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FRENELOPSIS HARRISII SP. NOV. FROM THE CRETACEOUS
OF TAJIKISTAN, USSR

Frenelopsis harrisii sp. nov. z kredy Tadżykistanu, ZSRR

ABSTRACT. In 1976 the material of *Frenelopsis harrisii* sp. nov. was found by M. P. Doludenko in the Cenomanian of Tajikistan, this being the second finding of the genus in the USSR. *F. harrisii* differs from other species by its unusual structure of the epidermis which is described in detail and illustrated with SEM micrographs. The outlines of the epidermal cells are marked by narrow grooves, the cell walls are built of two layers, an outer of a homogeneous substance and an inner of a granular or spongy substance. This epidermal structure is probably evidence of a very specialized habitat. Like other species of the genus, *F. harrisii* shows several xeromorphic characters. *F. harrisii* is compared with other species, a list of the species is given and the age of the genus is discussed.

INTRODUCTION

Reliable findings of the genus *Frenelopsis* Schenk, 1869 (*Coniferales*) have become known in many countries of Europe (Czechoslovakia, Poland, Portugal, Spain, France, Germany), in Asia, Africa and the USA. In the USSR some remains of *Frenelopsis* were recognized in the Albian deposits of the Ukraine (Pimenova 1939).

In autumn 1976 during the field works carried out in the Tajik SSR in the south-western spurs of the Darvaz range in the Bokodara gorge, M. P. Doludenko (1978) collected in calcareous sandstones numerous compressions of *Frenelopsis* branches. These plant remains were found in near-sea-shore deposits together with numerous remains of traces of fossil organism's activity (bioturbates or trace fossils) attributed to the genera *Scalarturba*, *Planolites*, etc., as well with two specimens of pelecypods identified by L. A. Anuprienko as *Chla-*

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mys sp. (? cf. *Chlamys elongatus* Lam.). L. A. Anuprienko considers this identification as rather tentative, because the poor preservation of the molluscs does not allow a more exact identification. *Chlamys elongatus* Lam. was observed in the Tajik depression in the Cenomanian and in the Late Albian — Cenomanian in England and France. The age interval of *Scalariturba* and *Planolites* is very wide, as they occur also in the Palaeozoic. They are associated with the zone of the shelf, being a good index of conditions of sedimentation.

AGE OF REMAINS OF THE GENUS *FRENELOPSIS*

Thus, in Tajikistan *Frenelopsis* was found in Cretaceous deposits just as in most other countries. Up to now the genus *Frenelopsis* has been known everywhere from Cretaceous deposits, only in Spain in the Lerida province, remains of *F. rubiesensis* were described by Barale (1973) from lithographic limestones attributed to the uppermost parts of the Upper Jurassic. Barale, not discussing the problem of the age of this formation in Spain, says, however, that if to be guided by our present day knowledge of the vertical distribution of the genus *Frenelopsis* throughout the Cretaceous, the finding of this genus in the lithographic limestones of Lerida would allow to attribute them to the Lower Cretaceous. One may assume, however, that *Frenelopsis*, its culmination being observed in the Cretaceous, was represented (in places, at least) by some species during the Upper Jurassic.

Below is given the list of the known at present species of *Frenelopsis* and their distribution, taking into account the recent revision of the material from Portugal by Alvin (1977) and from the USA by J. Watson (1977). The list reflects approximately the present knowledge of the genus, when certain old materials were reinvestigated, but others still await revision.

Proceeding from the available data and those presented in the list, we can say that the genus *Frenelopsis* appears for the first time in the uppermost parts of the Upper Jurassic of Spain. In the Lower Cretaceous this genus occurs already in Europe and in Africa (*F. hoheneggeri* in Czechoslovakia, Poland, Germany and *Frenelopsis* sp. in Sudan) and in North America (*F. ramosissima* in USA, Virginia). At the end of the Lower and during the Middle Cretaceous (Aptian-Cenomanian) the genus flourishes as several species are known from a number of countries. *F. ramosissima* in the USA and *F. occidentalis* from Portugal are known from the Aptian to the Albian, *F. alata* from Czechoslovakia, Portugal and the USA occurs from the Aptian to the Cenomanian and perhaps even to the Upper Cretaceous and *F. harrisii* possibly in the Cenomanian of Tajikistan. During the Upper Cretaceous the genus declines. There is known *F. obigostomata* from the Senonian of Portugal and *F. aff. alata* from the Turonian and Coniacian of Czechoslovakia. Apparently, the genus died out before the end of the Upper Cretaceous.

Considering the morphological resemblance, the genus *Frenelopsis* was attributed for a long time to the family *Cupressaceae*. However, as it has already

been noted by one of the authors (Reymanówna 1965, p. 23), the genus *Frenelopsis* shows some significant differences even from the most similar amongst the *Cupressaceae* genera *Callitris* and *Tetraclinis*. The study of the male cones of *Frenelopsis alata* from the Cenomanian of Czechoslovakia (Hluštík & Konžalová 1976) showed that abundant pollen grains contained in some of them belong to the genus *Classopollis* Pflug 1933, emend. Pocock and Jansonius 1961. Pollen grains of *Classopollis* were attributed up till now to the family *Cheirolepidiaceae* (= *Hirmeriaceae*) and their occurrence in a male cone of *Frenelopsis* raises the question of assigning the genus *Frenelopsis* to this family. The structure of epidermis in *Frenelopsis* (thick cuticle, entrance of stomatal pit surrounded by 4—5 subsidiary cells with thick papillae) speaks in favour of attributing this genus to the family *Cheirolepidiaceae*.

Below is given the description of a new species of *Frenelopsis* from Central Asia which is named *F. harrisii* in honour of Professor Thomas Maxwell Harris, F.R.S. who visited the Botanical Institute in Kraków, while both authors were working on this species.

SYSTEMATIC DESCRIPTION

Order *CONIFERALES*
 Family *Cheirolepidiaceae*
 Genus *Frenelopsis* Schenk 1869
Frenelopsis harrisii sp. nov.

Pl. I—VII

Holotype: Geological Institute of the Academy of Sciences of the USSR, N 3377/11, 11a (Pl. I, 3; Pl. II, 1—2; Pl. III, 1—7; Pl. IV, 3; Pl. V, 1-3). USSR, Tajikistan, south-western part of the Darvaz range, Bokodara gorge, Cenomanian (?).
 Diagnosis. Shoots branching in one plane (longest specimen 23 cm) lateral shoots alternating, arising at distances of about 8 mm at an angle of 20°—45°, but higher up frequently changing direction to a more vertical, lateral shoots giving up branches of the third order similarly arranged. Width of main shoots about 4 mm, of lateral shoots about 3 mm and of branches of third order 1—2 mm. Internodes 8—12 mm long. Leaves in alternating whorls of three, triangular, up to 1.5 mm long, 2 mm wide, with blunt apex, abaxial side without protruding ridges, adaxial side and leaf margin not known.

Cuticle of internodes typically with regularly spaced vertical rows of stomata, separated by 3—4 files of epidermal cells, stomata within a row separated by 2—3 cells.

Epidermal cells arranged in regular files, cells approximately square, occasionally polygonal, with rounded corners, typically 20—33 μm \times about 20 μm ,

their length 0.5—2 times their width, in section height of cells 2—3 times their width, periclinal and anticlinal walls very thick, cell lumen high and narrow. Outlines of epidermal cells marked by narrow grooves, surface of periclinal walls typically sunken in the middle, in certain regions bulging or rarely extending into a conical hair about 50 μm long.

Walls of epidermal cells consisting of two types of substance, an outer yellow homogeneous one and an inner darker granular or spongy one. Basal parts of anticlinal walls consisting of homogeneous substance gradually thinning upwards and acquiring on inner side a gradually thickening layer of granular substance; periclinal wall with very thin and frequently damaged outer homogeneous layer and up to 12 μm thick inner granular layer. Frequently inside granular substance present angular cavities about 1 μm in diameter, giving the substance a spongy consistency and suggesting that in the living plant they may have contained crystals. Angular cavities frequently forming a single layer below the surface of periclinal cell walls and grooves between them. Stomata inconspicuous, typically elliptical $45 \times 20 \mu\text{m}$, with 4—5 subsidiary cells forming a pit above sunken guard cells. Protruding upper parts of subsidiary cells either similar to those of ordinary epidermal cells but much smaller or in the shape of rounded lobes forming a dome over stomatal pit. On side facing stomatal pit each subsidiary cell bearing a large tongue-shaped papilla in the throat of pit and usually a small one at pit entrance. Papillae with specialized surface, fitting each other when closed. Guard cells rarely preserved, thin and indistinct.

Adaxial leaf cuticle unknown, abaxial consisting of files of cells converging towards apex, at base similar to cuticle of internode, higher up stomata rare and epidermal cells gradually elongating. Stomata on leaves more or less circular.

Hypodermis distinct on internode in the form of thinly cutinised, elongated cells between stomatal files.

DISCUSSION

Structure of epidermis. *Frenelopsis harrisii* shows an unusual structure of the surface and of the walls of the epidermal cells. The epidermis as seen in the SEM recalls a cobbled surface, because the periclinal portion of each cell is separated from others by narrow grooves. Such a structure does not occur typically in any other species of *Frenelopsis*. Only exceptionally in *F. alata* from Portugal Alvin (1977) observed that the cuticle on one side of the shoot had the outlines of epidermal cells marked by furrows. Dr Alvin thinks that this is perhaps due to degradation of the exposed side of the specimens since they were collected years ago. The limited amount of material did not allow him a closer investigation of this problem. As the cuticle preparations of *F. harrisii* were made in the first months after collecting, it appears that there was no degradation of this sort and we assume that this is the real structure of its epidermis.

Unusual is also the structure of the walls of the epidermal cells of *F. harrisii*. While in other species they are more or less homogeneous, in *F. harrisii* they look in the light microscope, as if built of a thin layer of a homogeneous substance, covered on the inside by a layer of a granular, secretion like substance. Usually the granular substance contains many small transparent spaces, angular in outline which suggests that in the living plant they may have contained crystals. The SEM appears to show no difference between the solid and granular substance, but the angular transparent spaces are seen in the SEM as cavities which gives the substance a spongy consistency.

It is not possible to decide, whether the granular substance represents really a secretion, or whether it is a different layer of the cutinised cell wall. It can only be stated that it is not soluble in concentrated nitric acid. In the periclinal wall of the epidermal cells the homogeneous substance is very thin and frequently damaged, showing the spongy substance below. This might indicate that only the homogeneous substance represents the real cell wall, however, there is not sufficient evidence for this interpretation.

It can be assumed that the unusual structure of the epidermal cells and their walls in *F. harrisii* is an indication that the plant lived in a very specialized habitat. It seems likely that this was some kind of xerophytic habitat, because, like other species of the genus, *F. harrisii* shows xeromorphic characters in its morphology and cuticle structure. The internodes have obviously taken over the function of photosynthesis, as they are covered with an epidermis showing numerous stomata, while the leaves are reduced. The stomata have deeply sunken guard cells and the stomatal pit may be closed at two levels by papillae. Structure of stomata. The stomata of *F. harrisii* are similar in type to those of other species, but differ in certain details. They are oval in shape and two times as long as wide, while in other species the stomata are circular. Circular stomata occur typically on leaves of *F. harrisii*. Unlike in most species, the stomata of *F. harrisii* are frequently inconspicuous, because the subsidiary cells may be similar to ordinary epidermal cells, though smaller. The papillae inside the stomatal pit show a system of grooves and ridges and also of small outgrowths and cavities which apparently fit together when the papillae adhere. A similar specialization of the surface of the papillae may occur also in other species, e.g. in *F. hoheneggeri*, but not to such a degree.

Comparisons. *F. harrisii* is different from all other species of the genus by the unusual structure of the epidermal cells and by its inconspicuous oval stomata. In addition, most species of *Frenelopsis* show a character which distinguishes it from *F. harrisii*. *F. rubiesensis* has much smaller leaves with protruding ridges which show as 4—5 furrows on the imprint of the leaf on the rock. *F. hoheneggeri* is different in having stomatal rows with closely spaced stomata which continue almost to the leaf apex. *F. ramosissima* is different in its very rich branching and in the presence of a papilla or conical hair on each epidermal cell. *F. occidentalis* differs from *F. harrisii* in having subsidiary cells which are flush with the surface of epidermal cells. *F. alata* differs in having stomata arranged in

Occurrence of the *Frenelopsis* species

Species	Country, age	References
<i>Frenelopsis</i> sp.	France, Upper Cretaceous	Broutin & Pons 1975
<i>F. oligostomata</i> Romariz	Portugal, Senonian	Romariz 1946; Alvin 1977
<i>F. hoheneggeri</i> (Ettingshausen) Schenk	France, Campanian, Turonian	Zeiller 1882; Carpentier 1933, 1937; Lecointre & Carpentier 1938
<i>F. aff. alata</i> (K. Feistmantel) Knobloch	Czechoslovakia, Turonian, Coniacian	Hluštík 1974
<i>F. alata</i> (K. Feistmantel) Knobloch = <i>F. bohémica</i> Velenovský	Czechoslovakia, Cenomanian	K. Feistmantel 1881; Velenovský 1887, 1888; Bayer 1921; Němejc 1926; Knobloch 1971; Hluštík 1972, 1974; Hluštík & Konzalová 1976
<i>F. alata</i> (K. Feistmantel) Knobloch = <i>F. lusitanica</i> Romariz	Portugal, Cenomanian	Romariz 1946; Alvin 1977
<i>F. harrisi</i> Doludenko et Reymanówna	USSR, Tajikistan, Cenomanian	The present paper
<i>F. elegans</i> Chow & Tsao	East China, Cretaceous	Chow & Tsao 1977
<i>F. alata</i> (K. Feistmantel) Knobloch	USA, Texas, Albian	Watson 1977
<i>F. ramosissima</i> Fontaine	USA, Virginia, Maryland Barremian-Albian	Fontaine 1889; Berry <i>et al.</i> 1911; Seward 1919; Watson 1977
† <i>F. occidentalis</i> Heer	Portugal, Aptian, Albian	Heer 1881; Alvin 1977
<i>F. hoheneggeri</i> (Ettingshausen) Schenk	Czechoslovakia, Moravia, Lower Cretaceous-USSR, Ukraine, Albian Germany, Barremian Poland, Hauterivian,	Ettingshausen 1852; Schenk 1869; Hluštík 1974 Pimenova 1939 Lipps 1932 Schenk 1869; Reymanówna 1965; Reymanówna & Watson 1976
<i>Frenelopsis</i> sp.	Czechoslovakia, Moravia, †Hauterivian)	Hluštík 1974
<i>Frenelopsis</i> sp.	Sudan, Lower Cretaceous	Edwards 1926; Watson & Alvin 1976; Watson 1977
<i>F. rubiesensis</i> Barale	Spain, †Uppermost, †Jurassic Valanginian-Barremian	Barale 1973

rather irregular stomatal rows. *F. elegans*, as far as can be judged from illustrations, differs in its stomatal rows in which the stomata are frequently not separated by ordinary epidermal cells.

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STRESZCZENIE

FRENELOPSIS HARRISII SP. NOV. Z KREDY TADŻYKISTANU, ZSRR

W 1976 r. jedna z autorek (M. P. Doludenko) znalazła materiał *Frenelopsis harrisii* sp. nov. w utworach kredowych (? cenoman) Tadżykistanu. Jest to drugie znalezienie *Frenelopsis* na terenie ZSRR. *F. harrisii* różni się od innych gatunków niezwykłą budową skórki, która została szczegółowo opisana i zilustrowana za pomocą fotografii z mikroskopu skaningowego. Zarysy komórek skórki są zaznaczone za pomocą wąskich rowków, a ściany komórek są zbudowane z dwóch warstw, zewnętrznej litej i wewnętrznej z ziarnistej lub gąbczastej substancji. Ta budowa skórki świadczy prawdopodobnie o bardzo wyspecjalizowanym siedlisku. Podobnie, jak inne gatunki tego rodzaju, *F. harrisii* posiada szereg cech kseromorficznych. Materiał *F. harrisii* porównano z innymi gatunkami, podano listę dotąd opisanych gatunków oraz przedyskutowano wiek tego rodzaju.

Plate I

Frenelopsis harrisii sp. nov.

1. Branch with well preserved leaves; No. 3377/66, $\times 1$
2. The same branch showing leaves distinctly visible under the binocular; No. 3377/66, $\times 1$
3. Holotype above, marked by an arrow; No. 3377/11, $\times 0.5$

Tablica I

Frenelopsis harrisii sp. nov.

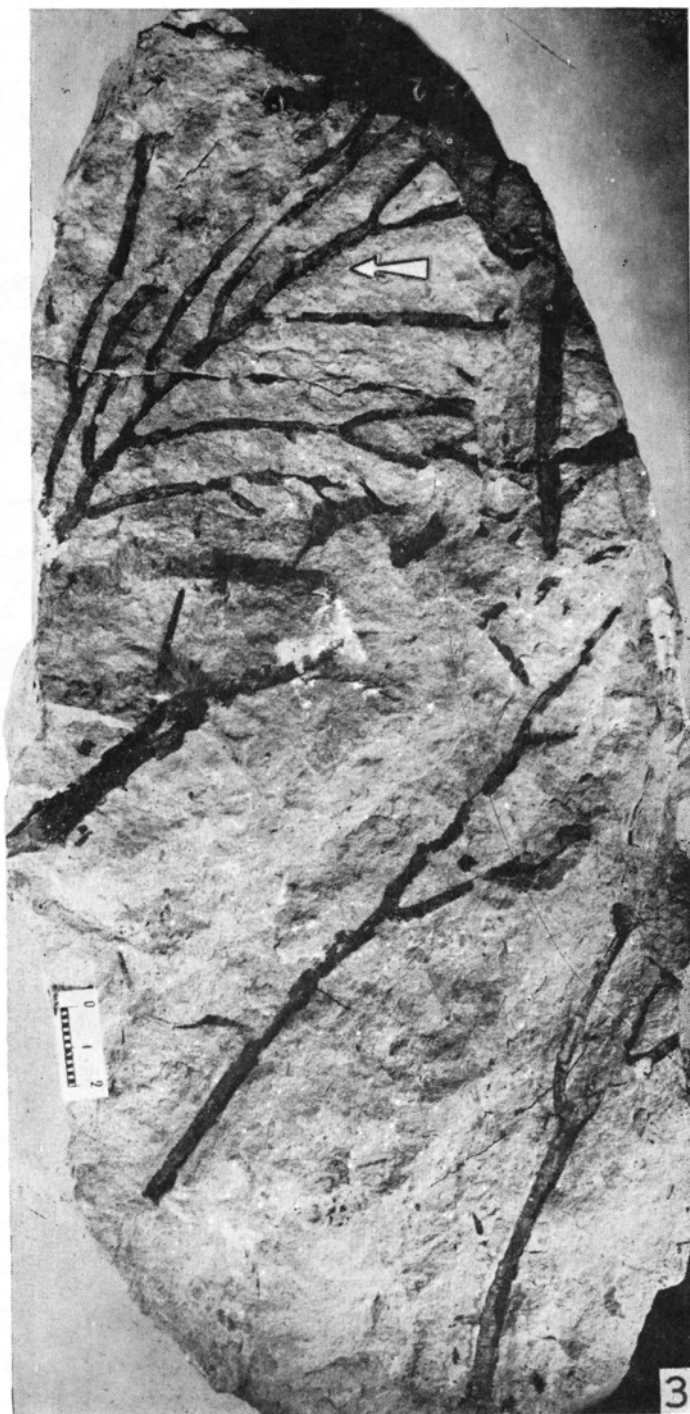
1. Gałązka z dobrze zachowanymi liśćmi; No. 3377/66, $\times 1$
2. Ta sama gałązka ukazująca liście dobrze widoczne pod lupą; No. 3377/66, $\times 1$
3. Powyżej holotyp, zaznaczony strzałką; No. 3377/11, $\times 0.5$



1



2



3

Plate II

Frenelopsis harrisii sp. nov.

1. Holotype, counterpart of the lower part of the branch; No. 3377/11a, × 1
2. Holotype, upper part of the branch; No. 3377/11, × 1

Tablica II

Frenelopsis harrisii sp. nov.

1. Holotyp, odwrotna strona dolnej części gałązki; No. 3377/11a, × 1
2. Holotyp, górna strona gałązki; No. 3377/11, × 1

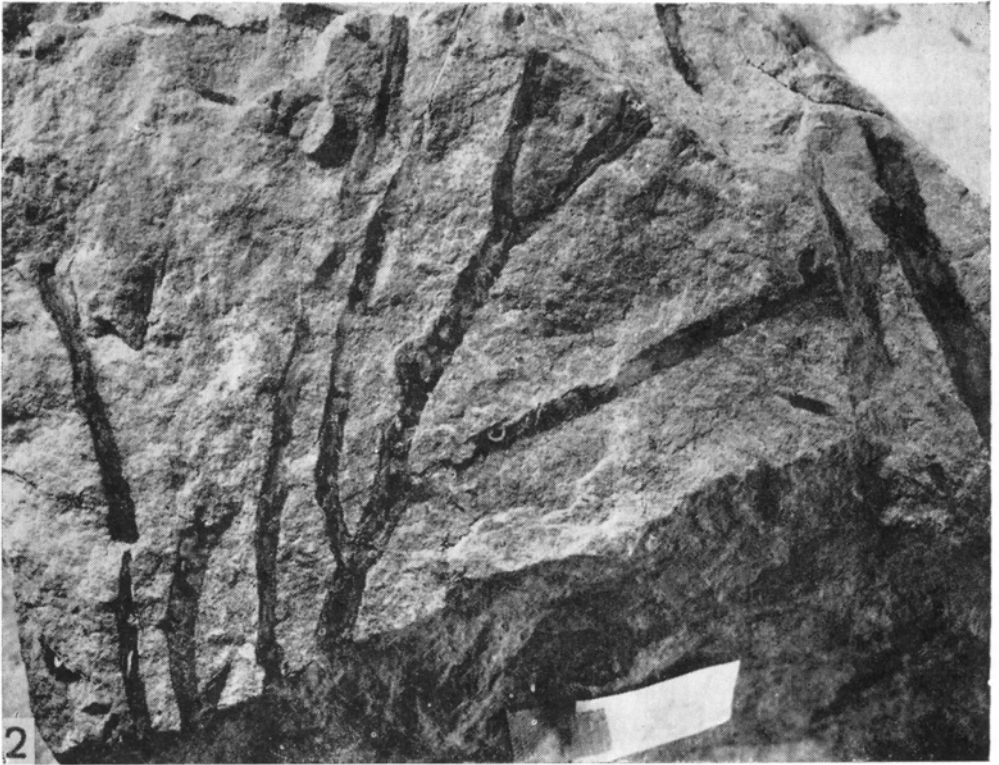
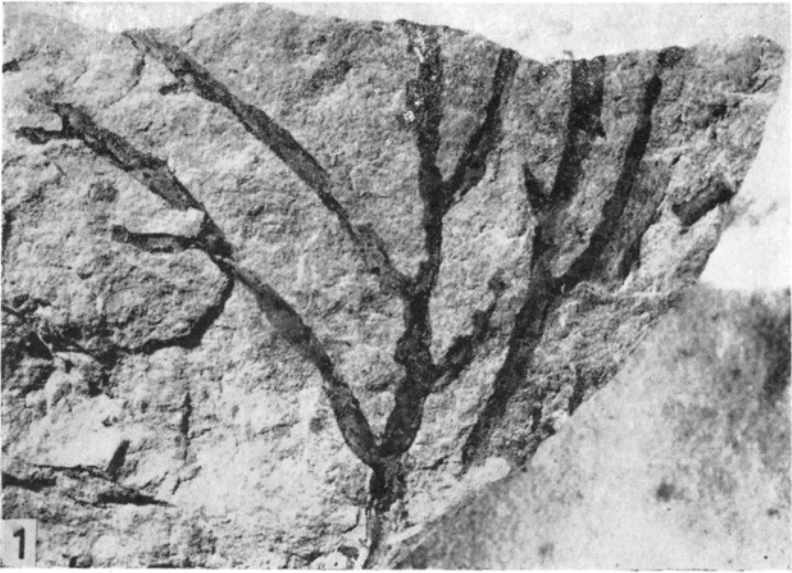


Plate III

Frenelopsis harrisii sp. nov.

- 1, 2. Leaves; No. 3377/11, $\times 25$
3. Internode cuticle with stomatal bands; No. 3377/11, $\times 25$
4. The same as 3, $\times 80$
5. Cuticle of the internal surface of the node (?) without stomata; No. 3377/11, $\times 75$
- 6, 7. Stomata and epidermal cells; No. 3377/11, $\times 300$

Tablica III

Frenelopsis harrisii sp. nov.

- 1, 2. Liście; No. 3377/11, $\times 25$
3. Kutykula międzywęzła z pasami szparkowymi; No. 3377/11, $\times 25$
4. To samo co 3, $\times 80$
5. Kutykula wewnętrznej powierzchni węzła (?) bez aparatów szparkowych; No. 3377/11;
 $\times 75$
- 6, 7. Aparaty szparkowe i komórki skórki; No. 3377/11, $\times 300$

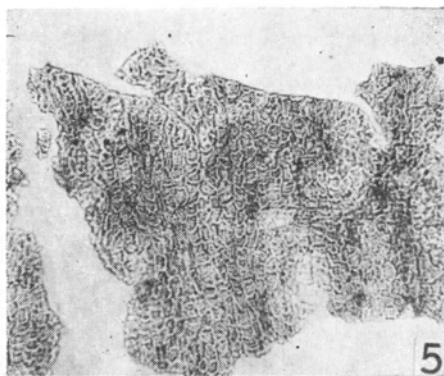
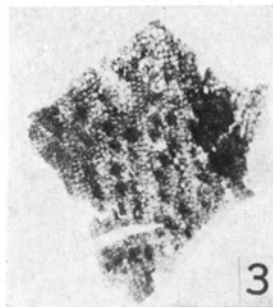
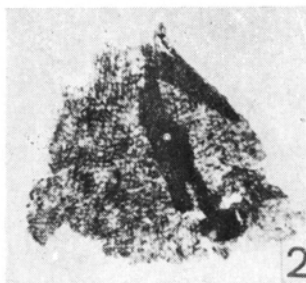
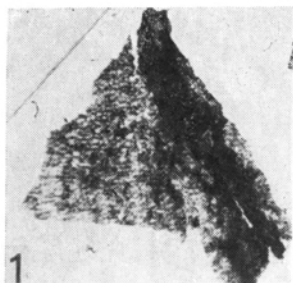


Plate IV

Frenelopsis harrisii sp. nov.

Scanning electron micrographs

1. External surface of cuticle showing epidermal cells, to the right with typical surface, to the left with unusual bulging surface or extending into conical hairs; 3377/66, \times 200
2. External surface of cuticle showing outlines of epidermal cells marked by grooves and stomata with subsidiary cells resembling epidermal cells. Epidermal cell surface frequently damaged; 3377/66, \times 500
3. External surface of cuticle, visible stoma with subsidiary cells in the form of rounded lobes; 3377/11, \times 600

Tablica IV

Frenelopsis harrisii sp. nov.

Fotografie z mikroskopu skaningowego

1. Zewnętrzna powierzchnia kutykuli ukazująca komórki skórki, po prawej z typowo wykształconą powierzchnią, po lewej o powierzchni wypukłej lub wyciągniętej w stożkowate włosy; 3377/66, \times 200
2. Zewnętrzna powierzchnia kutykuli ukazująca zarysy komórek epidermy zaznaczone przez wąskie rowki oraz aparaty szparkowe o komórkach pomocniczych podobnych do komórek skórki. Powierzchnia komórek skórki miejscami uszkodzona; 3377/66, \times 500
3. Zewnętrzna powierzchnia kutykuli, widoczny aparat szparkowy z komórkami pomocniczymi w postaci zaokrąglonych płatów; 3377/11, \times 600

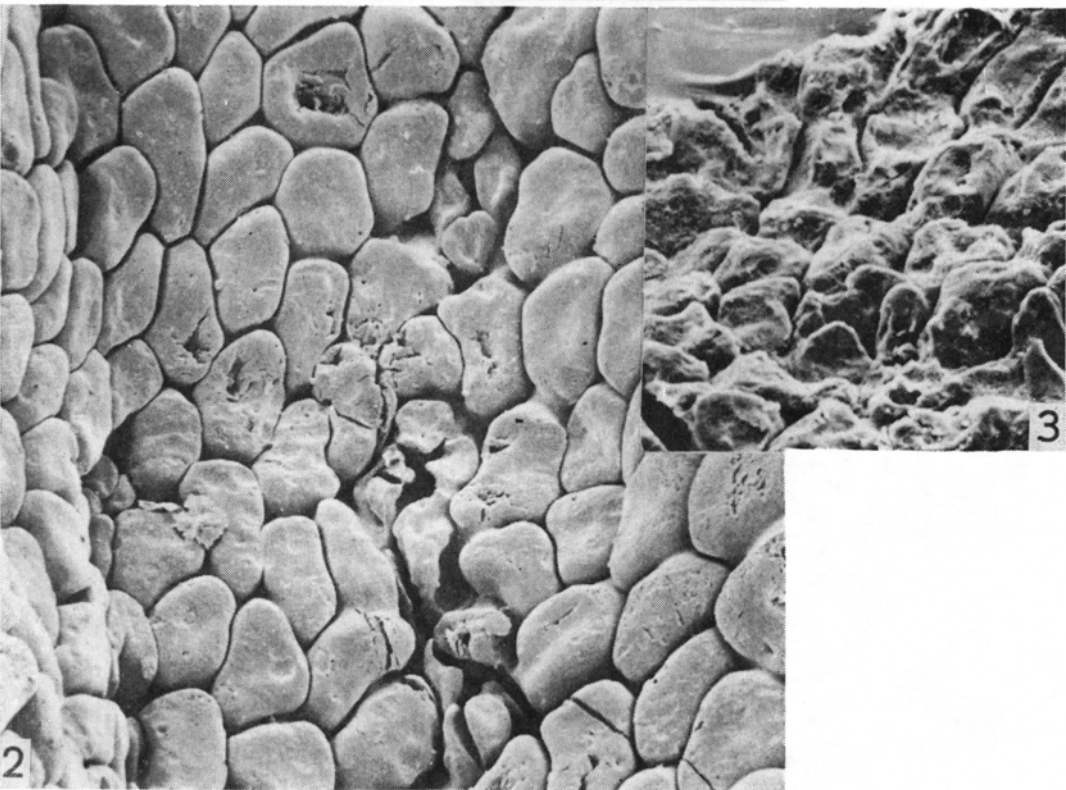
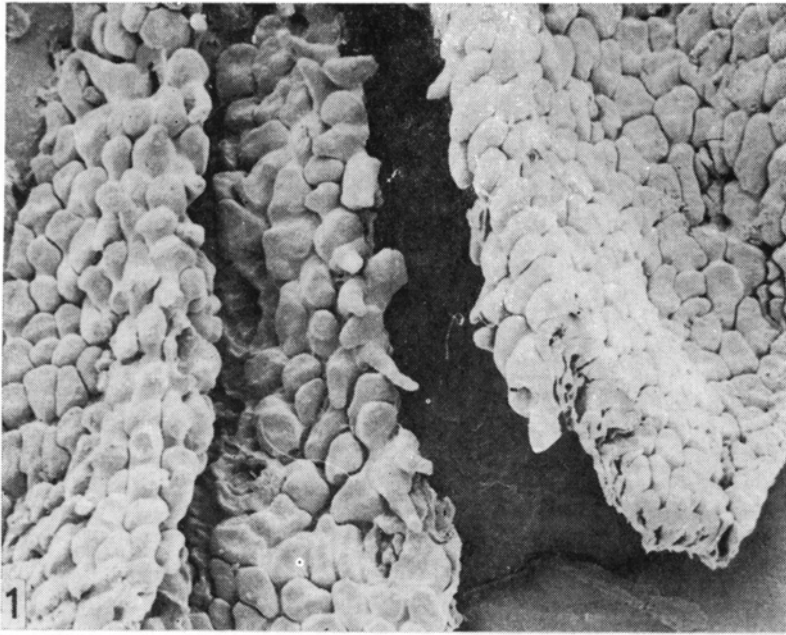


Plate V

Frenelopsis harrisii sp. nov.

Scanning electron micrographs

1. Internal surface of cuticle with stomata and hypodermis. The arrows mark the stomata presented in 2 and 3 of the same plate; 3377/11, \times 250
2. Stoma marked in 1 by upper arrow; 3377/11, \times 900
3. Stoma marked in 1 by lower arrow; 3377/11, \times 900

Tablica V

Frenelopsis harrisii sp. nov.

Fotografie z mikroskopu skaningowego

1. Wewnętrzna powierzchnia kutykuli z widocznymi aparatami szparkowymi i hypodermą. Strzałki oznaczają aparaty szparkowe przedstawione na 2 i 3 na tej samej tablicy; 3377/11, \times 250
2. Aparat szparkowy zaznaczony na 1 górną strzałką; 3377/11, \times 900
3. Aparat szparkowy zaznaczony na 1 dolną strzałką; 3377/11, \times 900

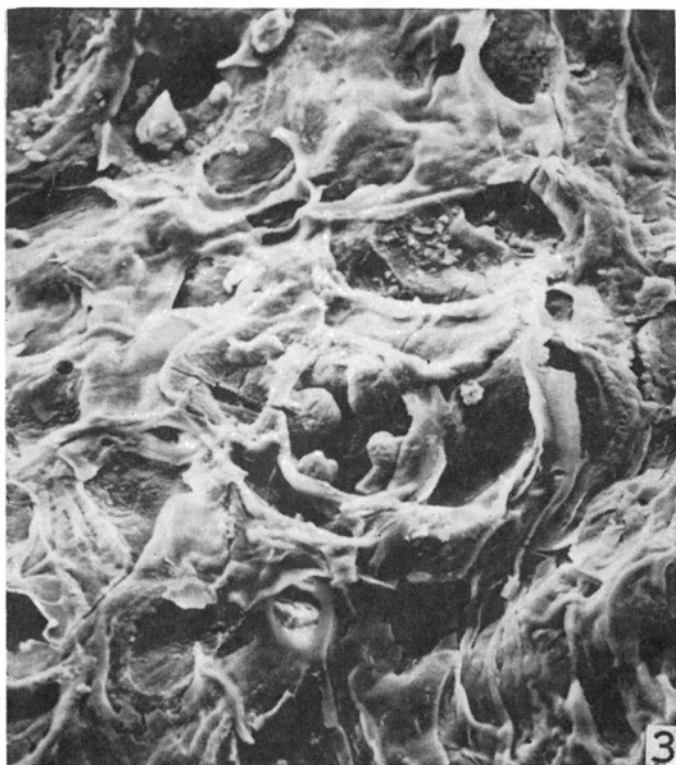
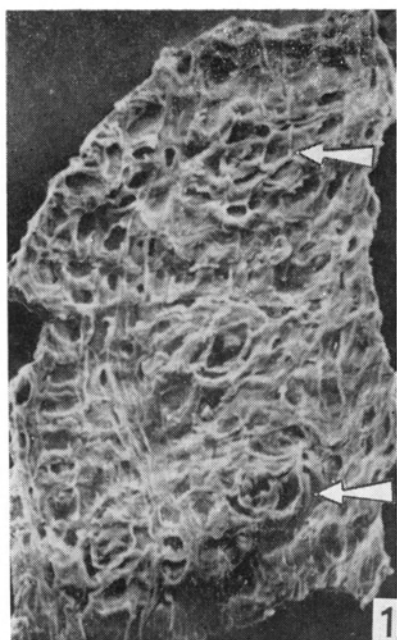


Plate VI

Frenelopsis harrisii sp. nov.

Scanning electron micrographs

1. Surface view of single stoma showing protruding lobes of subsidiary cells and papillae filling stomatal pit; 3377/66, \times 2000
2. Inside view of single stoma, showing ring of papillae in the stomatal pit; 3377/66, \times 2000

Tablica VI

Frenelopsis harrisii sp. nov.

Fotografie z mikroskopu skaningowego

1. Widok aparatu szparkowego od góry, ukazujący sterzące w postaci płatów komórki pomocnicze oraz papille wypełniające komorę szparkową; 3377/66, \times 2000
2. Aparat szparkowy widoczny od wewnątrz, widoczny pierścień papilli w komorze szparkowej; 3377/66, \times 2000

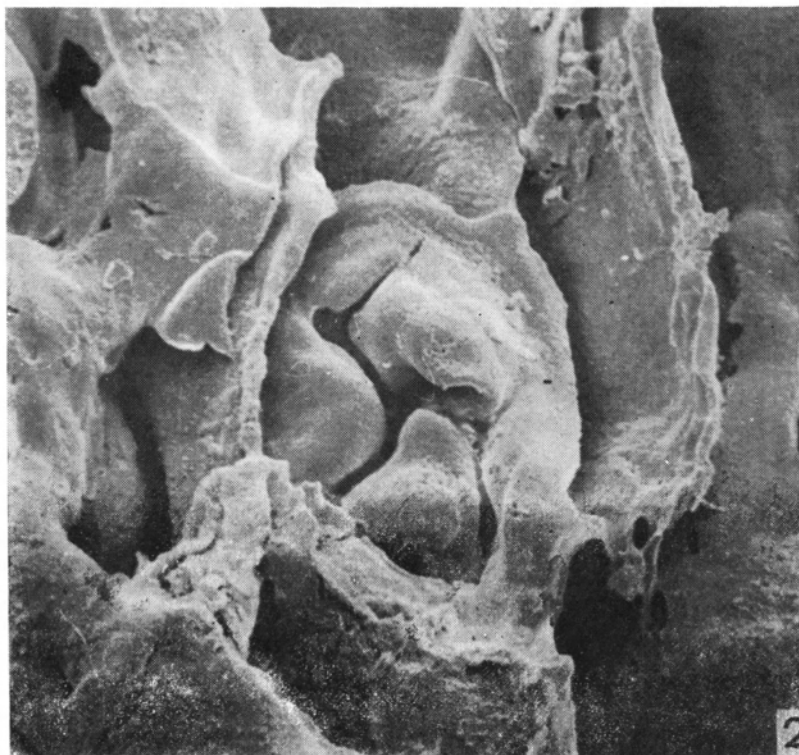
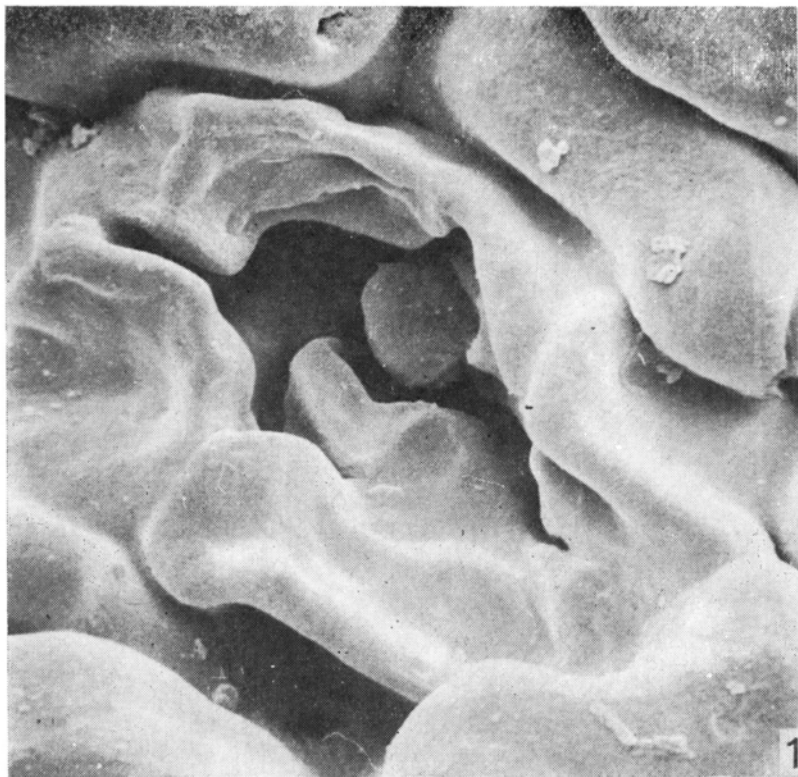


Plate VII

Frenelopsis harrisii sp. nov.

Scanning electron micrographs

1. Cuticle in section showing thick walls of epidermal cells differentiated into homogeneous and spongy substance, to the left stoma; 3377/66, $\times 1000$
2. Section of stoma showing large papillae in the stomatal pit; 3377/66, $\times 1000$

Tablica VII

Frenelopsis harrisii sp. nov.

Fotografie z mikroskopu skaningowego

1. Kutykula w przekroju ukazująca grube ściany komórek skórki, złożone z substancji litej i gąbczastej, po lewej aparat szparkowy; 3377/66, $\times 1000$
2. Przekrój aparatu szparkowego ukazujący wielkie papille w komorze szparkowej; 3377/66, $\times 1000$

