

Middle Jurassic Flora of the Peski Locality (Moscow Region): Systematics, Paleoecology, and Phytogeography

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Abstract—This paper describes the Middle Jurassic flora of the Peski locality (Moscow Region), a unique locality for fossil flora and fauna. The systematic composition, age of the flora, and plant taphonomy in context of paleorelief are considered. Plant associations are reconstructed. The paleogeographical significance of the flora is discussed.

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INTRODUCTION

The Middle Jurassic deposits of Central European Russia have been a classic object of stratigraphic and paleontological studies since the first half of the 19th century. The studies have focused mainly on marine deposits, because of their rich invertebrate fauna, a major source of stratigraphic information.

Apart from Middle Jurassic marine deposits, which are mostly Callovian in age, continental deposits are also present in Central Russia; they were formed before the Callovian transgression began. Paleontologically, they are poorly characterized. Palynologically, they are dated to the Bajocian–Late Bathonian (Volkova, 1952; Olfer'ev, 1986). The only information on the plant remains of these deposits are scattered in papers dealing with their lithology. Data on the Middle Jurassic flora of Central European Russia were virtually lacking in contrast to the coeval continental floras of Siberia, which were studied in great detail. The most probable explanation is that the Siberian Middle Jurassic deposits, developed in huge territories, are predominantly continental. Abundant plant remains here are the only reliable material for stratigraphic purposes.

The Middle Jurassic Peski locality, recently discovered in the Moscow Region, contains both plant remains and bones of various vertebrates, allowing one to fill this so far blank page of the paleontological record. The plant remains constitute a floristic assemblage that is comparable with the most representative floras of adjacent areas. The data obtained have refined the phytogeographical position of the Middle Jurassic flora of Central European Russia.

The locality was discovered in 1989 by A.V. Areshin and P.A. Fokin, who found, in the dumps for building materials of the Peski industrial complex remains of sharks, dipnoan fishes, and turtles of the Mesozoic type (Alekseev et al., 2001). The bedrocks that yielded the bones were exposed in the northern wall of the quarry in 1996. The deposits filled a karst cavity in Carboniferous limestones. In 1996, the first plant remains were also discovered. In 1998, two more karst cavities with similar deposits were exposed in the northern wall of the quarry. One of the cavities contained only plant remains, whereas numerous bones were found in the other in association with fossil plants. In 2000, the last cavity was exposed, with beds filled with complete skeletons of bony fishes. Plant remains in this cavity are infrequent and are represented mostly by wood fragments.

Two features of the Peski locality are unique: first, it is the only locality in European Russia that contains both Middle Jurassic vertebrates and plant remains, and, second, the preservation of the plant material is exceptional. For instance, the preservation allowed me to obtain for the first time data on the leaf anatomy of *Tritaenia* Mägdefrau et Rudolf (formal family "Miroviaceae" Bose et Manum).

Until recently, the Peski locality was the only locality in Central European Russia containing plant remains preserved as phytoleims with anatomical elements and cuticles. However, in 2003, I found a new promising locality with a Bathonian flora in the "Mikhailovskii Rudnik" quarry (near the town of Zheleznogorsk, Kursk Region) and published first data about this flora, including its generic and, in part, specific composition (Gordenko, 2004a, 2007).

Fossil flora is not only a source of stratigraphic information and an indicator of climate conditions, but also a basis of paleoecological reconstruction. In particular, a peculiar type of vegetation, which is not characteristic of the European–Sinian paleofloristic area, has been reconstructed on the basis of the Peski Flora.

CHAPTER 1. MATERIAL AND METHODS

The fossil plants (about 500 specimens) are kept as collection PIN, no. 4727 at the Paleontological Institute of the Russian Academy of Sciences. The plant remains were collected from the Middle Jurassic continental deposits of the Peski quarry, within 2 km of the railroad station Peski (Moscow Region, Kolomna district), situated about 100 km away from Moscow on the Moscow–Ryazan railroad (Fig. 1).

The plant remains include fragments of leaves and wood, seeds, and dispersed sporangia and cuticles.

The collection was amassed during field trips of 1997–2000 by scientists of the laboratory of paleobotany PIN S.A. Afonin, N.V. Gordenko, V.A. Krassilov, N.P. Maslova, with the participation of the researchers of other laboratories of PIN A.G. Sennikov, M.B. Efimov, and S.V. Moloshnikov.

Plant-bearing beds are predominantly plastic silty clays and, more rarely, clayey and silty sandstones.

The preservation of the plant material deserves special attention. Leaf fragments and seeds are phytoleims with well-preserved cuticles. In several cases, leaf anatomical elements, such as mesophyll and vascular bundles, are sufficiently well preserved. However, almost all the plant material, with a few exceptions, is represented by very fine debris and thus taxonomic determination can in some cases be hampered.

The leaf cuticles were macerated using the standard procedure and examined using an AXIOPLAN-2 light microscope and a CAMSCAN scanning electron microscope.

For comparative purposes, the leaf micromorphology of *Tritaenia linkii* Mägdefrau et Rudolf from the Lower Cretaceous of Germany and *T. scotica* (van der Burg et van Konijnenburg-van Cittert) Wilde from the Kimmeridgian of Scotland were studied. The specimens were kindly provided for this study by J. van Konijnenburg-van Cittert, (Utrecht University).

The terminology proposed by Krassilov (1968) and Meyen (1986) was used to describe cuticles. The vege-

tation was reconstructed using the methods of Krassilov (1971, 1972, 2003) and Spicer (1989a, 1989b).

CHAPTER 2. THE STRATIGRAPHIC POSITION AND AGE OF TAPHOFLORA OF THE PESKI LOCALITY

Historical Review. Jurassic Continental Deposits of the Moscow Syncline

The oldest Jurassic deposits of Central European Russia are continental. Palynologically, they are mostly dated to the Middle Jurassic (Bajocian–Early Callovian), although Early Jurassic deposits are possibly present at the very base (Unified ..., 1993).

Jurassic deposits of Central European Russia were first studied as early as the end of the 19th century. Shchurovskii (1866), Nikitin (1884), Dan'shin (1927, 1947), Zonov (1932, 1937), Zhukov and Kostantinovich (1951), Volkova (1952), Sazonov (1953, 1957), Gerasimov (1955, 1958, 1971), Sazonova (Sazonov and Sazonova, 1967), Gol'ts (1962), and Olfer'ev (1986) described them in their papers.

In spite of the long history of study, relatively little data on the Middle Jurassic continental deposits of Central European Russia have been accumulated. The deposits are poorly exposed (as a rule, available only by boring). In addition, they are usually poor in both plant and animal fossils. Olfer'ev (1986) proposed a chart subdividing the Middle Jurassic. Age determinations were predominantly based on data from pollen analysis or, more rarely, micropaleontology.

The Middle Jurassic deposits of Central European Russia are mostly confined to the Moscow Syncline, Ryazan-Saratov Depression, and the northern Voronezh Syncline. Continental deposits of this area are Bathonian and, in part, Lower Callovian. They have wide, but patchy, distribution, which significantly hampers facial analysis. They overlie Carboniferous–Triassic beds and are overlain by Callovian marine deposits (Volkova, 1952).

The distributional pattern of Jurassic continental deposits depends on the relief of the underlying Paleozoic and Triassic deposits, which were formed under continental conditions. Intense erosion occurred during this period. In the Middle Jurassic, a platform syncline was formed in the Volga Region. It had been sinking until the end of the Paleogene. The Dnieper-Donets and Mezen' depressions also experienced considerable submergence. The development of these three depressions and the uplifts separating them affected the Jurassic relief and, consequently, sedimentation. In the second half of the Middle Jurassic, a gradual land submergence began concurrently with the rise in the base level of erosion and accumulation of freshwater continental sediments predominantly in topographic depressions (Volkova, 1952). The elevation that separated the Dnieper-Donets depression from the northern slope of the Central Russian Upland served as an interfluvium

between two large river basins. The rivers of one of them flowed in the Dnieper-Donets depression, and the rivers of the other basin flowed eastward (Volkova, 1952). The Peski locality belongs to the second basin.

Two or, possibly, three large erosional valleys existed in this basin (Gol'ts, 1962). In the Middle Jurassic, clastic materials were accumulated along these valleys.

The first valley was discovered by Dan'shin (1927), and named the Main Moskva Pre-Jurassic erosional hollow. It starts near Moscow and runs eastward. In the upper course of the hollow, the height of the stream bed in the Jurassic deposits reaches 136 m above sea level; in the middle course, it decreases up to 60–80 m, and in the lower course, it is equal to 55–62 m. The hollow is relatively narrow in its upper course, subsequently it becomes wider, turning northward, and rounding the Moskva-Oka divide. The hollow again becomes narrower between the Suvoi and Cherusti elevations (Volkova, 1952). Hereafter, the river that flowed in this valley will be named the Proto-Moskva River. The second hollow, Oka hollow, appears slightly west of the town of Kaluga and runs northeastward. Several rather prominent left tributaries are present in its upper course; and right tributaries prevail in the lower course. The river that flowed in the Oka hollow will be named the Proto-Oka River. Opinions differ on the further direction of the Proto-Moskva and Proto-Oka rivers. The first idea is that the system of the Main Moskva hollow is margined on the north by an elevated band of Carboniferous deposits, which is latitudinally directed and passes through Rusa–Zelenograd–Moscow–Shchelkovo–Kudinovo–Gzhel'–Cherusti and farther eastward, up to the Oka-Tsna Ridge. This line is an interfluvium between the Main Moskva hollow and hollows running northward. The river system of the Main Moskva hollow ran into the Ulyanovsk-Saratov Syncline; and the system of rivers that ran northward was supposedly connected with the Mezen' Mesozoic depression. This idea was shared by many scientists, such as Dan'shin (1927), Volkova (1952), etc. Gol'ts (1962) developed another hypothesis. He revealed that in the north the bottom of Jurassic deposits considerably submerges, and a minor elevation of the roof of the Paleozoic and Triassic occurs only near Yaroslavl and north of the Oka-Tsna Ridge. Later studies have shown that one more, large Pre-Jurassic buried hollow exists along with the Main Moskva and Oka hollows. It was discovered by boring in the western Meshchera lowland. This valley appears slightly south of Ryazan and runs nearly meridionally northward. According to Gol'ts, the Main Moskva hollow is the left tributary of this valley. Consequently, he believed that this large basin ran northward down the dip of Paleozoic rocks, and the interfluvium situated between Ruza and the Oka-Tsna Ridge never existed.

The third opinion about the direction of the flow of the Proto-Moskva and Proto-Oka rivers was expressed by Olfer'ev (1986), who believes that not a vast alluvial

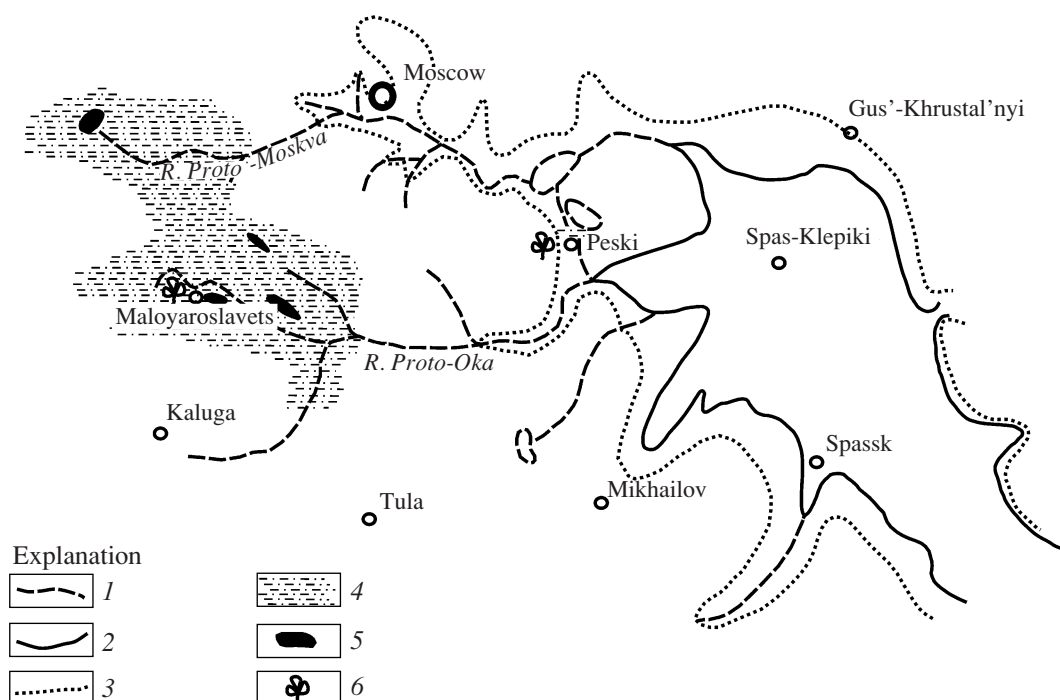


Fig. 1. Scheme of the paleohydrographic system in the Moscow Region (data of Volkova, 1952, are used): (1) river beds; (2) boundaries of a water body in drought season; (3) boundaries of a water body in wet season; (4) upland swamps; (5) lignites; (6) fossil plant localities.

valley, but a desalinated lagoon existed in the area (Fig. 1). In the east, it enters the Murom-Lomov depression of the Ulyanovsk-Saratov Syncline, from where shallow-water deposits are recorded. The supposed outline of the lagoon is shown in Fig. 1. I share the opinion of Olfer'ev.

The lithology of the Middle Jurassic continental deposits in Central European Russia is outlined below.

The base and the top of the Jurassic deposits under consideration contain coarse clastics, constituted by limestone and flint fragments and pebbles. These coarse clastics are only lacking in those areas where the surface of Carboniferous deposits was leveled and overlain by a relatively thick sequence of Jurassic continental beds.

The thickness of the deposits varies considerably: from 0 to 100 m, depending on the pre-Jurassic relief that they fill. The maximum thickness is in low topographic zones, and it is thin on interfluvies.

The lithological composition of the Jurassic continental deposits is also related to the pre-Jurassic relief. Volkova (1952) revealed in these deposits facies of interfluvies (refractory clays and lacustrine-paludal deposits), slopes (deluvial deposits), and lowlands (lacustrine-paludal and alluvial deposits).

Olfer'ev (1986; *Unified...*, 1993) proposed a regional stratigraphic chart of the Jurassic deposits in the Moscow Syncline, with seven structure-facial zones: the Yaroslavl-Ivanovo Volga Region, Kostroma

Trans-Volga Region, Kovernino Depression, Klin-Dmitrov Ridge and Teplyi Stan Hills, Vladimir-Yur'iev Opol'e and Meshchera Lowland, Northern slope of the Central Russian Upland, and Northern slope of the Oka-Don Lowland (Fig. 2). Within the Jurassic deposits, formations and sequences were described in each of these regions. The Peski locality is situated in the region of the Klin-Dmitrov Ridge and Teplyi Stan Hills, bordering on the Vladimir-Yur'iev Opol'e and Meshchera Lowland on the east and the Northern slope of the Central Russian Upland on the south. The Meshchera Series is developed in these zones, with three facially different sequences. The first, Kudinov Sequence, is up to 15 m thick, formed by light, often waxy hydromica-kaolin clays. This sequence entirely corresponds to the Kudinov clays of the southwestern Moscow Syncline and the Gzhel'-Kudinovo Formation (Olfer'ev, 1986), which was established by Sazonov and Sazonova (1967). The palynological assemblages extracted from these clays are dated to the Middle Jurassic (Olfer'ev, 1986). According to Olfer'ev, these clays are lacustrine, the lakes were predominantly karst in origin and developed when regional submergence took place during the Late Bajocian-Early Bathonian time. On the Northern slope of the Central Russian Upland, the Kudinov Sequence is replaced laterally by the Kireevo Sequence (so-called ore sequence), dated to the Bajocian-Early Bathonian. The third, the Moskva River Sequence, partially fills paleovalleys, in particular, Main Moskva, Venev, and Mikhailov hollows. The latter sequence shows a cyclic pattern. The

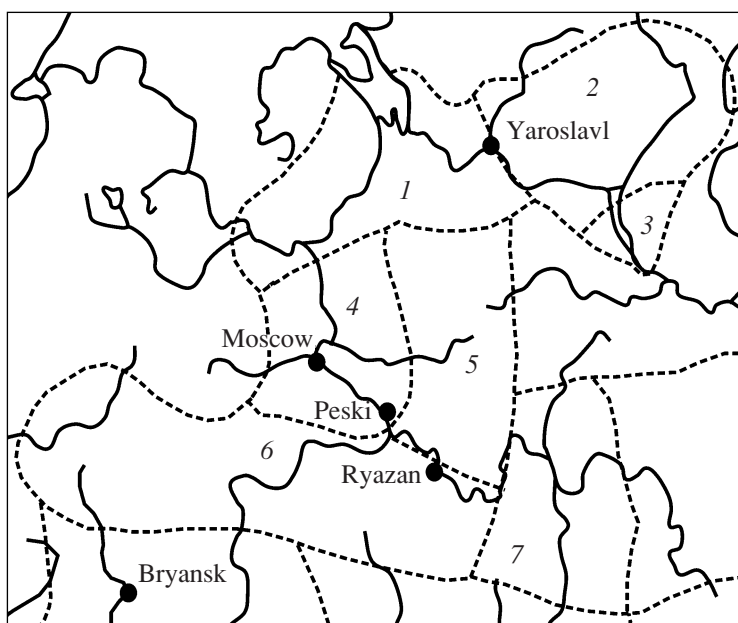


Fig. 2. Regions of the Jurassic deposits of the Moscow Syncline (Unified..., 1993): (1) Yaroslavl-Ivanovo Volga Region; (2) Kostroma Trans-Volga Region; (3) Kovernino Depression; (4) Klin-Dmitrov Ridge and Teplyi Stan Hills; (5) Vladimir-Yur'iev Opol'e and Meshchera Lowland; (6) Northern slope of the Central Russian Upland; (7) Northern slope of the Oka-Don Lowland. Dotted lines show the boundaries of the regions.

base of the cycle is formed by inequigranulate, predominantly white quartz sands with admixture of gravel and small pebbles of quartz reefs and quartzitic sandstones (channel facies), which are alternated by clayey silts and clays (floodland facies) with Bathonian palynological assemblages. This sequence is mostly composed of alluvial deposits. The Moskva River Sequence overlies the Kudinovo Sequence in some boreholes.

The Kudinovo and Moskva River sequences are united into the Meshchera Group, the concept of which corresponds to the Meshchera Sequence of the southwestern Main Moskva hollow. This sequence is formed by alluvial deposits of buried paleoterraces and reach 25 m in thickness. The Meshchera Horizon corresponds to the Meshchera Group.

Deposits which are analogous to the Meshchera Group are united into the Troyanovo Sequence in the upper courses of the Main Moskva and Oka hollows. This sequence is up to 13 m thick and is composed of irregularly alternating inequigranulate poorly sorted sands with wood fragments, coaly silts, black clays with plant remains and coal sublayers up to 3.7 m thick. The Troyanovo Sequence is particularly important for the purposes of the present study, since V.N. Kozlova and Gerasimov collected and A.S. Peresvetov determined (but did not figure) plant remains from these beds in the interfluvium of the Nara and Protva rivers: *Equisetites beanii* (Bunb.) Seward (now *Equisetum beanii* (Bunb.) Harris), *Equisetites* aff. *columnaris* (Brongn.) Phill. (= *Equisetum* aff. *columnaire* Brongn.), *Cladophlebis argutula* (Heer) Yok., *C. denticulata* (Brongn.) Font., *C. cf. haiburnensis* (L. et H.) Brongn.,

Eboracia lobifolia (Phill.) Thom., *Otozamites* sp., and *Nilssonia* sp. (Sazonov and Sazonova, 1967). Below, this locality will be named as the Narva-Protva interfluvium (Fig. 1). I believe that the fossil plant identified by Peresvetov as *Nilssonia* sp. is in fact *Nilssoniopteris* sp., as far as his preliminary determinations were accomplished without application of epidermal analysis. In the Peski locality it is *Nilssoniopteris*, which is similar in leaf morphology to *Nilssonia* Brongn., that shows a great diversity in combination with *Cladophlebis* Brongn., whereas no leaves of *Nilssonia* were found.

A different list of fossil plants is published in the *Unified Stratigraphic Scheme of the Jurassic Deposits of the Russian Platform* (1993): *Cladophlebis whitbienensis*, *C. argutula*, *C. denticulata*, *Eboracia lobifolia*, and *Equisetites beanii*.

According to Olfer'ev (1986), the Main Moskva hollow opened into a wide lagoon, bordered by an interfluvium to the north. To the east, the deposits of the supposed lagoon are replaced by coastal marine deposits. The supposed lagoonal deposits are united into the Moksha Sequence. These beds are up to 28 m thick and are characterized by rhythmically interbedded gray sands and light, bluish, and steel gray clays containing the shallow-water foraminifers *Ammodiscus colchicus* Thod. (determinations of N.T. Startseva). Ferruginous oolites and cavities of leached shells of the Middle Jurassic bivalves *Meleagrinella* aff. *doneziana* Bor. occur at the base of the beds (Sazonov and Sazonova, 1967).

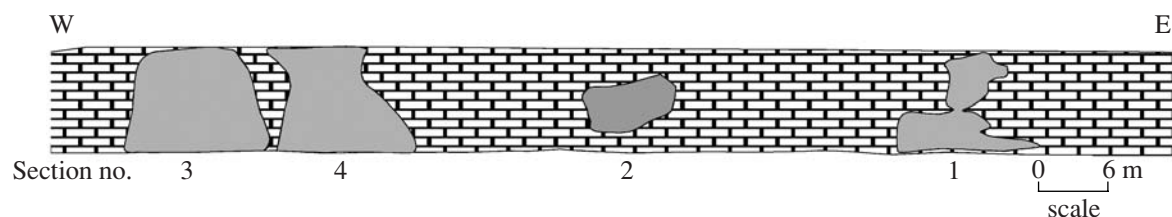


Fig. 3. The position of karst cavities filled with the Middle Jurassic continental deposits under study. Arabic numerals show the numbers of the sections in the order of their discovery.

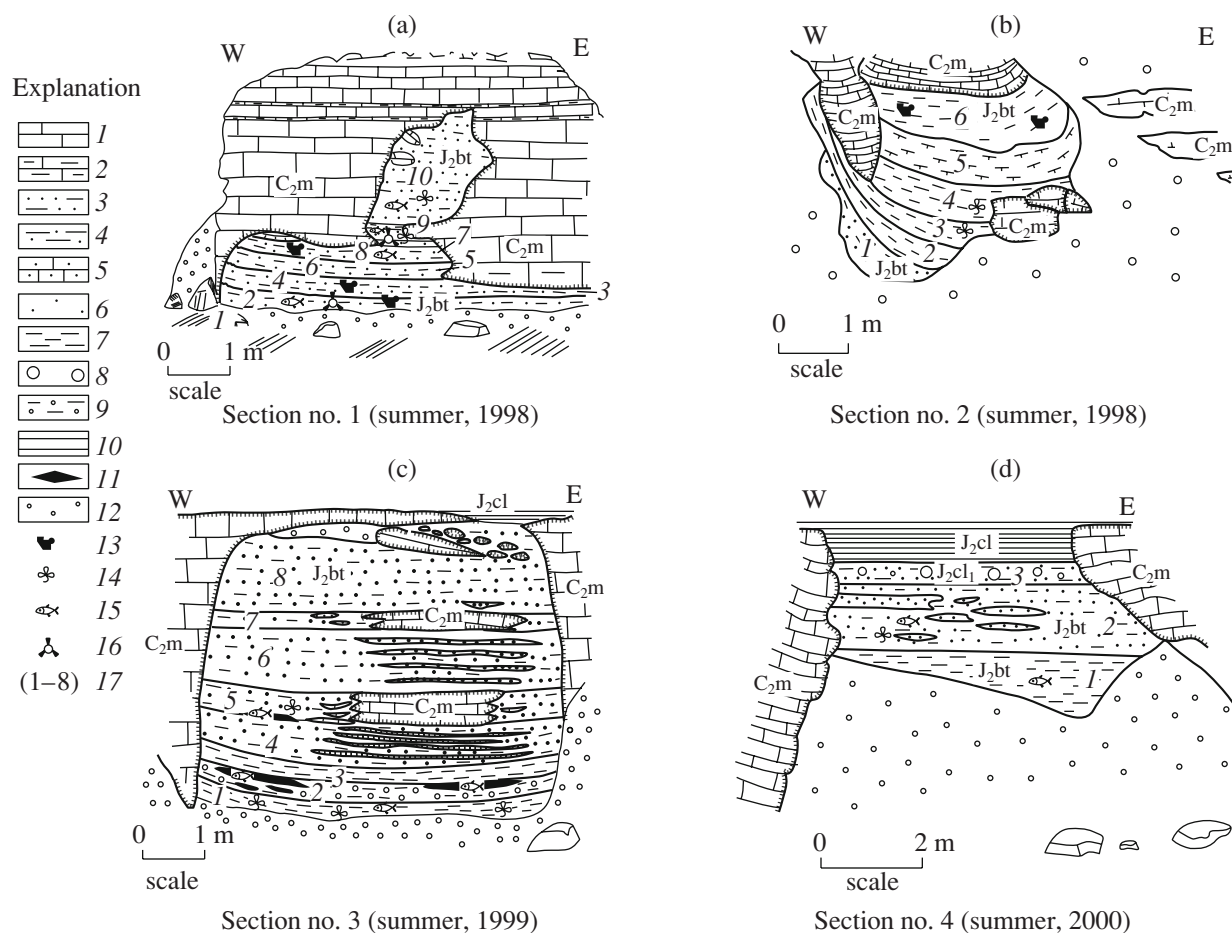


Fig. 4. Schemes of sections: (a) section, no. 1, 1998, summer; (b) section, no. 2, 1998, summer; (c) section, no. 3, 1999, summer; (d) section, no. 4, 2000, summer; (1) limestones C_2m ; (2) marls C_2m ; (3) silty sands, J_2bt ; (4) silty clays J_2bt ; (5) siltst J_2bt ; (6) sands J_2bt ; (7) clays J_2bt ; (8) calcic pebbles J_2cl_1 ; (9) clayey pebbles J_2cl_1 ; (10) marine clays J_2cl_2 ; (11) organic-rich layers; (12) Q_{IV} hillside; (13) pyrite concretions; (14) plant remains; (15) fish bones; (16) tetrapod bones; (1-8) numbers of layers.

The Meshchera Horizon is overlain by the Lower Callovian deposits of the Elat'ma Formation with a distinct washout. The marine Elat'ma Formation gives way to the coastal-marine Alpat'ev Formation between Shatura and Ryazan. The latter cuts off continental deposits of the Main Moskva hollow. Ammonites of the *Kepplerites goverianus* Sow. regional zone were found in deposits of the Alpat'ev Formation. In the west of the Main Moskva hollow, there is the Lyublino Sequence (up to 4 m thick), which is characterized by sands with Lower Callovian foraminifers and

ammonites *Cadoceras* sp. This sequence was probably replaced by continental deposits farther to the west. To summarize, the continental deposits of the Main Moskva hollow cannot be younger than the Late Bathonian.

Sections of the Continental Deposits of the Peski Quarry

The middle Jurassic deposits of the Peski Quarry are continental Bathonian and marine Callovian deposits. The continental deposits fill depressions in limestones

and karst cavities, supposedly formed in the limestones before the Bathonian. The limestones belong to the Moscovian Stage of the Middle Carboniferous. The Carboniferous limestones and Bathonian continental deposits filling roughnesses of the pre-Jurassic relief are overlain by a transgressive succession of Middle Callovian deposits.

This study mostly concerns Middle Jurassic continental deposits of the locality, which were described in 1997–2001. These deposits were uncovered by blasting operations in the northern wall of the quarry. In total, four outcrops were found during the above period (Figs. 3, 4). The outcrops are numbered according to the order they were discovered. The first outcrop is easternmost; the second is situated about 20 m west of the first outcrop along the wall of the quarry. The third is situated 60 m west of the first; and the fourth is 50 m west of the first.

The first and second outcrops were uncovered in 1996, and the third and fourth outcrops were uncovered in 1998. The deposits of the first outcrop have been studied in the most detail. Remains of primitive mammals, dinosaurs, eolacertilians, turtles, amphibians, and dipnoan fishes, as well as plants are known from this outcrop (Krupina, 1995; Novikov et al., 1998, 1999; Gordenko, 1999, 2000, 2004c, 2004d; Alekseev et al., 2001; Alifanov and Sennikov, 2001; Sukhanov, 2006). As early as 2000, these deposits were completely erased by bulldozer stripping. However, these operations showed how far the Bathonian deposits go into the wall of the quarry and allowed one to approximately reconstruct the outlines of the cavity they filled. The second and third outcrops were also destroyed, by blasting operations. Only the fourth outcrop remained, but now it is almost completely filled up with spoil heaps.

Data by Alifanov and Sennikov (2001) are used as a basis for the lists of fossil vertebrates given below. Cartilaginous fishes are determined by Bragina (2005); dipnoans, by Krupina (1995); ray-finned fishes, by Lebedev and Sychevskaya; amphibians, by Shishkin and Gubin; turtles, by Sukhanov (2006); eolacertilians, by Alifanov; dinosaurs, by Alifanov and Sennikov (2001); and mammals, by Gambarian and Averianov (2001).

Below descriptions of the Jurassic sections of the continental deposits in the Peski locality are given.

Jurassic system

Bathonian stage

Section no. 1 (Fig. 4a)

Layer 1 (visible base of the section). Sands are silty and brownish, 2 cm thick; sands are silty, strongly limonitized, 1 cm thick. The bedding is horizontal. The layer lies on breccia of Carboniferous limestones. The thickness is 3 cm. Incomplete skeletons of primitive

aquatic turtles *Heckerochelys romani* Sukhanov are found at the base of the layer.

Layer 2. The clays are silty, gray, and massive. The thickness is 30 cm.

Layer 3. The sands are fine-grained, silty, brownish, and with limonite sublayers. The bedding is horizontal. The thickness is 3 cm.

Layer 4. The clays are silty, gray, and massive. The thickness is 20 cm.

Layer 5. The sands are fine-grained, silty, brownish, with thin limonite sublayers. The bedding is horizontal. The thickness is 3 cm.

Layer 6. The clays are silty, gray, and massive. The thickness is 30 cm.

Layer 7. The sands are silty, brownish, with limonite sublayers. The bedding is horizontal. The thickness is 3 cm.

Layer 8. The clays are silty, grayish, with closely spaced thin (up to 0.3 mm) sublayers of limonite. The bedding is horizontal. The thickness is 20 cm.

Layers 1–8 contain skull imprints of cartilaginous fishes.

Layer 9. The interbedding of brownish silty sands, white carbonate sands, and bluish silty clays (silty sands prevail) contain a lens of plant debris up to 1.5 cm thick transforming into a bone-bearing lens. The bedding is horizontal. The layer yielded remains of the following fossil plants: *Sagenopteris rossica* Gordenko sp. nov., *Ptilophyllum riparium* Gordenko, 1999, *Otozamites paradoxus* Gordenko sp. nov., *Paracycas* sp., *Tritaenia glabra* Gordenko, 2004, *Tritaenia* sp., *Elatocladus* sp., and *Brachyphyllum* sp., isolated well-preserved seeds *Carpolithes* sp. 2, *Carpolithes* sp. 3, *Carpolithes* sp. 4, *Carpolithes* sp. 5, and *Carpolithes* sp. 6, and small fragments of fossil wood of *Podocarpoxylon* sp. The thickness is 30 cm.

The layer also contained fish bones (sharks *Hybodus hauffianus* Fraas; dipnoans *Ceratodus segnis* Krupina; palaeoniscoids of the order Ptycholepidiformes, *Ptycholepis* sp.; and neopterigians of the order Dapediidae, *Lepidotes* sp.); amphibians (labyrinthodonts cf. *Gobios* sp. and Caudata indet.); reptiles (eolacertilians, *Cteniogenis* sp.) and dinosaurs (Coelurosauria indet.), and primitive mammals (Morganucodontidae gen. et sp. indet.).

According to S.B. Smirnova, who studied a palynological spectrum from this layer, the abundance of *Sciadopityspollenites* increased up to 52% (Alekseev et al., 2001). In other characteristics, the spectrum resembles the spectra from the underlying layers.

Layer 10. The sands are silty, brownish, with repeated lenticular sublayers of limonite. Small concretions of brown iron ores, up to 3 cm, are present. Plant remains are represented by wood fragments of *Podocarpoxylon* sp. The thickness is 160 cm.

The visible thickness of the section is approximately 310 cm. The deposits are overlain by Carboniferous

limestones. Undulate textures are observed in the Jurassic deposits in the place of the lateral contact with the limestones. Within strata, the layers form undulate folds, with the undulation range reaching 10 cm. Such textures are explained by subsidence of the deposits forming the section, related to their consolidation and slumping.

The blasting operations and clearance with bulldozers revealed that the cavity that was filled by the deposits of the first sections was a fragment of a dead-ended cave, about 26 m long and 4 m wide.

Section no. 2 (Fig. 4b)

Layer 1 (visible base of the section). The sands are gray, silty, cross-bedded, and with admixture of carbonate particles. The thickness is 57 cm.

Layer 2 contains gray, silty, and massive clays. The thickness is 43 cm.

Layer 3 contains dark-gray clays with thin small limonite lenses. This layer contained numerous plant remains: *Stachypteris psammitica* Gordenko, 2000, *Sphenopteris* sp., *Sagenopteris rossica* sp. nov., *Otozamites paradoxus* sp. nov., and *Tritaenia glabra* Gordenko. The thickness is 47 cm.

Layer 4 contains black clays with limonite sublayers. Plant remains included *Sagenopteris rossica* sp. nov., *Otozamites paradoxus* sp. nov., *Williamsonia* sp., and *Tritaenia glabra*. The thickness is 69 cm.

Layer 5 contains carbonate, bluish-gray, and massive clays. The thickness is 57 cm.

Layer 6. The clays are black, strongly limonitized, massive, and with limonite concretions. The thickness is 79 cm.

Superimposed undulate textures are present in the layers. The textures are related to the subsidence and slumping. The layers form a concave rounded fold, related to their subsidence.

The deposits are overlain by strongly subsided Carboniferous limestones.

Section no. 3 (Fig. 4c)

Layer 1 (visible base of the section). The clays are black, silty with sublayers (up to 2 mm), enriched in carbonate material and sandy lenses. The following plant remains were found in the sandy lenses: *Cladophlebis denticulata* (Brongn.) Font., *Cladophlebis* sp., *Selenocarpus* sp., *Clathropteris* sp., *Sagenopteris rossica* sp. nov., *Anomozamites* aff. *minor* (Brongn.) Nath., *Nilssoniopteris vittata* (Brongn.) Florin, *Nilssoniopteris* sp., *Tritaenia striata* Gordenko, 2004, *Oswaldheeria* aff. *macrophylla* (Florin) Bose et Manum, and *Cephalotaxopsis* sp.

Vertebrate remains are palaeoniscoids *Ptycholepis* sp. The thickness is 40 cm.

Layer 2. There are small clay pebbles in clay matrix. Small lenses of light sand occur at the base of this cross-bedded layer. Numerous ichthyodorulites of sharks *Hybodus hauffianus* were found in the layer. The thickness is 50 cm.

Layer 3 shows interbedding of silty clays and sublayers with clayey pebbles. There are black sublayers with charred organic material. They are situated in the upper portion of the layer, at a distance of 5 cm from each other. No bedding was observed. Ichthyodorulites of sharks *Hybodus hauffianus* were found in the layer. The thickness is 70 cm.

Layer 4. The sandstones are silty, brownish, with numerous lenses of poorly rounded quartz sands, which contained fragmentary bones of dipnoans *Ceratodus segnis* and small bony fishes (determination by Gordenko), ichthyodorulites of sharks *Hybodus hauffianus*, and plant remains *Sagenopteris rossica* sp. nov., *Nilssoniopteris infera* Gordenko, sp. nov., *Nilssoniopteris* sp., and *Anomozamites* aff. *minor*. No bedding was observed. The thickness is 90 cm.

Layer 5. Weathered limestones of a crumbled part of the roof in the silty matrix. The thickness is 60 cm.

Layer 6. The sands are silty, brownish, with numerous lenses of small-grained quartz sands with bony debris, and cross-bedded. The thickness is 130 cm.

Layer 7. The limestones are weathered, from a crumbled part of the roof. The thickness is 30 cm.

Layer 8. Gray silts. The thickness is 130 cm.

Layer 8 is overlain by slightly subsided Carboniferous limestones. Upward in the section, Upper Callovian clays are present. The Bathonian deposits contact with the Callovian deposits in the top right part of the outcrop. The Callovian deposits overlie the Bathonian deposits with a distinct washout. The width of the contact is about 50 cm.

Section no. 4 (Fig. 4d)

Layer 1 (visible base of the section). Black clays are alternating with bluish carbonate clays. The layer contains a vertical succession of mass accumulations of complete skeletons of ray-finned fishes (order *Ptycholepiformes*, *Ptycholepis* sp.) and neopterigians (order *Dapediidae*, *Lepidotes* sp.). The bedding is horizontal. Large wood fragments of *Araucarioxylon* sp. and *Taxaceae* gen. indet. also occur in the layer. The thickness is 150 cm.

Layer 2. The clays are dark, silty, with lenses of sands and with clay pebbles. Fine indeterminable plant debris is present. Other plant remains include a seed of *Carpolithes* sp. 1 and leaf fragments and cuticles of *Oswaldheeria* aff. *macrophylla*. The thickness is 170 cm.

Layer 3. Conglomerate of calcic boulders and clayey pebbles in clayey-sandy matrix. The thickness is 50 cm. These are coastal marine deposits of the Lower-

Middle Callovian, indicating the beginning of a marine transgression.

Layer 3 is overlain by black marine Upper Callovian clays.

*The Age of the Jurassic Continental Deposits
in the Peski Quarry*

First of all, the age of the continental deposits in question can be estimated based on the fact that they are underlain by Middle Carboniferous deposits, which, in their turn, are overlain by marine Upper Callovian and Oxfordian deposits in most of the Peski Quarry area. Since the Jurassic continental deposits predominantly fill karst cavities in Carboniferous deposits, they are laterally contacting. They are also overlain by Carboniferous limestones. The third section, where the part of the roof of the cave fell down, shows a small area of contact with the Callovian clays. Transgressive overlapping of conglomerates was only observed in the upper part of the fourth section, the conglomerates give way to light gray marine clays with belemnites. There are grounds for believing that these deposits are Early Callovian in age, since they are transgressive and contain marine invertebrates (belemnites). The light gray clays are overlain by dark gray Upper Callovian–Oxfordian clays. Therefore, the upper limit of the age of the deposits under description is bounded by the beginning of the Callovian transgression. Therefore, it is necessary to determine the lower limit.

First we will analyze available lithological data. Although a general rule of cavity filling was observed that clayey deposits are substituted by sandy deposits upward the section, some differences in the lithological composition were observed between the described sections. Let me compare the deposits of the Peski locality and the beds established by Olfer'ev. The first section is most comprehensively studied. Palynologically, these deposits belong to the Moskva River Sequence of the Meshchera Horizon (Alekseev et al., 2001). As was said above, these beds occur in several pre-Jurassic paleovalleys and are alluvial formations. The Peski locality is situated on a small interfluvium, at a distance from the channels of the Proto-Oka and Proto-Moskva rivers; moreover, these deposits lack cyclicity characteristic of the Moskva River Sequence. Lithologically, the deposits of the first section more closely resemble the deposits of the Moksha Sequence because of the presence of sublayers of blue and gray clays and ferruginous concretions. However, the Moksha Sequence is characterized by the presence of brackish-water foraminifers. The deposits in question in the Peski locality and, in particular, the deposits of the first section, do not contain foraminifers (with the exception of a lens of black clays, which was exposed by bulldozer stripping in the first section and most probably represents a later inwash).

The lithology of the deposits of the second section has much in common with the Troyanovo Sequence, which is characterized by unevenly alternating poorly sorted sands with wood fragments, coaly silts, and black clays. Supposedly, the Troyanovo Sequence is of lacustrine-paludal genesis. Similarly to the Troyanovo Sequence, the deposits of the section in question contain *Otozamites* Braun. However, remains of *Equisetites* sp. or other Equisetopsida are lacking.

The deposits of the third section resemble those of the Moskva River Sequence, but do not show cyclicity characteristic of the latter formation. The base and middle portion of the section contain plant remains comparable with those found in the Troyanovo Sequence and teeth of *Ceratodus segnis* and ichthyodorulites of sharks (*Hybodus hauffianus*), identical to those of the first section. In addition, a few complete skeletons of ray-finned fishes-palaeoniscoids have been encountered at the base of the section.

Apparently, the deposits of the fourth section are not identical in lithology to any sequence established by Olfer'ev, as far as their lower part represents alternating thin silt layers and thin black layers filled with complete skeletons of ray-finned fishes. In my opinion, these layers reflect seasonal fish kills. Thin fine-grained silty sands are situated above the zone of fish kill. To date, the origin of these deposits has been a matter of debate. There is a possibility that layers in the first section with alternating gray and bluish carbonate clays with relatively complete skeletons of aquatic turtles and skulls of cartilaginous fishes partially correspond to the seasonal deposits of the fish kill. As far as the sands of the fourth section are overlain with a washout by deposits lithologically comparable with the Lower Callovian Alpat'evo Formation, they can be dated Late Bathonian.

The deposits of the Peski locality are of particular interest because of their occurrence in karst caves and cavities on an interfluvium, features that are at first glance comparable with the deposits of the Kudinov Sequence, which are connected with interfluvium lakes formed on karst. However, the vertebrate assemblage of the Peski locality implies the existence of a large water body. Such a water body could not have been situated on an interfluvium. In addition, the facies in this locality differ from deposits of "karst lakes."

Now let me consider the available data on plant macrofossil remains. First of all, it should be decided where these plant remains constitute a single assemblage.

Let me compare sections 1 and 2. Fossil plants were found in layer 9 of section 1 and layers 3, 4 of section 2. These three layers share the following fossil plants: *Sagenopteris rossica* sp. nov., *Otozamites paradoxus* sp. nov., and *Tritaenia glabra*.

The above-listed species are most numerous in the plant-bearing layers of sections 1 and 2 and exhibit identical degrees of preservation. Of importance is the fact that all three species are endemics of the locality under consideration. Thus, definite indications exist

that the plant remains of sections 1 and 2 belong to a single assemblage.

The comparison between sections 1 and 2 and section 3 is much more difficult, since the plant remains of section 3 differ considerably from those of sections 1 and 2. Layers 1 and 4 are plant-bearing in section 3. These layers share the only species with sections 1 and 2, namely, *Sagenopteris rossica* sp. nov. The genus *Tritaenia* Mägdefrau et Rudolf is represented by a different species, *T. striata*. Bennettites of section 3 belong to *Nilssoniopteris* Nath. and *Anomozamites* Schimp., which are lacking in sections 1 and 2. In addition, section 3 contains ferns *Clathropteris* Brongn., *Cladophlebis*, and *Selenocarpus* Schenk and conifers *Cephalotaxopsis* sp. and *Oswaldheeria* aff. *macrophylla*. Therefore, the presence of *Sagenopteris rossica* sp. nov. is the only feature common to section 3 and sections 1 and 2.

It should be considered that this sharp difference in the composition of ferns, bennettites, and conifers of these sections might in fact be caused by facial differences. Krassilov (1971, 1972, 2003) studied in detail the formation of taphonomic assemblages in the Kamenka locality (Donets Basin, Ukraine) of the Bathonian and, in part, Early Callovian age. He showed by this example that such cyclic processes as the riverbed migration and changes in the delta lead to cyclic redistribution of the riverside vegetation. The replacement of the channel of deltaic facies is accompanied by the replacement of plant taphonomic assemblages. This vertical succession of taphonomic assemblages corresponds to the succession of catena units. A catena reflects the successive alternation of vegetation from the water line to interfluvium. Each catena unit corresponds to a particular plant association; extreme units of the catena differ significantly in their floristic composition. Thus, *Ptilophyllum* Morris and *Nilssoniopteris* belong to different associations in the Kamenka locality. The former genus is anthracophobic and usually occurs in plant associations of coastal-marine and deltaic facies, whereas the latter is related with inland paludal facies. *Ptilophyllum* is a member of the association with *Elatides* Heer, caytonias (*Sagenopteris* Presl), and ferns (*Todites williamsonii* (Brongn.) Sew. and *Dictyophyllum rugosum* L. et H.). *Nilssoniopteris* associates with caytonias (*Sagenopteris*), ferns (*Cladophlebis denticulata*), and conifers of the genus *Pityophyllum*. It should be pointed out that *Sagenopteris* is present in both associations.

Although the Peski associations slightly differ from the above associations in the Kamenka locality, in general, they are equivalent. One association corresponds to the association with *Ptilophyllum*; the other, to that with *Nilssoniopteris*, and *Sagenopteris* occurs in both associations. By analogy with the Kamenka locality, I believe that the two associations are parts of a single flora in the region under consideration and reflect facies alternation.

Now let me compare sections 3 and 4. Leaf fragments and dispersed cuticles of *Oswaldheeria* aff. *macrophylla* were extracted by bulk maceration from layer 2 of section 4. Leaves of this species were also found in layer 1 of section 3 suggesting that the plant remains in both sections belong to the same floristic assemblage.

Therefore, below all plant remains found in the Peski locality will be considered as members of a single floristic assemblage.

Conceivably the deposits of all four sections are more or less coeval, but some other data should also be included in the analysis to support this assumption. Apart from plant remains, sections 1, 3, and 4 contain fairly numerous bones of various vertebrates, and the sections can be compared using these remains. Thus, sections 1 and 3 are comparable in the presence of ichthyodorulites of sharks *Hybodus hauffianus* and teeth of dipnoans *Ceratodus segnis*. Sections 3 and 4 are comparable in the presence of palaeoniscoids *Ptycholepis* sp. Therefore, bone remains of vertebrates also imply that the deposits of the four sections are approximately coeval.

The described floristic assemblage is characterized by the following typical Mesozoic genera: *Stachypteris* Pomel, *Cladophlebis*, *Clathropteris*, *Sagenopteris*, *Ptilophyllum*, *Otozamites*, *Nilssoniopteris*, *Anomozamites*, *Tritaenia*, and *Oswaldheeria* Bose et Manum. *Stachypteris* and *Oswaldheeria* do not occur before the Middle Jurassic, and the last members of *Clathropteris* only survived until the Bathonian (Vachrameev et al., 1970). These data definitely point to the Middle Jurassic age of the assemblage. At the specific level, the assemblage under consideration is relatively highly endemic, thus making comparison with other floristic assemblages difficult. Thus, the genus *Stachypteris* is represented by the endemic species *S. psammitica*; *Sagenopteris*, by *S. rossica* sp. nov.; *Ptilophyllum*, by *P. riparium*; *Otozamites*, by *O. paradoxus* sp. nov.; and *Tritaenia*, by *T. glabra* and *T. striata*. Apart from the previously known species of *Nilssoniopteris*, *N. infera* sp. nov. is present. The comparison between such endemic species is conceivable on the basis of some similarities in the epidermal structure. Thus, *Ptilophyllum riparium* shows much in common in its epidermal structure with other species of the genus, which were united by Doludenko and Svanidze (1964) in one group on the basis of epidermal structure: *P. pecten* (Phill.) Morris and *P. hirsutum* Thom. et Bancroft from the Bajocian of Yorkshire (England), *P. caucasicum* Dolud. et Svan. from the Bajocian of western Kazakhstan and the Bathonian and Callovian of western Georgia, and *P. ukrainense* Dolud. from the Bathonian–Callovian of western Ukraine. In my opinion, this group also includes *P. vasekgahense* Barnard et Miller from the Middle Jurassic of Iran (Schweitzer and Kirchner, 2003), which resembles *P. riparium* in epidermal structure. All these related species of *Ptilophyllum* occur in the Middle Jurassic, from the Bajocian to the Callovian.

In epidermal structure, *Otozamites paradoxus* sp. nov. is closest to *O. pulcher* Barnard et Miller and *O. harri-sianus* (Kilpper) Schweitzer et Kirchner from the Lower–Middle Jurassic of Iran; apparently, these species are closely related. Members of *Otozamites* with similar epidermal structure are absent in deposits of other regions. In epidermal structure, *Nilssoniopteris infera* sp. nov. shows a close similarity to such species from the Callovian of Georgia as *N. vulgaris* Dolud., *N. angustifolia* Dolud., and *N. muchlensis* Dolud. In sum, bennettites also testify to the Middle Jurassic age of the deposits of the Peski locality.

To determine the stage on the basis of plant remains is much more difficult, among other things because of the high endemism at the species level. According to Vachrameev, the Aalenian floristic assemblages are characterized by a low species diversity of the ferns *Coniopteris* Brongn. (no more than two or three species) and high diversity of *Nilssonia* (six or more species). The typical Aalenian floristic assemblage was described from the Karakhskaia Formation in Dag-estan, where the following plant remains were found: *Equisetum beanii*, *E. ferganensis* Sew., *Marattiopsis muensteri* (Goep.) Schimp., *Coniopteris hymenophyl-loides* (Brongn.) Sew., *C. murrayna* (Brongn.) Brongn., *C. magnifolia* Brick, *C. whitbiensis* (Brongn.) Brongn., *Sagenopteris phillipsii* (Brongn.) Presl, *Anomozamites minor*, *Pterophyllum andreanum* Schimp., *P. brau-nianum* (Goep.) Schenk, *Cycadites rectangularis* Brauns, *Taeniopteris densinervis* Feist., *Ptilophyllum acutifolium* Morris, *P. cutchense* Morris, *Nilssonia acuminata* Presl, *N. dentata* Brick, *N. formosa* Vachr. et Vasina, *N. mediana* (Leck.) Fox-Str., *N. orientalis* Heer, *N. polymorpha* Schenk, and *N. vittaeformis* Pryn. (Vachrameev, 1989). The comparison between the assemblage from the Peski locality and this Aalenian assemblage shows a significant difference at the generic level: such genera as *Equisetum* L., *Marattiop-sis* Schimp., *Cycadites* Sternb., *Pterophyllum* Brongn., and *Nilssonia* are totally absent. Moreover, the floristic assemblage under consideration also lacks reliable remains of *Coniopteris*. On the other hand, *Ano-mozamites* aff. *minor* is present. *Anomozamites minor* is believed to disappear in deposits younger than the Aalenian (Vachrameev, 1989). Therefore, the assem- blage under consideration is only similar to the Aalen- ian assemblage in the presence of *Anomozamites*, *Ptilo- phyllum* and *Sagenopteris*.

The typical Bajocian flora is the flora of Yorkshire (England). Since the list of Yorkshire species exceeds 150 species (Harris, 1961, 1964, 1969, 1979; Harris and Millington, 1974), it is not reproduced here, but only distinctive features of this assemblage are dis- cussed. In the Bajocian, *Coniopteris* reached its great- est diversity. Members of *Nilssonia* were still diverse. Typical Aalenian genera and species continued to exist, although some new genera appeared, such as *Klukia* Racib., *Stachypteris*, and *Pachypteris* Brongn. *Ptilo- phyllum* and *Otozamites* reached the greatest species

diversity, represented by three and nine species, corre- spondingly. Caytonias were also numerous.

In the Peski locality, *Stachypteris* is found, but *Klukia* and *Pachypteris* are lacking. Leaves of cayto- nias are numerous (*Sagenopteris*), but they are repre- sented by a newly discovered species. *Otozamites* includes a single species. The only species common to Yorkshire and Peski are *Cladophlebis denticulata* and *Nilssoniopteris vittata*, but they are not index species. In sum, a close similarity to the Bajocian assemblage is not observed.

The type flora of the Bathonian is the flora described from the Tkvarcheli coal basin in western Georgia (Vachrameev, 1989). A characteristic feature of the local Bathonian flora is the decline in the species diver- sity of the fern *Coniopteris* down to two species, which survived since the Bajocian. The species diversity of *Nilssonia* is also reduced. Bennettites of the genera *Ptilophyllum* and *Otozamites* are still relatively diverse. *Pachypteris lanceolata* Brongn. and the conifers *Pagiophyllum* Heer and *Elatides* become common. As far as the diversity of ferns *Coniopteris* and cycads *Nilssonia* reduces in the Bathonian, the Bathonian assemblage shows a significant similarity to the assem- blage from the Peski locality. However, such an impor- tant element as *Pachypteris* is unknown from the Peski locality.

In the Callovian, the diversity of ferns was greatly reduced, nilssonias nearly disappeared, *Pachypteris*, *Nilssoniopteris*, *Otozamites*, *Pterophyllum*, *Pseudocte- nis* Sew., *Brachyphyllum* Brongn., and *Pagiophyllum* became common (Vachrameev, 1989). The similarity between the Callovian assemblage from Georgia and the assemblage from the Peski locality includes the high species diversity of *Nilssoniopteris*: this genus is represented by three species in the Peski locality, two of which resemble Callovian species from Georgia in epi- dermal structure. *Ptilophyllum* is represented by *P. riparium*, a species related with the Callovian *P. cau- casicum*. The low diversity of ferns is also a feature common to both assemblages. They share the species *Cladophlebis denticulata*. However, only one small fragmentary shoot of *Brachyphyllum* was found in the Peski locality, and the pollen genus *Classopollis* Pflug, which is thought to be associated with such shoots, is also rare, which testifies to the difference between the Georgian and Peski assemblages.

Thus, the Peski Assemblage shows the closest simi- larity to the Bathonian and Callovian assemblages. However, a specific feature of the Callovian is the wide occurrence of conifers with scaly leaves (*Brachyphyl- lum* and *Pagiophyllum*), and this is not the case in the Peski Assemblage, so the deposits of the Peski locality are dated to the Late Bathonian by floristic data.

Of extreme importance is the find in the Peski locality of members of *Tritaenia*. Previously, only three species of *Tritaenia* were known, the most ancient (*T. scotica*) appears in the Upper Jurassic

deposits of the Kimmeridgian of Scotland. The other two species are known from the Cretaceous. The family Miroviaceae, which includes the genus *Tritaenia*, appears in the Middle Jurassic. Keeping in mind that the deposits under description are no younger than Late Bathonian–early Early Callovian, the present record is the earliest record of the genus. Usually, leaves of *Tritaenia* tend to form monodominant aggregations. This trend is not very distinct in the Peski locality. To date, available data on floristic assemblages containing *Tritaenia* are insufficient; nonetheless, such assemblages obviously differ from the type assemblages, which were formed by coastal vegetation, a fact that explains the relative ease of determining their age. Therefore, certain difficulties appear in the comparison between the assemblage from the Peski locality and the type assemblages from western Europe.

The palynological assemblage was studied by Smirnova only from section 1 (Aleksiev et al., 2001). According to Smirnova, layers 1–8 are characterized by a single palynological assemblage. Among spores, “Gleicheniaceae” are numerous (8–25%), represented by *Plicifera delicata* (Bolch.) Bolch., *P. decora* (Chlon.) Bolch., *Gleicheniidites senonicus* Ross, *G. laetus* (Bolch.) Bolch., *G. umbonatus* (Bolch.) Bolch., *G. apilobatus* Dör., and *Ornamentifera* sp. Spores of “Cyatheaceae” are *Cyathidites minor* Coup. and *C. australis* Coup. (2–10%). Other, less numerous, ferns are *Osmundacidites jurassicus* (Bolch.) Kuz., *O. wellmanii* Coup., *Marattisporites scabratus* Coup., *Sestrisporites pseudoalveolatus* Coup., etc. Lycopod microspores occur: *Lycopodiumsporites* sp., *Neorastrickia rotundiformis* (K.-M.) Tarass., *Densoisporites velatus* Weyl. Et Krieg., *Staplinisporites caminus* (Balme) Dett., *S. rotalis* Dör. Horsetails are represented by *Equisetosporites* sp. Spores of sphagnum (*Sphagnumsporites suflatus* Bolch. and liverworts (*Coocsonites* sp.) occur more rarely.

Pollen grains constitute 70% or more of the assemblage. Pollen grains of *Sciadopityspollenites* sp. are the most numerous members of the assemblage (12%). Bisaccate pollen grains, which are more typical of the Lower Jurassic, are numerous: *Alisporites* sp., *Ovalipollis* sp., and *Protoconiferus funarus* Bolch. However, more advanced morphotypes are also present: *Pinuspollenites divulgatus* (Bolch.) Petr., *Piceapollenites mesozoicus* (Bolch.) Chlon., *Cedripites admirabilis* (Bolch.) Poc., and *Phillocladidites memorabilis* Petr. Non-saccate pollen grains are less numerous: *Classopollis* sp. (0–4%), Taxodiaceae–Cupressaceae (up to 9%), Araucariaceae (up to 4%), *Cycadopites* sp. (up to 2%), and single specimens of ephedras. Solitary pollen grains of caytonias (*Caytonipollenites palludus* (Reiss.) Coup.) were found as well as *Eucommiidites troedssonii* Erdt., *Perotriletes elatoides* Coup., *Callialaesporites dampieri* (Balme) Dev., *C. trilobatus* (Balme) Dev., *Chasmatosporites* sp., *Exesipollenites tumulus* Balme, *Inaperturopollenites turbatus* Balme, and others.

Layer 9 of section 1, which contained plant macrofossil remains, is characterized by a different palynological assemblage. The abundance of *Sciadopityspollenites* sp. is sharply increased (up to 52%), whereas the other members of the spectrum do not change.

Palynologically, the deposits of section 1 are dated to the Late Bathonian. The main criterion is the low proportion (no more than 4%) of *Classopollis* sp. (Aleksiev et al., 2001).

Below, the vertebrate remains found in section 1 will be discussed in the context of dating deposits under consideration. Hibodont sharks were dominating predators in the Triassic and Jurassic (Carroll, 1988). *Ceratodus* is known from the Lower Triassic–Paleocene deposits. Ray-finned fishes are represented by palaeoniscoids (order Ptycholepidiformes, *Ptycholepis* sp.) and neopterigians (order Dapediidae, *Lepidotes* sp.). *Ptycholepis* Agassiz is known from Middle Triassic–Lower Jurassic deposits, and *Lepidotes* Agassiz is known from Upper Triassic–Lower Cretaceous deposits. Alifanov and Sennikov (2001) believe that the tetrapod assemblage from the Peski locality is archaic for the Jurassic. Turtles, which were found at the very base of the section, are represented by the new family Heckerochelyidae, and the genus and species *Heckerochelys romani*, combining characters of Triassic and Early Jurassic members of the Cryptodira, whereas the second half of the Jurassic in Europe is characterized by relatively advanced members of the family (Sukhanov, 2006). Labyrinthodonts and eolacertilians mostly occurred in the Permian and Triassic; they became relicts in the beginning of the Jurassic (Carroll, 1988). The last of the labyrinthodonts survived until the Middle Jurassic. Members of *Ctenioagenis* are only known from the Upper Jurassic of Europe. Alifanov and Sennikov (2001) noted that dinosaurs of the *Coelurosauridae*, found in the Peski locality, are common in Upper Jurassic and Cretaceous deposits. Triconodonts (primitive mammals) are reliably known from Lower Jurassic–Lower Cretaceous deposits (Carroll, 1988). In general, the vertebrate assemblage, although the majority of the members are archaic, implies a Jurassic age. Similar vertebrate assemblages are known from the Bathonian of Yorkshire (Metcalf, 1993; Evans and Milner, 1994), Upper Jurassic of Karatau and Mongolia (Nesov and Kaznyshkin, 1985; Krupina, 1994); however, direct comparison with the assemblage from the Peski locality seems impossible.

Having analyzed all available data, the four sections studied are dated to the Late Bathonian.

CHAPTER 3. SEDIMENTATION CONDITIONS IN THE PESKI LOCALITY IN RELATION TO THE BURIAL OF PLANT AND VERTEBRATE REMAINS

As the above descriptions show, the sections in the Peski localities are not lithologically identical. Differ-

ences in occurrence of vertebrate bones and plant remains also take place.

Section no. 1 is studied in maximal detail. It is a filling of a dead-ended cave in Carboniferous limestones. In the lowermost part of the section, a breccia is situated that is formed by limestone debris of the fallen roof of the karst cave. Virtually complete skeletons and fragmentary carapaces of aquatic turtles were found directly on the breccia.

The lower part of the section is dominated by distinctly rhythmic clayey deposits (see description). Judging from the size of the particles, which are pelitic and silty, the deposits were accumulated in relatively quiet water. Nearly complete skulls of cartilaginous fishes, ichthyodorulites of sharks *Hybodus hauffianus*, and fine plant debris (particles no more than 2 mm) are known from this part of the section.

The preservation of the turtles and sharks testifies that they died in close proximity to the place of burial. Alifanov and Sennikov (2001) share this opinion. These animals died in the labyrinths of the karst cavity, where they may have been trapped. Apparently, the turtles swam into the grotto, failed to find the exit, and died. This hypothesis is supported by evidence from modern marine turtles. Karst cavities with a complex system of labyrinths occur in coral reefs, and turtles that enter them often cannot get out. Large accumulations of dead turtles form in such cavities. The burial under consideration is probably a similar case.

Sharks and turtles live in large water bodies. Hibodont sharks were large freshwater predators; their body length reaches 2 m (Carroll, 1988). Sharks can only live in high-oxygen water; and modern water turtles prefer large, open water bodies. Nowadays, both freshwater and marine turtles exist; however, in the Middle Jurassic, turtles had not colonized the sea (Sukhanov, 1964). In Jurassic deposits, aquatic turtles and ceratodontids occur in lagoonal and lacustrine-paludal deposits (Krupina, 1994).

In all probability, the system of grottos of the karst cave was flooded by a relatively large body of water. The absence of shallow-water microfauna suggests that this water body was fresh or characterized by low salinity. The deposits under consideration are situated on a small interfluvium (Fig. 2). Therefore, the water level at the moment of the burial of the sharks and turtles reached the level of the interfluvium. The cave with its grottos was situated in the coastal area of the water body. The rhythmic sedimentation of this time was probably related to cyclical changes in the water body regime.

The period under consideration corresponds to the time when layers 1–8 were accumulated. In that time, the water body apparently represented a large lagoon of low salinity, into which several rivers flowed.

Upward in the section, the mode of sedimentation changes after a short washout. Layer 9 contains a lens with plant debris laterally substituted by a bone-bearing

lens. This layer also contains plant remains outside the lens. The plant material is preserved as phytolite.

The plant debris in the lens is represented by numerous fragmentary leaves and cuticles of the conifer *Tritaenia glabra*, rare fragmentary leaves of the bennettites *Otozamites paradoxus* sp. nov. and *Ptilophyllum riparium*, small wood fragments, and seeds. The size of the leaf fragments does not exceed 1 cm, and the wood fragments are no greater than 5 cm in size. Of importance is the fact that virtually all small wood fragments and some leaf remains bear spherical fungal fruiting bodies 1–3 mm in diameter. Apparently, the wood was crushed before it was transported by the water. Outside the lens, plant remains include rare leaf fragments of the cycad *Paracycas* sp., bennettites *Otozamites paradoxus* sp. nov. and *Ptilophyllum riparium*, *Sagenopteris rossica* sp. nov., conifers *Tritaenia glabra* and *Marskea* sp., and a single small fragment of a leafy shoot of the conifer *Brachyphyllum* sp. Leaf fragments outside the lens are larger than within the lens: up to 4.5 cm long. Complete and nearly complete conifer leaves are found here. Fungal fruiting bodies also occur on leaves found outside the lens. Obviously, these fungi were not parasites, but detritivores inhabiting dead pieces of plants. Therefore, before burial, the plant debris either lay for a while in the forest litter or participated in filling peat bogs. After that, the accumulated debris was washed out by water and partially buried in the karst cavity.

Plant remains that formed the lens were dragged on the bottom before burial. Apart from the plant debris, the lens contains fine reworked fragmentary skeletons of Carboniferous invertebrates: fusulinids, brachiopods, crinoids, and echinoids. Some wood fragments and leaves of *Tritaenia* were pyritized, evidence of reducing conditions, caused by the accumulation of the plant debris. Probably, leaves that were buried outside the lens were not dragged on the bottom, but floated for some time on the surface of the water body. The weak current brought them into the karst cavity, where they sank. This model at least explains the irregular distribution of plants within the layer of massive silty clays. Pyritization is not developed on detached leaf fragments.

Teeth of dipnoan fishes and bones of amphibians, eolacertilians (Eolacertilia, Kuehneosauridae), dinosaurs, and mammals were extracted from the bone-bearing lens mostly by elutriation. Detached bones of eolacertilians, dinosaurs, and mammals were found, some of them were rolled, indicating that they had been transported for long distances.

Apparently, the water body commenced shoaling when layer 9 was accumulated. The hydrodynamics that became (slightly) more intense and was connected with the formation of the lens with the plant debris also supports this idea.

During the third stage of the cavity filling, sands were accumulated in indistinct bedding. Relatively large wood fragments, detached scales of ray-finned

fishes, and teeth of dipnoan fishes occur throughout the layer. Apparently, the shoaling of the water body increased, and coarser sediments were accumulated. Consequently, section no. 1 reflects at least three stages of the water body development.

Section no. 2. Deposits of this section fill a large karst cave and differ from the deposits of section no. 1, although they contain a phytoorictocenosis that is similar both in preservation and composition of the fossil plants. The sedimentation took place in the karst cavity, as indicated by the presence of relatively large limestone lumps (pieces of the destroyed roof of the cave), occurring in the section. The small sizes of particles forming the section (pelitic and silty particles with admixture of fine-grained quartz sand) also confirm that the hydrodynamics was low.

The lower part of the section corresponds to relatively strong hydrodynamics, which is supported by accumulated silty sands with fragments of reworked Carboniferous faunal remains.

Upward in the section, the silty sands are replaced by clays of high organic content. Layers 2–6 correspond to the clay accumulation. Clays of layer 2 contain small amounts of organic matter in the form of fine plant debris: the sizes of the particles do not exceed 3 mm. The amount of organic matter increases in layer 3. The following plant remains were found in this layer: *Stachypteris psammitica*, *Sphenopteris* sp., *Sagenopteris rossica* sp. nov., *Otozamites paradoxus* sp. nov., *Tritaenia glabra*, and small wood fragments. The sizes of the leaf fragments do not exceed 3 cm. The plant debris forms several bedding planes. Each debris layer is no thicker than 2 mm. The amount of organic matter increases even more in layer 4. *Sagenopteris rossica* sp. nov., *Otozamites paradoxus* sp. nov., *Williamsonia* sp., *Tritaenia glabra*, and small wood fragments were found in this layer. Layers 3 and 4 are comparable with layer 9 of section 1 in the preservation and taxonomic composition of the plant remains.

The addition of organic matter sharply reduced during the accumulation of layer 5. The amount of organic matter sharply increases in layer 6, but no determinable plant remains were found.

As was mentioned above, the deposits of section 2 have a similarity to the Troyanovo Sequence, occurring on the northern slope of the Central Russian Upland, in particular, in the upper reaches of the Main Moskva hollow. The Troyanovo beds fill in depressions of the bottom of Carboniferous limestones and are alternating dark-gray coaly thin-laminated sandy-silty clays, gray clayey siltstones, and loose black coals with concretions and pseudomorphs of pyrites after wood remains. Such facies are interpreted as lacustrine-paludal or facies of raised bogs, where coals were accumulated (Olfer'ev, 1986). The Troyanovo Sequence also contains plant remains.

The deposits of the section under consideration differ from those of the Troyanovo Sequence, because thin

lamination is not expressed here, and limonitization is developed, instead of pyritization. There is a possibility that the deposits of section 2 resulted from the washout and redeposition of sediments which were originally accumulated under conditions similar to those of the Troyanovo Sequence. In other words, a lake or swamp was situated near the karst cavity, which was washed out for any reason (for example, a creek had its source in it). A proportion of the material was redeposited in the second karst cavity. Such a small lake or swamp should have been situated on the nearest interfluvium.

Apparently, the plant material of the debris lens in layer 9 of section 1 came from the same lake or swamp.

Section no. 3. Deposits of this section also fill a karst cavity. Unlike sections 1 and 2, the deposits of section 3 correspond to more active hydrodynamics.

The first visible layer of the section is composed of silty clays with a high organic content. The layer includes closely spaced sublayers, enriched in reworked Carboniferous faunal remains, and small light sandy lenses with the following plant remains: *Clathropteris* sp., *Selenocarpus* sp., *Cladophlebis denticulata*, *Cladophlebis* sp., *Sagenopteris rossica* sp. nov., *Anomozamites* aff. *minor*, *Nilssoniopteris vittata*, *Tritaenia striata*, and *Cephalotaxopsis* sp. The plant remains do not form lenticular aggregations. The remains were apparently brought by weak water currents and sank directly in the karst cavity. Rare virtually complete skeletons of bony fishes were found in this layer.

Layer 2 overlies layer 1 with a distinct washout, as testified by the presence of clayey pebbles, resulted from the destruction of layer 1 by an increased current, and small lenses of poorly sorted and unrolled sand. The layer contains lenses rich in black organic matter (destroyed bone material), with numerous shark ichthyodolites and ceratodontid teeth. Layer 3 is lithologically similar to layer 2: it also contains black sublayers with a high organic content, containing shark ichthyodolites.

When layers 2 and 3 were deposited in the karst cavity, water level lowering apparently took place, which was accompanied by increased stream power, washout of the underlying layer, and condensation of bone material.

A new sedimentation stage commenced, which embraces layers 4–8 (see the description of the sections). Bulk maceration showed that particles in sandy lenses are poorly sorted; about 90% of the particles are unrolled quartz particles and well-faceted small crystals and druses of quartz. The silty sands have a better sorted sandy fraction, but the sand grains are predominantly weakly rolled. Since the clastic material in the sandy lenses is not sorted, it did not undergo a long transportation. Therefore, this material is not normal river alluvium, which is characterized by well-sorted particles, at least within a layer (Frolov, 1993, 1995). Eolian transportation is excluded, since it is also characterized by well-sorted small sandy particles (no more than 0.2 mm), which are striated or polished (Frolov,

1993, 1995). Consequently, most of the sandy and pebble material is a result of the destruction of the Carboniferous limestones of the karst cavity or adjacent diagenetic quartz veins, developed in fissures of the limestones. Only a small part of the sandy material was brought from remote sites. Pelitic and silty fractions prevail, which corresponds to sedimentation under conditions of swampy lowland. Bulk maceration extracted leaf fragments, dispersed cuticles, and resin canals of *Tritaenia striata* and *Oswaldheeria* sp., small slightly rolled wood fragments, ceratodontid teeth, small rolled bones of vertebrates, and numerous coprolites no more than 4 mm in size. The coprolites contain small undigested fragments of cuticles and resin canals of *Tritaenia* and small wood fragments.

The uppermost part of layer 4, at its boundary with layer 5, a small sandy lens with rare fragmentary plant remains was found. The fossil plants include *Sagenopteris rossica* sp. nov., *Nilssoniopteris infera* sp. nov., *Nilssoniopteris* sp., *Anomozamites* aff. *minor*, and *Cephalotaxopsis* sp. Apart from plant remains, numerous detached indeterminable bone fragments were found.

The taphonomic assemblage of section 3 represents another plant association, dominated by *Sagenopteris rossica* sp. nov. and *Cephalotaxopsis* sp. As in the first association, *Sagenopteris rossica* sp. nov. is among the dominants. Ferns of *Cladophlebis* are numerous; bennettites are represented by different genera (*Anomozamites* and *Nilssoniopteris*).

Section no. 4 is the only section, where the continental deposits have a wide area of contact with marine deposits at the upper part of the section.

Black clays of the lower layer contain mass agglomerations of full skeletons of ray-finned fishes, reflecting seasonal fish kills. The combination of bluish clays and a fish-kill layer corresponds to one year. The average thickness of this rhythm is 2 mm, that allows me to estimate the time when the deposits of this layer were accumulated. Fish kills took place during about 750 years. Therefore, 1 m of the sediments corresponds to a temporal interval of 500 years. This way, a certain understanding was obtained about the sedimentation rate during fish kills.

The layer with seasonal bedding is overlain by dark silty clays with lenses of sands and clayey pebbles, containing fine indeterminable plant debris (no more than 2 mm in size) and large (up to 30 cm in length) slightly rolled wood fragments of *Araucarioxylon* sp., and *Taxaceae* gen. indet. One seed of a caytonia was found. Apparently, this layer is comparable with the upper layer of section 1 and layers 4–8 of section 3. All these layers reflect shoaling of the water body.

Upward in the section, deposits of the next layer are washed out. The deposits are represented by a conglomerate of limestone boulders and clayey pebbles in clayey-sandy matrix. Belemnites were found in this layer. This layer is not formed by continental, but

coastal-marine deposits, which are supposedly dated to the Early Callovian and indicates the beginning of a marine transgression. Middle–Upper Callovian black clays overlie the layer.

Currently, the karst cavities of the Peski locality are situated 75 m above sea level. In the Middle Jurassic, they should have been situated at a much lower level. The plant material came to the karst cavities from the adjacent interfluvies. It is difficult to reveal the direction of the runoff, since the locality is situated in the area of facial transition from alluvial to lacustrine-paludal deposits. Typically alluvial deposits are lacking in the sections under description. Most probably, they combine lacustrine (lacustrine-lagoon), alluvial, and proluvial genesis.

Hence, the depositional environment can be reconstructed as follows. Most part of the time, karst cavities were filled with relatively stagnant water, where clayey and silty material deposited. In some cases, this process shows a seasonal character. Fish kills or imprints of complete skulls of cartilaginous fishes and nearly complete skeletons of aquatic turtles are restricted to clayey layers in some cavities. Periodically, water flow increased in the cavities, resulting in accumulation of either fine plant debris with sand admixture or nearly without admixture of terrigenous material, or in accumulation of bone fragments of vertebrates (sharks, ceratodontids, dinosaurs, and primitive mammals) with coarse sand, clayey pebbles, and gruss. Rapid current facilitated the accumulation of bone debris, whereas more or less complete vertebrate remains are restricted to quiet sedimentary sites. Fine bone fragments, similarly to fine plant debris, came from the interfluvial; complete remains belong to aquatic vertebrates. In the case of section 1, the system of submerged grottos served as a trap. Section 4 reflects seasonal oscillations of the level of the water body, which retreated during drought leaving small disjunct water bodies, where fish kills occurred. Three phases can be traced in the sedimentation in the sections of the Peski locality. Burials of turtles and fishes predominantly belong to the first phase. Plant remains in the first layer of section 3 belong to the same phase. Seasonal fluctuations in the water level took place during this phase, documenting at least 750 years of the history of the water body.

The seasonal character of the climate is additionally confirmed by the preliminary analysis of growth rings in wood remains from sections 3 and 4 (wood remains from sections 1 and 2 were not included in the analysis because of insufficient preservation). The width (no more than 2 mm) and presence of false growth rings in the growth rings of studied specimens of *Podocarpoxylon* sp. and *Taxaceae* gen. indet. point to a seasonally dry climate and periodical water deficiency. The climate was already seasonally dry during the first phase, as indicated by the presence of growth rings in the wood fragments and fish kill layers in section 4. Similar woods were described from the Bathonian of Yorkshire

(Morgans, 1999). In the Bathonian, a winter-humid climate of the Mediterranean type existed in this region, as testified by so-called charcoals, deposits with wildfire traces (Morgans, 1999; Morgans et al., 1999).

Plants of sections 1 and 2 were buried during the second phase. In that time, the large water body apparently became smaller. The shores and adjacent interfluvies were swampy.

Poorly sorted silty sands with wood fragments and detached bones of vertebrates were accumulated during the third phase, which most probably was related with a further reduction of the water body. The cause could have been an increasing aridization before the Callovian transgression.

The vertebrate assemblage of the Peski locality generally resembles assemblage of other Jurassic localities. In particular, there is similarity to Upper Jurassic assemblages of Mongolia and Fergana Depression. All these assemblages usually include hibodont sharks, ceratodontids, various palaeoniscoids, labyrinthodonts, aquatic turtles, and primitive mammals (Nesov and Kaznyshkin, 1985; Krupina, 1994; Efimov, 1997). Facies in Mongolia where such assemblages occur are considered as lacustrine-paludal or lagoonal; facies in the Fergana depression are considered as facies of desalted lagoons or silted estuaries.

However, Alifanov and Sennikov (2001) point out that the tetrapod assemblage from the Peski locality is peculiar, differs from coeval European assemblages, and characterizes an earlier unknown page of the geological history of Europe. According to these authors, the specific features are the presence of such relict groups as Labyrinthodontia and Eolacertilia, the heyday of which took place in the pre-Jurassic time, and archaic turtles, on the one hand, and the occurrence of the dinosaurs of the Coelurosauria, common in the Late Jurassic and Cretaceous and previously unknown from such old deposits.

Ceratodontids can confirm the existence of drought periods. It is believed that fossil ceratodontids lived in lagoons and silted estuaries with lowered salinity; however, ceratodontids from lacustrine-paludal deposits are also reported (Krupina, 1994). No typically marine fossil species are known in the family Ceratodontidae Gill. Their modern descendants, *Neoceratodus*, only live in Australia, where they inhabit small rivers, which dry in drought seasons, separating into a chain of shallow pools overgrown by green algae. Since the abundance of the algae prevents the oxygen level dropping below certain limits, *Neoceratodus* survives drought seasons in such pools, not bedding into mud and/or falling into anabiosis, as is characteristic of modern African dipnoans (Grigg, 1965a, 1965b). It is conceivable that fossil ceratodontids lived not only in lakes and lagoons, but in intermittent rivers. The presence of sharks, ceratodontids, and turtles indicates that the water body itself did not dry completely. Most probably, rivers that

flowed into this water body separated into a chain of small lakes or pools.

The following landscape reconstruction is proposed. There was a large lake with swampy shores. Several rivers with swampy banks flowed into the lake. During draught seasons, the lake shoaled, and the rivers partially dried. Judging from early/late wood ratio in the growth rings, the drought season was not long, but the plants often suffered from water deficiency. Before the beginning of marine transgression, aridization increased.

CHAPTER 4. THE RECONSTRUCTED VEGETATION

Since any information on the vegetation of Central European Russia and, in particular, Moscow Region, was virtually absent, the study of the Peski Flora allows one to fill this gap.

Plants do not inhabit sites at random, but form permanent communities with special environment = phytocenoses (Larcher, 1976). The reconstruction of vegetation cover is impossible through reconstructing paleophytocenoses alone. Krassilov (1971, 1972, 2003) developed in detail a method to reconstruct paleophytocenoses. The method is based on the study of a given taphonomic assemblage, revealing autochthonous and allochthonous components and compensation of information losses and distortion (Krassilov, 1971). Association, union (formation), and class (geoflora) were used as elements of the classification.

Since all plant remains of the Peski locality are allochthonous, and the facies are not very diverse, there are several restrictions on the application of the method. Therefore, I have resorted to some additional expedients. Data on the paleorelief and supposed runoff areas, sources of the plant material, were used.

To reconstruct a plant community, the life habits of its members should be understood. It was long done for most plants constituting the Peski community. The life habit of the fern *Stachypteris psammitica* was reconstructed on the basis of the material from the Peski locality (Gordenko, 2001; Gordenko and Krassilov, 2006).

Some plants, mostly bennettites, show a relatively high specific diversity, but are represented by a few specimens. It is impossible to assign them to a plant association via lithological-facial analysis. A considerable amount of information is lost, since this group was important in Jurassic plant communities. These losses are proposed to be compensated for by cuticular analysis, which reveals adaptations of the leaf and plant to the environment.

Reconstruction of the Life Habit of Stachypteris psammitica

A fertile pinna of the fern *Stachypteris* (Pl. 1, fig. 1) with saccate pollen grains of *Caytonipollenites palli-*

dus adhering to the sporangia (Pl. 2, figs. 1, 4–6) was found in the deposits of section 2. Numerous fragmentary leaves of *Sagenopteris rossica* sp. nov. were found in the same layer. These leaves belong to plants of the order Caytoniales, which produced pollen of the *Caytonipollenites*-type.

Usually, pollen grains of caytonias are rare in palynological assemblages (Krassilov, 1972), and the Peski Assemblage is no exception: although saccate pollen grains are numerous, *C. pallidus* is represented by single specimens (Aleksiev et al., 2001). Conversely, fragmentary leaves of caytonias are numerous in three sections of the locality, indicating a considerable role of the parent plants in the community.

Fifteen pollen grains of *C. pallidus* were found on one of the sporangia of *Stachypteris psammitica*, testifying that caytonialean synangia with mature pollen were situated in the close proximity to this sporangia. This supposition is additionally substantiated by the fact that a relatively high concentration of caytonialean pollen grains was registered only on leaves of *Sagenopteris rossica* sp. nov. Consequently, although only one pinna of *Stachypteris psammitica* and numerous leaves of *Sagenopteris rossica* sp. nov. were found in the locality, I believe that *Stachypteris psammitica* grew together with caytonias.

Finds of shoots of caytonias show that they were trees (Harris, 1964). By analogy with modern *Ginkgo* L. and other gymnosperms, one can suppose that caytonias commenced pollen production at the age of about 20, when the trees become relatively large. Like the *Ginkgo*ales, they were deciduous, that explains the abundance of leaves of *Sagenopteris rossica* sp. nov. in the locality.

To explain the high concentration of pollen grains of caytonia on a fern pinnule, the life habit of the fern should be reconstructed. A scandent leaf liana climbing tree trunks and resembling the modern fern *Lygodium* Swartz (Schizaeaceae) seems to be the most probable life habit. The morphology of sporangia of this fern shows that *Stachypteris* also belongs to the family Schizaeaceae (Gordenko, 2000). Morphologically, fertile parts of *Lygodium* are similar to those of *Stachypteris* and are similarly separated from the sterile part of the frond. However, the frond of *Stachypteris* is dissected in a greater degree than that of *Lygodium*.

The presence of vessels in vascular bundles of pinnules of this fern is an added reason for its reconstruction as a leaf liana (Pl. 2, figs. 8–10). It is common knowledge that vessels are mostly present in angiosperms; but recently, ferns and lycopods in increasing frequency have been found to have vessels (Schneider and Carlquist, 1997, 2000). In particular, it was revealed that vessel formation was caused in these plants by water deficiency (Schneider and Carlquist, 2000). The frond of *Stachypteris* has a distinct xeromorphic appearance, also indicating water deficiency. However, as far as *Stachypteris psammitica* grew in the

same habitat as caytonias, which were hydrophilic plants (Krassilov, 1972), the water deficiency was most probably caused not by soil water deficiency, but other reasons. I believe that the water deficiency and related appearance of vessels can be explained by the life habit of this fern: a leaf liana.

To conclude, the life habit of *Stachypteris psammitica* is reconstructed as a leaf liana climbing on trunks of caytonias (Fig. 8; Gordenko and Krassilov, 2006). It should be pointed out that it does not come to a constant synecological relation between *Stachypteris* and *Caytonia*. This fern could have easily climbed other trees sharing the association with caytonias.

Cuticular Analysis as a Tool to Reconstruct the Environment (by the Example of Bennettites)

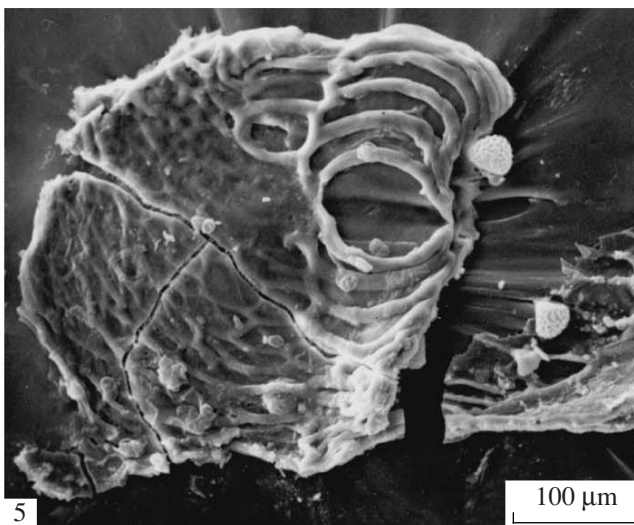
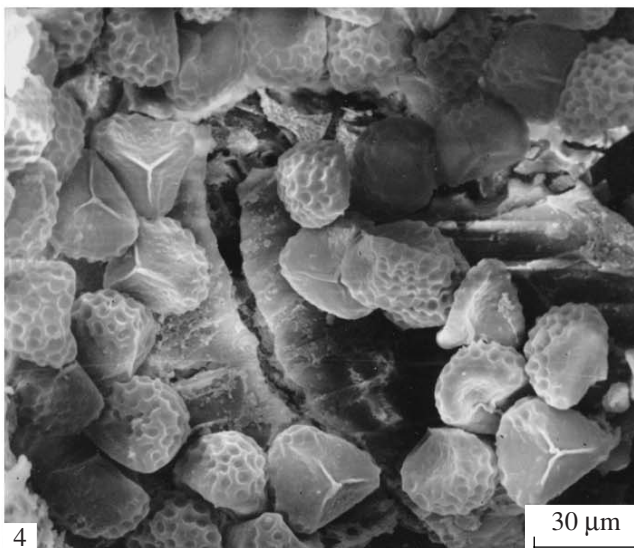
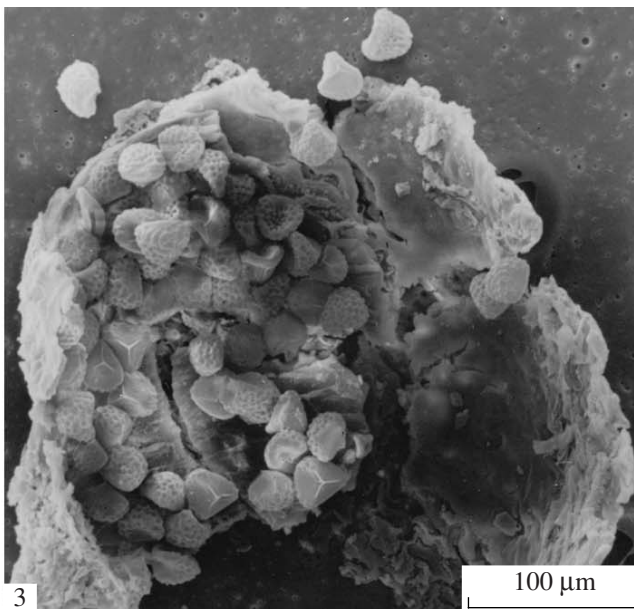
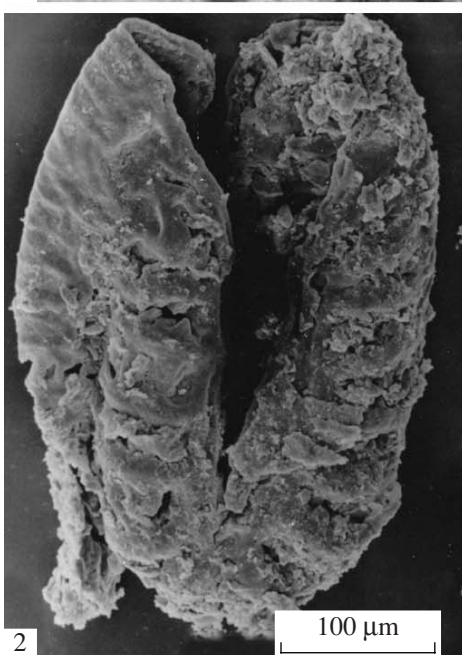
Below I consider a method developed on the basis of cuticular analysis that allows one to reconstruct the environment where bennettites grew.

Characters of cuticle and epidermis are an important source of information about the plant. Thus, they have been long used in taxonomy. They include epidermis topography, arrangement and morphology of stomatal apparatuses, the presence of trichomes and hairs, and cutinization of periclinal and anticlinal cell walls. Such characters are also usable for paleoenvironmental reconstruction. They include the cuticle thickness, epidermis topography, number of stomata per a leaf surface unit, degree in which stomata are protected, presence/absence of trichomes, and trichome morphology. The term micromorphotype is proposed to classify combinations of these characters. Micromorphotype is an artificial concept reflecting general trends in epidermal morphology. There is no strict correlation between micromorphotypes and members of plant system: epidermal characters of different species, genera, and families, etc. are attributable to the same micromorphotype.

Usually, micromorphological characters attract the attention of paleobotanists in the context of paleoclimatology (Spicer, 1989a; Barale, 1997). For example, xeromorphic characters in plants are conventionally considered as a clue that these plants grew under conditions of an arid climate. However, these might have been conditions of a particular ecotope, and the characters can reflect insolation or soil peculiarities of the sites where the plants grew. Micromorphological characters have not been hitherto analyzed in this aspect.

Bennettites have been chosen for such analysis for two reasons. First, all species of bennettites from the Peski locality are represented by single specimens. All plant remains of this locality are allochthonous. Therefore, the ecological niche of bennettites and their position in the catena cannot be determined by lithological-facial or statistic analyses, which are usually applied to reconstruct plant communities (Krassilov, 1972, 2003; Spicer, 1989b). Second, this group is very suitable for

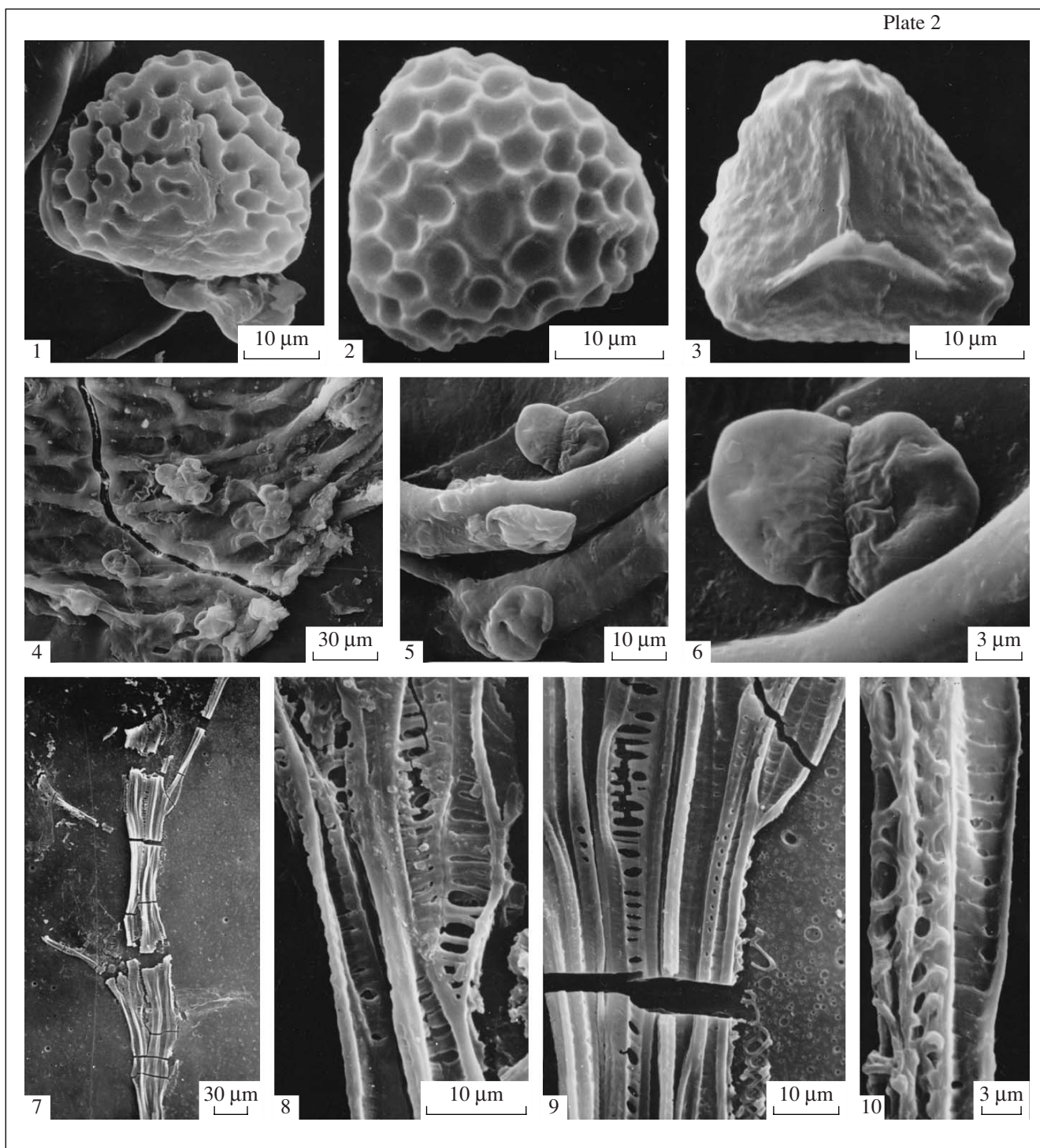
Plate 1



Explanation of Plate 1

Figs. 1–5. *Stachypteris psammitica* Gordenko: (1, 2, 5) holotype PIN, no. 4727/226; (1) fragment of a fertile pinna, $\times 13$; (2) sporangium with a well-preserved apical ring, SEM; (5) fragment of a sporangium with an additional incomplete ring, SEM; (3, 4) PIN, no. 4727/227; (3) partially destroyed sporangium (spores are visible), SEM; (4) spore mass, SEM.

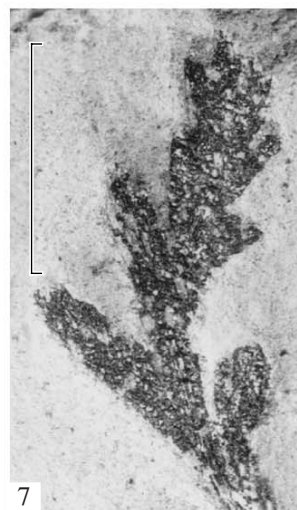
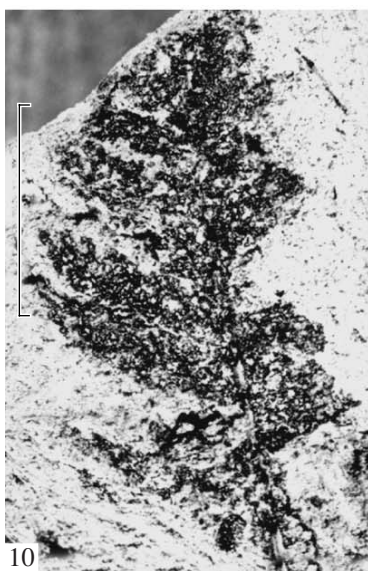
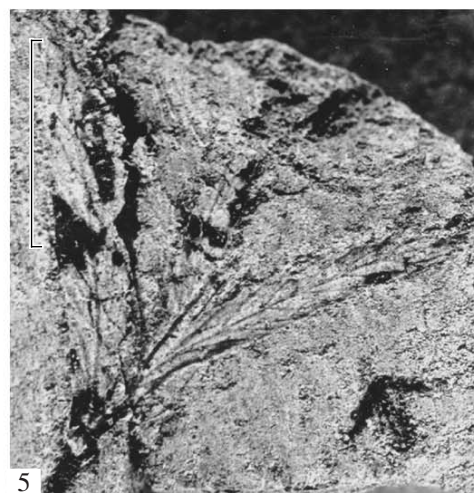
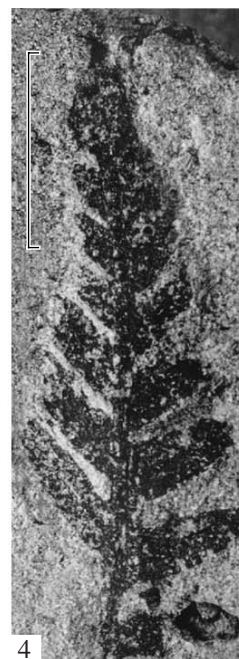
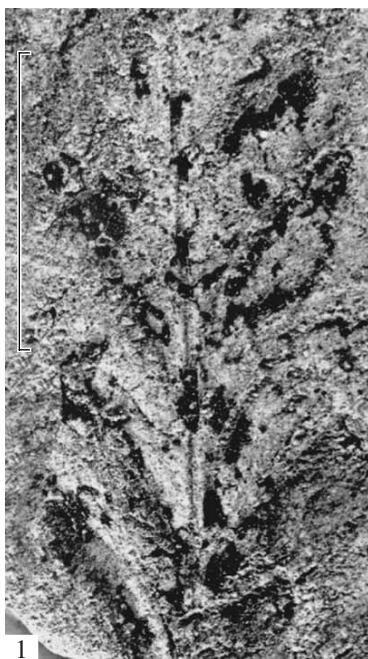
Plate 2



Explanation of Plate 2

Figs. 1–10. *Stachypteris psammitica* Gordenko: (1, 4–6) holotype PIN, no. 4727/226; (1) spore, distal view, a pollen grain of *Caytonipollenites pallidus*, SEM; (4) sporangial wall with attached pollen grains of *Caytonipollenites pallidus*, SEM; (5) pollen grains of *Caytonipollenites pallidus* on sporangial wall, SEM; (6) pollen grain on sporangial wall, SEM; (2, 3) PIN, no. 4727/227; (2) spore, distal view, SEM; (3) spore, proximal view, SEM; (7–10) PIN, no. 4727/228, details of a vascular bundle, SEM.

Plate 3



micromorphological analysis, because it shows a high diversity of epidermal characters.

Now I consider epidermal characters revealed in bennettites from the Peski locality, taking into account the following parameters: cutinization of ordinary epidermal cells and cells of stomatal apparatuses; differentiation on costal and intercostal stomatal zones; orientation of stomata; presence of various papillae and trichomes; and others. Four bennettite micromorphotypes have been revealed in the Peski locality by combination of the above characters.

The first micromorphotype includes leaf cuticles of *Nilssoniopteris vittata* and *N. infera* sp. nov. The cuticles of these species are thin, and their maceration resistance is low. No stomatal and non-stomatal zones are developed in the lower epidermis. Stomatal apparatuses are distributed evenly and orientated irregularly (Pl. 9, fig. 10; Pl. 17, fig. 4). This suggests that veins in these leaves were sunk in the mesophyll, and the leaf lamina was relatively fleshy. Cells of the lower epidermis bear hollow and variously developed papillae or hair bases (Pl. 9, figs. 7, 11). The stomatal apparatuses are superficial. Only guard cells are significantly cutinized; subsidiary cells do not differ by their cutinization from ordinary epidermal cells. A thin cuticle that does not prevent active cuticular transpiration and superficial position of stomata testifies that such a leaf was poorly protected from desiccation (Larcher, 1976). Plants with the first micromorphotype were most probably hygrophytes.

The second micromorphotype includes relatively thick leaf cuticles of *Anomozamites* aff. *minor* and *Nilssoniopteris* sp. Costal and intercostal zones are distinct in the epidermal topography of these leaves. Within the intercostal zones, stomata are distributed regularly, within any preferred orientation. The guard cells of stomata are without papillae. They are slightly sunken below the cuticle surface and strongly cutinized; the subsidiary cells are cutinized to a lesser degree than the guard cells, but to a greater degree than ordinary cells of the lower epidermis. No trichomes are found on the epidermal cells (Pl. 16, figs. 1, 3–5). Bennettites of the second micromorphotype were most probably mesophytes.

The third micromorphotype is a character of leaves of *Otozamites* sp. and *O. paradoxus* sp. nov. The cuticle is very thick. The lower epidermis shows distinct costal and intercostal zones of an approximately equal width (Pl. 9, figs. 1, 2; Pl. 13, figs. 1, 3–5). Sto-

mata within intercostal zones are arranged in one to three indistinct rows and predominantly orientated across the veins. The stomatal apparatuses are considerably sunken in the cuticle surface; the subsidiary and guard cells are strongly cutinized (Pl. 14, figs. 1, 2). Encircling cells form conical elevations, which trap near-surface air and form a microclimate (Pl. 8, fig. 8; Pl. 9, figs. 1, 3; Pl. 15, figs. 1, 3). In addition, subsidiary cells bear hollow clavate papillae, which interlock over the stomatal aperture, additionally protecting the stomata (Pl. 9, fig. 4; Pl. 15, figs. 2–5). The protected stomata and thick cuticle testify that the leaves were effectively protected from desiccation. Bennettites of this micromorphotype were xerophytes.

The fourth micromorphotype is specific of the leaf cuticle of *Ptilophyllum riparium*. The cuticle is very thick; cells of the lower epidermis are considerably cutinized: the anticlinal walls are completely cutinized, and the inner periclinal walls are occasionally cutinized. The cuticle is divided into costal and intercostal zones of an approximately equal width (Pl. 10, fig. 4; Pl. 12, fig. 13). The anticlinal cellular walls that are parallel to veins are cutinized more strongly than the perpendicular anticlinal walls; because of this the cells are aligned in distinct rows, separated from each other by thick longitudinal anticlinal walls, fused in a solid continuous row (Pl. 12, fig. 1). The intercostal zones are situated at a lower level than the costal zones, forming low grooves on the upper surface of the cuticle. Stomatal apparatuses within intercostal zone are arranged in one to three indistinct rows and mostly transversely orientated (more rarely, obliquely orientated stomata occur). The stomatal apparatuses are deeply sunken; and the subsidiary and guard cells are strongly cutinized (Pl. 12, fig. 2). The subsidiary cells hang over the guard cells and bear hollow clavate papillae, which may interlock over the aperture (Pl. 12, fig. 3). One of the subsidiary cells of each stomatal apparatus contacts with a cell bearing a rounded trichome base (Pl. 12, fig. 3). All ordinary cells of the lower epidermis bear peculiar hollow peltate trichomes (Pl. 9, fig. 14; Pl. 11, figs. 3–5). The stomata were protected in part at the expense of air space in the depression under the papillae and in part at the expense of peltate trichomes, which densely cover the surface of the lower epidermis, making stomata hardly visible. The morphotype also testifies that the leaves were effectively protected from desiccation. Bennettites of the fourth morphotype were also xerophytes.

Explanation of Plate 3

Figs. 1–7. *Selenocarpus* sp.: (1) PIN, no. 4727/383; pinna fragment; (2, 3) PIN, no. 4727/370, pinna fragment; (4) PIN, no. 4727/349, part and counterpart of a pinna fragment; (5, 6) PIN, no. 4727/384; (5) pinna fragment; (6) pinnules, note details of venation; (7) PIN, no. 4727/381, pinna fragment.

Figs. 8–11. *Cladophlebis denticulata* (Brongniart) Fontaine: (8) PIN, no. 4727/349, pinna fragment, note venation; (9) PIN, no. 4727/392, pinna fragment; (10) PIN, no. 4727/385, pinna fragment; (11) PIN, no. 4727/391, pinna fragment.

Scale bar 1 cm.

Plate 4

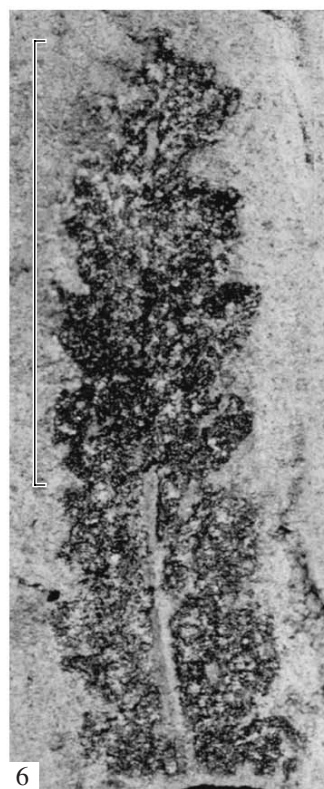
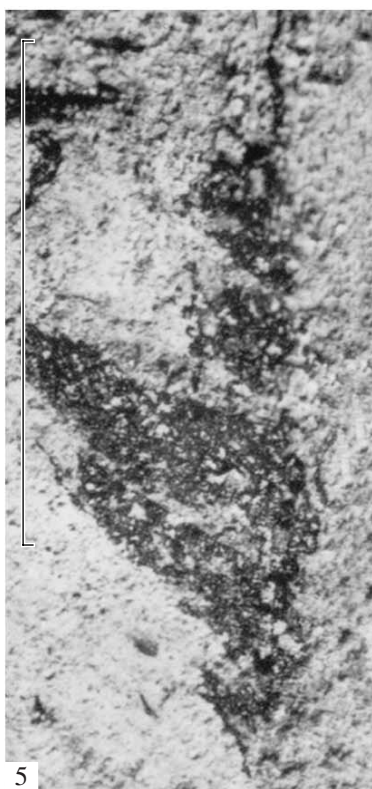
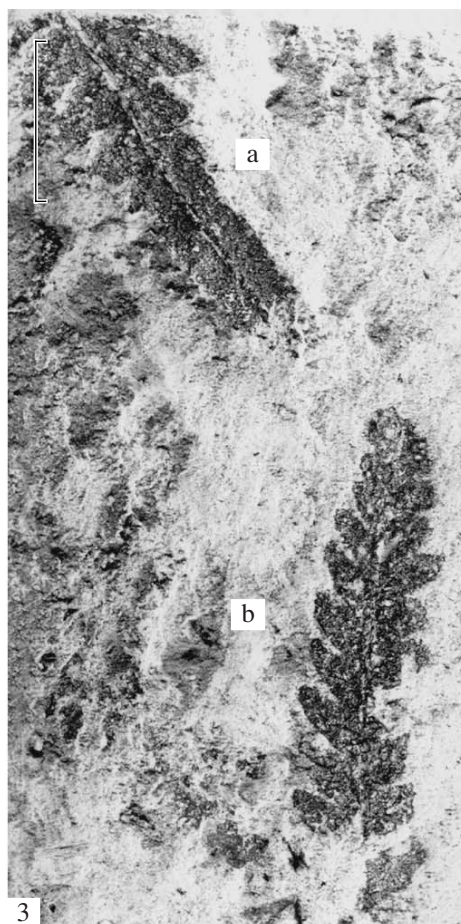
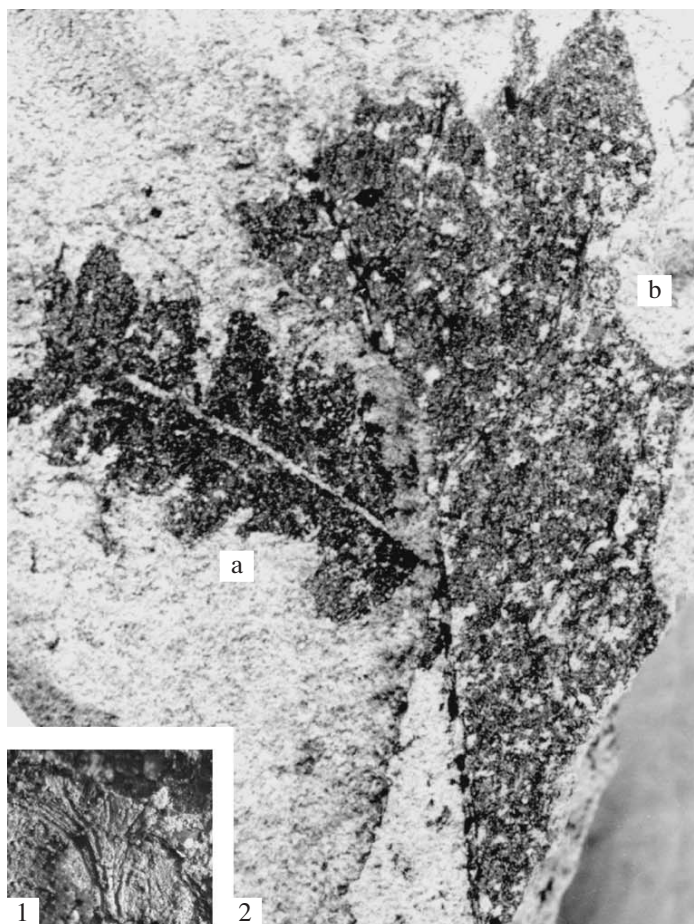


Table 1. Epidermal characters in bennettites from the Peski locality. Legend: (+) character present; (–) character lacking. Hygrophytic characters are in white, mesophytic and xerophytic characters are in gray; and xerophytic characters are in deep gray

Micromorpho- type	Species name	Venation	Stomatal bands	Ordinary epidermal cells are cutinized	Papillae on ordinary epidermal cells	Bases of hairs, or trichomes	Papillae on subsi- diary cells	Specialized encircling cells form elevations over stomatal apertures	Stomatal apparatus is sunken
I	<i>Nilssoniopteris vittata</i>	–	–	slightly	–	+	–	–	–
	<i>Nilssoniopteris infera</i> sp. nov.	–	–	slightly	small, dome- shaped	–	small	–	–
II	<i>Nilssoniopteris</i> sp.	+	+	moderately	–	–	–	–	slightly
	<i>Anomozamites</i> aff. <i>minor</i>	+	+	moderately	–	–	–	–	slightly
III	<i>Otosamites paradoxus</i> sp. nov.	+	+	conside- rably	–	–	clavate	+	conside- rably
	<i>Otozamites</i> sp.	+	+	conside- rably	–	–	clavate	+	conside- rably
IV	<i>Ptilophyllum riparium</i>	+	+	conside- rably	peltate	+	clavate	–	conside- rably

Therefore, among the bennettites of the Peski locality hygrophytes (first micromorphotype), mesophytes (second micromorphotype), and xerophytes (third and fourth micromorphotype) occurred (Table 1). Hygrophytes supposedly inhabited strongly moist sites that could have been periodically flooded. This is supported by the absence of adaptations of the epidermis to overtranspiration. Rachis glands could have removed surplus water. Therefore, these bennettites did not suffer from water deficiency. They most probably belonged to floodplain and swale vegetation.

Mesophytes are relatively moisture-loving plants, but are able to grow in dryer sites as well. This is supported by their thicker cuticle and thin leaf lamina with distinct venation. These bennettites could have grown in moist understorey, forest edges, as well as swamps.

Xeromorphic characters are more difficult to interpret, since they do not always indicate soil water deficiency (Larcher, 1976). Thus, xeromorphic members of *Ptilophyllum* occurred along coasts of saline lagoons, as testified by finds of their leaves in dolomites (Krassi-

lov, 1972), and were present in mangrove communities of marine coasts (Doludenko and Svanidze, 1969; Krassilov, 1972). This xeromorphism is explained by physiological dryness, related to saline soil. Distinct xeromorphic features are also developed in leaves of plants growing in raised bogs. In this case, xeromorphism is caused by surplus phosphorus in the soil. At a high concentration of phosphorus in leaves, they become vulnerable to sun rays and photosynthesis becomes impeded. Such protective adaptations as a thick cuticle and dense hairs facilitating light scattering significantly reduce plant vulnerability (Larcher, 1976).

The taphonomic assemblages of sections 1 and 2 are characterized by bennettites with xeromorphic features, whereas the assemblage of section 3 contains hygrophytes and mesophytes as well. This distribution is nonrandom, but shows that these two types of taphonomic assemblages correspond to two different plant communities. Most bennettites were shrubs. Most probably, *Otozamites* and *Ptilophyllum* avoided forest phytocenoses. The cenophobic character of bennettites

Explanation of Plate 4

Fig. 1. *Sphenopteris* sp., PIN, no. 4727/2260, fragment of a sterile pinna, $\times 3$.

Figs. 2a, 3, 4, 6. *Cladophlebis* sp.: (2a) PIN, no. 4727/385, pinna fragment; (3a) PIN, no. 4727/365, pinna apex; (3b) PIN, no. 4727/366, pinna apex; (4) PIN, no. 4727/2366, pinna fragment; (6) PIN, no. 4727/377, pinna fragment.

Fig. 5. *Cladophlebis denticulata* (Brongniart) Fontaine, 1889, PIN, no. 4727/372, pinna fragment.

Fig. 2b. *Clathropteris* sp., PIN, no. 4727/3850, pinna fragment.

Figs. 2–6. Scale bar 1 cm.

Table 2. Occurrence of leaf remains in the sections. Legend: (+) character present; (–) character lacking; (=) in parallel to bedding; (#) at an angle to the bedding plane; (L.f.) leaf fragment; (Ll.f.) leaflet fragment; (Sh.f.) shoot fragment; (P.f.) pinna fragment; (Pl.f.) pinnule fragment; (S.b.) sterile bracts

Species	Section no. 1	Layer no.	Number of specimens	Preservation	Orientation	Section no. 2	Layer no.	Number of specimens	Preservation	Orientation	Section no. 3	Layer no.	Number of specimens	Preservation	Orientation	Section no. 4	Layer no.	Number of specimens	Preservation	Orientation
<i>Stachypteris psammitica</i>	–					+	3	1		=	–					–				
<i>Clathropteris</i> sp.	–					–					+	1	1	P.f.	=	–				
<i>Selenocarpus</i> sp.	–					–					+	1	5	P.f.	=	–				
<i>Sphenopteris</i> sp.	–					+	3	1	Pl.f.		–					–				
<i>Cladophlebis denticulata</i>	–					–					+	1	5	P.f.	= #	–				
<i>Cladophlebis</i> sp.	–					–					+	1	7	P.f.	=	–				
<i>Sagenopteris ros-sica</i> sp. nov.	+	9	3	Ll.f.	=	+	3, 4	22	Ll.f.	= #	+	1, 4	41	Ll.f.	= #	–				
<i>Paracycas</i> sp.	+	9	1	L.f.	=	–					–					–				
<i>Ptilophyllum riparium</i>	+	9	5	L.f.	=	–					–					–				
<i>Otozamites paradoxus</i> sp. nov.	+	9	2	L.f.	=	+	3, 4	3	L.f.	= #	–					–				
<i>Otozamites</i> sp.	–					+	4	1	L.f.	#	–					–				
<i>Anomozamites</i> aff. <i>minor</i>	–					–					+	1, 4	5	L.f.	=	–				
<i>Nilssoniopteris vittata</i>	–					–					+	1	1	L.f.	=	–				
<i>N. infera</i> sp. nov.	–					–					+	1	1	L.f.	=	–				
<i>Nilssoniopteris</i> sp.	–					–					+	2	2	L.f.	#	–				
<i>Williamsonia</i> sp.	–					+	4	1	S.b.	#	–					–				
<i>Tritaenia striata</i>	–					–					+	1	9	L.f.	= #	–				
<i>T. glabra</i>	+	9	55	L.f.	= #	+	3, 4	30	L.f.	= #	–					–				
<i>Tritaenia</i> sp.	+	9	2	L.f.	=	–					–					–				
<i>Oswaldheeria</i> aff. <i>macrophylla</i>	–					–					+	1	3	L.f.	#	+	2	1	L.f.	#
<i>Marskea</i> sp.	+	9	1	L.f.	#	–					–					–				
<i>Brachyphyllum</i> sp.	+	9	1	Sh.f.	=	–					–					–				
<i>Elatocladus</i> sp.	+	9	1	L.f.	=	–					–					–				
<i>Cephalotaxopsis</i> sp.	–					–					+	1	11	L.f.	=	–				

is indirectly testified by their entomophilous and self-pollination adaptations (Krassilov, 1977). Indeed, insect-pollination is only effective in open sites, and self-pollination facilitates population reproduction when new sites are inhabited.

Hygrophytes and mesophytes inhabited river banks, swales, and forest edges. Apparently, the xerophytes *Ptilophyllum* and *Otozamites* were less specific and adapted to a broader variety of environments. Krassilov (1971) pointed out that they could have grown both in wetlands (mangroves and swamps) and in dry sites

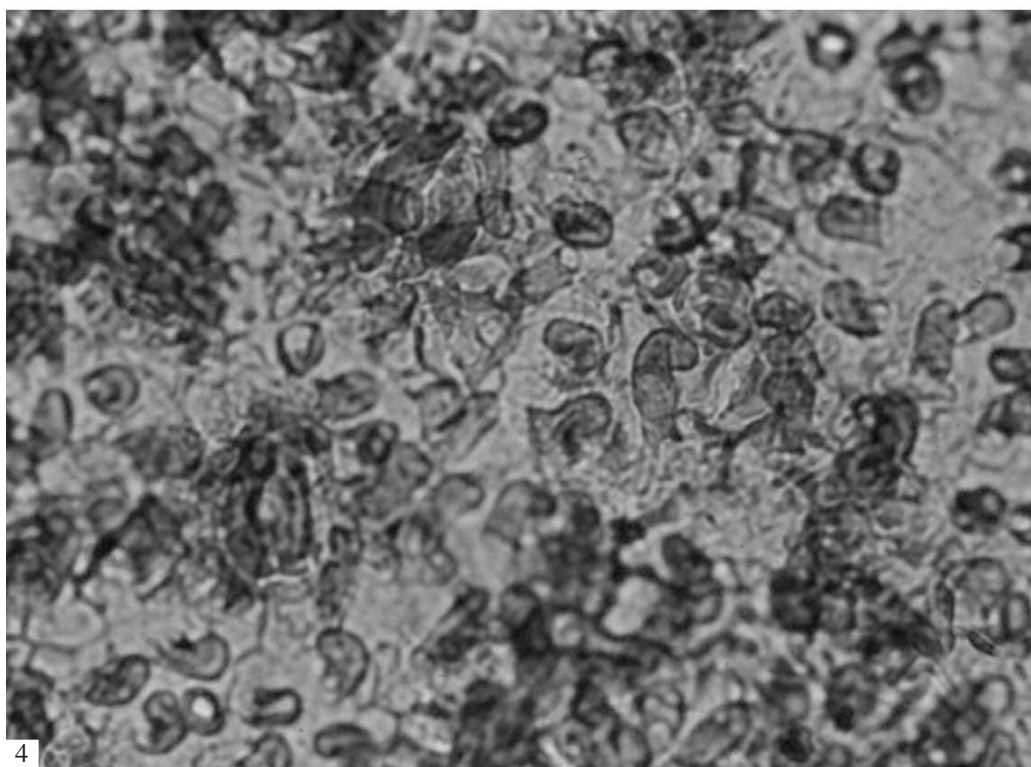
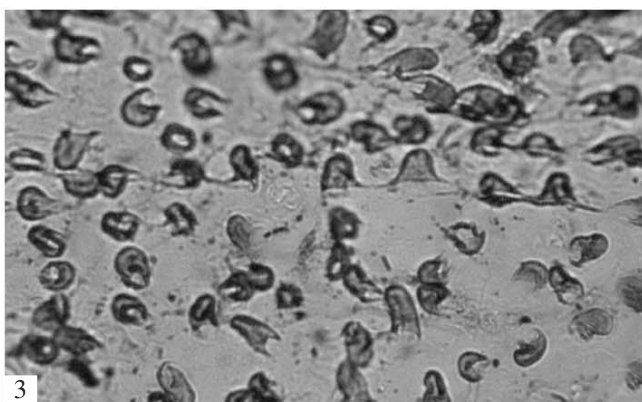
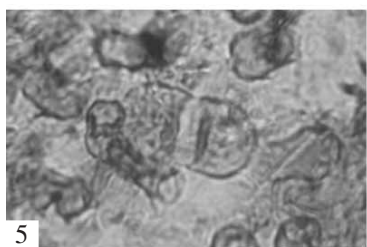
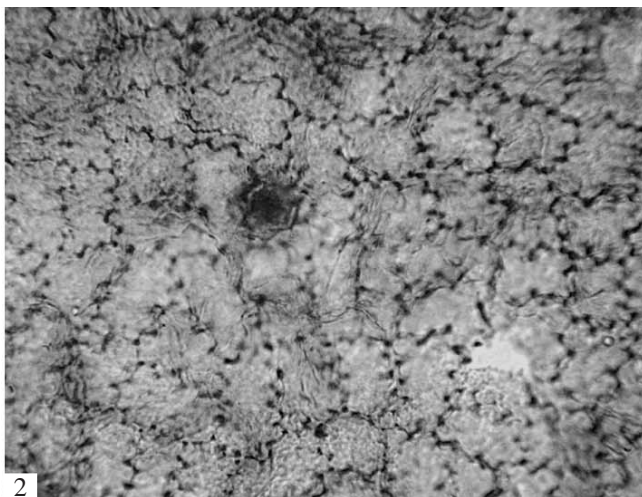
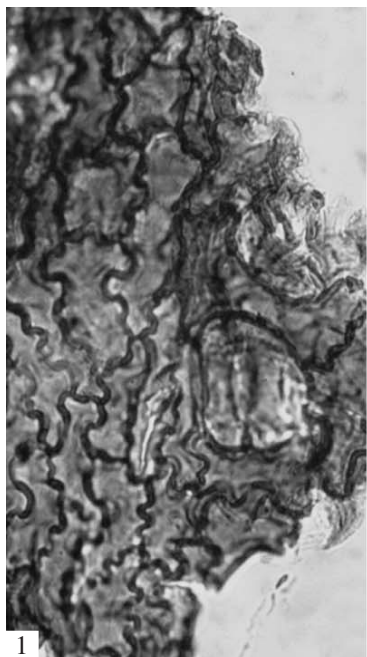
forming communities resembling modern chaparral. In the Peski locality, they could have inhabited upland swamps, elevated slopes, and barren land.

Reconstruction of Plant Associations and Paleocatena

To reconstruct paleocatena, the correlation between plant remains and particular lithological beds or facies was traced, and the preservation of the plant fossils was taken into consideration (Tables 2, 3). In addition, data were

Table 3. Taphonomic assemblages of the Peski locality

Section no.	Layer no.	Thickness	Bedding	Lithological composition of the layer	Genesis	Taphonomic assemblage	Species composition
1	9	30 cm	lenticular	Interbedding of brownish silty sands, white carbonate sands, and bluish silty clays containing a lens of plant debris (up to 15 mm thick) passing laterally into a bone-bearing lens	Sediments deposited by a small stream with varying water-flow velocity	Leaf and stem assemblages. Predominantly as plant debris. Leaf fragments, wood fragments, seeds, dispersed cuticle particles. Preserved as phytoliteims	<i>Sagenopteris rossica</i> sp. nov., <i>Paracycas</i> sp., <i>Ptilophyllum riparium</i> , <i>Otozamites paradoxus</i> sp. nov., <i>Tritania glabra</i> , <i>Tritania</i> sp., <i>Brachyphyllum</i> sp., <i>Carpolithes</i> sp. 2, <i>Carpolithes</i> sp. 3, <i>Carpolithes</i> sp. 4, <i>Carpolithes</i> sp. 5, ? <i>Podocarpoxylon</i> sp.
	3	47 cm	horizontal	Dark gray clays with thin small limonite lenses	Sediments deposited by a slow stream	Leaf and stem assemblages. Fragmentary plant remains (debris). Leaf fragments, wood fragments, dispersed cuticle particles. Preserved as phytoliteims	<i>Stachypteris psammitica</i> , <i>Sphenopteris</i> sp., <i>Sagenopteris rossica</i> sp. nov., <i>Otozamites paradoxus</i> sp. nov., <i>Tritania glabra</i>
	4	69 cm	horizontal	Black clays with limonite sublayers	Sediments deposited by a slow stream	Leaf and stem assemblages. Fragmentary plant remains (debris). Leaf fragments, wood fragments, dispersed cuticle particles, fragments of sterile bracts. Preserved as phytoliteims	<i>Sagenopteris rossica</i> sp. nov., <i>Otozamites paradoxus</i> sp. nov., <i>Otozamites</i> sp., <i>Williamsonia</i> sp., <i>Tritania glabra</i>
3	1	40 cm	absent	Black silty clays with sublayers enriched in carbonate material and light-colored sandy lenses	Sediments deposited by a rapid water stream	Leaf and stem assemblages. Large and small leaf fragments, wood fragments, and dispersed cuticle particles. Preserved as phytoliteims	<i>Clathropteris</i> sp., <i>Selenocarpus</i> sp., <i>Cladophlebis denticulata</i> , <i>Cladophlebis</i> sp., <i>Sagenopteris rossica</i> sp. nov., <i>Nilssoniopteris</i> sp., <i>Anomozamites</i> aff. <i>minor</i> , <i>Tritania striata</i> , <i>Oswaldheeria</i> aff. <i>macrophylla</i> , <i>Cephalotaxopsis</i> sp., <i>Podocarpoxylon</i> sp.
	4	90 cm	lenticular	Brownish silty sandstones with closely spaced lenses of poorly rounded quartz sands	Sediments deposited by a small water stream	Leaf assemblages. Leaf fragments and dispersed cuticle particles	<i>Sagenopteris rossica</i> sp. nov., <i>Nilssoniopteris infera</i> sp. nov., <i>Anomozamites</i> aff. <i>minor</i>
4	1	150 cm	horizontal	Interbedding of black clays (fish kill layers) and bluish carbonate clays	Sediments of a marginal zone of a seasonally intermittent stream	Stem assemblages. Tree stem fragments.	<i>Araucarioxylon</i> sp., <i>Taxaceae</i> gen. indet.
	2	170 cm	lenticular	Dark silty clays with sandy lenses containing clayey pebbles	Sediments of a rapid stream	Leaf and stem assemblages. Fine leaf debris, dispersed cuticle particles, seeds, and small wood fragments	<i>Oswaldheeria</i> aff. <i>macrophylla</i> , <i>Carpolithes</i> sp. 1



used about the paleorelief and supposed area of runoff which provided the plant material (Volkova, 1952).

The upper courses of the rivers were swampy as evidenced by coal beds of lacustrine genesis in the upper courses of the Proto-Moskva River (interfluvium of the Nara and Protva rivers) with plant remains (Olfer'ev, 1986). The Peski locality is situated on a slope of a small interfluvium. Consequently, the sections of the locality should be dominated by plant remains of two types of vegetation: raised bogs and river banks.

Tables 2 and 3 show that the taphonomic assemblages of sections 1 and 2 are similar in their taxonomic composition and preservation of the plant fossils. Leaves with thick cuticles are predominantly preserved as fine debris. *Sagenopteris rossica* sp. nov., *Otozamites paradoxus* sp. nov., and *Tritaenia glabra* occur in both taphonomic assemblages and apparently constituted one and the same association. Since *Sagenopteris rossica* sp. nov. and *Stachypteris psammitica* were synecologically related, the latter species also was a member of this association. Moreover, cuticular analysis shows that *Otozamites paradoxus* sp. nov. and *Ptilophyllum riparium* occupied similar environments; therefore, *P. riparium* also could be a component of the association under consideration. *Paracycas* sp., *Brachyphyllum* sp., *Marskea* sp., and *Elatocladus* sp. probably represent allochthonous elements.

The taphonomic assemblages of section 3 considerably differ from those of sections 1 and 2 in the taxonomic composition and degree of preservation. The only element shared by sections 1 and 2 is *Sagenopteris rossica* sp. nov. The leaves are also fragmentary, but the fragments are several times larger. The facies of section 3 that contain plants are sandier, and the fragments mostly belong to plants with thin cuticles. These are indications of albeit considerable but shorter transportation of the material than in section 1. *Oswaldheeria* aff. *macrophylla* is the only exception: it has a thick cuticle, but is preserved as small fragments and dispersed cuticles. Obviously, it is a foreign element. Other plants of this taphonomic assemblage constituted one association.

Accordingly, two plant associations have been defined in the Peski locality.

Association *Ptilophyllo-Tritaenietum*
Gordenko ass. nov.

Nomenclatural type: Peski locality (Moscow Region), section 2, layers 3, 4.

These communities occurred in the upper courses of rivers and in raised bogs. The association corresponds to the middle unit of the catena. *Tritaenia glabra* and *Caytonia* (*Sagenopteris rossica* sp. nov.) were the main trees, and *Otozamites paradoxus* sp. nov., *Otozamites* sp., and *Ptilophyllum riparium* were shrubs. Herbs were represented by the leaf liana *Stachypteris psammitica*. Judging from the presence of bennettites, the forest was light. Currently, associations containing *Tritaenia* or other members of the Miroviaceae are poorly understood; however, their main characteristic feature is low specific diversity. Miroviaceous leaves often form monospecific stands.

Association *Nilssoniopteridi-Cephalotaxopsietum*
Gordenko ass. nov.

Nomenclatural type: Peski locality (Moscow Region), section 3, layer 1.

These communities occurred in floodplains and lowlands. The association corresponds to the lower unit of the catena. Main trees were *Cephalotaxopsis* sp. and *Caytonia* (*Sagenopteris rossica* sp. nov.). *Tritaenia striata* rarely occurred. Shrubs were represented by the bennettites *Nilssoniopteris* sp., *N. vittata*, *N. infera* sp. nov., and *Anomozamites* aff. *minor*. Tree ferns included *Cladophlebis* sp. and *C. denticulata*, and herbaceous ferns were *Clathropteris* sp. and *Selenocarpus* sp.

This association shows features common with the association *Nilssoniopteridi-Pitiophylletum*, described by Krassilov (1971).

CHAPTER 5. THE IMPORTANCE OF THE PESKI FLORA FOR PALEOPHYTOGEOGRAPHY

Until now, more or less complete data on the Middle Jurassic flora of Central European Russia have been lacking, and some paleophytogeographic problems have remained unsolved. It is important to understand the position of the Peski Flora in the existing paleophytogeographic schemes and how the data obtained about the Peski Flora update these schemes.

Since this flora is dated as Bathonian, it should be compared with coeval floras of adjacent areas. To begin, the formation of the knowledge about the climatic and botanical-geographical zones of the Jurassic in Eurasia should be briefly outlined.

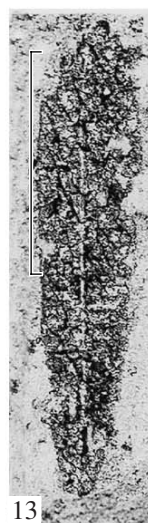
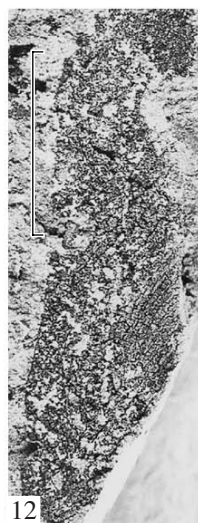
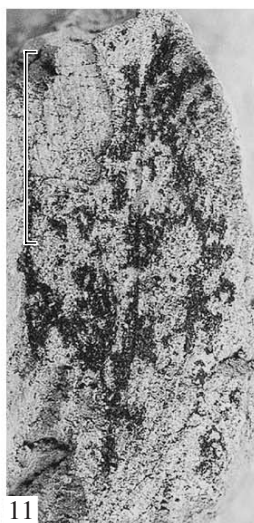
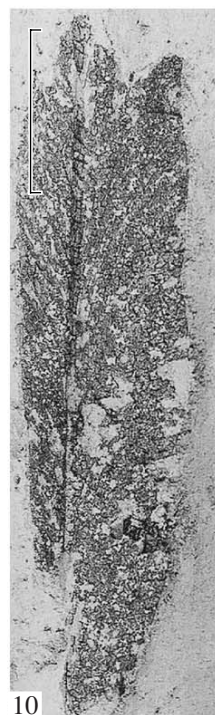
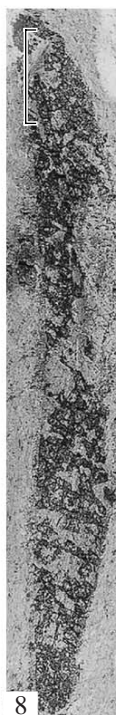
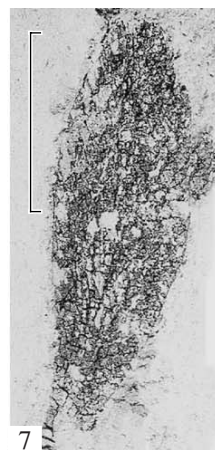
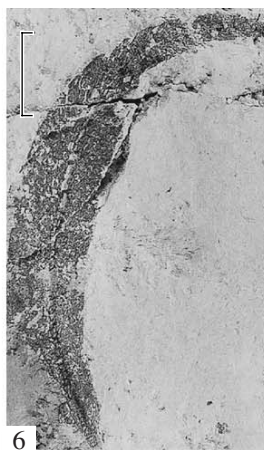
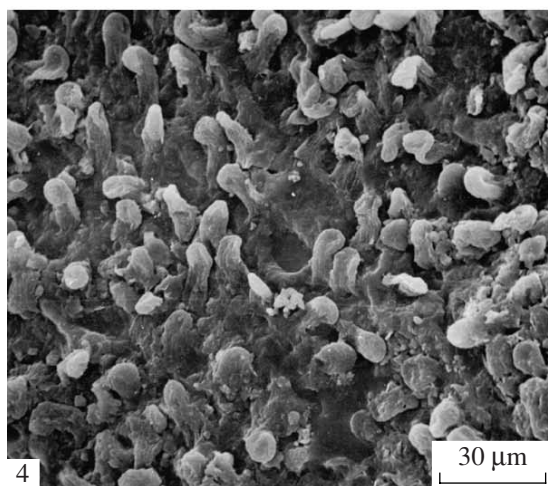
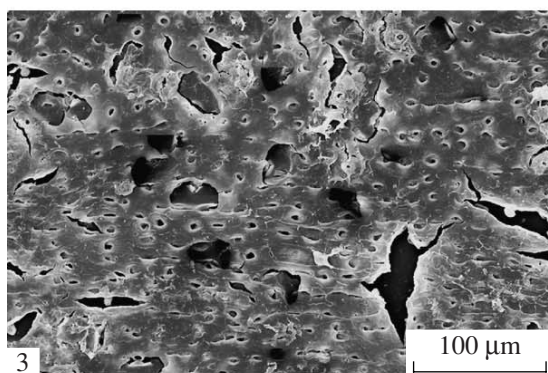
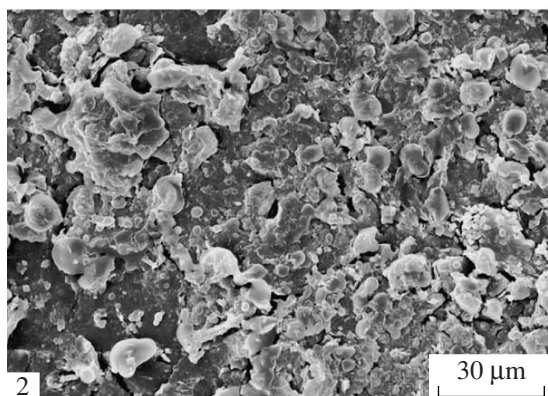
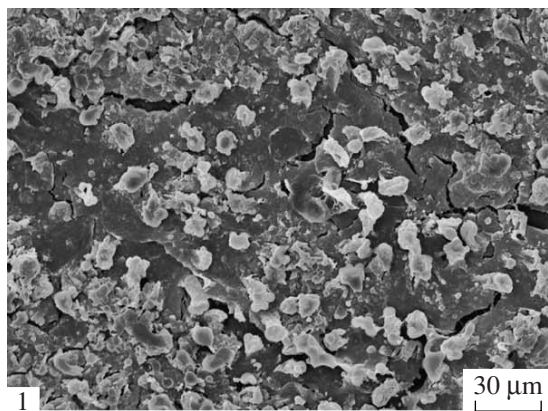
Krishtofovich (1939) was the first to suppose that climatic zones existed in the Mesozoic. Later, Prynada (1944), Vachrameev (1957, 1964, 1970, 1975, 1988,

Explanation of Plate 5

Fig. 1. *Selenocarpus* sp., PIN, no. 4727/384, lower epidermis cuticle of a leaf, a stoma is visible, $\times 600$.

Figs. 2–5. *Sagenopteris rossica*, sp. nov.: (2) PIN, no. 4727/70, upper epidermis cuticle, triangular thickenings are visible in the points of bends of anticlinal walls, $\times 360$; (3–5) holotype PIN, no. 4727/410; (3) cuticle of a costal zone of the lower epidermis, $\times 450$; (4) cuticle of an intercostal zone of the lower epidermis, $\times 900$; (5) lower epidermis cuticle with attached pollen grain of *Caytonipollenites pallidus*, $\times 900$.

Plate 6



1990), and Krassilov (1972, 1974, 2003) studied the phytogeography and climatic zones of this time.

Prynada (1944) studied Jurassic floras of Siberia and was the first to use the term Siberian province. He noted that coeval European floras differ from Siberian floras. Later, Vachrameev renamed the Siberian province as the Siberian area, which, in its turn, was later renamed by him as the Siberian-Canadian area, and, finally, the original name was returned. He united the other, more southern, Eurasian floras into Indian-European area with four provinces: European, Central Asian, East Asian, and Indian (Vachrameev, 1957). Vachrameev (1975) divided the Indian-European area into two subareas: European-Sinian and Australian. According to this subdivision, the Indian province belonged to the Australian subarea. In his later papers, Vachrameev gave a status of an area to the European-Sinian subarea and subdivided the Australian subarea into Equatorial and Notal (Australian) areas. It should be noted that Vachrameev identified phytogeographic areas with climatic zones. Thus, he believed that the Siberian phytogeographic area corresponded to the warm-temperate zone; the European-Sinian area, to the subtropical zone of the Northern hemisphere; the Equatorial area, to the tropical zone; and the Australian, to the subtropical zone of the Southern hemisphere (Vachrameev, 1985). In reality, the boundaries of phytochoria and climatic zones do not coincide. Moreover, the boundaries of phytochoria do not correspond to boundaries between different types of vegetation (Takhtajan, 1974). The term phytochorium concerns the degree of isolation and endemism of a given flora. The term vegetation fits to the totality of live forms of a definite type (irrelevant to the systematic composition). The climatic zone is a geographical term, primarily related to the distribution of air masses (Alisov and Poltarau, 1974). In general, vegetation reflects the climatic zonation. However, it should be taken into account that, for example, the modern tropical vegetation includes both the vegetation of tropical rain forests and arid vegetation.

Krassilov (1972) showed that the boundary between the Siberia and Indian-European (=European-Sinian in modern terms) areas was not a boundary between phytochoria. In his opinion, this boundary corresponds to a boundary between two types of vegetation. Such a vast phytochorium as an area implies the presence of endemic families; whereas Siberia lacks even endemic genera, and ecotones are traced between typical Siberian and European floras (Krassilov, 1972, 1974). The

presence of ecotones indicates changes in vegetation, not in phytochoria. The following criteria are used to define the boundary between the Middle Jurassic European-Sinian and Siberian areas: noticeably reduced diversity of the genera *Nilsson* and *Taeniopteris* Brongn., disappearance of bennettites *Ptilophyllum*, *Williamsonia*, and *Cycadites* and conifers *Brachyphyllum* and *Pagiophyllum*, appearance of *Phoenicopsis* Heer, and the increased diversity of *Czekanowskia* Heer in the Siberian area. Since in fact one type of vegetation gives way to another, Krassilov defined three geofloras: the geoflora with *Phoenicopsis* (corresponds to the Siberian area in terms of Vachrameev), geoflora with *Cycadeoidea* Buckland (approximately equal to the European-Sinian area of Vachrameev), and geoflora with *Pentaxylon* Srivastava (corresponds to the Equatorial and Notal areas of Vachrameev). According to Krassilov (2003), geoflora is equal to class, a high-rank unit used in geobotanical classification. Consequently, the boundary between the European-Sinian and Siberian areas are considered here as a change from one type of vegetation to another and, in part, as a change from one climatic type to another, but not as a change from two phytochorium to another. Seemingly, the change from one province to another also reflects the change in the type of vegetation and in local climatic conditions.

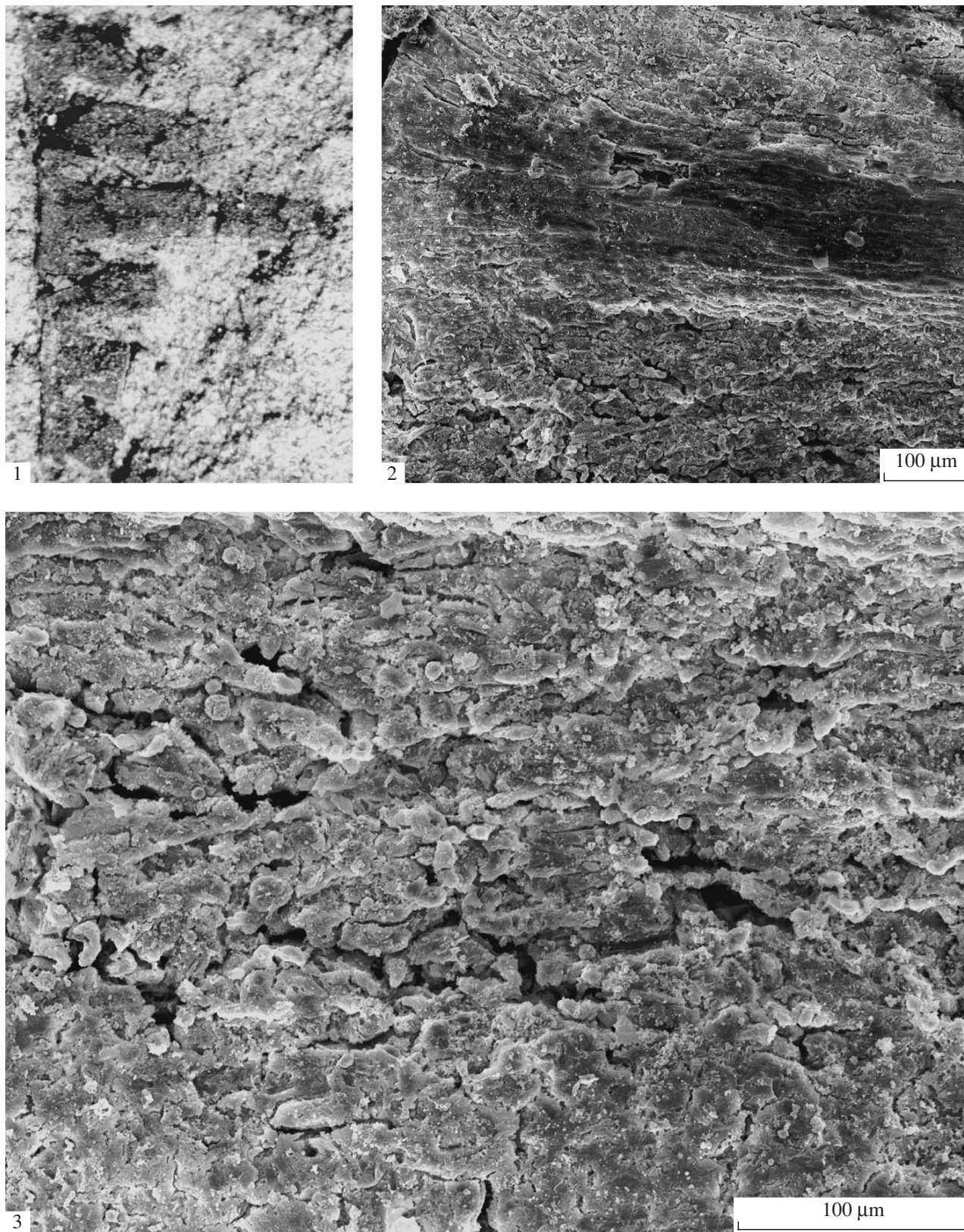
Vachrameev drew the boundary between the Siberian and European-Sinian areas in Eastern Europe on the basis of palynological data; since data on Middle Jurassic macroflora of central Russia were insufficient, and publications supplemented by descriptions and figures of fossil plants were virtually lacking. Some papers on the Jurassic stratigraphy of Central European Russia (Sazonov and Sazonova, 1967) contain merely a list of plant taxa determined by Peresvetov in the mid-20th century from the interfluvium of the Narva and Protva rivers. This list, which I have brought up to date with current taxonomy, contains *Equisetum beani*, *E. aff. columnare*, *Cladophlebis argutula*, *C. denticulata*, *C. cf. haiburnensis*, *Eboracia lobifolia*, *Otozamites* sp., and *Nilssoniopteris* sp. The nearest coeval localities in which fossil plants were described and figured are the Samara Bend and the Severnaya Dvina River basin. From the Samara Bend Prynada (1927) described *Hausmannia crenata* (Nath.) Moeller, *H. volgensis* Pryn., *Feildenia cupsiformis* (Heer) Nath., *Elatides curvifolia* (Dunk.) Nath., and *Conites* sp. Vachrameev (1964) described from the basin of the Severnaya Dvina River a new fern genus and species: *Jarenga rosanovii*

Explanation of Plate 6

Figs. 1–13. *Sagenopteris rossica*, sp. nov.: (1–4, 9) holotype PIN, no. 4727/410; (1, 2) topography of the lower epidermis (upper surface), SEM; (3) inner surface of the lower epidermis cuticle, bases of papillae are visible; (4) stoma surrounded by papillae, SEM; (5) PIN, no. 4727/396, leaflet fragment; (6) PIN, no. 4727/395, leaflet fragment; (7) PIN, no. 4727/336, leaflet fragment; (8) PIN, no. 4727/36, leaflet fragment; (9) leaflet fragment; (10) PIN, no. 4727/397, leaflet fragment; (11) PIN, no. 4727/389, leaflet fragment; (12) PIN, no. 4727/349, leaflet fragment; (13) PIN, no. 4727/229, leaflet fragment.

Figs. 5–13. Scale bar 1 cm.

Plate 7



Explanation of Plate 7

Figs. 1–3. *Paracycas* sp. PIN, no. 4727/119: (1) fragment of a pinnate leaf, $\times 33$; (2) upper surface of the lower side of a segment, non-stomatal and two stomatal zones are visible, SEM; (3) upper surface of the lower side of a segment in a stomatal zone, SEM.

Vachr. *Cladophlebis nebbensis* (Brongn.) Nath. and *Sphenopteris* sp. were also found in this locality. The paucity of fossil remains did not allow a representative floristic assemblage to be defined or the flora of Central Russia to be assigned to a particular paleofloristic area. The boundary was drawn by extrapolation between the floras of Georgia, Ukraine, and Caspian Depression, on the one hand, and the Yorkshire flora, on the other hand.

Since a particular floristic assemblage was discovered from the Peski locality, it will be compared with the most representative coeval assemblages of adjacent localities. Such a comparison will refine the phytogeographic position of the Middle Jurassic flora of the Moscow region. New data on the Peski Flora and corrected list of species from the interfluvium of the Nara and Protva rivers will be considered.

The Peski Flora apparently characterizes inland vegetation. In the Middle Jurassic, an archipelago of numerous small islands existed in Western Europe, whereas Eastern Europe still represented a vast landmass in the Bathonian. According to the paleogeographic schemes proposed by Vachrameev (1988, 1990) in different papers, the Peski locality belongs alternatively to European-Sinian and Siberian areas. Recent data, including those about the locality under study, allows one to correct this boundary for the Bathonian. For this purpose, the European-Sinian and Siberian areas in the Middle Jurassic will first be characterized in terms of Vachrameev (1990).

European-Sinian area. In the Middle Jurassic, the European-Sinian area is characterized by several genera, which are absent in the Siberian paleofloristic area. These are *Dictyozamites* (Oldham) Medlicott et Blandford, *Sphenozamites* (Brongn.) Miquel, *Zamites* Brongn., *Ptilophyllum*, *Otozamites*, and *Cycadites*. Among conifers, *Brachyphyllum* and *Pagiophyllum* are prominent. Large horsetails of *Equisetites* (*Equisetum*) are common. Dipteridaceous ferns still occur. These are *Clathropteris obovata*, the latest species of this genus, and *Dictyophyllum rugosum*, which replaced extinct Lower Jurassic members of *Dictyophyllum*. Schizaeaceae ferns *Klukia* and *Stachypteris* appear. *Klukia* is represented by several species, among which *Klukia exilis* (Phlill.) Racib. is the most common. The genus *Coniopteris* reaches its greatest diversity. The earliest members of *Gleichenia* Smith (= *Gleichenites* Sew.) appear. The genus *Pachypteris* was quite usual, with the most common species *P. lanceolata*.

Below the main criteria to delimit provinces within the European-Sinian area will be outlined.

European province is characterized by endemic *Stachypteris spicans* and *Ctenozamites cycadea* (Berger) Schenk, common *Equisetites beanii* (*Equisetum beanii*), *Klukia exilis*, and *Dictyophyllum rugosum*, constantly occurring *Ptilophyllum*, and frequent finds of *Otozamites*.

Central Asian province is characterized by the presence of *Nilssonia acuminata*, *N. dentata*, *N. orskica*

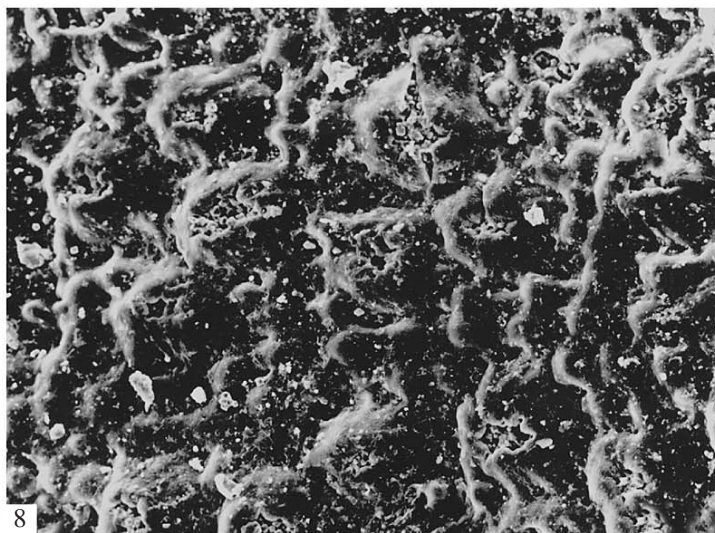
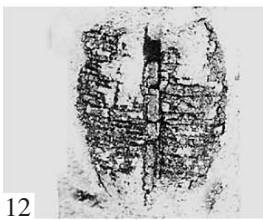
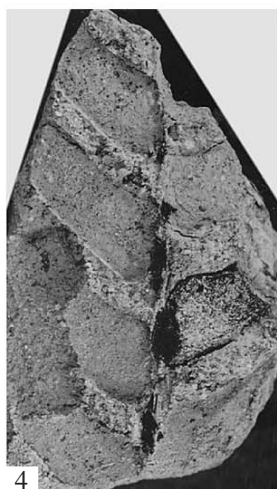
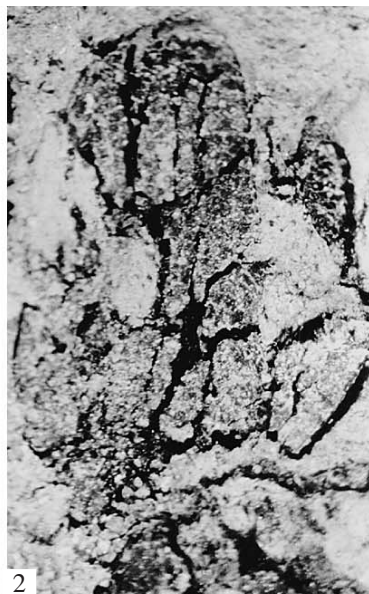
Genkina, *N. serrata* Pryn., and *N. vittaeformis*. According to Vachrameev, a nearly total absence of *Otozamites* is one more distinguishing feature of this province. *O. graphicus* (Leck.) Schimp occurs only in few Bathonian localities (e.g., Gissar Range). Recent data on the Bathonian flora of Iran and Afghanistan, which belongs to the Central Asian province, show that bennettites of the genus *Otozamites* are quite diverse, but combine epidermal characters of *Otozamites* and *Ptilophyllum* (Schweitzer and Kirchner, 2003). The conifers *Podozamites* (Brongn.) Braun and *Ferganiella* Neuburg are present. However, genera that are characteristic of the European province also occur. Moreover, this province exhibits a high diversity of the Ginkgoales and Czekanowskiales, two times as high as in the European province. In addition to *Czekanowskia*, members of *Phoenicopsis* are present. The total number of ginkgoalean and czezanowskialean species reaches 40.

Vachrameev believed that the Central Asian province was a transitional zone between the European-Sinian and Siberian areas.

Hitherto, Middle Jurassic floras have not been found in the East-Asian province.

Siberian area. No members of *Neocalamites* Halle is present in the area, except *N. pinitoides* (Chachlov) Chachlov. The ferns *Coniopteris*, *Cladophlebis*, and *Raphaelia* Debey et Ettingshausen are common. Some of their members are endemic: *Coniopteris angarensis* Pryn., *C. jurensis*, *C. ircutensis* Pryn., *C. krasnopolskii* Pryn., *C. maakiana* (Heer) Pryn., *Cladophlebis czulmakensis*, *C. maicubensis* Orlovskaja, *C. multinervis* Golova, and *C. prynadae* Orlovskaja. Some species are shared with the Central Asian province. Thus, dipteridaceous ferns include several species of *Hausmannia* and one species of *Clathropteris*, *C. obovata*. *Klukia*, a characteristic genus of the European-Sinian area, is absent. Bennettites and cycads are rare in the Siberian area. *Anomozamites lindleyanus* Schimp., *A. minor*, *Ctenis* sp., *Butefia ensifopmis* (Heer) Dobruskina, *Nilssonia acuminata*, *N. cf. comptula* Heer, *N. aff. linearis* Sze, *N. mediana*, *N. cf. muensteri*, *N. orientalis*, *N. villosa* Dervis in Teslenko, *Pterophyllum cf. inconstans* (Braun) Goep., *P. irkutense* Pryn., *Taeniopteris cf. spathulata* McClelland, and *T. vittata* Brongn. are only known. *Elatides*, *Pityophyllum*, and *Podozamites* are characteristic conifers. At one time, endemic cycadophytes were believed to occur in the Siberian area, but Krassilov (1974) disproved this suggestion.

Since the indicators of subtropical climate *Stachypteris*, *Ptilophyllum*, and *Otozamites* are found in the Peski locality, and leaves of the Ginkgoales, Czekanowskiales, and *Podozamites* are absent, the Peski Flora can be assigned to the European-Sinian area of Vachrameev and the geoflora with *Cycadeoidea* of Krassilov. Keeping in mind the aforesaid, the comparison will be accomplished with coeval floras in the Donets Basin, Lvov Region (Ukraine), Caspian Depression (Kazakhstan), Georgia, and Yorkshire (England).



Among these localities, those of the Donets Basin and Caspian depression are geographically closest.

Eichwald (1865) was the first to describe plant remains from one of the Middle Jurassic localities of the Donets Basin that are faunistically dated to the Late Bathonian–Early Callovian, a locality near the town of Izyum. The determinations made by Eichwald are now obsolete. Later, this flora was monographically studied by Thomas (1911) and Stanislavsky (1957). The last author provided the following list of species: *Palaeohopatica rostafinskii* Racib., *Annulariopsis inopinata* Zeill., *Neocalamites* sp., *Equisetites beanii*, *Equisetites hallei* Thom., *Equisetites* sp., *Hymenophyllites* cf. *zeilieri* Racib., *H. kamenkensis* Pryn., *Coniopteris hymenophylloides*, *Dicksonites* sp., *Phlebopteris* sp., *Todites princeps* (Presl) Goth., *T. cf. roessertii* (Presl) Zeill., *Osmundopsis sturi* (Racib.) Harris, *Klukia exilis*, *Gleichenites cycadina* (Schenk) Sew., *Gleichenites* sp., *Marattiopsis muensteri*, *Eboracia lobifolia* (Phill.) Thom., *Cladophlebis whitbiensis* (Brongn.), *C. kamenkensis* Thom., *P. denticulata*, *C. nalivkinii* Thom., *C. crenata* Font., *Sphenopteris acutiloba* Heer, *S. cf. zarczyński* (Racyb.) Thom., *Sphenopteris* sp. 1, *Sphenopteris* sp. 2, *Thinnfeldia rhomboidalis* Ett., *Sagenopteris phillipsii*, *Taeniopteris vittata* Brongn., *Williamsonia pecten* (Phill.), *Williamsonia gigas* (L. et H.) Carruthers, *Otozamites iziumensis* Thom., *O. giganteus* Thom., *O. cf. obtusus* (L. et H.), *Otozamites* sp., *Cycadeoidea* sp., *Pterophyllum nathorstii* Sew., *Nilssonina orientalis*, *N. inouyei* Yok., *N. compta* (Phill.) Brongn., *N. donetziana* Stanislavsky, *Nilssonina* sp. 1, *Nilssonina* sp.? 2, *Nilssonina* sp.? 3, *Ctenis* sp. 1, *Ctenis* sp. 2, *Pseudoctenis* sp., *Zamites denticulatus* (Thom.) Stanislavsky, *Androstrobis jamnitschenkoii* Stanislavsky, *Beania* sp., *Cycadolepis* cf. *villosa* Zeill., *Ginkgo digitata* (Brongn.) Heer, *Ginkgo* sp.?, *Ginkgodium nathorstii* Yok., *Czekanowskia rigida* Heer, *Feildenia* sp., *Elatides setosa* (Phill.) Stanislavsky, *E. curvifolia*, *Elatocladus* sp. 1, *Elatocladus* sp. 2, *Pagiophyllum* sp., *Brachyphyllum* sp. 1, *Brachyphyllum* sp. 2, *Abietites densifolia* Thom., *Pityophyllum angustifolium* (Nath.) Moell., *Schyzolepis moelleri* Sew., *Drepanolepis charkoviensis* Stanislavsky, *Podozamites lanceolatus* (L. et H.) Schimp., *P. kamenkensis* Stanislavsky, and *Nageiopsis* sp.?

I have made several corrections in this list concerning modern names of the species, namely: *Equisetites beanii* now is *Equisetum beani*, *Thinnfeldia rhomboidalis* Ett. is *Pachypteris* sp., *Sagenopteris phillipsii* is *Sagenopteris* sp., *Nilssonina orientalis* is *Nilssoniopteris* sp. (Doludenko, 1963b), *Nilssonina* sp. 1 is *Nilssoniopteris* sp., *Williamsonia pecten* (Phill.) is *Ptilophyllum* sp., and *Otozamites iziumensis* Thom. is *Otozamites* sp.

The floras of the Donets Basin and Moscow Region share such species as *Equisetum beani*, *Eboracia lobifolia*, and *Cladophlebis denticulata*, and genera *Sagenopteris*, *Ptilophyllum*, *Otozamites*, and *Nilssoniopteris*. However, the flora of the Donets Basin contains numerous *Pachypteris*, *Ginkgo*, *Czekanowskia*, *Brachyphyllum*, *Pagiophyllum*, and *Podozamites*.

The flora of the Donets Basin is considered as transitional between the European and Central Asian provinces, since it includes *Klukia exilis*, *Pachypteris*, *Ptilophyllum*, and *Otozamites*, which are characteristic of the European province, and *Podozamites*, which is characteristic of the Central Asian and Siberian provinces. The flora of the Moscow Region lacks species that are characteristic of the Central Asian province.

Doludenko (1963a, 1963b) provided the following list of plants, which she determined in collaboration with Vachrameev from southwestern Ukraine (Lvov Region): *Equisetites* sp., *Sphenopteris* sp., *Ptilophyllum sokalense* Doludenko, *P. ukrainense*, *Ptilophyllum* sp., *Nilssoniopteris* aff. *vittata*, *Pseudocycas* sp., *Pterophyllum* sp., *Williamsonia* sp., *Nilssonina* sp., *Phoenicopsis* sp., *Sciadopitytes ukrainensis* Doludenko, *Pityophyllum* ex gr. *nordenskioldii* (Heer) Nath., *Sagenopteris* sp., *Elatides* sp., and *Brachyphyllum* sp. Sveshnikova (1981) converted *Sciadopitytes ukrainensis* Doludenko into *Sciadopityoides ukrainensis* (Doludenko) Sveshnikova.

The West Ukrainian flora shows a greater similarity. The genera in common are *Equisetum*, *Sphenopteris*, *Ptilophyllum*, *Nilssoniopteris*, *Williamsonia*, *Brachyphyllum*, and *Sagenopteris*. Remarkable is the prevalence of bennettites over cycads and low diversity of the Ginkgoales and Czekanowskiales in this flora. In addition, *Sciadopityoides ukrainensis* was found in this flora. It is a member of the Miroviaceae, which appeared as late as the Middle Jurassic and still had a rather small geographical range. The Peski locality also

Explanation of Plate 8

Figs. 1, 4–8. *Otozamites paradoxus*, sp. nov.: (1) PIN, no. 4727/120, fragment of a pinnate leaf, ×2; (4–6, 8) holotype PIN, no. 4727/107; (4) pinnate leaf fragment, ×2; (5) segment fragment showing the epidermis topography, ×7; (6) blowing up of Fig. 5, ×14; (7) PIN, no. 4727/179, pinnate leaf fragment, ×2; (8) upper surface of the lower epidermis, conical elevations are visible formed by encircling cells of stomata, SEM.

Figs. 2, 3. *Otozamites* sp., PIN, no. 4727/148: (2) small fragment of a pinna, only one segment is visible, ×7; (3) counterpart of the part shown in Fig. 2, venation is distinct, ×7.

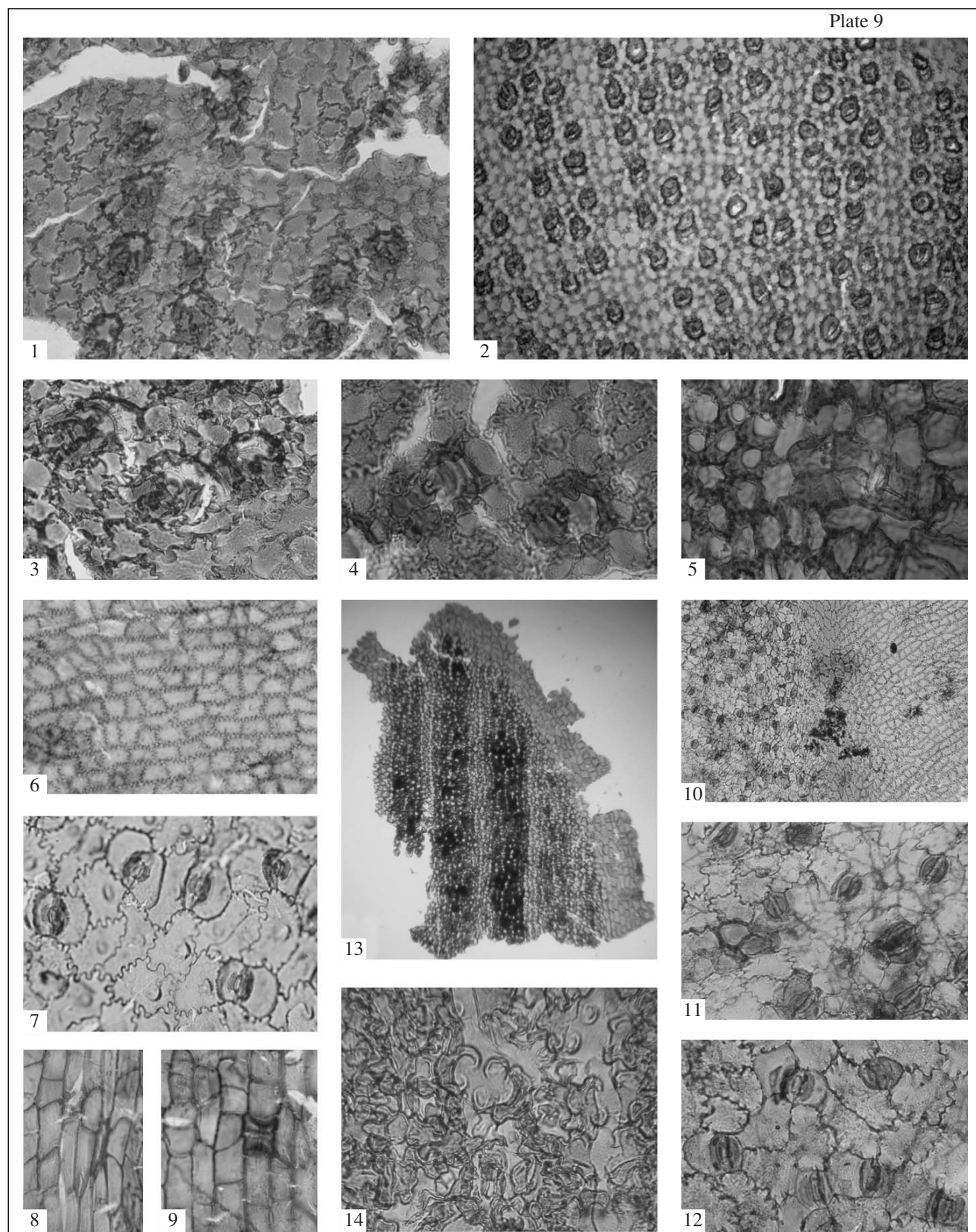
Fig. 9. *Nilssoniopteris vittata* (Brongniart) Florin, 1933, PIN, no. 4727/357, leaf, × 2.

Fig. 10. *Anomozamites* aff. *minor* (Brongniart) Nathorst, 1878, PIN, no. 4727/777, pinnate leaf fragment, ×2.

Fig. 11. *Nilssoniopteris infera*, sp. nov., holotype PIN, no. 4727/352, leaf fragment, ×2.

Fig. 12. *Nilssoniopteris* sp., PIN, no. 4727/405, leaf fragment, ×2.

Plate 9



contains members of this family, although they belong to other genera: *Tritaenia* and *Oswaldheeria*. Apparently, the floras of the Moscow Region and western Ukraine correspond to the same type of vegetation. However, the latter includes *Phoenicopsis*, that testifies to the ecotone character of the flora.

The Central Asian province is exemplified by the Upper Bathonian flora of the northern Caspian Region. The assemblage includes *Neocalamites* sp., *Equisetites beani* (now *Equisetum beani*), *Equisetites lateralis* (Phill.) Phill., *Equisetites* sp., *Marattiopsis* sp., *Coniopteris simplex* (L. et H.) Harris, *C. cf. furssenkoi* Pryn., *C. cf. hymenophylloides*, *C. cf. spectabilis* Brick., *C. vialovae* Tur.-Ket., *Coniopteris* sp., *Klukia exilis*, *Cladophlebis denticulata*, *C. whitbiensis* (Brongn.) Brongn., *Cladophlebis* sp., *Lobifolia lobifolia* (Phill.) Rasskaz. et Leb., *Anomozamites* sp., *Pseudocycas baranovae* Kiritchk., *P. cf. sajghanensis* K. Jacob et Schukla, *Ptilophyllum caucasicum* Dolud. et Svan., *Nilssonina dentata*, *N. polymorpha*, *N. cf. mediana*, *N. vittaeformis* Pryn., *Nilssonina* sp., *Sphenobaiera* sp., *Phoenicopsis* ex. gr. *angustifolius* Heer, *Podozamites angustifolius* (Eichw.) Heer, *P. lanceolatus* (L. et H.) Braun, *Podozamites* sp., *Ferganiella lanceolata* Brick, *Ferganiella* sp., *Pagiophyllum setosum* (Phill.) Sew., *Pagiophyllum* sp., *Elatides* sp., and *Pityophyllum* ex gr. *nordenskioldii* (Baranova et al., 1975). *Cladophlebis denticulata*, *Anomozamites*, and *Ptilophyllum* are present in both this and the Moscow Region Flora. The cooccurrence of the subtropical genus *Ptilophyllum* with temperate *Ferganiella* and *Phoenicopsis* testifies to the ecotone character of the flora under consideration. The absence of members of the Miroviaceae should be pointed out.

To date, the flora of the Yorkshire Deltaic Series (England) is the most completely studied flora of the Middle Jurassic. Three main series are defined in the locality: the Lower Deltaic, Middle Deltaic, and Upper Deltaic Series, which are dated to the Early Bajocian, Middle Bajocian, and Bathonian, respectively. In the present time, this locality and the Peski locality are situated in virtually the same latitude. Fossil plants from the Yorkshire Deltaic Series were mostly studied by Seward (1900) and Harris (1961, 1964, 1969, 1979). Millington and Miller collaborated with Harris (Harris

et al., 1974), who also published a compiled multivolume paper with detailed descriptions of fossil plants.

The total list of Middle Jurassic plants of Yorkshire enumerates more than 150 species. Comparing to the Bajocian, the diversity of the Bathonian genera and species strongly decreases in the Yorkshire. Since the present study deals with the Bathonian, it is pertinent to reproduce in full the list of the Bathonian plants of Yorkshire: *Thallites* sp., *Equisetum beani*, *Todites denticulatus* (rare), *T. williamsoni*, *T. princeps* (Presl) Goth., *Phlebopteris woodwardi* Leck., *Coniopteris bella* Harris, *C. himenophylloides* (rare), *Eboracia lobifolia*, *Zamites gigas* (L. et H.) Morris, *Otozamites beani* (L. et H.) Brongn., *O. graphicus*, *O. thomasi* Harris, *O. venosus* Harris, *O. penna* Harris, *O. marginatus* Saporta, *Nilssoniopteris vittata*, *N. major* (L. et H.) Florin, *Pterophyllum thomasi* Harris, *P. cycadites* Harris et Rest, *Caytonia nathorsti* (Thomas) Harris, *Nilssonina tenuinervis* (Phill.) Fox-Str., *N. revoluta* Harris, *Ctenozamites leckenbyi* (Leck.) Nath., *C. cycadea*, *C. megalostoma* Harris, *Ctenozamites* sp. A, *Ctenis exilis* Harris, *C. cf. stewardiana* Harris, *Pachypteris lanceolata*, *Stenopteris williamsoni* (Brongn.) Harris, *S. nana* Harris, *Ginkgo huttoni* (Sternberg) Black, *G. whidbiensis* Harris, *Baiera furcata* (L. et H.) Braun, *Eretmophyllum whitbiense* Thom., *Pseudotorellia tibia* Harris, *Czekanowskia blacki* Harris, *Sphenarion muiriae* Harris, *Brachyphyllum mamillare* L. et H., *B. cricus* Kendall, *Pagiophyllum kurrii* (Schimper) Salfeld, *P. fragilis* (Bose) Harris, *P. maculosum* Kendal, *P. ordinatum* Kendall, *Hirmerella estonensis* (Kendall) Harris, *H. kendaliae* Harris, *Geinitzia rigida* (Phill.) Harris, *Elatides thomasi* Harris, *Cyparissidium blakii* (Harris) Harris, *Pityanthus scalbiensis* van Konijnenburg-van Cittert, *Scarburgia hillii* Harris, *Pityocladus scarburgensis* Harris, *Schizolepis liasokeuperianus* C.F.W. Braun, *Torreya valida* Florin, *Bilsdalea dura* Harris, and *Trulla nitens* Harris.

First of all, the absence of the fern *Stachypteris* and bennettites of the genus *Ptilophyllum* in the Bathonian assemblage has engaged the attention. In the Bajocian, the latter genus is represented by three species: *P. pectinoides*, *P. hirsutum*, and *P. pecten*. The number of species of *Otozamites* was reduced from 11 to 5. Bennettites of the genus *Anomozamites* disappear. Moreover,

Explanation of Plate 9

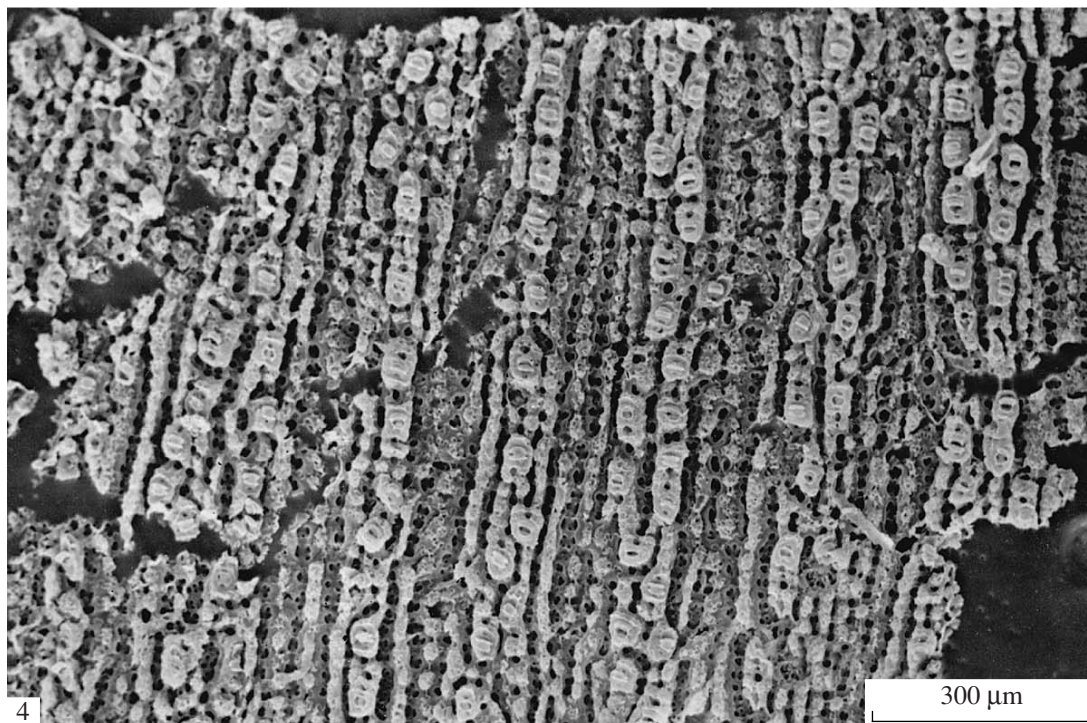
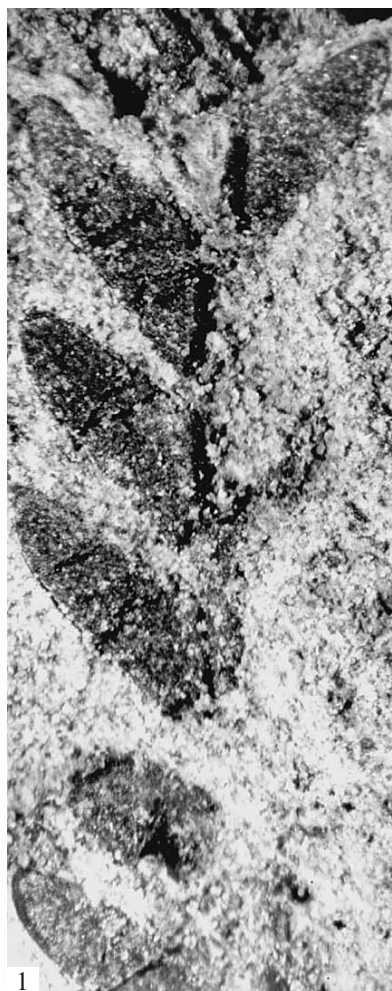
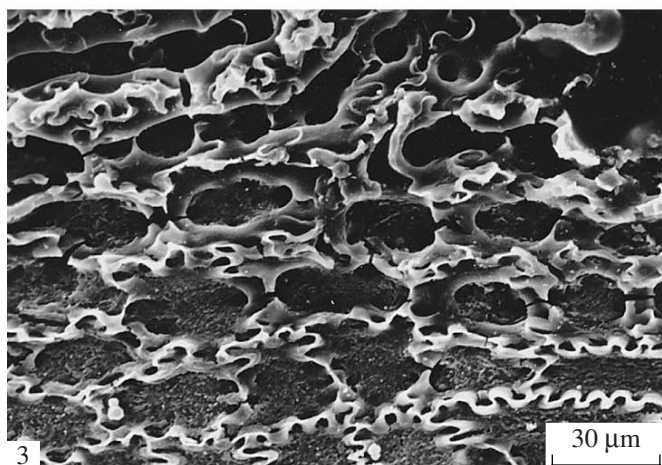
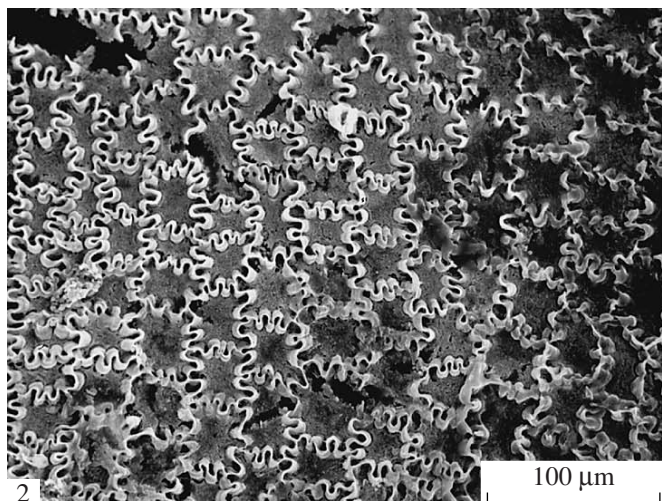
Figs. 1, 3, 4. *Otozamites* sp., PIN, no. 4727/148: (1) topography of lower epidermis cuticle, $\times 230$; (3) lobe fragment, upper focus of stomata, note conical elevations formed by encircling cells, $\times 500$; (4) lobe fragment, lower focus of stomata, papillae on subsidiary cells are visible, $\times 560$.

Figs. 2, 5. *Otozamites paradoxus*, sp. nov., holotype PIN, no. 4727/107: (2) lobe fragment showing the topography of the lower epidermis, $\times 40$; (5) lobe fragment, a gland is visible at the leaf base, $\times 800$.

Figs. 6–9. *Nilssoniopteris infera*, sp. nov., holotype PIN, no. 4727/352: (6) upper epidermis cuticle, $\times 70$; (7) lower epidermis cuticle, $\times 100$; (8, 9) glands on the rachis, $\times 200$.

Figs. 10–12. *Nilssoniopteris vittata* (Brongn.) Florin, 1933, PIN, no. 4727/357: (10) topography of the lower and upper epidermises, $\times 40$; (11, 12) lower epidermis cuticle, note stomatal apparatuses and trichomes, $\times 160$.

Figs. 13, 14. *Ptilophyllum riparium* Gordenko, 1999, holotype PIN, no. 4727/108: (13) lower epidermis topography, $\times 20$; (14) peltate trichomes, $\times 600$.



caytonias virtually disappear in the Bathonian, whereas their remains are represented both by leaves (*Sagenopteris*) and by reproductive structures (*Caytonia* and *Caytonanthus* Harris) in the Bajocian. In general, the number of index species of the European-Sinian area was reduced. Of importance is the fact that members of the Miroviaceae are lacking in such a thoroughly studied locality as the Yorkshire Deltaic Series.

One more important flora is situated in the Caucasus. Caucasian fossil plants were studied by Delle (1960, 1962, 1967) and Doludenko and Svanidze (1969). The list of Bathonian species includes *Neocalamites hoerensis* (Shimp.) Halle, *Equisetum beani*, *E. laterale* Phill., *Equisetum* sp., *Marattia muensteri* (Goep.) Delle, *Osmundopsis prynadae* Delle, *Todites princeps*, *T. williamsonii*, *Klukia exilis*, *Coniopteris* ex. gr. *hymenophylloides*, *C. murrayana* (Brongn.) Brongn., *Gonatosorus lobifolius* Burak., *Clathropteris* sp., *Dicthyophyllum rugosum*, *Cladophlebis* ex. gr. *lobifolia* (Phill.) Brongn., *Pachypteris lanceolata*, *P. multiformis* Delle, *Ctenozamites cycadea* (Berger) Nath., *Sagenopteris* cf. *fillipsii* (Brongn.) Presl, *Williamsonia whitbiansis* Nath., *Williamsonia* sp., *Anomozamites* sp. (?), *Cycadolepis rugosa* (Halle) Harris, *Otozamites graphicus* (Leck.) Schimp., *Ptilophyllum acutifolium*, *P. acutifolium* f. *latum* Delle, *P. cutchense*, *Pseudocycas* cf. *saiganensis* K. Jacob et Shukla, *Ctenis pontica* Delle, *Nilssonsonia* cf. *kendalli* Harris, *N. grandifolia* Delle, *N. princeps* (Oldham et Morris) Sew., *N. variabilis* Pryn., *N. vittaeformis*, *Paracycas brevipinnata* Delle, *Pseudoctenis weberi* (Sew.) Pryn., *Cycadites rectangularis*, *Taeniopteris* sp. cf. *Nilssoniopteris vittata*, *Baiera inaequilobata* Delle, *Ginkgo digitata* (Brongn.) Heer, *Ginkgo* sp., *Sphenobaiera colchica* (Pryn.) Delle, *Czekanowskia* cf. *rigida* Heer, *Podozamites* cf. *lanceolatus* (L. et H.) Schimp., *Araucarioxylon* sp., *Pityophyllum* ex gr. *nordenskioldii* (Heer) Nath., *Xenoxylon latiporosum* (Cram.) Goth., *Pagiophyllum* sp., cf. *Haiburnia setosa* (Phill.) Harris, *Carpolithes* aff. *minor* Pryn., *Carpolithes* sp. a, *Carpolithes* sp. b, and *Carpolithes* sp. c.

This flora belongs to the European province, but the presence of *Podozamites* makes it slightly similar to Central Asian floras. No members of the Miroviaceae were found.

There are a considerable number of species shared with the flora of the Moscow Region: *Equisetum*, *Clathropteris*, *Cladophlebis*, *Sagenopteris*, *Williamsonia*, *Nilssoniopteris*, *Anomozamites*, *Otozamites*, *Ptilophyllum*, *Paracycas*, *Araucarioxylon*, and *Carpolithes*. However, conifers of the Peski locality are represented

by other genera, and the diversity of ferns and cycads is much lower.

The comparison between the flora of the Moscow region and the most important coeval floras reveals that the former shows the closest similarity to the flora of western Ukraine. In particular, both floras contain members of the Miroviaceae. The earliest members of the Miroviaceae were found in the Middle Jurassic of Europe. It is possible to outline their geographic range in the Middle Jurassic. The southernmost reliable record is situated on latitude 50° N, western Ukraine (Doludenko, 1963b); and the northernmost locality, on 70° N, northern Norway (Bose and Manum, 1990). The westernmost locality is situated in Poland, and the easternmost, in the Moscow Region (Peski locality). Revising the Angren flora of Uzbekistan, Nosova (1998) mentioned the presence of *Tritaenia* sp. and *Oswaldheeria* sp.; in her opinion, the latter represents a new species. However, she neither described nor figured the plants. If the presence of the above-mentioned plants in Angren flora is confirmed, the southern boundary of the range of the Miroviaceae will reach the modern latitude 40° N, and the eastern boundary will retreat beyond the Ural Mountains. It should be pointed out that the Angren flora is considered as transitional between subtropical and warm temperate floras. The Middle Jurassic Polish locality includes the type species of the Miroviaceae, *Mirovia szaferi* Reymanówna. *M. szaferi* cooccurs with *Sagenopteris colpodes*, *Pterophyllum cycadites*, *Pseudotorellia grojecensis* Reymanówna, *Brachyphyllum* sp., and *Allicospermum retemirum* Harris (Reymanówna, 1985).

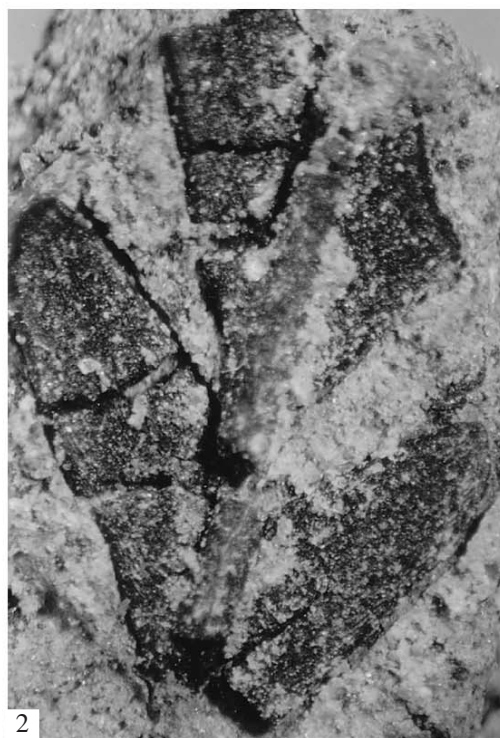
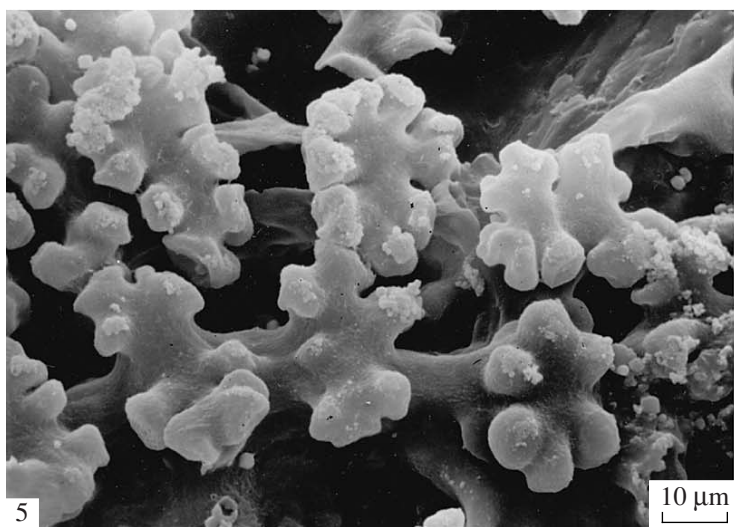
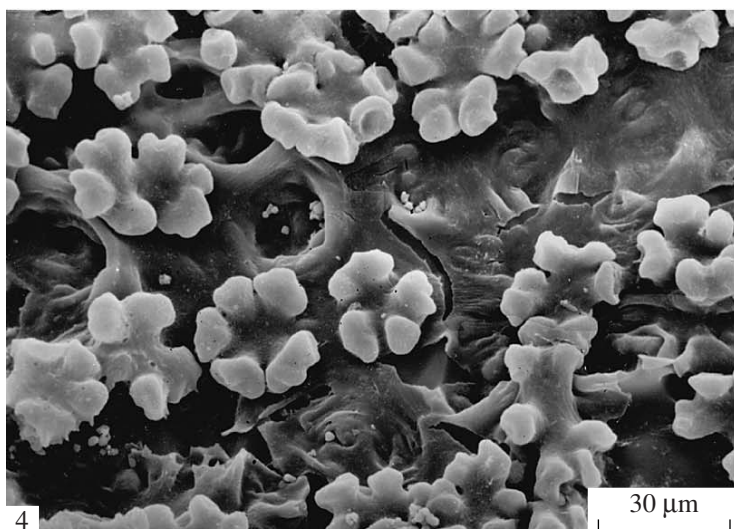
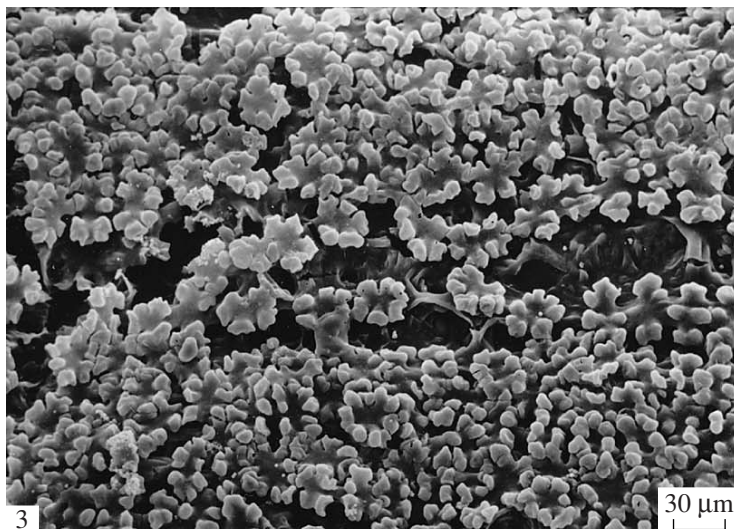
Recently, I have discovered one more Late Bathonian locality in the Kursk Region (near the town of Zheleznogorsk) that contains miroviaceous remains. Mass accumulations of leaves of *Oswaldheeria eximia* Gordenko (Miroviaceae) were found (Gordenko, 2007), as well as *Ginkgo huttoni*, *Pachypteris* sp., numerous trunk fragments of *Podocarpoxylon* sp., and various seeds.

The Miroviaceae are generally characterized by leaf mat formation, which is also characteristic of the Ginkgoales, Pseudotorelliaceae, and Czekanowskiales. The environments where miroviaceous plants grew were probably similar to those of the above groups. This is in part confirmed by leaf mats with *Oswaldheeria eximia* and *Ginkgo huttoni* found in the Kursk Region. Ecologically, the Miroviaceae can be considered as an analogue of the Ginkgoales, Pseudotorelliaceae, and Czekanowskiales in northern European province. Members of the Miroviaceae were prominent in plant communities in Central European Russia, where a vast mainland

Explanation of Plate 10

Figs. 1–4. *Ptilophyllum riparium* Gordenko, 1999: (1) PIN, no. 4727/110, fragment of a pinnate leaf, $\times 7$; (2–4) holotype PIN, no. 4727/108; (2) upper epidermis cuticle, SEM; (3) cuticle of the marginal zone of the lower epidermis, SEM; (4) topography of the lower epidermis cuticle, SEM.

Plate 11



apparently existed during this time. In the Early Cretaceous, these plants already have a relatively wide geographic range: they are known from Spain (Gomez, 2002), Greenland (Bose and Manum, 1990), and Siberia and Primorye (Nosova, 2001). Most probably, their range was circumpolar in that time, and, in comparison with the Middle Jurassic, some members reached more southern regions. Consequently, the Middle Jurassic is a starting epoch in the history of the Miroviaceae, and this start took place in Eastern Europe.

To date, the Peski Assemblage is the only representative floristic assemblage showing the vegetation of Central European Russia during the Bathonian. *Phoenicopsis*, *Eretmophyllum* Thomas, *Czekanowskia*, and *Podozamites*, which are usual indicators of ecotone floras, are absent. However, the oldest known remains of *Tritaenia* have been found in the locality as well as members of the genus *Oswaldheeria*. In the Middle Jurassic, the geographical range of *Oswaldheeria* reached northern Norway (Bose and Manum, 1990; Manum et al., 1991), where Siberian elements prevail in the vegetation, but some European-Sinian indicators also occur. The following plants were found: *Nilssoniopteris norvegicus*, *Pachypteris* sp. cf. *P. lanceolata*, *Ginkgo dahlei* Manum et Bose, *Pseudotorellia heeri* Manum, ?*Czekanowskia* sp., *Oswaldheeria macrophylla*, *Oswaldheeria* sp. cf. *O. hallei* (Florin) Bose et Manum, and *Ramsaia ednyana* Manum et Bose. Large accumulations of leaves of *Oswaldheeria* in the Mikhailovskii Rudnik locality (Kursk Region) testify that these plants were prominent in the vegetation cover. Keeping in mind that the Miroviaceae occurred only in the Northern Hemisphere, and the boundary of their range does not drop below 40°N, I propose to consider them as an ecotone indicator. I believe that in the Bathonian the boundary between the European-Sinian and Siberian areas in Eastern Europe became wider and rose northward relatively abruptly (Figs. 9, 10), the ecotone was wide: started about 40°–50° N and continued at least up 60° N.

CHAPTER 6. SYSTEMATIC PALEOBOTANY

DIVISION POLYPODIOPHYTA

Order Polypodiales

Family Schizaeaceae Martius, 1834

Genus *Stachypteris* Pomel, 1849

Stachypteris psammitica Gordenko, 2000

Plate 1, figs. 1–5; Plate 2, figs. 1–10

Stachypteris psammitica: Gordenko, 2000, pl. 4, figs. 1–4; pl. 5, figs. 1–6.

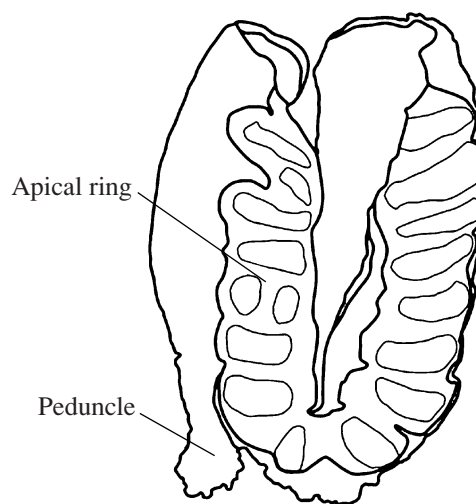


Fig. 5. Schematic drawing of a sporangium of *Stachypteris psammitica* Gordenko, detached from the fertile area of the holotype.

Holotype. PIN, no. 4727/226, leaf impression with a phytolaim, layer no. 3, section no. 2, Peski open mine, within 1.5 km of the Peski railway station, Kolomna district, Moscow Region, Middle Jurassic, Bathonian, Meshchera horizon.

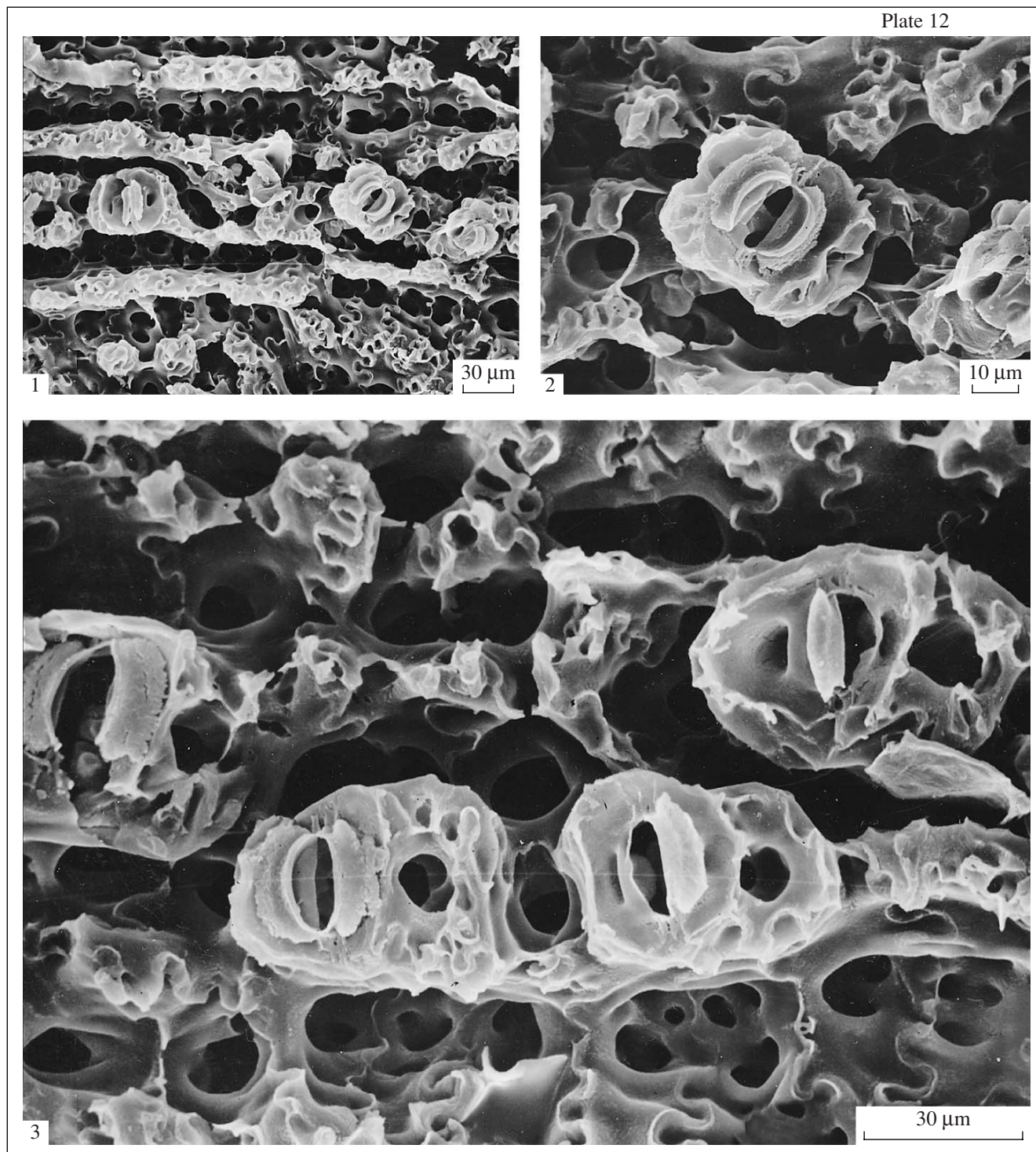
Description (Fig. 5). A pinna fragment is 11 mm long and 3.1 mm wide, becomes narrower toward the apex (Pl. 1, fig. 1). The rachis is a groove, 0.18 mm thick, reaches the apex, sinuous, changing the direction in the point where pinnules are attached. The pinnules are alternating, with a small distance between adjacent pinnules, catadromous, deviate from the rachis at an angle of 30°. Their outlines are elongated lanceolate. The pinnules are straight or, occasionally, weakly falcate. The length of the pinnules is 0.9–3.7 mm, and the width in the middle part is 0.5–1 mm. The pinnules are entire-margined, with acuminate or obtuse apices, constricted by decurrent bases bordering the rachis. Veins that enter the pinnule are simple, reaching the apex, and occasionally once or, more rarely, twice dichotomizing.

Conductive elements of xylem are 5–10 µm in transverse section, with walls of 0.3–0.5 µm thick, and are perforated with scalariform bordered pits (Pl. 2, figs. 7–10). The long axis of the bordered pits is 1–5 µm, and the short axis is 0.5–3.6 µm. The conductive elements are ended with rather primitive perforated plates, formed by five to seven scalariform bordered pits with reduced

Explanation of Plate 11

Figs. 1–5. *Ptilophyllum riparium* Gordenko, 1999: (1, 3–5) holotype PIN, no. 4727/108; (1) fragment of a pinnate leaf, ×8; (3) upper surface of the lower epidermis cuticle in the area of a stomatal zone, peltate trichomes are visible, SEM; (4) upper surface of the lower epidermis cuticle, note stomatal pits and peltate trichomes, SEM; (5) peltate trichomes fused with their bases, SEM; (2) PIN, no. 4727/106, fragment of the apex of a pinnate leaf, ×16.

Plate 12



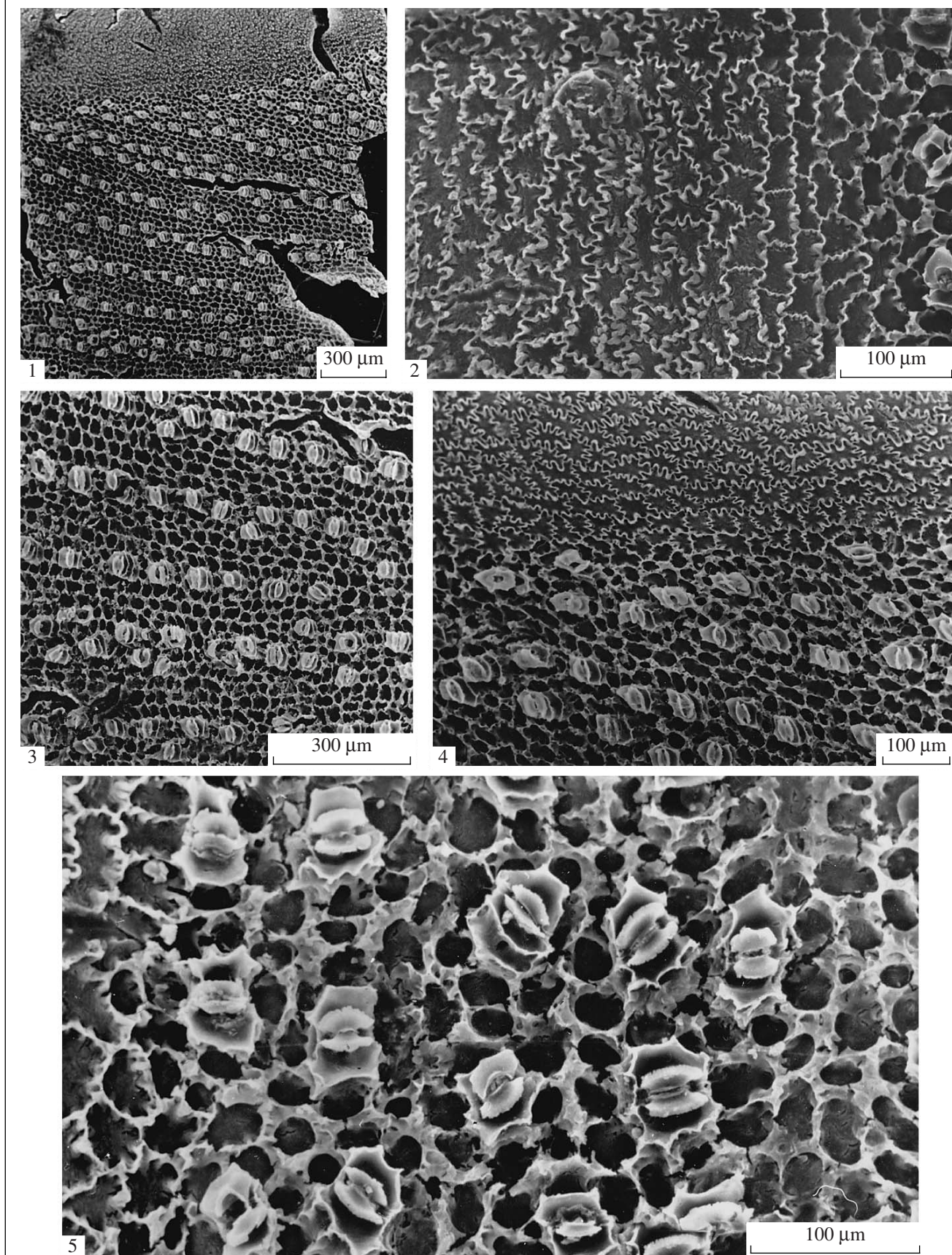
Explanation of Plate 12

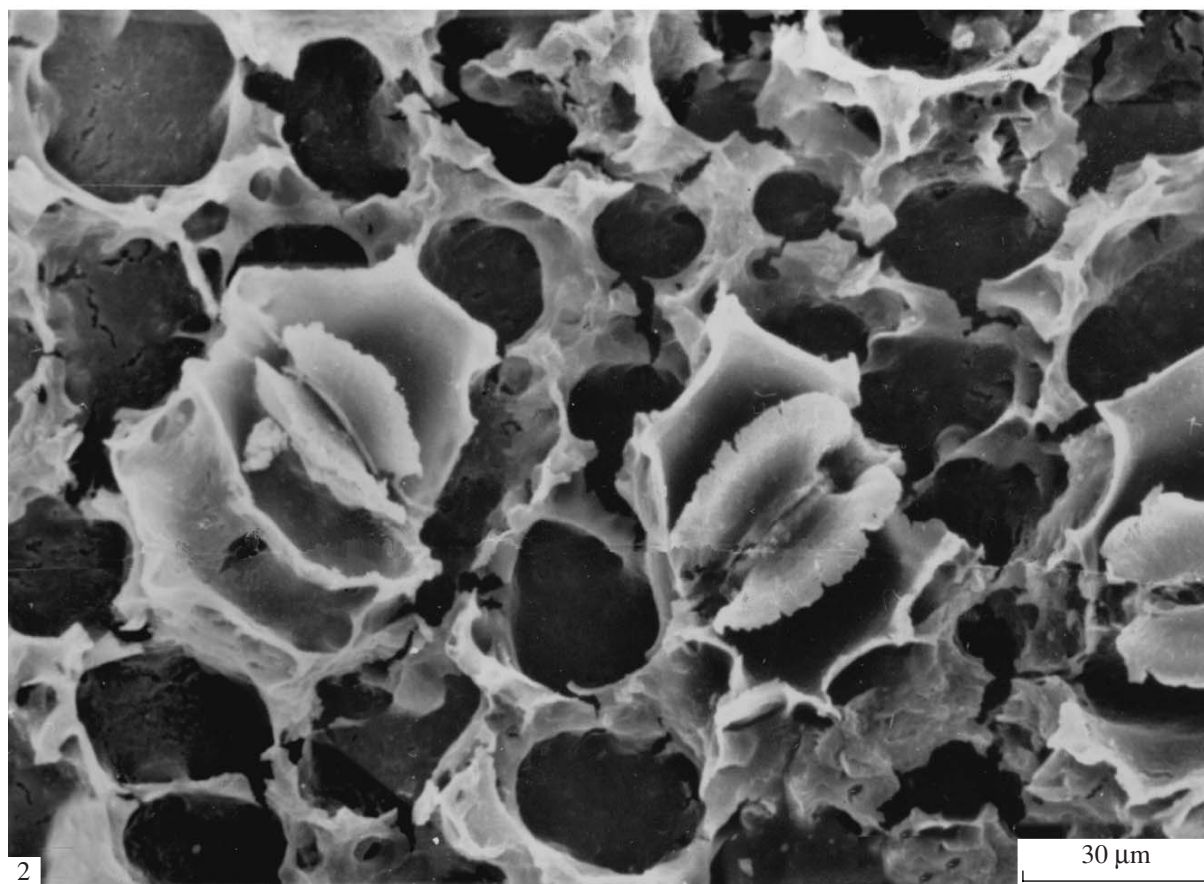
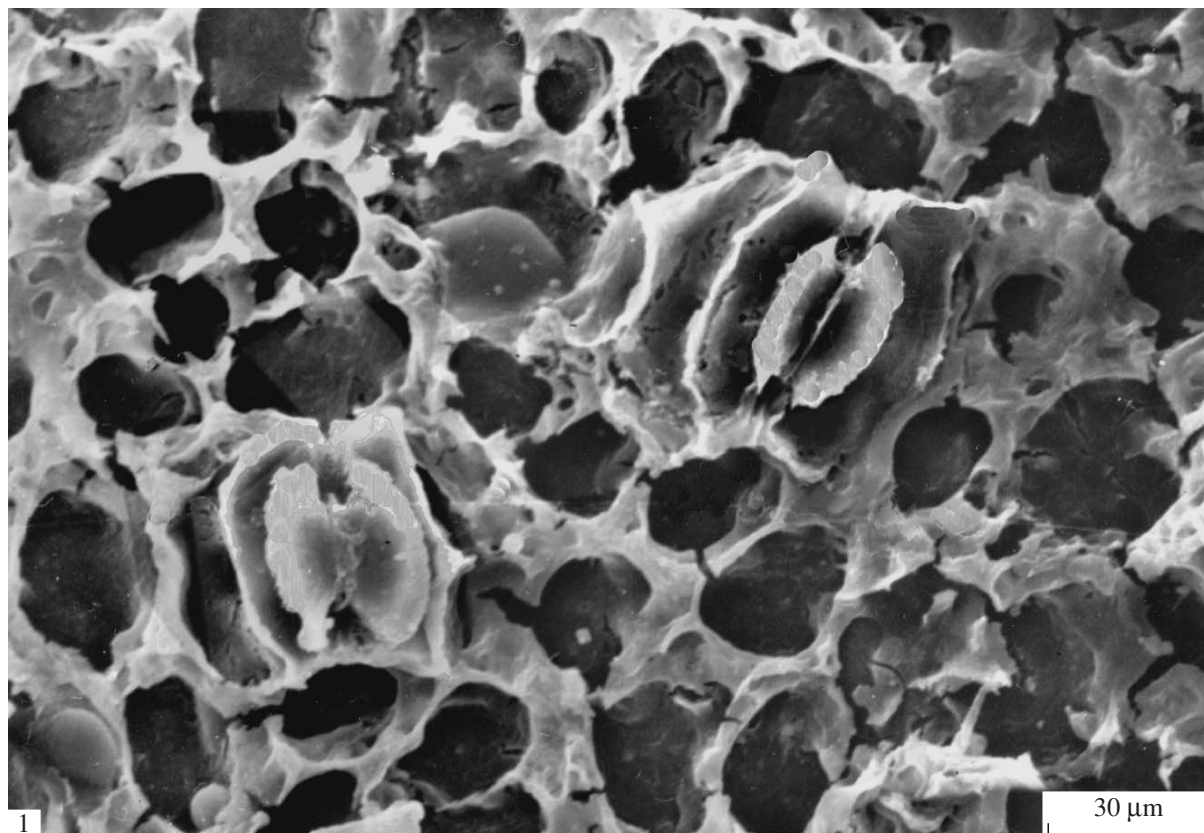
Figs. 1–3. *Ptilophyllum riparium* Gordenko, 1999, holotype PIN, no. 4727/108; (1) fragment of a stomatal zone, SEM; (2) obliquely orientated stomatal apparatus, SEM; (3) stomatal apparatuses, note papillae on guard cells with adjacent trichomes, SEM.

Explanation of Plate 13

Figs. 1–5. *Otozamites paradoxus*, sp. nov., holotype PIN, no. 4727/107; (1) epidermis topography, SEM; (2) cuticle of the upper epidermis, SEM; (3) stomata arranged in one row, SEM; (4) stomata arranged in two rows, SEM; (5) variously orientated stomatal apparatuses, SEM.

Plate 13





membranes (Pl. 2, figs. 8, 9). I consider these elements as vessels.

The fertile part is separated from the sterile part and forms a terminal spike of 4 mm long and 1.1 mm wide, which consists of eight basiscopic and seven acroscopic pinnules. The fertile pinnules are narrowly elliptical, acuminate, and approximately three times as small as the sterile pinnules. Each fertile pinnule bears one sporangium.

There are 15 abaxial sporangia in the fertile part (Pl. 1, fig. 1). They are ellipsoidal (Pl. 1, figs. 2, 3) and shortly pedunculate. The long axis of the sporangia is about 450 μm , and the short axis is 290 μm . The sporangial wall is one-layered, about 9 μm thick, and consists of elongate cells with distinct anticlinal walls. The sporangial ring is subapical, horizontal, about 60 μm high, ellipsoidal, measuring approximately 120 \times 60 μm , consists of 15 thick-walled cells arranged in one row (Pl. 1, fig. 2; Fig. 1).

The spores are trilete, rounded-triangular in equatorial view, 30–35 μm in diameter (Pl. 1, fig. 4; Pl. 2, figs. 1–3). The proximal scar is distinctly striate, bordered, and reaches 1/3–2/3 of the spore radius. The proximal surface is covered with scattered small verrucae, many of which are fused in small short ribs (Pl. 2, fig. 3). The distal surface is alveolate (Pl. 2, figs. 1, 2). The alveolae are 2.5–3 μm , from rounded-polygonal to rounded, occasionally fused with each other, with the walls of 0.5–3 μm wide.

Comparison. *Stachypteris psammitica* closely resembles other species of this genus, which is characterized by small catadromous pinnules with simple or, more rarely, branching veins, a fertile part of the pinna separated from the sterile part and bearing solitary sporangia without indusium. In the outline and arrangement of sterile pinnules the species resembles *S. turkestanica* Tur.-Ket. from the Jurassic of Karatau, which has alternating, lanceolate, decurrent pinnules, separated by small spaces (Doludenko and Orlovskaya, 1976). However, *S. psammitica* has slightly wider pinnules, a smaller fertile spike, and less numerous sporangia. The spore morphology shows an important difference: the spores *S. psammitica* bear sculptural elements, and the spores of *S. turkestanica* are psilate.

The morphology of spores of *S. psammitica* is very close to that of *S. spicans* Pomel from the Upper Jurassic of Europe (Harris, 1961; Barale, 1981). *S. psammitica* differs from this species by the outline and size of sterile pinnules: *S. psammitica* has relatively long and narrow (narrowly lanceolate) pinnules with acuminate apices, whereas *S. spicans* has short and rounded pinnules. In addition, the spores of *S. psammitica* are much smaller than *S. spicans*.

S. alata Zhou from the Jurassic of China (Zhou, 1994) has larger pinnules, which virtually do not become narrower and have rounded apices. No data on the morphology of sporangia and spores are available.

S. ketovae Krassilov from the Lower Cretaceous of the Russian Far East is distinct by its narrow, nearly needle-shaped pinnules. Sporangial rings in this species are not in the subapical, but in apical position.

Occurrence. Type locality.

Material. Two specimens: a pinna impression and its counterpart with a phytolite and one dispersed sporangium.

Family Dipteridaceae Seward et Dale, 1907

Genus *Clathropteris* Brongniart, 1828

Clathropteris sp.

Plate 4, fig. 7

Description. The fragment of a sterile pinna is 29 mm long and 10 mm wide (Pl. 4, fig. 7). The pinna margin is toothed, with the teeth of 2 mm high curved toward the apex. The distance between adjacent teeth is about 8 mm. The venation is pinnate-reticulate. The midrib is prominent, 0.3 mm wide. Less distinct lateral veins deviate from the midrib at an angle of 60°–70° and reach the apices of the teeth. The distance between the bases of the lateral veins is 10–15 mm. Weak tertiary veins deviate from the lateral veins at an angle that is close to 90°. Their ends are blind. Occasionally, veins of the fourth order are visible. They serve as anastomoses between the tertiary veins. The tertiary veins form a meshwork of open orthogonal meshes, with an average size of 0.5 cm.

Comparison. The specimen closely resembles *Clathropteris obovata* Oishi from the Upper Triassic of Japan (Oishi, 1932). The similarities include lateral veins deviating from the midrib at an acute angle, insignificant veins of the third and fourth orders, and small teeth. However, since the fragmentary preserved specimen does not provide sufficient information about the leaf lamina morphology, it is described as *Clathropteris* sp.

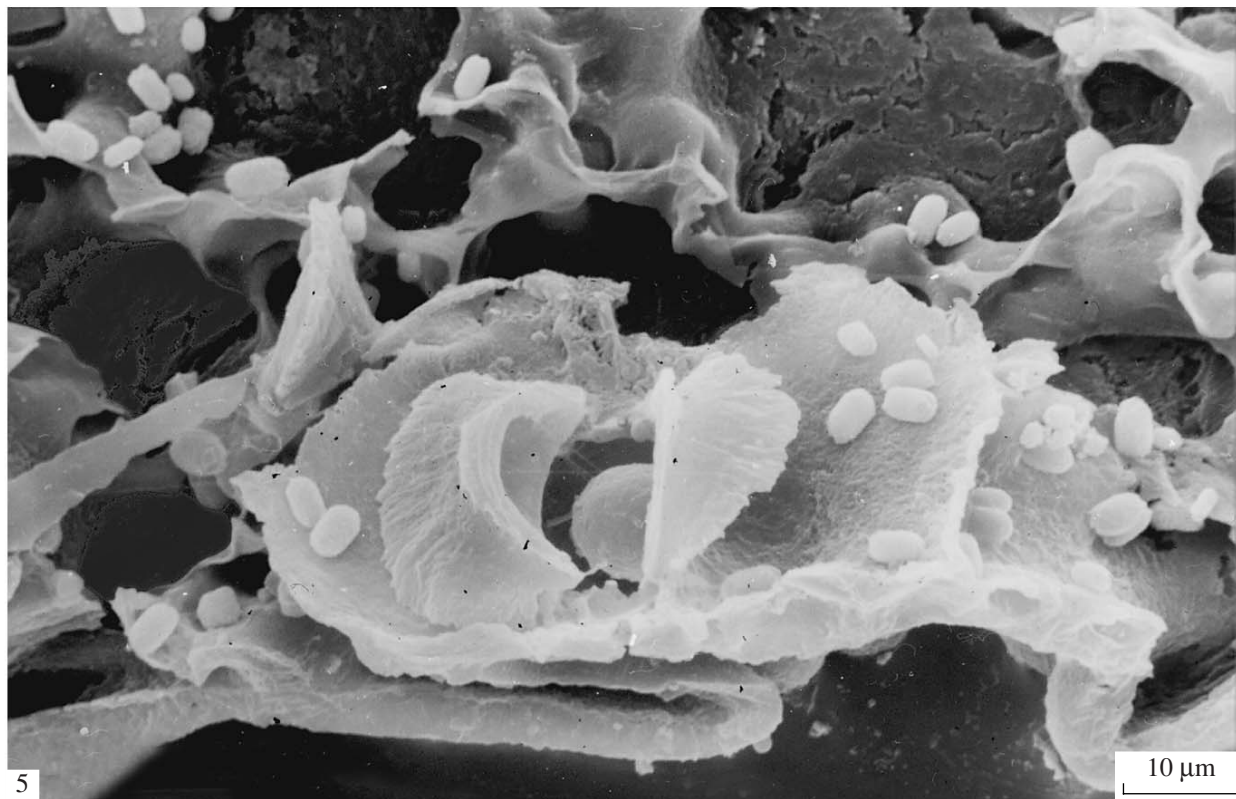
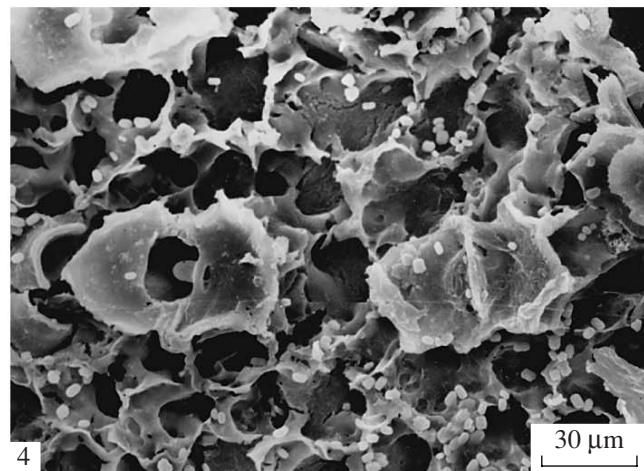
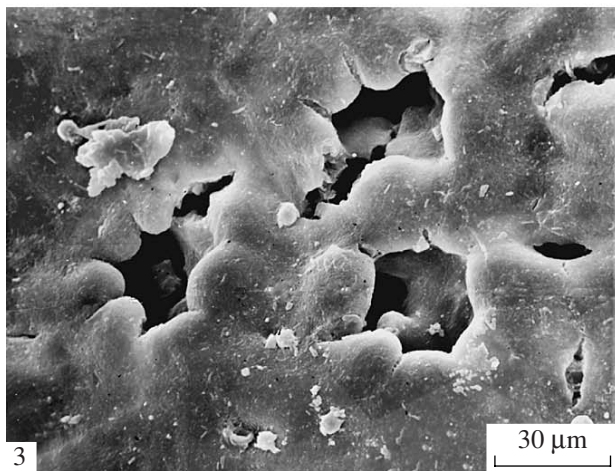
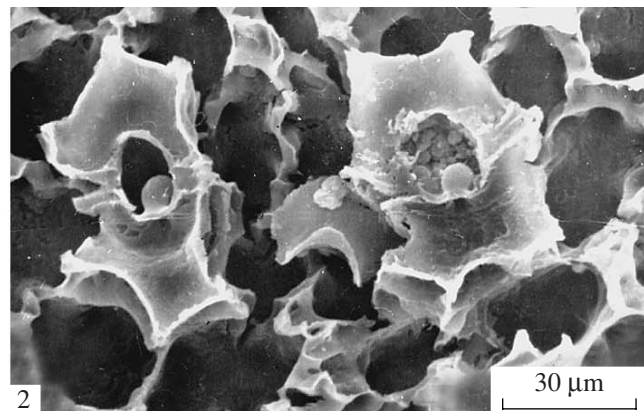
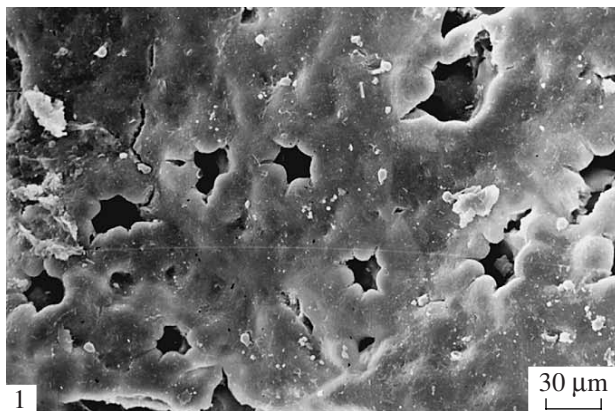
Two other species of the genus, *C. meniscioides* Brongn. from the Upper Triassic of Sweden (Brongniart, 1828) and *C. elegans* Oishi (Oishi, 1932), have larger teeth and tertiary veins that serve as anastomoses of secondary veins resulting in close rectangular meshes.

Material. One specimen consisting of an impression of a fragmentary sterile pinna, its counterpart, and the phytolite.

Explanation of Plate 14

Figs. 1, 2. *Otozamites paradoxus*, sp. nov., holotype PIN, no. 4727/107, stomatal apparatuses with a encircling cell bearing a papilla, SEM.

Plate 15



Explanation of Plate 15

Figs. 1, 3–5. *Otozamites* sp., PIN, no. 4727/148; (1) external surface of the lower side of a segment, stomatal pits are visible, SEM; (3) encircling cells forming conical elevations over stomatal apparatuses, SEM; (4) fragment of a stomatal zone, SEM; (5) stomatal apparatus with preserved cutinized plates of the guard cells, SEM.

Fig. 2. *Otozamites paradoxus*, sp. nov., holotype PIN, no. 4727/107, stomatal apparatuses with remote guard cells, papillae of subsidiary cells are visible, SEM.

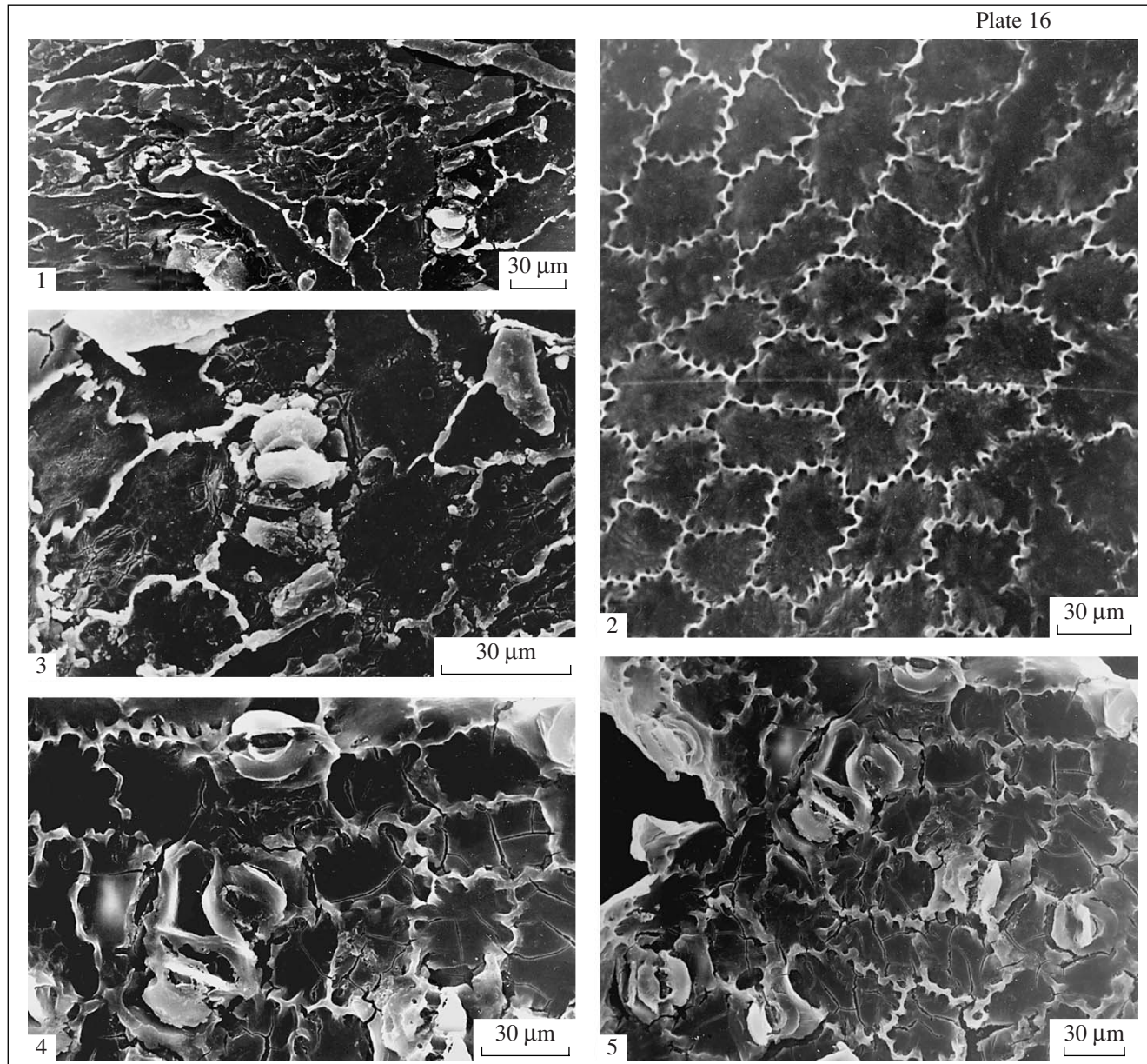
Family Matoniaceae Presl, 1848**Genus *Selenocarpus* Schenk, 1867***Selenocarpus* sp.

Plate 3, figs. 1–7; Plate 5, fig. 1

Description. The collection contains small fragments of incomplete sterile pinnae. The rachis is

straight, thin, 0.3–0.5 mm wide, rounded tetragonal in transverse section. The pinnules are alternating, at a distance of 2–4 mm from each other, nearly contacting in one of the specimens. The length of pinnules in the middle part of the pinna varies from 10 mm to 19–20 mm, and the width is 2.5–3 mm. Toward the apex,

Plate 16

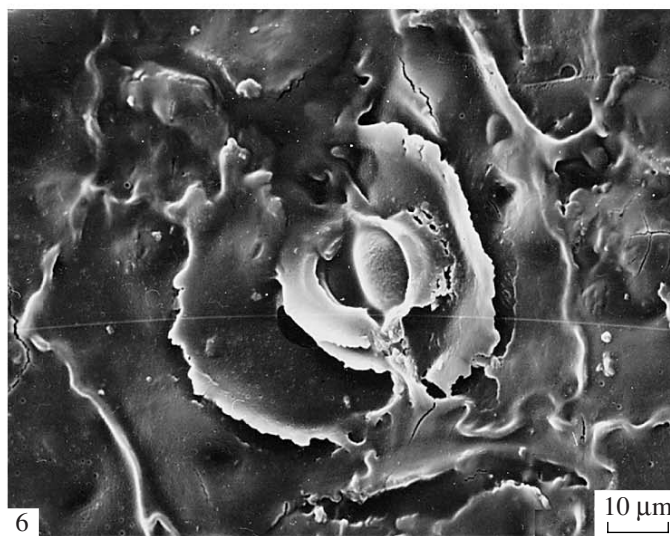
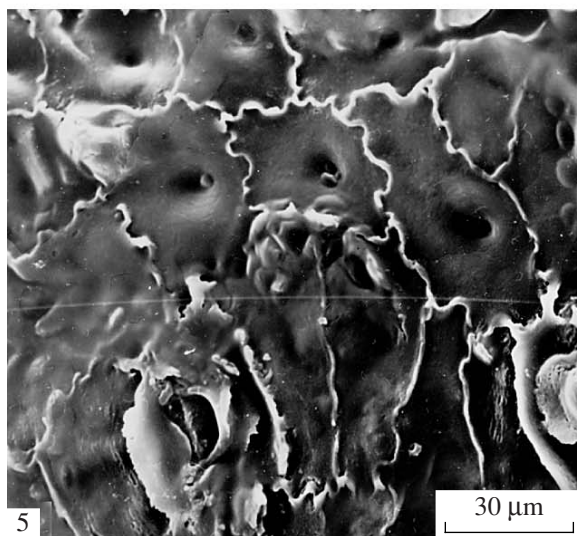
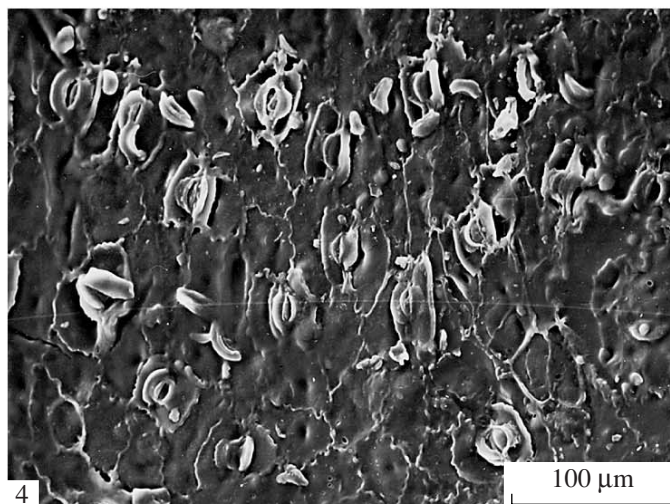
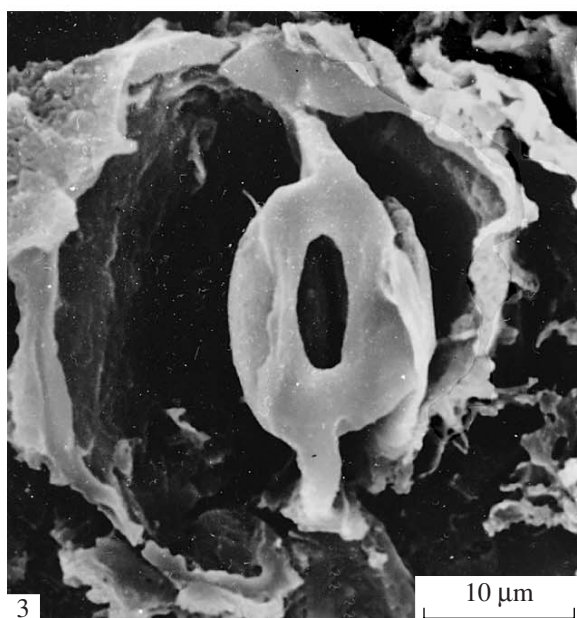
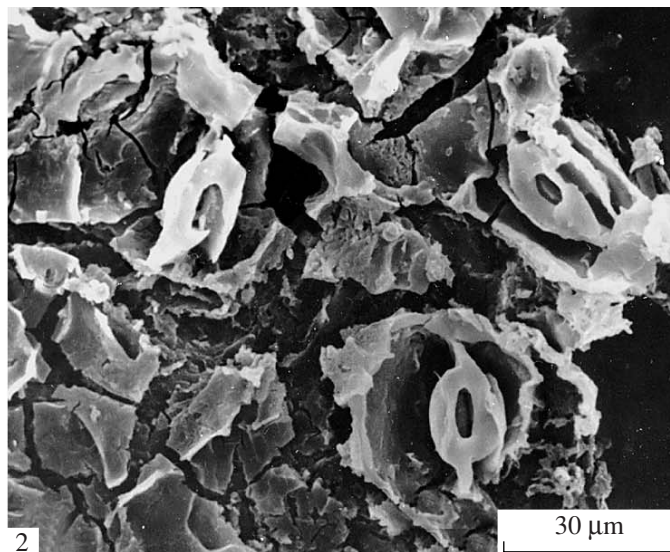
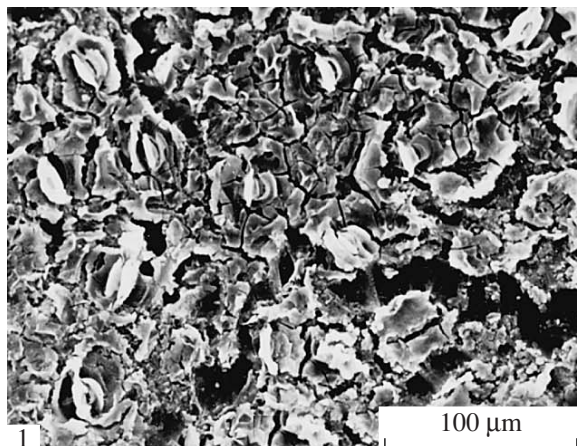


Explanation of Plate 16

Figs. 1–3. *Nilssoniopteris* sp., PIN, no. 4727/405: (1) cuticle of the lower epidermis, SEM; (2) cuticle of the upper epidermis, SEM; (3) stomatal apparatus, subsidiary cells were destroyed, SEM.

Figs. 4, 5. *Anomozamites* aff. *minor* (Brongniart) Nathorst, 1878, PIN, no. 4727/777, cuticle of the lower epidermis, SEM.

Plate 17



the pinnules gradually become smaller. The pinnules are attached to the rachis laterally, at an angle of 20°–40° or, more rarely 50°. They are lanceolate, with acuminate apices. The bases of the pinnules are slightly constricted from the acroscopic margin and decurrent and bordering the rachis from the basiscopic margin. The pinnule venation is pinnate-dichotomous. The midrib is distinct, reaching the pinnule apex. Secondary veins are catadromous, connivent in pairs, simple, or once (more rarely, twice) dichotomizing. They deviate from the midrib at an angle of 15°–45°, reach the leaf margin and occasionally end in small teeth sloping toward the apex (Pl. 3, fig. 6). The height of the teeth does not exceed 0.4 mm.

The cuticle is thicker than usually in ferns and resistant to maceration. The cuticles of the lower and upper epidermis are equal in thickness. The thickness of the cuticle is about 1 µm.

The leaf lamina is hypostomous. Ordinary cells of the upper epidermis are longitudinally elongated, with nearly straight anticlinal walls in costal zones and undulate in intercostal zones, with the range of undulations 3–5 µm. Trichomes are lacking.

Rounded-fusiform or rounded-rectangular longitudinally elongated cells with nearly straight or slightly sinuous anticlinal walls are present in costal zones of the lower epidermis. Cells of intercostal zones are longitudinally elongate, amoeboid, with the range of undulations 3–5 µm. Stomatal apparatuses are situated in intercostal zones. They are longitudinally or obliquely orientated and lack specialized subsidiary cells (Pl. 5, fig. 1). The guard cells are bean-shaped. The average length of stomata is 30 µm, and width, 20–30 µm. Adjacent stomata may share a subsidiary cell. Trichomes are lacking.

Comparison and remarks. The pinnule outlines, mode and angle of their attachment to the rachis, and patterns of venation are significantly similar to those of the only species of the monotypic genus *Selenocarpus*, *S. muensterianus* (Schenk, 1867; Harris, 1961). However, some specimens studied here are supplied with small and hardly visible teeth, whereas *S. muensterianus* has entire margins of pinnules. In addition, pinnules of the specimens from the Peski locality are slightly larger than those of *S. muensterianus*.

It should be pointed out that leaves of this genus are characterized by sporangia arranged in sori without indusia and situated over lateral veins and palmate arrangement of pinnae. The specimens studied are too fragmentary to prove such an arrangement. Complete

fertile leaves of *S. muensterianus* are known from the type Lower Liassic locality in southwestern Germany (Franconia). Small fragments of sterile leaves are known from the Middle Jurassic of Yorkshire, similar in preservation to the specimens under consideration. Harris (1961) assigned these fragments to *S. muensterianus* based on the same criteria that I used to assigned the specimens from the Peski locality to *Selenocarpus*: dimensions, angle of pinnule attachment, and venation pattern. Harris believed that the very small angle of attachment of pinnules to the rachis (about 45°) is an important characteristic feature of the genus.

The epidermal morphology of the specimens under description additionally proves their assignment to the Matoniaceae, a family to which belong the genus *Selenocarpus*. So far, no information has been available about the epidermal morphology of type specimens of *S. muensterianus*. However, it was only studied in some other fossil members of the Matoniaceae. Thus, the epidermal morphology of *Phlebopteris polypodioides* Brongn. from the Middle Jurassic of Yorkshire (Harris, 1961) is very similar to that of the specimens studied.

Therefore, the specimens under discussion are reliably assigned to *Selenocarpus*. However, some of their peculiarities do not allow to assign them confidently to *S. muensterianus*. Since the erection of a new species seems inexpedient, they are reported as *Selenocarpus* sp.

Material. Five specimens represented by impressions and phytoliteims.

Ferns of Formal Genera

Genus *Cladophlebis* Brongniart, 1849

Cladophlebis denticulata (Brongniart) Fontaine, 1889

Plate 3, figs. 8–11; Plate 4, fig. 5

Pecopteris denticulata: Brongniart, 1828–1836, pl. XCVIII, figs. 1, 2.

Cladophlebis denticulata: Fontaine, 1889, pl. VII, fig. 7; Briq, 1935, pl. 1, figs. 1, 2; Genkina, 1963, pl. X, figs. 2–6, pl. XI, figs. 1, 2.

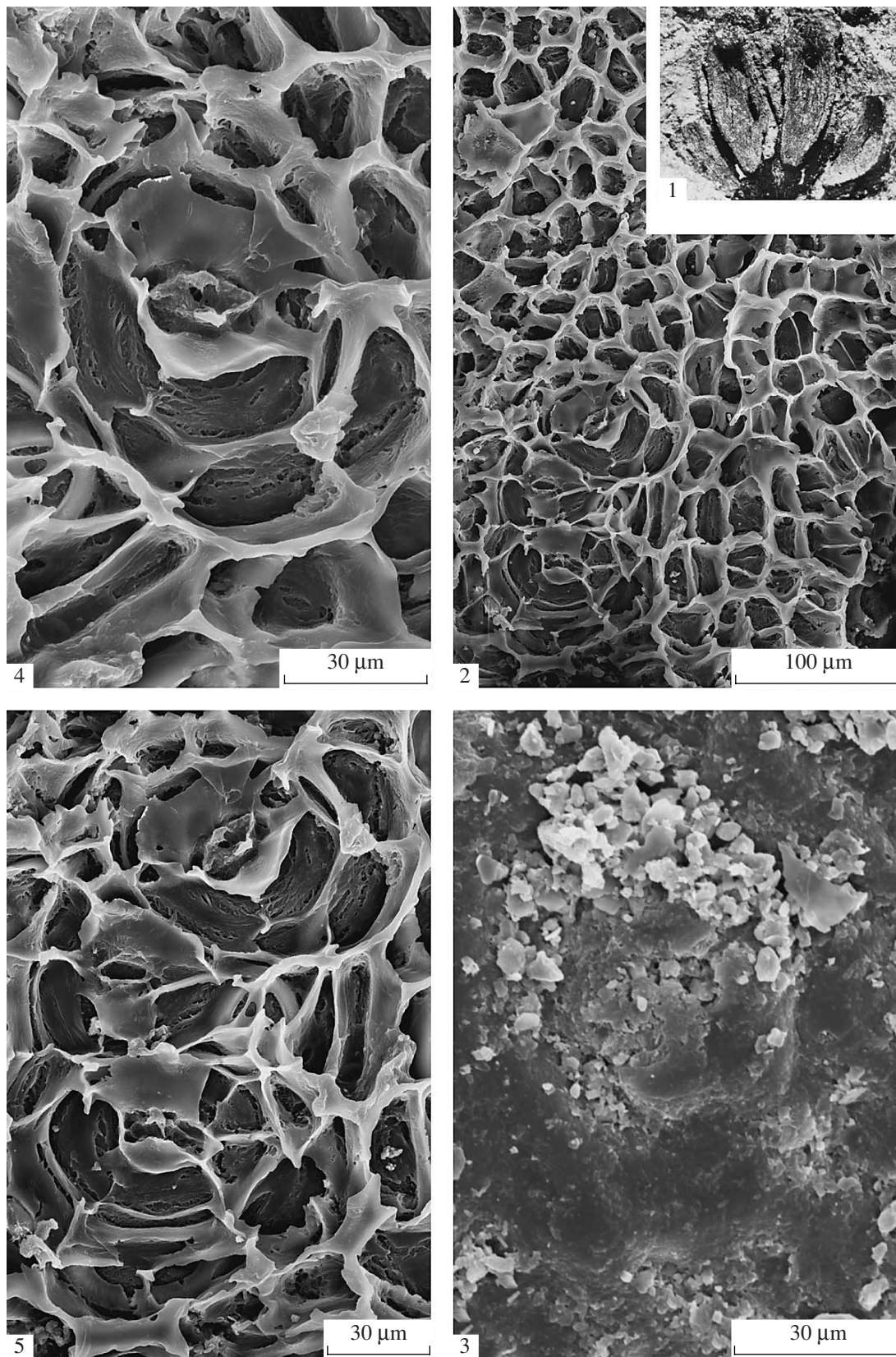
Holotype. A specimen without number figured in Fontaine (1889, pl. VII, fig. 7), Jurassic (?) of North America. The place where the specimen is kept is not designated.

Description. The collection contains small fragments of sterile leaves (Pl. 3, figs. 8–11, Pl. 4, fig. 5). The rachis is distinct, 0.5–0.7 mm thick. The pinnules are alternating, connivent in pairs, with contacting bases, attached to the rachis at an angle of 70°–90°. The pinnules are nearly triangular, with apices sloping toward the acroscopic margin and slightly falcate

Explanation of Plate 17

Figs. 1–3. *Nilssoniopteris vittata* (Brongniart) Florin, 1933, PIN, no. 4727/357: (1) lower epidermis topography, SEM; (2) variously orientated stomatal apparatuses, SEM; (3) stomatal apparatus with a preserved cutinization of inner periclinal walls of the guard cells, SEM.

Figs. 4–6. *Nilssoniopteris infera* Gordenko, sp. nov., holotype PIN, no. 4727/352: (4) lower epidermis topography, SEM; (5) papillae on ordinary cells of the lower epidermis, SEM; (6) stomatal apparatus with papillae on the subsidiary cells, SEM.



toward the pinna apex. The length of the pinnules is 11–13 mm, and their width at the base is 3–4.5 mm. The pinnule margin is toothed (Pl. 3, fig. 11). The teeth are small, occasionally hardly distinguishable because of the preservation. The midrib is distinct, occasionally reaching the apex. Secondary veins deviate from the midrib and dichotomize once.

Comparison and remarks. The toothed margin of the pinnules, their outline, and venation allow me to assign the fragments to *C. denticulata*, common in the Mesozoic of the Northern Hemisphere.

Harris (1969) revealed that fronds of *C. denticulata* from the Middle Jurassic of Yorkshire are identical to sterile fronds of *Todites denticulatus* (Brongn.) Krasser, included into the Osmundaceae on the basis of the morphology of the sporangia. It is possible that leaves of *C. denticulata* from the Peski locality belong to the same ferns. However, as far as no fertile leaves were found, the leaves under consideration cannot be reliably assigned to *T. denticulatus* and are determined as *C. denticulata*.

Occurrence. Triassic–Cretaceous of the Northern Hemisphere.

Material. Five specimens represented by impressions and phytoleims of sterile pinnae.

Cladophlebis sp.

Plate 4, figs. 2a, 3, 4, 6

Description. The collection contains small fragments of sterile pinnae (Pl. 4, figs. 2a, 3, 4, 6). The rachis is distinct, about 0.2–0.5 mm thick. The pinnules are connivent, with a slightly decurrent acroscopic margin. They are attached to the rachis at an angle of 70°–80°. The pinnules are tongue-shaped in outline, their apices are slightly sloping toward the acroscopic margin and, occasionally, slightly falcate. The length of the pinnules is 4–8 mm, and the width at the base is 3–5 mm. Toward the apex of the pinna, pinnules become smaller and fuse by their bases, bordering the rachis. Near the apex, one apical pinnule with basally undulate margins is formed by the increasing fusion of the pinnules (Pl. 4, fig. 3). The leaf lamina is imparipinnate. The pinnule venation is nearly indistinguishable because of the insufficient preservation. Only midrib is visible in some specimens.

Remarks. The absence of specimens showing venation pattern prevents the comparison with other members of the genus. Therefore, these specimens are described as *Cladophlebis* sp.

Material. Seven phytoleims and fragmentary impressions of sterile leaves.

Genus *Sphenopteris* Brongniart, 1828

Sphenopteris sp.

Plate 4, fig. 1

Description. The specimen is a fragment of a sterile pinnule (Pl. 4, fig. 1). The pinnule is obovate-triangular, with a wedge-shaped base. The length is 6 mm, the maximum width is 6 mm, and the width of the base is 0.5 mm. The upper part of the pinnule is divided into two small unequal lobes with finely serrate margins. The venation is irregularly pinnate.

Remarks. The wedge-shaped base and irregularly pinnate venation make this specimen close to *Coniopteris* Brongn., common in the Jurassic and Lower Cretaceous of the Northern Hemisphere. However, as far as the pinnule is sterile and fragmentary, it cannot be confidently assigned to a particular species of this genus and is determined here as *Sphenopteris* sp. within the artificial system.

Material. One specimen represented by an impression and the counterpart of a fragmentary sterile pinnule.

DIVISION PINOPHYTA

Order Caytoniales

Genus *Sagenopteris* Presl, 1838

Sagenopteris rossica Gordenko, sp. nov.

Plate 5, figs. 2–5; Plate 6, figs. 1–13

Etymology. From the Latin *rossicus* (Russian).

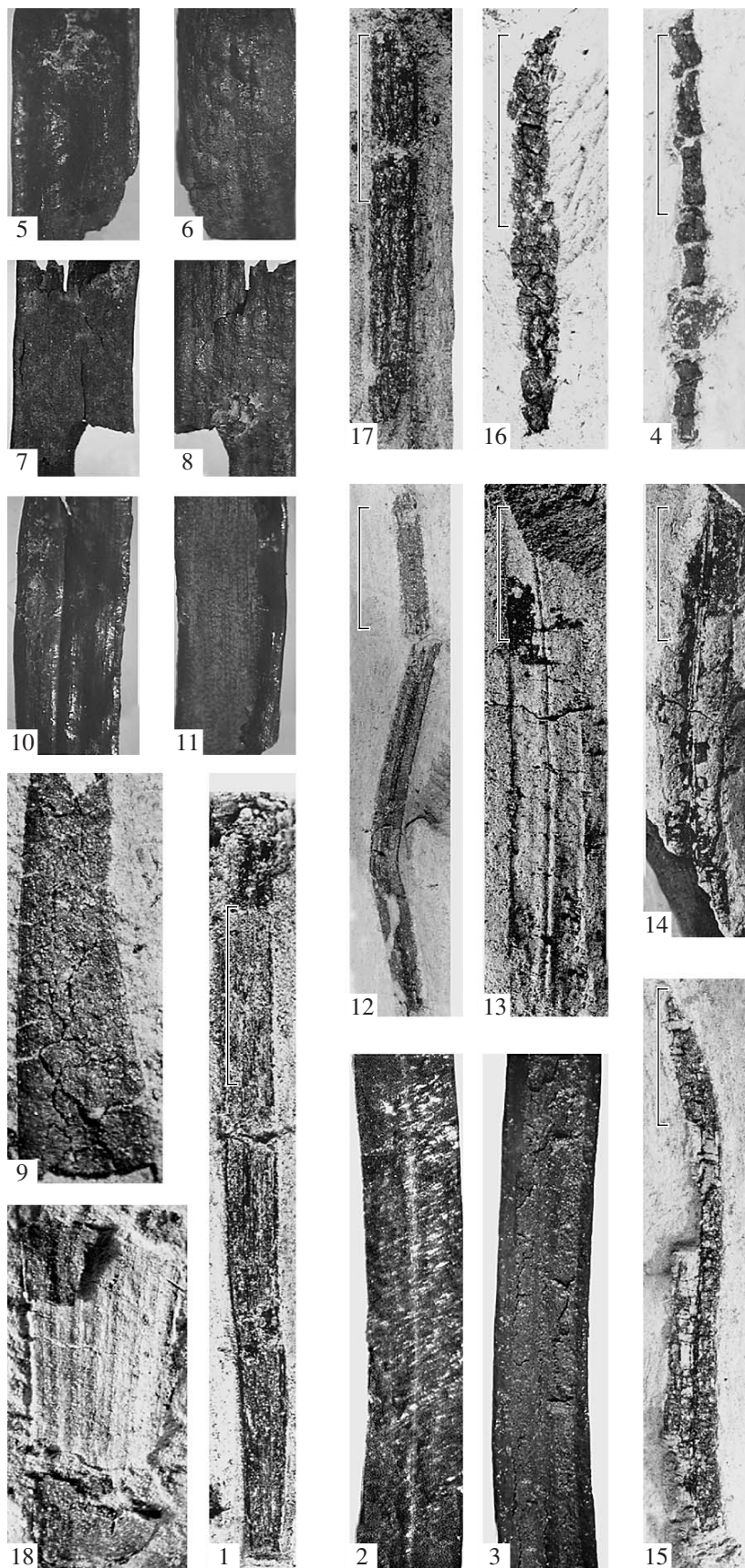
Holotype. PIN, no. 4727/410; leaf impression with a phytoleim; layer no. 1, section no. 3, Peski open mine, 1.5 km from the Peski railway station, Kolomna district, Moscow Region, Middle Jurassic, Bathonian, Meshchera horizon (Pl. 6, fig. 9).

Diagnosis. Leaflets from narrowly elliptical to narrowly obovate. Bases of leaflets wedge-shaped, apices from acute to rounded. Leaves hypostomous. Upper epidermis composed of triangular to pentagonal cells with sinuous anticlinal walls. Triangular cuticular thickenings in bends of anticlinal walls. Lower epidermis composed of amoeboid cells bearing clavate or calyptriform hollow papillae.

Description. The collection contains numerous detached leaflets of palmate leaves. Their outlines vary from narrow elliptical to narrow obovate. The bases of the leaflets are wedge-shaped. The apices are acute, falcate, up to rounded. The length of leaflets is 20–70 mm, and the width in the middle part is 5–20 mm. The venation of the lobes is pinnate-reticulate. The midrib is distinct, nearly reaching the lobe apex or, more rarely, traceable only in the lower third of the lobe. The meshes formed by anastomosing veins are elongated in

Explanation of Plate 18

Figs. 1–5. *Williamsonia* sp., PIN, no. 4727/140: (1) sterile bracts, $\times 2$; (2) epidermis topography of the upper surface of the bract, SEM; (3) papillae formed by encircling cells of a stomatal apparatus, SEM; (4, 5) stomatal apparatuses, SEM.



parallel to secondary veins and have pentagonal to heptagonal outlines. The length of the meshes is 1–5 mm, and the width is 1–2 mm.

The cuticle is relatively thin and resistant to maceration. The leaves are hypostomous. The upper epidermis is formed of triangular to pentagonal cells with sinuous anticlinal walls. Triangular thickenings are present in bends of the anticlinal walls. The cells are 20–50 µm in size, the range of undulations of the anticlinal walls is about 3 µm.

The cells of the lower epidermis are amoeboid, about 30 µm in size. Each cell bears a hollow clavate or calyptriform papilla. The length of the papillae is 20 µm, and the diameter of its base is about 7 µm. Epidermal cells of costal zones are slightly elongated along veins. Stomatal apparatuses are situated in intercostal zones and orientated irregularly. The stomata are haploheilig. The guard cells are non-sunken, bean-shaped, with a small cutin rim surrounding the aperture. The average size of stomata is 20 µm; however, some stomata are two times as large as other stomata. The larger stomata constitute about 30% of the total. The subsidiary cells of the stomata do not differ from ordinary epidermal cells.

Comparison. *S. rossica* sp. nov. is close in the leaflet morphology to *S. phyllipsii* (Brongn.) Presl (Seward, 1900) and *S. colpodes* Harris (Harris, 1964) from the Middle Jurassic of England, but differs from the former species in the sinuous anticlinal walls of the upper and lower epidermises and in the presence of papillae on cells of the lower epidermis. *S. rossica* sp. nov. differs from the latter species, which also has sinuous anticlinal walls of epidermal cells, in the presence of papillae on cells of the lower epidermis.

S. rossica sp. nov. differs from *S. hallei* Harris from Lower Jurassic of Greenland (Harris, 1964) and *S. pilosa* Barbacka (Barbacka, 1991) from the Lower Jurassic of Poland, which have papillae on ordinary cells of the lower epidermis, in the sinuous anticlinal walls. Moreover, hairs of *S. hallei* and *S. pilosa* have a base consisting of several cells.

The new species differs from *S. nilssoniana* (Brongn.) Ward and *S. undulata* Halle from the Rha-

etian–Liassic of Sweden (Halle, 1910) in the sinuous anticlinal walls, presence of papillae on ordinary epidermal cells, and absence of bases of multicellular hairs.

Papillae on ordinary epidermal cells are also present in *S. pualensis* Barbacka from the Lower Jurassic of Alaska (Barbacka et al., 2006), but the latter species differs from *S. rossica* sp. nov. in the presence of papillae on both lower and upper epidermis. In addition, bases of hairs are also present in this species.

The new species differs from *S. serrata* Harris from the Lower Jurassic of Greenland (Harris, 1932) in the smooth (without teeth) margin of the leaf lamina.

Material. Seventy-six isolated leaflets and leaflet fragments of various preservation.

Order Cycadales

Genus *Paracycas* Harris, 1964

Paracycas sp.

Plate 7, figs. 1–3

Description. The collection contains a small fragment of a simple pinnate leaf (Pl. 7, fig. 1). The leaf rachis is thin, about 0.5 mm wide. The segments are attached to the rachis laterally, at an angle of 90°. The segments are linear, basally widening and apically narrowing. The apex of the only complete segment is rounded. The segment length is 15 mm, the width at the base is 4 mm, and the width in the middle area is 2.5 mm. The segment is entered by a solitary vein reaching the segment apex.

The cuticle is thin and does not resist maceration. The leaf is hypostomous. There are two wide stomatal bands, divided by a median non-stomatal zone, which corresponds to the midrib (Pl. 7, fig. 2). The width of stomatal bands is about 250 µm; and the width on non-stomatal zone is also about 250 µm. The stomatal apparatuses are haploheilig. There are five or six subsidiary cells (Pl. 7, fig. 3). Each subsidiary cell bears a small cutinized papilla, hanging over the stomatal aperture.

Remarks. The presence of several characteristic features, such as linear segments with a solitary midrib, hypostomous leaf lamina, and haploheilig stomatal apparatuses with papillose subsidiary cells, hanging

Explanation of Plate 19

Figs. 1–6. *Tritaenia glabra* Gordenko, 2004: (1) holotype PIN, no. 4727/76, leaf, lower surface; (2, 3) PIN 4727/200, leaf fragment (upper and lower surfaces), ×7; (4) PIN, no. 4727/778, leaf fragment; (5, 6) PIN, no. 4727/602, leaf fragment, upper and lower surfaces, ×4.

Figs. 7–9. *Tritaenia striata* Gordenko, 2004: (7, 8) PIN, no. 4727/600, leaf fragment, lower and upper surfaces, ×4; (9) holotype PIN, no. 4727/368, leaf fragment, upper surface, ×4.

Figs. 10, 11. *Oswaldheeria* aff. *macrophylla* (Florin) Bose et Manum, 1990, PIN, no. 4727/603, leaf fragment, upper and lower surfaces, ×4.

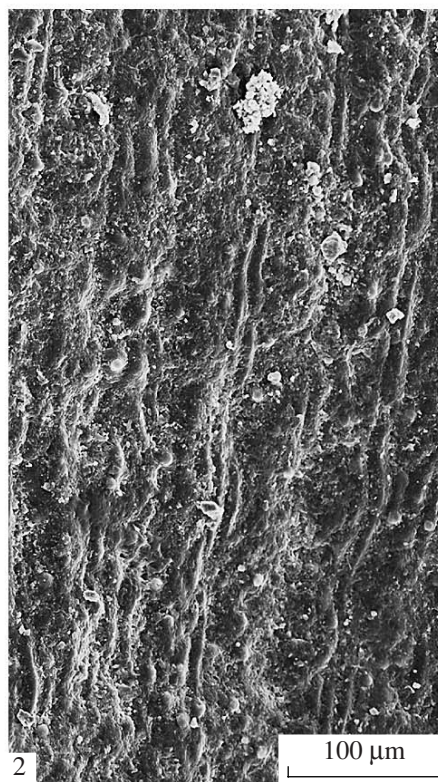
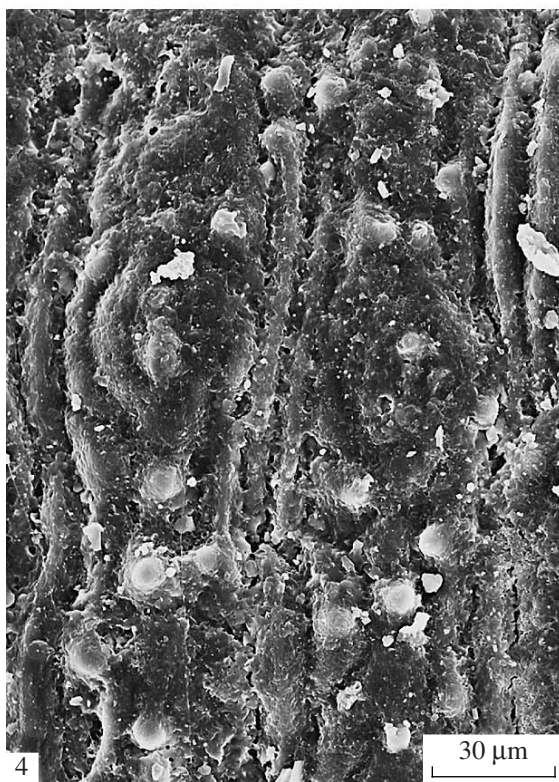
Fig. 12. *Marskea* sp., PIN, no. 4727/116, leaf fragment.

Figs. 13–15. *Cephalotaxopsis* sp.: (13) PIN, no. 4727/779, leaf fragment; (14) PIN, no. 4727/356, leaf fragment; (15) PIN, no. 4727/347, leaf fragment.

Fig. 16. *Brachyphyllum* sp., PIN, no. 4727/117, shoot fragment.

Fig. 17. *Elatocladus* sp., PIN, no. 4727/351, leaf fragment.

Figs. 1, 12–17. Scale bar 1 cm.



over guard cells, allows me to consider this specimen within the genus *Paracycas*. Unfortunately, the fragmentary state of the specimen prevents the comparison with other species of the genus.

Material. One specimen that includes an impression and phytoleim.

Order Bennettitales

Family Williamsoniaceae Carruthers, 1870

Genus *Ptilophyllum* Morris, 1840

Ptilophyllum riparium Gordenko, 1999

Plate 9, figs. 13, 14; Plate 10, figs. 1–4; Plate 11, figs. 1–5; Plate 12, figs. 1–3

Ptilophyllum riparium: Gordenko, 1999, p. 126, pl. IX, figs. 1–3.

Holotype. PIN, no. 4727/108, leaf impression with a phytoleim; layer no. 9, section no. 1, quarry Peski, 1.5 km from the Peski station, Kolomna district, Moscow Region, Middle Jurassic, Bathonian, Meshchera horizon.

Description. Leaves are elongated lanceolate, simple pinnate (Pl. 10, fig. 1; Pl. 11, fig. 1). The width of the leaf lamina is 4.5–8 mm. The rachis is smooth, 0.5–1 mm wide, narrowing toward the leaf apex. The segments are decurrent, connivent in pairs, attached to the upper surface of the rachis. They either contact with each other (do not superimpose) or are spaced about 0.3–0.5 mm apart. The basiscopic margin of the segment is situated at an angle of 45°–60° to the rachis. The acroscopic margin has an indistinct weak constriction. An auricle at the base of the basiscopic margin is lacking or very weakly developed. The acroscopic angle is about 55°–75°.

The segments are elongated, linguete, 4–5 mm long, and 1.5–2 mm wide. The bases of the segments are asymmetric, with upwardly oblique, slightly acuminate or rounded apices. The venation is nearly parallel. The veins dichotomize and slightly come apart approaching the segment apex. There are eight or nine veins per each segment.

The cuticle is thick and maceration-resistant. The lower cuticle is thicker than the upper cuticle. The leaf is hypostomous. Cells of the upper epidermis are uniform, rounded-rectangular, occasionally trapezoidal or rounded-triangular, with sinuous anticlinal walls and straight periclinal walls (Pl. 10, fig. 2). The cells are up to 50 µm wide. The range of sinuosity of the anticlinal cells is about 10 µm.

The lower epidermis is differentiated into stomatal and non-stomatal zones (Pl. 10, fig. 4). The non-stomatal zones are 90–200 µm wide (three or four cells). Cells in the non-stomatal zones are rounded-triangular, arranged in relatively distinct rows, and transversely

orientated to veins. The cells of the non-stomatal zones are 30–55 µm, the anticlinal walls are sinuous (range of sinuosity is up to 10 µm), and the periclinal walls bear peltate trichomes.

Stomatal zones are sunken in shallow grooves. These zones are 90–250 µm wide (three to five cells), 65–114 µm on average. Stomatal apparatuses are situated in one to three indistinct row and are usually transversely oriented. About 13% of the stomatal apparatuses are obliquely orientated, making an angle of 45° to the stomatal zone (Pl. 12, figs. 1, 2). The distance between stomatal apparatuses within one stomatal zone is equal to one or two cells (30–90 µm).

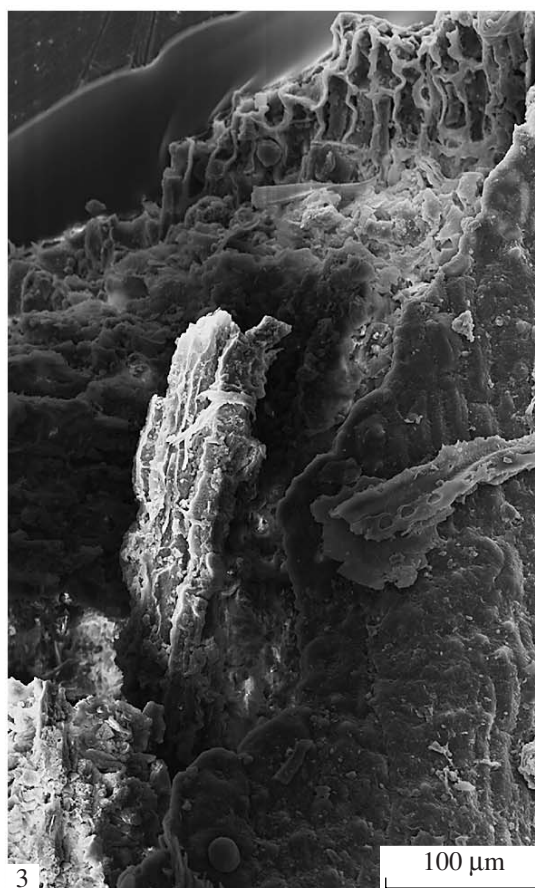
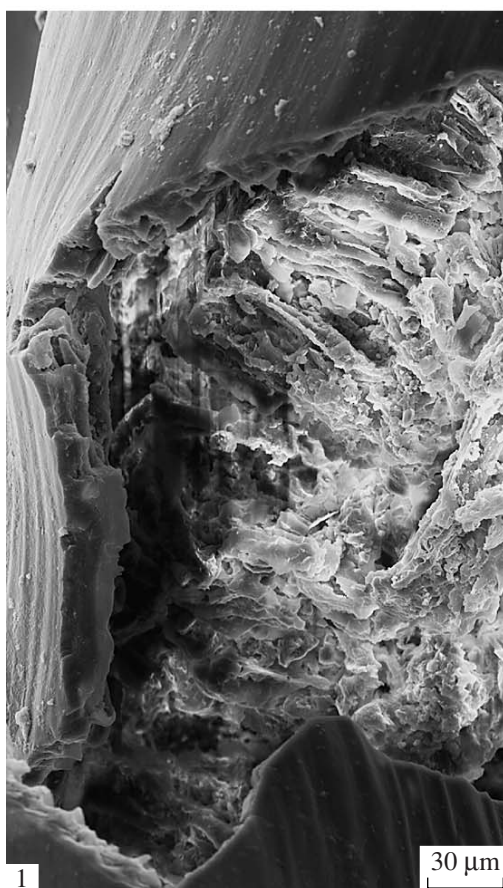
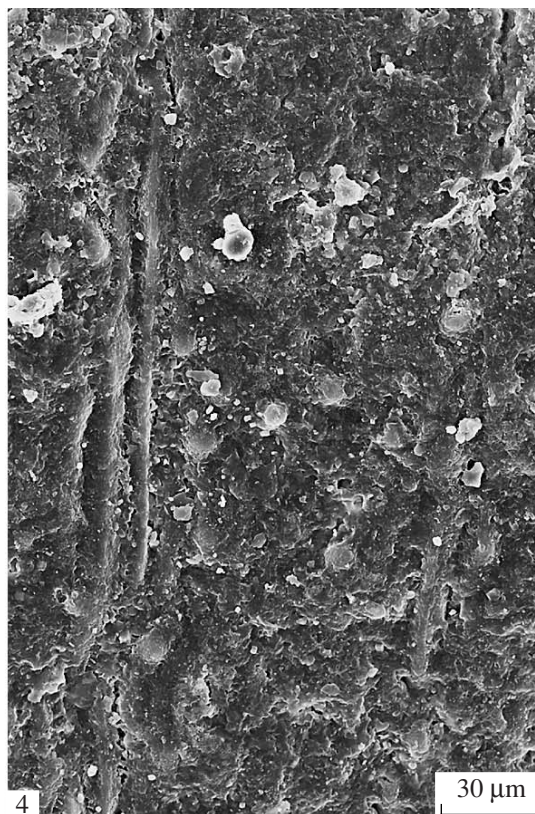
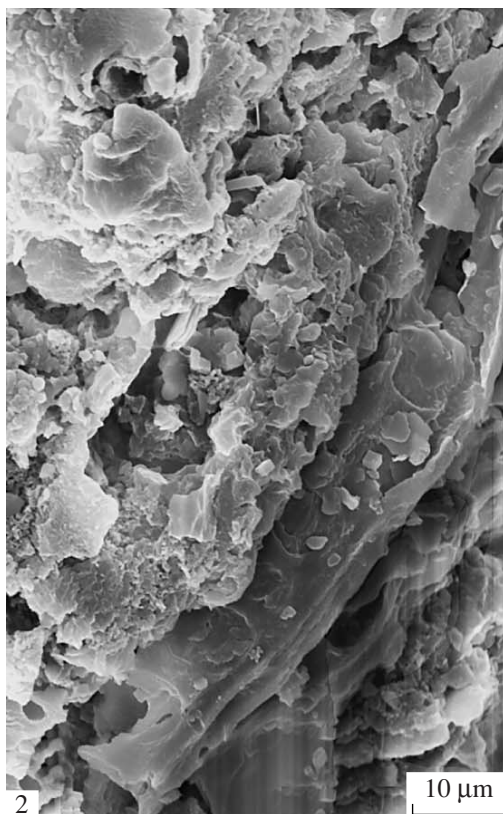
The stomatal apparatuses are syndetoheilic, 25 µm long, and 30 µm wide. The subsidiary and guard cells are bean-shaped and strongly cutinized (Pl. 12, figs. 2, 3). The subsidiary cells bear one clavate papilla with an irregularly oval base. The length of the papillae is up to 9 µm and the width of their bases is up to 5 µm. Epidermal cells laterally bordering on one of the subsidiary cells bear strongly cutinized bases of trichomes about 27 µm in diameter (Pl. 12, fig. 3). Ordinary epidermal cells of stomatal and non-stomatal zones bear peltate trichomes (up to 25 µm in diameter) with several rounded papillae on the margins of the pelta (Pl. 11, figs. 3–5). The density of the peltate trichomes varies. Trichomes are arranged in distinct longitudinal rows in the middle area of the pinnule. Contacting with their margins, they virtually hide the outlines of the epidermal cells. Marginally, the trichomes are situated less often and regular (Pl. 10, fig. 3).

Comparison and remarks. In leaf morphology, the species is close to *P. pecten*, *P. pectinoides* (Phill.) Harris, and *P. hirsutum* from the Middle Jurassic of Yorkshire (Harris, 1969), *P. cuthense* Oldham et Morris from the Lower Cretaceous of India (Bose and Dev, 1957), and *P. caucasicum* from the Callovian of Tkvarcheli coal basin of Georgia (Doludenko and Svanidze, 1964). All these species belong to one morphological group (Doludenko and Svanidze, 1964), which, in my opinion, also includes *P. riparium*. Their epidermis is characterized by strongly sinuous anticlinal cells of the upper epidermis, stomatal and non-stomatal zones, proximal papillae on subsidiary cells, and periclinal papillae on ordinary epidermal cells of stomatal zones.

By the epidermal morphology, *P. riparium* maximally resembles *P. pectinoides*, *P. caucasicum*, *P. pecten*, and *P. hirsutum*. The upper cuticle of *P. riparium* shows no significant differences from the cuticle of *P. caucasicum*, and only differs from the cuticle of *P. pecten*, *P. hirsutum*, and *P. pectinoides* in the lesser range of

Explanation of Plate 20

Figs. 1–4. *Oswaldheeria* aff. *macrophylla* (Florin) Bose et Manum, 1990, PIN, no. 4727/604: (1) leaf fragment, stomatal zone up, SEM; (2) stomatal zone fragment, SEM; (3) Florin ring over stomatal apparatuses and longitudinal striation, SEM; (4) stomatal apparatuses, dense papillae and longitudinal striation, SEM.



sinuosity of cellular walls. The lower cuticle shows more significant dissimilarities. Within stomatal zones, stomata are situated in one or two, or, more rarely, in three rows in *P. riparium*, and in two or three rows in *P. pecten*, *P. caucasicum*, and other related species (Doludenko and Svanidze, 1964; Harris, 1969). *P. riparium* has slightly smaller papillae, which do not contact over the stomatal apertures, as in *P. pecten* and *P. caucasicum*.

The sharpest distinctions are the size and shape of trichomes on the lower cuticle, cutinization of the anticlinal cells of the lower epidermis, and the arrangement of rounded bases of trichomes contacting with subsidiary cells, a feature typical of the new species. In *P. riparium*, cells bearing trichome bases adjoin subsidiary cells of stomata on one side or, more rarely, on both sides (Pl. 12, fig. 3). This arrangement of hair bases seems quite predictable. The comparison between *P. riparium* and related species shows that trichomes of *P. riparium* maximally resemble those of *P. caucasicum*. However, trichomes of the latter species fuse with each other within a row. Trichomes of *P. pecten* are hollow dome- or mushroom-shaped papillae, situated on ordinary epidermal cells of stomatal and non-stomatal zones. In *P. hirsutum*, papillae on epidermal cells vary in shape from conical and dome-shaped to mushroom-shaped. They nearly completely cover the epidermal cells. *P. pectinoides* and *P. riparium* are similar in having circular bases of trichomes; however, trichomes are rarely present on the boundary with subsidiary cells in the former species, but it is a characteristic feature of the latter species. In addition, no peltate trichomes were found in the latter species.

In *P. pectinoides*, anticlinal walls of cells at the boundary between rows are cutinized stronger than those within the row. Longitudinal thickenings of cells form ribs on the inner cuticle surface; such striation is lacking in other related species.

Bose and Dev (1957) reported that the morphologically close species *P. cuthense* is characterized by two or three papillae on cells of stomatal and non-stomatal zones (however, it should be pointed out that the microstructure of type specimens of this species was not studied).

Another dissimilarity is that stomata of the lower cuticle of *P. riparium* are situated in distinct zones, whereas no zonation is observed in *P. hirsutum*, and only indistinct zonation is expressed in *P. pectinoides*.

P. choshiense Kimura, Okubo et Miyahashi from the Lower Cretaceous of Japan also has some morphological features in common with the new species. However, the cuticle structure shows remarkable differences. The Japanese species is characterized by an irregular distri-

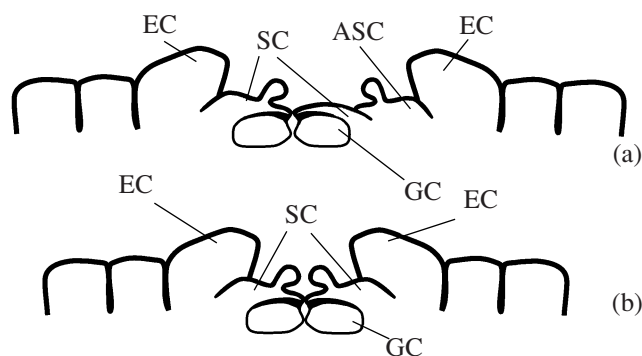


Fig. 6. Schematic reconstruction of a transverse section through a stomatal apparatus: (a) *Otozamites paradoxus*, sp. nov.; (b) *Otozamites* sp.; (GC) guard cells; (SC) subsidiary cells; (ASC) additional subsidiary cell; (EC) encircling cells.

bution of stomata and by intercellular trichomes of a different shape (Kimura et al., 1991). The European Lower Cretaceous species are characterized by a similar arrangement of stomata and trichomes (Watson and Sincok, 1992).

Occurrence. Type locality.

Material. Five incomplete leaves (impressions and phytoteleims).

Genus *Otozamites* Braun, 1842

Otozamites paradoxus Gordenko, sp. nov.

Plate 8, figs. 1, 4–8; Plate 9, figs. 2, 5; Plate 13, figs. 1–5;
Plate 14, figs. 1, 2; Plate 15, fig. 2

E t y m o l o g y. From the Latin *paradoxus* (contraversional).

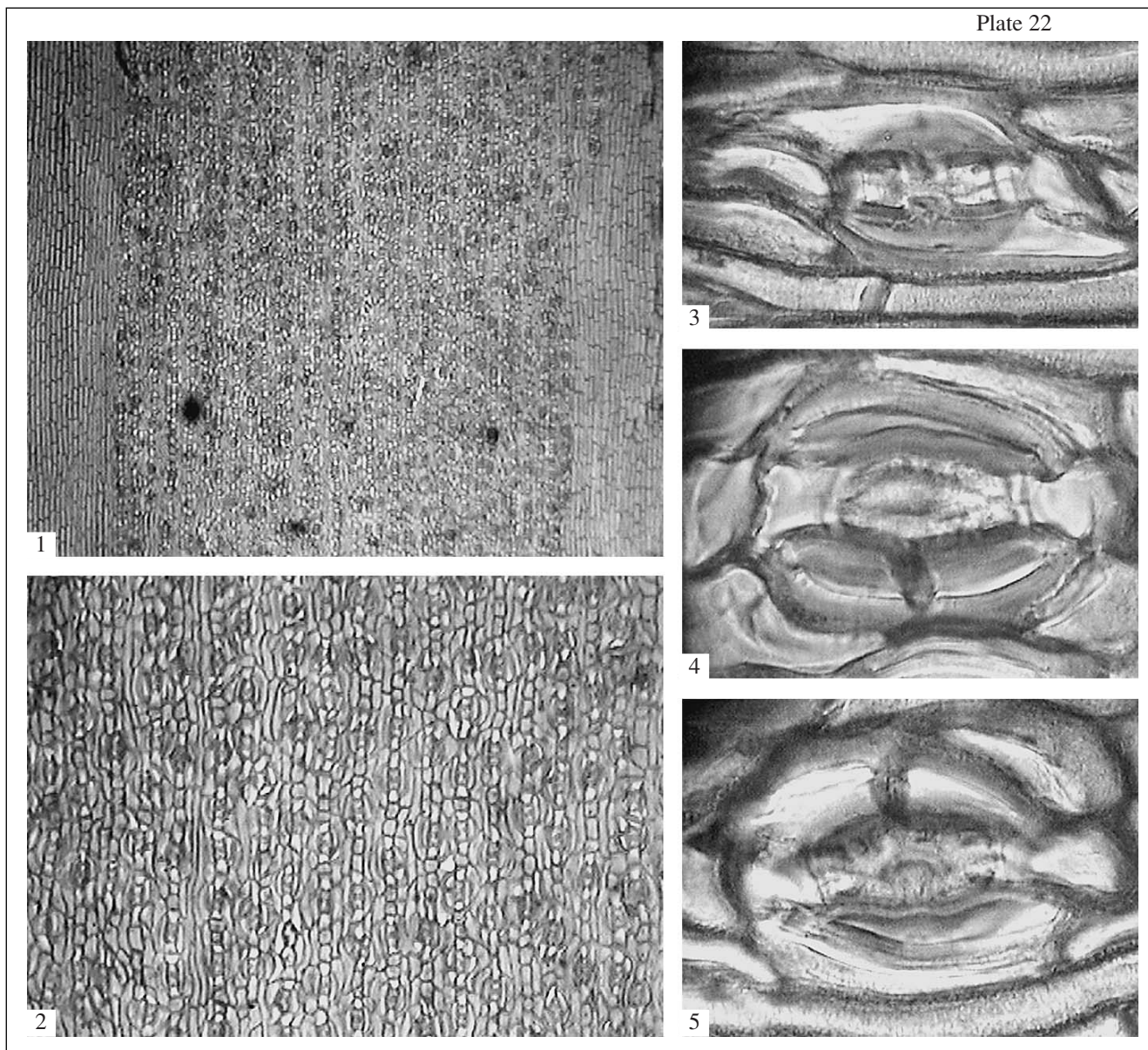
H o l o t y p e. PIN, no. 4727/107, leaf impression with a phytoteleim, layer no. 9, section no. 1, quarry Peski, 1.5 km from the Peski station, Kolomna district, Moscow Region, Middle Jurassic, Bathonian, Meshchera horizon (Pl. 8, fig. 4).

D i a g n o s i s. Leaves once-pinnate, pinnae linguulate with auricles at base of acroscopic margin. Pinnae are attached to rachis laterally, arising at acute angle. Upper cuticle lacking both stomata and trichomes. Lower cuticle without trichomes. Stomata in one to four indistinct files per intercostal stomatal zone, syndetoheilic. Subsidiary cells with papillae. Stomatal pit covered with epidermal cells which form dome-shaped roof with stellate hole. Ordinary epidermal cells of upper and lower epidermis without trichomes.

D e s c r i p t i o n (Fig. 6a). Leaves are once-pinnate, with a thin rachis (Pl. 8, figs. 1, 4, 7). The width of the rachis is usually less than 1 mm. Segments are

Explanation of Plate 21

Figs. 1–4. *Oswaldheeria* aff. *macrophylla* (Florin) Bose et Manum, 1990, PIN, no. 4727/604: (1) sclerified palisade mesophyll is visible, SEM; (2) tracheid of a vascular bundle with bordered pits, SEM; (3) vascular bundle, SEM; (4) dense papillae of marginal areas of the leaf, SEM.



Explanation of Plate 22

Figs. 1–5. *Oswaldtheeria* aff. *macrophylla* (Florin) Bose et Manum, 1990, PIN, no. 4727/603; (1) stomatal zone, $\times 45$, (2) fragment of a stomatal zone, $\times 150$; (3–5) stomatal apparatuses, note papillae on subsidiary cells.

attached to the rachis laterally, at an angle of 70° – 90° . The segments are linguete and slightly curved. Their apices are oblique toward the acroscopic margin and slightly rounded (Pl. 8, figs. 1, 7). The average length of the segments is 10 mm. The width of the segment in the middle area is 3 mm and 1 mm at the base. Basally, the segment bears a round auricle on the acroscopic side; on the basiscopic side the segment is rounded (Pl. 8, fig. 5). The average width of the segment near auricle is 4 mm. The venation is fan-shaped dichotomizing (Pl. 8, fig. 6). The veins dichotomize two or three times and disappear slightly before the leaf margin. The segments

are connivent in pairs, not contacting with each other. The average distance between adjacent is 2 mm.

The leaf is hypostomous. The cuticle is thick and resistant to maceration. The lower cuticle is thicker than the upper cuticle.

The upper epidermis has isodiametric or nearly isodiametric cells with sinuous anticlinal walls (Pl. 13, fig. 2). The cells are 30–40 μm . The sinuosity range is about 15 μm . Trichomes are lacking.

The cuticle of the lower epidermis is subdivided into stomatal and non-stomatal zones (Pl. 9, fig. 2; Pl. 13, figs. 1, 3, 4). The stomatal zones are intercostal. Ordi-

nary cells of the lower epidermis are nearly isodiametric, occasionally slightly elongated in longitudinal direction, with thick and slightly sinuous walls. The average size of ordinary cells is 45–50 μm . The sinuosity range of the anticlinal walls is 5–15 μm . Trichomes are lacking.

Stomatal apparatuses are syndetoheilic, transversely orientated, situated in one to three or, more rarely, four longitudinal rows within a stomatal zone (Pl. 9, fig. 2; Pl. 13, figs. 1, 3, 5). The distance between stomatal apparatuses within a stomatal zone is 30–90 μm (one to three cells). The guard cells of the stomatal apparatuses are bean-shaped. Subsidiary cells bear one clavate papillae (Pl. 15, fig. 2). The height of the papillae is 8–10 μm , and the diameter is 6 μm at the base. In most stomata, a subsidiary cell that is situated closer to the base of the segment is divided into two cells, in parallel to the orientation of the stomatal apparatus. In this case, a papillae is present not on a cell contacting with the guard cells, but on the next lateral encircling cell (Pl. 14, figs. 1, 2; Fig. 6a). This encircling cell has the same mother cell as guard and subsidiary cells have. Encircling cells hang over the stomatal apparatus forming a conical elevation 10–15 μm high, which protects the stomatal aperture. There are six or, more rarely, five or seven encircling cells. These encircling cells have a different ontogenesis than lateral encircling cell: they are specialized epidermal cells. Proximal margins of the encircling cells form an opening over the stomata and bear dense papillae (Pl. 8, fig. 8).

Comparison. *O. paradoxus* sp. nov. is closest to *O. simpsoni* Harris from the Middle Jurassic of Yorkshire (Harris, 1969) in the leaf morphology, but differs in the morphology of the epidermis. A considerable morphological similarity is also observed between some other European species; however, the morphology of the lower epidermis is very different. In *O. paradoxus* sp. nov., cells of the lower epidermis lack trichomes, whereas other members of this genus bear hollow papillae and rounded hair bases. In addition, the species under description is characterized by the presence of clavate papillae on subsidiary cells of stomatal apparatuses, that is untypical of the genus *Otozamites*. This feature was not observed in other European members of the genus.

The epidermal morphology of the species significantly resembles *O. pulcher* from the Lower–Middle Jurassic of Iran (Barnard and Miller, 1976; Schweitzer and Kirchner, 2003). The latter has encircling cells hanging over stomatal apparatuses and papillae on subsidiary cells. Unlike *O. paradoxus* sp. nov., *O. pulcher* has small hollow papillae on ordinary epidermal cells. One more characteristic feature of *O. paradoxus* sp. nov. is an additional lateral cell, resulted from the division of a subsidiary cell. Segments of *O. pulcher* are more elongated than those of *O. paradoxus* sp. nov.

Material. Five incomplete leaves with phytoliteims.

Otozamites sp.

Pl. 8, figs. 2, 3; Pl. 9, figs. 1, 3, 4; Pl. 15, figs. 1, 3–5

Description. The leaf is simple pinnate. The rachis is narrow, smooth, 2 mm wide. The segments are connivent in pairs, not contacting. The segments are tongue-shaped, up to 10 mm long, and up to 6 mm wide in the middle area of the segment (Pl. 8, figs. 2, 3). A small auricle is present at the base of the acroscopic margin. The apices of the segments are rounded, slightly oblique toward the acroscopic margin. The basiscopic and acroscopic margins are slightly constricted at the base. The venation is fan-shaped-dichotomous. The veins dichotomize one to three times reaching the leaf margin.

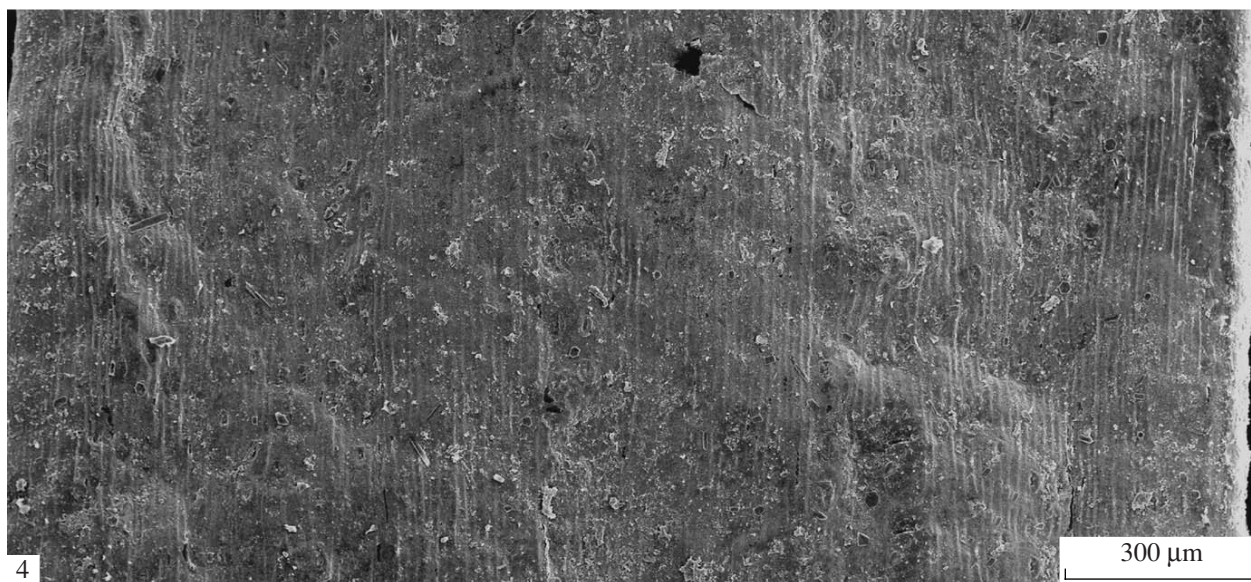
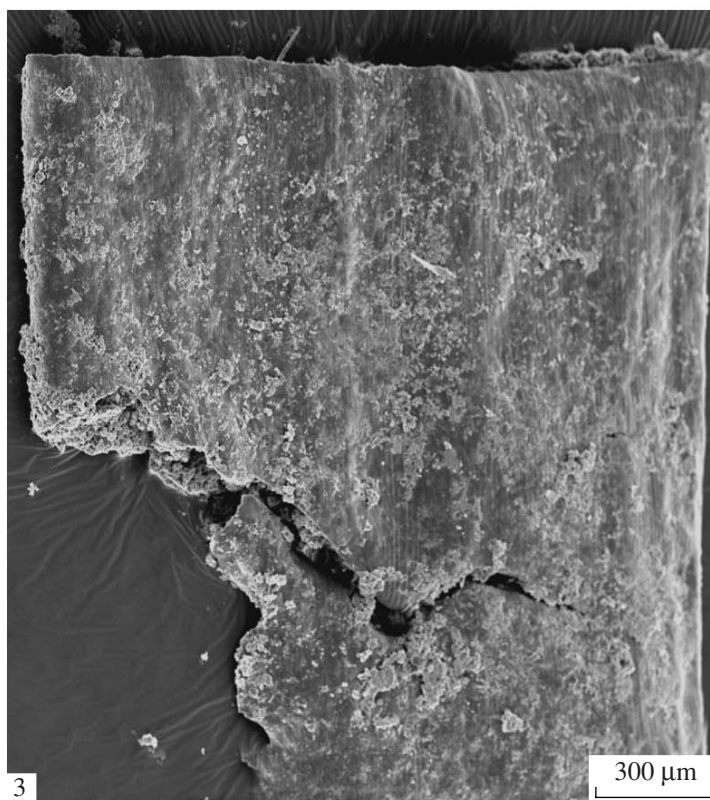
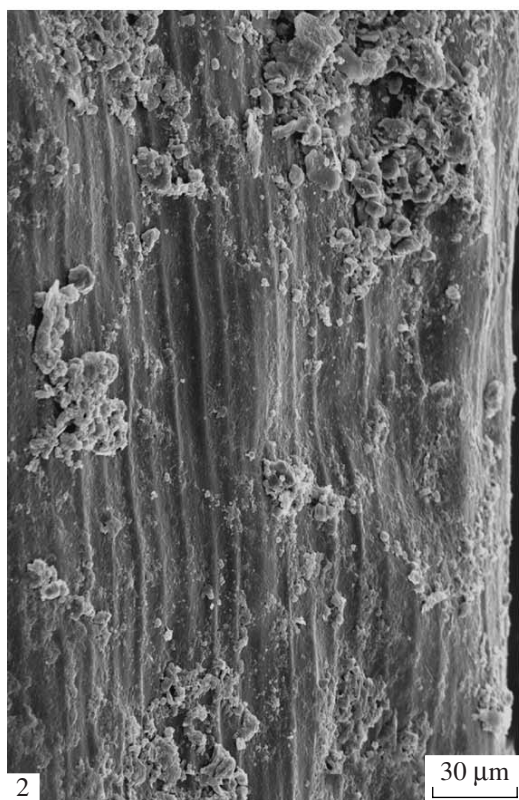
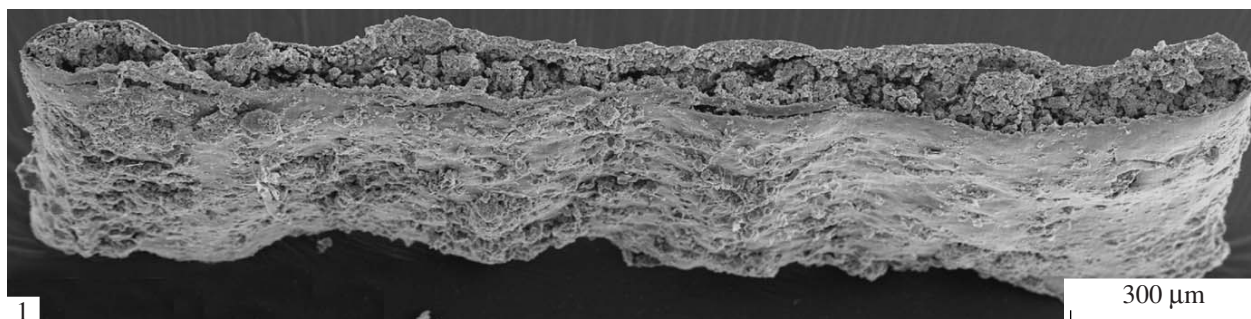
The cuticle is thick and maceration-resistant. The leaf is hypostomous. Cells of the upper epidermis are nearly isodiametric, with strongly sinuous anticlinal walls. They do not form rows. The cells are 30–40 μm in size; the range of sinuosity is 10–15 μm . Trichomes are lacking.

The cuticle of the lower epidermis is subdivided into stomatal and non-stomatal zones (Pl. 9, fig. 1).

Ordinary cells of the lower epidermis show no regular arrangement. Their outlines are irregularly tetragonal; the anticlinal walls are strongly cutinized. The sizes of the ordinary epidermal cells vary from 15 to 40 μm . The range of sinuosity of the walls is 5–10 μm .

The stomatal apparatuses are syndetoheilic, deeply sunken under the cuticle surface (Pl. 9, figs. 3, 4; Pl. 15, figs. 3–5). The guard and subsidiary cells are strongly cutinized. The subsidiary cells bear hollow clavate papillae (Pl. 15, figs. 3–5). On average, the papilla is 6 μm in diameter at its base and 8–9 μm in height. On average, the stomatal apparatuses are 53–60 μm wide and 33 μm long. They form one to three indistinct rows within a stomatal zone. Within a row, the distance between stomata is one to three cells. The stomatal apparatuses occupy about 40% of the surface of the lower epidermis. The stomatal apparatuses are surrounded by encircling cells, which form over them conical elevations 15–20 μm high (Pl. 9, figs. 1, 3, 4; Pl. 15, figs. 1, 3, 5).

Comparison. The specimen is closest to *O. paradoxus* sp. nov. by the epidermal morphology. However, *O. paradoxus* sp. nov. is characterized by the presence of stomatal apparatuses with an additional papilla-bearing subsidiary cell, resulted from the division of a subsidiary cell into two cells. Such stomatal apparatuses were not found in *Otozamites* sp. One might have supposed that such leaves are variations of *O. paradoxus* sp. nov., but the two species have different segment outlines. The former has tongue-shaped and wide segments with a rounded apex and a poorly defined auricle. The latter has narrow and long segments with an acuminate apex and a distinct auricle at the base. The material is too fragmentary to describe a new species, and the specimen is considered in open nomenclature.



Material. One incomplete leaf, represented by a phytoleim, impression, and the counterpart.

Genus *Anomozamites* Schimper, 1870

Anomozamites aff. *minor* (Brongniart) Nathorst, 1878

Plate 8, fig. 10; Plate 16, figs. 4, 5

Description. The fragmentary leaf is lanceolate and simple pinnate, about 20 mm wide (Pl. 8, fig. 10). Only the middle part of the leaf is preserved. The rachis is distinct, 0.8 mm wide.

The segments are attached to the upper side of the rachis. They are nearly square, entire-margined, and 10 mm long. Basally, they become slightly wider, from both acroscopic and basiscopic margins. The angles of segments that are off the rachis are slightly rounded. The segmentation is regular. The distances between the segments are 1–1.5 mm, widened bases of the segments can contact. The segment venation is parallel. There are 18–20 veins in each segment. The distance between veins is about 0.5 mm. The basiscopic and acroscopic angles of the segments are 90°.

The leaf is hypostomous. The cuticle of the upper epidermis is relatively thin: 1–1.5 µm. Ordinary cells of the upper epidermis vary from rounded-square to rounded-rectangular. Their sizes are 30–50 µm. The anticlinal walls are sinuous; the curves are sharp, forming a polygonal, not undulate curve. The sinuosity range is 5–7 µm. No trichomes are present on cells of the upper epidermis.

The cuticle of the lower epidermis is thicker than the cuticle of the upper epidermis (2 µm) and is resistant to maceration. It is subdivided into narrow non-stomatal (costal) and wide stomatal (intercostal) zones. Cells within the stomatal zone are irregularly arranged and orientated (Pl. 16, fig. 5). They are rounded-tetragonal or oval, with sinuous anticlinal walls. The sinuosity range of the anticlinal walls is 6–7 µm. Trichomes are lacking.

The stomatal apparatuses do not form rows within the stomatal zone. The width of the stomatal zone is 12–14 cells (500–600 µm). The stomatal apparatuses are syndetoheilig. The strongly cutinized guard cells are wings-shaped. The subsidiary cells are also relatively strongly cutinized. The average width of the stomatal apparatuses is 40 µm, and the length is 30–34 µm. The width without subsidiary cells is 26 µm. Occasionally, groups of stomatal apparatuses are present sharing adjacent subsidiary cells. The stomatal apparatuses occupy about 40% of the surface of the lower epidermis.

Comparison and remarks. The leaf is closest by the outlines and sizes of the segments to *A. ishpushtensis* Schweitzer et Kirchner from the Bajocian–Bathonian of Iran (Schweitzer and Kirchner, 2003), *A. nillsoni* (Phill.) Sew. and *A. thomasi* Harris from the Middle Jurassic of Yorkshire (Harris, 1969), *A. quadratus* Prosviriakova from the Jurassic of Mangyshlak in Kazakhstan (Prosviriakova, 1966), *A. elegans* Orlovskaja from the Lower Jurassic of Karatau Range in southern Kazakhstan (Doludenko and Orlovskaja, 1976), *A. embensis* Kiritchkova from the Middle Jurassic of western Kazakhstan (Baranova et al., 1975), and *A. minor* (Brongn.) Nath. from the Upper Triassic of Sweden (Nathorst, 1878). No data on the epidermal morphology are available for *A. quadratus* and *A. elegans*. *A. embensis* has cells of the lower epidermis with indistinct papillae; and its anticlinal walls of the upper epidermis have omega-shaped sinuosity. *A. ishpushtensis* and *A. nillsoni* have rounded trichomes on the lower epidermis. In addition, *A. thomasi* has rounded hollow central papillae on ordinary epidermal cells. By contrast, the leaf from the Peski locality lacks both trichomes and papillae. *A. minor* shows a considerable similarity to the leaf from the Peski locality by the epidermal morphology; however, unlike *A. minor*, segments of the Peski leaf do not become wider toward the base.

The epidermal morphology of the leaf is close to that of *A. angulatus* Heer from the Upper Jurassic of the Amur River (Heer, 1876) and *A. pterophylloides* Kiritchkova from the Middle Jurassic of western Kazakhstan (Baranova et al., 1975); however, the specimen differs from the above species by leaf morphology. The leaf under description has veins deviating from the rachis at an angle of 90° and nearly square segments. *A. angulatus* has rectangular segments with rounded apices and veins deviating from the rachis at an angle of 70°. *A. pterophylloides* has much narrower segments. The specimens from the Peski locality lack papillae; curves of the anticlinal walls of the upper epidermis form a polygonal, not undulate curve.

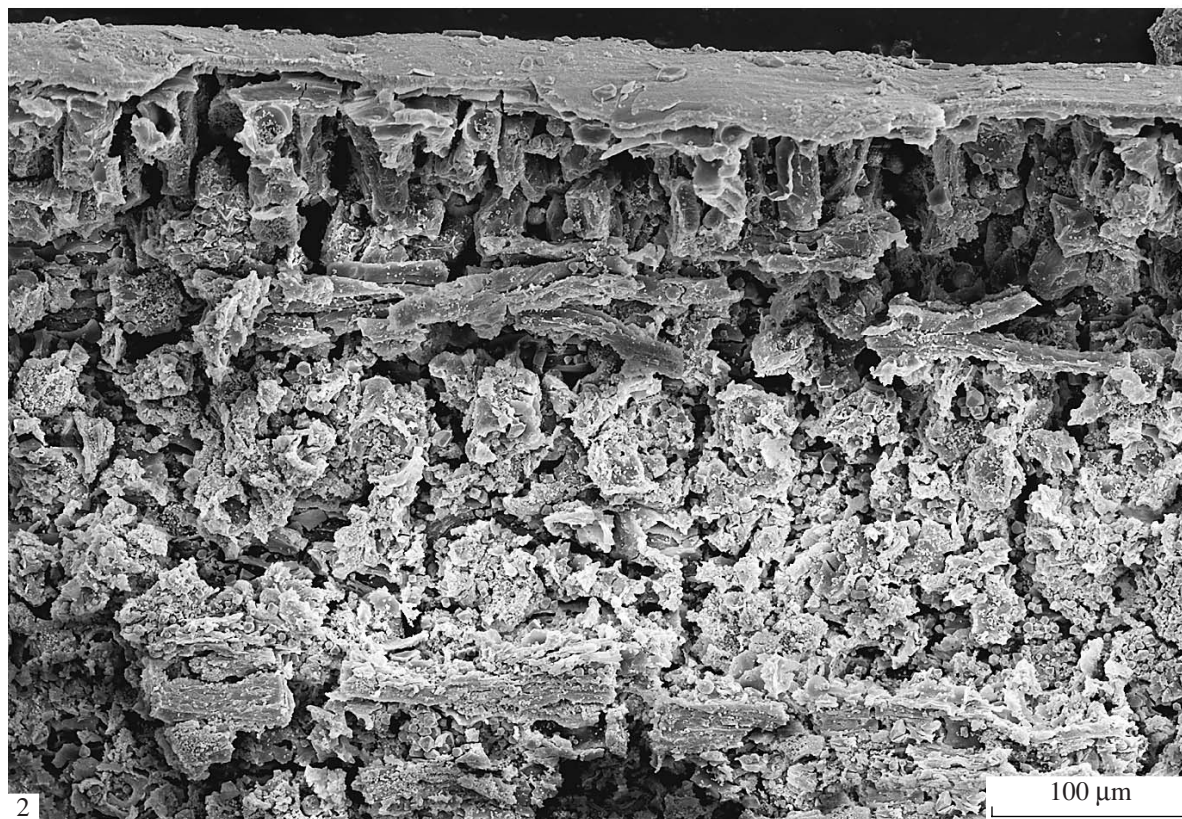
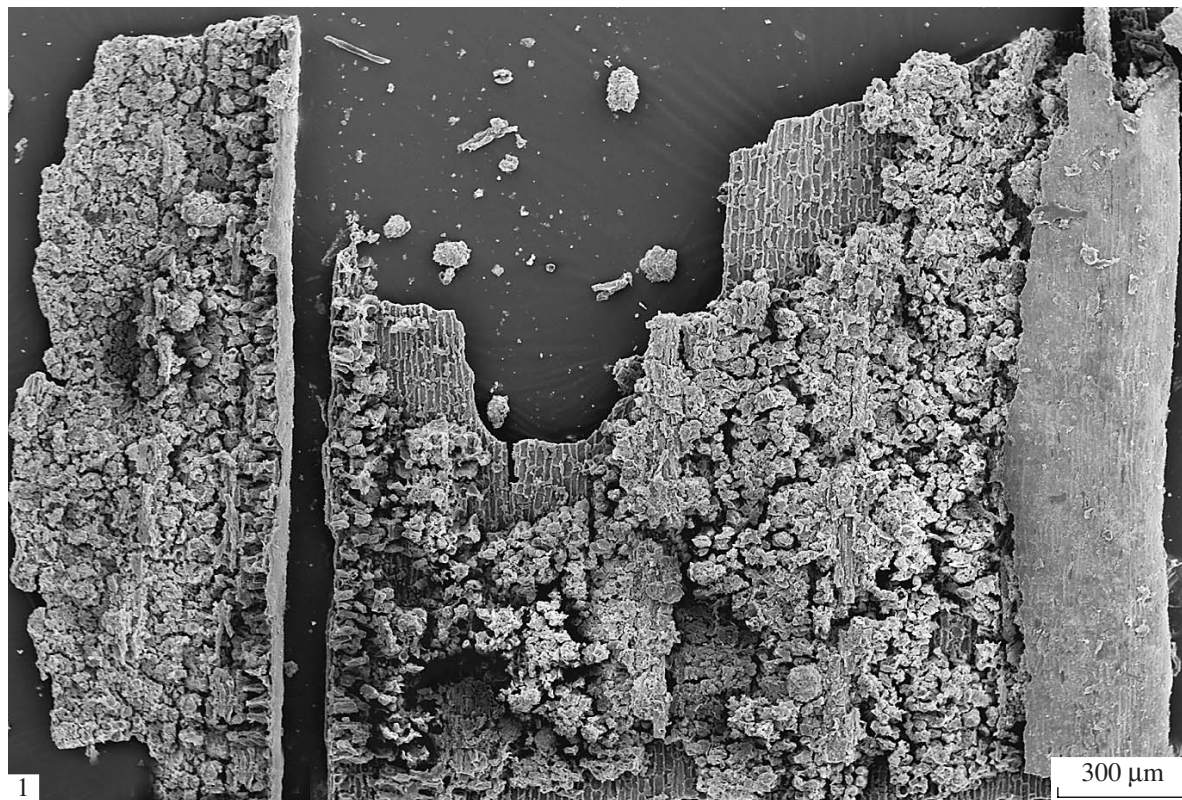
The specimens markedly differ from other species of this genus in the segment outlines and epidermal morphology. The other species are characterized by narrower rectangular (not square) segments and the cuticle of the lower epidermis with rounded bases of numerous hairs.

As the specimens under description only differ from *A. minor* in the widened base of segments, I consider them in open nomenclature as *Anomozamites* aff. *minor*.

Material. Two specimens represented by an imprint, counterpart, and a phytoleim and by imprint and a phytoleim of a detached segment.

Explanation of Plate 23

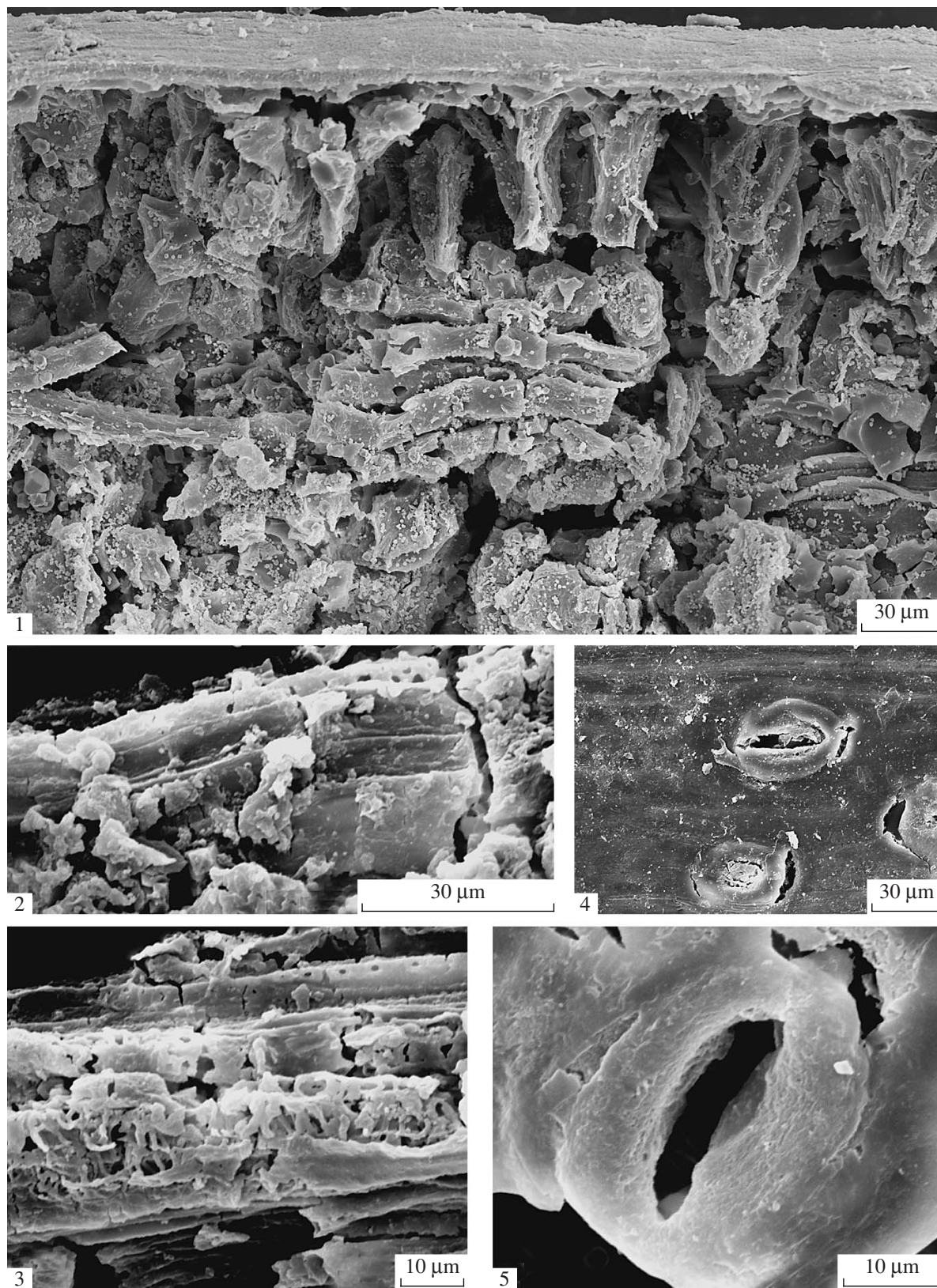
Figs. 1–4. *Tritaenia glabra* Gordenko, 2004, PIN, no. 4727/200: (1) transverse section of leaf, SEM; (2) longitudinal striation in the marginal zone of leaf, SEM; (3) fragment of the upper side of leaf, four veins are visible, SEM; (4) fragment of the lower surface of leaf, note three stomatal bands, SEM.



Explanation of Plate 24

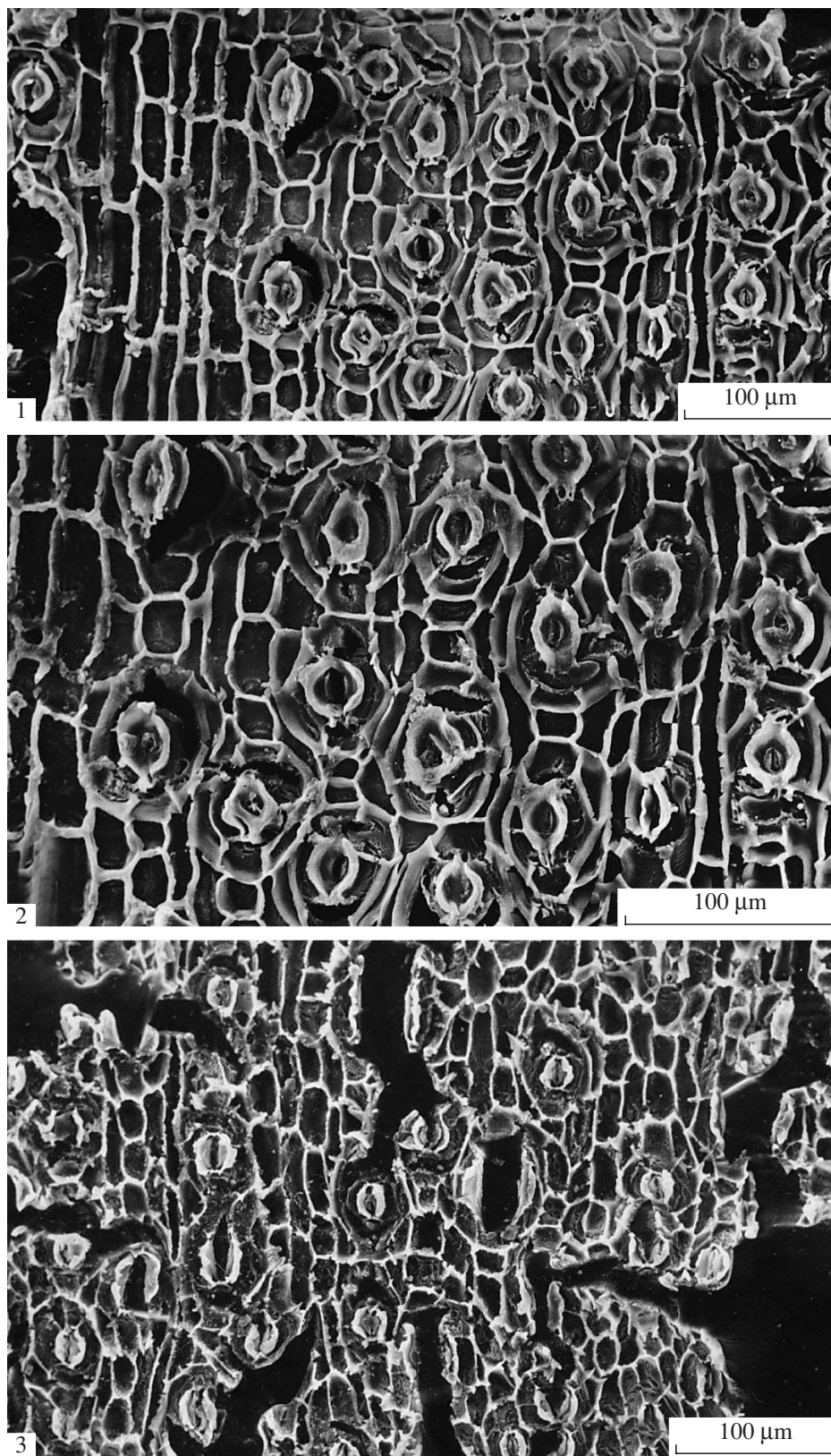
Figs. 1, 2. *Tritaenia glabra* Gordenko, 2004, PIN, no. 4727/200: (1) epidermis is removed to show vascular bundles and resin canals, SEM; (2) vascular bundle (below) and resin canal (above), sunken in mesophyll, SEM.

Plate 25



Explanation of Plate 25

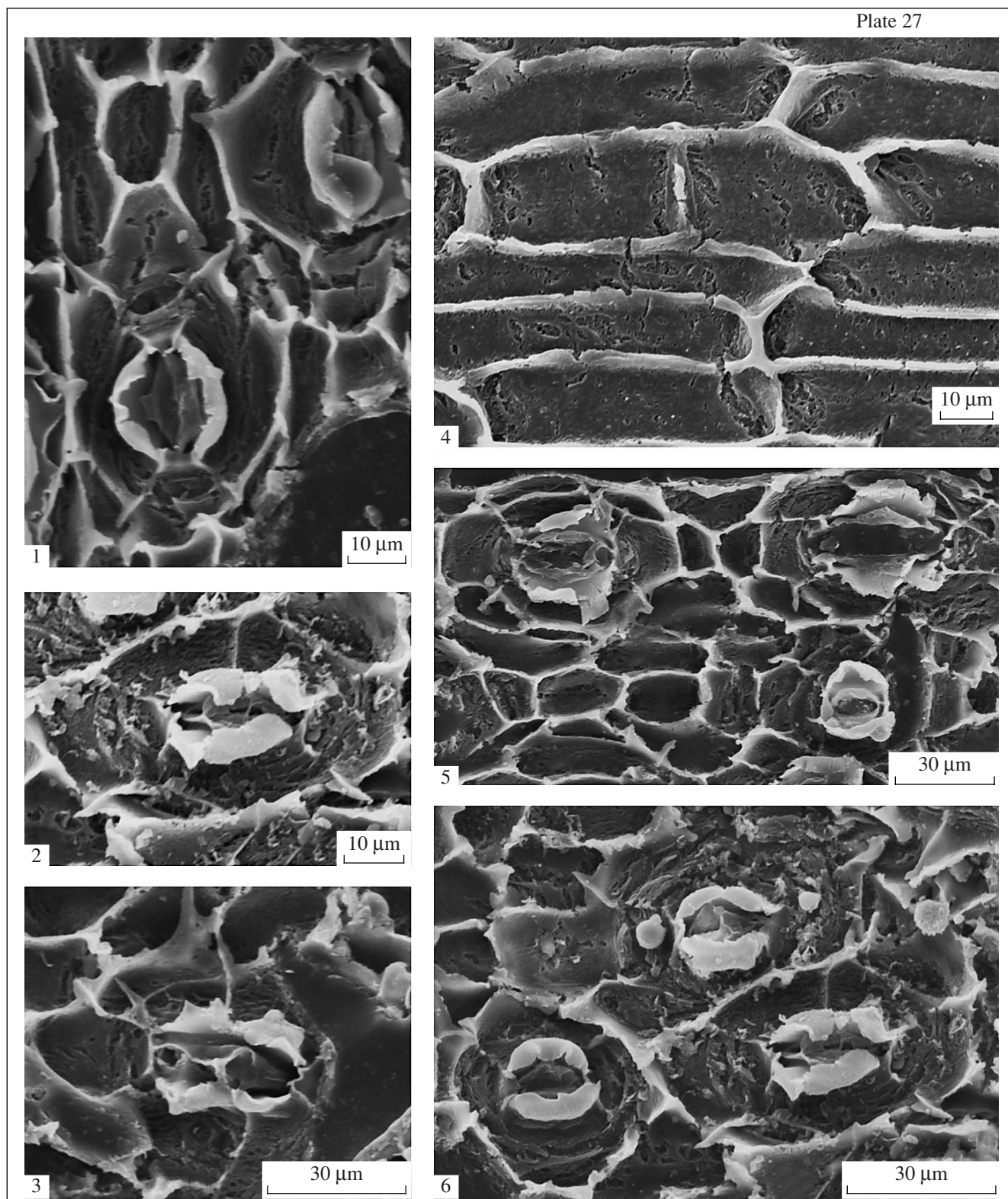
Figs. 1–5. *Tritaenia glabra* Gordenko, 2004: (1) PIN, no. 4727/200, sclerified cells of palisade mesophyll, hanging over a fragmentary resin canal, SEM; (2–5) PIN 4727/26; (2, 3) details of a vascular bundle, pitted tracheids are visible, SEM; (4, 5) Florin rings over stomatal apparatuses, SEM.



Explanation of Plate 26

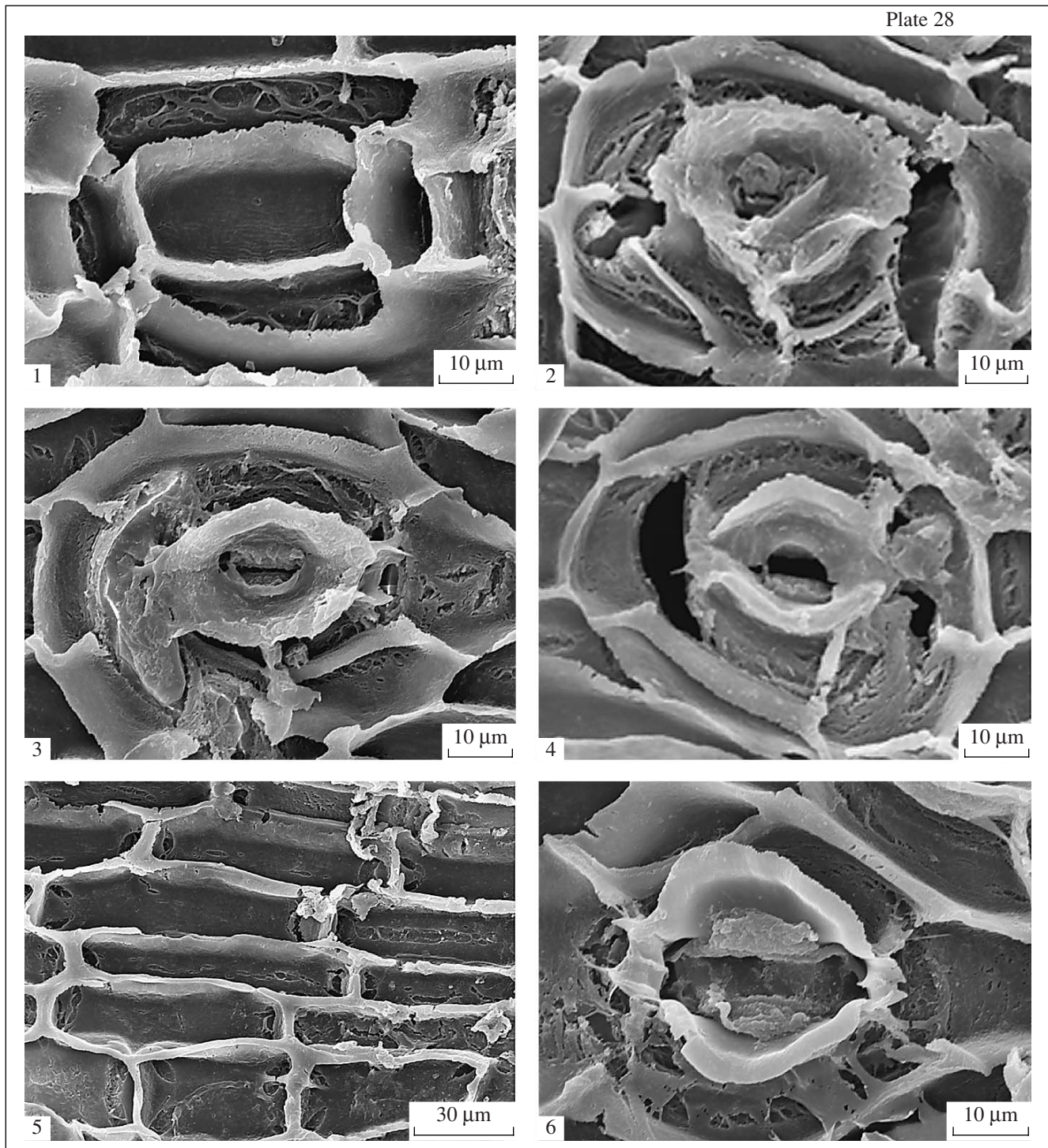
Figs. 1–3. *Tritaenia glabra* Gordenko, 2004: (1, 2) PIN, no. 42727/200; (1) epidermis topography, SEM; (2) stomatal band, SEM; (3) holotype PIN, no. 4727/76, stomatal band, SEM.

Plate 27



Explanation of Plate 27

Figs. 1–6. *Tritaenia glabra* Gordenko, 2004, holotype PIN, no. 4727/76: (1, 5, 6) fragments of a stomatal band, SEM; (2) normal stomatal apparatus, SEM; (3) abnormal (double) stomatal apparatus, SEM; (4) fragment of a non-stomatal band, SEM.



Explanation of Plate 28

Figs. 1–6. *Tritaenia glabra* Gordenko, 2004, PIN, no. 4727/200: (1) developing stomatal apparatus, SEM; (2–4, 6) stomatal apparatuses, SEM; (5) fragment of a non-stomatal band, SEM.

Genus *Nilssoniopteris* Nathorst, 1909

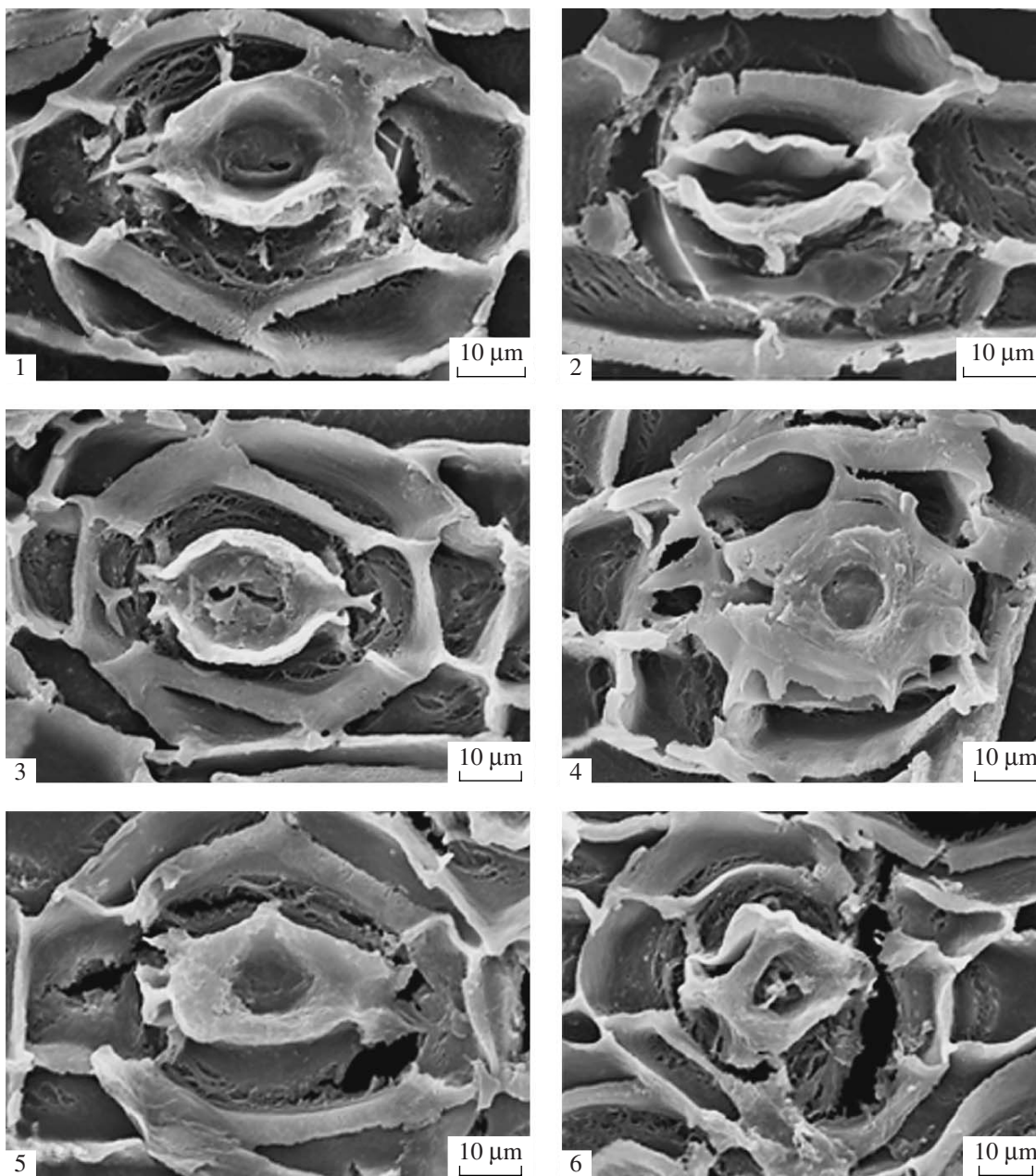
Nilssoniopteris infera Gordenko, sp. nov.

Plate 8, fig. 11; Plate 9, figs. 6–9; Plate 17, figs. 4–6

Etymology. From the Latin *inferus* (situated below).

Holotype. PIN, no. 4727/352, leaf impression with a phytolite, layer no. 4, section no. 3, Peski open mine, 1.5 km from the Peski railway station, Kolomna district, Moscow Region, Middle Jurassic, Bathonian, Meshchera horizon.

Plate 29



Explanation of Plate 29

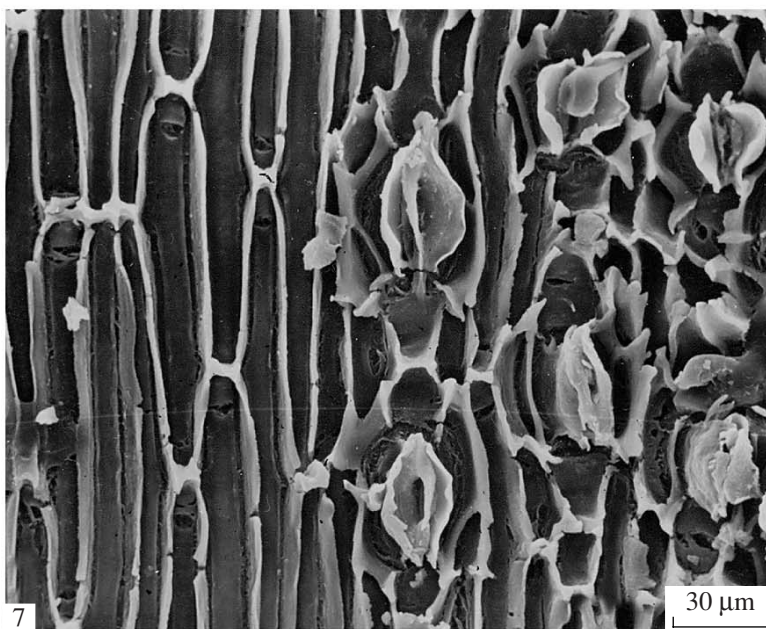
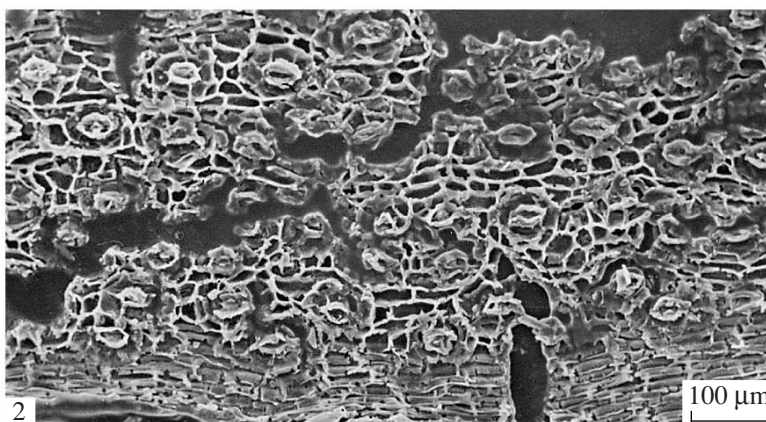
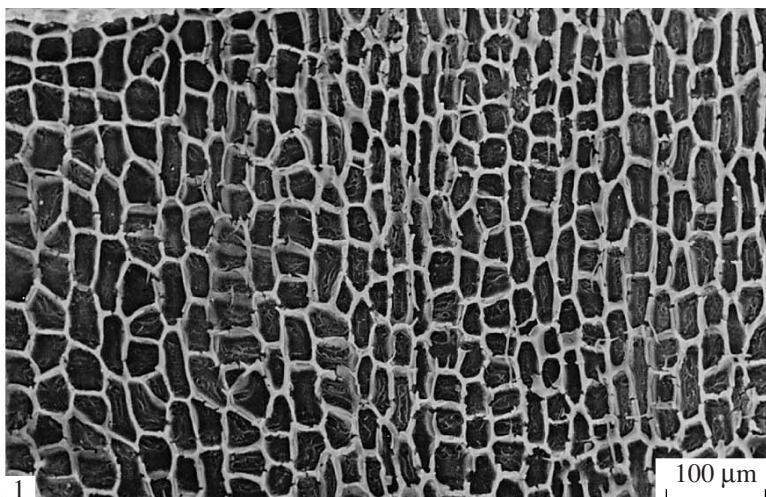
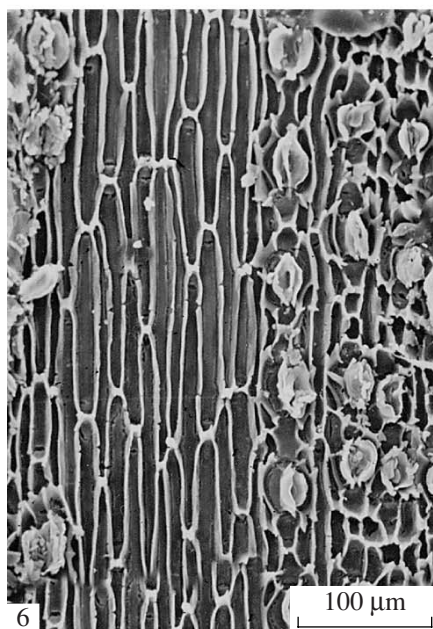
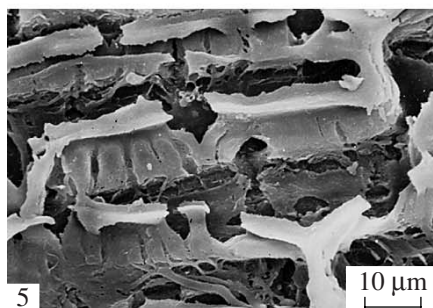
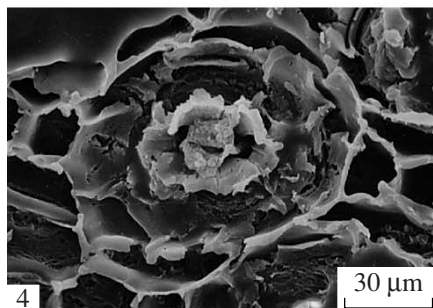
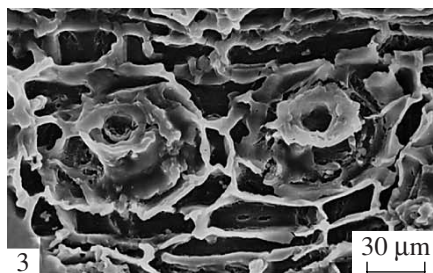
Figs. 1–6. *Tritaenia glabra* Gordenko, 2004, PIN, no. 4727/200; (1, 3–6) stomatal apparatuses with preserved cutinization of inner periclinal walls, SEM; (2) forming stomatal apparatus, SEM.

Diagnosis. Leaves linear-lanceolate. Upper cuticle lacking both stomata and trichomes. Lower cuticle with irregularly arranged stomata. Epidermal cells with small dome-shaped papillae. Rachis thick and glandular.

Description. The leaf is linear-lanceolate and entire-margined (Pl. 8, fig. 11). The apex and base are not preserved. The rachis is thick and rounded in section, 2 mm wide. The leaf lamina is thick. It is attached to the upper third of the rachis. The width of the leaf

lamina is 11 mm; the length of the fragment is 21 mm. The venation is not expressed.

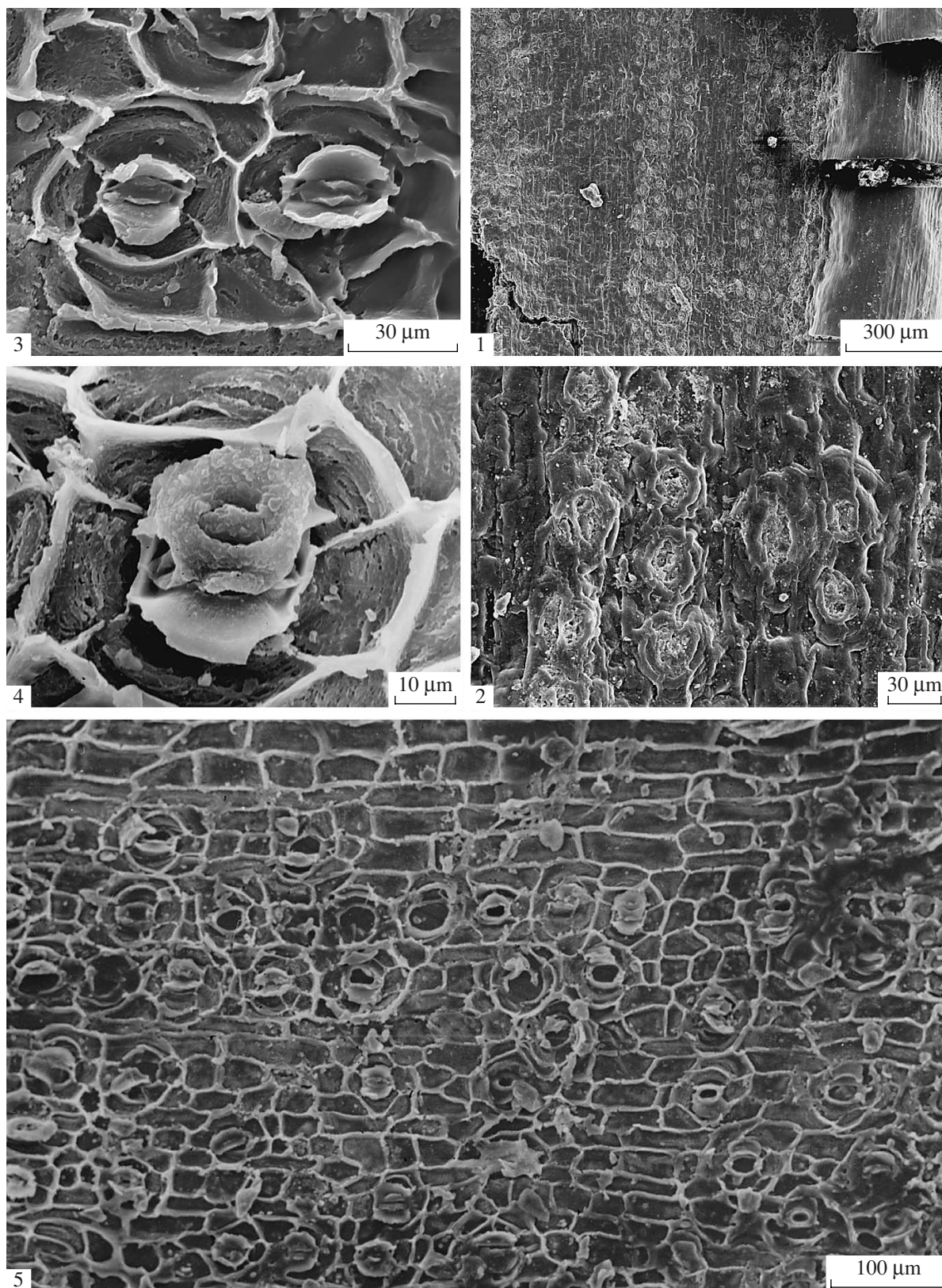
The leaf is hypostomous. The cuticle is 1.5–2 µm thick, but resistant to maceration. The upper epidermis is with tetragonal and rounded-triangular cells with sinuous anticlinal walls (Pl. 9, fig. 6). The size of the cells is 30–40 µm. The curves of the walls are sharp, forming acuminate teeth. The sinuosity range of the anticlinal walls is 3–5 µm. Trichomes are lacking.



Explanation of Plate 30

Figs. 1–7. *Tritaenia glabra* Gordenko, 2004: (1–5) PIN, no. 4727/4; (1) upper epidermis topography, SEM; (2) stomatal band, SEM; (3, 4) stomatal apparatuses, SEM; (5) ordinary epidermal cells of non-stomatal zone, SEM; (6, 7) PIN, no. 4727/15; (6) non-stomatal band, surrounded by stomatal bands, SEM; (7) blowing up of (6), note incomplete amphicyclic stomatal apparatuses, SEM.

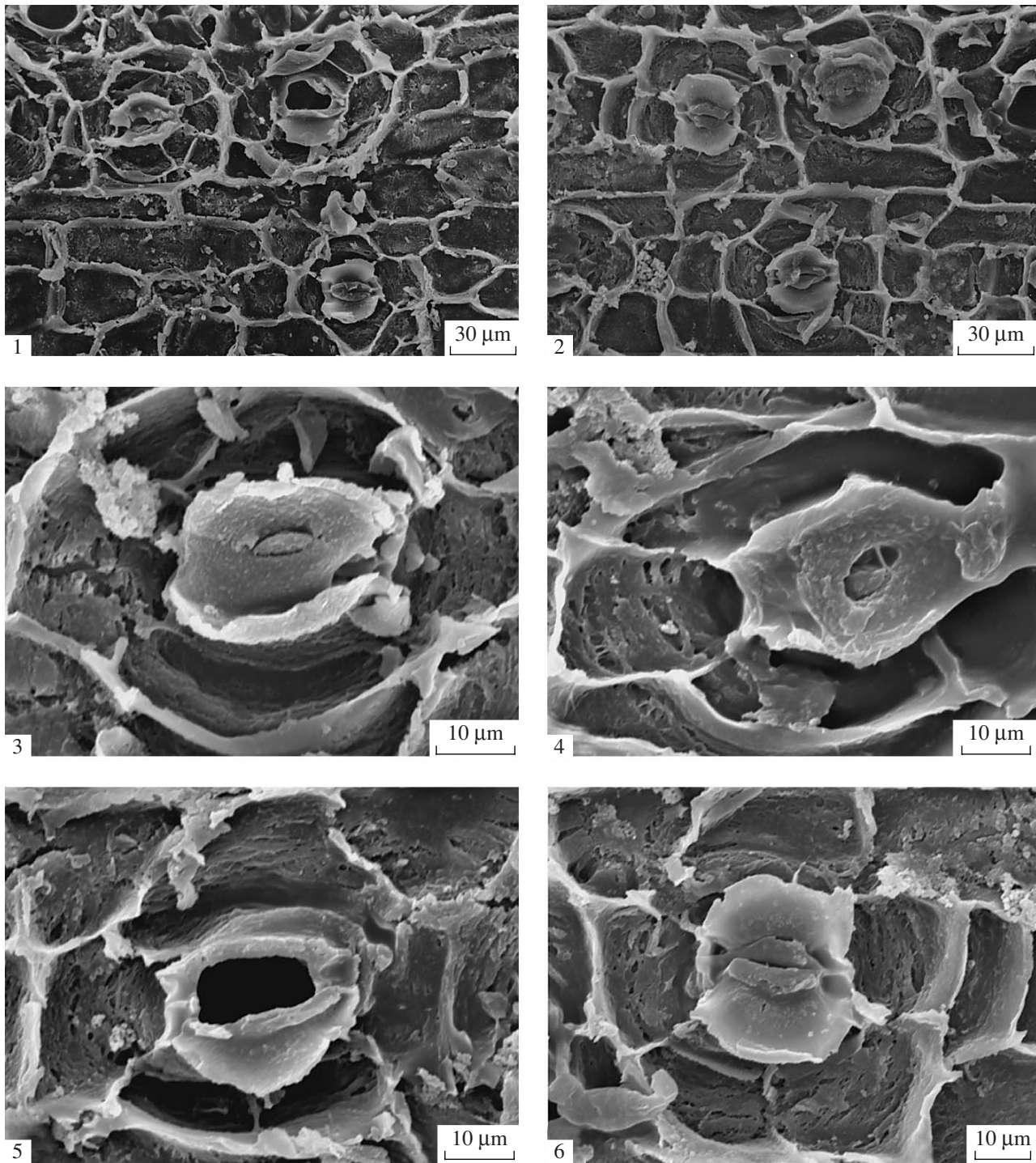
Plate 31



Explanation of Plate 31

Figs. 1–5. *Tritaenia* sp., PIN, no. 4727/14: (1) fragment of the external surface of the lower side of the leaf, SEM; (2) stomatal band, external surface, SEM; (3) incomplete amphicyclic stomatal apparatuses, SEM; (4) monocyclic stomatal apparatus with preserved cutinization of inner periclinal walls, SEM; (5) fragment of a stomatal band, inner surface, SEM.

Plate 32



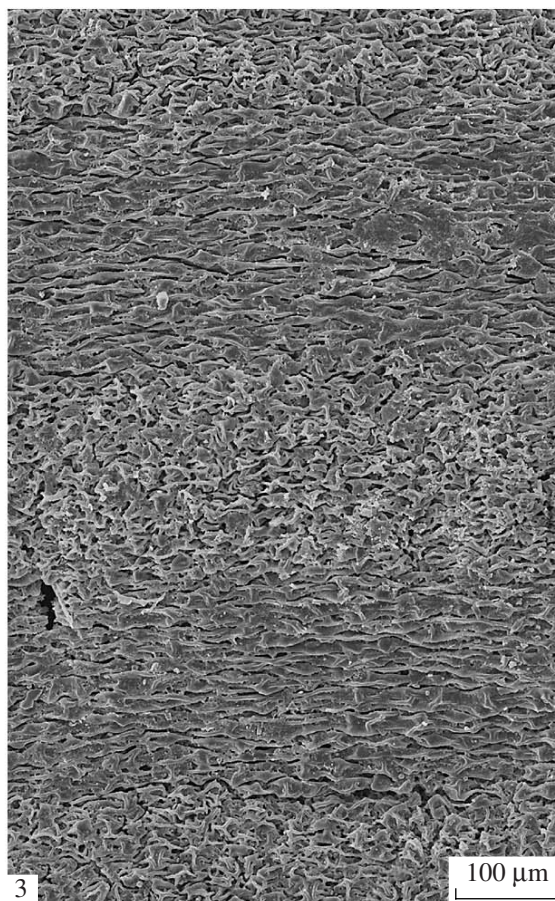
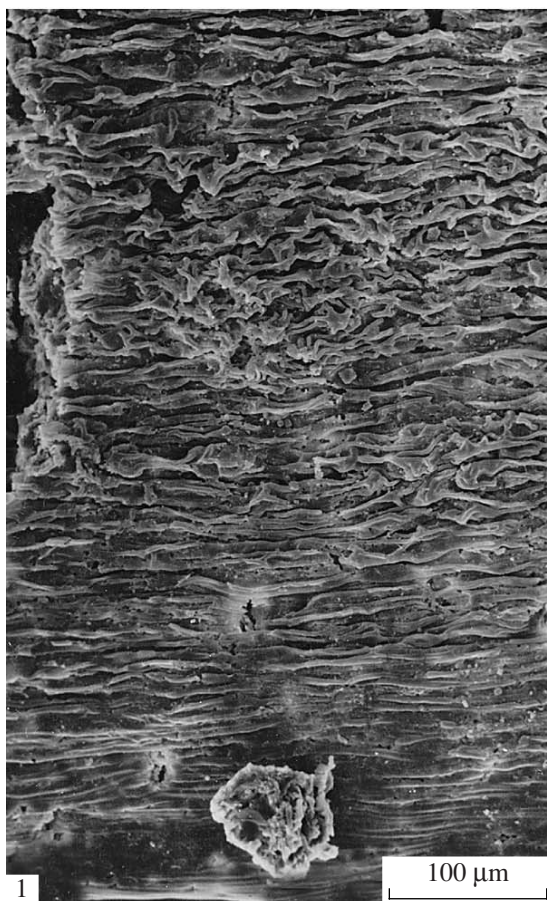
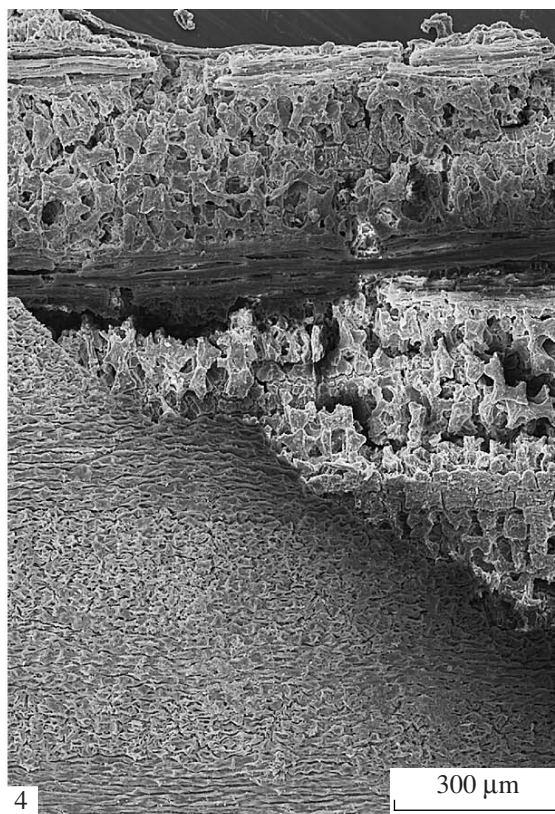
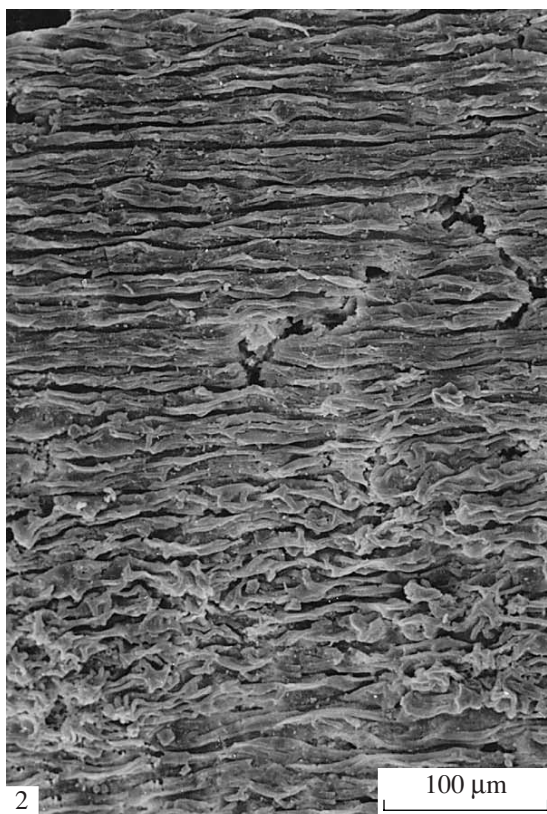
Explanation of Plate 32

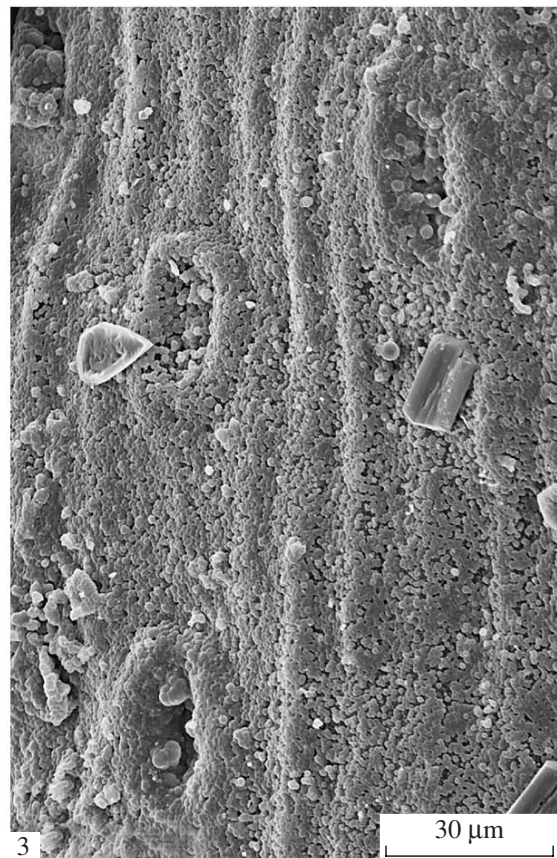
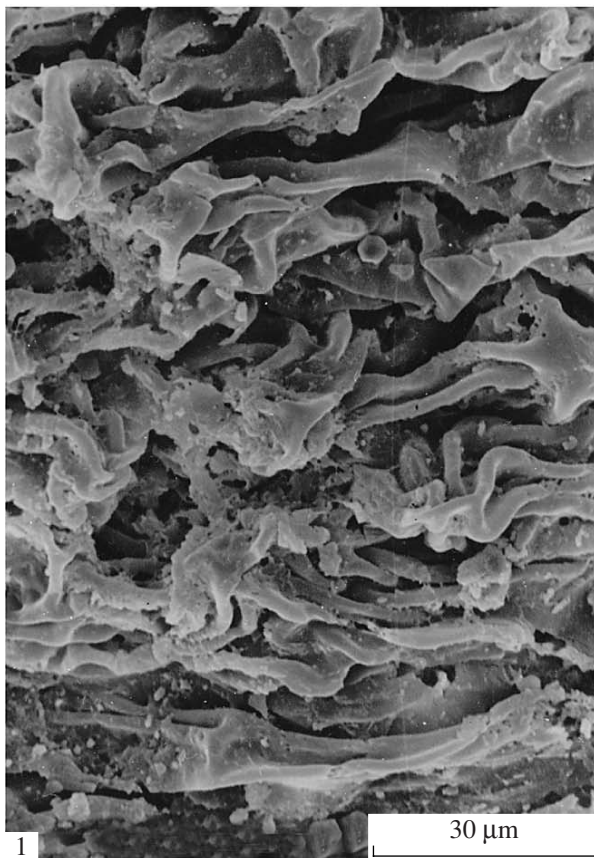
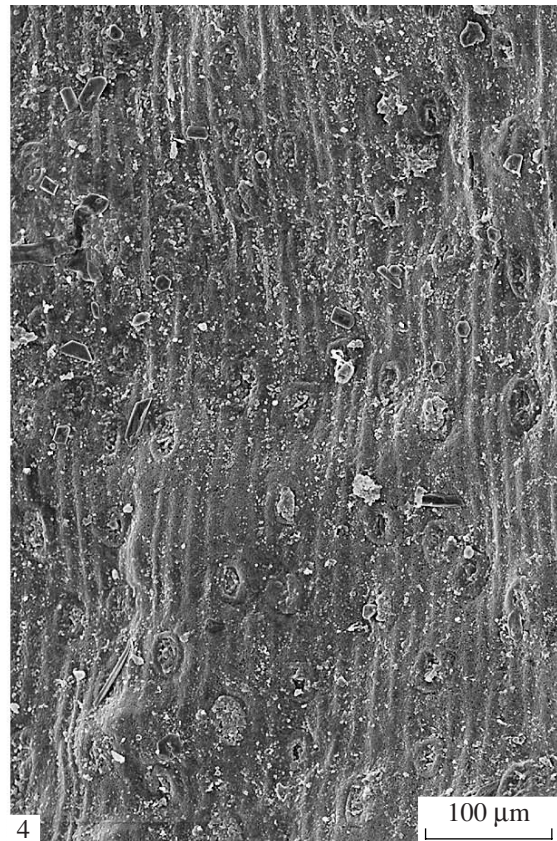
Figs. 1–6. *Tritaenia* sp., PIN, no. 4727/14: (1, 2) fragments of a stomatal band, SEM; (3, 4) stomatal apparatuses with preserved cutinization of inner periclinal walls of the guard cells, SEM; (5, 6) stomatal apparatuses, external periclinal walls are visible, SEM.

Explanation of Plate 33

Figs. 1–4. *Tritaenia striata* Gordenko, 2004: (1, 2) holotype PIN, no. 4727/368; (1) external surface of the marginal zone of a leaf, SEM; (2) sculpture of the external surface over a stomatal zone, SEM; (3, 4) PIN 4727/600; (3) external surface of the lower epidermis, SEM; (4) epidermis is removed to show three vascular bundles sunken in the mesophyll, SEM.

Plate 33





The lower epidermis has tetragonal to pentagonal cells with sinuous anticlinal walls and small hollow papillae in the center of each periclinal cellular wall (Pl. 9, fig. 7; Pl. 17, figs. 4, 5). The sinuosity range of the anticlinal walls is 2–5 μm . The diameter of the papillae is about 10 μm at the base; and their average height is 4–5 μm . Stomatal apparatuses do not form definite stomatal bands and are irregularly orientated (Pl. 9, fig. 7). The stomatal apparatuses are syndetoheilic. On average, the width of the stomata is 49 μm , and the length is 44–45 μm . Subsidiary cells of the stomatal apparatuses are non-sunken; they do not differ from ordinary cells of the epidermis by cutinization and often bear hollow papillae, not differing from papillae of ordinary epidermal cells. Their proximal parts slightly hang over the guard cells and enclose the space over the stomatal aperture with small dense papillae (Pl. 17, fig. 6). The guard cells are strongly cutinized. The distance between the stomatal apparatuses within a stomatal zone is one to three cells (=30–100 μm). The stomatal apparatuses occupy about 50% of the surface of the lower epidermis.

The cuticle of the rachis is thick, with rectangular longitudinally elongated epidermal cells with straight walls. The length of the cells is 40–50 μm , and the width is 20 μm . In addition to ordinary cells, the epidermis includes glands. Their apertures are formed by four–six cells (Pl. 9, figs. 8, 9). The margins of cells forming the gland aperture are strongly cutinized and bearing indistinct dense papillae.

Comparison. In the morphology of the leaf lamina and epidermis, *N. infera* sp. nov. resembles *N. vulgaris* from the Middle Jurassic of Georgia (Doludenko and Svanidze, 1969), but differs from it in the absence of hair bases on the cuticle of the lower epidermis and in the presence of glands on the rachis. In addition, *N. infera* sp. nov. has some similarities with *N. angrenica* Gomolitzky in the morphology of the leaf lamina and epidermis (Gomolitzky, 1974). Similarly to *N. angrenica*, *N. infera* sp. nov. has dense papillae on subsidiary cells of stomata, closing the stomatal aperture. However, *N. angrenica* has hair bases on the lower epidermis.

N. infera sp. nov. shares the morphology of the upper epidermis with many other species of this genus. However, members of *Nilssoniopteris* with small rounded papillae on the cells of the lower epidermis occur quite rarely. Such small papillae are occasionally present in members of *Anomozamites*. Moreover, *N. infera* sp. nov. lacks hair bases, characteristic of many members of the genus. Therefore, in spite of fragmentary material, I assign the leaf to a new species.

Material. One specimen represented by an impression and phytolite of an incomplete leaf.

Nilssoniopteris vittata (Brongniart) Florin, 1933

Plate 8, fig. 9; Plate 9, figs. 10–12; Plate 17, figs. 1–3

Taeniopteris vittata: Brongniart, 1828, p. 62; Brongniart, 1831, p. 263, pl. LXXXII, figs. 1–4.

Nilssoniopteris vittata: Florin, 1933, p. 4; Harris, 1969, p. 28, text-fig. 32.

Holotype. The specimen without number figured in Brongniart, 1831 (Pl. LXXXII, fig. 1), Middle Jurassic, Yorkshire, England. The repository of the specimen is not specified.

Description. The leaf is lanceolate and entire-margined (Pl. 8, fig. 9). The length is 38 mm, and the maximum width is 9 mm. The leaf lamina is symmetrical, with a rachis along the middle line. The rachis is gradually narrowing from the base towards the apex, where it becomes nearly indistinct. The leaf margin is slightly undulate, with weakly distinct, nearly symmetrical lobes (there are four lobes on each sides). The venation is parallel, but is not expressed on the surface of the leaf lamina, because the veins are deeply sunken in the mesophyll.

The leaf is hypostomous. The cuticle is thin (1–1.5 μm), but maceration-resistant. The cuticle of the upper epidermis is thinner than the cuticle of the lower epidermis. The upper epidermis is formed by nearly isodiametric tetragonal or rounded-triangular cells (Pl. 9, fig. 10). Anticlinal cellular walls are sinuous, forming in plane a polygonal line with acute teeth at the points of curve. Trichomes are lacking.

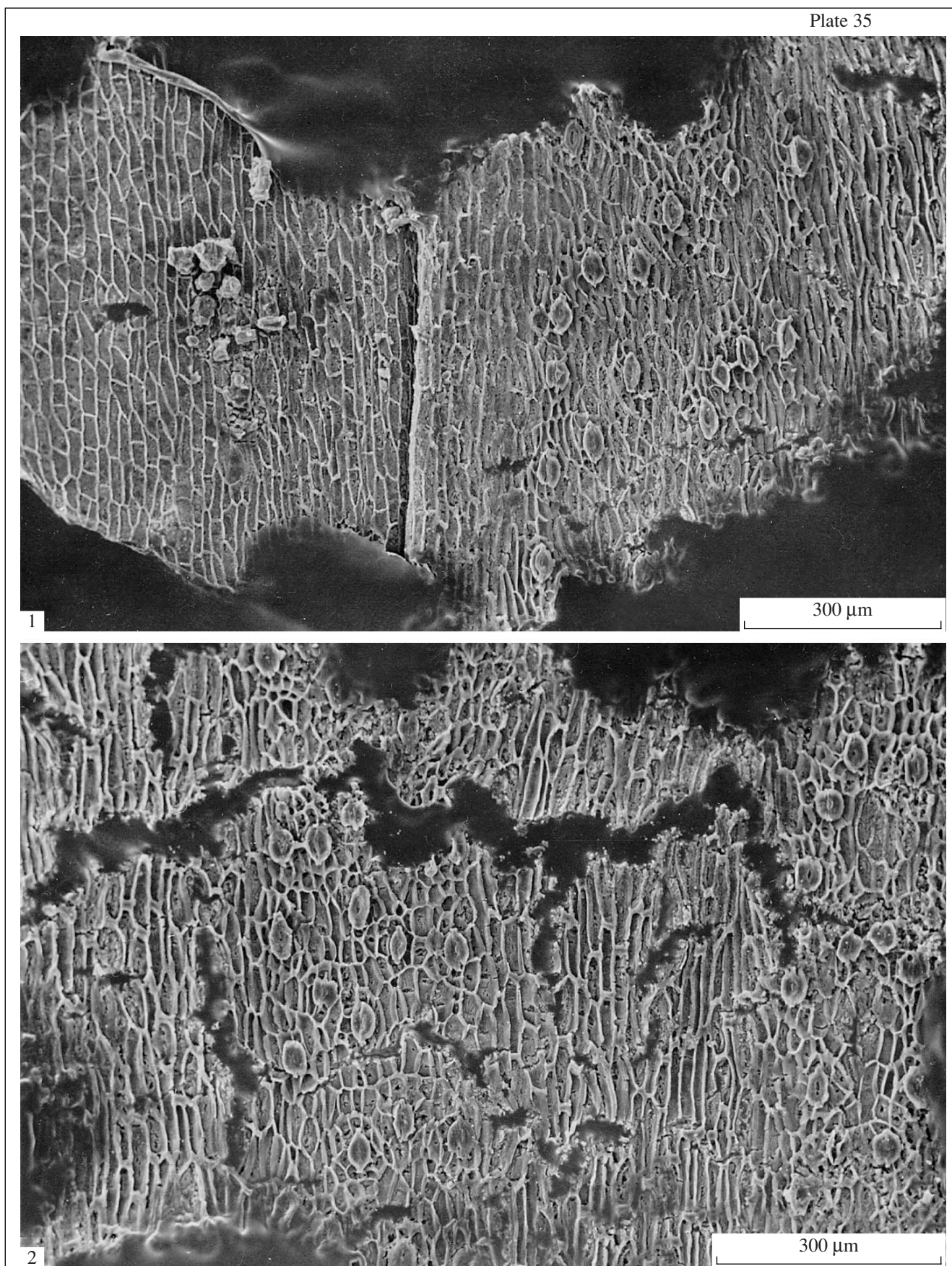
Ordinary cells of the lower epidermis are rounded-triangular or rectangular with sinuous anticlinal walls. Trichomes are present on the periclinal walls of many cells (Pl. 9, fig. 11). These are hollow conical papillae up to 10 μm in length and 4–5 μm in diameter at the rounded base or rounded hair bases 20 μm in diameter. The hair bases are strongly cutinized.

Stomatal apparatuses are syndetoheilic. They are irregularly distributed and orientated (Pl. 17, figs. 1–3). The distance between the stomatal apparatuses is one or two cells (=25–60 μm). The stomatal apparatuses occupy nearly 60% of the surface of the lower epidermis. Costal and intercostal zones are not expressed. Therefore, venation is not expressed in the topography of the lower epidermis. The guard cells are small. Their external periclinal walls are wing-shaped and relatively strongly cutinized. In a number of cases, cutinization of the inner periclinal walls of the guard cells is preserved

Explanation of Plate 34

Figs. 1, 2. *Tritaenia striata* Gordenko, 2004, holotype PIN, no. 4727/368; (1) external surface of the lower side of a leaf in the area of a stomatal zone, note cutin ribs and papillae hanging over stomatal apparatuses, SEM; (2) external surface of the lower side of a leaf in the area of non-stomatal zone, note sculpture, SEM.

Figs. 3, 4. *Tritaenia glabra* Gordenko, 2004, PIN, no. 4727/200: (3) Florin rings, SEM; (4) stomatal band, SEM.



(Pl. 17, fig. 3). Subsidiary cells are crescent, with virtually straight anticlinal walls, and strongly cutinized (Pl. 17, fig. 2). The length of stomatal apparatuses are 20–25 μm . The width of stomatal apparatuses with subsidiary cells is 28–30 μm , and their average width without subsidiary cells is 15 μm .

Remarks. By leaf lamina morphology, the specimen from the Peski locality is close to *N. vittata* from the Middle Jurassic of Yorkshire, which has an oval-lanceolate leaf lamina. The specimen from the Peski locality has identical trichomes, similar outlines of the anticlinal walls of the upper and lower epidermises. It only differs from the Middle Jurassic specimens from Yorkshire in having deeply sunken veins. This difference is probably caused by different ecological conditions and hardly can serve for specific diagnostic.

Occurrence. Middle Jurassic of Yorkshire (England), Moscow Region (Russia), and Donets Basin (Ukraine).

Material. One specimen represented by impression, its counterpart, and phytoleim.

Nilssoniopteris sp.

Plate 8, fig. 12; Plate 16, figs. 1–3

Description. The leaf is linear-lanceolate and entire-margined (Pl. 8, fig. 12). The rachis is distinct, 1 mm wide. The leaf lamina is attached to the upper third of the rachis. The leaf venation is pinnate. The veins are parallel, deviating from the rachis at an angle of 90°. Occasionally, they dichotomize at the very base. There are about 20 veins per 1 cm. The leaf lamina margins are rolled down. On average, the visible width of the leaf in its middle area is 11 mm.

The cuticle is moderately thick. The leaf is hypostomous. The cuticle of the upper epidermis has uniform rectangular and triangular cells (Pl. 16, fig. 2). The cell sizes are 30–35 μm . Anticlinal cellular walls are sinuous. The sinuosity is sharp, forming a polygonal line. The cuticle becomes thicker at the points of curves. The sinuosity range is 4 μm on average. Trichomes are lacking.

Ordinary cells of the lower epidermis are weakly sinuous, rounded triangular to pentagonal, 10–40 μm . The stomatal apparatuses are small and syndetoheilig. The length of the stomatal apparatuses are 17 μm ; the width with subsidiary cells is 28–30 μm ; the width without subsidiary cells is 17 μm . The guard cells of the stomatal apparatuses are strongly cutinized (Pl. 16, figs. 1, 3); the subsidiary cells are cutinized in a lesser degree. Trichomes on the cells of the lower epidermis are apparently lacking. The distance between adjacent stomata without a stomatal zone is equal to three or four cells.

Remarks. The leaf lamina morphology, sinuosity of the anticlinal walls of ordinary epidermal cells, and the morphology of stomatal apparatuses allow me to assign this specimen to the genus *Nilssoniopteris*. In leaf lamina morphology (leaf width, number of veins, and rolled down margin of the leaf lamina), the specimen under description resembles *N. mikailovii* (Sadovnikov) Schweitzer et Kirchner from the Rhaetian–Liassic deposits of Iran (Schweitzer et Kirchner, 2003), *N. angrenica* Gomolitzky from the Middle Jurassic of Angren in Uzbekistan (Gomolitzky, 1974), *N. longifolia* Doludenko from the Middle Jurassic of Georgia (Doludenko and Svanidze, 1969), *N. taeniata* Samylina from the Lower Cretaceous of the Primorye Region (Samylina, 1961), *N. prynadae* Samylina from the Lower Cretaceous of the Kolyma River Basin (Samylina, 1963), and *N. beyrichii* Shenghui from the Lower Cretaceous of northern China (Shenghui, 1995).

The fragmentary preservation of the cuticle prevents the comparison on the epidermal morphology between the specimen under description and other species of the genus, because of this the specimen is described in open nomenclature as *Nilssoniopteris* sp.

Material. One specimen represented by an impression, its counterpart, and phytoleim of an incomplete leaf.

Genus *Williamsonia* Carruthers, 1870

Williamsonia sp.

Plate 18, figs. 1–5

Description. Four sterile bracts are preserved. The bracts are virtually ellipsoidal. The length of the bracts is 10 mm, and the width is 3 mm.

The cuticle is thick and resistant to maceration. Ordinary epidermal cells are tetragonal to pentagonal and nearly isodiametric. The diameter of the ordinary epidermal cells is 8–42 μm . Stomatal apparatuses are rare and irregularly distributed over the surface of the bract (Pl. 18, fig. 2). Usually, they form compact aggregations of two to five stomata. The guard cells of stomatal apparatuses are wide, wing-shaped, and with a well-developed rim near the aperture. The guard cells are surrounded by three to five subsidiary cells, two of which are lateral, and others are polar (Pl. 18, figs. 4, 5). The guard cells are strongly cutinized, whereas lateral cells usually do not differ from ordinary epidermal cells by the degree of cutinization. The outer periclinal walls of the subsidiary cells are swollen (Pl. 18, fig. 3). Occasionally, normal syndetoheilig stomatal apparatuses are present with strongly cutinized subsidiary cells. The length of the guard cells is 29–32 μm and the width of the stomata is 36–42 μm .

Explanation of Plate 35

Figs. 1, 2. *Tritaenia striata* Gordenko, 2004, holotype PIN, no. 4727/368; (1) spread cuticle of the marginal area of a leaf, SEM; (2) stomatal zones, SEM.

Comparison and remarks. As far as only sterile bracts are present, the comparison with other species of the genus is difficult. The specimen shows similarity to many members of the genus in the epidermal-cuticular characters; therefore, it is described here in open nomenclature.

Williamsonia sp. and leaves of *Otozamites paradoxus* sp. nov. were found in the same bed, therefore there is a possibility that the bract and leaves could have belonged to the same plant.

Material. One specimen represented by the impression and phytolaim.

Order Coniferales

Family Miroviaceae Bose et Manum, 1990

Genus *Tritaenia* Mägdefrau et Rudolf, 1969

Tritaenia glabra Gordenko, 2004

Plate 19, figs. 1–6; Plate 23, figs. 1–4; Plate 24, figs. 1, 2; Plate 25, figs. 1–5; Plate 26, figs. 1–3; Plate 27, figs. 1–7; Plate 28, figs. 1–6; Plate 29, figs. 1–6; Plate 30, figs. 1–7; Plate 34, figs. 3, 4; Plate 37, figs. 1–4

Tritaenia glabra: Gordenko, 2004, p. 100, pl. X, figs. 1–3; pl. XI, fig. 4.

Holotype. PIN, no. 4727/67, leaf impression with a phytolaim, layer no. 9, section no. 1, quarry Peski, 1.5 km from the Peski station, Kolomna district, Moscow Region, Middle Jurassic, Bathonian, Meshchera horizon.

Description (Fig. 7a). The collection contains numerous fragments of linear leathery leaves with a more or less distinct median groove (Pl. 19, figs. 1–6). Nearly complete leaves with a rounded apex and gradually tapering base occur more rarely. The width of the leaves in the middle area varies from 2 to 3 mm. The length of the only preserved complete leaf is 45 mm and the width is 2 mm (Pl. 19, fig. 1). The venation of the lower surface of the leaf is not expressed. After maceration and removing the upper cuticle, the relief of the upper surface of the leaf shows four parallel veins (Pl. 23, fig. 3; Pl. 24, fig. 1; Fig. 7a). The same number of veins is observed on the transverse sections of leaf phytolaims (Pl. 23, fig. 1). Intercostal resin canals are present (Pl. 24, figs. 1, 2).

The leaves are hypostomous. The cuticle is thick and resistant to maceration. The upper cuticle is with longitudinally elongated tetra- or pentagonal cells with slightly rounded angles, 30–100 μm long and 20–30 μm wide. The anticlinal cellular walls are straight or, more rarely, slightly sinuous. The external surface of the upper epidermis is covered with continuous parallel ribs (Pl. 23, fig. 2). Trichomes are lacking.

The lower cuticle is thinner than the upper cuticle, with distinct costal and intercostal bands. The relief of the cuticle is formed by thin parallel ribs (Pl. 23, fig. 4; Pl. 34, figs. 3, 4). There are three or, more rarely, two stomatal bands (Pl. 19, fig. 3; Pl. 23, fig. 4; Pl. 37, fig. 1). The median stomatal band is very narrow, consisting of one to four or, more rarely, five longitudinal rows of

stomata, and often interrupted. The width of marginal stomatal bands is about 700 μm ; the width of the median stomatal band is about 60 μm ; and the width of non-stomatal zones is about 500 μm . Cells in non-stomatal zones are two times as large as in stomatal zones. Ordinary epidermal cells have straight or slightly sinuous anticlinal walls and smooth periclinal walls. Stomatal apparatuses within a stomatal zone form seven or eight interrupted longitudinal rows (Fig. 2a). Ordinary epidermal cells within the rows are rounded-rectangular or hexagonal. They are nearly isodiametric or slightly elongated transversely or, more rarely, longitudinally, 14–35 μm long and 21–30 μm wide. Ordinary epidermal cells between stomatal rows are longitudinally elongated, wedge-shaped, rectangular, or fusiform, 15–65 μm long and 7–15 μm wide. Ordinary epidermal cells of non-stomatal zones are rounded-rectangular or, more rarely, trapezoidal, 30–80 μm long and 15–30 μm wide (Pl. 27, fig. 4; Pl. 28, fig. 5, Pl. 30, figs. 5, 6).

The stomatal apparatuses are amphicyclic (Pl. 28, figs. 2, 3; Pl. 29, figs. 1, 3–5; Pl. 30, figs. 3, 4), more rarely, incomplete amphicyclic (Pl. 27, fig. 2; Pl. 28, fig. 6; Pl. 29, fig. 2; Pl. 30, fig. 7), or monocyclic (the leftmost stoma, Pl. 27, fig. 7). The external periclinal walls of the guard cells are bean- or wing-shaped, with slightly undulate and rolled down external margins (Pl. 27, figs. 1, 2, 7; Pl. 28, fig. 6; Pl. 29, fig. 2; Pl. 30, fig. 7). The guard cells are unevenly cutinized: in a greater degree in the middle part of the dorsal plate and in a lesser degree toward the periphery. The inner near-apertural ridge is well developed. The length of the guard cells is 20–35 μm , and the width is 20–32 μm . Polar extensions are dovetailed, with a thin median ridge. The width of the polar extensions is 5–6 μm . The cuticle of the external periclinal walls of the guard cells is smooth (Pl. 28, fig. 6), and the cuticle of the inner periclinal walls is granular (Pl. 28, figs. 2, 3).

The guard cells of the stomatal apparatuses are surrounded by two to four lateral and two or three polar subsidiary cells, forming an elliptic Florin ring around the stomatal aperture (Pl. 25, figs. 4, 5; Pl. 34, fig. 3). Occasionally, lateral subsidiary cells are divided together with the guard cells (Pl. 27, fig. 3). In this case, double stomatal apparatuses are formed. The number of the encircling cells varies from two to four. Various abnormal stomatal apparatuses are observed, which have more than four subsidiary cells. Trichomes are lacking.

Comparison. *T. glabra* does not differ in the leaf lamina morphology from *T. scotica* from the Upper Jurassic of Scotland, *T. linkii* from the Lower Cretaceous of Germany, *T. crassa* (Seward) Bose et Manum from the Lower Cretaceous of western Norway (Manum et al., 2000), and *T. striata* from the Peski locality. Similarly to these species, *T. glabra* has hypostomous leaves with a longitudinal groove on the upper

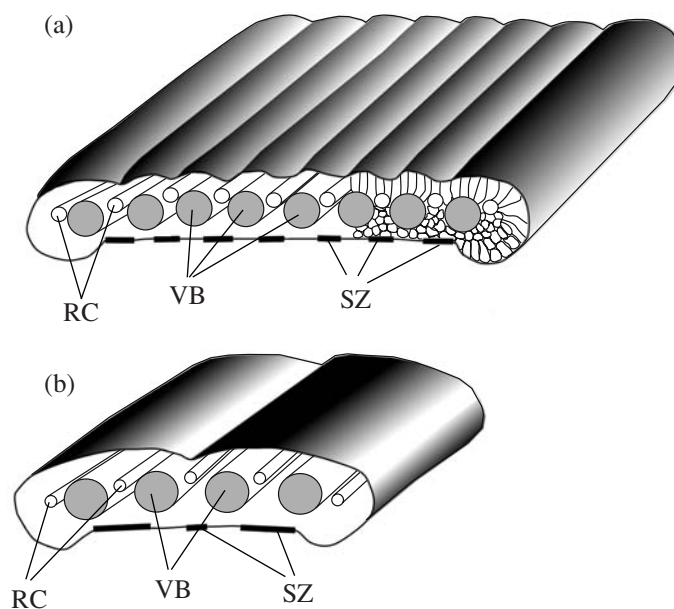


Fig. 7. Some details of leaf lamina anatomy reconstructed in *Tritaenia*, transverse section: (a) *T. glabra* Gordenko; (b) *T. striata* Gordenko; (VB) vascular bundle; (RC) resin canal; (SZ) stomatal zone.



Fig. 8. Life habit reconstructed for the fern *Stachypteris psammitica*.

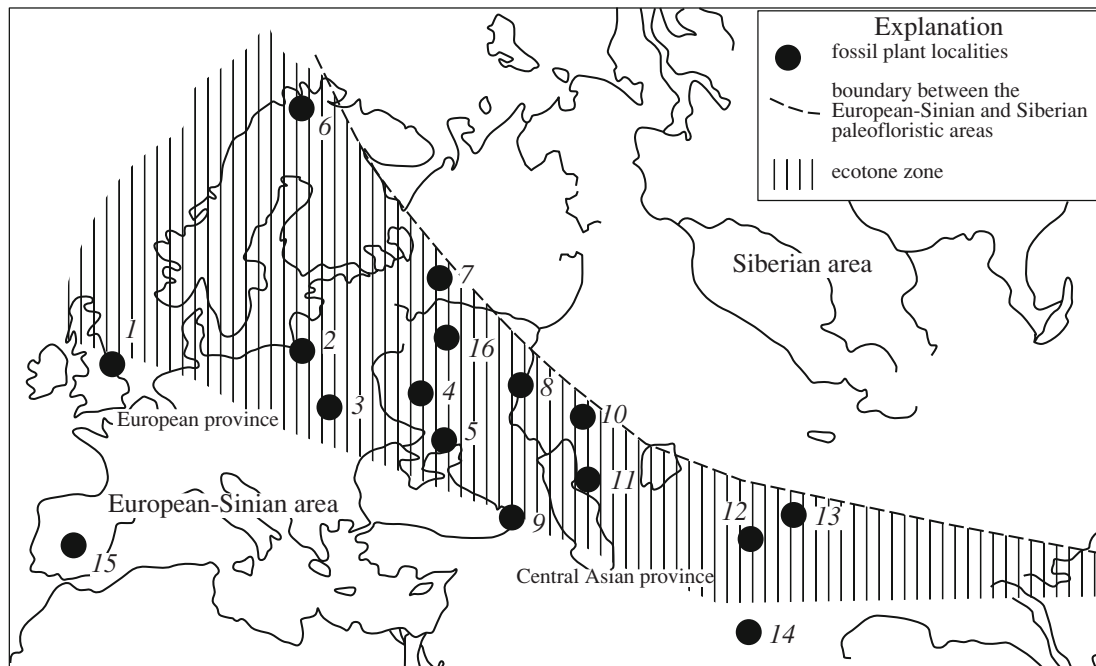


Fig. 9. Supposed position of the boundary between European-Sinian and Siberian areas in the Bathonian in western Eurasia. The position of Bathonian floras of the European-Sinian or transitional aspects are indicated: (1) Yorkshire (England); (2) Poland; (3) western Ukraine; (4) Zheleznogorsk (Kursk Region, Russia); (5) Donets Basin (Ukraine); (6) northern Norway; (7) Vychegda River (Vologda Region, Russia); (8) Samarskaya Luka (Samara Region, Russia); (9) Transcaucasia (Georgia); (10, 11) northern Caspian depression (Kazakhstan); (12) Gissar Ridge (Tadzhikistan); (13) Fan-Yagnob (Kazakhstan); (14) Afghanistan; (15) France; (16) Peski.

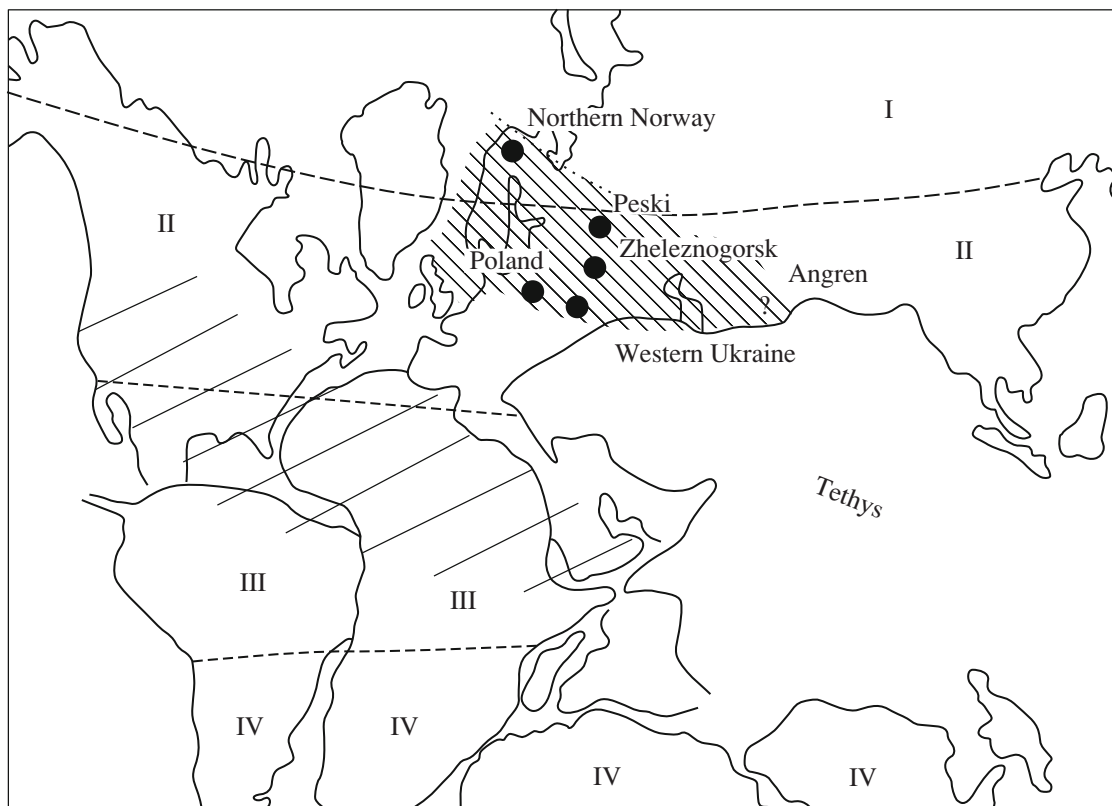


Fig. 10. Climatic zones (dotted line) and the position of the continents in the Middle Jurassic according to the mobilism scheme (after Vachrameev, 1988, changed). Localities with the Miroviaceae are indicated, and the supposed boundary between the European-Sinian and Siberian areas in the Bathonian time is dotted. Left-tilting lines indicate the ecotone zone in the Bathonian time; right-tilting lines indicate the arid zone. Legend: (I) Siberian area; (II) European-Sinian area; (III) Equatorial area; (IV) Notal area.

side. By the relief of the cuticle of the lower leaf side, *T. glabra* is mostly similar to *T. crassa*, which only has thin strands in costal zones and lacks trichomes. In addition, a considerable similarity is revealed in the morphology of stomatal apparatuses: both *T. glabra* and *T. crassa* are characterized by the differentiation of subsidiary cells into two lateral and two polar, absence of papillae on subsidiary cells, and the presence of two to four encircling cells. The main distinctive feature of the species under consideration is the presence of two or three stomatal bands, with an interrupted median band of one to four rows of stomata; by contrast, the number of stomatal bands varies from three to five in *T. crassa*, and the median band is relatively wide. Moreover, *T. glabra* has stomatal apparatuses orientated exclusively longitudinally, whereas many obliquely and transversely orientated stomata are observed in *T. crassa*. A weakly developed or reduced median stomatal band differentiates *T. glabra* from other species of this genus, *T. scotica* and *T. linkii*, as well. In addition, it differs from *T. scotica* and *T. linkii* in the absence of papillae on subsidiary cells.

In all probability, the number of vascular bundles is constant in this species, whereas it can slightly varies in *T. crassa* and *T. scotica*.

Unlike *T. glabra*, *Tritaenia striata* has more than three stomatal bands, papillae on subsidiary cells, and peculiar ribs on the surface of the lower epidermis.

Occurrence. Type locality.

Material. One complete and 84 fragmentary leaves preserved and impressions and phytoleims.

Tritaenia striata Gordenko, 2004

Plate 19, figs. 7–9; Plate 33, figs. 1–4; Plate 34, figs. 1, 2; Plate 35, figs. 1, 2; Plate 36, figs. 1–4; Plate 37, figs. 9, 10; Plate 38, figs. 1–4

Tritaenia striata: Gordenko, 2004, p. 97, pl. X, figs. 4–7.

Holotype. PIN, no. 4727/368, leaf impression with a phytoleim, layer no. 1, section no. 3, Peski open mine, 1.5 km from the Peski railway station, Kolomna district, Moscow Region, Middle Jurassic, Bathonian, Meshchera horizon.

Description (Fig. 7b). The collection contains leaf fragments having parallel margins in the middle area and tapering toward the acuminate apex (Pl. 19, figs. 7–9). The length of the fragments does not exceed 15 mm, and their maximum width is 5 mm. The venation is parallel. There are seven to nine veins per the median area of the leaf, which usually are distinct in the relief of the upper surface of the leaf lamina (Fig. 7b). Conductive bands are thin, straight, lined with isodiametric parenchyma cells, and sunken in the mesophyll (Pl. 33, fig. 4). Resin canals are intercostal.

The cuticle is thick and resistant to maceration. The upper cuticle is thinner than the lower cuticle. The epidermis is hypostomous. The cells of the upper epidermis is triangular to hexagonal, longitudinally elongated, 20–50 μm long and 10–30 μm wide (Pl. 36,

fig. 1). The anticlinal walls of the cells are straight. The transverse anticlinal walls are cutinized in a greater degree than the longitudinal anticlinal walls. The periclinal cellular walls are flat. Trichomes are lacking.

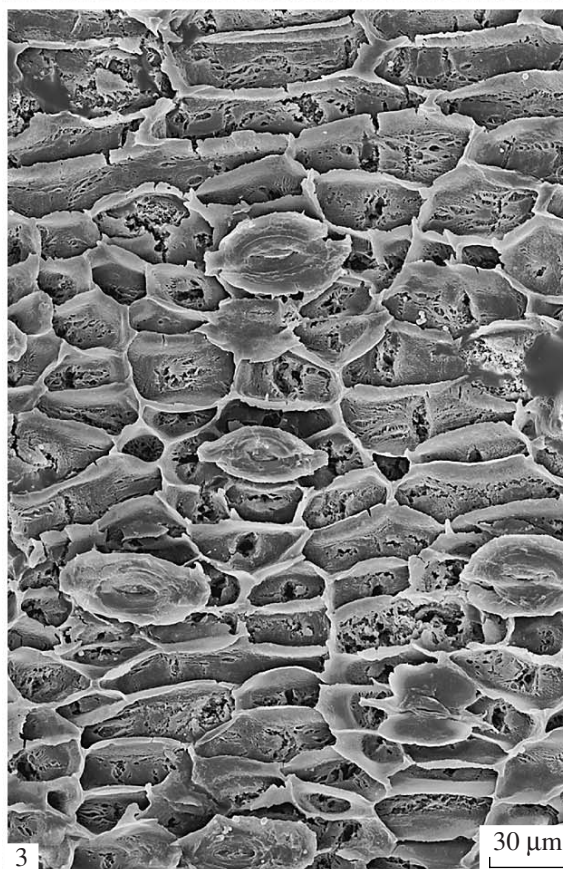
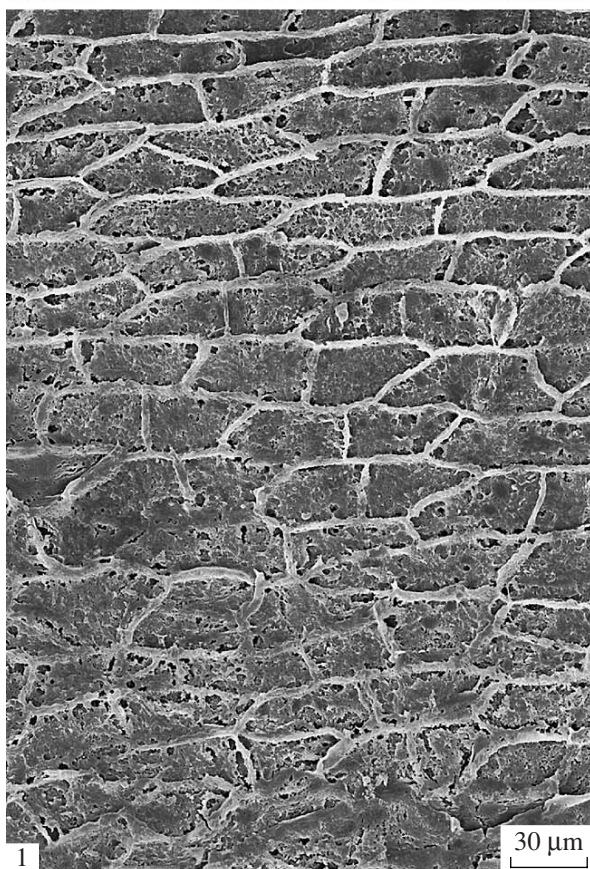
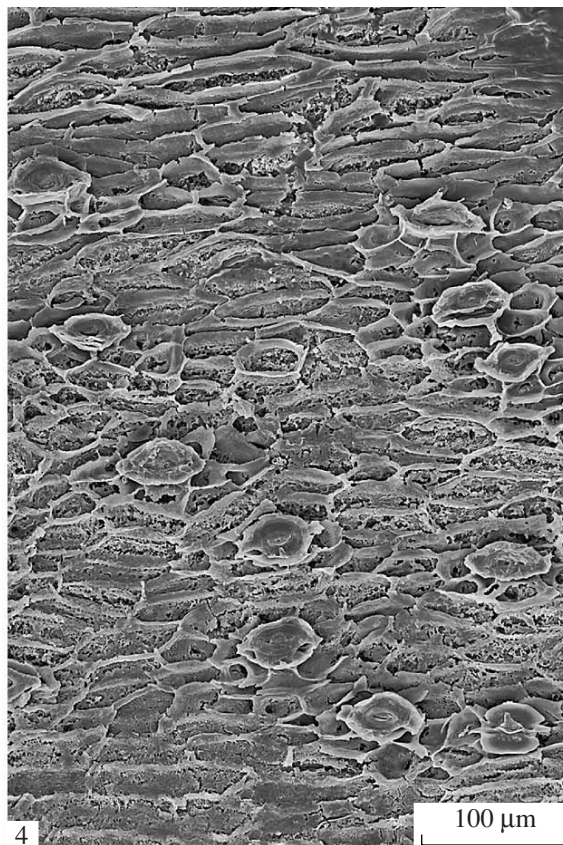
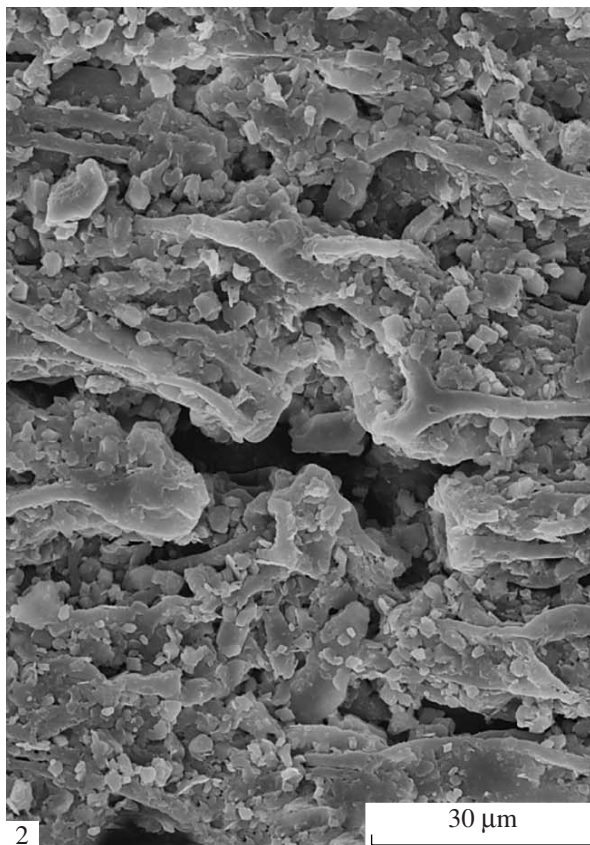
The cuticle of the lower epidermis is subdivided into stomatal (intercostal) and non-stomatal zones (Pl. 33, figs. 1–4; Pl. 35, figs. 1, 2; Pl. 36, fig. 4; Pl. 37, figs. 9, 10). They vary in number from five to seven, depending on the number of veins. The average width of the stomatal bands is 300 μm , and the width of non-stomatal zones is 400 μm . The external surface of the lower cuticle shows a compound relief, which is not reflected on its inner surface. Marginal leaf zones are nearly smooth; in non-stomatal zones, the cuticle forms long and weakly elevated longitudinal ribs, which are densely adpressed to each other (Pl. 33, figs. 1, 2). The cuticle of the stomatal zones is sinuously grooved, with nodular longitudinal ridges coalescing over stomatal pits (Pl. 33, figs. 1–3; Pl. 34, fig. 1; Pl. 36, fig. 2).

Ordinary epidermal cells within the stomatal bands are tetragonal to hexagonal, from isodiametric to longitudinally elongated, 16–50 μm long and 10–31 μm wide; within the non-stomatal bands, ordinary epidermal cells are strongly elongated, 40–120 μm long and about 30 μm wide (Pl. 34, fig. 2; Pl. 37, fig. 10). The anticlinal walls of the ordinary epidermal cells of the lower epidermis are straight and smooth; the transverse walls are thicker than the longitudinal walls.

The stomatal apparatuses do not form distinct rows (Pl. 36, fig. 4). They are longitudinally orientated and incompletely amphicyclic (Pl. 38, figs. 1, 4), more rarely, monocyclic (Pl. 37, fig. 2), or amphicyclic (Pl. 37, fig. 3). The cutinization of the external walls of the guard cells is bean- or wing-shaped, with a thickened ridge surrounding the aperture (Pl. 37, fig. 2). Polar extensions are narrow and dovetailed (Pl. 37, figs. 2–4). The length of the stomata is 40–46 μm and the width is 23–30 μm . The length of the polar extensions is 8–9 μm , and the width is about 3 μm . The cuticle of the inner periclinal walls of the guard cells is smooth and has thin concentric folds (Pl. 37, fig. 1).

There are four to seven subsidiary cells. Each subsidiary cell bear a small obtusely conical and covered with thin ribs papillae, hanging over the aperture (Pl. 34, fig. 1; Pl. 36, fig. 2). Encircling cells differ from ordinary epidermal cells in the smaller sizes, nearly isodiametric outline, and radial arrangement. As a rule, they form an incomplete ring of two to four cells.

Comparison. Morphologically, leaves of species of *Tritaenia* are slightly different from each other. *T. striata* is closer to *T. scotica* in the leaf apex outline; however, a longitudinal groove is not expressed in the latter species. The variability ranges in leaf width and number of veins approximately coincide for these species. The main distinctive features are epidermal-cuticular. The species under study has the upper surface of the cuticle of the lower epidermis with sinuous grooves over stomatal bands, whereas *T. scotica* has distinct



longitudinal ribs on the entire external surface of the cuticle of the lower epidermis. The type species *T. linkii* has straight or slightly sinuous cuticular rims over all external surface of the cuticle of the lower epidermis, which transform in some specimens into wide irregularly thickened longitudinal ribs.

As a rule, subsidiary cells in the species under consideration are more numerous than in *T. scotica* and *T. linkii*, although the variability ranges are overlapping. Manum et al. (2000) reported isolated resin bodies in *T. linkii*. However, the study of specimens from the type locality showed the presence of continuous resin canals (Gordenko, 2004b, 2004d). Therefore, the three species of *Tritaenia* are similar by this character.

The species under consideration differs from *T. crassa* (Sew.) Bose et Manum and *T. glabra* in the presence of papillae on subsidiary cells of stomatal apparatuses and a more elaborated relief of the cuticle of the lower surface of the leaf.

Occurrence. Type locality.

Material. Nine impressions and phytoleims of fragmentary leaves.

Tritaenia sp.

Plate 19, fig. 18; Plate 31, figs. 1–5; Plate 32, figs. 1–6; Plate 37, figs. 5–8

Description. The collection contains fragmentary linear-lanceolate leaves. The length of the biggest fragment is 15 mm, the width at the base is 2 mm, and the maximum width is 7 mm. Most probably, this fragment is the base of a leaf lamina (Pl. 19, fig. 18). The apex was not preserved. The venation is parallel. There are eight veins in the middle area of the leaf. Intercostal resin canals are present.

The leaf is hypostomous. The cuticle is thick and resistant to maceration. The upper cuticle is thicker than the lower.

The cuticle of the upper epidermis shows longitudinally elongated epidermal cells, which are predominantly rounded-tetragonal or nearly oval in outlines. The periclinal cellular walls are straight. The length of the ordinary epidermal cells is 23–125 μm , and the width is 10–30 μm . The external surface of the cuticle is covered with continuous longitudinal cutin ribs. Trichomes are lacking.

The cuticle of the lower epidermis is subdivided into stomatal and non-stomatal zones (Pl. 31, fig. 1). In total, six wide parallel stomatal zones are present, separated by relatively narrow non-stomatal zones. The width of the stomatal zones varies between 210 and 300 μm . The width of non-stomatal zones is about 200 μm . Epidermal cells of marginal and non-stomatal

leaf zones are strongly elongated in longitudinal direction. The majority of other epidermal cells are nearly isodiametric and tetragonal to heptagonal. The length of the cells is 15–90 μm , and the width is 10–30 μm . The anticlinal walls of the epidermal cells are straight or weakly sinuous and smooth. Epidermal cells within the non-stomatal zones are strongly elongated. Stomata are irregularly distributed within the stomatal zones (Pl. 31, fig. 5; Pl. 37, fig. 5). Often, they form longitudinal or transverse chains of 4–11 stomata which have adjacent subsidiary cells or even shared them. The stomatal apparatuses are amphicyclic (Pl. 32, fig. 3; Pl. 37, fig. 6), incompletely amphicyclic (Pl. 32, figs. 4–6), or, more rarely monocyclic (Pl. 31, fig. 4; Pl. 37, fig. 8). The external periclinal walls of the guard cells are wing-shaped, often rolled down (Pl. 31, fig. 3; Pl. 32, figs. 2, 6). The guard cells are unevenly cutinized. Areas near apertures and median areas of the upper periclinal walls of the guard cells are most strongly cutinized. Cutinization of the inner periclinal walls is often preserved (Pl. 31, fig. 4; Pl. 32, figs. 3, 4). Usually, the width of a guard cell is 15 μm . Polar extensions of the guard cells are wide and short, slightly widening as a dovetail (Pl. 32, fig. 5). The length of the polar extensions is 2–3 μm , and the width is 3–4 μm . Usually, there are four or five subsidiary cells. There are two polar and two or three lateral subsidiary cells. The subsidiary cells form a Florin ring over the stomatal aperture. Usually, there are two to four encircling cells.

Abortive stomata occur quite often. Occasionally, abnormal stomatal apparatuses are observed, with three polar and three or four lateral subsidiary cells.

The stomatal apparatuses can be subdivided into two size groups. Among normal stomata of 30 μm long, very large stomata are visible, two times as large as the normal stomata (Pl. 32, fig. 1). Such large stomata make up to about 20%. Trichomes are lacking.

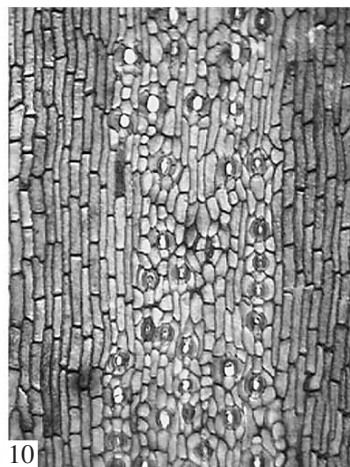
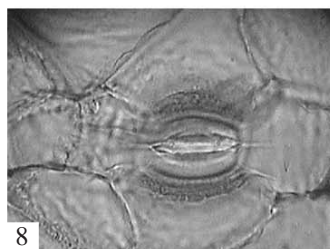
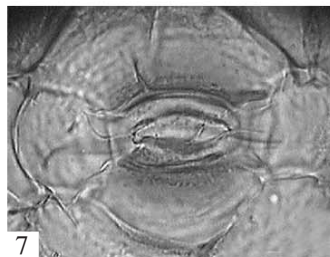
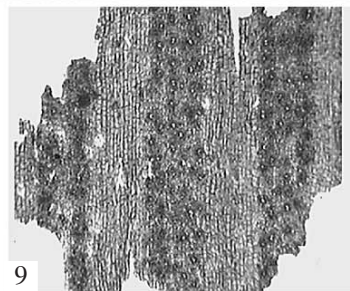
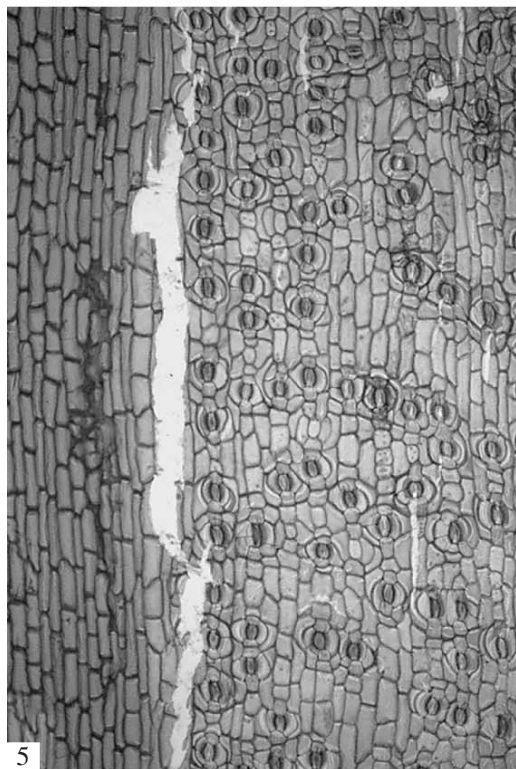
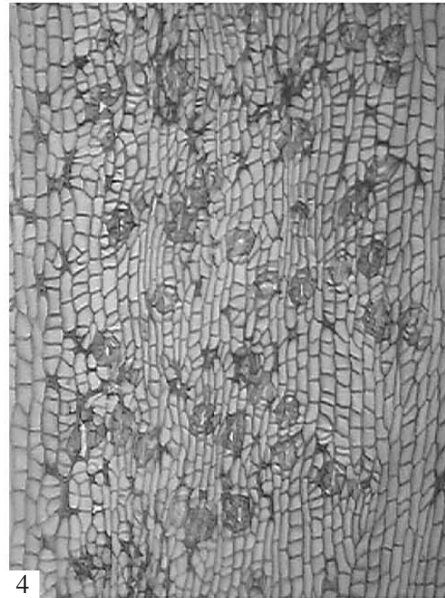
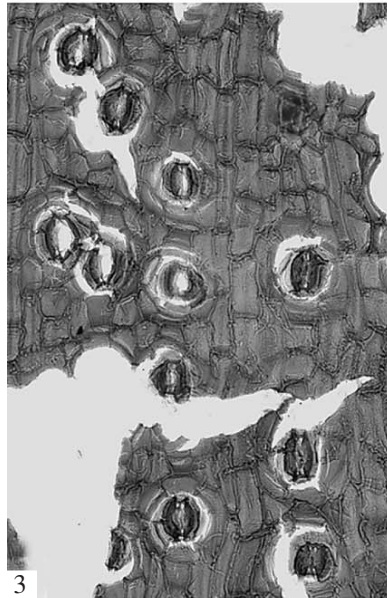
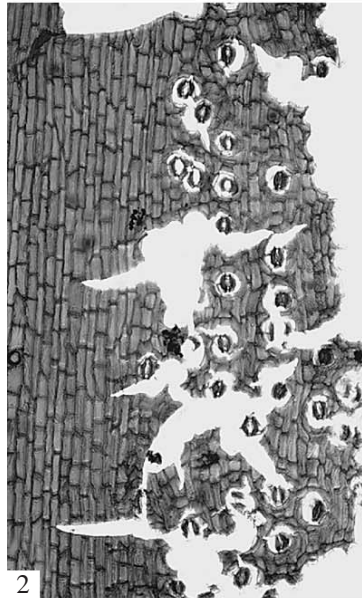
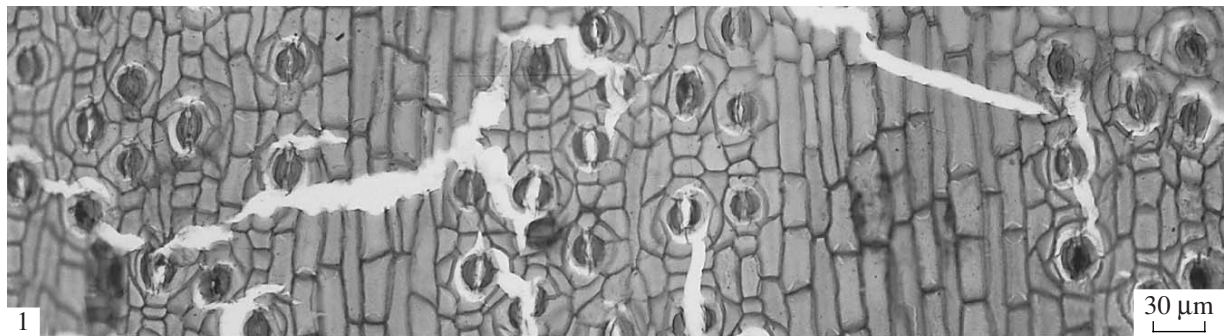
Comparison and remarks. All members of *Tritaenia* have uniform leaf lamina morphology and are only reliably differentiated on the basis of epidermal characters. The specimen under description is virtually identical to *T. striata* and *T. glabra* from the same deposits, *T. scotica* from the Upper Jurassic of Scotland, *T. linkii* from the Lower Cretaceous, and *T. crassa* from the Upper Cretaceous.

The leaf lamina morphology of *Tritaenia* sp. shows the greatest similarity to that of *T. striata*: a median groove on the upper side of the leaf lamina is not developed. All other members of the genus have a developed median groove.

Tritaenia sp. most resembles *T. crassa* both in the relief of the cuticle of the lower side of the leaf lamina

Explanation of Plate 36

Figs. 1–4. *Tritaenia striata* Gordenko, 2004, holotype PIN, no. 4727/368: (1) cuticle of the upper epidermis, SEM; (2) papillae hanging over a stomatal apparatus, SEM; (3) fragment of a stomatal band, note an abortive stoma, SEM; (4) stomatal band with amphicyclic stomatal apparatuses, SEM.



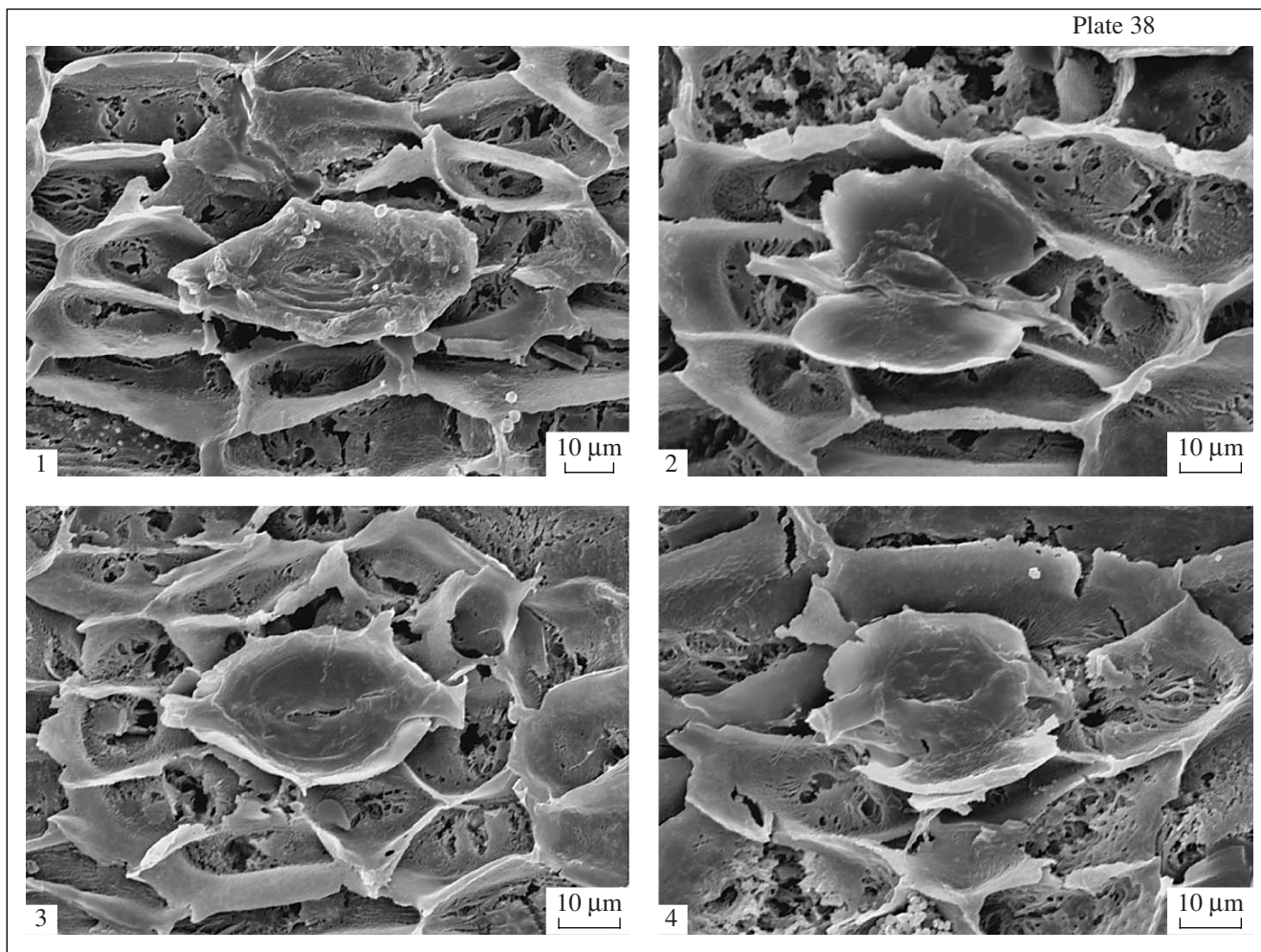
Explanation of Plate 37

Figs. 1–4. *Tritaenia glabra* Gordenko, 2004: (1) PIN 4727/200, lower epidermis topography, three stomatal bands are visible; (2, 3) PIN 4727/26; (2) spread of leaf margin, $\times 80$; (3) detail of a stomatal band, $\times 160$; (4) PIN, no. 4727/602, stomatal band with abnormal stomatal apparatuses, $\times 100$.

Figs. 5–8. *Tritaenia* sp., PIN, no. 4727/14: (5) spread of leaf margin, $\times 100$; (6) developing stomatal apparatus, $\times 600$; (7, 8) stomatal apparatuses, $\times 600$.

Figs. 9, 10. *Tritaenia striata* Gordenko, 2004, PIN, no. 4727/601: (9) lower epidermis topography, $\times 20$; (10) stomatal band, $\times 80$.

Plate 38



Explanation of Plate 38

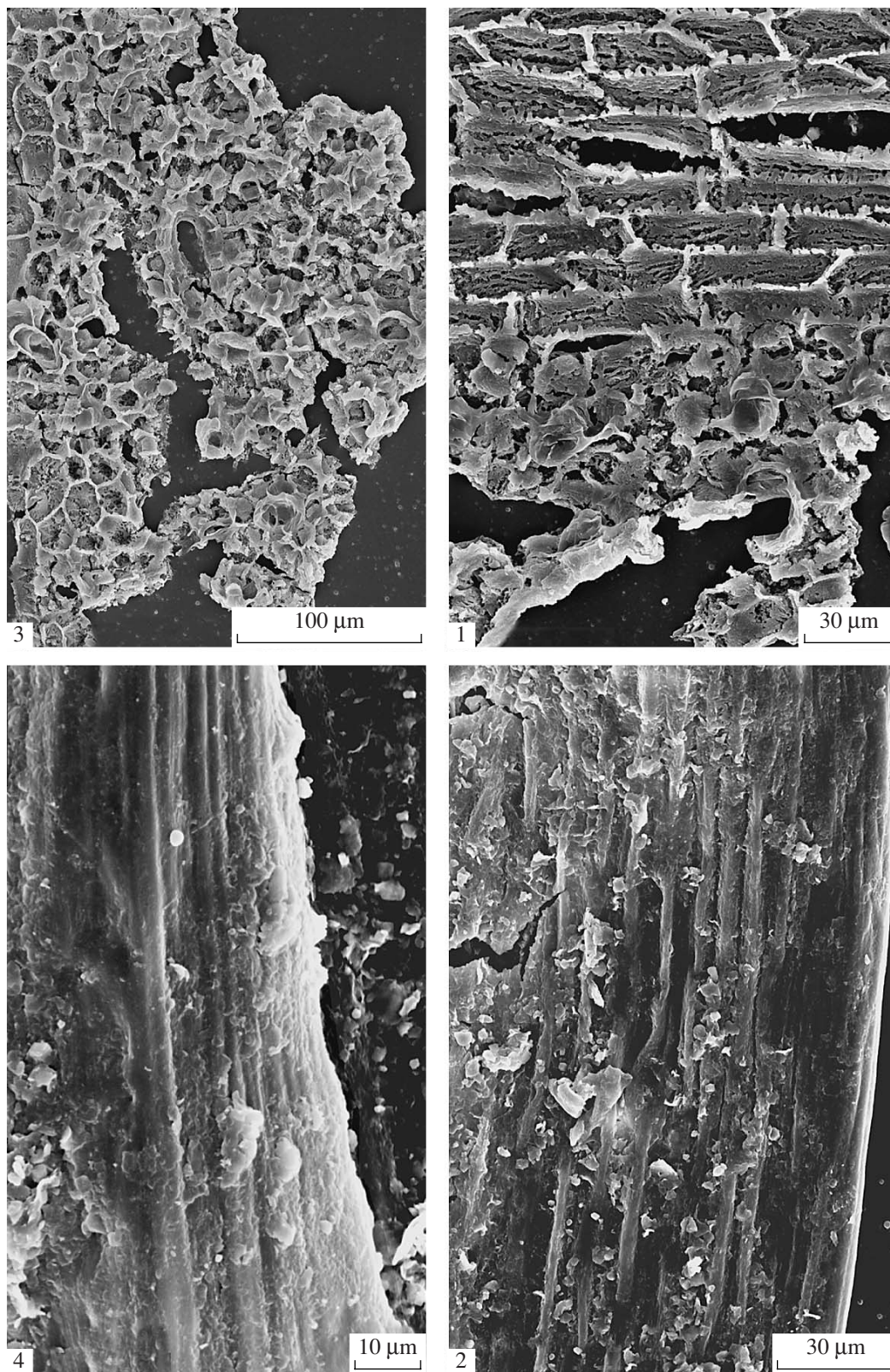
Figs. 1–4. *Tritaenia striata* Gordenko, 2004, holotype PIN, no. 4727/368, stomatal apparatuses, SEM.

and in the morphology and arrangement of stomatal apparatuses: *T. crassa* has thin ribs in costal zones and lacks trichomes. Both *Tritaenia* sp. and *T. crassa* are characterized by subsidiary cells differentiated into two lateral and two polar cells, absence of papillae on subsidiary cells, and the presence of two to four encircling cells. *Tritaenia* sp. has seven stomatal bands; *T. crassa* has three to five stomatal bands and relatively wide median band. Both *Tritaenia* sp. and *T. crassa* have numerous obliquely or transversely orientated stomata. As far as the available material includes only two fragmentary leaves showing mosaic characters, that pre-

vents their assignment to earlier described species, it is reported here as *Tritaenia* sp.

A certain similarity in the stomatal morphology is present between *Tritaenia* sp. and *T. glabra*. However, the latter species is characterized by a weakly developed or reduced median stomatal band. In addition, *Tritaenia* sp. differs from *T. scotica*, *T. linkii*, and *T. striata* in the absence of papillae on subsidiary cells.

Material. Two specimens represented by impressions and phytoleims of fragmentary leaves.

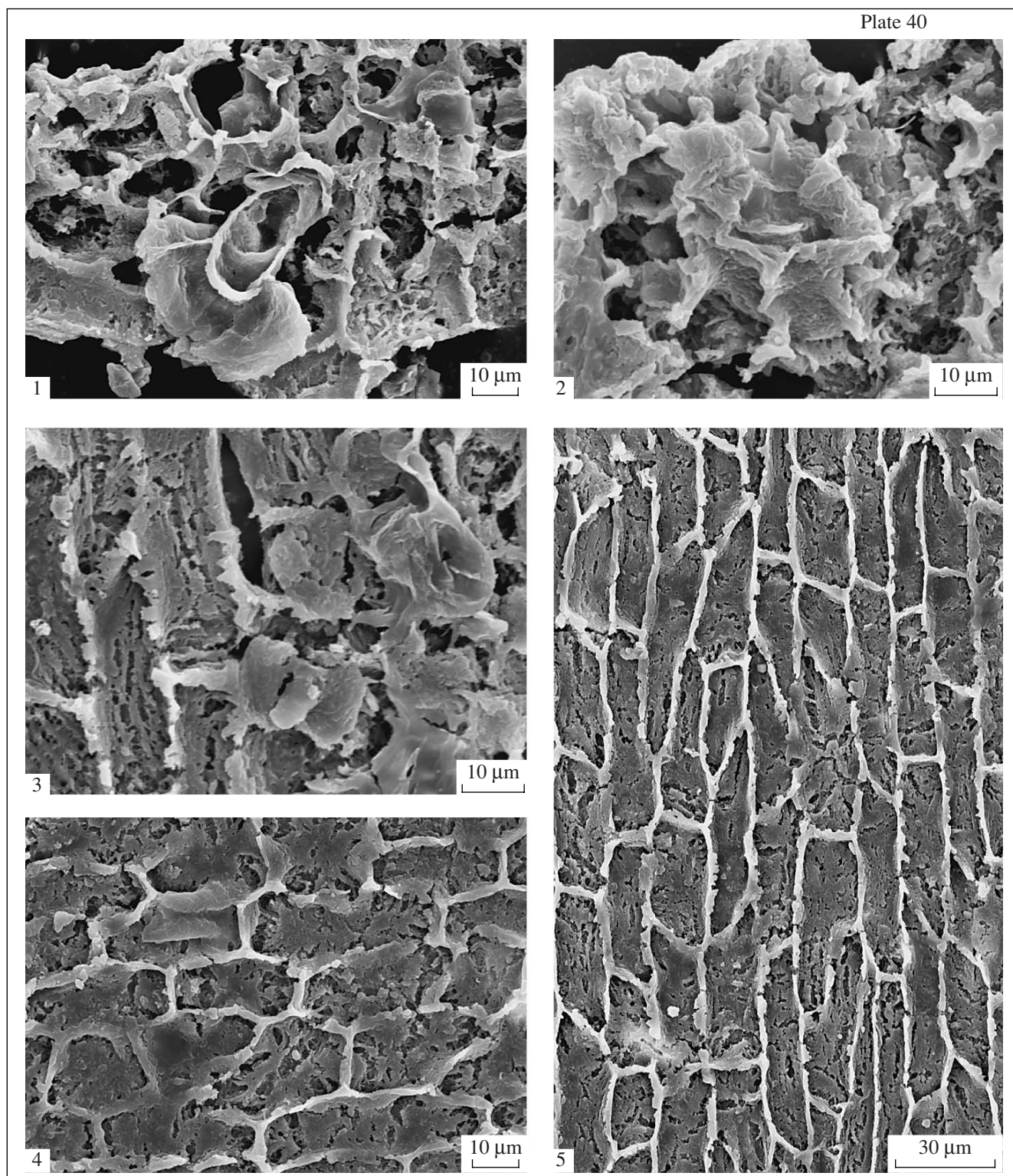


Explanation of Plate 39

Figs. 1–3. *Marskea* sp., PIN, no. 4727/116: (1) Marginal zone of leaf; (2) longitudinal striation of marginal zones of a leaf, SEM; (3) fragment of a stomatal band, SEM.

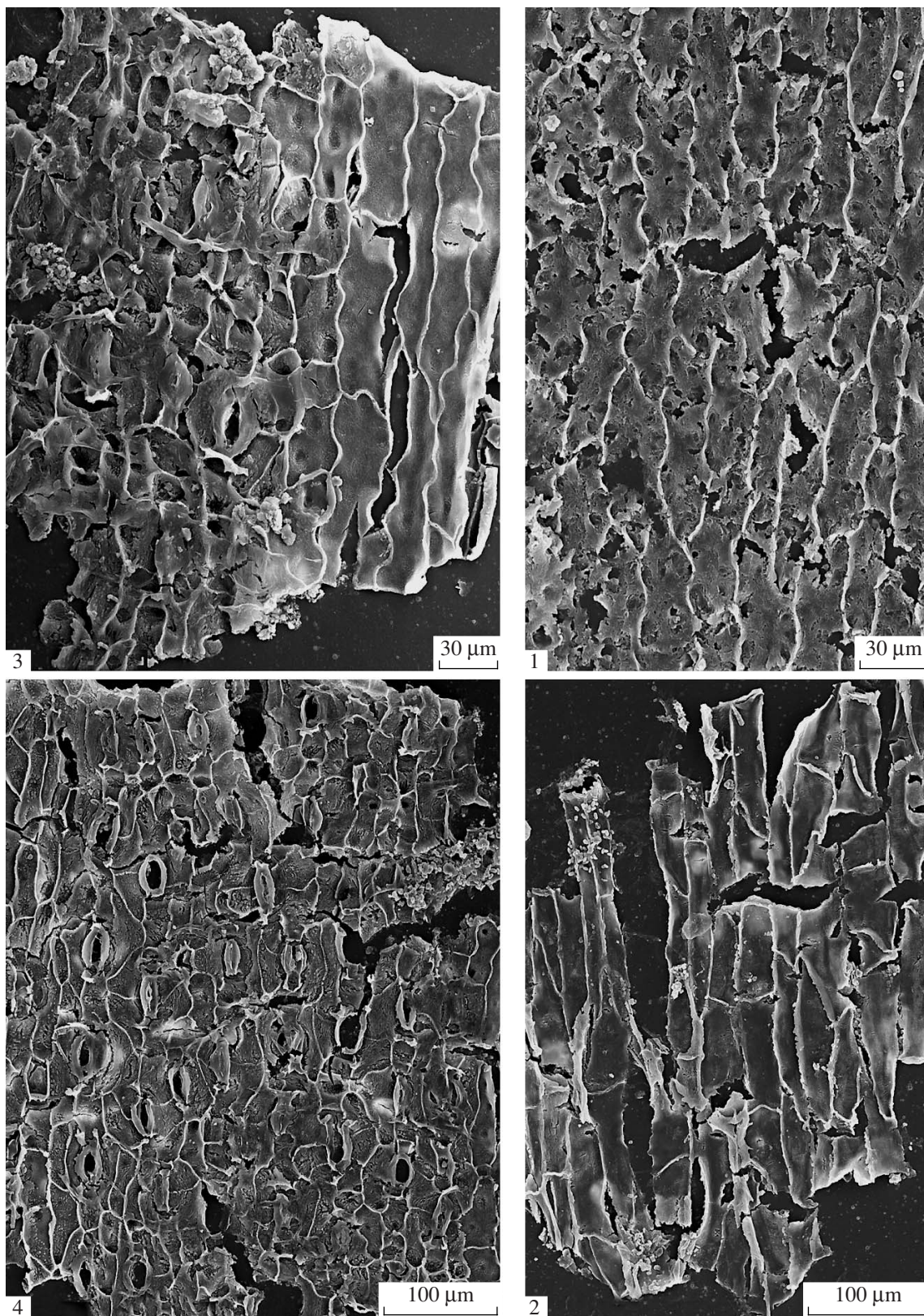
Fig. 4. *Elatocladus* sp. 2, PIN, no. 4727/345, longitudinal striation of marginal zones of a leaf, SEM.

Plate 40



Explanation of Plate 40

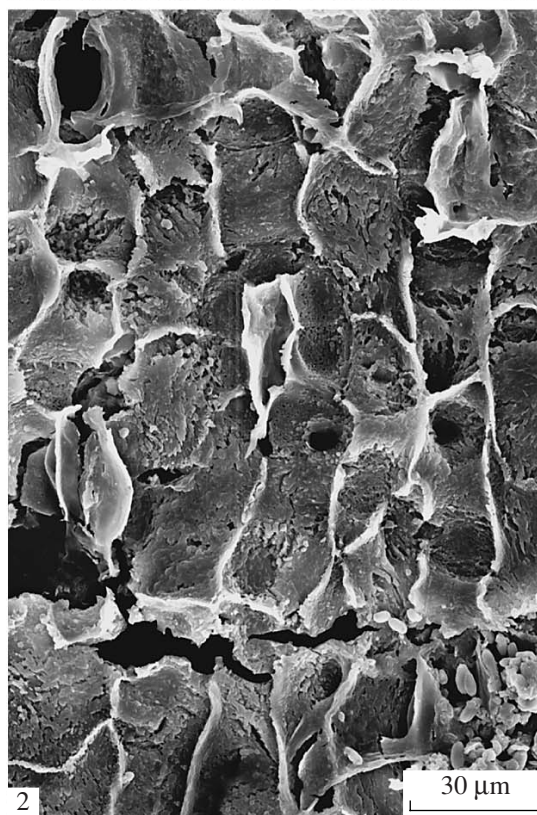
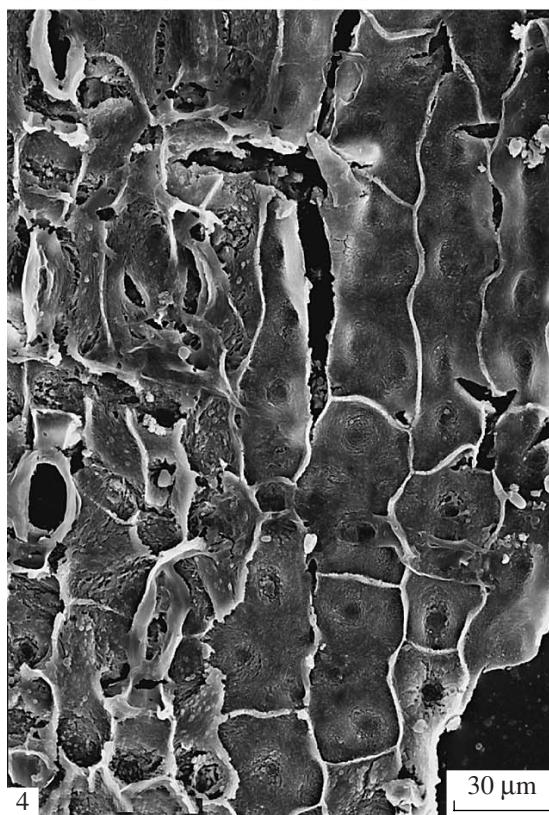
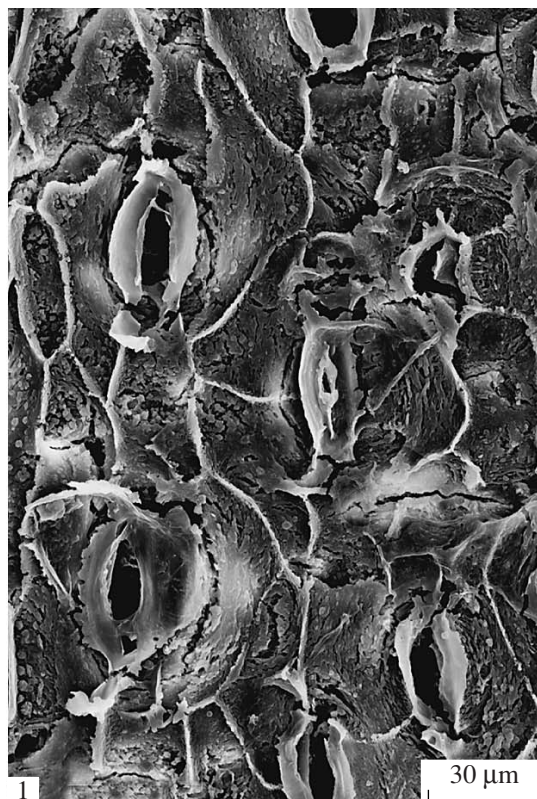
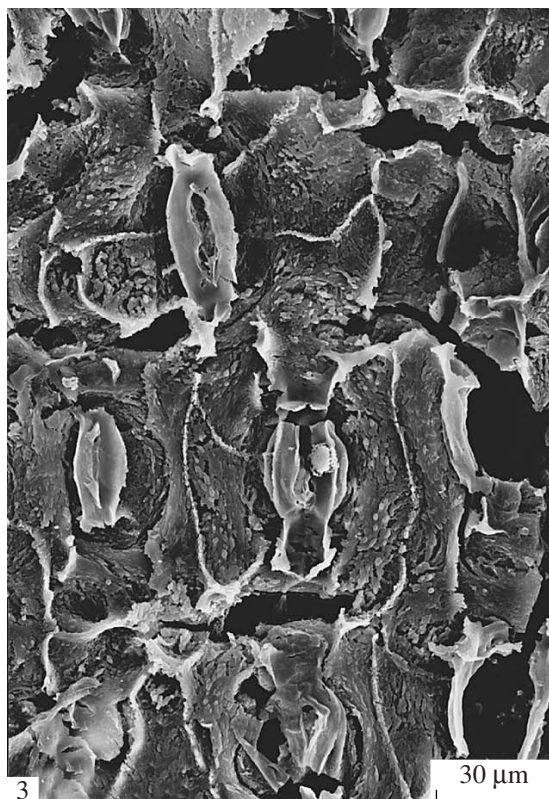
Figs. 1–5. *Marskea* sp., PIN, no. 4727/116: (1) stomatal apparatus, SEM; (2) abnormal stomatal apparatus, SEM; (3) boundary between stomatal and non-stomatal zones, SEM; (4) cuticle of the upper epidermis in the marginal zone, SEM; (5) cuticle of the upper epidermis over the midrib, SEM.



Explanation of Plate 41

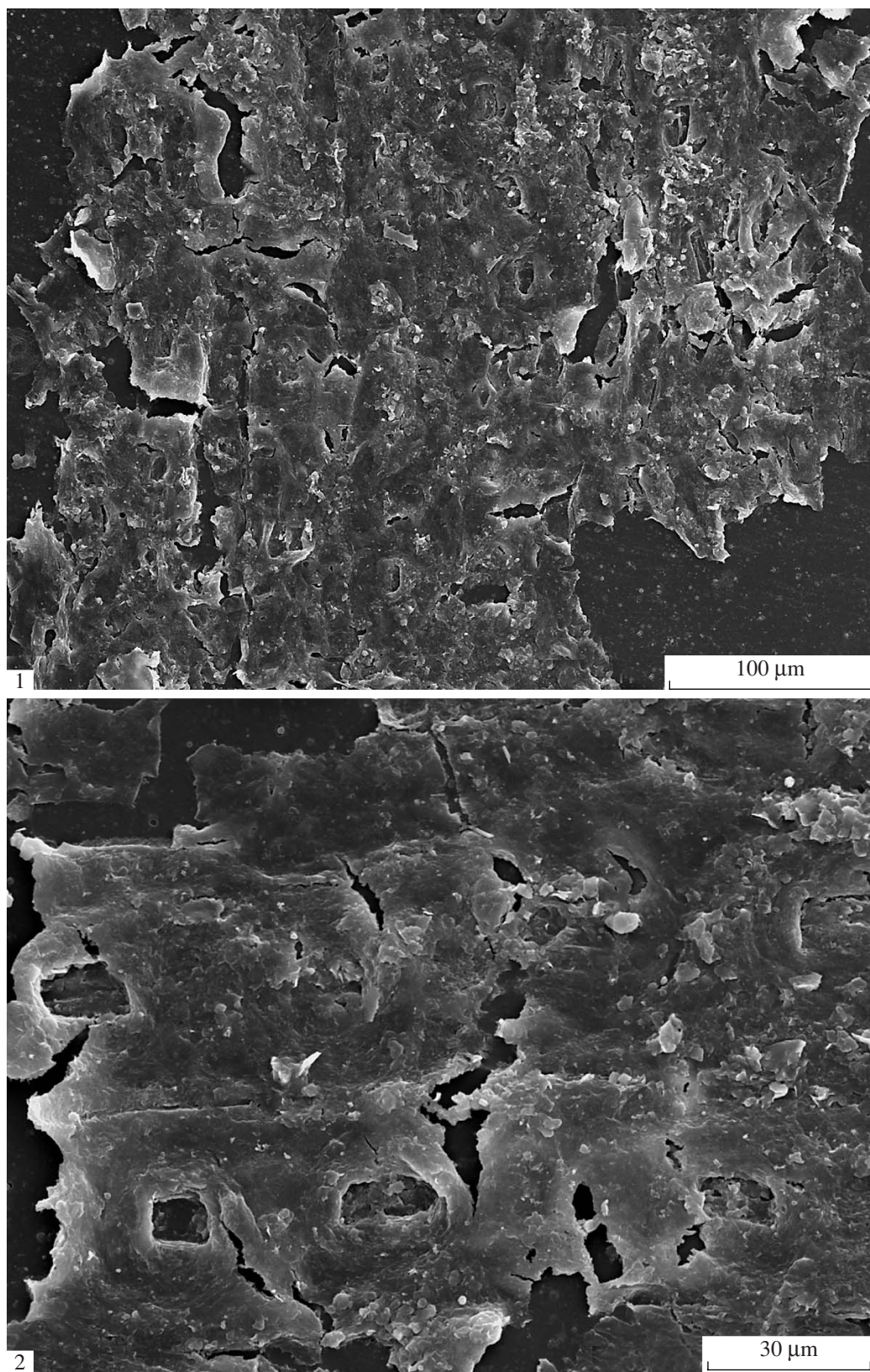
Figs. 1–4. *Elatocladus* sp., PIN, no. 4727/351; (1) cuticle of the upper epidermis, SEM; (2) cuticle of the epidermis over a vein, SEM; (3) marginal zone of a leaf, papillae on ordinary epidermal cells are visible, SEM; (4) stomatal band, SEM.

Plate 42



Explanation of Plate 42

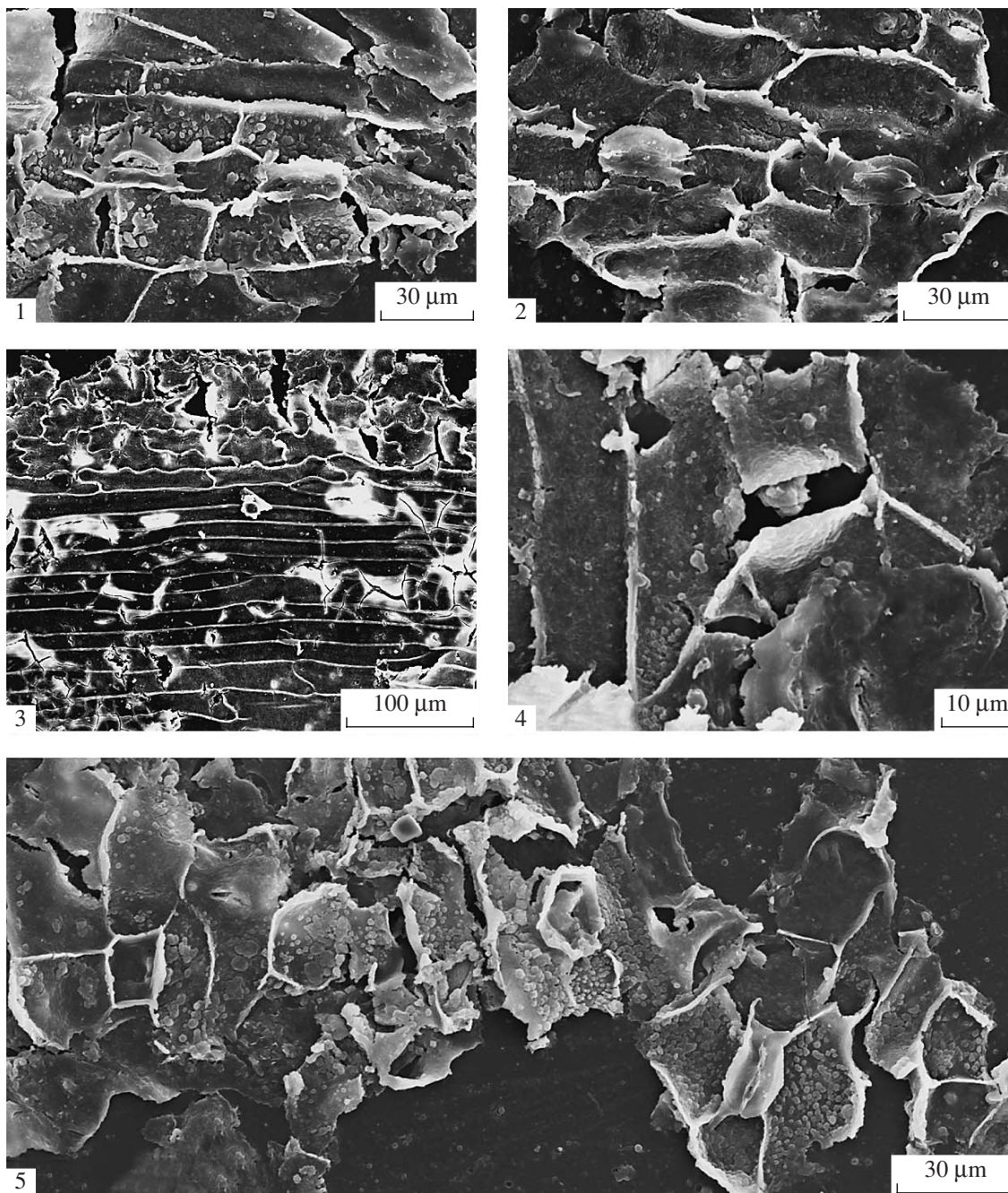
Figs. 1–4. *Elatocladus* sp., PIN, no. 4727/351; (1–3) fragments of a stomatal band, SEM; (4) small hollow papillae on ordinary epidermal cells, SEM.



Explanation of Plate 43

Figs. 1, 2. *Cephalotaxopsis* sp., PIN, no. 4727/345; (1) external surface of the lower epidermis in the area of a stomatal zone, SEM; (2) Florin rings over stomatal apparatuses, SEM.

Plate 44



Explanation of Plate 44

Figs. 1–5. *Cephalotaxopsis* sp., PIN, no. 4727/345: (1, 2) longitudinally orientated stomatal apparatuses, SEM; (3) epidermis cuticle of the marginal zone of a leaf, SEM; (4) transversely orientated stomatal apparatus, SEM; (5) fragment of a stomatal zone, SEM.

Genus *Oswaldheeria* Bose et Manum, 1990

Oswaldheeria aff. *macrophylla* (Florin) Bose et Manum, 1990

Plate 19, figs. 10, 11; Plate 20, figs. 1–4; Plate 21, figs. 1–4; Plate 22, figs. 1–5

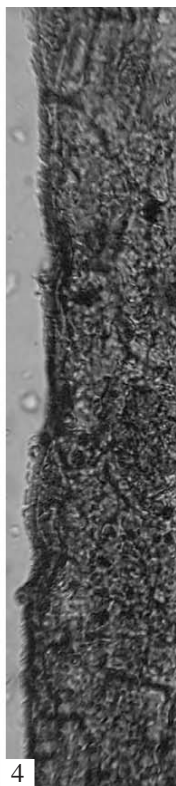
Description. The material represents fragmentary leaves without apices and bases (Pl. 19, figs. 10, 11; Pl. 20, fig. 1). The average leaf width is 3 mm. A longitudinal groove is situated on the upper side of

the leaf lamina. The venation is parallel. At least two veins occur per the leaf width. There are intercostal resin canals. (Pl. 20, fig. 2).

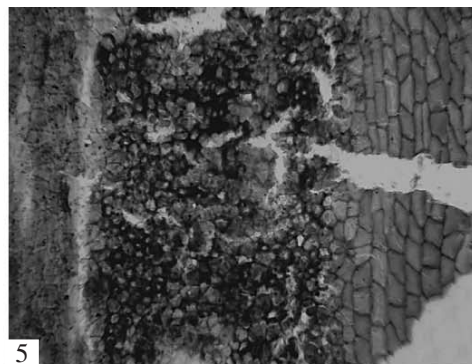
The leaves are hypostomous. The cuticle of the upper epidermis is 4 µm thick, as thick as the cuticle of the lower epidermis. The upper epidermis shows tetrapentagonal longitudinally elongated cells, 30–60 µm



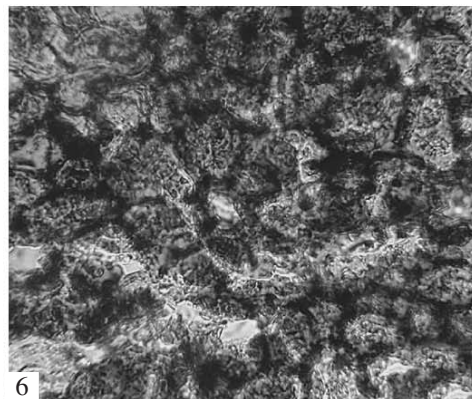
1



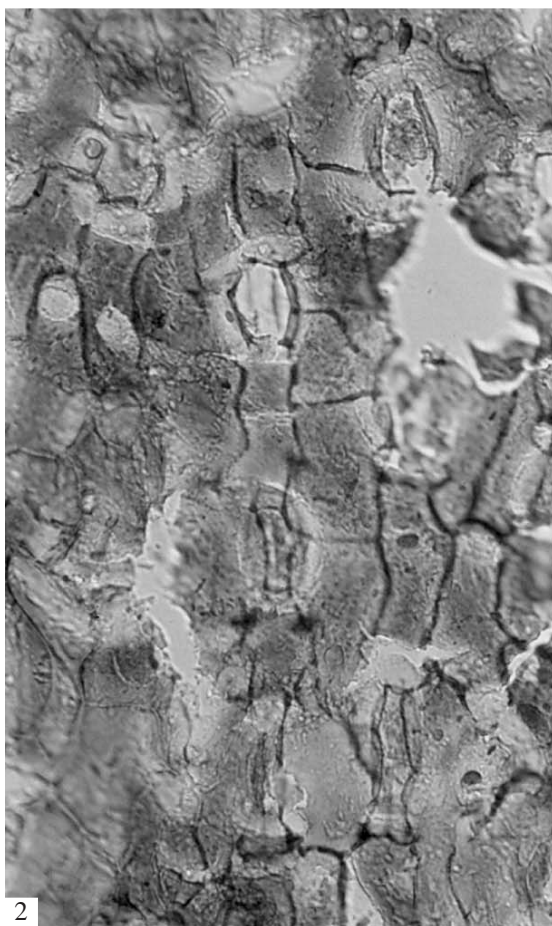
4



5



6



2



3

long and 10–20 μm wide. The upper surface of the cuticle is covered with thin longitudinal continuous ribs (Pl. 21, fig. 1). Trichomes are lacking.

The cuticle of the lower epidermis shows the only stomatal band and two marginal non-stomatal zones (Pl. 20, fig. 1; Pl. 22, fig. 1). The width of the stomatal zone is 1300–1500 μm , and the width of the marginal zones is 500 μm . Ordinary cells of the marginal zones are indistinguishable from those of the upper epidermis. Within the stomatal zone, the stomata are arranged in interrupted chains and the orientated longitudinally (Pl. 22, fig. 2). Ordinary epidermal cells within the stomatal chains are much smaller than those between the chains: 20–30 μm long and 10–20 μm wide. Ordinary cells between the chains are 40–150 μm and 10–20 μm wide. The stomatal apparatuses vary from monocyclic (Pl. 22, fig. 3) to amphicyclic (Pl. 22, fig. 5). The length of the guard cells of the stomatal apparatuses is 35–45 μm ; the width of the stomata is 25–35 μm . There are four or five, or, more rarely, six subsidiary cells. Two or three of them are polar, and the others are lateral. Each subsidiary cell usually bears one dome-shaped papilla. The papillae close over the stomatal aperture (Pl. 22, figs. 3, 5). However, there is a considerable number of stomatal apparatuses with subsidiary cells lacking papillae. The external surface of the cuticle of the stomatal zone is covered with longitudinal interrupted ribs (Pl. 20, figs. 2, 4) and dense papillae 7–8 μm in diameter (Pl. 20, figs. 3, 4; Pl. 21, fig. 4).

Comparison and remarks. Such character as the presence of papillae on subsidiary cells of stomatal apparatuses makes the specimens under description similar to *O. macrophylla* Bose et Manum from the Middle Jurassic of northern Norway and *O. arctica* Bose et Manum from the Lower Cretaceous of the Arctic Canada (Bose and Manum 1990), and *O. samylinae* (Sveshnikova) Hvalj and *O. latiuscula* Nosova from the Lower Cretaceous of the Lena River Basin (Nosova, 2001). The main characters of the specific diagnostic in the genus *Oswaldheeria* are the leaf length and the presence/absence of papillae on subsidiary cells of stomatal apparatuses. For example, *O. macrophylla* and *O. arctica* have papillae on subsidiary cells and only differ in the leaf length: the latter species has nearly two times shorter leaves. All specimens from the Peski locality are incompletely preserved leaves; therefore, a reliable determination up to the species level is difficult. In addition, *O. macrophylla* has distinct papillae on both ordinary cells of the lower epidermis and subsidiary cells of stomatal apparatuses. Specimens from the Peski locality have small dense papillae on epidermal cells, different from those of *I. macrophylla*; papillae

on subsidiary cells are not always present. Keeping in mind the Middle Jurassic age of the specimens under consideration and their vague differences from *O. macrophylla* (only development of papillae), they are reported here as *Oswaldheeria* aff. *macrophylla*.

Material. Four phytoliteims of incomplete leaves and dispersed cuticle obtained by bulk maceration.

Family Taxodiaceae Lindley, 1838

Genus *Marskea* Florin, 1958

Marskea sp.

Plate 19, fig. 12; Plate 39, figs. 1–3; Plate 40, figs. 1–5; Plate 45, figs. 4–6

Description. The material represents one nearly complete linear leaf with a distinct midrib (Pl. 19, fig. 12). The leaf apex and base are not preserved. The length of the leaf is 35 mm, and the width is 2 mm. The width of the midrib is 0.5 mm.

The leaf is hypostomous. The cuticle of the upper epidermis is thicker than the cuticle of the lower epidermis. Ordinary cells of the upper epidermis are trihedral to hexahedral, with slightly curving unevenly cutinized toothed anticlinal walls. In marginal zones, they are nearly isodiametric (Pl. 40, fig. 4) and up to weakly longitudinally elongated (Pl. 40, fig. 5); over the midrib, they are strongly longitudinally elongated. The length of the cells is 40–60 μm , and the width is 20–30 μm .

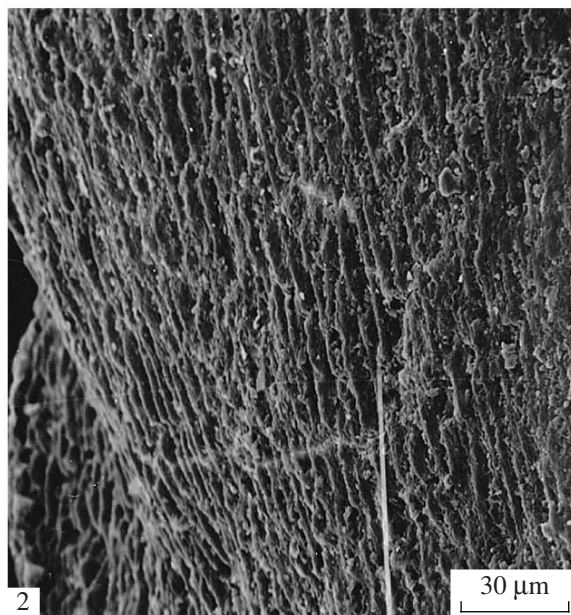
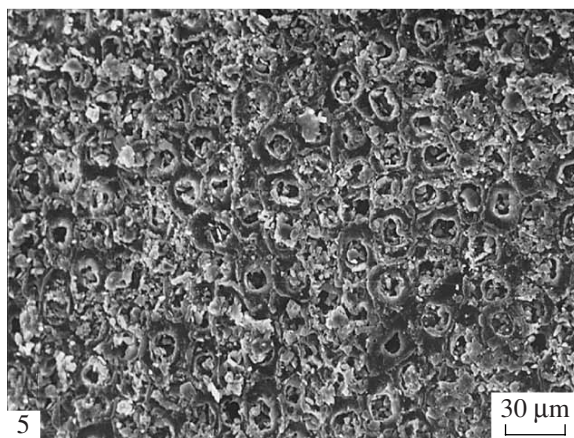
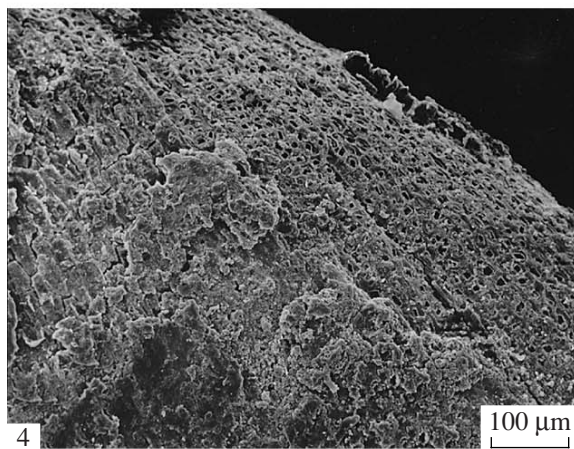
The stomata are grouped into two stomatal bands, separated by a non-stomatal band, corresponding to the midrib. The width of the stomatal bands is about 600 μm . The width of the median non-stomatal band is 500 μm . The width of marginal non-stomatal bands is about 200 μm . Ordinary epidermal cells of the non-stomatal zones are three times as large as those within the stomatal bands (Pl. 39, fig. 1). The length of the epidermal cells in non-stomatal zones is 40–70 μm , and the width is about 20 μm . Ordinary cells within the stomatal bands are isodiametric, 10–25 μm in diameter. The stomatal apparatuses are irregularly arranged within the stomatal bands (Pl. 39, fig. 3; Pl. 40, fig. 5). The stomatal apparatuses are sunken, monocyclic, with a predominant longitudinal or (more rarely) oblique orientation. The external periclinal walls of the guard cells of the stomatal apparatuses are wing-shaped (Pl. 40, figs. 1, 3); very rarely, the guard cells are not cutinized (Pl. 40, fig. 2). The cutinization of the inner periclinal walls of the guard cells is often preserved (Pl. 40, fig. 3). The length of the stomatal apparatuses is about 25 μm .

There are six to eight subsidiary cells. They bear small and strongly cutinized proximal papillae closing over the aperture (Pl. 45, fig. 6). Adjacent stomatal

Explanation of Plate 45

Figs. 1–3. *Elatocladus* sp., PIN, no. 4727/351: (1) stomatal band, $\times 100$; (2) stomatal apparatuses, $\times 400$; (3) cuticle of the upper epidermis.

Figs. 4–6. *Marskea* sp., PIN, no. 4727/116: (4) marginal part of a leaf with small cutin tooth, $\times 500$; (5) stomatal band, $\times 50$; (6) stomatal apparatus, $\times 400$.



apparatuses occasionally share lateral and polar subsidiary cells.

Thin longitudinal ribs are observed in the marginal zones of the leaf lamina (Pl. 39, fig. 2). Small teeth are developed along the leaf margin (Pl. 45, fig. 4).

Comparison and remarks. The specimen from the Peski locality shows the greatest similarity in the leaf lamina morphology to *Marskea sibirica* Samylina from the Jurassic of Siberia (Samylina, 1994), but differs from the latter species in the width of the stomatal bands: they are three times as wide and are comparable with the stomatal bands of *M. jurassica* Harris from the Middle Jurassic of Yorkshire (Harris, 1968). However, *M. jurassica* is characterized by relatively short leaves (20–25 µm), whereas the leaf length of the specimen from the Peski locality is 35 mm. Other species of this genus differ from the specimen under consideration both in size and in epidermal morphology.

It should be noted that the specimen studied has virtually straight anticlinal cellular walls (weak sinuosity only is observed in marginal zones), a feature that is not characteristic of the genus *Marskea*. However, other epidermal characters support such generic affiliation. As far as the collection only contains one incomplete leaf, the erection of a new species seems unjustified: it is described here in open nomenclature.

Material. One specimen represented by an impression and a phytolite.

Family Cephalotaxaceae Neger, 1907

Genus *Cephalotaxopsis* Fontaine, 1889

Cephalotaxopsis sp.

Plate 19, figs. 13–15; Plate 39 fig. 4; Plate 43, figs. 1, 2; Plate 44, figs. 1–5

Description. The collection contains numerous fragments of linear-lanceolate leaves (Pl. 19, figs. 13–15). Middle parts of leaves prevail: apices occur less often. Bases are not preserved. The margins of the leaf lamina are straight and often slightly rolled down. The leaves are gradually tapering toward the apex. The apices are acuminate. The width of the leaf lamina in the middle part is 4–5 mm. The midrib is distinct and reaches the leaf apex. The width of the midrib is 0.5 mm.

The cuticle is very thin. As a rule, only the cuticle of marginal zones of the leaf and the cuticle over the midrib survive maceration. The cuticle of the stomatal zones is only preserved in some specimens.

The leaf is hypostomous. The upper epidermis over the stomatal bands is constituted of rectangular, trapezoidal, and fusiform cells with sinuous anticlinal walls. The length of the cells is 63–116 µm, and the width is 15–31 µm.

The cuticle of the lower epidermis is subdivided into two stomatal zones, separated by three non-stomatal

zones. The width of the stomatal zones is 500–700 µm. The median non-stomatal zone corresponds to the zone of a vascular bundle. Ordinary cells of the median zone are rectangular or fusiform and strongly elongated in the longitudinal direction. Ordinary cells of marginal zones are tetra- or pentagonal, strongly longitudinally elongated (Pl. 44, fig. 3). Their length is 90–230 µm, and the width is 22–48 µm. Ordinary cells of the marginal zones of the lower epidermis are amoeboid and slightly elongated in the longitudinal direction (Pl. 44, fig. 3). The external epidermal surface in the marginal zones is covered with thin longitudinal ribs (Pl. 39, fig. 4). The stomatal apparatuses within the stomatal zones form relatively distinct longitudinal rows (Pl. 43, figs. 1, 2; Pl. 44, figs. 1, 2). The stomatal apparatuses are orientated in longitudinal or, more rarely, in transverse direction (Pl. 44, figs. 1, 2, 4, 5); they are monocyclic. There are four or five or, more rarely, six subsidiary cells (Pl. 57, figs. 1, 2, 4, 5). Within rows, stomatal apparatuses usually shared polar subsidiary cells. Subsidiary cells of the stomatal apparatuses form distinct Florin rings (Pl. 53, fig. 2). The guard cells of the stomatal apparatuses are narrowly wing-shaped. They are identical to ordinary epidermal cells in the degree of cutinization. The length of the stomata is 25–30 µm, and the width is 14–24 µm. Polar extensions of the guard cells are wide and relatively long (4–10 µm).

Resin canals are lacking; however, maceration reveals rounded resin bodies.

Comparison. The leaf and epidermal morphology of the specimens under consideration suggests their relation with members of the Cephalotaxaceae. The studied leaves most closely resemble in leaf and epidermal morphology *Cephalotaxopsis* Font. (Fontaine, 1889), known in the Northern Hemisphere from the Jurassic onward. However, as far as the attachment of these leaves to the shoot is unknown, they are determined here as *Cephalotaxopsis* sp.

Remarks. The relation with the Cephalotaxaceae seems most probable by the morphology of the leaf lamina and epidermal characteristics.

Material. Eleven specimens represented by phytolites and impressions of incomplete leaves.

Formal Genera of Conifers Introduced on the Basis of Leaf Remains

Genus *Brachyphyllum* Brongniart, 1828

Brachyphyllum sp.

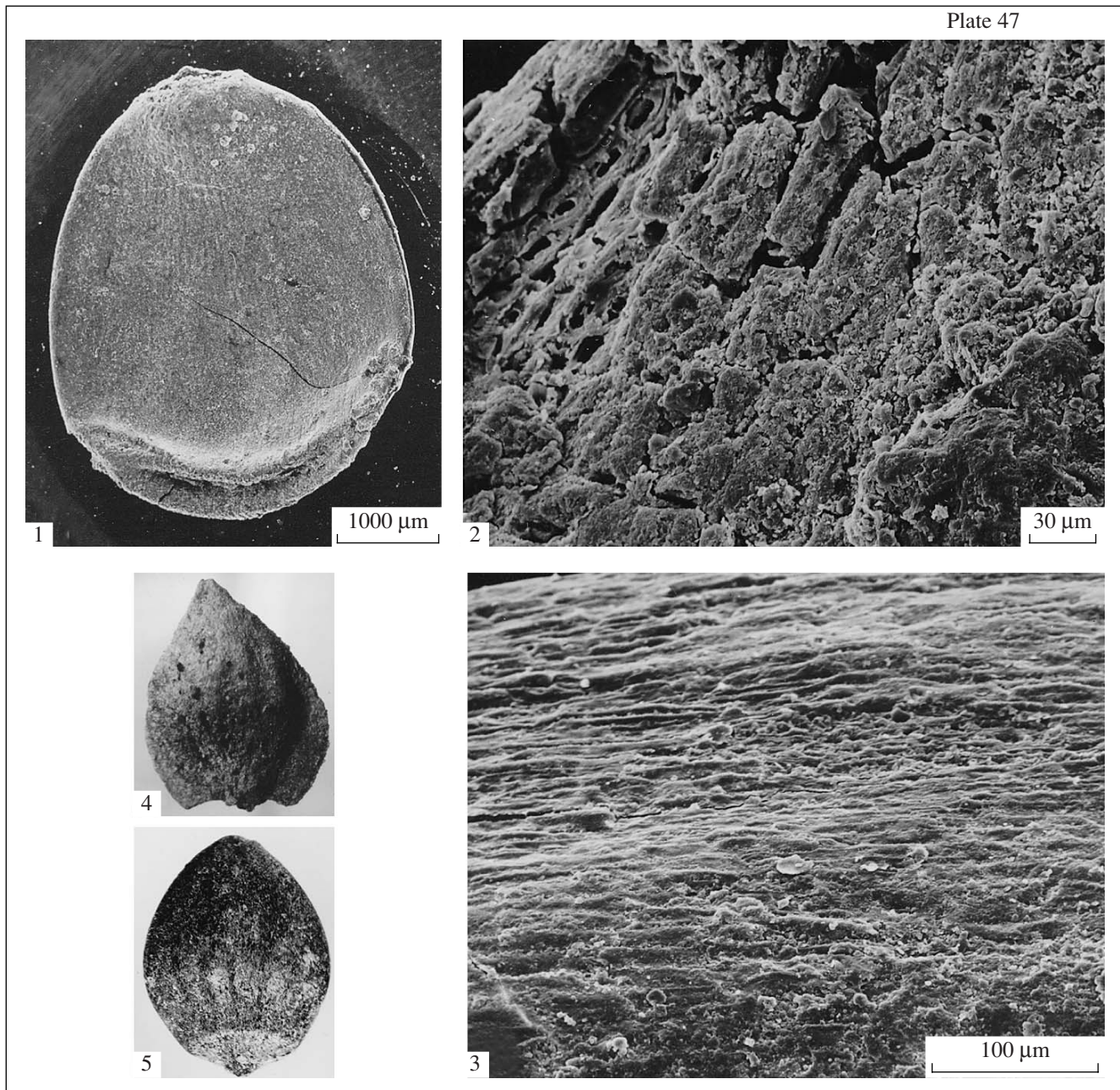
Plate 19, fig. 16

Description. A shoot fragment bear helically arranged scaly leaves (Pl. 19, fig. 16). The length of the

Explanation of Plate 46

Figs. 1, 2. *Carpolithes* sp. 1, PIN, no. 4727/905: (1) seed, general view, SEM; (2) seed surface, a detail, SEM.

Figs. 3–5. *Carpolithes* sp. 2, PIN, no. 4727/904: (3) seed, general view, SEM; (4) epidermal and sclerified cells of the integument, SEM; (5) sclerified cells of the integument, SEM.



Explanation of Plate 47

Figs. 1–3. *Carpolithes* sp. 3, PIN, no. 4727/908; (1) seed, general view, SEM; (2) epidermal and sclerified cells of the integument, SEM; (3) seed surface, SEM.

Fig. 4. *Carpolithes* sp. 5, PIN, no. 4727/906, seed, general view, $\times 3.8$.

Fig. 5. *Carpolithes* sp. 4, PIN, no. 4727/909, seed, general view, $\times 3.9$.

fragment is 22 mm, and the width is 2.5 mm. There are three leaves per one half of the convolution. Lower leaves imbricate over upper leaves covering their bases. The leaves are scaly, oval-rhomboidal, with an acuminate base. The midrib is not visible on the surface of the leaf lamina. A keel in the lower part of the upper side of the leaf lamina is indistinct. The leaf length is 2–2.5 mm, and the width is 1–1.2 mm.

The cuticle is not preserved.

Remarks. The arrangement of leaves on the shoot and the leaf outline allow one to assign this specimen to the formal genus *Brachyphyllum* Brongn. As far as the cuticle was not preserved, the specific determination is impossible.

Material. One specimen represented by a fragmentary leafy shoot, preserved as an impression and phytoliteim.

Genus *Elatocladus* Halle, 1913*Elatocladus* sp.

Plate 19, fig. 17; Plate 41, figs. 1–4; Plate 42, figs. 1–4

Description. The leaf fragment is up to 30 mm long and 2.5 mm wide (Pl. 19, fig. 17). The midrib is distinct, about 0.2 mm wide. The leaf lamina margin is slightly curved down.

The leaf is hypostomous. The upper cuticle is slightly thicker than the lower cuticle. The thickness of the upper cuticle is 2.3 μm . Ordinary cells of the upper epidermis are rounded-rectangular, strongly longitudinally elongated, up to 150 μm long (Pl. 45, fig. 3). Ordinary epidermal cells of marginal zones of the upper epidermis are fusiform, more rarely rectangular, or trapezoidal. The anticlinal cellular walls are weakly sinuous (Pl. 41, fig. 1). The length of the ordinary epidermal cells in marginal zones is 60–85 μm , and the width is 20–37 μm .

The anticlinal walls become less sinuous toward the midrib; the sinuosity disappears completely in the area of the midrib (Pl. 41, fig. 2). The epidermal cells over the midrib are 80–130 μm long and 13–60 μm wide.

The lower epidermis shows two stomatal zones separated by a non-stomatal zone that corresponds to the midrib. The width of stomatal zones is about 400 μm (Pl. 41, fig. 4; Pl. 45, fig. 1). The width of the median non-stomatal zone is 1000 μm . Ordinary epidermal cells of marginal zones are rectangular, with weakly sinuous anticlinal walls. Each cell bears one to four papillae, 6–9 μm in diameter at the base (Pl. 45, fig. 4).

The stomatal apparatuses within the stomatal zone form longitudinal, occasionally indistinct, rows (Pl. 42, figs. 1, 3; Pl. 45, fig. 2). There are eight to ten such rows per width of the stomatal zone. The stomatal apparatuses are orientated longitudinally and are monocyclic. The guard cells are narrow, nearly rod-like, with a narrow rim around the aperture, not differing from ordinary epidermal cells in the degree of cutinization. The inner periclinal walls of the guard cells are cutinized. The length of the guard cells of the stomatal apparatuses is 30–45 μm , and the width is 18–20 μm . Polar extensions of the guard cells are long, dove-tailed, 9–10 μm long. Subsidiary cells are non-specialized, but their periclinal walls are slightly thicker than those in ordinary epidermal cells. The stomatal apparatuses have four to eight subsidiary cells, two of which are polar. The subsidiary cells hang over the guard cells forming a Florin ring. Rows of stomatal apparatuses tightly contact with each other (Pl. 42, figs. 1–3), ordinary cells within stomatal zones occur extremely rarely. Occasionally, ordinary and subsidiary cells of stomatal apparatuses bear small hemispherical papillae, 6–9 μm in diameter at the base. One cell bears one to three papillae (Pl. 42, figs. 2, 4).

Resin canals are lacking, but maceration reveals spherical resin bodies.

Comparison. In leaf lamina morphology, the specimen under description shows features common

with the Jurassic conifers *Podocarpophyllum* Gomolitzky, *Storgaardia* Harris, *Tomharrisia* Florin, *Torreya* Arnott, and formal genus *Elatocladus* Halle.

In the morphology of the upper epidermis and marginal zones of the lower epidermis, the specimen shows a significant similarity with *Marskea jurassica* (Florin) Harris from the Middle Jurassic of Yorkshire (Harris, 1979), but differs in the morphology and arrangement of stomatal apparatuses within the stomatal zone. *Elatocladus ramosus* (Florin) Harris from the Middle Jurassic of Yorkshire (Harris, 1979) is also significantly similar to the specimen under consideration, but it has teeth in the marginal areas of the leaf; in addition, stomatal apparatuses of this species are situated within the stomatal zone in a different way.

Remarks. The epidermal morphology allows one to consider the specimens within the Taxodiaceae. As far as *Elatocladus* includes fossil leaves of the Taxodiaceae, the specimen is assigned to this genus as *Elatocladus* sp.

Material. One specimen represented by an impression and phytolite.

*Gymnosperms of Unknown Systematic Position***Genus *Carpolithes* Sternberg, 1825***Carpolithes* sp. 1

Plate 46, figs. 1, 2

Description. The seed is elliptic, apparently radial. The chalazal part is destroyed, but apparently was rounded (Pl. 46, fig. 2). The length of the cells is 15–150 μm , and the width is 10–15 μm . The thickness of the integument is about 133 μm . A layer under the epidermis consists of rounded sclerified cells. Most probably, the micropyle was short.

Remarks. The singleness of the material did not allow maceration, and the seed is described in open nomenclature.

Material. One phytolite.

Carpolithes sp. 2

Plate 46, figs. 3–5

Description. The seed is bilateral, oval. The chalaza is rounded, and the micropyle is attenuated (Pl. 46, fig. 3). The length of the seed is 4.6 mm, and the width is 3.2 mm.

The upper cuticle of the epidermis is relatively thin. The epidermal cells are tetragonal to hexagonal, with straight anticlinal walls, slightly elongated in longitudinal direction (Pl. 46, fig. 4). The length of the epidermal cells is 40–60 μm , and the width is 20–26 μm . A layer of sclerified cells, which are rounded in plane, is discovered under the epidermis (Pl. 46, fig. 5). The average diameter of the sclerified cells is 25 μm .

Remarks. The singleness of the material did not allow maceration, and the seed is described in open nomenclature.

Material. One phytolite.

Carpolithes sp. 3

Plate 47, figs. 1–3

Description. The seed is bilateral, ellipsoidal. The chalazal part of the seed is rounded (Pl. 47, fig. 1). The seed is slightly tapering toward the micropyle. The micropyle is destroyed; most probably, it was not strongly attenuated.

The external cuticle of the integument is thick. Epidermal cells are rounded tetragonal to hexagonal and longitudinally elongated (Pl. 47, fig. 2). Stomata are lacking. A layer of sclerified cells is present under the epidermis (Pl. 47, fig. 3). On average, these rounded in plane cells are 25 µm in diameter. The micropylar canal is short.

Remarks. The singleness of the material did not allow maceration, and the seed is described in open nomenclature.

Material. One phytolite.

Carpolithes sp. 4

Plate 46, fig. 4

Description. The seed is ovoid, bilateral, 10 mm long, 8 mm wide, and broadly oval in transverse section. The chalaza is flattened, about 4 mm in diameter. A conical elevation is situated in the center of the chalaza, 2 mm in diameter at the base and 1 mm high. The seed is slightly tapering toward the micropyle. Short ribs about 3 mm long run from the chalaza toward the micropyle. They are better developed on one side of the seed. The distance between adjacent ribs is 1 mm.

The external cuticle of the integument is thin.

Remarks. The morphology of *Carpolithes* sp. 4 resembles the Taxaceae. The singleness of the material did not allow maceration, and the seed is described in open nomenclature.

Material. One phytolite.

Carpolithes sp. 5

Plate 47, fig. 5

Description. The seed is ovoid, 9 mm long, and 8 mm wide. The chalazal part is destroyed. The seed is tapering toward the micropyle. The micropyle is attenuated. In transverse section, it is fusiform. A thickening in the middle area of the seed corresponds to the nucellar cavity. Therefore, the thickness of the integument is uneven.

The nucellus only fuses with the integument in the chalazal area. The cuticle of the nucellus is relatively thick. The cavity where the nucellus was situated makes two-thirds of the total height of the seed. The nucellus is rounded, 5 mm in diameter. The micropyle is 3 mm in length.

Remarks. The bilateral symmetry of the seed and the morphology of the nucellus imply that the seed belonged to the Ginkgoales. However, the seed is

described in open nomenclature because of singleness of the material.

Material. One specimen represented by an impression and phytolite.

CONCLUSIONS

Plant remains of the four sections studied from the Peski locality are Late Bathonian in age and represent a single paleofloristic assemblage. Taxa revealed in the locality belong to two divisions of the higher plants: Pteridophyta and Pinophyta. The majority of the genera found were common in the Middle Jurassic time. The only exception is *Tritaenia*: previously, members of this genus were reliably reported from Upper Jurassic deposits (starting from the Oxfordian) and Cretaceous of Western Europe. It seems likely that the earliest members of *Tritaenia* (as well as members of other genera of the family) appeared in Asia, spread in Eastern Europe in the Middle Jurassic, and colonized Western Europe as late as the Late Jurassic time. The comparison between the Peski locality and adjacent coeval floras shows the peculiarity of the floristic assemblage of the former. It shows the greatest similarity to the floristic assemblage of western Ukraine in the generic composition. In particular, the Ukrainian assemblage contains miroviaceous genera. In the Middle Jurassic, members of this group were prominent in plant associations of Central European Russia and had not yet occurred in Western Europe (with the exception of northern Norway). Some members of the Miroviaceae probably were ecological analogues of the Ginkgoaceae, Pseudotorreliaceae, and Czekanowskiaceae, characteristic members of the Siberian area.

The flora of the Peski locality is interesting because it reflects inland, not coastal, vegetation. This is the reason of its peculiarity. The plant community of the Peski locality includes two associations: *Ptilophyllum*–*Tritae-nietum* ass. nov., which occurred in the upper reaches of rivers and could have reached swamps, and *Nilssoniop-teridi-Cephalotaxopsietum* ass., which corresponded to lowland and floodplain vegetation. *Brachyphyllum*, *Marskea*, and *Elatocladus* sp. are allochthonous elements, which were failed to be related with the established associations. *Brachyphyllum* and *Marskea* represent water-divide (not swamp) vegetation, whereas *Elatocladus* sp. is an element of swamp vegetation. *Ptilophyllum* and *Otozamites* from the Peski locality show ecology unusual for bennettites: they grew on swampy interfluvies. Leaves of *Ptilophyllum* and *Otozamites* are common in deposits of lagoons and marine estuaries. They are often considered as mangrove elements in the Jurassic. Such a wide range of adaptations testifies that the two genera were cenophobic. Results of epidermal and taphonomical analyses show that epidermal characters of bennettites reflect local conditions of the ecotope rather than regional climatic characteristics.

The thickness of growth rings in wood remains found in the Peski locality testifies to the existence of a warm and seasonably dry climate in the Moscow Region during the Late Bathonian time. The seasonality is also confirmed by fish kill layers. Thermophilic bennettites *Ptilophyllum* and *Otozamites* and schizaeaceous fern *Stachypteris* also indicate a warm climate. To refine the boundary between zones of warm and warm temperate climates, data on the geographical range of the Miroviaceae were used. It is proposed to use the presence of the Miroviaceae in floristic assemblages as an indicator of an ecotone zone (Gordenko, 2004). Taking into account the obtained data on the geographical range of the Miroviaceae, the boundary between the European-Sinian and Siberian areas in Eastern Europe is refined: it was situated closer to the north than it was previously believed and deviate in northwestern direction at an acute angle to the modern latitude 50° N.

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