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Istchenkophyton filiciforme gen. et sp. nov., a New Small Vascular Plant with Thick Cuticle from the Devonian of Voronezh Region (European Russia)

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Abstract—Remains of a new small vascular plant, *Istchenkophyton filiciforme* gen. et sp. nov., are described from the Upper Givetian strata of Pavlovsk vicinity (Voronezh Region). The plant is characterized by a very thick cuticle (up to 300 μm), complex branching pattern, similar to that of a frond rachis, anomocytic stomata, and a well-developed vascular bundle with a central elongated in transversal section protoxylem strand and massive metaxylem composed chiefly of scalariform bordered-pitted tracheids. A reconstruction of the new plant is proposed; its ecology and systematic position are considered. In the light of new data relationships of problematic Devonian plants with thick cuticle are discussed.

Key words: Middle Devonian, Voronezh Region, plant fossils, Spongiophytales, morphology, anatomy, ecology.

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INTRODUCTION

Despite of long, more than centenarian, study of problematic Devonian plants with a very thick cuticle, they are still a subject of acute discussion of paleobotanists. These plants are often considered within the group Spongiophytales, established by Sommer (1959); homogeneity of the group and the systematic position of its members are disputable. Different authors attributed members of the group to higher plants, algae, or their intermediates, sometimes regarded them as peculiar primitive plants, adapted for life on land (Zalessky, 1915; Ergolskaya, 1936; Kräusel and Venkatachala, 1966; Chaloner et al., 1974; Istchenko and Istchenko, 1981; Krassilov, 1981; Meyen, 1987; Gensel and Johnson, 1994; Snigirevskaya and Nadler, 1994; Gomankov et al., 2004; etc.). Recently, *Spongiophyton* from North America was reinterpreted as a lichen (Stein et al., 1993; Taylor et al., 2004). Thick-cuticled plants are widespread in Middle Devonian and rarer in Lower Devonian strata of the world; occasionally they form paper coals ("barzassits"). Some classic localities of plants under discussion are situated in the southern part of the Voronezh Region (European Russia). This paper describes a new thick-cuticled plant from this area, *Istchenkophyton filiciforme* gen. et sp. nov. The plant is named in honor of the Ukrainian paleobotanists Tamara Anastas'evna and Alla Antonovna Istchenko, who described for the first time thick-cuticle plants from the Devonian of the Voronezh Region and accomplished of one of the most important works on this plant group. Exceptional importance of this find is determined by the well-preserved anatomical structure of the new plant, studied for the first time in the plant assignable to spongiophytes. The new data allow reconsidering some questions related to the systematic position and ecology of plants of the group.

MATERIAL AND METHODS

The material was collected during several field trips by A.V. Broushkin, O.V. Shatalova and D.V. Zbukova (VSEGEI) from the deposits of the Yastrebovka Formation of Shkurlat (Pavlovsk) quarry near the town of Pavlovsk, Voronezh Region. The Yastrebovka Formation corresponds to the Pashiya Regional Stage, earlier dated to the Early Frasnian and now considered as Late Givetian (Rzhonsnitskaya, 2000; *Zonal* …, 2006; etc.). Remains of the plant under consideration occur throughout the whole section of the Yastrebovka Formation of the locality, being alluvial in genesis, confined mostly to very thin clayey lenses and accumulations of small plant debris on the bedding surfaces of light gray or greenish cross-bedded channel tuffstones. Here they associate with remains of other land plants, including archaeopterids (Krassilov et al., 1987), stenokolealeans, lycopods, as well as thick-cuticled plants described by Istchenko and Istchenko (1981) from this area. The material is represented by small fragments of plant branching axes preserved as thick cuticular coverings with coalified or, more rarely, permineralized inner tissues.

The plant remains were extracted from the rock matrix using steel needles, then small particles of matrix were removed in water with help of needles and brushes; bulk maceration was also accomplished. The anatomy of permineralized specimens was studied in fractured and polished surfaces under reflected polarized light and in thin sections in transmitted light; the anatomy of coalified specimens was studied in longitudinal splits using SEM. For the study of epidermal structure, the plant remains were macerated with concentric hydrofluoric acid, then cleared after standard technique in concentric nitric acid followed by potassium hydroxide. Some fragments were mounted for the SEM study untreated. Observations and photography were carried out using a Leica-MZ6 stereomicroscope, Leica-DMRX microscope, Leica-DC200 digital camera and a CAMSCAN scanning electron microscope.

MATERIAL

The collection PIN, no. 5267 is kept at the Paleontological Institute of the Russian Academy of Sciences.

SYSTEMATIC PALEOBOTANY
PLANTAE VASCULARES INCERTAE SEDIS

Istchenkophyton Broushkin et Gordenko, gen. nov.

E t y m o l o g y. In honor of T.A. Istchenko and A.A. Istchenko, who described for the first time thick-cuticled plants from the Devonian of the Voronezh Region; Greek φυτον (plant).

T y p e s p e c i e s. *Istchenkophyton filiciforme* Broushkin et Gordenko, gen. et sp. nov.

D i a g n o s i s. Axes thin, round or elliptical in cross section. Branching typically frequent, regular, pseudomonopodial, with laterals alternating in two rows, opposed or orientated at angle to each other. Length of internodes and laterals complexity decrease distally. Main axes (first order) more robust, with long internodes, bear lateral branching systems, principal branching of which occurs in plane more or less perpendicular to that of main axis. Primary axes of lateral branching systems (second order) with short internodes; first ramifications (third order) of each secondary axes depart in one and the same direction in relation to first order axis. Further branching of lateral branching systems occurs usually in the same general plane and manner, with catadromous first ramifications (fourth and all subsequent orders); in distal parts occasionally present nearly isotomous branching in different planes. Axes apices are coiled on dorsal side. Vascular strand (axes of first and second orders) slightly elliptical and stout. Xylem centrarch; protoxylem strand in cross section distinctly elongated (elongation coincides with axis branching plane) and comprises spiral tracheids. Metaxylem massive, composed of tracheids with scalariform and, more rarely, circular bordered pits. Xylem strand encircled by variable in thickness zone of poorly preserved cells, apparently corresponded to phloem or possibly also to inner cortex, composed of thin-walled prosenchymatous elements. Outer cortex of elongated relatively thick-walled cells, with prominent intercellular spaces. Epidermis one-cell thick, consists of cells similar to those of outer cortex; covering cells longitudinally elongated, with strongly cutinized anticlinal walls. Cuticle very thick, resistant to maceration; cutinization of axes often irregular. Over the stomatal pore, cuticle abruptly attenuates, forming conical depression. Stomata relatively rare, more or less regularly spaced over entire surface of axes, orientated longitudinally or, more rarely, oblique. Stomatal apparatuses anomocytic; guard cells bean-shaped or, more rarely, baculiform and slightly sunken relative to ordinary epidermal cells. Stomatal aperture well cutinized.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. *Istchenkophyton* gen. nov. differs sharply from the other Devonian thick-cuticle plants by its specialized branching type, irregular in other members of the group, as well as by the stomatal organization and some other morphological and epidermal characters. The anatomical structure of other Devonian thick-cuticled plants is unknown. *Istchenkophyton* gen. nov. exhibits a substantial similarity with the monotypic genus *Dalejophyton* Obrhel from the Middle Devonian (Eifelian) of the Czech Republic (Obrhel, 1957), which is characterized by a branching type, similar to that of lateral branching systems of the new plant, coiled on one side axes tips, and by comparable measurements. The structures interpreted by Obrhel as sporangia of *Dalejophyton* supposedly represent unflattened coiled tips of its sterile axes. Anatomical and epidermal structure of *Dalejophyton* is unknown. Judging by its form of preservation, this plant did not possess a thick cuticle; thus, its resemblance to *Istchenkophyton* gen. nov. is confined to the similarity in morphology of vegetative axes, which cannot serve as a reliable basis for assimilation of the two plants.

R e m a r k s. Poorly preserved plant remains, described by Istchenko and Istchenko (1981, pp. 29–30; pls. XXIII–XXIV) as *Orestovia* sp. from slightly older, Middle (?) Givetian, strata of the same area most likely belong to *Istchenkophyton* gen. nov.

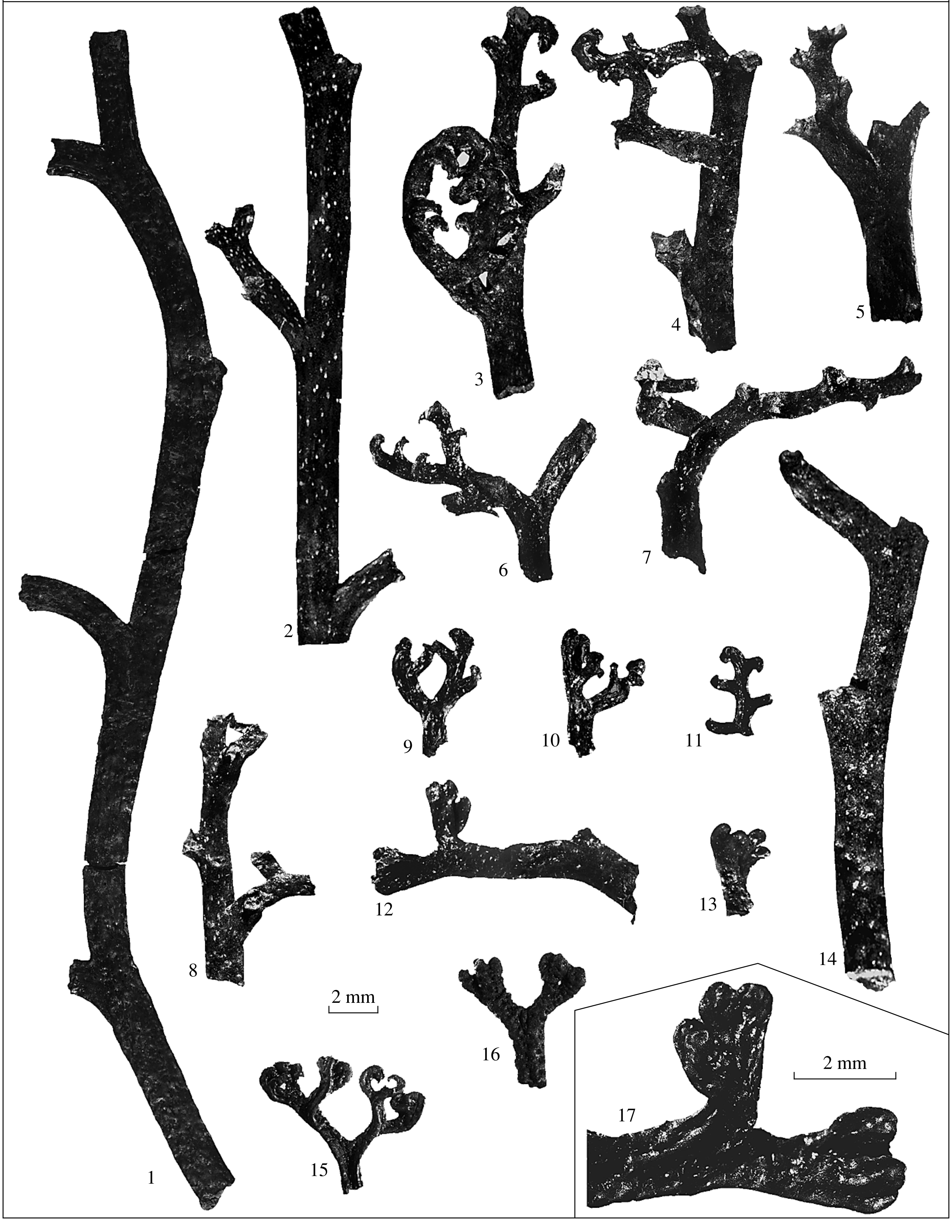
Istchenkophyton filiciforme Broushkin et Gordenko, sp. nov.

Plate 5, figs. 1–17; Plate 6, figs. 1–12; Plate 7, figs. 1–9; Plate 8, figs. 1–7; Plate 9, figs. 1–8.

E t y m o l o g y. After the superficial similarity of the plant axes with immature fern leaves.

H o l o t y p e. PIN, no. 5267/1; upper part of main (first order) axis with partially preserved lateral branching systems, represented by cuticle covering with coalified tissues; Shkurlat (Pavlovsk) quarry near the town of Pavlovsk, Voronezh Region, European Russia; Yas-

Plate 5



Explanation of Plate 5

Figs. 1–17. *Istchenkophyton filiciforme* gen. et sp. nov., European Russia, Voronezh region, vicinity of the town of Pavlovsk, Shkurlat (Pavlovsk) quarry; Yastrebovka Formation, Upper Givetian; (1–6) fragments of main (first order) axes with partially preserved lateral branching systems, ramifying in planes, perpendicular to those of main axes: (1) PIN, no. 5267/2, large fragment of a curved axis; two first laterals depart in the same direction; (2) PIN, no. 5267/3, fragment of the main axis with bases of lateral branching systems; the main axis deviates in the upper node; (3) holotype, PIN, no. 5267/1, upper part of a main axis with well-preserved coiled lower lateral branching system; principal axis of the lateral branching system (second order) and first lateral of the third order are developed considerably stronger than followed laterals and are close to the main axis in its level of development (axis of the third order is visible incompletely because of convolution in plane perpendicular to image plane); tips of last laterals of the main axis are coiled on its (nominally) dorsal side, first ramifications (third order) of lateral branching systems depart in two rows on the same side; (4) PIN, no. 5267/4, fragment of a main axis with rows of laterals, orientated at an angle about 90° to each other; (5) PIN, no. 5267/5, a small fragment of an axis of the first order with partially preserved lateral branching system; (6) PIN, no. 5267/6, fragment of a main axis with well-preserved lateral branching system, an irregular development of the third order axes is visible; (7) PIN, no. 5267/7, fragment of large lateral branching system, ramifying in one plane; (8) PIN, no. 5267/8, fragment of a main axis with partially preserved lateral branching systems; (9–11) fragments of small axes, in their branching type corresponding to lateral branching systems parts and demonstrating varying development level relative to a main axis: (9) PIN, no. 5267/9, a first lateral on its development level nearly comparable with deviated principal axis; (10) PIN, no. 5267/10, a first lateral is well-developed, principal axis is straight; (11) PIN, no. 5267/11, distinct domination of a principal axis, ramifications are poorly developed; (12) PIN, no. 5267/12, fragment of an axis with laterals, branching nearly isotomously in different planes; last ramifications are contiguous, their apices are nearly straight, incised on tip; (13) PIN, no. 5267/13, small fragment of an axis with nearly dichotomous branching; (14) PIN, no. 5267/14, fragment of a main axis with preserved poorly developed lateral branching system; (15, 16) fragments of small axes with the thickest cuticle, exhibiting similar to isotomous branching in different planes: (15) PIN, no. 5267/15; (16) PIN, no. 5267/16, last ramifications are contiguous, apices are coiled inside; (17) PIN, no. 5267/12, detail of axis, figured on fig. 12, incisions on tips of the last order ramifications are visible.

trebovka Formation, Middle Devonian, Upper Givetian; Pl. 5, fig. 3.

Diagnosis. As for the genus. Axes up to 5 mm in width; rows of laterals orientated at angle approximately 60°–180° to each other, maximal length of main axes internodes more than 4.2 cm. Vascular strand constitutes 1/5–1/3 of total axis diameter; protoxylem tracheids approximately 5–20 μm, metaxylem tracheids up to 60 μm in diameter; diameter of outer cortex cells 20–50 μm. Epidermal cells longitudinally elongated, attain length 850 μm, up to 65 μm in diameter; cuticle 20–300 μm (usually 60–110 μm) thick; stomata guard cells 60–70 μm long and 23–50 μm wide.

Description (Figs. 1–3). The material studied is represented by small, up to 10 cm long, fragments of branching axes of the plant, up to 5 mm wide.

The axes of the plant are characterized by a regular, dense, and pseudomonopodial branching with alternation of branches in two rows, orientated at an angle of 60°–180° to each other. The length of internodes decreases distally, as well as the degree of the development of laterals (the last often decreases abruptly and irregularly). Ultimate branches and apices of the axes are coiled on their dorsal side; occasionally, whole axes with their laterals are coiled (Pl. 5, figs. 3, 4, 6, 7, 9–11, 13–16; Figs. 1c, 1d, 1f, 1g, 1i–1k, 1m–1p, respectively; Pl. 6, figs. 3, 4, 6–12), that endows the entire branching system an immature appearance. Some axes bear, in their apical parts, compactly situated primordia of axes of the next order (Pl. 6, fig. 7). As a rule, remains of branching systems found in rock are incomplete and strongly flattened during fossilization process, that sufficiently complicates reconstitution of the plant habitus.

In the most completely preserved specimens (Pl. 5, figs. 1–6, 8, 14; Fig. 1), *the main axis* and *lateral branching systems*, branching in a plane which is more or less perpendicular to a branching plane of the main axis, are distinctly recognizable (Fig. 2; more precisely, this is a particular case; when the main axis and lateral branching systems ramify not in plane, instead of their branching planes we have to do with planes perpendicular to their planes of symmetry).

Main axes (first order; the orders of axes are defined here provisionally, according to the plant architecture) are characterized by a relatively large diameter, 1.5–5 mm in the proximal parts, and long internodes with the maximal length more than 4.2 cm; fragments of axes with length up to 10 cm were found. Branching is pseudomonopodial, the rows of laterals are orientated to each other at an angle of about 180° or, more rarely, 90°. Fragments of the main axes are straight along the entire length (Pl. 5, figs. 3, 4, 8; Fig. 1), or irregularly sinuous due to the lateral deviation of the main axis in some nodes (Pl. 5, figs. 1, 2, 14); supposed aberrations were observed, when two lateral axes depart one after the other in the same direction (Pl. 5, fig. 1). The laterals (second order) depart at an angle of 30°–90° and often immediately after this bend out at a greater angle (Pl. 5, figs. 1, 6, 8).

Principal axes of *lateral branching systems* (second order) usually have a smaller diameter and considerably shorter internodes than the main axes (Pl. 5, figs. 2–6, 8). The branching is pseudomonopodial, the rows of laterals are orientated at an angle of about 60°–180° to each other; further the laterals often bent inwards in a varying degree, towards the dorsal (adaxial) side of the principal axis. The first ramifications (third order; Pl. 5, figs. 1–6, 8, 14; noted by black arrows in Figs. 1, 2) usually depart near the bases of secondary axes, at an angle of approximately 90° to the main axis branching plane (that coincides with general orientation of lateral branching systems relative to the main axis), and in the

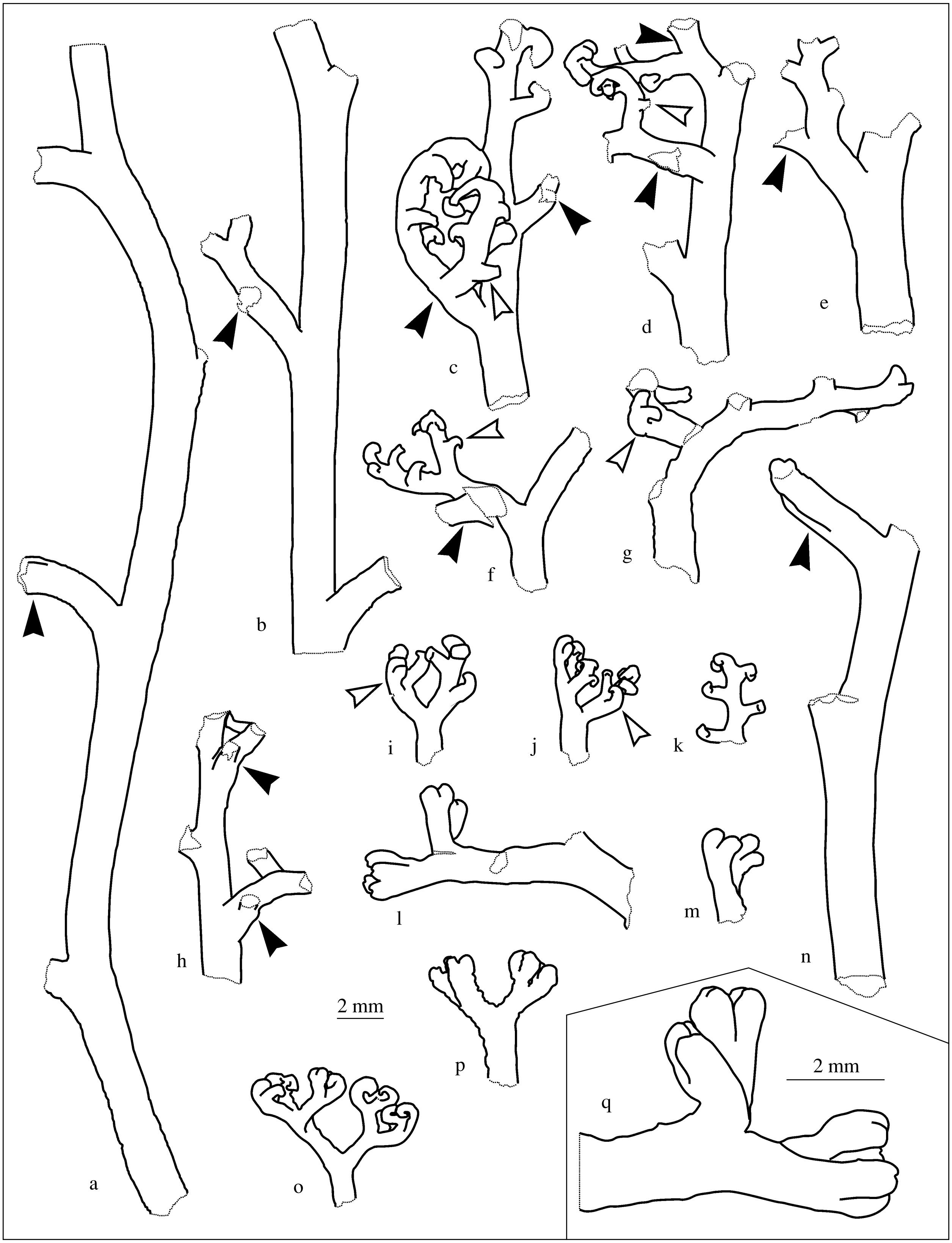


Fig. 1. *Istchenkophyton filiciforme* gen. et sp. nov.: (a–q) line drawings of the specimens figured in Pl. 5 (figs. 1–17, correspondingly). Black arrows indicate the first ramifications of the third order, departing perpendicularly to the plane of branching of main axis; contour arrows indicate the basiscopic first ramifications of the fourth and all subsequent orders.

lateral branching systems of both rows, the first ramifications of the third order depart to one and the same side (Pl. 5, figs. 3, 4; Figs. 1, 2).

Further branching of lateral branching systems commonly is analogous to the branching of their principal axes and occurs approximately in the same general plane (Pl. 5, figs. 3, 4, 6; Figs. 1, 2); the first laterals (axes of the forth and all following orders) are basiscopic (Pl. 5, figs. 3, 4, 6; contour arrows; Figs. 1, 2); consequently, the branching of the lateral branching systems corresponds to the branching of the catadromous pinnate leaf rachis. Laterals of ultimate orders often retain signs of flattening in a plane different from the bedding plane (Pl. 6, figs. 9, 10), that may indicate the original nature of the flattening. The fact that axes of lower orders are often flattened in the bedding plane, independently on their orientation in relation to the bedding plane (Pl. 5, figs. 1–6, 8, 14), is an indication that they were originally rounded or slightly elliptical in section.

The branching of the overwhelming majority of small fragments of axes, kept in the collection, corresponds to the branching of the lateral branching systems (Pl. 5, figs. 7, 9–11; Pl. 6, figs. 3, 4, 8–10). In comparison with the principal axis, the development of the laterals is highly variable (Pl. 5, figs. 9–11). In distal parts, under similar development of the principal axis and its laterals, branching can resemble isotomous; occasionally, successive divisions occur in different planes (Pl. 5, figs. 12, 13, 15–17; Pl. 6, figs. 5, 6). In this case, the last ramifications are usually contiguous; their apices are coiled inside or nearly straight, apically incised (incipient next order axes; Pl. 5, figs. 12, 17; Fig. 1).

The anatomical structure is known in first and second order axes; it is identical in all specimens. Only primary tissues are present; vascular strand is central, constitutes from 1/5 to more than 1/3 of the total diameter of the axis. In cross section, it is lenticular in shape due to compression during fossilization (which is suggested by significant compression of tracheids); original outline of the strand must have been rounded or slightly elliptical. Protoxylem is central, comprises spiral tracheids approximately 5–20 μm in diameter (Pl. 7, figs. 1, 2, 9). In cross section, the protoxylem is flattened, i.e., it has the shape of a narrow elongated strand, orientation of which coincides with the branching plane of the axis; however, the orientation of the strand can be perpendicular to the plane of the axis compression. A compaction zone in the central part of the protoxylem strand is supposedly a result of obliteration of protoxylem tracheids or parenchyma cells. Metaxylem is massive, composed of tracheids up to 60 μm in diameter, with scalariform (Pl. 7, figs. 3, 7, 8) or, rarely, circular (Pl. 7, fig. 8) bordered pits. The scalariform bordered pits are 5–13 μm wide and 2–3 μm high; the circular bordered pits are about 4 μm in diameter. A space between the xylem strand and outer cortex does not usually retain

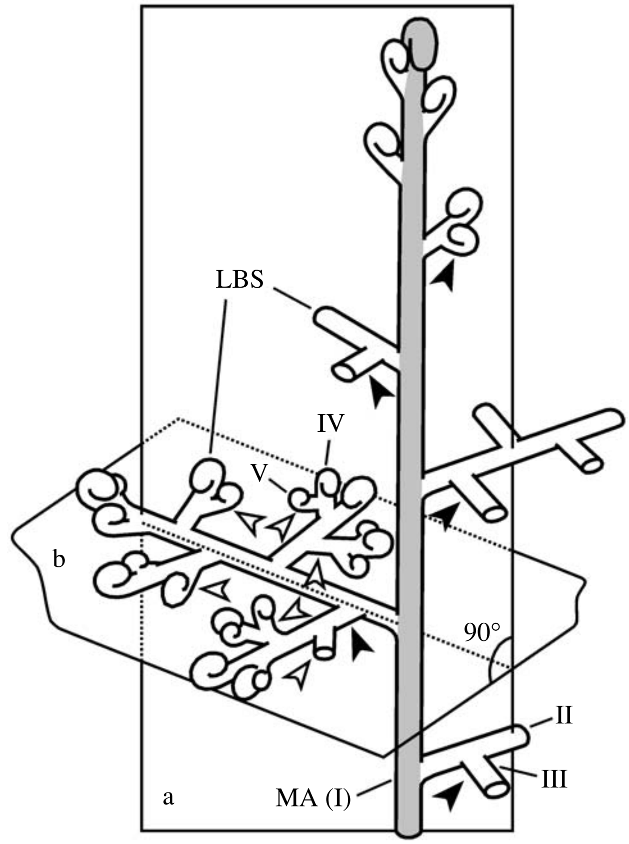
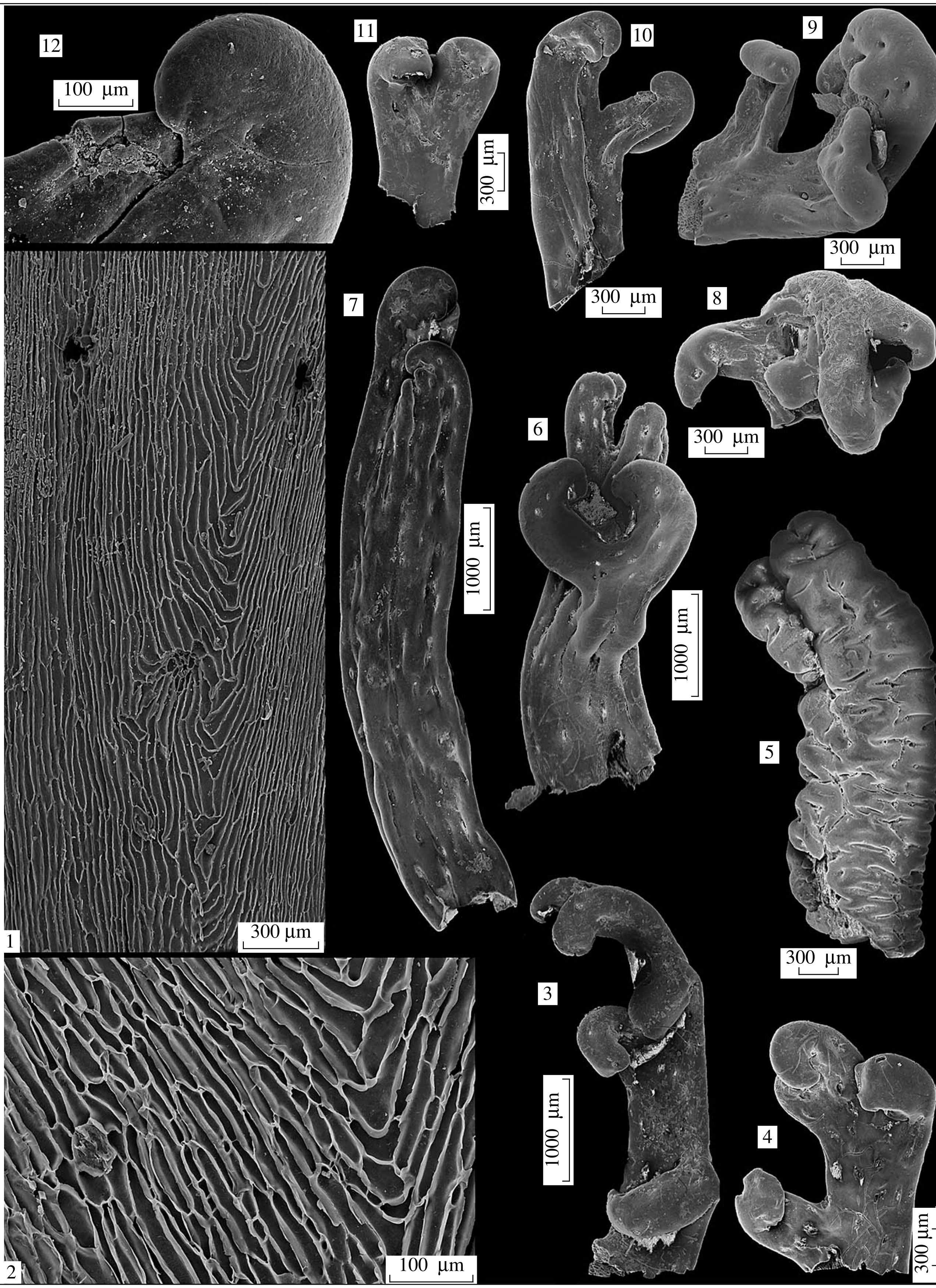


Fig. 2. *Istchenkophyton filiciforme* gen. et sp. nov., scheme of branching, view from the (nominally) dorsal side of the main axis. The main axis (first order; MA, stippled) bears in pseudomonopodial distichous mode lateral branching systems (LBS), branching planes of which are perpendicular to the branching plane (plane a) of the main axis; only one of the lateral branching systems with its branching plane (plane b) is completely shown. The first ramifications on the lateral branching systems (tertiary axes, noted by black arrows) depart correspondingly at the right angle to the main axis branching plane; they are directed in one and the same side in lateral branching systems of both rows. The first ramifications of the fourth and fifth orders (noted by contour arrows) are basiscopic. Axes orders are indicated by roman numerals.

preserved cells; more rarely strongly deformed thin-walled prosenchymatous elements are preserved here; this space corresponds to the phloem and probably also to inner cortex. Detached cells of a supposed phloem 17–19 μm in diameter were observed in coalified specimens under SEM (Pl. 7, fig. 6). The outer cortex is homogenous, composed of prosenchymatous cells with relatively thick walls, 20–50 μm in diameter and up to 800 μm long, with prominent intercellular spaces (Pl. 7, figs. 1, 4, 5). The epidermis is one cell thick, composed of cells similar to those of the outer cortex (Pl. 7, fig. 5). Cells of the cortex and epidermis are often filled with a

Plate 6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100 μm
11
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10
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9
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1
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3
1000 μm
4
300 μm
2
100 μm

coalified matter, probably remnants of cellular protoplasts.

The cuticle is very thick, 20–300 μm wide (usually 60–110 μm), resistant to maceration. The cutinization of axes is often irregular, with short longitudinal or, more rarely, cushion-like transverse thickenings. The thickness of the cuticle of the dorsal and ventral sides in the main (first order) axes is more or less the same; in axes of the lateral branching systems, the cuticle of the dorsal side is often significantly thinner (two to five times in distal parts) than cuticle of ventral side; the thinnest and often fractured cuticle is present near coiled tips of axes (Pl. 7, fig. 12). Its maximal width, 200–300 μm, the cuticle attains in some small axes with nearly isotomous branching type; the surface of these axes often appears textured due to irregular transverse thickenings of the cuticle (Pl. 5, figs. 15, 16; Pl. 6, fig. 5; Pl. 8, fig. 5). Usually, the outer surface of axes is more or less smooth (Pl. 6, figs. 3, 4, 9, 11) or with longitudinal folds (Pl. 6, figs. 6, 7; Pl. 8, fig. 4). The cuticular structure in splits is more or less homogenous, small spherical cavities occasionally occur (Pl. 8, figs. 1, 3).

The epidermal cells are up to 850 μm in length and to 65 μm in diameter, from quadrangular–hexagonal to fusiform, wedge-shaped in places of axes departing or with irregular outlines; in axes of the first order, they are strongly longitudinally elongated and occasionally septate (Pl. 6, figs. 1, 2). The anticlinal walls of cells are straight and strongly cutinized (Pl. 6, fig. 2; Pl. 8, fig. 1); the cutinization penetrates deeply and corresponds to a height of the anticlinal wall.

Stomata are more or less regularly distributed on the whole surface of axes and relatively rare; the average stomata distribution is 7 stomata per mm^2 on the main axes and 12–24 per mm^2 on the axes of the lateral branching systems. The stomatal apparatuses are longitudinally orientated (Pl. 8, fig. 7; Pl. 9, figs. 2–5) or, more rarely, oblique (Pl. 9, fig. 1). The epidermis around the stomata is slightly elevated above its common surface; a deep conical depression is formed on the outer side of cuticle, over a stomatal pore, by an abrupt thinning of cuticle (Pl. 8, figs. 1, 3, 6; Fig. 3). The stomatal apparatuses are anomocytic. The guard cells are baculiform (Pl. 9, figs. 3, 5) or, more rarely, been-

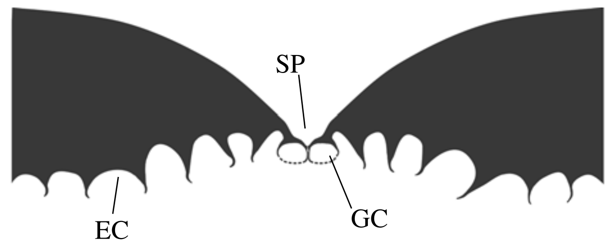


Fig. 3. *Istchenkophyton filiciforme* gen. et sp. nov., schematic transversal section through stomatal apparatus and epidermal cells. Legends: (GC) guard cell; (EC) epidermal cell; (SP) stomatal pore; cutinized parts shown in gray and approximate contours of uncutinized parts of guard cells drawn in dashed line.

shaped (Pl. 9, figs. 2, 6), 60–70 μm long and 23–50 μm wide. The anticlinal wall, delimiting the polar areas of guard cells, is usually weakly cutinized. The stomatal aperture is well cutinized (Pl. 8, fig. 7); the stomata are usually closed, the line of closure is occasionally toothed and resembles a zipper (Pl. 9, fig. 5). The guard cells are slightly sunken relative to ordinary epidermal cells (Pl. 8, fig. 2). The epidermal cells, adjacent to guard cells of stomata, are unspecialized and correspond to other epidermal cells in their shape and dimensions (Pl. 9, figs. 3, 5), or they are shorter than the latter; in the last case they occasionally form an irregular ring around a stoma (Pl. 9, fig. 1). Abortive stomata occur (Pl. 9, fig. 4).

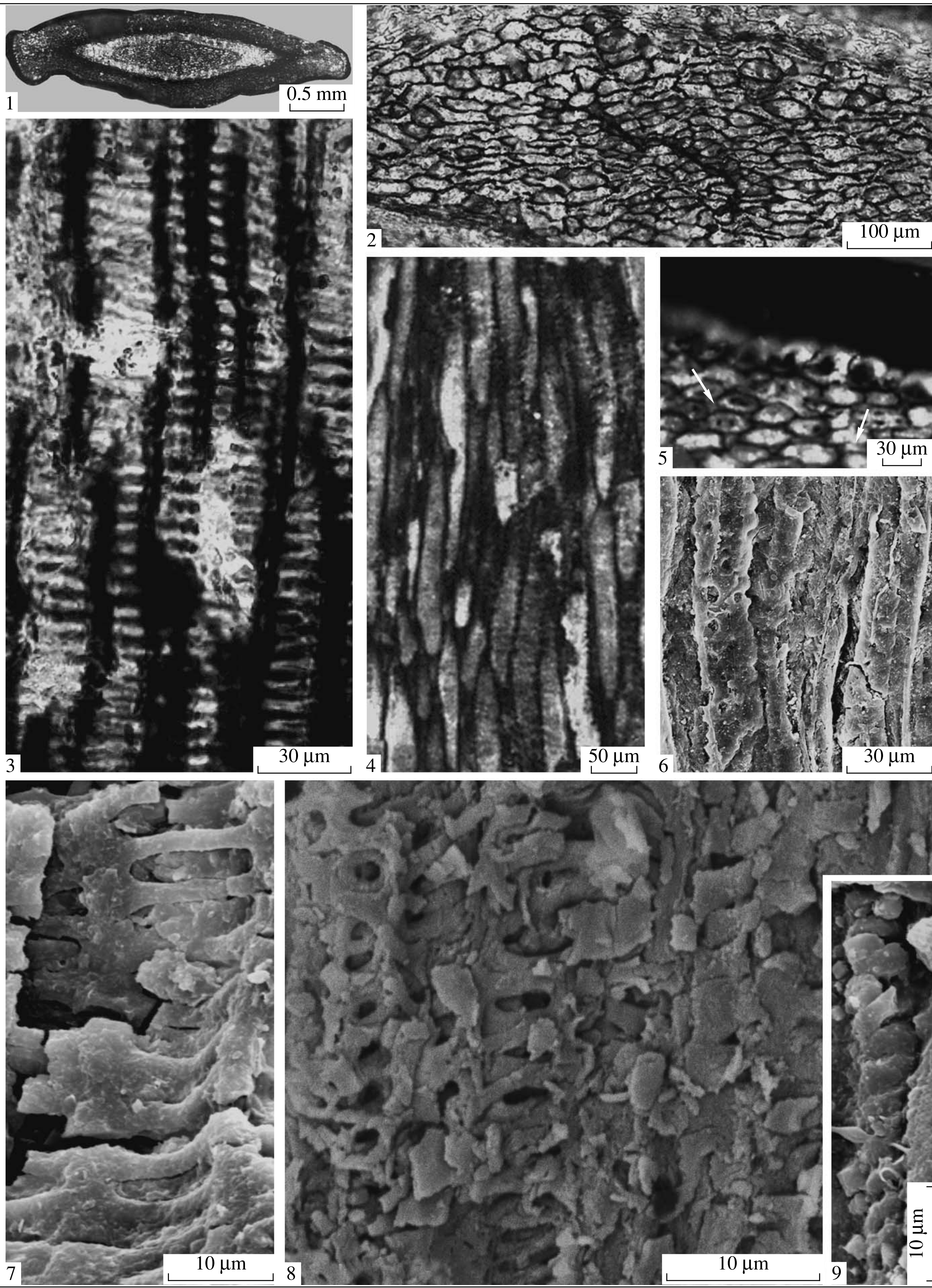
Abundant traces of fungal attacks occur on the surface, within the cuticle and in the cortical cells of the plant (Pl. 6, figs. 4, 6, 8; Pl. 8, fig. 5; Pl. 9, figs. 7, 8). The most conspicuous are traces of profusely branching hyphae on the outer surface of the plant cuticle, represented by thin, up to 15 μm wide, smooth or moniliform, resembling arthroconidia, furrows, "etched" in the cuticle. Most of them are spreading along the plant surface, occasionally resulting in its irregular-reticulate appearance (Pl. 6, fig. 8; Pl. 8, fig. 5), while others penetrate through the cuticle, as is visible in their cross section (Pl. 9, fig. 7).

M a t e r i a l. More than 200 specimens, represented by small fragments of the plant branching axes pre-

E x p l a n a t i o n o f P l a t e 6

Figs. 1–12. *Istchenkophyton filiciforme* gen. et sp. nov., European Russia, Voronezh region, vicinity of the town of Pavlovsk, Shkurlat (Pavlovsk) quarry; Yastrebovka Formation, Upper Givetian; SEM: (1, 2) PIN, no. 5267/17; (1) the topography of epidermis of the first order axis in the area of lateral axis departing; (2) detail of the epidermal topography of the main axis; epidermal cells with strongly cutinized anticlinal walls, longitudinally elongated, occasionally septate, wedge-shaped in place of axis departing; an anomocytic stoma is visible to the left; (3, 4) small fragmentary axes, in their branching type corresponding to parts of lateral branching systems: (3) PIN, no. 5267/18; (4) PIN, no. 5267/19; (5) PIN, no. 5267/20, fragment of a small axis with very thick cuticle (visible on split), the axis surface is covered with irregular transverse thickenings of the cuticle; (6) PIN, no. 5267/21, fragment of a small axis with laterals, branching nearly dichotomously; (7) PIN, no. 5267/22, fragment of a distally branching axis; ramifications apices bear concentrated primordia of the next order axes; (8), PIN, no. 5267/23, fragment of a small coiled axis; abundant traces of destruction by fungal hyphae are visible on the surface of cuticle; (9, 10) fragments of small axes, in their branching type corresponding to parts of lateral branching systems; signs of original axes flattening in plane, differing of compression plane, are visible: (9) PIN, no. 5267/24; (10) PIN, no. 5267/25; (11) PIN, no. 5267/26, small fragment of a branching axis with coiled apices; (12) PIN, no. 5267/25, detail of fig. 10, a coiled axis apex, thin fractured cuticle of the dorsal side is visible.

Plate 7



served as thick cuticular coverings with coalified or, more rarely, permineralized inner tissues, or filled with matrix.

DISCUSSION

Istchenkophyton filiciforme gen. et sp. nov. most likely was a small plant, not much than 30–40 cm high. Mutual orientation of its main (first order) axes and lateral branching systems suggests that the former in living plant were more or less upright and the latter were horizontally expanded (Fig. 4). Architecturally, main axes of *Istchenkophyton filiciforme* gen. et sp. nov. are comparable to vertical frond rachises of some ferns (e.g., phyllophores of certain "coenopteridaleans"), with lateral branching systems corresponding to their pinnae. Often irregularly flexuous aspect of main axes, together with distichous organotaxis and unequal development of ramifications (in particular, the holotype has a lower secondary axis and its first branch resembling the main axis in the degree of development; Pl. 5, fig. 3; Fig. 1c) indicate that main axes were not self-supporting and could retain more or less vertical position through leaning against other plants or each other in dense stands (leaner habit).

Main axes and axes of lateral branching systems of *Istchenkophyton filiciforme* gen. et sp. nov. belong to the same structural type, characterized by dorsoventral symmetry (distichous organotaxis, coiled on one side axes tips, and in main axes also identical orientation of the first ramifications of the third order), which is primarily an attribute of plagiotropic plant organs (Sinnott, 1960). Lack of specialization in orthotropic axes and the fact that all axes belong to the same structural type suggest the possibility of changing roles of axes in ontogenesis (ability to become upright in plagiotropic axes and to lie down in orthotropic axes). Absent in strata basal parts of the plant probably were of the same general type and were represented by unspecialized trailing axes or/and formed by lying down orthotropic axes.

An exceptional importance of *Istchenkophyton filiciforme* gen. et sp. nov. is determined by its completely preserved anatomical structure, for the first time studied in a plant, assignable to spongiophytes (previously, only accumulations of tracheids from inner parts of cuticular sheaths in some plants of the group were known). The new data allow estimating the systematic position and ecology of this plant, as well as reconsideration of a number of questions related to the group.

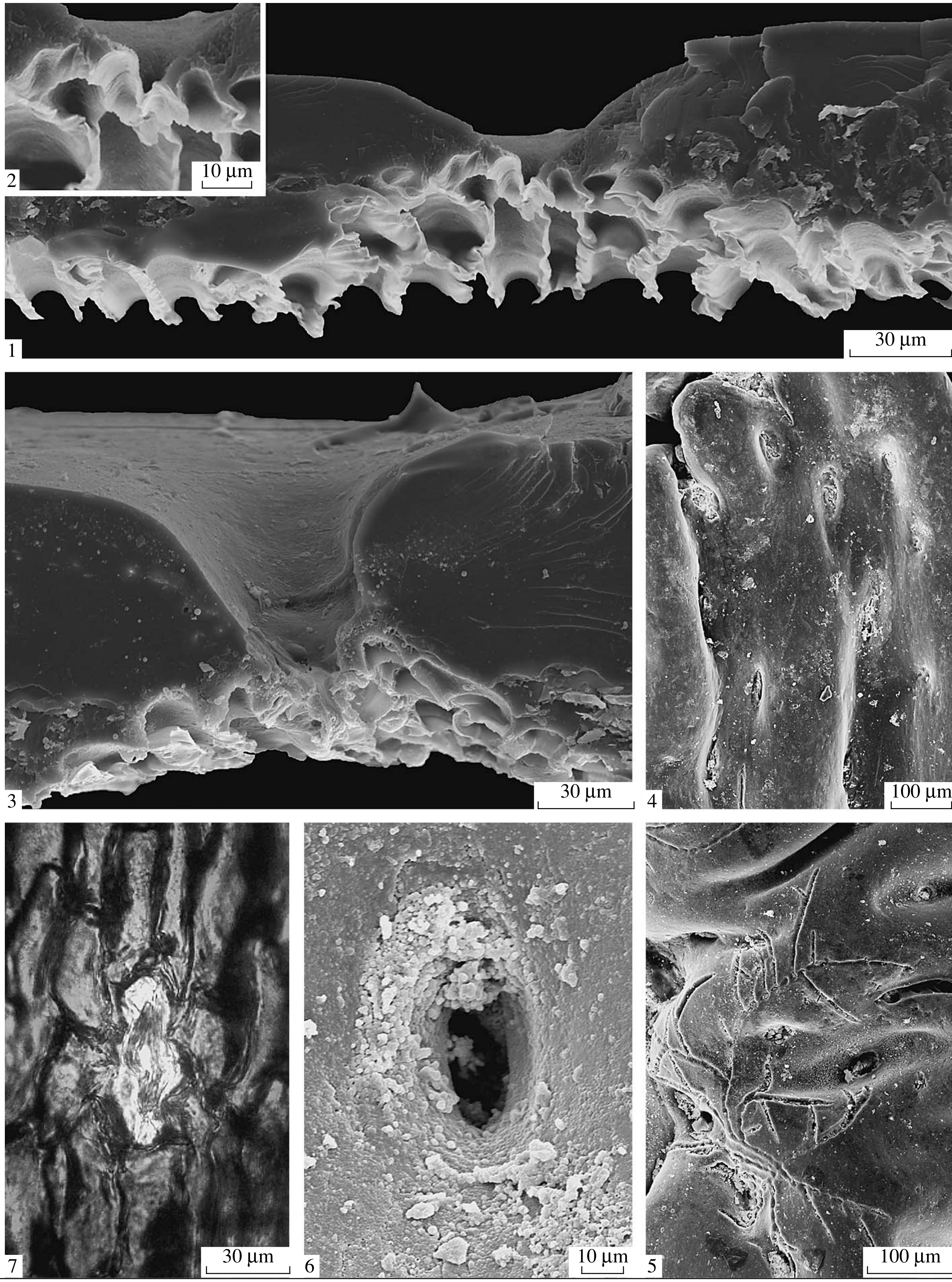
Fig. 4. Reconstruction of *Istchenkophyton filiciforme* gen. et sp. nov., upper part of main axis with departing lateral branching systems.

The development of vascular tissue, in particular, the nature of protoxylem and the type of metaxylem tracheids pitting, along with specialized branching pattern and determined growth suggest that *Istchenkophyton filiciforme* gen. et sp. nov. was a relatively advanced vascular plant, corresponding in the level of development to the most advanced members of Propteridophyta. It is related to them (in terms of Meyen (1987),

Explanation of Plate 7

Figs. 1–9. *Istchenkophyton filiciforme* gen. et sp. nov., European Russia, Voronezh region, vicinity of the town of Pavlovsk, Shkurlat (Pavlovsk) quarry; Yastrebovka Formation, Upper Givetian: (1, 2) PIN, no. 5267/27, cross section of a petrified axis of the first order: (1) general view; cuticle, outer cortex, zone of poorly preserved cells, corresponding to a phloem and inner cortex (?), and xylem, from peripheral to a central part, are visible; (2) detail of a vascular strand exhibits an elongated central protoxylem strand with compression in the central part, supposedly corresponding to a zone of obliterated cells; metaxylem tracheids are strongly flattened; (3) PIN, no. 5267/28, metaxylem tracheids with scalariform bordered pits, LM; (4) PIN, no. 5267/32, cells of outer cortex in nearly longitudinal section; (5) PIN, no. 5267/29, cross section through a part of outer cortex with intercellular spaces (indicated by arrows), the cuticle and epidermal cells are visible in the upper part; (6, 7) PIN, no. 5267/30; (6) cells of phloem (?), SEM; (7) tracheids of metaxylem with scalariform bordered pits, SEM; (8, 9) PIN, no. 5267/25; (8) tracheids of metaxylem with scalariform and circular bordered pits, SEM; (9) tracheid of protoxylem with spiral thickening, SEM.

Plate 8



as a grade-group) by an axial organization without distinct differentiation of different orders axes, haplostelic structure, and the absence of secondary tissues. However, the absence of spore-bearing organs and ambiguity of morphological data prevent the assignment of the plant to any certain phylogenetic line of tracheophytes. The anatomical structure (particularly, the character of protoxylem and type of metaxylem tracheids pitting) is similar to that of trimerophytes and their derivatives. On the contrary, a number of morphological and epidermal characters, such as a coiled grows, axes branching type, presence of thick, resistant to maceration cuticle, and stomatal structure, are more characteristic of plants of zosterophyll lineage.

The level of development of *Istchenkophyton filiciforme* gen. et sp. nov. shows that ordinary vascular land plants at least were able to produce the unique very thick cuticular covering. The occurrence of the assemblage which includes remains of the plant under study in channel facies of alluvial deposits suggest a removal of plant remains found here from inner parts of a land, from different sites within a floodplain. All this, as well as the level of development (essentially, vascular tissues) of the plant, its stereotypic for contemporaneous vascular plants anatomical structure, and clearly expressed xeromorphic features (thick cuticle and sunken stomata with tightly closing apertures, resembling a zipper), indicates that *Istchenkophyton filiciforme* gen. et sp. nov. might have occupied relatively dry sites, or rather areas with casual (seasonal?) water-short. Here it might have formed relatively dense stands (which is suggested by their leaner habit), probably, together with other thick-cuticled plants, found in the association.

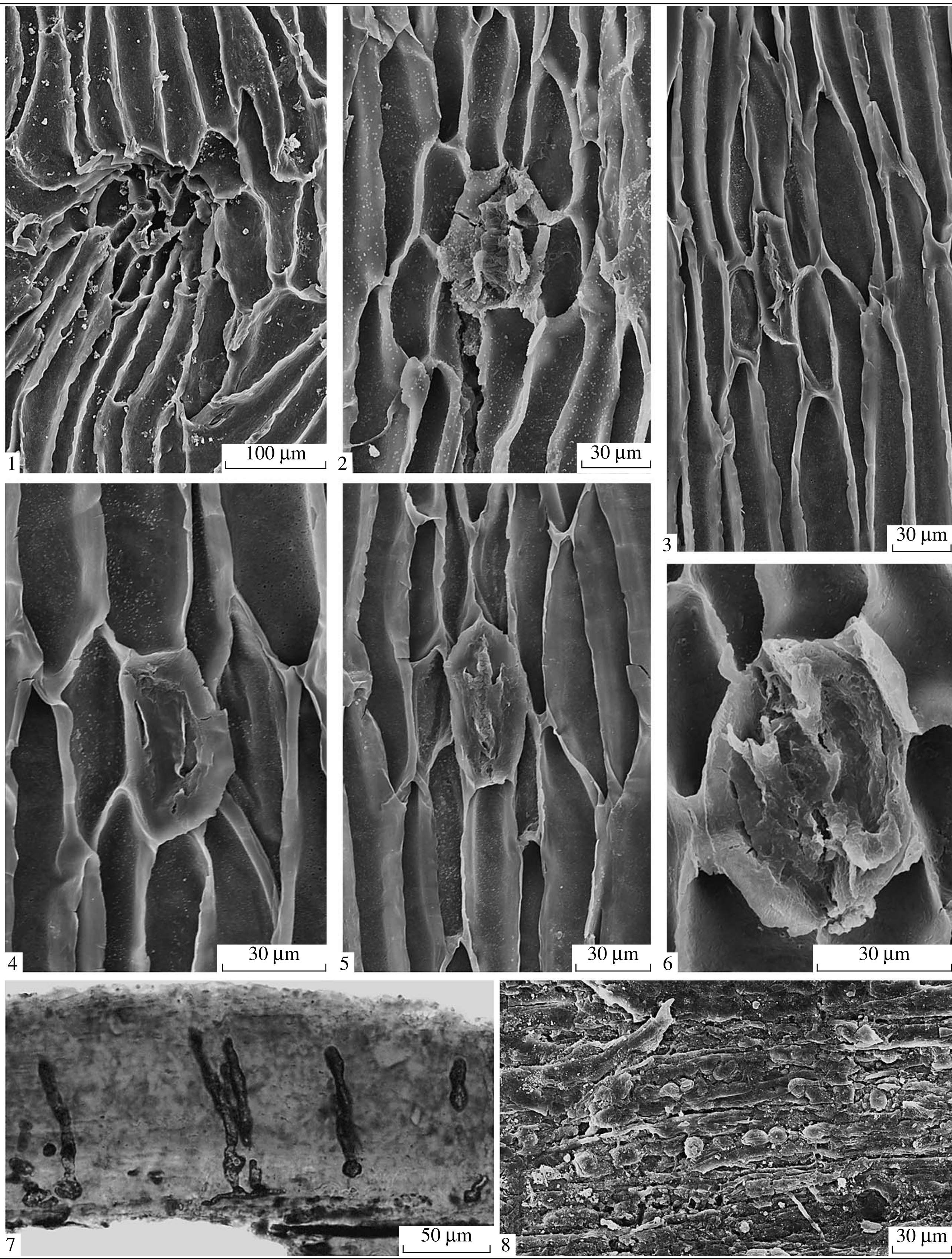
Coiled axes tips with thinning cuticle in the coiled part, likening the plant branching system to an immature developing structure, and primordia, concentrated in the apical parts of axes, probably testify that the distal parts of the plant retained dormant meristems, by means of which growth of axes might have recommenced after an unfavorable period finishing. Analogous function in other thick-cuticle plants might have been performed by commonly found undeveloped branches (“lobes”).

Significant differences between *Istchenkophyton filiciforme* gen. et sp. nov. and other Devonian thick-cuticled plants, as well as the fact that they are studied in a much less degree, prevent direct extrapolation of the data obtained on the whole group. In authors' opinion, however, at least most of spongiophytes belong to vascular plants. Stomata and tracheids were reported in *Orestovia* from the Middle (?) Devonian of the Kuznetsk basin in Siberia (Ergolskaya, 1936; Krassilov, 1981; Gensel and Johnson, 1994) and *Orestovia* (*Schuguria*) from the Givetian of the East-European Platform (Snigirevskaya, 1993; Gomankov et al., 2004); similar stomata were observed also by the present authors in several *Orestovia*-like plants from the Voronezh Region. It is possible that *Spongiophyton* also belongs to vascular plants. Recently, the most wide-spread became the opinion about its lichen affinities, based mainly on the discovery of abundant fungal hyphae in the cuticle-like covering and the interior of *S. minutissimum* from the Emsian of Canada (Stein et al., 1993; Taylor et al., 2004; etc.). Unfortunately, the permineralized material reported by Stein et al. (1993) is not yet published; structures observed by Taylor et al. (2004), in our opinion, are equally can be interpreted as fungal borings and/or peculiarities of the ultrastructure, often observed in the cuticle of *Orestovia*-like plants, perhaps caused by its chemical decomposition. Abundant fungal hyphae observed in the remains of *Istchenkophyton filiciforme* gen. et sp. nov. might belong to some saprotrophic or parasitic fungi. Similar traces of fungal activity were described earlier in remains of *Spongiophyton nanum* from the Middle Devonian of Ghana and Brazil (Chaloner et al., 1974, pl. 121, figs. 1, 4; pl. 124, figs. 1, 2). Along with the occurrence of fungal hyphae in the remains of *Istchenkophyton filiciforme* gen. et sp. nov., traces of fungal attacks were observed in remains of other Devonian vascular plants with thick cuticle. Cuticle borings (Gensel and Johnson, 1994) and ascomycete fruiting bodies (Krassilov, 1981) were found in remains of *Orestovia* from Siberia; fungal hyphae on the surface of cuticle as well as fruiting bodies or pycnidia of asco- or deuteromycetous fungi were observed by the present authors in *Orestovia* (*Schuguria*) and some other *Orestovia*-like plants from the Voronezh Region. In our opinion, “hemispherical bodies”, described by Istchenko and Istchenko (1981, pl. XXV, figs. 1a, 1c; pl. XXX, figs. 1a–1c) in *Orestovites* and *Rhytidophyton*, also could represent fungal reproductive structures. Frequent association of Devonian thick-cuticled plant remains with traces of presumed saprotrophic and/or parasitic fungi may imply that the fungus found in the remains of *Spongiophyton* was of the same nature. Occurrence in the deposits of similar genesis and age, identical form of preservation, similarities in overall morphology, cuticle ultrastructure, often

Explanation of Plate 8

Figs. 1–7. *Istchenkophyton filiciforme* gen. et sp. nov., European Russia, Voronezh region, vicinity of the town of Pavlovsk, Shkurlat (Pavlovsk) quarry; Yastrebovka Formation, Upper Givetian: (1–3, 7) PIN, no. 5267/17; (1) section through the cuticle across a stomatal pore, SEM; (2) fragment of fig. 1, stoma, SEM; (3) section through the cuticle across a stomatal pore, SEM; (7) stoma, well-developed cutinization of stomatal pore is visible, LM; (4) PIN, no. 5267/22, axis surface with longitudinally folded cuticle, stomatal pores are visible, SEM; (5) PIN, no. 5267/20, relief outer surface of an axis with very thick cuticle, abundant branching fungal hypha are visible on the surface, SEM; (6) PIN, no. 5267/31, outer surface of axis with a stomatal pore, formed by an abruptly thinned cuticle, SEM.

Plate 9



Explanation of Plate 9

Figs. 1–8. *Istchenkophyton filiciforme* gen. et sp. nov., European Russia, Voronezh region, vicinity of the town of Pavlovsk, Shkurlat (Pavlovsk) quarry; Yastrebovka Formation, Upper Givetian: (1–6) PIN, no. 5267/17, anomocytic stomata, slightly sunken relative to adjacent ordinary epidermal cells, on the inner side of cuticle, SEM: (1) obliquely orientated stoma; epidermal cells adjacent to the guard cells are shorter and form an irregular ring around the stoma; (2) stoma with bean-shaped guard cells; (3) stoma with baculiform guard cells; (4) abortive stoma; (5) stoma with transitional between baculiform and bean-shaped guard cells; the line of closure of aperture is toothed and resembles a zipper; (6) stoma with bean-shaped guard cells; (7) PIN, no. 5267/28, cross section through the cuticle (outer surface is above); note traces of fungal hypha, passing through the cuticular layer, LM; (8) PIN, no. 5267/30, traces of fungal attack in the cortex.

with a spongy layer present, occasionally preserved cell outlines on the inner surface of the cuticle and resemblance of *Spongiophyton* pores to poorly preserved stomata of some *Orestovia*-like plants (e.g., Kräusel, 1954, pl. 24, figs. 35–36; Gensel et al., 1991, text-fig. 5B) may indicate their relationship and thus tracheophyte affinities for *Spongiophyton*. However, the present state of our knowledge on this plant precludes any definite conclusions on its nature; to test our hypothesis an additional study of well-preserved material of *Spongiophyton* is required.

The above expressed hypothesis about xerophytic nature of *Istchenkophyton filiciforme* gen. et sp. nov. may be also correct for other Devonian thick-cuticled plants. Their unique specialization is due to an adaptation not to terrestrial life (i.e., colonization of land), as is sometimes regarded, but to land habitats with unfavorable conditions, most probably to those which experienced a temporary (seasonal?) water deficit, such as relatively raised spots in a floodplain, banks of ephemeral streams, etc. These plants, relatively primitive in comparison with general developmental level of land flora of the late Early–Middle Devonian, might have been driven out in such habitats by more competitive contemporaries.

It is still open questions, what caused such overdevelopment of cuticle covering in these plants (its maximal thickness exceeds that of all known fossil and living plants in approximately 15 times), and whether such cuticle is the unique feature of a certain plant group or an adaptation appeared independently in nonrelated plants.

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