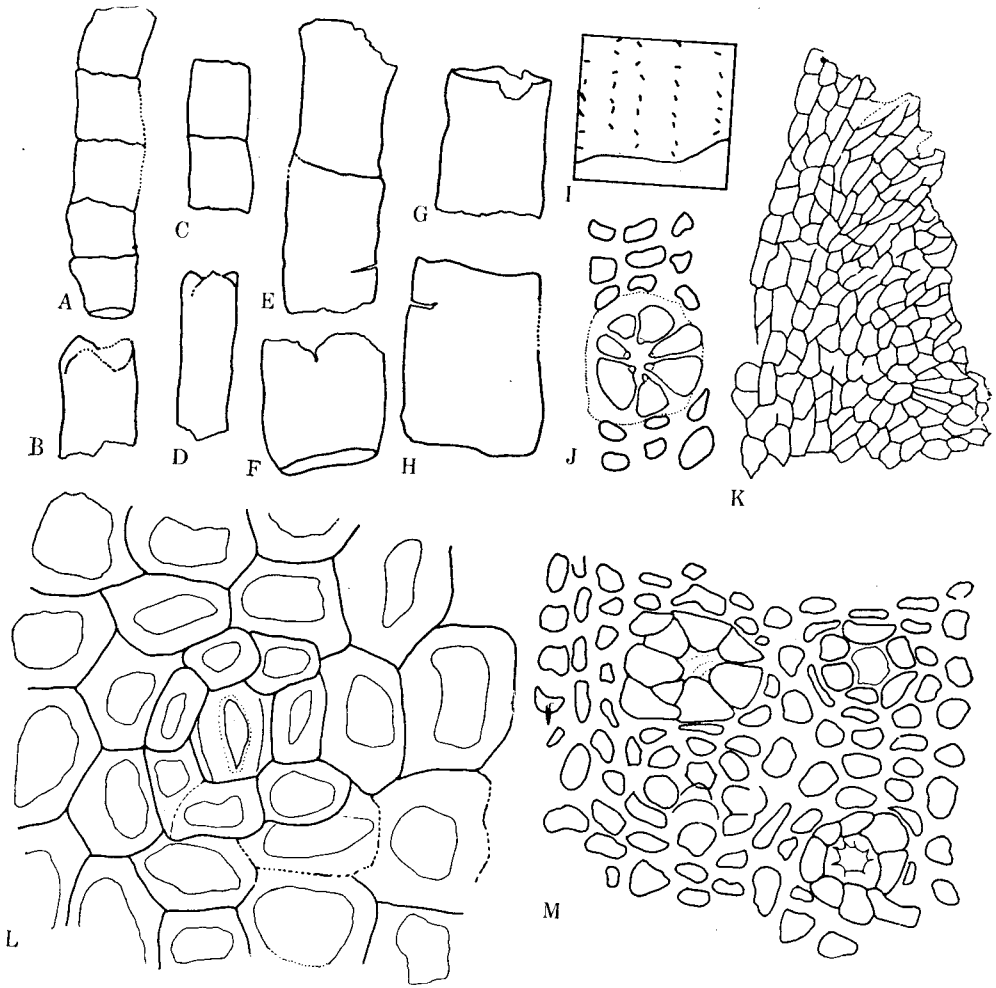
Description. Shoots without dorsiventral differentiation, consisting of flat, rectangular, easily separated internodes, 3—12 mm. long, 2—5 mm. wide.

Leaves (rarely preserved) triangular, about 1 mm. long, growing in whorls of three on upper edge of internode, in contact at bases, appressed, not decurrent. Lower (abaxial) leaf surface showing about 15 strongly marked ridges, converging towards apex.

Cuticle of internode very thick, without sutures, showing parallel longitudinal rows of stomata over its entire surface, 5 rows per mm. Strands of hypodermal cells running between stomatal rows. In a row the stomata separated from each other by 1—4 epidermal cells, rarely subsidiary cells of adjacent stomata in contact. Stomatal rows separated by 2—4 rows of rectangular epidermal cells. Epidermal cells without pitting or papillae. About 50 stomata occurring in 1 sq. mm.; apertures orientated in all directions.

Stomatal apparatus circular, sometimes oval, from 75—100 μ across. Guard cells sunken, thinly cutinised, surrounded by a ring of 4—8 raised

and overhanging subsidiary cells; all subsidiary cells of similar size and shape, occasionally thinner and smaller than ordinary epidermal cells. In most stomata inner tangential wall of subsidiary cells bearing a papilla; papillae often extended and closing the aperture of the stomatal pit. An incomplete ring of cells present around the subsidiary cells.



Text-fig. 2. *Frenelopsis Hoheneggeri*. A, shoot consisting of five internodes, × 2. B—H, internodes, × 4, S 223. I, distribution and orientation of stomata in one square mm., S 212. J, stomata showing papillae, × 200, S 211. K, fragment of inner cuticle of leaf, × 100, S 209. L, stoma without papillae, × 400, S 207. M, cuticle showing three stomata, × 200, S 210.

Ryc. 2. *Frenelopsis Hoheneggeri*. A, fragment pędu złożony z pięciu segmentów, × 2. B—H, segmenty, × 4, S 223. I, rozmieszczenie i orientacja kierunkowa szparek na 1 mm², S 212. J, aparat szparkowy z widocznymi papillami, × 200, S 211. K, część wewnętrznej kutykuli liścia, × 100, S 209. L, aparat szparkowy bez papilli, × 400, S 207. M, fragment kutykuli z trzema szparkami, × 200, S 210.

Cuticle of abaxial leaf surface similar to that of internode, growing thinner towards the apex. Stomatal rows continuous with those of internodes and converging towards apex. Cuticle of adaxial leaf surface much thinner, without stomata, consisting of rectangular cells, arranged in longitudinal rows; towards the margin, cells placed transversely or obliquely to those of the rest of the leaf.

Occurrence, 1. Lipnik near Bielsko. 2. Przenosza near Skrzydlna.

Material. The fragments of *Frenelopsis* were cleaned in the same way as *Weichselia*. They are very tough and maceration in cold HNO_3 gave no results, so they were heated in concentrated HNO_3 and then treated with ammonia in the usual way in order to obtain cuticle preparations.

The material consists of about 100 single internodes, deriving mostly from Przenosza. Only a few joined internodes were obtained, though in the rock the shoots may consist of several internodes. Only 12 internodes bore leaves.

The leaves proved brittle and crumbled easily during maceration. One specimen, however, provided most of the inner cuticles of a whorl of leaves and the basal parts of the upper cuticles. Leaves were found in the material from Przenosza.

A few internodes show dark hypodermal strands adhering to the cuticle and running between the rows of stomata. On certain macerated specimens in the same place strands are seen, consisting of 2 or 3 rows of elongated cells. Some internodes show distinct parallel ridges, probably resulting from these hypodermal strands.

On certain specimens the stomata are clogged with a dark substance.

Discussion and comparison. The genus *Frenelopsis* is usually classified with the *Cupressaceae*. This is confirmed by the present material where leaves are in whorls of three like in many members of this family and the structure of the stomata is also encountered in other *Cupressaceae*.

I was able to see only the material of *Frenelopsis bohemica* Vel. described by Němejc (1926) and this convinced me that my fossil belonged to the same genus but to a different species. They share such characters as the rectangular shape of the internode, the lack of sutures, the arrangement of leaves in whorls of three, and the distribution of stomata over the whole internode and leaves. *Frenelopsis bohemica* is different from my material in its more slender shoots, its much thinner cuticle, and in having stomata arranged in irregular rows.

I was not able to see the type material of the genus, which is *Frenelopsis Hoheneggeri* described by Schenk (1869) from the Lower Cretaceous of the Silesian Carpathians. I have looked for it in Poland and Czechoslovakia without success.

The description and figures of *Thuites Hoheneggeri* Ettingshausen (1852), which S c h e n k (l. c.) regarded as identical to *Frenelopsis Hoheneggeri,* do not show the stomata arrangement and therefore I leave it out of comparison.

On the whole, comparison with descriptions and figures of similar fossils is difficult and not satisfactory, because they do not provide enough details. The descriptions of fossils named *Frenelopsis* are contradictory as to the number and arrangement of leaves. It is possible that when the whole material is revised the genus which is here regarded as *Frenelopsis* will receive a different name.

The literature concerning *Frenelopsis* and similar fossils is discussed in detail in the paper of Dr. Joan W a t s o n - H e n d e r s o n (in print). Therefore I shall here refer only to a few fossils which seem to be closest to the material from the Carpathians.

The species most similar to my fossil is *Frenelopsis Hoheneggeri.* The figures of S c h e n k (1869) show that the internodes of the two plants agree in size, in their rectangular shape and lack of sutures, and in the appearance of their leaves. The internodes of *F. Hoheneggeri* are marked by regular longitudinal rows of dots which certainly correspond to stomata and are distributed just like the stomata in my material.

There is one important difference. According to the text of S c h e n k, the leaves of *F. Hoheneggeri* are borne in opposite decussate pairs.

For two reasons, however, I am inclined to think that my fossil is identical with *F. Hoheneggeri* of S c h e n k. Firstly, the figures of S c h e n k are strikingly similar to my material. Secondly, I found my fossil also in the Silesian Carpathians and in a locality called Lipnik which is the name of one of S c h e n k's localities with *F. Hoheneggeri.*

The age of the beds is the same.

It appears to me that the difference in the arrangement of leaves might be the result of a mistake, or even that *F. Hoheneggeri* might have had both types of leaf arrangement, decussate pairs of leaves on certain shoots and whorls of three on others, as have certain recent *Cupressaceae,* e. g. *Juniperus chinensis.*

Finally, I decided to assign the fossil to *F. Hoheneggeri,* because before the reexamination of the type material there is no evidence that they are different.

Also *Frenelopsis Hoheneggeri* from the Lower Cretaceous of Portugal described by R o m a r i z (1946) and T e i x e i r a (1948) is very similar. It seems to have rectangular internodes and the structure and arrangement of stomata in regular longitudinal rows is the same as in my material. The leaves are not known.

Two species from the Upper Cretaceous of Portugal, *F. lusitanica* and *F. oligostomata,* differ from *F. Hoheneggeri* in having stomata arranged in an irregular way.

F. Hoheneggeri has certain characters in common with *Manica parceramosa* from the English Wealden, as described by Dr. J. Watson-Henderson (in print). The leaves of *Manica* consist of a small free part and of a leaf base which surrounds the stem. The leaf base often forms a complete cylindrical sheath and is then very similar to the internodes of *F. Hoheneggeri* because the structure and arrangement of stomata is the same in the two fossils. But *Manica* is different in having spirally arranged leaves.

Among recent plants the most similar to *F. Hoheneggeri* are shoots of those species of *Callitris* which have their leaves arranged in whorls of three. *Callitris,* however, is different in having distinct sutures between the decurrent parts of the leaves.

I have macerated a few internodes of *Callitris Drummondi* and found that they easily divide into three leaves along the sutures. In *F. Hoheneggeri,* however, the internodes do not show sutures and do not divide during maceration. *Callitris Drummondi* is also different from. *F. Hoheneggeri* in having stomata arranged in two bands along the leaf and in having subsidiary cells of the stomatal apparatus differentiated into polar and lateral ones.

Tetraclinis articulata is different from *F. Hoheneggeri* in having leaves in false whorls of four. The leaves are decurrent and the stomata are not evenly distributed over the internode.

Age and distribution. The genus *Frenelopsis* is known only from the Cretaceous of Europe and Northern America (cf. map in Florin (1963). The oldest species is *F. Hoheneggeri* which is known from the Lower Cretaceous of Poland (Hauterivian), Czechoslovakia (probably Hauterivian), Germany (Barremian, Lipps 1932), and Portugal (Romariz 1946, Teixeira 1948). Pimienova (1939) described *F. Hoheneggeri* from the Cenomanian of the Ukraine. It has also been recorded from the Campanian and Turonian of France (Carpentier 1937, Zeiller 1882). However, the cuticle of the Turonian material figured by Carpentier looks more like *F. lusitanica.*

F. bohemica occurs in the Upper Cretaceous (Cenomanian) of Czechoslovakia, *F. lusitanica* and *F. oligostomata* in the Upper Cretaceous of Portugal.

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I wish to express my gratitude to Professor F. Němejc (Prague) and to the Authorities of the National Museum in Prague for putting at my disposal the material of *Frenelopsis bohemica;* and to Dr. K. L. Alvin (London) for showing me the *Weichselia reticulata* from the Bommer Collection.

I wish to thank Dr. Joan Watson-Henderson (St. Andrews University) for discussions and for allowing me to read her manuscript.

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STRESZCZENIE

WEICHSELIA RETICULATA I *FRENELOPSIS HOHENEGGERI* Z KARPAT ZACHODNICH

Najlepiej znanymi mezofitycznymi roślinami z Karpat są skamieniałe pnie *Cycadeoidea*, pochodzące najprawdopodobniej z dolnej kredy. Oprócz nich są znane jeszcze inne rośliny dolnokredowe. Po raz pierwszy w 1852 Ettingshausen wymienił kilka gatunków ze stanowisk w Bramie Morawskiej i na Pogórzu Śląskim w okolicy Cieszyna. W 1869 roku Schenk opisał z tego właśnie obszaru 22 gatunki roślin dolnokredowych z 7 miejscowości.

W 1960 roku znalazłam w Przenoszy koło Skrzydlnej (Beskid Średni), a więc znacznie dalej na wschód, niż poprzednie stanowiska, łupki zawierające drobne, lecz oznaczalne szczątki roślinne. W pobliżu tego właśnie miejsca został poprzednio znaleziony pień *Cycadeoidea*. W tym samym roku dr W. Nowak z Karpackiej Stacji Terenowej IG w Krakowie wskazał mi łupki zawierające te same rośliny w Lipniku koło Bielska (Pogórze Śląskie).

W Lipniku poziom zawierający rośliny należy według Gerocha i Nowaka (1963, str. 247, 261, 262) do łupków grodziskich i jest wieku dolnokredowego.

Ogromną większość szczątków roślinnych w tych łupkach tworzą dwie rośliny: *Weichselia reticulata* i *Frenelopsis Hoheneggeri*.

Weichselia reticulata (*Filicinae incertae sedis*) posiada charakterystyczną siatkowatą nerwację, co pozwala je oznaczyć, nawet gdy znajduje się pojedyncze odcinki liści. Oprócz tego znaleziono tarczkowate indusia tej rośliny. *Weichselia reticulata* występuje w dolnej kredzie Europy, a także w Północnej Afryce, w Azji oraz Ameryce Północnej.

Frenelopsis Hoheneggeri (*Coniferae, Cupressaceae*) tworzy pędy złożone z małych, prostokątnych segmentów, które często są znajdowane oddzielnie. Charakterystyczną cechą *F. Hoheneggeri*, różniącą go od innych gatunków europejskich, jest ustawienie szparek w regularne, równoległe rzędy wzdłuż segmentu. Rodzaj *Frenelopsis* występuje tylko w kredzie Europy i Ameryki Północnej, gatunek *F. Hoheneggeri* niemal wyłącznie w dolnej kredzie Europy.

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Plate I

All figures are unretouched photographs

Frenelopsis Hoheneggeri Schenk

Fig. 1. Cuticle with stomata, × about 150, S 207.
Fig. 2. Cuticle of inner (adaxial) side of two leaves, × 25, S 209.
Fig. 3. Two joined internodes without leaves, showing arrangement of stomata, × 8, S 223.
Fig. 4. Upper part of an internode with a whorl of three leaves, on this side two leaves are visible, × 7, S 222.
Fig. 5. Other side of the same specimen showing the third leaf, × 7, S 222.
Fig. 6. Cuticle showing arrangement of stomata, × 50, S 207.

Weichselia reticulata Stokes et Webb

Fig. 7. Indusium seen from below, showing incurved margin and stalk, × about 40, S 205.
Fig. 8. Pinna from under side, showing venation, × 10, S 206.
Fig. 9. Rachis with smaller rounded pinnae standing upright, × about 10.
Fig. 10. Same indusium as in Fig. 7 seen from above, × about 40, S 205.
Fig. 11. Under side of pinna fragment showing venation, × about 10.

Tablica I

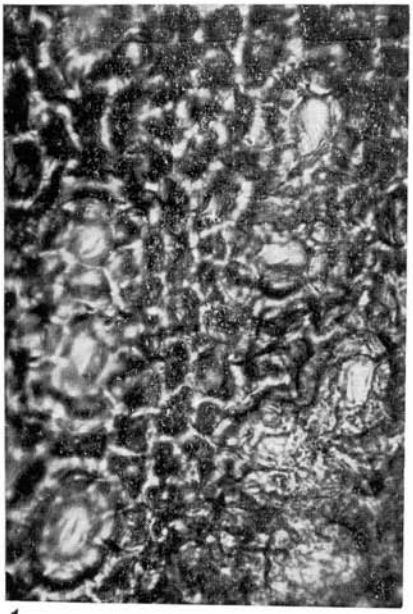
Wszystkie ryciny są nieretuszowanymi fotografiami

Frenelopsis Hoheneggeri Schenk

Fig. 1. Kutykula z widocznymi aparatami szparkowymi, × około 150, S 207.
Fig. 2. Kutykula wewnętrznej strony dwóch liści, × 25, S 209.
Fig. 3. Dwa połączone bezlistne segmenty, widoczne rozmieszczenie aparatów szparkowych, × 8, S 223.
Fig. 4. Górna część segmentu z okółkiem z trzech liści, ukazująca dwa liście, × 7, S 222.
Fig. 5. Odwrotna strona tego samego okazu, widoczny trzeci liść, × 7, S 222.
Fig. 6. Kutykula ukazująca rozmieszczenie aparatów szparkowych, × 50, S 207.

Weichselia reticulata Stokes et Webb

Fig. 7. Indusium widziane od dołu, widoczny zawinięty brzeg oraz trzonek, × około 40, S 205.
Fig. 8. Odcinek liściowy od dołu z widocznym unerwieniem, × 10, S 206.
Fig. 9. Małe zaokrąglone odcinki liściowe stojące pionowo na osi, × około 10.
Fig. 10. To samo indusium co na Fig. 7, tu widziane od góry, × około 40, S 205.
Fig. 11. Dolna strona odcinka liściowego z widocznym unerwieniem, × około 10.



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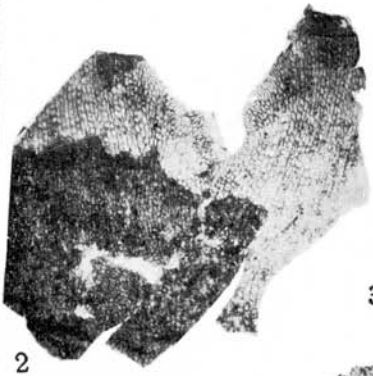

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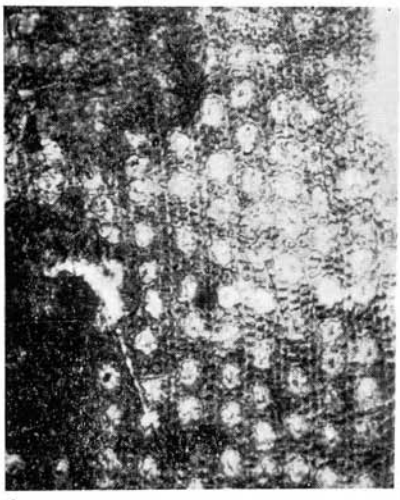

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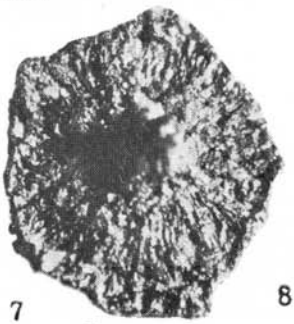

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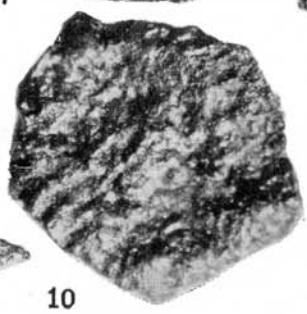

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