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NEW DATA AND REVISON OF THREE GYMNOSPERMS FROM THE CENOMANIAN OF BOHEMIA – *SAGENOPTERIS VARIABILIS* (VELENOVSKÝ) VELENOVSKÝ, *MESENEA BOHEMICA* (CORDA) comb. n. AND *ERETMOPHYLUM OBTUSUM* (VELENOVSKÝ) comb. n.

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Abstract. New data from cuticular analysis are provided for three fossil plant taxa from the Cenomanian of Bohemia. *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ is newly revised and its comparison with *S. mantelii* is discussed. Leaves of *S. variabilis* are peltate, consisting of 3-(?5) lanceolate pinnae with reticulate venation. The new genus *Mesenea* is compared with similar Mesozoic genera *Almargemia* FLORIN, *Ticoa* ARCHANGELSKY and *Ctenozamites* NATHORST. The species *Mesenea bohemica* (CORDA in REUSS) comb. n., newly recorded from several Bohemian Cenomanian localities, is compared with *Kirchnera arctica* Heer and considered to be of cycadalean affinity. The tripinnate fronds consist of entire-margined or loosely dentate pinnae with odontopteroid venation. Its cuticle shows typical characters of cycads including haplocheilic stomata and small thick–walled cells. The ginkgoalean leaf *Eretmophyllum obtusum* (VELENOVSKÝ) comb. n. is synonymized with *Nehvizdya obtusa* (VELENOVSKÝ) HLUŠTÍK and *Podozamites obtusus* VELENOVSKÝ. Its relationship with *E. andegavense* is discussed. It shows obtuse entire-margined leaves with typically forking venation and extremely thick cuticle.

■ Upper Cretaceous, Cenomanian, Fossil Plants, Gymnosperms, *Sagenopteris, Eretmophyllum, Mesenea.*

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Introduction

Cenomanian sediments yielding abundant plant remains are exposed in the southern edge of the Bohemian Cretaceous Basin in the west and central part of the Czech Republic (Central Europe). Past investigations of the Cenomanian flora were largely done during 19th century by Velenovský (1882, 1883, 1884, 1885ab, 1887, 1888a,b, 1889), Bayer (1900, 1914, 1921), and later by Velenovský and Viniklář 1926, 1927, 1929, 1931). Cuticles of the Cenomanian plants were at first studied by Bayer (1914, 1921) and by Němejc (1926). During the 1960s authors began selected revisions (Hluštík 1974, 1980) based on cuticular analyse which are continued in the present paper.

This contribution is focused on the Lower Cretaceous or Jurassic fossil plant taxa *Sagenopteris* and *Eretmophyllum* and one enigmatic plant - *Mesenea.* They co-occur in plant assemblages with developing and spreading taxodiaceous conifers and angiosperms. These archaic reminders of Mesozoic gymnospermous floras, including other groups described elsewhere (Kvaček 1995, Kvaček and Knobloch 1997, Knobloch and Kvaček 1997, Kvaček in press) survived during the Cenomanian and are recorded from numerous localities of the Bohemian Cretaceous Basin. Accessories to the above mentioned genera are recorded also higher in Cretaceous (e.g. Krassilov 1979 – *Sagenopteris microphylla*, Hluštík 1978 - *Frenelopsis* aff. *alata,* Alvin 1977 - *Frenelopsis oligostomata*). It is remarkable, that none of these plants persisted into the Tertiary.

The material was recovered from the localities that belong to the Peruc - Korycany Formation of the Bohemian Cretaceous Basin (as defined by Čech et al. 1980). Data on sedimentology and palaeoecology of the formation in Pecínov open clay pit were published by Uličný and Špičáková (1996) and Uličný et al. (1997). Palynological data indicate late middle Cenomanian age for this formation (Pacltová 1977).

Material and methods

New fossil material has been collected at the localities Praha - Hloubětín brick-kiln, Pecínov, and Horoušany - Kamenná Panna clay pits. Historical specimens were studied in the collections of the National Museum, Prague. They came from localities that no longer exist: Praha – Malá Chuchle, Praha – Slivenec, Mšené-lázně, and Nehvizdy.

The fossil plants studied are preserved as carbonized compressions. Fresh material from Praha Hloubětín (brick-kiln), Pecínov and Kamenná Panna (near Horoušany) was partly bulk-macerated using H_2O_2 and HF for disintegration. Leaves of *Eretmophyllum obtusum* were carefully

washed in water and picked out manually. The collected material is stored in glycerin on preparation glasses covered by a thin plastic film ("UMAFAN" used by philatelists).

Clean cuticles obtained by sampling or bulk maceration were prepared for bleaching procedure with Schulze's reagent: HNO_3 + $KClO_3$. A weak solution of KOH was used for washing out the oxidized coal matter. The time for oxidation was estimated according to coalification of compressed specimens (few minutes for the material from the locality Lipenec, 6-24 hours for the material from the localities of the Praha - Hloubětín brickiln, and Pecínov). The material from the locality Praha–Malá Chuchle was naturally oxidized, only few minutes in KOH solution was sufficient to prepare them for microscopical study. Specimens were examined using Olympus BX 40 light microscope. Cuticlesprepared for SEM observations were mounted in water on photographic film, then dried and mounted on stubs. For preparing thick cuticles of *Eretmophyllum* it was necessary to dry the cuticles before gluing them to the stubs to prevent breakage during evaporation. Observations were done by Tesla scanning electron microscope.

The specimens studied are housed in the collections of the Department of Palaeontolgy of the National Museum, Prague (abbreviated as NM), in the Faculty of Sciences of the Charles University (abbreviated as UK), in the British Museum (Natural History) (abbreviated as BMNH) and in the Naturhistoriska Riksmuseet, Stockholm (abbreviated as NRS).

Systematic part

Order: **Caytoniales**

Genus: ***Sagenopteris*** PRESL in STERNBERG 1838: 164

Type: *Sagenopteris rhoifolia* PRESL in STERNBERG, 1838: 65, pl. 35, fig. 1, type presently missing or of unknown repository.

Diagnosis was emended by Harris (1932, 1964).

Sagenopteris variabilis (VELENOVSKÝ) VELENOVSKÝ

Pl. 1, figs 1-7, Pl. 2, figs 1-6

Basionym: *Thinfeldia variabilis* VELENOVSKÝ1885a: 6

1885a *Thinfeldia variabilis* VELENOVSKÝ: 6, pl. 2, figs 1-5, pl. 3, fig. 12 (non *T. variabilis* FONTAINE 1889: 110, pl. 17, figs 3-7, pl. 18, figs 1-6, nom. illegit.)
1889 *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ: 48, 52, 56, 73 (non *S. variabilis* CHxxx 197x, nom illegit.)
1901 *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ; Frič & Bayer: 85, text-fig. 35
1903 *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ; Frič & Bayer: 85, text-fig. 35
1914 *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ; Bayer: 17, text-fig. 9
1920 *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ; Bayer: 19, text-fig. 9
1921 *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ; Bayer: 49, 53, text-figs 1, 2
1969c *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ; Knobloch: 130

Lectotype: No F 237, Velenovský 1885a, pl. 2, fig. 1, (herein Pl. 1, fig. 2), housed in the National Museum, Praha.
Type locality: Praha - Malá Chuchle (Kuchelbad).
Type horizon: Cretaceous, Cenomanian, Peruc- Korycany Formation.

Diagnosis [Taken partly from Velenovský (1885a) and Bayer (1914)]: Leaves compound, palmately tri (? penta) foliate; Leaflets entire-margined, medial almost symmetrical, broadly lanceolate to ovate, lateral asymmetrically triangular, rounded at base. Midrib usually disappearing below the apex. Secondary veins running at sharp angles from the midrib, forming reticulate pattern. Leaves hypostomatic; adaxial cuticle thin, showing polygonal cells, abaxial cuticle with costal and intercostal zones; costal zones displaying rows of elongate tetragonal cells; intercostal zones showing polygonal cells with scattered, irregularly orientated stomata; stomata haplocheilic guard cells sunken in pits overarched by a ring of papillae on 5-8 subsidiary cells.

Specimens studied: F 237, F 1426, F 1427, F 2264 - F 2272, F 2332 - F 2334, F 2388 - F 2392, F 2719, F 2723, F 2724, (coll. NM), Pb 18, Pb 19 (coll. UK).

Occurrence: Praha–Malá Chuchle, Praha - Slivenec, Tachlovice

Description: The lectotype, F 237 (Pl. 1, fig. 2), represents a nearly entire, large lateral leaflet (25 x 65 mm) preserved as leaf-impression. It has a well-pronounced petiolule 3 mm long.

Most of the material studied consists of detached leaflets. Only one small tri- (or ? 5-) foliate leaf has been recovered (Pl. 1, fig. 6); its leaflets are attached on a 15 mm long petiole. The medial leaflet is 15 mm long, the lateral ones reach 8 mm. In several cases three or maybe five leaflets are arranged on the bedding plane in a position suggesting palmate arrangement. The specimen figured by Bayer (1914, 1920) which consists of two leaflets, was not available for the present study. Detached leaflets vary from lanceolate to broadly ovate. The medial, symetrical leaflets are rarely preserved (Velenovský 1885a pl. 3, fig. 12, F 610) and show a rather contracted base (Pl. 1, fig. 1). Asymmetrical lateral leaflets vary in shape and size ranging from 12-70 mm in length and 12-35 mm in width. The apex of the leaflets is usually obtuse or slightly acute, base asymmetrical, gradually narrowing, sub-sessile, minutely stalked. The leaflets show reticulate venation with the midrib usually disappearing below the apex. Velenovský's type material from Praha - Malá Chuchle lacks cuticles. On the other hand, many of Bayer's specimens from the same locality are well preserved leaf compressions (F 237, F 1426, F 1427, F 2269, F 2333). In addition, Bayer collected compressed fragments of cuticles separately and made cuticle preparations. Bayer's material is still available in the National Museum. Among the cuticle preparations made for the present study, the best were obtained from the specimen F 2269 (Pl. 1, fig. 3). Leaves of *S. variabilis* are hypostomatic. The adaxial cuticle is thin, bearing tetragonal or polygonal cells (Pl. 1, fig. 7) with inconspicuous differentiation of costal and intercostal zones. The costal cells (15-25 x 55-75 μm) are tetragonal and arranged in rows. The intercostal cells (30-40 x 30-55 μm) vary from tetragonal to polygonal, and are arranged in short rows. Both types of cells have similar straight or curved anticlinal walls. The abaxial cuticle shows well distinguished costal and intercostal zones (Pl. 1, fig. 5). The costal cells (20-35 x 40-75 μm) are tetragonal, running in rows. The intercostal zones contain ordinary cells tetragonal or polygonal in shape (20-45 x 35-65 μm) and stomata. Both

types of cells show slightly sinuous anticlinal walls. Stomata are haplocheilic and irregularly scattered. Guard cells (5-15 x 50-70 μm) are surrounded by thickly cutinized 5-8 subsidiary cells (Pl. 2, figs 1, 5, 6), that are typically smaller (10-20 x 10-35 μm) than the ordinary cells (Pl. 2, figs 5, 6). The guard cells are sunken in stomatal pits, surrounded by a cutinized rim of irregular papillae (Pl. 2, figs 3, 4).

Almost all of our knowledge on *S. variabilis* is based on the specimens from the Praha - Malá Chuchle locality. Only two incomplete leaf compressions come from the locality Tachlovice [collected by Velenovský and Viniklář in 1913, now housed in the collection of the Faculty of Science, Praha, Pb 18, Pb 19 (Pl. 1, fig. 4)]. They display the same cuticle arrangement (compare Pl. 2, fig. 2) as the type.

Secimens from the Slivenec locality include three impressions of detached leaflets (F 2719, F 2723, F 2724). The specimen F 2724 shows a well-preserved short petiolule.

Discussion: The leaf morphology of *Sagenopteris variabilis* (VELENOVSKÝ) VELENOVSKÝ is so similar to *S. mantellii* (DUNKER) SCHENK that Seward (1894) decided to unite those species. Although similar in number of subsidiary cells (5-8) and similarly arranged stomata sunken in pits surrounded by a rim of papillae, recent investigations in the Wealden Formation in Germany (Wilde oral communication 1999) have shown one important difference: numerous trichome bases on cuticle of *S. mantelii.* This character, observed also by Carpentier (1939, pl. 4, fig 10) is not known in any cuticle of *S. variabilis.*

Sagenopteris microphylla KRASSILOV (1979, pl. 7, figs 6-9, pl. 8, figs 1-9) from the Cretaceous of Sakhalin differs from *S. variabilis* in sinuous anticlinal walls of adaxial cuticle and exposed stromata. It has similar type of stomata and size and shape of pinnae.

Bayer (1914) pointed out that *S. variabilis* bears only bifoliate leaves. However, also one small trifoliate (or pentafoliate) leaf has recently been recovered (Pl. 1, fig. 6).

Ecological remarks: *S. variabilis* occurs only in a restricted area around the locality Praha - Malá Chuchle in a taphocoenose with *Zamites bayeri* J. KVAČEK, *Nilsonia bohemica* VELENOVSKÝ, *"Dryandra" cretacea* VELENOVSKÝ, *Platanus rhomboidea* (VELENOVSKÝ) VELENOVSKÝ, *Dalbergites pulcherrimus* (BAYER) SEWARD. Stomata surrounded by papillae on the abaxial cuticle and foliage disintegrated in the sediment are characters, which probably suggest *S. variabilis* as a member of upland vegetation. Moreover, its restriction into the Palaeozoic limestone fabric area suggests that it was calciphilous.

Order: **Cycadales**

Several genera in the Cenomanian of Bohemia are assumed to represent cycads: *Nilsonia, Jirusia, Dioonites* and *Microzamia* (see J. Kvaček 1995, 1997, Kvaček and Knobloch 1997). The new genus *Mesenea* is tentatively placed in the order Cycadales based on its cycad-like epidermis.

Genus: ***Mesenea*** gen. n.

Type: *Pecopteris bohemica* CORDA in REUSS 1846: 95, pl. 49, fig. 1 *Mesenea bohemica* (CORDA in REUSS) comb. n., No F 586, coll. NM.

Diagnosis: Tripinnate fronds. Shape of primary pinnae unknown, apical parts of secondary pinnae lanceolate, partly overlapping, axis robust. Tertiary pinnae lanceolate, parallel-sided in the basal and medial parts, gradually narrowing to the apex. Pinnule lanceolate or oblong, shortly decurrent, with one or more teeth, attached at an angle of 40°, apex shortly acute. Venation inconspicuous, veins delicate. Midrib of the pinnules not prominent and not reaching the apex, accompanied at the base by smaller separate parallel veins. Lateral veins arising at sharp angles from the midrib, simple or once forked. No pinnae occurring on secondary rachises. Adaxial cuticle with elongate cells, some of them conspicuously strongly cutinized, abaxial cuticle with haplocheilic stomata sunken in pits.

Discussion: The genus *Mesenea* is similar to the genera *Ticoa* ARCHANGELSKY and *Ctenozamites* NATHORST from the Cretaceous of Argentina and the Rhaeto-Liassic of Germany. It differs from the genus *Ticoa* in having the odontopteroid type of pinnule (pinnule lanceolate or oblong, shortly decurrent, pinnule venation with a short midrib not reaching the apex, accompanied at the base by smaller separate parallel veins, with more than one vein entering the pinnule base). It differs from *Ctenozamites* in the lack of pinnules on the secondary rachises. The pinnules of *Mesenea* are attached only to tertiary rachises. On the other hand, both genera are similar to *Mesenea* in the cycadalean type of cuticle (Archangelsky 1963, Harris 1964, 1961). They show the closest relationship to a cycad called *Almargemia* FLORIN (1933a) from the Lower Cretaceous of Portugal. This is similar to *Mesenea* in dentate pinnules, but differs in simply pinnate leaves, parallel venation and long decurrent leaf bases. A close relationship of *Mesenea* to *Almargemia* is stressed by similar cuticle patterns including haplocheilic stomata and small thickly cutinised cells on adaxial cuticle. Odontopteroid type of pinnule of *Mesenea* resemble the Carboniferous form genus *Odontopteris* BRONGNIART, but also Jurassic genus *Dichopteris* ZIGNO. The last genus differs from *Mesenea* in lack of a midrib in the pinnules.

Fronds similar to *Mesenea* are known also from North America (Fontaine 1889), Greenland (Heer 1874), and Europe (Velenovský 1888). The fronds have several characters in common: they are bi- or tri-pinnate bearing no pinnules on primary and secondary rachises and having the odontopteroid type of venation. Heer (1874) identified them with the genus *Thinfeldia* ETTINGSHAUSEN (*Thinfeldia arctica* HEER 1874). Velenovský (1888) subsequently transferred *T. arctica* into the genus *Kirchneria* (i.e. *K. arctica* (HEER) VELENOVSKÝ; *Kirchneria* F. BRAUN = *Thinfeldia* ETTINGSHAUSEN sensu Gothan 1914). Fontaine (1889) described this type of foliage from the Cretaceous of the Potomac Group as *Ctenopteris integrifolia* FONTAINE, *C. angustifolia* FONTAINE, *C. insignis* FONTAINE, and *C. minor* FONTAINE, although they do not agree with the generic diagnosis of *Ctenopteris* SAPORTA = *Ctenozamites* NATHORST sensu Gothan (1914).

Fontaine (1889) atributed similar fronds from the Potomac Formation to the genus *Scleropteris* SAPORTA (1872) emended by Frenguelli (1943). The type of the genus *Scleropteris* is *S. pomelii* SAPORTA 1872 from the Oxfordian of Verdun. The type specimen of *S. pomelii* is a leaf im-

pression without cuticle preservated. Barale (1981) therefore transferred it with along the other French representatives of the genus, preserved as leaf impressions, into the genus *Sphenopteris* BRONGNIART.

The genus *Pachypteris* BRONGNIART (= *Thinfeldia* ETTINGSHAUSEN; see Doludenko 1969) differs from *Mesenea* in having only simple pinnate fronds, strongly decurrent pinnules and a different cuticle pattern. The adaxial cuticle of *Pachypteris* shows mostly isodiametric ordinary cells, which are not thickly cutinised, and there are sunken stomata on both surfaces of the pinnules.

Mesenea bohemica (CORDA in REUSS) comb. n.

Pl. 3, figs 1-5, Pl. 4, figs 1-5, Pl. 5, Pl. 6, figs 1-8, Pl. 7, figs 1-6

Basionym: *Pecopteris bohemica* CORDA in REUSS 1846: 95, Die Versteinerungen der böhmischen Kreideformation, pl. 49, fig. 1

1846 *Pecopteris bohemica* CORDA in REUSS: 95, pl. 49, fig. 1
1888 *Kirchnera arctica* (HEER) VELENOVSKÝ: 16, pl. 2, figs 12-16
1901 *Kirchnera arctica* (HEER) VELENOVSKÝ; Frič & Bayer: 82, text-fig. 27
1903 *Kirchnera arctica* (HEER) VELENOVSKÝ; Frič & Bayer: 80, text-fig. 27
1927 *Kirchnera arctica* (HEER) VELENOVSKÝ; Velenovský & VINIKLÁŘ: 4, 30, pl. 12, fig. 1
1971 *Kirchnera arctica* (HEER) VELENOVSKÝ; Knobloch: 52
1986 *Kirchnera arctica* (HEER) VELENOVSKÝ; Knobloch: 21

Holotype: No F 586, CORDA in REUSS: 95, pl. 49, fig. 1 (herein Pl. 3, fig. 3), housed in the National Museum, Praha.
Type locality: Mšené-lázně (Msseno).
Type horizon: Cretaceous, Cenomanian, Peruc- Korycany Formation.
Etymology: From the type locality Mšené.

Emended diagnosis: Fronds tripinnate, large. Shape of primary pinnae unknown, apical parts of secondary pinnae lanceolate, partly overlapping, rachis robust. Tertiary pinnae lanceolate, parallel-sided in the basal and medial parts, gradually narrowing to the apex. Pinnules lanceolate or oblong, shortly decurrent, with acute apex, bearing one or several teeth on abmedial margin. Venation very inconspicuous; one primary vein and several secondary veins entering the pinnules at the base. Pinnules coriaceous, bearing thick cuticle. Adaxial cuticle showing elongate cells; some of them conspicuously smaller and thickly cutinized. Abaxial cuticle consisting of tetragonal or polygonal cells, bearing haplocheilic stomata, irregularly orientated. Stomatal apparatus incompletely dicyclic, guard cells sunken, overlapped by 4(6) subsidiary cells which form an oval or circular border around the stomatal pit; two of subsidiary cells in lateral position, two others in polar position. Trichome bases rounded, frequent near the rachis. Some of ordinary cells thickly cutinized.

Specimens studied: F 230, F 577, F 586, F 590, F 596, F 598, F 599, F 600, F 1459, F 2459 - F 2480 (coll. NM); B 151 (coll. UK).

Occurrence: Mšené-lázně, Vyšehořovice, Strakonice Kounice, Pecínov- Babín North quarry, unit 2; Horoušany-Kamenná Panna; Praha – Malá Chuchle, Mělník (after Velenovský 1889), Otruby Harcov (after Frič and Bayer 1901, 1903).

Description: The studied material of *Mesenea bohemica* consists of small or larger parts of fronds. The holotype, which is the only specimen from Mšené-lázně, is the apical part of a tertiary pinna bearing lanceolate pinnules (Pl. 3, fig. 3, Pl. 4, fig. 2). The pinnules vary in size (4 x 12 – 1 x 7 mm). Although the cuticle is poorly preserved, the epidermal pattern is still recognizable (Pl. 6, fig. 7, Pl. 7, fig. 5). Abaxial cuticle bears haplocheilic stomata, in which the guard cells are surrounded by 4-6 subsidiary cells (Pl. 6, fig. 7); adaxial cuticle displays elongate cells orientated parallel to veins accompanied with smaller, more cutinized cells. The largest collection of leaf impressions (partly compressions) comes from Vyšehořovice. The biggest specimen (B 151) was collected there by Viniklář in 1924 and published by Velenovský and Viniklář (1927 pl. 12, fig. 1). The specimen represents a 300 mm long part of a tripinnate frond impression (Pl. 5). It consists of six secondary pinnae arranged in a position suggesting their attachment to the primary axis. The primary rachis and the shape of the primary pinna are not known. Secondary pinnae are lanceolate, in the medial part nearly parallel-sided and partly overlapping each other. The largest secondary pinna is 220 mm long and bears 16 pairs of tertiary pinnae identical in shape to the secondary pinnae (Pl. 5). The largest tertiary pinna is 55 mm long. Pinnules of the pinnae measure 1-4 x 4-8 mm and bear several teeth. The National Museum collection includes several specimens showing secondary pinnae. The most complete specimens, F 2461 and F 2479, show several primary pinnae attached to a robust axis (Pl. 3, fig. 1). Specimens usually display lanceolate or oblong, shortly decurrent pinnules 1-4 x 5-12 mm in width and length. Their venation is inconspicuous, showing one main vein and several other basal veins entering the pinnula base (F 230, F 2480, Pl. 4, fig. 1). Other leaf impressions are known from the localities: Stradonice, Kounice, Otruby, Mělník, Praha - Malá Chuchle, and Harcov.

The best preserved material was newly recovered in the open clay pits Pecínov and Kamenná Panna near Horoušany (Pl. 3, fig. 2, pl. 4, fig. 3). The newly recovered leaf compressions are coriaceous with good cuticles, and are hypostomatic. Their adaxial cuticle is thicker, consisting of elongate cells (15-30 x 75-140 µm); some of them are conspicuously small (10-15 x 30-50 µm) and more cutinized (Pl. 6, figs 2, 4, Pl. 7, figs 2, 4). Circular trichome bases occur attached to one or two cells. Abaxial cuticle shows tetragonal or polygonal ordinary cells (12-40 x 30-60 µm, Pl. 7, figs 5, 6). They have thin, curved or straight anticlinal walls. Haplocheilic, incompletely dicyclic stomata consist of guard cells surrounded by 4-6 rather more cutinized 20-25 x 25-55 µm large subsidiary cells (Pl. 6, figs 5-8), which form a small rim around the stomatal pit (Pl. 6, fig. 3). Lateral subsidiary cells are usually slightly more cutinized (Pl. 7, fig. 6), while guard cells are seldom cutinized.

Discussion: *Mesenea bohemica* differs from *Kirchnera dentata* VELENOVSKÝ 1888b [*Sphenopteris dentata* (VELENOVSKÝ) SEWARD (1926)] in having a robust rachis, odontopteroid venation and coriaceous pinnae (see Pl. 4, fig. 4). As pointed out already by Antevs (1914), *K. dentata* is probably identical with *Onychiopsis capsulifera* (VELENOVSKÝ) NATHORST. Although this idea is highly probable, it was impossible to prove because the type material of *K. dentata* is very poorly preserved (see Pl. 4, fig. 4).

Although Velenovský (1888) described *Mesenea bohemica* as a true fern, he subsequently pointed out its striking similarity to the Palaeozoic seed fern foliage *Odontopteris* and *Neuropteris*. He did not link the foliage *K. arctica* with Corda's *Pecopteris bohemica*. New investigation of Corda's type ma-

terial, particularly cuticle ana-lysis of tiny fragments of cuticle, allowed to merge *Kirchnera arctica* (sensu Velenovský 1888) with *Pecopteris bohemica* CORDA in REUSS 1846. Coriaceous leaves, haplocheilic stomata, small thickly cutinized cells on adaxial cuticle have suggested that this foliage is most similar to that of cycads. Similar cuticle can be found in *Almargemia dentata* (HEER) FLORIN from the Portuguese Cenomanian (Florin 1933). *A. dentata* differs, as mentioned above, in having simply pinnate fronds with parallel venation and longly decurrent pinnule bases. The specimens from the locality Sao Mamede, Belas (the Cenomanian of Portugal) figured by Teixeira (1948, pl. 21, figs 6, 7) and identified as ? *Almargemia dentata* do recall *M. bohemica* in shape and size of pinnae, but due to the small photographs provided it is difficult to determine more details to confirm their identity.

Order: **Ginkgoales**

Genus: ***Eretmophyllum*** THOMAS 1913: 259

syn:
Euryspatha PRINADA 1956: 244
Nehvizdya HLUŠTÍK 1977: 174

Type: *Eretmophyllum pubescens* THOMAS 1913: 256, pl. 6, No V.27704 (coll. BMNH).
Diagnosis as emended by Harris & Millington (1974) is accepted here.

Discussion: The genera *Nehvizdya* and *Euryspatha* mentioned in the synonymy are so similar in morphology and in epidermis anatomy, that both have been suggested to be included in *Eretmophyllum.* The genus *Euryspatha* and its type *E. rarinervis* PRINADA (1956: 245, pl. pl. 42, fig. 5) was included into the genus *Eretmophyllum* by Krassilov (1972), who considered it as a synonym of *E. glandulosum* (SAMYLINA) KRASSILOV. Based on the present investigations *Nehvizdya* is also placed in synonymy with *Eretmophyllum.* The main characteristics of the genus *Eretmophyllum,* as defined by Thomas (1913: 259) and emended by Harris & Millington (1974: 56) are identical to *Nehvizdya* HLUŠTÍK (1977: 174): Leaves simple oblanceolate, entire-margined, petiolate; apex usually rounded; veins dichotomously branched, parallel, slightly convergent to the apex (compare Pl. 27, fig. 5); epidermal cells polygonal, more or less isodiametric, subsidiary cells regularly surrounding stomata.

According to Hluštík (1977: 182) *Nehvizdya* differs from the type of *Eretmophyllum,* i.e. *E. pubescens* THOMAS (1913: 256, pl. 6, herein Pl. 9, fig. 5), in the lack of secretory tracts, and from *E. whitbiense* THOMAS (1913: 259, pl. 7) in the lack of interstitial veins. Nevertheless, the present author observed resin bodies in the leaves of *E. obtusum* (Pl. 27, fig. 3) and does not consider the lack of interstitial veins as a diagnostic character at the generic level. Moreover, neither of these characters are included in the original diagnosis of *Eretmophyllum* (see Thomas 1913). Harris and Millington (1974), emending the diagnosis, do not consider the presence of resin bodies (secretory tracts by Thomas 1913) as an obligatory generic character. They only state: "Round to spindle-shaped resin bodies often present". The argument that *Eretmophyllum* is typical of and limited to the Jurassic (Hluštík 1977: 182) cannot be accepted, because some species (*E. glandulosum, E. andegavense* - see table 1) were recorded also from Cretaceous strata. Furthermore, other genera occurring in the Jurassic such as *Sagenopteris, Nilsonia, Nilssoniopteris,* are present in the Bohemian Cenomanian as well.

The genus *Feildenia* HEER 1878 (superfluous to *Torellia* Heer 1870) was used for a new combination *Feildenia obtusa* by Velenovský and Viniklář (1929). The monotypic genus *Torellia* (*T. rigida* (HEER) FLORIN) described from the Tertiary of Spitzbergen differs from *E. obtusum* in narrow leaf lamina, sinuous anticlinal walls and more elongate ordinary cells.

Eretmophyllum obtusum (VELENOVSKÝ) comb. n.

Pl. 8, figs 1-6, Pl. 9, figs 1-6, Pl. 10, figs 1-5

Basionym: 1885a *Podozamites obtusus* VELENOVSKÝ: 9, Die Gymnospermen der böhmischen Kreideformation, pl. 1, figs 8-9

1885a *Podozamites obtusus* VELENOVSKÝ: 9, pl. 1, figs 8, 9
1901 *Podozamites obtusus* VELENOVSKÝ; Frič et Bayer: 90
1903 *Podozamites obtusus* VELENOVSKÝ; Frič et Bayer: 88
1921 *Podozamites obtusus* VELENOVSKÝ; Bayer: 44, 54, text-figs 3, 4
1926 *Podozamites obtusus* Velenovský; VELENOVSKÝet VINIKLÁŘ: 7, 34, pl. 4, figs 1, 2, pl. 6, figs 11-13
1926 *Pseudozamites* VELENOVSKÝet VINIKLÁŘ, nom. nud.: 8, 35
1927 *Podozamites obtusus* VELENOVSkÝ; Velenovský et VINIKLÁŘ: 6, 33
1929 *Feildenia obtusa* (VELENOVSKÝ) VELENOVSKÝet VINIKLÁŘ: 7, 24
1968 *Phyllotenia obtusa* (VELENOVSKÝ) KNOBLOCH in KNOBLOCH et al., comb. inval.: 214
1977 *Nehvizdya obtusa* (VELENOVSKÝ) HLUŠTÍK: 174, pls 1-4
1980 *Nehvizdya obtusa* (VELENOVSKÝ) HLUŠTÍK; Hluštík: 26, pl. 3, fig. 1
1986 *Nehvizdya obtusa* (VELENOVSKÝ) HLUŠTÍK; Hluštík: 100, pls 1-4
1986 *Nehvizdya obtusa* (VELENOVSKÝ) HLUŠTÍK ssp. *obtusa*; Hluštík: 110

Holotype: No F 3, Velenovský 1885a, pl. 1, fig. 8, (herein Pl. 26, fig. 1), housed in the National Museum, Praha.
Type locality: Nehvizdy.
Type horizon: Cretaceous, Cenomanian, Peruc-Korycany Formation.

Emended diagnosis [After Hluštík 1977, 1980]: Leaf coriaceous, entire-margined, oblanceolate, petiolate; petiole widening gradually into a narrow cuneate base of leaf lamina; apex rounded, partly asymmetrical; veins parallel - subparallel, branching dichotomously, of uniform thickness, 8 - 12 per cm of the leaf width; only few medial veins reaching the top of apex, the other entering the converging apex margins; leaf substance very thick, small rounded or narrow spindle-shaped resin bodies present in the mesophyll tissue. Leaves usually hypostomatic; adaxial cuticle heavily cutinized, cells polygonal, isodiametric (to slightly elongate), arranged in longitudinal rows; anticlinal walls straight or slightly bent. Abaxial cuticle also heavily cutinized, showing costal and intercostal bands; intercostal cells polygonal, elongate, forming longitudinal rows; costal bands built of strongly cutinized polygonal,

isodiametric ordinary cells and randomly scattered stomata (or arranged in short rows). Stomata haplocheilic (perigenous), monocyclic or incompletely dicyclic, irregularly orientated, guard cells, sunken in stomatal pits, surrounded by 4-6 subsidiary cells. Subsidiary cells strongly cutinized, usually bearing papillae that form a rised coronal rim.

Specimens studied: F 3-15, F 112-134, F 189-191, F 2281, F 2293, F 2481-2483, F 2497-F 2500 (coll. NM).

Occurrence: Nehvizdy, Praha - Vysočany, Lipenec, Praha, Hloubětín, Praha - Prosek, Vyšehořovice, Horoušany - Kamenná Panna - clay pit, Lobeč, Pecínov- Babín North quarry, unit 3, ?Lidice (Velenovský 1889).

Description: The holotype (Pl. 8, fig. 1) is a leaf impression of an oblanceolate leaf (10 x 23 mm) with a thick petiole (3 mm). Well-pronounced veins fork three times (Pl. 8, fig. 3) in their course. Additional material of Velenovský, probably collected later (labeled year 1886 on the specimen No F 8), consists of two specimens from Vysočany (F 10, F 11, Pl. 8, fig. 4) and one from Lipenec (F 8, F 9, part and counterpart, Pl. 9, fig. 1). The latter specimen is a well-preserved basal part of the leaf compression (22 x 50 mm). The other specimens studied by Hluštík (1977, 1986) are isolated leaf compressions. Hluštík (1977), after the studying numerous specimens, stated that "the length varies from 30 to 100 mm, the width from 5 to 30 mm.... petiole is 1,5 to 3 mm wide". I have not found any leaves outside of this size range. Hluštík (1974) figured also many variously shaped apices of *E. obtusum* to show a quite high variability of the leaf apex (Hluštík 1974, text-figs 1-5, F 114). However, from my experience when collecting the fossil material in the localities Praha - Hloubětín, Pecínov and Horoušany, aberrantly shaped apices are rare. The most illustrative are the naturally translucent specimens F 115 - F 120 (Pl. 8, figs 2, 3, 5, 6). They display distinct venation patterns. Two veins enter the petiole, then fork three or four times in the basal part of the lamina forming a longitudinal parallel venation. The most dense branching is concentrated at the base where the petiole enters the leaf. Anastomosing of veins is rare (Pl. 8, fig. 3). This unique case is shown on the apex of specimen F 117 (Pl. 8, fig. 5). Resin bodies occur frequently; they are rounded (200-500 µm in diameter) or spindle-shaped (150-350 x 600 - 1500 µm, Pl. 9, fig. 3). Hluštík (1986, pl. 1, figs 4, 5, pl. 2, figs 3-6, pl. 3, figs 1-6) separated spindle-shaped bodies in the preparation F 112 prep. 39, rounded in F 112 prep. 38. The specimen F 2483 collected by the present author shows round and spindle-shaped (250 x 1050 µm) resin bodies in situ (Pl. 9, fig. 3).

Leaves of *E. obtusum* are hypostomatic, but sometimes (F 112, prep. 10) several stomata appear on the adaxial cuticle (Pl. 9, fig. 2). The adaxial cuticle is very thick. Tetragonal or polygonal isodiametric cells (20-40 x 25-50 µm) of the adaxial cuticle are arranged in ill-defined rows (Pl. 10, fig. 1). The anticlinal walls are straight or curved (5-10 µm thick). The preparation No F 112 prep. 10, displays stomata irregularly scattered in the apical part of the adaxial cuticle (Pl. 9, fig. 2). They are of the same type as those on the abaxial side (see below). The abaxial cuticle displays poorly differentiated costal and intercostal bands (Pl. 10, fig. 2). The costal bands show tetragonal or polygonal, isodiametric or slightly elongate cells (15-50 x 40-100 µm) with straight or bent anticlinal walls that are 3-6(10) µm thick. External surface of cuticle (Pl. 10, fig. 5) seen in the SEM shows elongate striations in the costal area. The intercostal bands display polygonal isodiametric or elongate cells (15-50 x 25-75 µm) with straight or bent 5-20 µm thick anticlinal walls (Pl. 10, fig. 4). Haplocheilic stomata are monocyclic or incompletely dicyclic, irregularly orientated, with guard cells sunken in oval pits (Pl. 10, figs 3-5). They are surrounded by tetragonal or polygonal, heavily cutinized subsidiary cells (20-45 x 35-70 µm), which form a stomatal rim. Remains of guard cells are preserved as cutinized ledges in pits.

Discussion: Hluštík (1986) proposed *E. obtusum* to be very similar to *Glossophyllum florinii* KRÄUSEL (1938) from the Triassic of Lunz, Austria. This hypothesis would assign *E. obtusum* to the family Glossophyllaceae (Tralau 1968). Hluštík argued that both taxa have leaves arranged in a spiral on the axis and not in bundles (compare Hluštík 1986, text-fig. 9). (Hluštík based his argument on the lack of dwarf-shoots with attached leaves of *E. obtusum* in the sediment.) On the other hand, *Glossophyllum florinii* lacks resin bodies in mesophyll tissue and differs in cuticle pattern (compare Kräusel, 1938). Due to fragmentary data on reproductive structures, it is presently not possible to assign *E. obtusum* to any family within the order Ginkgoales.

The most similar to *E. obtusum* are leaves of *Eretmophyllum andegavense* PONS, BOUREAU et BROUTIN (1976) from the French Cenomanian of Anjou (Pl. 9, fig. 6). Their similarity is so suggestive, that Hluštík (1986) decided to reduce *E. andegavense* to a subspecies of *Nehvizdya obtusa* and thus he recognized two subspecies: *N. obtusa* (VELENOVSKÝ) HLUŠTÍK ssp. *obtusa* and *Nehvizdya obtusa* (VELENOVSKÝ) HLUŠTÍK ssp. *andegavensis* (PONS, BOUREAU, BROUTIN) HLUŠTÍK.

The presence of epidermal secretory cells and amphistomatic leaves are two main characters that were supposed by Hluštík (1986) to occur in *E. andegavense* contrary to *E. obtusum.* However, the former is no longer valid. The occasional occurrence of stomata on the abaxial surface in preparation F 112 prep. 10 (Pl. 9, fig. 2) of *E. obtusum* shows that the second mentioned epidermal character can vary. However, the present author prefers to leave the two species separate, until the type material of *E. andegavense* is thoroughly revised. Relevant *Eretmophyllum* species are compared in the table 1.

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Table 1. Comparison of some species of *Eretmophyllum*.

species and location	stratigraphy	stomatal distribution	trichome bases	papillae around pits	resin bodies
E. glandulosum (Samylina) Krassilov, 1972: 50 Aldan River, Bureia Basin, Siberia	Lower Cretaceous	hypostomatic	present	present	present
E. pubescens Thomas, 1913: 256, Yorkshire, England	Middle Jurassic	amphistomatic	rarely present	present	present
E. whitbiense Thomas, 1913: 259, Yorkshire, England	Middle Jurassic	amphistomatic	absent	present	present
E. lovisatoi Edwards, W. N., 1929: 388, Sardinia	Jurassic	amphistomatic	absent	present	present
E. boroldaicum Orlovskaya in Doludenko et Svanidze, 1976: 70, Karatau, south Kazakhstan	Middle Jurassic	amphistomatic	?	present	absent
E. saighanense (Seward) Seward, 1919: 60, Afghanistan	Jurassic	?	?	?	?
E. magnum Doludenko in Doludenko et Orlovskaya, 1976: 113, Karatau, south Kazakhstan	Upper Jurassic	?	?present	present	?
E. thomasii Doludenko et Svanidze, 1969: 71, Georgia (Middle Asia)	Upper Jurassic	hypostomatic	absent	present	absent
E. baikonuricum Orlovskaya, 1962: 166, Kazakhstan	Jurassic				
E. ovatum Teslenko, 1970: 166, Kuzbas, Lower Jurassic south western Siberia	?	?	?	?	
E. ketoviae Gomolitzky, 1965: 129, Gissar Mts., Uzbekistan	Middle Jurassic	hypostomatic	absent	present	? abs.
E. pulchellum (Heer, 1876) Nathorst, 1919: Spitzbergen	Jurassic	?	?	?	?
E. tetonense Kimura et Sekido, 1965: 1, Hokaido, Japan	?	?	?	?	?
E. harrisii Gomolitzky, 1987: 127, Gissar Mts., Uzbekistan	Middle Jurassic	hypostomatic	absent	present	present
E. andegavense Pons, Boureau et Broutin, 1976: 358, Anjou, France	Upper Cretaceous	amphistomatic	absent	absent	present
E. obtusum (Velenovský) comb. n., Bohemia, Czech Republic	Upper Cretaceous	hypostomatic	absent	present	present

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Explanations to the plates

(numbers in parenthesis indicate negative numbers for SEM photos; SEM = scanning electron micrograph, LM = light micrograph)

PLATE 1

Sagenopteris variabilis (VELENOVSKÝ) VELENOVSKÝ

1. Terminal pinula, Velenovský 1885a, pl. 2, fig. 3, Praha - Malá Chuchle; F 610, × 2.
2. Lectotype, pinula, Velenovský 1885a, pl. 2, fig. 1,Praha - Malá Chuchle; F 237, × 1.
3. Lateral pinula, Praha - Malá Chuchle; F 2269, × 2.
4. Lateral pinula, Tachlovice; Pb 19, × 2.
5. Abaxial cuticle, Praha - Malá Chuchle, LM micrograph; F 2269a, × 100.
6. Trifoliate leaf, Praha - Malá Chuchle; F 2271, × 2.
7. LM of adaxial cuticle, Praha - Malá Chuchle; F 2269a, × 150.

PLATE 2

Sagenopteris variabilis (VELENOVSKÝ) VELENOVSKÝ

1. SEM of abaxial cuticle, inner surface, Praha - Malá Chuchle; F 2269b (4194), × 300.
2. LM of abaxial cuticle, Tachlovice; Pb 19a, × 250.
3. SEM of abaxial cuticle, outer surface, Praha - Malá Chuchle; F 2269c (4193), × 150.
4. SEM of abaxial cuticle, outer surface, Praha - Malá Chuchle; F 2269c, × 750.
5. LM of stomata, adaxial cuticle, Praha - Malá Chuchle; F 2269a, × 800.
6. SEM of stoma, abaxail cuticle, inner surface, Praha - Malá Chuchle; F 2269b (4200), × 800.

PLATE 3

Mesenea bohemica (CORDA in REUSS) comb. n.

1. Part of bipinnate frond, Vyšehořovice; F 2461, × 1.5.
2. Simply pinnate frond, Pecínov, Babín North; F 2459, × 2.
3. Holotype, Mšené-lázně; F 586, × 1
4. Part of bipinnate frond, Vyšehořovice; F 596, × 1.5.
5. Part of bipinnate frond, Vyšehořovice; F 598, × 1.5.

PLATE 4

Mesenea bohemica (CORDA in REUSS) comb. n.

1. Simply pinnate frond, Vyšehořovice; F 599, × 2.
2. Holotype, terminal part, Mšené-lázně; F 586, × 2.
3. Simply pinnate frond, Horoušany, Kamenná Panna; F 2460a, × 2.

Sphenopteris dentata (VELENOVSKÝ) SEWARD

4. Bipinnate frond, Kounice; F 577, × 1.

Mesenea bohemica (CORDA in REUSS) comb. n.

5. LM of both sides of cuticle showing two marginal teeth, Pecínov, Babín North; F 2459a, × 100.

PLATE 5

Mesenea bohemica (CORDA in REUSS) comb. n.
Part of tripinnate frond, Vyšehořovice; B 151, (coll. UK) × 0.5.

PLATE 6

Mesenea bohemica (CORDA in REUSS) comb. n.

1. SEM of abaxial cuticle, inner surface, Pecínov; F 2459b (4359), × 500.
2. SEM of adaxial cuticle, inner surface, Pecínov; F 2459c (4337), × 300.
3. SEM of stoma, abaxial cuticle, outer surface, Horoušany; F 2460ab (4357), × 800.
4. SEM of adaxial cuticle, inner surface, Pecínov; F 2459b (4365), × 1000.
5. LM of stoma, abaxial cuticle, Horoušany; F 2460ab, × 1000.
6. SEM of stoma, abaxial cuticle, inner surface, Pecínov; F 2459b (4362), × 1000.
7. Holotype, LM of stoma, abaxial cuticle, Mšené-lázně; F 586a, × 800.
8. LM of stoma, abaxial cuticle, Pecínov; F 2459a, × 800.

PLATE 7

Almargemia dentata FLORIN

1. LM of adaxial cuticle, original Florin's preparate, Almargem, (coll. NRS) × 500.

Mesenea bohemica (CORDA in REUSS) comb. n.

2. Holotype, LM of adaxial cuticle, Mšené-lázně; F 586a, × 500.
3. LM of cells under the midrib, Pecínov; F 2459a, × 200.
4. LM of adaxial cuticle, Pecínov; F 2459a, × 200.
5. Holotype, LM of abaxial cuticle, Mšené-lázně; F 586a, × 500.
6. LM of abaxial cuticle, Pecínov; F 2459a, × 500.

PLATE 8

Eretmophyllum obtusum (VELENOVSKÝ) comb. n.

1. Holotype, Nehvizdy; F 3, × 1.
2. Naturally translucent specimen, Praha, Hloubětín; F 115, × 2.
3. Basal part of naturally translucent specimen, Praha, Hloubětín; F 116, × 2.5.
4. Specimen from the type collection, Praha, Hloubětín; F 11, × 3.
5. Naturally translucent specimen, Praha, Hloubětín; F 117, × 3.
6. Apical part of naturally translucent specimen, Praha, Hloubětín; F 120, × 3.

PLATE 9

Eretmophyllum obtusum (VELENOVSKÝ) comb. n.

1. Specimen from Velenovský's type collection, Lipenec; F 09, × 1.5.
2. LM of adaxial cuticle, stomata, Praha, Hloubětín; F 112/10, × 400.
3. Macerated specimen showing resin bodies, Praha, Hloubětín, F 2483, × 5.
4. Seed enclosed in cupula, Pecínov; F 2281, × 3.

Eretmophyllum pubescens THOMAS

5. Holotype, Cloughton Wyke, Great Britain; V.27704 (coll. BMNH), × 2.5.

Eretmophyllum andegavense PONS, BOUREAU et BROUTIN

6. LM of abaxial cuticle, Anjou, France; prep. S. Opluštil, × 400.

PLATE 10

Eretmophyllum obtusum (VELENOVSKÝ) comb. n.

1. LM of adaxial cuticle, phase contrast, type collection, Praha, Hloubětín; F 8, × 200.
2. LM of abaxial cuticle, Praha, Hloubětín; F 8, × 40.
3. SEM of abaxial cuticle, Pecínov; F 2481b (4032), × 500.
4. LM of abaxial cuticle, type collection, Praha, Hloubětín; F 8, × 200.
5. SEM of abaxial cuticle, outer surface, Pecínov; F 2481b (4027), × 100.


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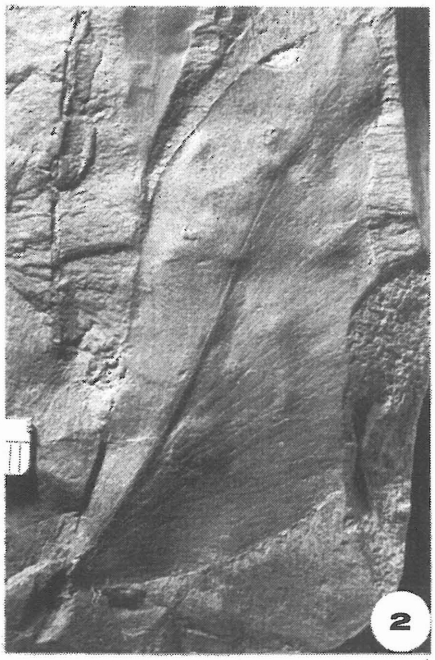
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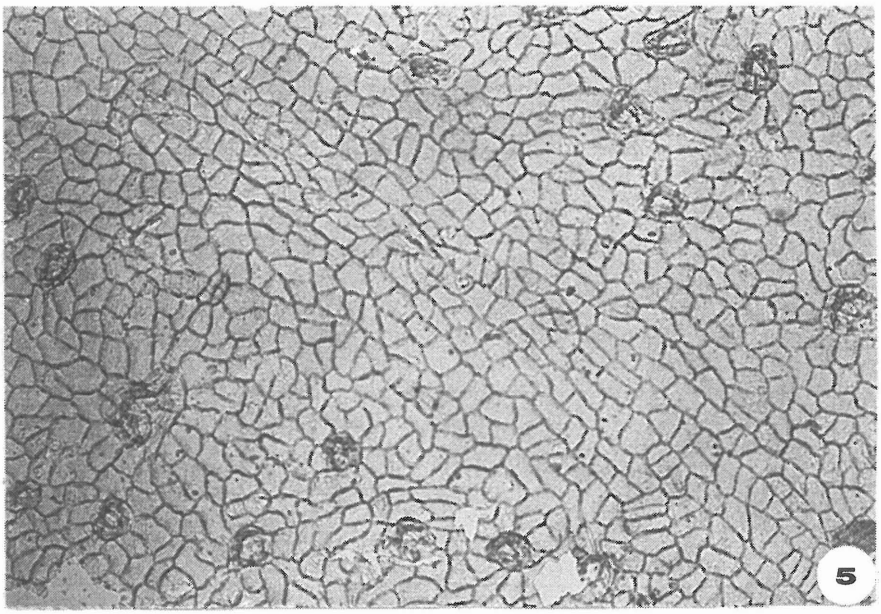
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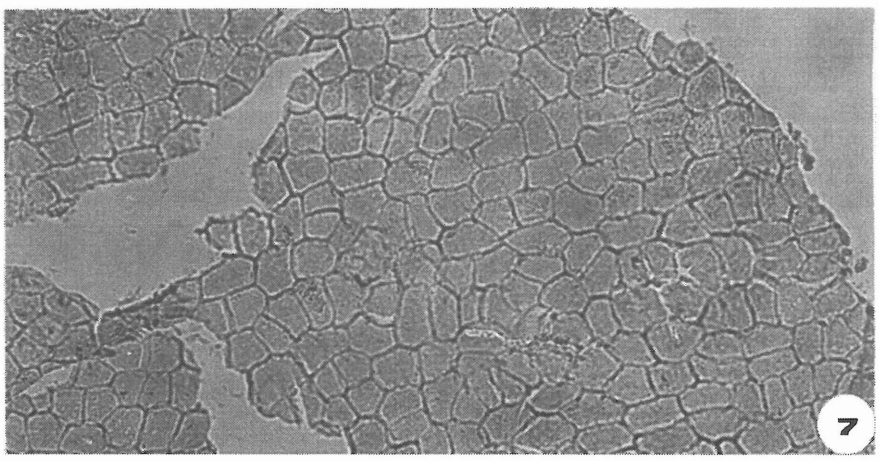
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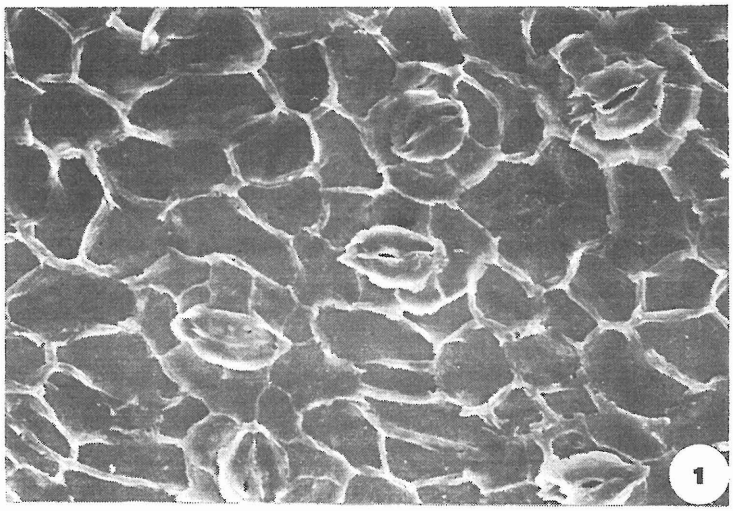
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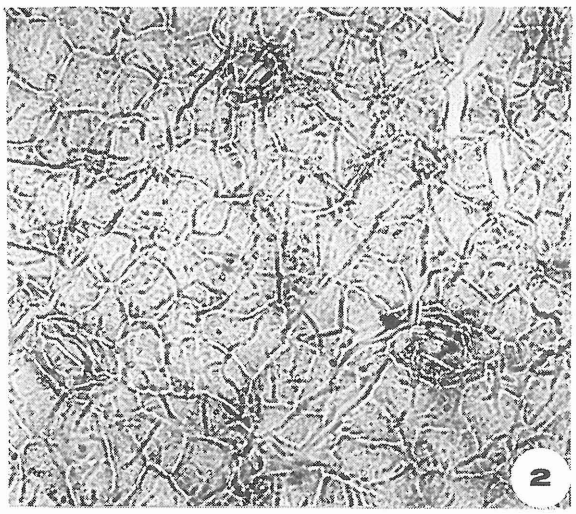
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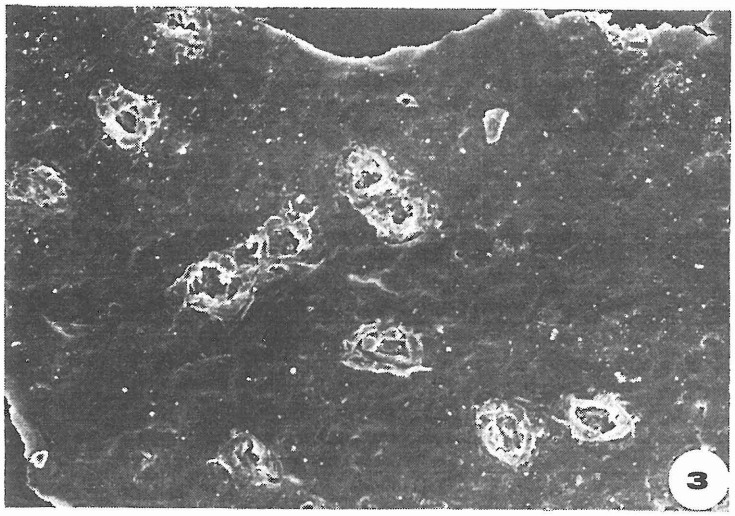
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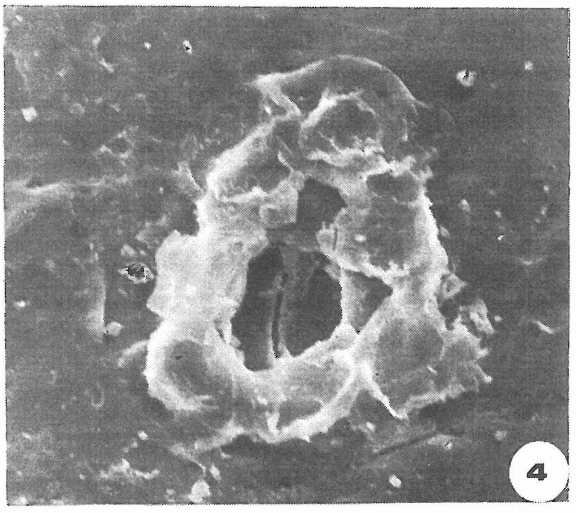
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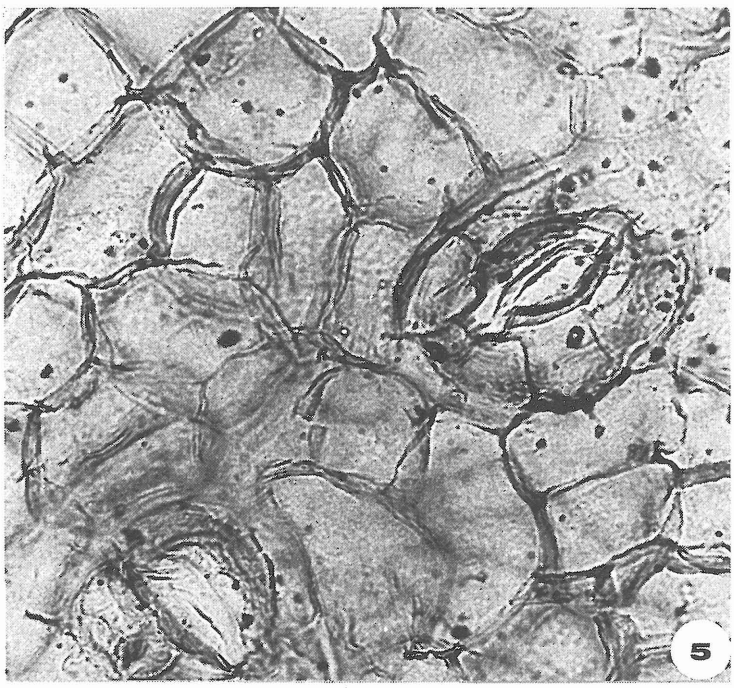
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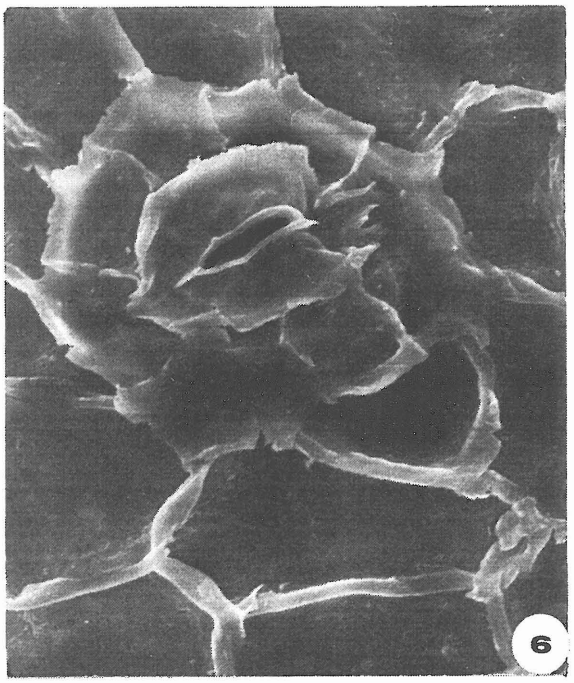
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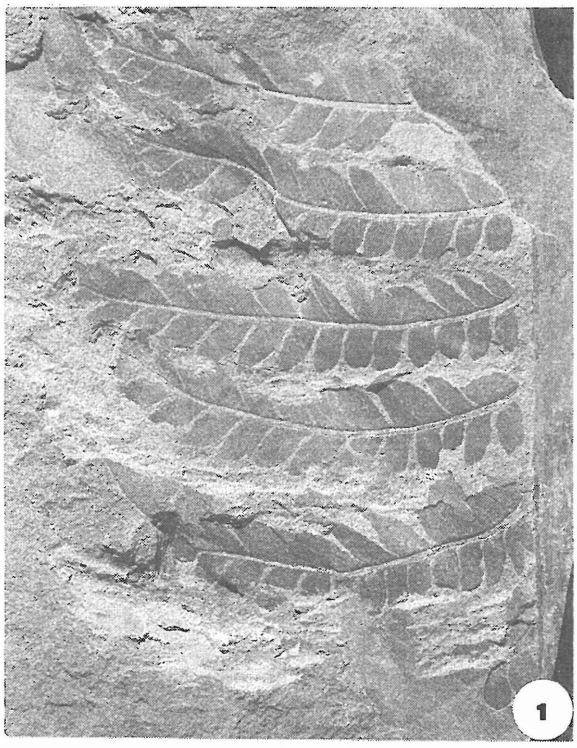
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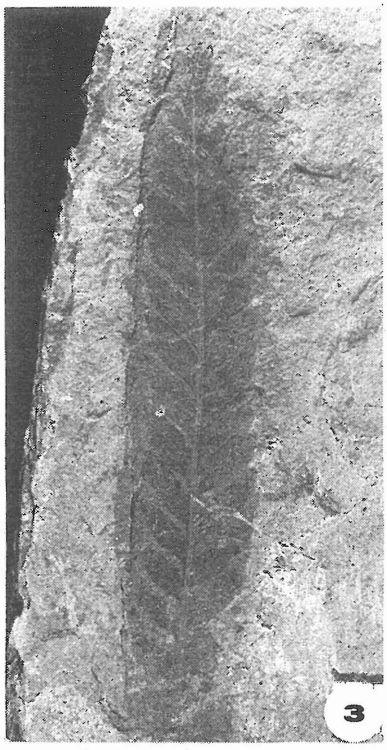
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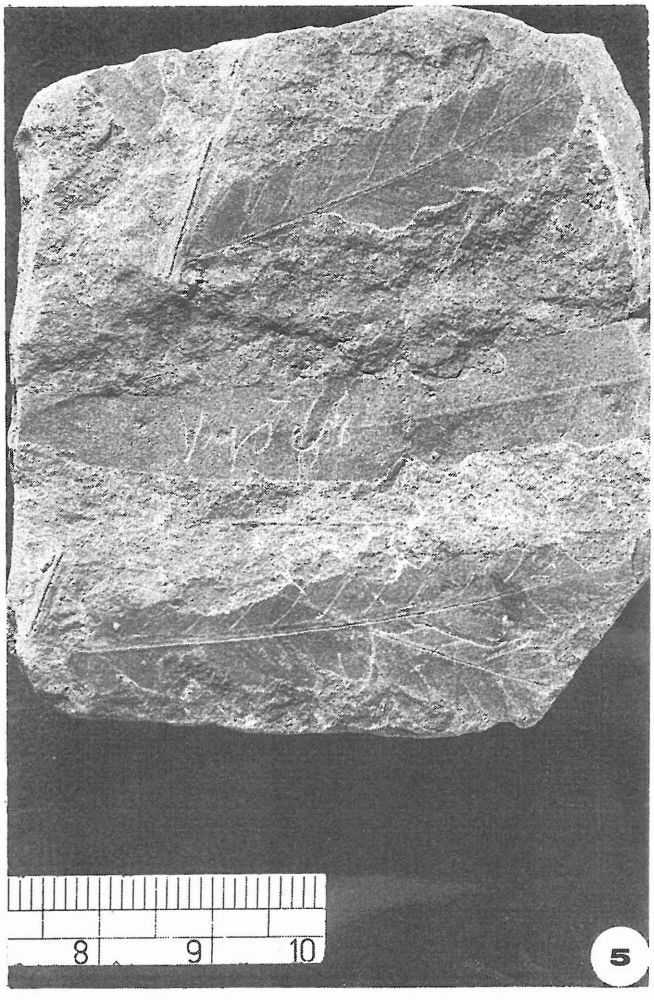
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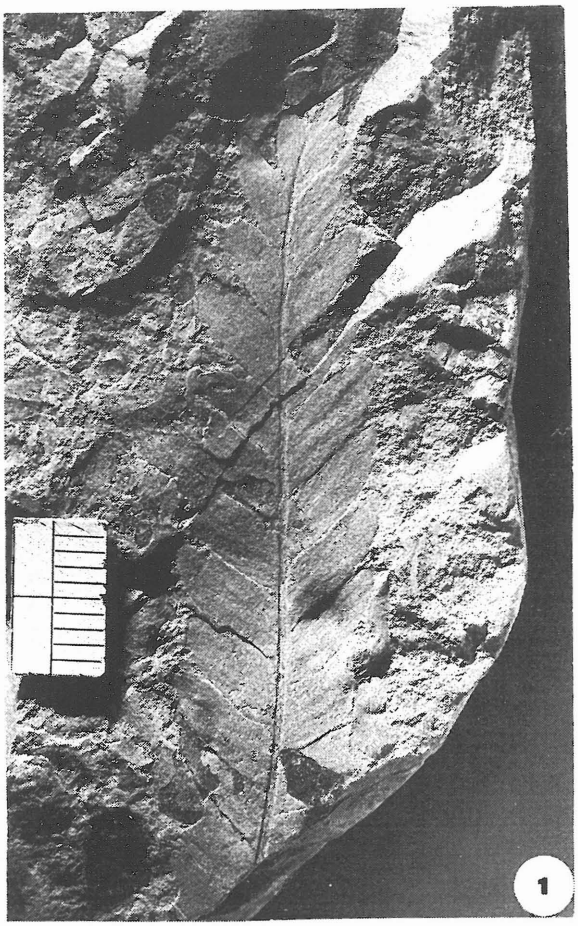
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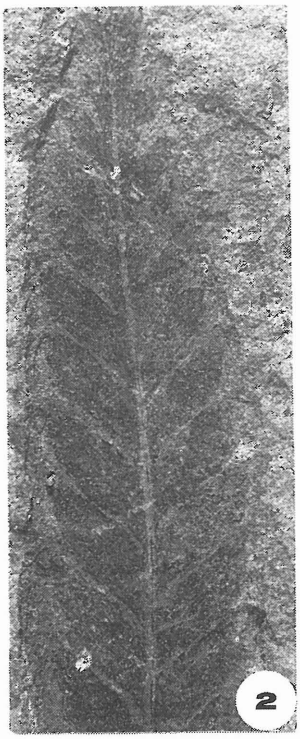
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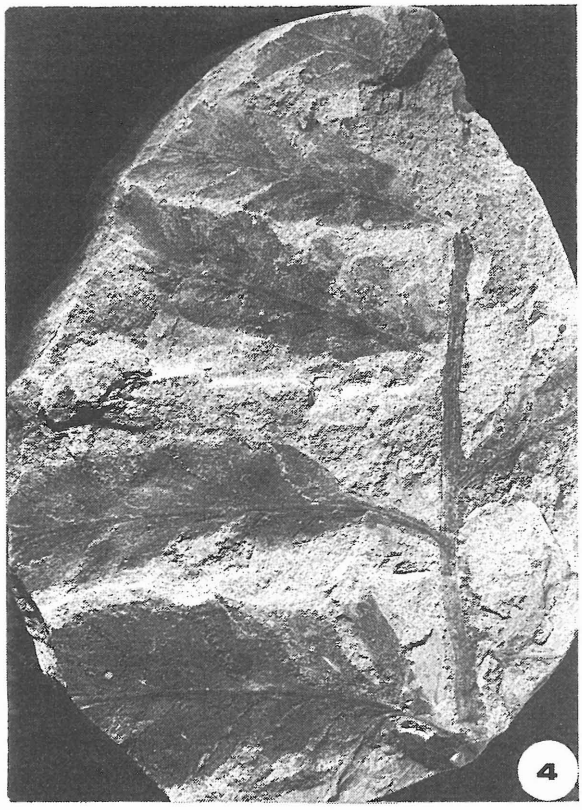
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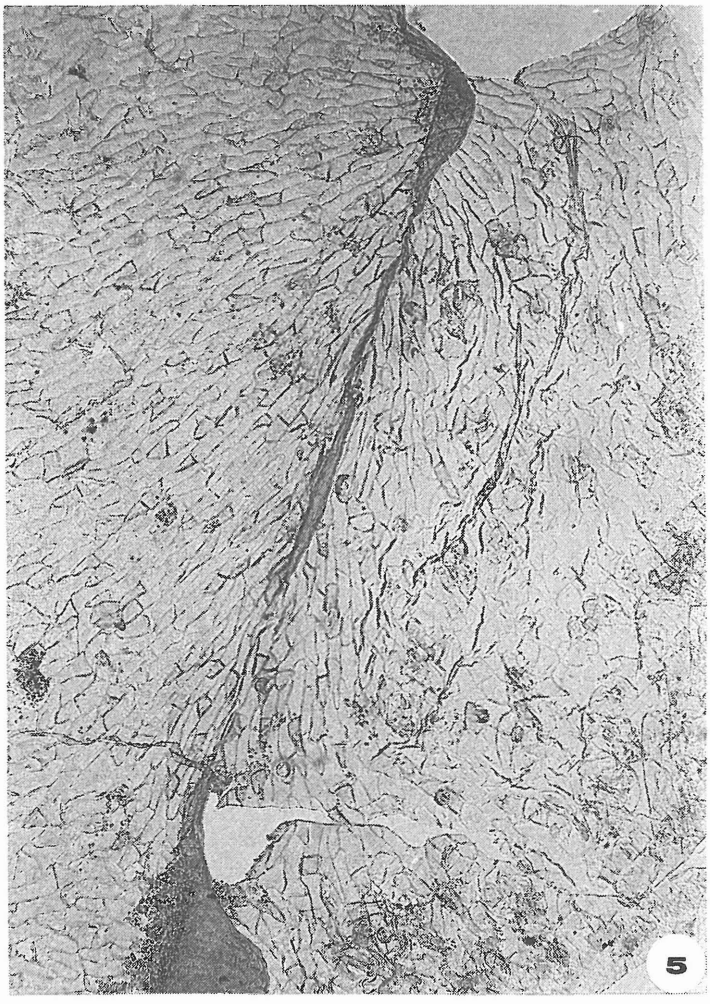
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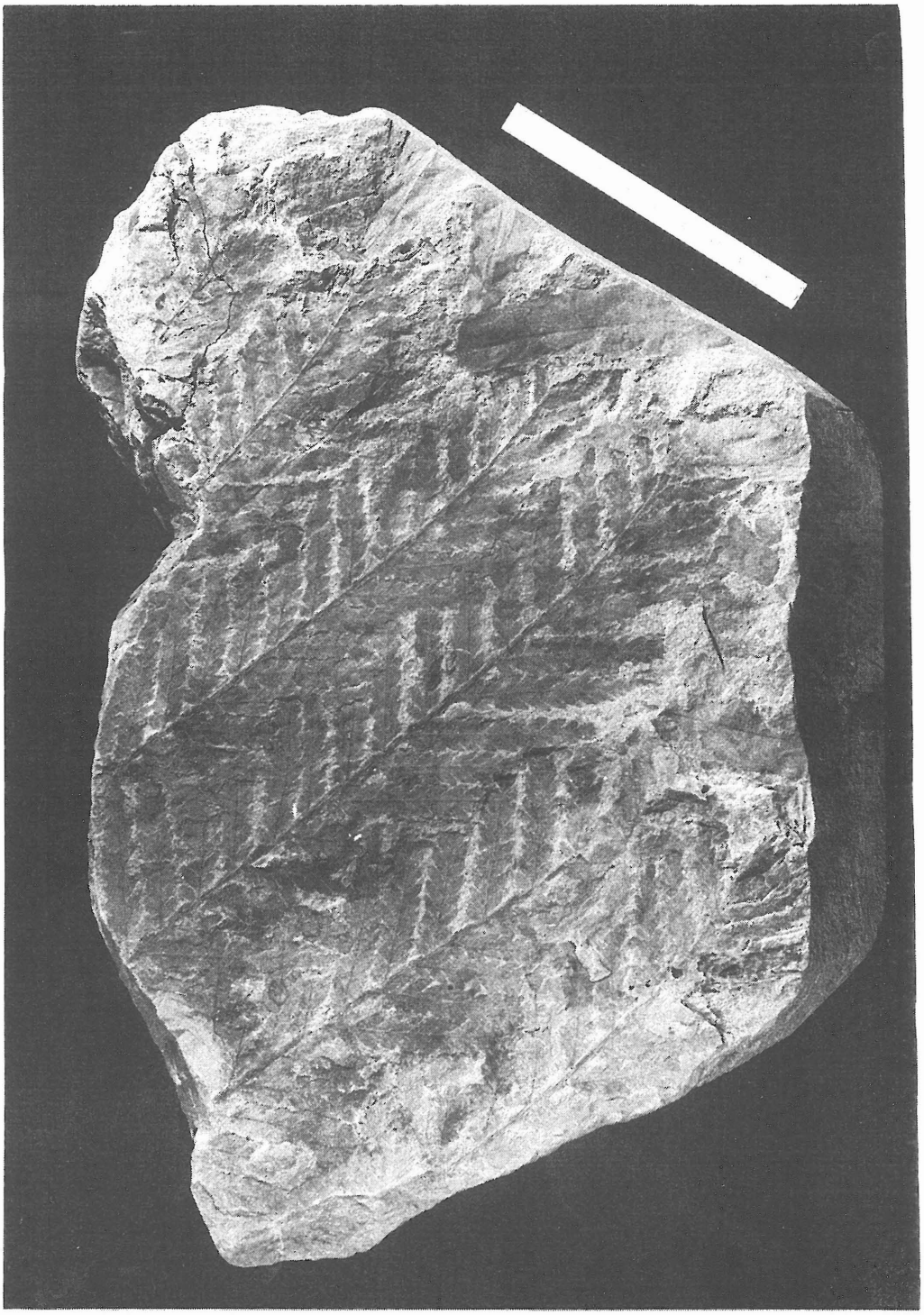

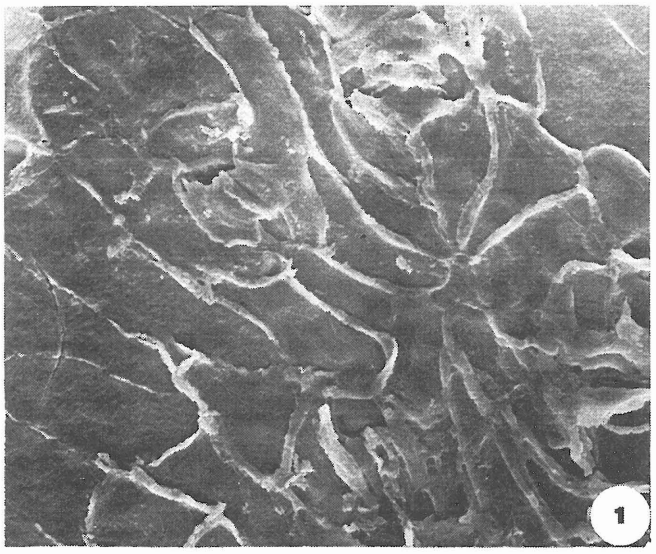
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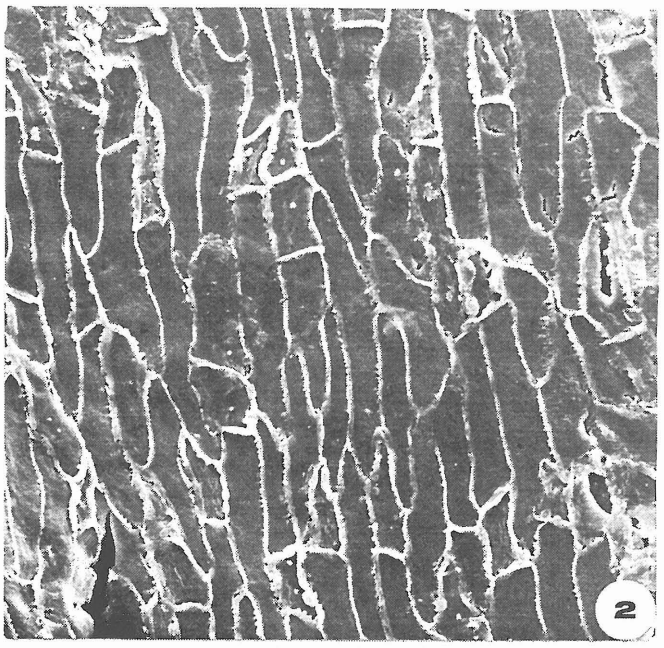
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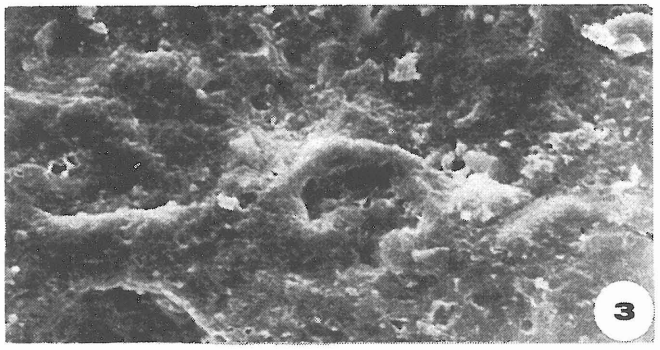
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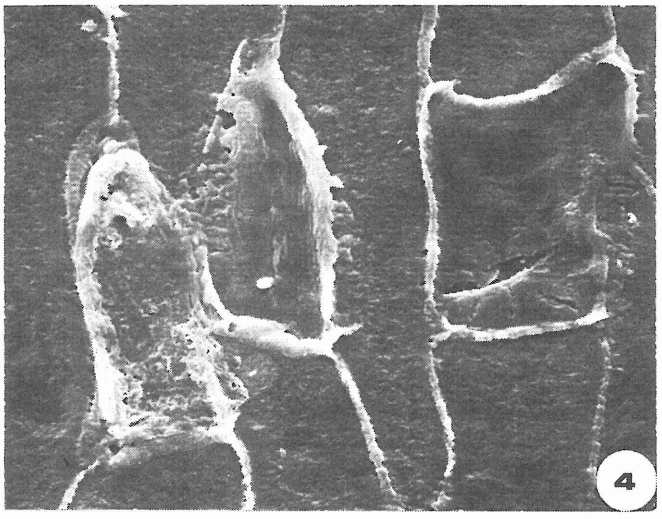
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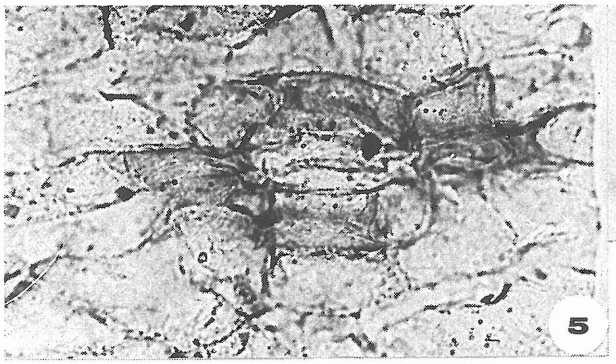
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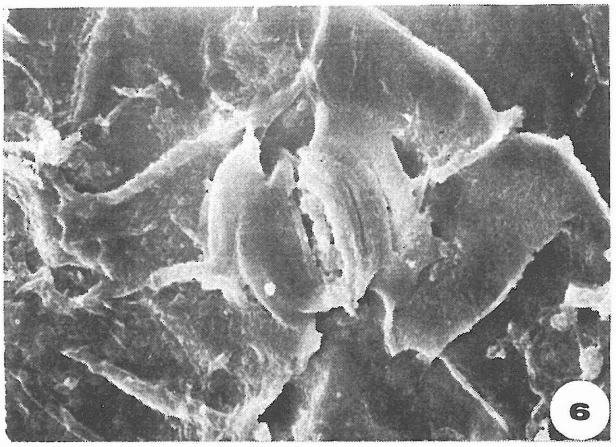
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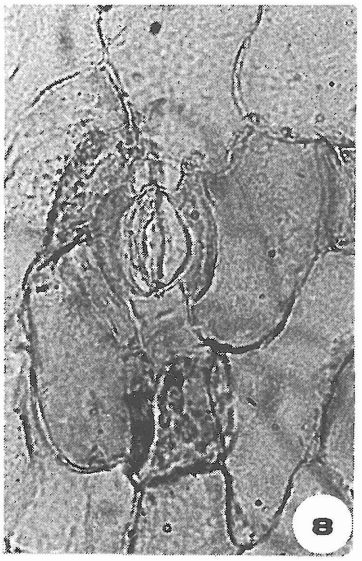
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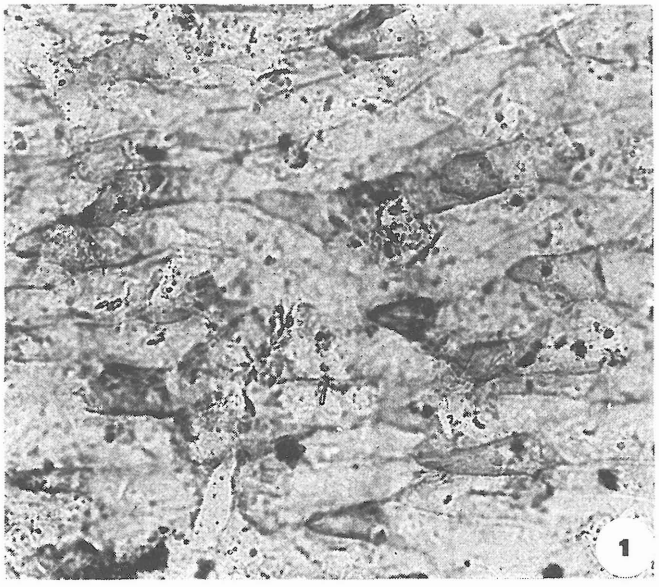
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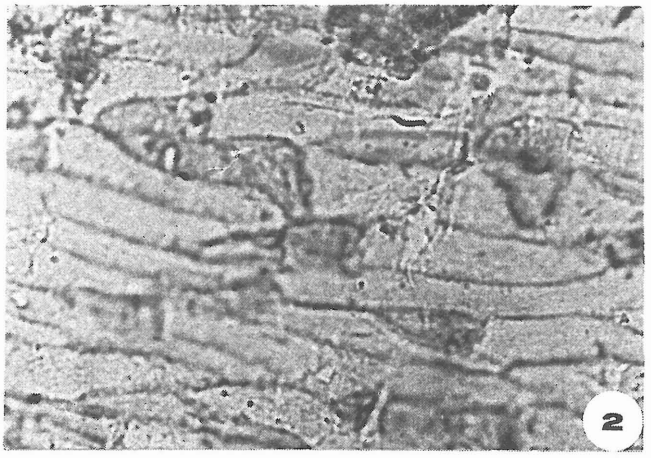
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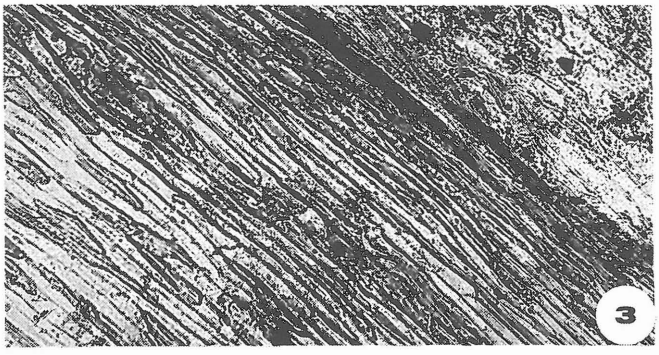
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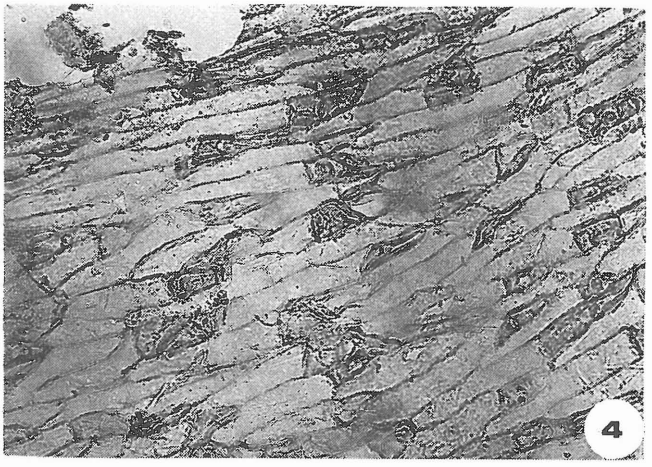
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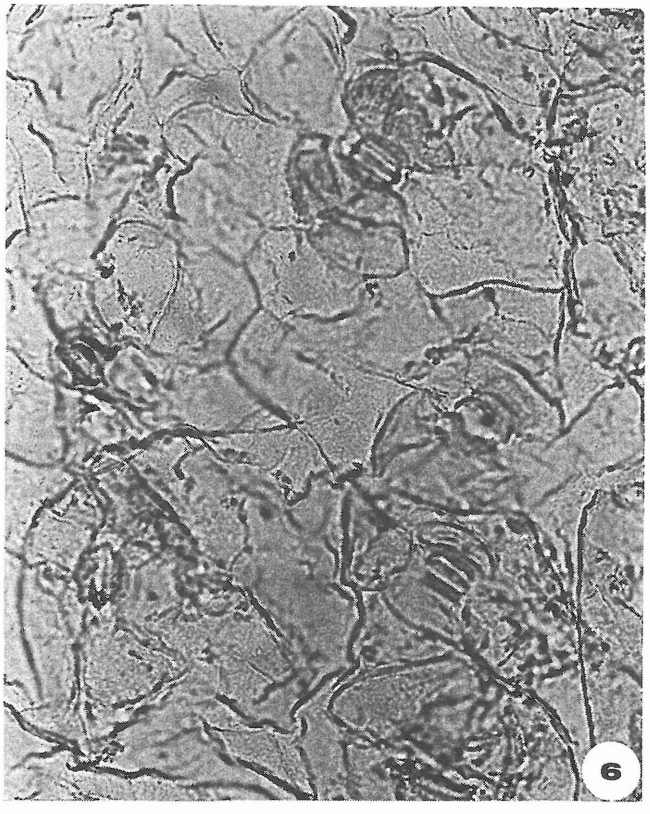
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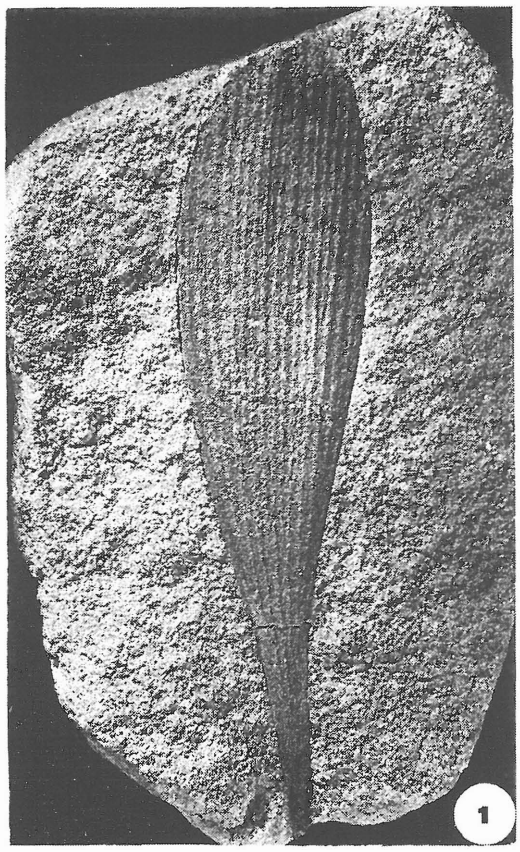
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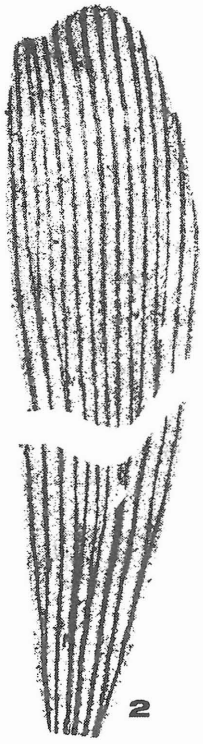
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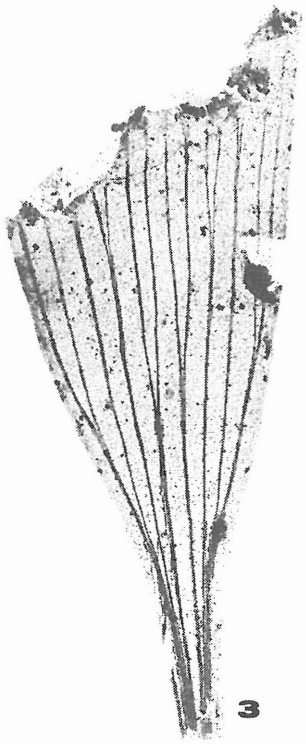
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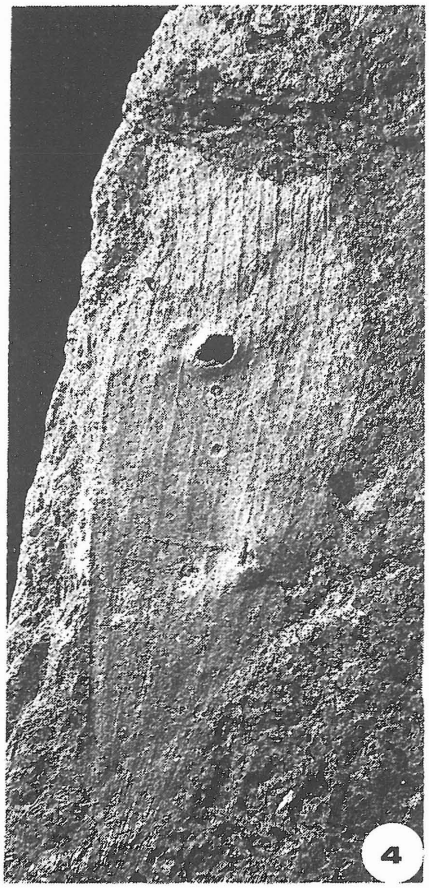
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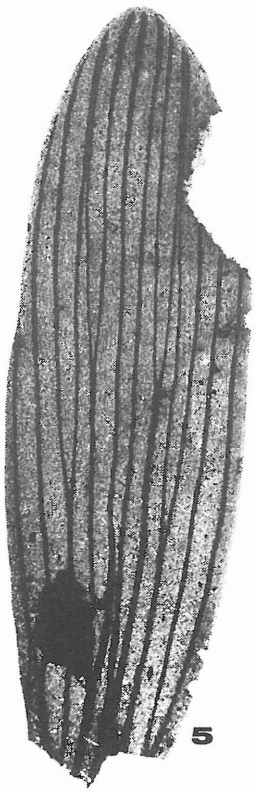
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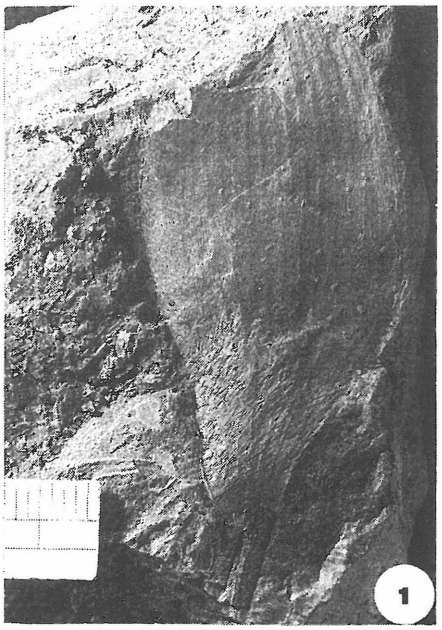
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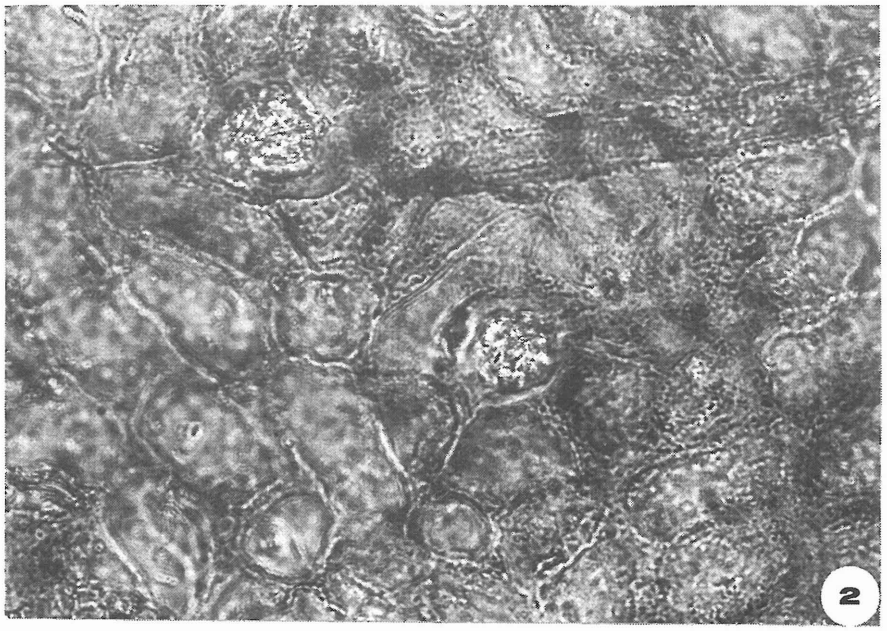
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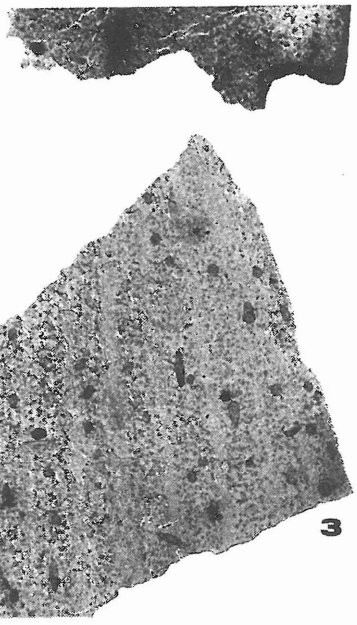
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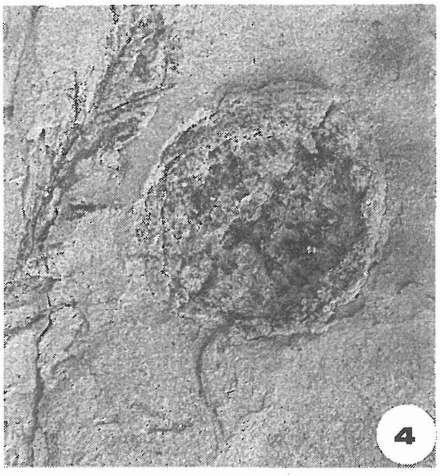
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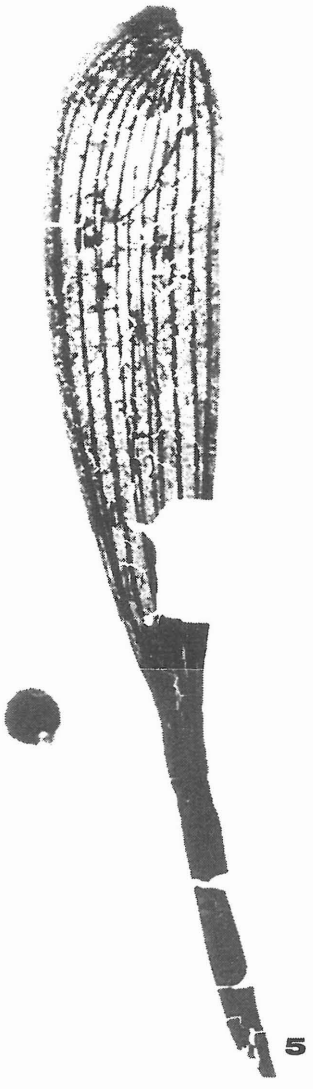
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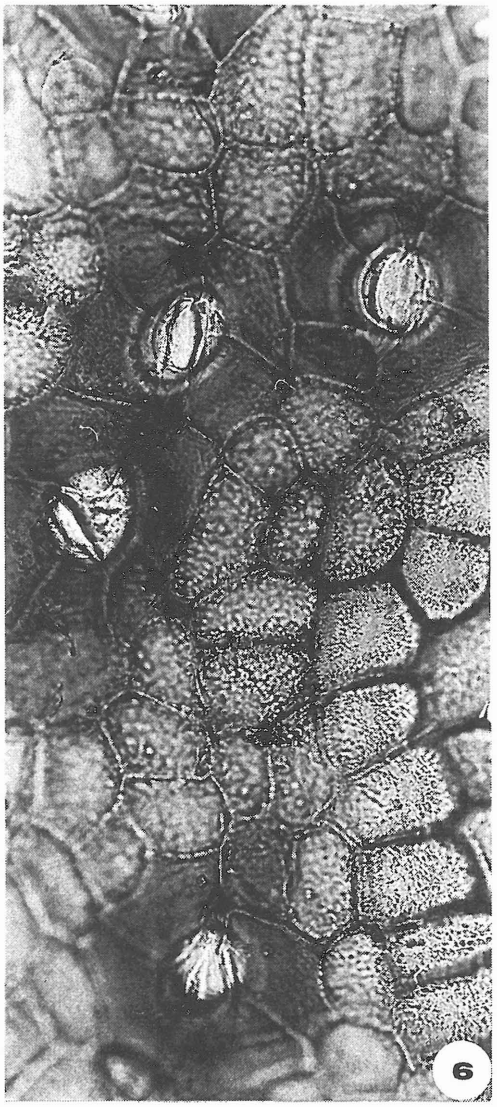
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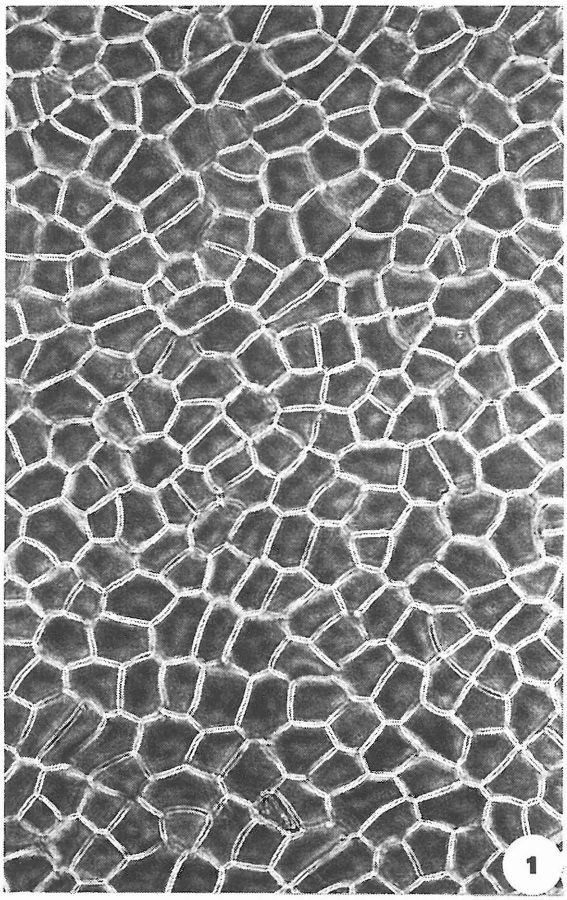
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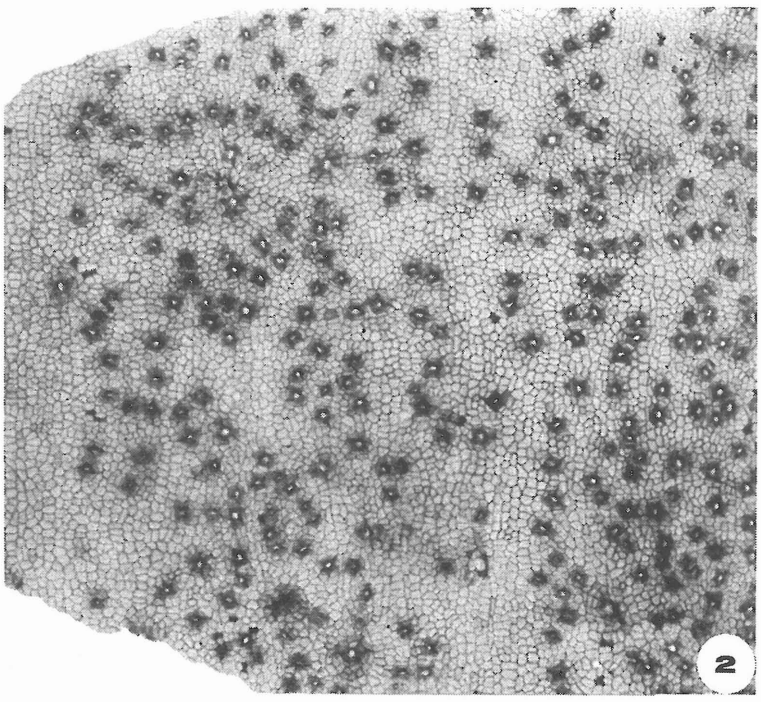
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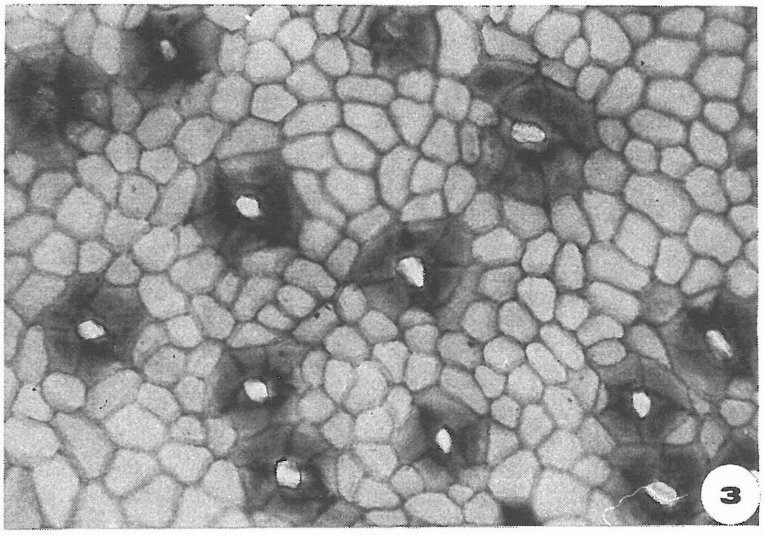
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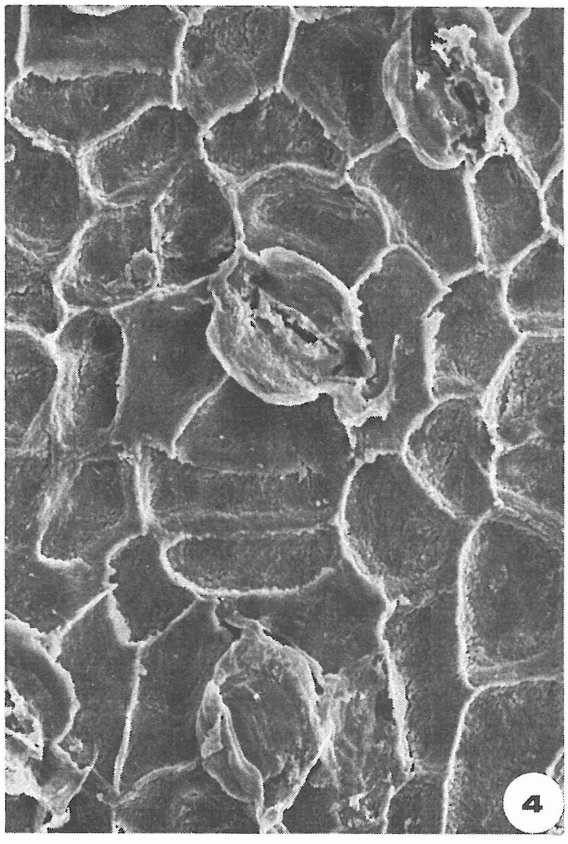
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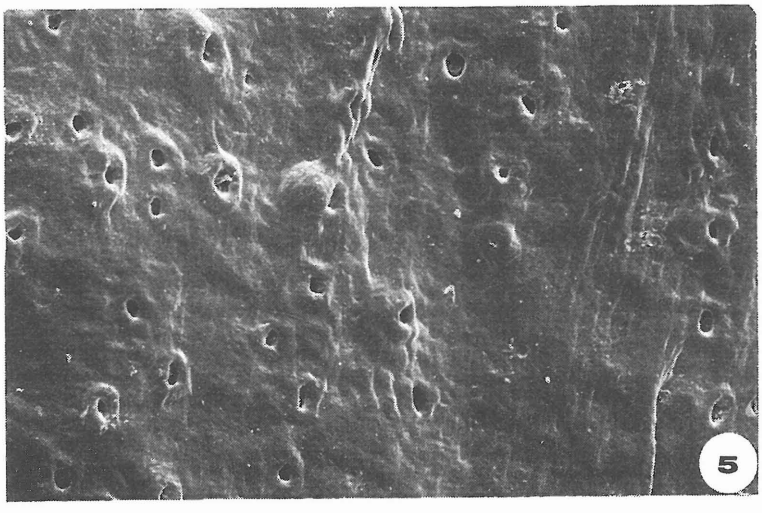
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