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THE GENUS *FRENELOPSIS* SCHENK AND THE TYPE SPECIES *FRENELOPSIS HOHENEGGERI* (ETTINGSHAUSEN) SCHENK

Rodzaj *Frenelopsis* Schenk i jego gatunek typ *Frenelopsis hoheneggeri* (Ettingshausen) Schenk

ABSTRACT

In the absence of the type material of the Lower Cretaceous conifer *Frenelopsis hoheneggeri* (Ettingshausen) Schenk it is proposed that the plant with three leaves described in 1965 by Reymanówna from the Lower Cretaceous in the Carpathians from the locality at Przenosza be accepted as identical with this species. It appears certain that the material of Schenk and of Reymanówna was heterogeneous and contained also a second plant with only one leaf at a node which is called *Manica* Watson. The genera *Frenelopsis* and *Manica* are classified in the family *Cheirolepidiaceae* on evidence obtained by other authors that both produced male cones yielding *Classopollis* Pflug pollen.

An emended diagnosis of the genus *Frenelopsis* and of the type species *Frenelopsis hoheneggeri* are given. A lectotype for *Frenelopsis hoheneggeri* and a neotype for its epidermal structure are selected. The structure of the epidermis and stomata is described in detail on the evidence of SEM micrographs. The list of the known species of *Frenelopsis* is given.

The articulated shoots of *Frenelopsis* and *Manica* have a succulent appearance recalling the halophyte *Salicornia (Chenopodiaceae)*. This would suggest a xerophytic and/or halophytic habitat for these fossil plants.

INTRODUCTION

In 1852 Ettingshausen described conifer shoots collected by Mr. Hohenegger of Teschen (now Cieszyn in Poland) from Lower Cretaceous rocks in the Carpathians. He figured two specimens collected from Murk, near

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Neutitschein (now in Czechoslovakia) and named them *Thuites hoheneggeri*. In 1869 Schenk described further material, from another Carpathian locality (Leipnik), which he considered identical with Ettingshausen's material. At the same time he removed the plants to a new genus, *Frenelopsis*, because he considered them to be closer to the living genus *Frenela*, now a synonym of *Callitris* of the *Cupressaceae*.

Efforts by several palaeobotanists have failed to locate any of Ettingshausen's or Schenk's specimens. The absence of this important material has long impeded progress in elucidating an ill-defined genus which has been used by numerous authors.

New material was collected by Reymanówna (1965) from a few localities in the Polish Western Carpathians, mainly at Przenosza near Limanowa, S. E. of Kraków. The plants appeared identical with those described by Schenk (1869) and were from the Grodziszcze Beds of Hauterivian age, though from localities further to the east and north.

Hitherto, the definition of the genus *Frenelopsis* has been based only on the descriptions and drawings of Ettingshausen and Schenk and the most important characters, leaf number and arrangement, have been in doubt. Ettingshausen's plate 1, fig. 7 (1852) clearly shows cyclic leaf arrangement and his diagnosis suggests that there are four leaves in a whorl. Schenk (1869) interpreted the leaf arrangement of some of his specimens as opposite and decussate (e. g. Schenk 1869, pl. VI, fig. 6). The material collected by Reymanówna has yielded numerous specimens bearing 3 leaves per node but not one with opposite and decussate pairs. We believe that Ettingshausen and Schenk were mistaken and were dealing with plants having leaves in whorls of three. It seems clear that Schenk studied only internodes attached to the rock, never freed from it. Unless one can turn the specimen over it is easy to confuse alternating whorls of three with an opposite and decussate arrangement (see Barale 1973, text. fig. 1 and plate II, fig. 1).

The material from Przenosza was described by Reymanówna (1965) as *Frenelopsis hoheneggeri*. Further studies have shown the material to be heterogeneous, containing a mixture of shoots with three leaves per node and shoots with one leaf per node (but at first thought to have no leaves).

On studying Schenk's figures (1869) we are sure that he also had heterogeneous material. One can see in his plate VI, figs. 1, 3 and 6 that the specimens have more than one leaf per node whilst plate IV. figs. 5 and 6 and plate VI, fig. 2 show internodes apparently without leaves. Clearly there are strong reasons for supposing that Schenk and Reymanówna were dealing with the same two species.

There can be no doubt that both Ettingshausen and Schenk thought that their plant had more than one leaf per node and therefore the one with three leaves at the node should be given the name *Frenelopsis* Schenk. On that basis we propose a new diagnosis of the genus.

We further propose that the Przenosza species with three leaves should

be accepted as identical with the type species *Frenelopsis hoheneggeri* (Ettingshausen) Schenk.

Dr. Hluštik is investigating *Frenelopsis*-like plants from localities of Ettingshausen and Schenk which are in Czechoslovakia and he will continue to search for the type material. Clearly his results may change what we have said in this paper but in the meantime we hope it will serve as a useful basis for redescription and comparison of other species which are currently undergoing revision by several workers.

The other species present in the Przenosza material (and presumably in Schenk's) is now known to be *Manica parceramosa* (Fontaine) Watson (1974) which has one very small leaf per node. This is a widely distributed species also known from the Lower Cretaceous of U. S. A. (Fontaine, 1889; Watson in preparation), England (Watson 1964 and in preparation), Portugal (Alvin in press) and Africa (Chaloner, pers. comm.). Amongst the English material of *Manica parceramosa* (Fontaine) are male cones which have yielded *Classopollis* Pflug pollen. *Classopollis* has also been found by Hluštik and Konzalová (1975) in cones attributed to *Frenelopsis alata* (K. Feistmantel) and it now seems that these plants hitherto regarded as *Cupressaceae* should be classified in the family *Cheirolepidiaceae*.

SYSTEMATIC DESCRIPTIONS

Order *Coniferales*

Family *Cheirolepidiaceae*

Genus *Frenelopsis* Schenk 1869:13

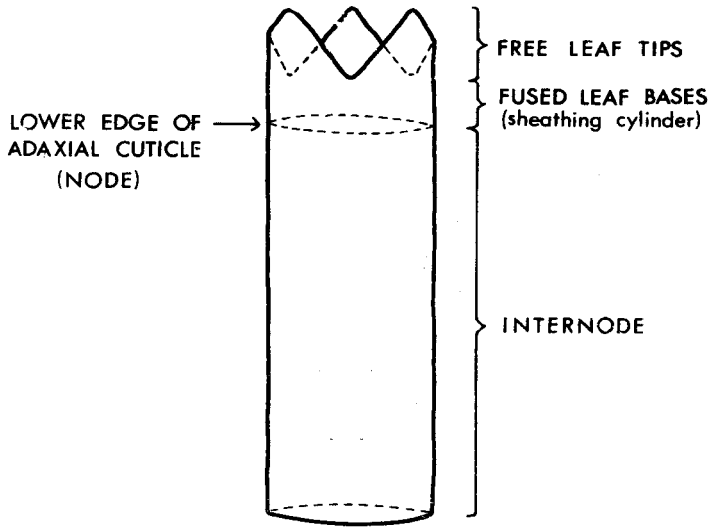
Emended diagnosis. Branching, articulated shoots consisting of cylindrical internodes each extending at the upper margin into a whorl of normally three scale-like, adpressed, triangular leaves; successive whorls alternating; internode surface smooth showing no grooves or sutures. Stoma circular, monocyclic or incompletely amphicyclic having guard cells sunken below a ring of subsidiary cells which form a stomatal pit.

Type species. *Thuites hoheneggeri* Ettingshausen 1852: 26

A minimal diagnosis for *Frenelopsis* has been given in order that it may, at least temporarily, serve to accommodate all the three-leaved species which are currently undergoing revision.

Frenelopsis Schenk as diagnosed above consists of units in which there is no visible demarcation between leaf and internode on the abaxial surface. *Manica* Watson is similar but the leaves are borne singly in a simple helix. Because the leaf and internode are continuous certain difficulties arise in de-

scribing these cheirolepidiaceous conifers. Text-fig. 1 shows a typical *Frenelopsis* internode plus whorl of leaves and the terminology we have employed here. The line along which the adaxial cuticle joins the base of the internode above we shall call the node; the surface of the stem below this level we shall



Text-fig. 1. Diagrammatic representation of a disarticulated unit of *Frenelopsis hoheneggeri* labelled to show the terminology used in the text

Ryc. 1. Schematyczne przedstawienie pojedynczego członu *Frenelopsis hoheneggeri* z objaśnieniem terminologii użytej w tekście, po lewej: dolny brzeg doosiowej kutikuli (węzeł); po prawej od dołu ku górze: międzywęźle, zrośnięte nasady liści, wolne końce liści

call the internode. However we clearly do not know how much of it was contributed developmentally by leaf or axis. In *Cupressinocladus* Seward (Chaloner, Lorch 1960) the stem shows separate cushions below the leaves with distinct grooves or sutures between them.

Frenelopsis hoheneggeri (Ettingshausen) Schenk

Pl. I, II, III, IV; Text-figs. 1, 2

1852 *Thuites hoheneggeri* Ettingshausen: 26, pl. 1, figs. 6—7.
1869 *Frenelopsis hoheneggeri* (Ettingshausen) Schenk (pro parte): 13, pl. 6, figs. 1, 3, 6.
1965 *Frenelopsis hoheneggeri* (Ettingshausen); Reymanówna (pro parte): 19, pl. I, figs. 2, 4—5; text fig. 2 B, D, K,

Emended diagnosis. Elongated internodes up to 10 times as long as wide, typically 8 mm × 3 mm; triangular leaves, 3 per whorl, up to 1·5 mm long × up to 2·5 mm wide with blunt apex, joined basally to form sheathing cylinder about 1 mm deep. Abaxial surface of leaf showing about 15 protruding ridges converging towards leaf apex; margin of leaf scarious. Thickly cutinised internodes

with regularly spaced vertical rows of less thickly cutinised stomata, 10 to 12 rows per mm; stomatal rows continuing onto abaxial surface of leaf, converging towards leaf apex. Stomatal rows typically separated by 2—4 files of square or elongated epidermal cells; stomata within a row separated by 1—4 epidermal cells, occasionally with subsidiary cells adjacent. Stoma circular, 60 to 70 μ diameter with 4—6 (most often 4) subsidiary cells forming a pit above sunken guard cells. Subsidiary cells each topped by a large, hollow papilla and having a large tongues haped papilla inside stomatal pit; lower papillae filling stomatal pit and obscuring guard cells. Guard cells arranged more or less transversely, broadly elliptic. Anticlinal walls of subsidiary cells thin (3—4 μ); anticlinal walls of ordinary epidermal cells very thick (10—12 μ). Hypodermis present, having narrow, elongated cells between stomatal rows and square cells below stomatal rows. Adaxial cuticle thinly cutinised, without stomata, consisting of diverging rows of cells.

MATERIAL

Lectotype. We select plate 1 fig. 7 of Ettingshausen 1852 as the lectotype of *F. hoheneggeri* and we propose that specimen No. S 222 of Reymanówna 1965, plate I figs. 4—5 and present paper plate I fig. 1 should serve as neotype for epidermal details.

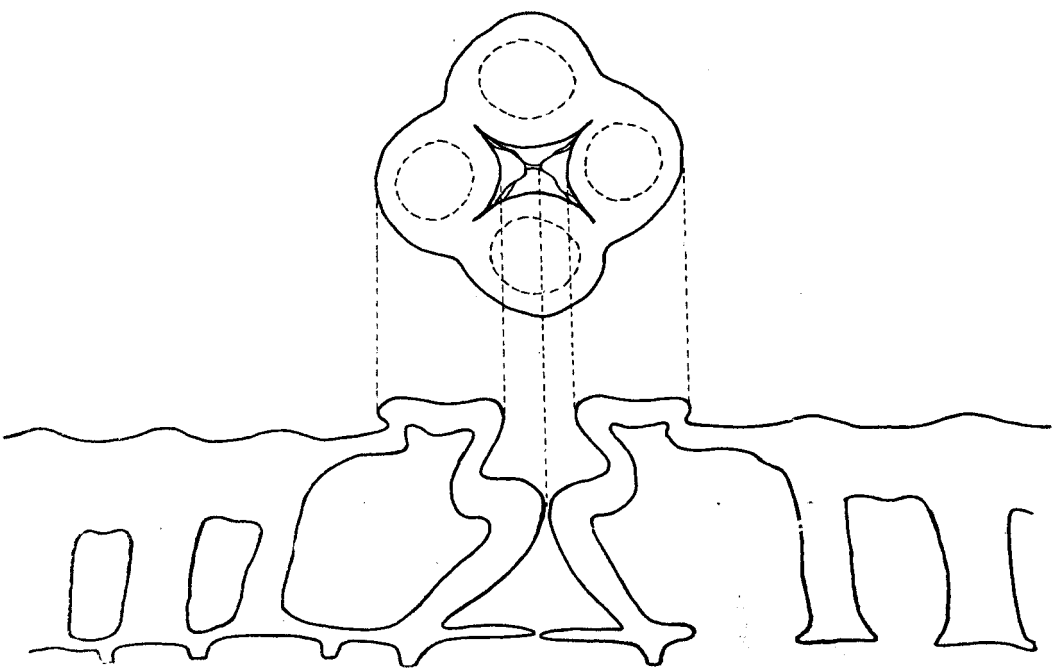
The material described here occurs abundantly in three localities in the Polish Carpathians, Przenosza, Wiśniowa and Lipnik near Bielsko. According to Doc. Dr J. Burtan in the outcrop at Wiśniowa and at Przenosza the fossil plants occur in Grodziszcze-Cieszyn Beds of Hauterivian age from the Sub-Silesian unit (Burtan and others 1974, p. 102—109). At Lipnik near Bielsko they occur in Grodziszcze Shales of Hauterivian-Lower Barremian? age (Geroch, Nowak 1963). It now seems certain according to J. Guzik (personnal communication) that the locality Leipnik of Schenk (1869) is in Czechoslovakia and is not Lipnik near Bielsko.

DISCUSSION AND COMPARISON

All the recently collected material consists of numerous isolated internodes and short lengths of assembled shoot but there are no specimens showing branching.

In this heterogeneous material the cuticle of *Manica parceramosa* (Fontaine) is generally better preserved and microscopic details given by Reymanówna (1965) were based entirely on this species. The complex stoma of *Frenelopsis hoheneggeri* is not easy to understand with light microscope preparations of

indifferent preservation and the SEM has been invaluable. The micrographs in Plate III figs. 1 and 4 show the variability that occurs in surface details and also that many of the stomata are eroded. Plate III figs. 2 and 3 show good examples of well preserved stomata in which the pouchlike papillae on the subsidiary cells coalesce to form a prominent rosette around the rim of the stomatal pit. This feature is not always so well developed as is seen in Plate III figs. 4 and 5. The large papillae inside the stomatal pit (Plate IV fig. 2) are the strongest feature of the stoma under the light microscope (Plate IV fig. 6) but are difficult to find with the SEM when the guard cells and hypodermis are intact (Plate IV, fig. 1). The sections of stomata seen in the SEM (Plate III, fig. 6 and Plate IV, fig. 3) are not entirely satisfactory but were used to help reconstruct the vertical section of the cuticle in text-fig. 2.



Text-fig. 2. *Frenelopsis hoheneggeri* (Ettingshausen) Schenk Diagram of surface view of stoma related to a reconstruction of a section through cuticle; × 1000

Ryc. 2. *Frenelopsis hoheneggeri* (Ettingshausen) Schenk Schematyczny rysunek powierzchni aparatu szparkowego wyjaśniający rekonstrukcję przekroju przez kutikulę; × 1000

This type of stoma with large papillae situated in the stomatal pit is now known in several species of *Frenelopsis* (Alvin, in press; Watson, in preparation) and in one species of *Cupressinocladus* (Watson, in preparation).

A similar mixture of a *Frenelopsis* species and a *Manica* species has been found in silicified material from the Sudan (Watson, Alvin, 1976; Watson, in preparation).

With the imminent publication of several new descriptions, detailed comparison of *F. hoheneggeri* with other species must be deferred but of the species formerly assigned to *Frenelopsis* Schenk we know that the following can be retained in the genus: *F. ramosissima* Fontaine (1889); *F. alata* (K. Feistmantel) Knobloch (Němejc, 1926; Hluštik, 1974; Alvin, in press); *F. oligostomata* Romariz (Romariz, 1946; Alvin, in press); *F. rubiesensis* Barale (Barale, 1973). Unnamed forms with three leaves from the Upper Cretaceous of France and Portugal (Broutin and Pons, 1975) also belong in *Frenelopsis* Schenk.

Amongst these species there is considerable variety in degree of branching, in the extent of the decurrent leaf sheath (Text-fig. 1) and in microscopic details. Some of them show the converging ridges on the triangular leaf. They appear to be associated with dark hypodermal strands which resist maceration. The stomatal rows occur both on and between the ridges (plate II, figs 1—2).

The most striking feature about all the species of *Frenelopsis* Schenk and *Manica* Watson is that the articulated shoots have a succulent appearance resembling some stem of succulent dicotyledons rather than any living conifer. They remind us of *Salicornia* of the *Chenopodiaceae* which flourishes on mud laden with salt or soda and it is interesting to note that the similarity was also mentioned by the early palaeobotanists, e. g. Zeiller (1872). There is strong evidence that one of the Lower Cretaceous species from U. S. A. (Watson, in preparation) was distinctly succulent with a very limited amount of wood and it seems that a xerophytic and/or halophytic habitat is indicated.

ACKNOWLEDGEMENTS

We are very grateful to Doc. J. Burtan for showing us the locality at Wiśniowa and for discussion of the age of the beds with *Frenelopsis* at Wiśniowa and Przenosza. We are most grateful to Dr K. L. Alvin for access to his manuscript on Portuguese conifers, also to Prof. T. M. Harris for discussion and helpful suggestions. The SEM work was done in the Department of Textile Technology, Manchester University and the photography by Mr. Brian Atherton, except for plate 1, figs 1—2 which were photographed by Dr Z. Dzwonko.

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STRESZCZENIE

RODZAJ *FRENELOPSIS* SCHENK I JEGO GATUNEK TYP *FRENELOPSIS HOHENEGGERI* (ETTINGSHAUSEN) SCHENK

Materiał, na podstawie którego został opisany rodzaj rośliny szpilkowej *Frenelopsis* Schenk i gatunek *Frenelopsis hoheneggeri* (Ettingshausen) Schenk z dolnej kredy Zachodnich Karpat, nie został na razie odnaleziony. Utrudnia to postęp badań nad tym rodzajem, prowadzonych obecnie w różnych krajach. W 1965 r. Reymanówna opisała nowy materiał z warstw grodziskich w Karpatach ze stanowisk położonych bardziej ku wschodowi, głównie ze stanowiska

Przenosza koło Limanowej. Wiek warstw grodziskocieszyńskich z roślinami w Przenoszy został określony przez geologów jako hoteryw (Burtan i inni, 1974). Wydaje się, że materiał roślinny z Przenoszy jest identyczny z opisanym przez Schenka, chociaż okazy z Przenoszy posiadają liście ustawione po trzy w okółkach, a nie nakrzyżlegle, jak to podaje Schenk w swej diagnozie.

Autorki sądzą, że materiał opisany jako *Frenelopsis hoheneggeri* przez Schenka i Reymanówną dotyczy dwóch różnych roślin. Jedna z nich posiadała trzy liście wyrastające z węzła, a druga jeden niepozorny liść wyrastający z węzła. Jak się wydaje, zarówno Ettingshausen, jak i Schenk uważali za *Frenelopsis* roślinę posiadającą więcej niż jeden liść w węźle, dlatego roślina o trzech listkach powinna nosić nazwę *Frenelopsis*. Roślina posiadająca jeden listek w węźle należy do rodzaju *Manica* Watson. Obydwa te rodzaje zostały zaliczone do rodziny *Cheirolepidiaceae*, ponieważ u przynależnych do nich szyszeczek pyłkowych inni autorzy stwierdzili ziarna pyłku *Classopollis* Pflug.

Proponuje się, by okazy z Przenoszy o trzech listkach uznać za identyczne z gatunkiem *Frenelopsis hoheneggeri* (Ettingshausen) Schenk. Podana jest poprawiona diagnoza rodzaju *Frenelopsis* Schenk oraz gatunku typu *Frenelopsis hoheneggeri* (Ettingshausen) Schenk. Wybrano lektotyp dla *Frenelopsis hoheneggeri* oraz neotyp dla budowy jego epidermy. Opisano szczegółowo budowę epidermy i aparatów szparkowych na podstawie mikrofotografii z mikroskopu skaningowego (SEM). Podano również listę opisanych dotychczas gatunków *Frenelopsis* mieszczących się w obecnej diagnozie rodzaju.

Złożone z członów pędy *Frenelopsis* i *Manica* mają wygląd rośliny gruboszowatej, a w szczególności przypominają solirodek (*Salicornia*) z rodziny *Chenopodiaceae*. Pozwala to przypuszczać, że *Frenelopsis* i *Manica* rosły na siedliskach słonych, a być może i suchych.

Plate I

Frenelopsis hoheneggeri (Ettingshausen) Schenk

1, 2. light micrographs; 3. scanning electron micrograph. Specimen numbers prefixed V. refer to collection in British Museum (Natural History), specimen numbers prefixed S refer to collection in Institute of Botany, Polish Academy of Sciences.

1. Neotype, node from the side showing two leaves (leaf to the right hand side damaged photographs of the undamaged specimen from both sides in paper of 1965, Pl. I, figs 4—5); S 222; × 8
2. Adjacent internodes showing one leaf and bases of the two adjacent ones; S 226; × 8
3. Oblique view of internode and broken leaf apex (towards top left hand corner) showing protruding ridges; V. 58651; × 50

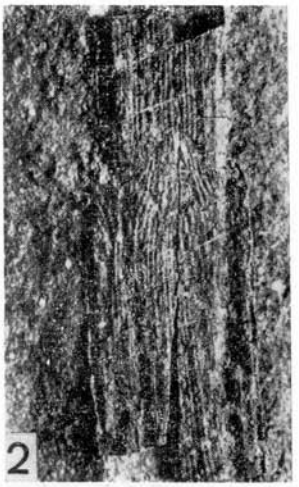
Tablica I

Frenelopsis hoheneggeri (Ettingshausen) Schenk

1, 2. fotografie spod lupy; 3. fotografie spod mikroskopu skaningowego. Okazy, których numer jest poprzedzony literą V., znajdują się w kolekcji British Museum (Natural History), okazy poprzedzone literą S znajdują się w kolekcji Instytutu Botaniki PAN.

1. Neotyp, węzeł od strony ukazującej dwa liście (liść po prawej stronie uszkodzony; zdjęcia tego samego okazu nieuszkodzonego znajdują się w pracy z 1965 r., Tabl. I, fig. 4—5); S 222; × 8
2. Sąsiednie człony z widocznym jednym liściem i nasadami dwóch sąsiednich liści; S 226; × 8
3. Ukośny widok członu i uszkodzonego szczytu liścia (w górnym lewym rogu), ukazujący sterczące żeberka; V. 58651; × 50


1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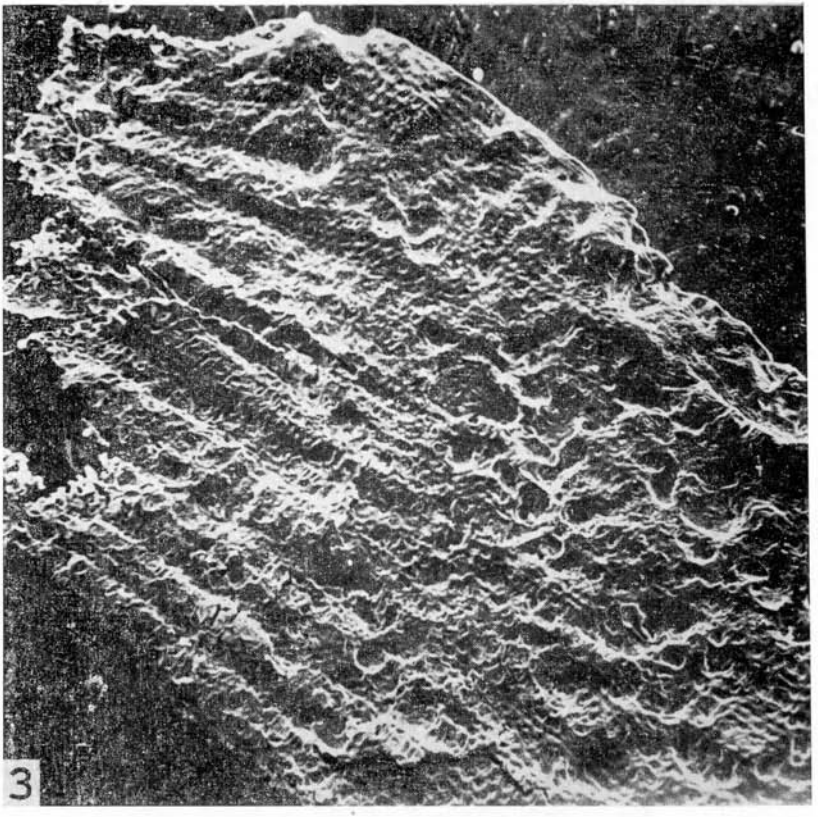
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Plate II

Frenelopsis hoheneggeri (Ettingshausen) Schenk

Scanning electron micrographs

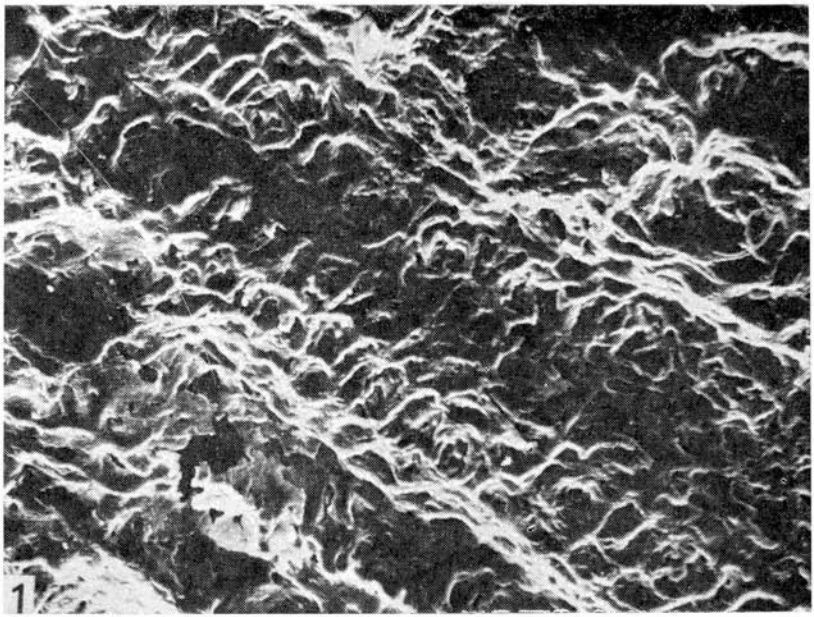
1, 2. Oblique views of leaf showing stomatal rows present both on the ridge and in furrows between them; V. 58651; fig. 1, ×100; fig. 2. ×250

Tablica II

Frenelopsis hoheneggeri (Ettingshausen) Schenk

Fotografie spod mikroskopu skaningowego

1, 2. Ukośny widok liścia ukazujący rzędy aparatów szparkowych obecne zarówno na żeberku, jak i na bruzdach między nimi; V. 58651; fig. 1, ×100; fig. 2, ×250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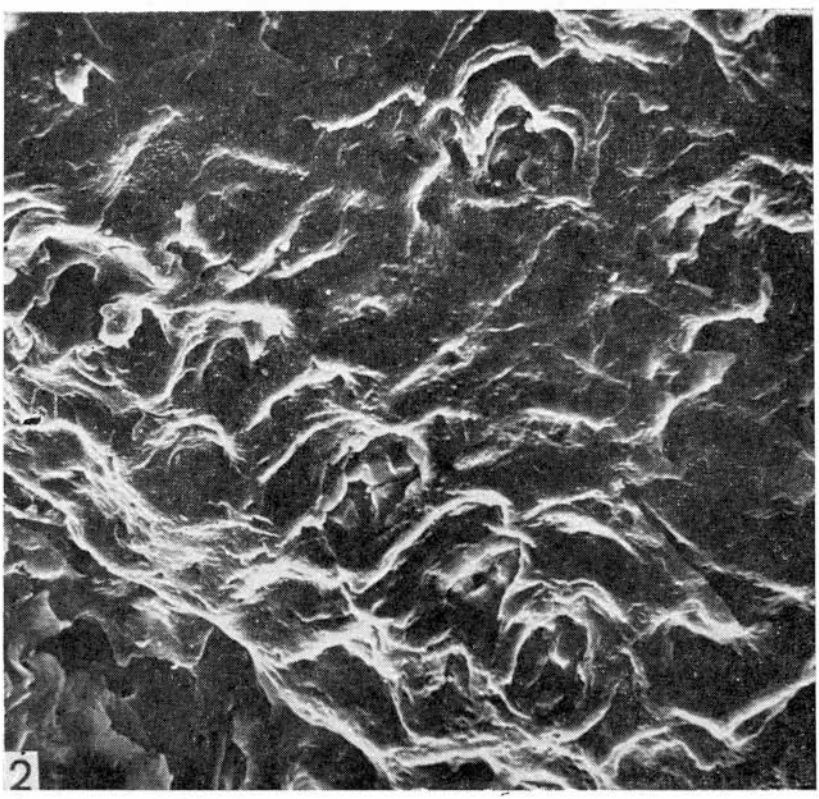
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Plate III

Frenelopsis hoheneggeri (Ettingshausen) Schenk

All scanning electron micrographs

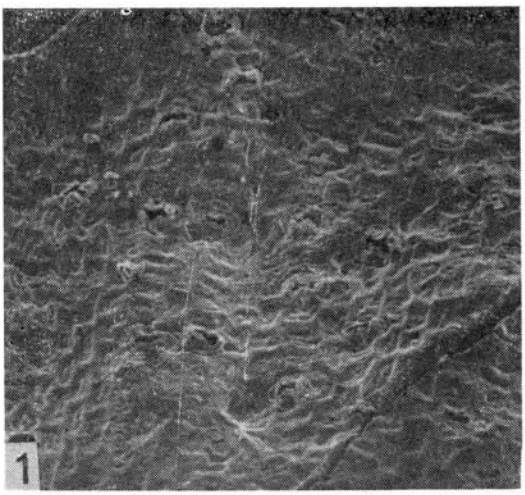
1, 2. External surface of internode cuticle; V. 58650; fig. 1, × 150; fig. 2, × 250
3. Surface view of single stoma showing papillae forming "rosette" around stomatal pit and large papillae filling pit below; V. 58650; × 1000
4, 5. External surface of specimen with less prominent outer papillae; V. 58651; fig. 4, × 150; fig. 5, × 1000
6. Section of stoma; V. 58650; × 500

Tablica III

Frenelopsis hoheneggeri (Ettingshausen) Schenk

Wszystkie fotografie spod mikroskopu skaningowego

1, 2. Zewnętrzna powierzchnia kutikuli międzywęźla; V. 58650; fig. 1, × 150; fig. 2, × 250
3. Widok aparatu szparkowego od góry ukazujący papille tworzące „rozetkę" naokoło jamy szparkowej, jak też duże papille wypełniające komorę poniżej; V. 58650; × 1000
4, 5. Zewnętrzna powierzchnia okazu z mniej wydatnymi zewnętrznymi papillami; V. 58651; fig. 4, × 150; fig. 5, × 1000
6. Przekrój aparatu szparkowego; V. 58650; × 500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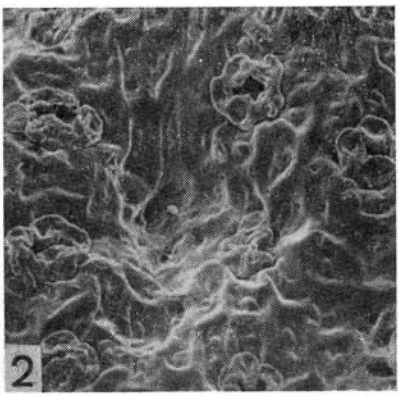
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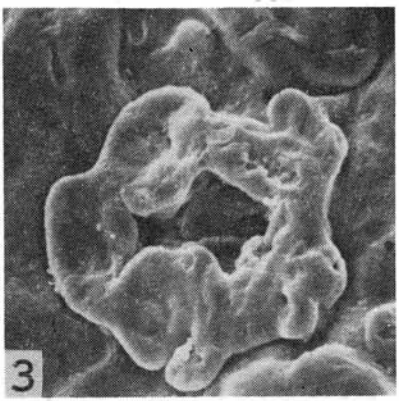
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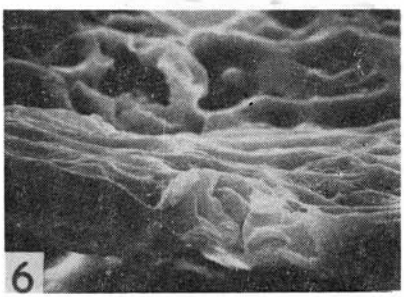
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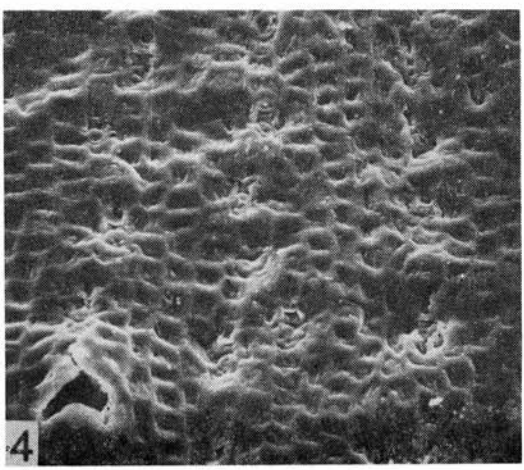
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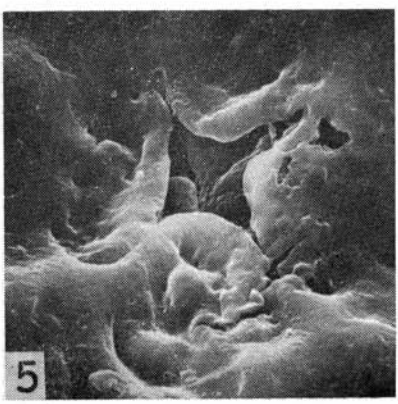
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Plate IV

Frenelopsis hoheneggeri (Ettingshausen) Schenk

1 — 3. Scanning electron micrographs; 4 — 6. light micrographs

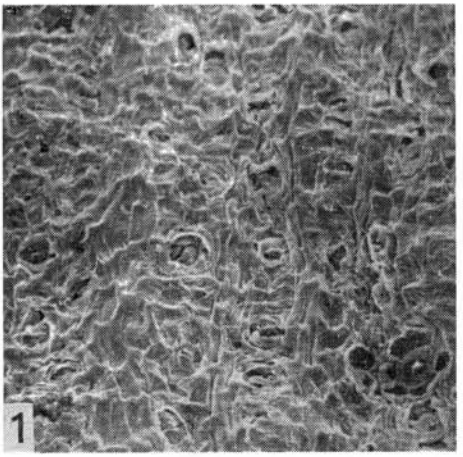
1. Inside view of internode cuticle; V. 58650; × 150
2. Inside view of single stoma. Papillae in stomatal pit can be seen because guard cells are missing; V. 58650; × 1000
3. Section of stoma showing two outer papillae and one papilla in the stomatal pit; V. 58650; × 1000
4. Low power view of cuticle showing stomatal rows; V. 58650; × 100
5. Single stoma in high plane of focus showing "rosette" of papillae around rim of stomatal pit
6. Same stoma in low plane of focus showing papillae in stomatal pit; V. 58650; × 600

Tablica IV

Frenelopsis hoheneggeri (Ettingshausen) Schenk

1 — 3. fotografie spod mikroskopu skaningowego; 4 — 6. fotografie spod mikroskopu świetlnego

1. Kutikula międzywęźla widoczna od wewnątrz; V. 58650; × 150
2. Aparat szparkowy widoczny od wewnątrz. Papille w jamie szparkowej są widoczne ponieważ brak jest komórek szparkowych; V. 58650; × 1000
3. Przekrój aparatu szparkowego ukazujący dwie zewnętrzne papille oraz jedną papillę w komorze szparkowej; V. 58650; × 1000
4. Widok kutikuli spod małego powiększenia ukazujący rzędy aparatów szparkowych; V. 58650; × 100
5. Pojedynczy aparat szparkowy, górny poziom ostrości, widoczna "rozetka" z papilli naokoło brzegu komory szparkowej
6. Ten sam aparat szparkowy, dolny poziom ostrości, widoczne papille w komorze szparkowej; V. 58650; × 600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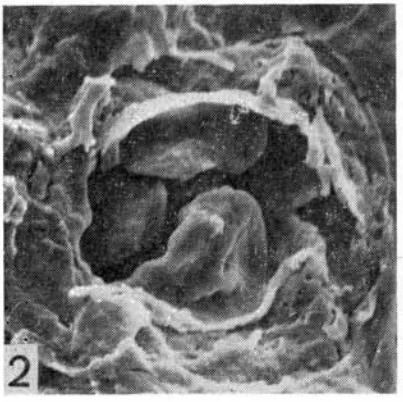
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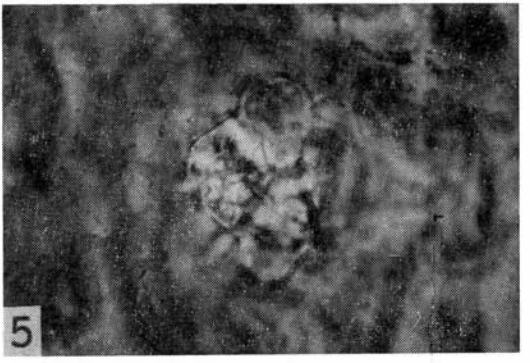
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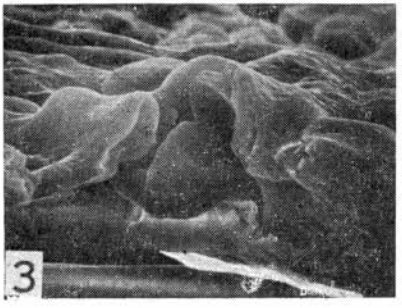
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