

A New Bennettitalean Genus from the Middle Jurassic of the Mikhailovskii Rudnik Locality (Kursk Region, Russia)

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Abstract—Bennettitalean leaves with unusual morphology were found in the Middle Jurassic (Bathonian) deposits of Mikhailovskii Rudnik locality (Kursk Region, European Russia). This morphotype derived on the basis of *Pterophyllum*-like pinnate leaves by coherent coalescence of segments, through which superficial similarity of leaves of the new genus to *Nilssoniopteris* Nath., possessing entire leaf blade, is achieved. Each of coalescent segments was completely isolated from neighboring segments by massive cuticular wall. This character distinguishes leaves of the new genus from coherent leaves, known in other gymnosperms. The unique preservation type characteristic of plant remains of the Mikhailovskii Rudnik locality, allowed us to study some details of anatomical structure of leaf segments in the new genus. In particular, it was established, that palisade mesophyll in segments was poorly developed, and metaxylem in vascular bundles comprises tracheids with scalariform to circular bordered pits.

Key words: Middle Jurassic, Bathonian, gymnosperms, Bennettitales, morphology, anatomy, systematics.

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INTRODUCTION

Bennettitalean leaves do not exhibit high morphological diversity (Doludenko and Svanidze, 1969; Harris, 1969, 1973; Watson and Sincock, 1992; Schweitzer and Kirchner, 2003); therefore the find of a new morphotype in the Jurassic of Northern Hemisphere, thoroughly studied in the aspect of floristic diversity, is unexpected and very interesting.

As yet, the data on anatomical features of bennettitalean leaves are scanty. The most detailed information is available for mineralized leaves of *Otozamites kerae* Ohana et Kimura from the Upper Jurassic of Japan (Ohana and Kimura, 1991) and leaves of *O. mertonii* Dower, Bateman et Stevenson from the Middle Jurassic of Scotland (Dower et al., 2004). It was found, that segments of *O. kerae* possess hypodermal tissue, well developed palisade mesophyll, and sclereids, concentrated above and below vascular bundle; xylem conducting elements in vascular bundles are represented by annular and scalariform tracheids. Vascular bundles in petiole of this species are arranged U-shapely. In *O. mertonii*, the anatomical structure of petiole is similar to that of *O. kerae*.

Recently, the data on leaf anatomical structure in *Nilssoniopteris oishii* Yamada, Legrand et Nishida from the Lower Cretaceous of South-Western Japan were obtained (Yamada et al., 2009); in this species, anatomical structure of rachis was studied. In the whole, it is the same as in other studied bennettitalean leaves.

Below we give the description of a new unusual morphotype of bennettitalean leaves from the Middle Jurassic Mikhailovskii Rudnik locality (Kursk Region, European Russia); we had possibility to study some details of its anatomical structure.

MATERIAL AND METHODS

The studied material was collected by authors during two field seasons in 2007–2008. Plant remains were found in sandy siltstones of 1.5 m thick plant-bearing lens, situated in the northern wall of the Northern open mine of Mikhailovskii Rudnik (near Zhelesnogorsk town, Kursk Region), in the continental deposits of the Arkinsk Formation hypostratotype section (Middle Jurassic, Upper Bathonian). The studied lens is situated in the base of the section, near the contact with the Late Proterozoic ferruginous quartzites. The Upper Bathonian deposits of Mikhailovskii Rudnik are of predominantly alluvial genesis. Besides leaves of the new genus, there are abundant remains of other plants, cryptogams and gymnosperms (Gordenko, 2008).

The material is represented by leaf fragments, preserved as phytoliteims. The organic content of leaf segments tissues, during treatment with the nitric acid, is not dissolved completely. Cell walls are dissolved, leaving indissoluble residue, which fills cell interior and formed cast of the leaf anatomical structure. The organic residue consists of resin-like matter, but any

resin canals were not found in leaf segments. Such a preservation of tissues is characteristic also for other plants from the locality and, probably, related to the taphonomic features. Most probably, this matter is the product of cell walls degradation and cell content transformation. As it was shown by Harris (1973), sacchariferous leaf matter could be transformed into indissoluble resin-like matter under conditions of slow coalification.

The preservation of the material allowed investigation of not only epidermal structure, but also some details of leaf segments anatomical structure.

To obtain cuticle preparations, phytolaims initially were placed in concentrated hydrofluoric acid to remove matrix, and subsequently macerated by standard method in concentrated nitric acid. Obtained cuticle preparations were studied using light microscopy (LM) and scanning electron microscopy (SEM). Individual fragments were prepared for study under SEM without maceration.

Collection no. 5137 is kept in the Borissiak Paleontological Institute, Russian Academy of Sciences.

SYSTEMATIC PALEOBOTANY
DIVISION GYMNOSPERMAE
CLASSIS CYCADOPSIDA
Order BENNETTITALES Engler, 1892

Genus *Sympterophyllum* Gordenko et Broushkin, gen. nov.

Etymology. From the Latinized Greek *sym* (together), *pterus* (pinna), and *phyllum* (leaf).

Type species. *Sympterophyllum sympinnatum* gen. et sp. nov.

Diagnosis. Leaves ribbon-shaped, entire because of coherent coalescence of leaf segments. Leaf blade pulpy. Rachis thick, leather-like. Segments attached to upper third of rachis. Venation of segments parallel, not expressed in segment surface relief. Adjacent segments have common cuticle in marginal zones.

Leaves hypostomous. Stomatal apparatuses syndetohealic, generally amphycyclic. Each segment with single stomatal band, in which stomata more or less regularly distributed and randomly orientated. Numerous unicellular and bicellular trichome bases developed in stomatal band area.

Comparison. The new genus demonstrates most similarity to *Pterophyllum* on its morphology, as well as on epidermal structure. The distinction consists in coherent coalescence of segments in the new genus, through which leaf is no longer pinnate and resembles in outward appearance *Nilssoniopteris* leaves.

From all other bennettitalean genera, identified by their leaves, it sufficiently differs in the leaf blade morphology.

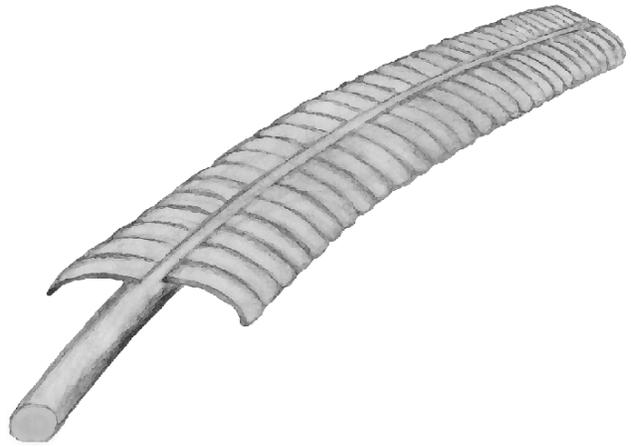


Fig. 1. Reconstructed leaf of *Sympterophyllum sympinnatum* gen. et sp. nov.

Remarks. The new genus is rather similar to *Pterophyllum*. In particular, significant similarity was found in epidermal structure of their segments. Leaves of the new genus are not an aberration of *Pterophyllum* leaves in the given locality, where the latter was not found. The find of similar leaves in the Upper Triassic of China, Sichuan Province (Wu, 1998), points on antiquity of origin of the morphotype with coherent segments. Though, they were mistakenly described as a new species of *Nilssonia* Brongn. (*N. loriformis* Wu). We do not place the latter in the new genus, because the epidermal structure of leaves from China is unknown, and the presence of the leaf structure parallelism in cycads and bennettitaleans do not exclude the origin of similar morphotype in the former.

Generic composition. Type species.

***Sympterophyllum sympinnatum* Gordenko et Broushkin, sp. nov.**

Pl. 22, figs. 1–4; Pl. 33, figs. 1–6; Pl. 24, figs. 1–4;
Pl. 25, figs. 1–6; Pl. 26, figs. 1, 2; Pl. 27, figs. 1–6;
Pl. 28, figs. 1–6; Pl. 29, figs. 1–5

Etymology. From the Latinized Greek *sympinnatus* (sympinnate).

Holotype. PIN, no. 5267/30; leaf fragment, preserved as a phytolaim; Russia, Kursk Region, Zhelesnogorsk town vicinity, Mikhailovskii open mine; Middle Jurassic, Upper Bathonian, Arkinsk Formation (Pl. 22, fig. 1).

Diagnosis. As for genus.

Description (Figs. 1, 2). The collection contains fragments of ribbon-shaped leaves (Pl. 22, figs. 1, 2; Fig. 1). The largest segment is 70 mm long. Rachis is very massive, about 6 mm wide.

Leaf blade attached to the upper third of the rachis. Segments depart from the rachis at a right angle, occasionally with small deviation towards leaf apex (basis-copic and acroscopic angles are about 90°). Segments are linear, rounded-rectangular in the transverse section. Segments are about 15 mm long, 3–3.5 mm

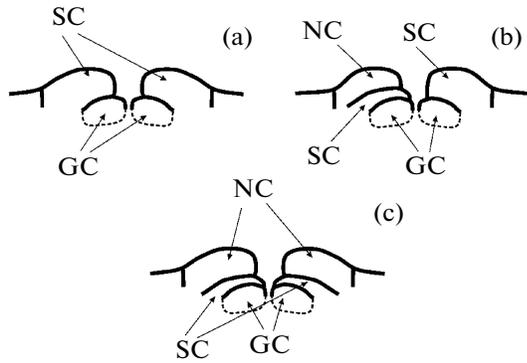


Fig. 2. *Sympterophyllum sympinnatum* gen. et sp. nov. Schematic transverse sections through stomatal apparatuses, demonstrating variability in their structure. Legend: (GC) guard cells; (SC) subsidiary cells; (NC) neighboring cells. Cutinization of cells is shown by full black line; supposed outlines of the guard cells are traced by dotted line.

wide, and 0.3–1 mm thick; acroscopic margin of each segment fused to basisopic margin of the next following one. The leaf margin is slightly bent down.

Leaves are hypostomous. The lower epidermis cuticle is thicker than the upper: 5–7 μm and 1.5–2 μm respectively. The venation is not expressed in the topography of the upper and lower epidermises.

The upper epidermis is composed of slightly transversely elongated ameba-like cells, 30–90 μm long, 25–40 μm wide, with sinuous anticlinal walls, amplitude of sinuosity is up to 15 μm .

Lateral parts of segments have common cuticular wall (Pl. 23, figs. 1, 4–6). Lower epidermis of each of coalescent segments exhibits a wide stomatal zone and distinct marginal nonstomatal zones (Pl. 23, fig. 2). Pavement cells in the marginal nonstomatal zones are slightly transversely elongated, more rarely isometric or longitudinally elongated (Pl. 24, fig. 1). Their anticlinal walls are sinuous, periclinal walls are smooth. Trichomes are absent. Pavement cells in stomatal zone nearly do not differ from the cells in marginal nonstomatal zones, but have more rounded outlines. Stomatal apparatuses within stomatal zone show more or less regular distribution and random orientation (Pl. 23, fig. 3; Pl. 24, figs. 1, 2). They are syndetocheilic (Fig. 2 a), and often one (Pl. 27, fig. 4; Fig. 2b) or both subsidiary cells (Pl. 27, fig. 5; Fig. 2c) form a neighboring cell by longitudinal division. The cuticle of subsidiary cells, as a rule, is radially striated (Pl. 22, figs. 3, 4; Pl. 27, figs. 3–5). The stomatal apparatuses are deeply sunken, with subsidiary cells sunken at the expense of neighboring cells, and guard cells sunken at

the expense of subsidiaries. Subsidiary and neighboring cells without papillae, form indistinct Florin's ring above stoma (Pl. 27, figs. 1, 2). Trichome bases are numerous, distributed only on the lower surface of segments, within stomatal zone. There are numerous rounded unicellular (Pl. 22, fig. 4; Pl. 27, fig. 6; Pl. 28, figs. 1–4) or bicellular (Pl. 22, fig. 3; Pl. 28, figs. 5, 6) trichome bases.

Size and cutinization rate of cells, bearing trichome bases, vary. As a rule, their anticlinal and periclinal walls are more cutinized, than those of pavement cells. The diameter of rounded trichome bases is 12–17 μm .

The cuticle of rachis is thick, up to 8–9 μm , identical for the upper and the lower side of a leaf (Pl. 29, figs. 1–5). The pavement cells of epidermis are longitudinally elongated, from tetragonal–hexagonal to nearly oval. The anticlinal cell walls are from straight to unevenly beaded thickened and slightly sinuous (Pl. 29, figs. 2, 5). Stomatal apparatuses in the rachis are less numerous, scattered mainly in its marginal areas, and longitudinally or obliquely orientated (Pl. 29, figs. 2, 4). They are smaller than stomatal apparatuses in leaf segments; the pair of guard cells is about 30 μm long and 28–30 μm wide. The guard cells are deeply sunken (Pl. 29, fig. 3).

Palisade mesophyll is located below upper epidermis (Pl. 24, fig. 4), consists of short, prismatic, nearly isodiametric cells, 20–40 μm in diameter. Above vascular bundles, sclerenchyma is developed instead of mesophyll (Pl. 24, figs. 1, 2, 4). Sclereids are thick-walled, mainly fusiform, vary in size, 10–40 μm in diameter, up to 90 μm long and more. As a rule, they possess circular pits (Pl. 24, fig. 2).

Vascular bundles in segments are parallel, sunken, relatively closely spaced (about six vascular bundles per segment width). Vascular bundles are up to 150 μm in diameter, composed of tracheids with scalariform to circular bordered pits, often with inner thickenings (Pl. 25, figs. 1–6). Pits are uniseriate, in close arrangement. Casts of tracheids are 4–11 μm in diameter and more than 400 μm long. Bordered pits in tracheids are about 3–5 μm in diameter.

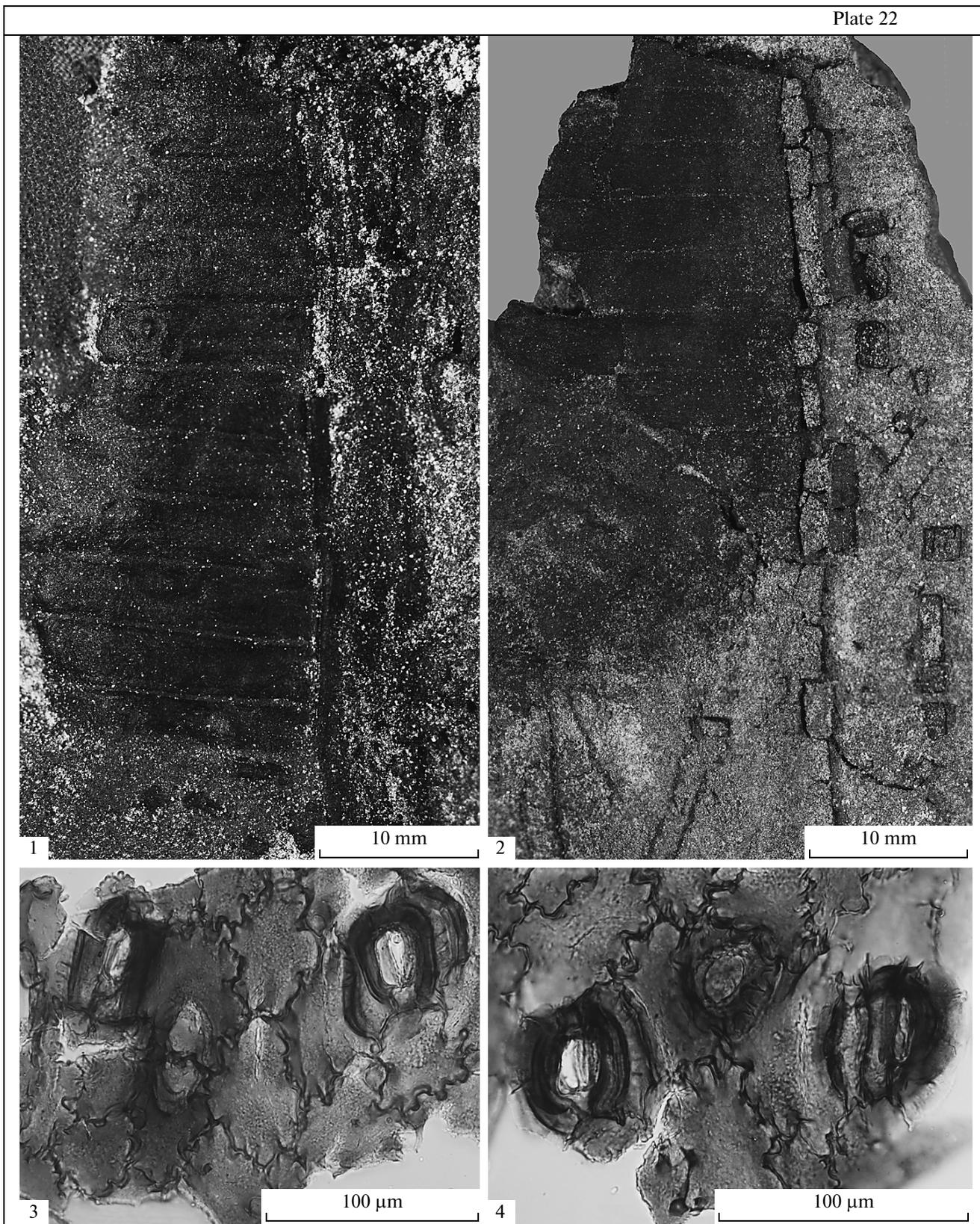
Remarks. The whole length of leaf was not stated, because of fragmentary material. Along the all preserved leaf blade length, the decrease of leaf width was not observed, therefore, the leaves, most probably, were ribbon-shaped (Fig. 1).

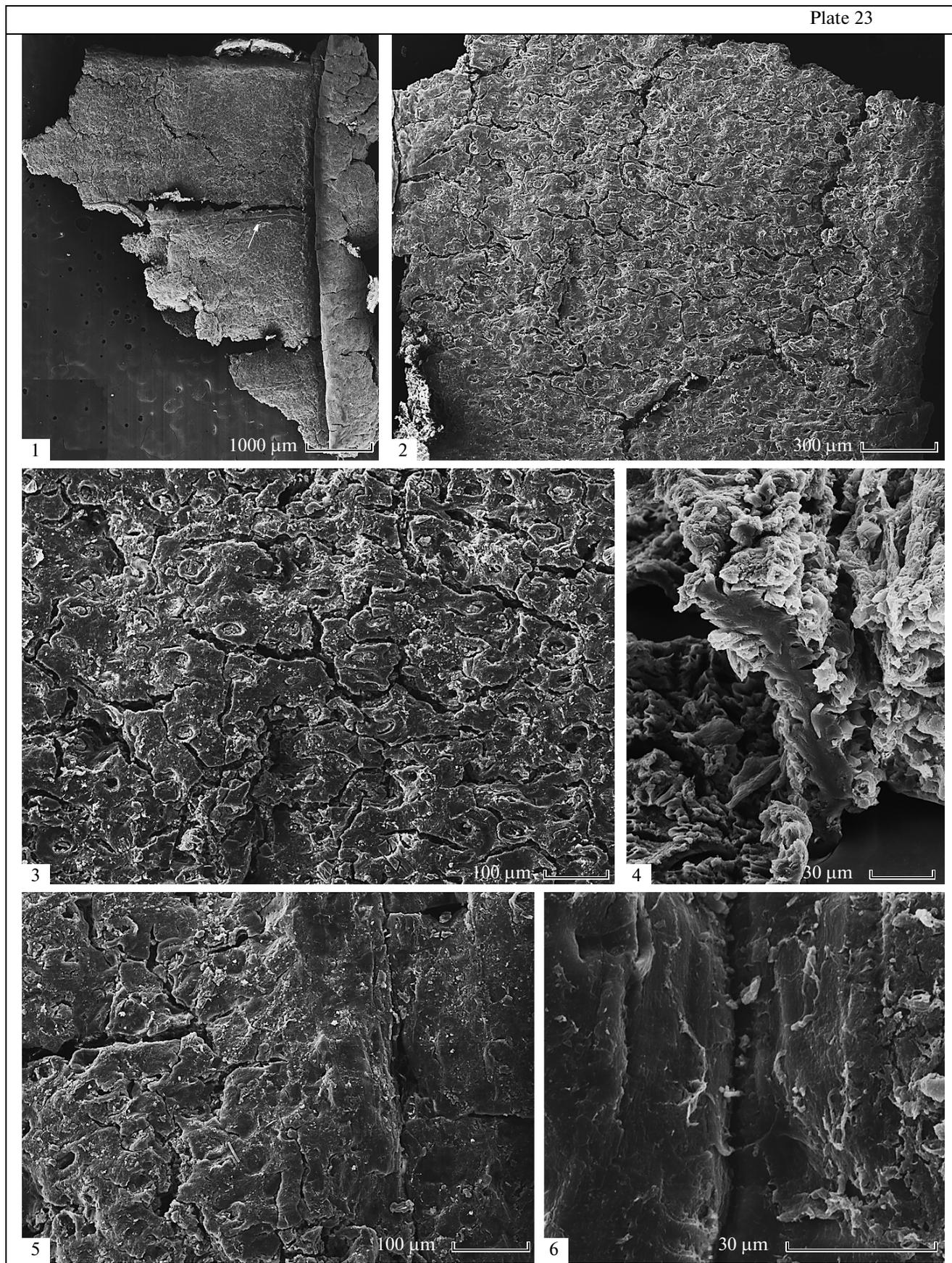
Material. Four exemplars, represented by phytolims of incomplete leaves.

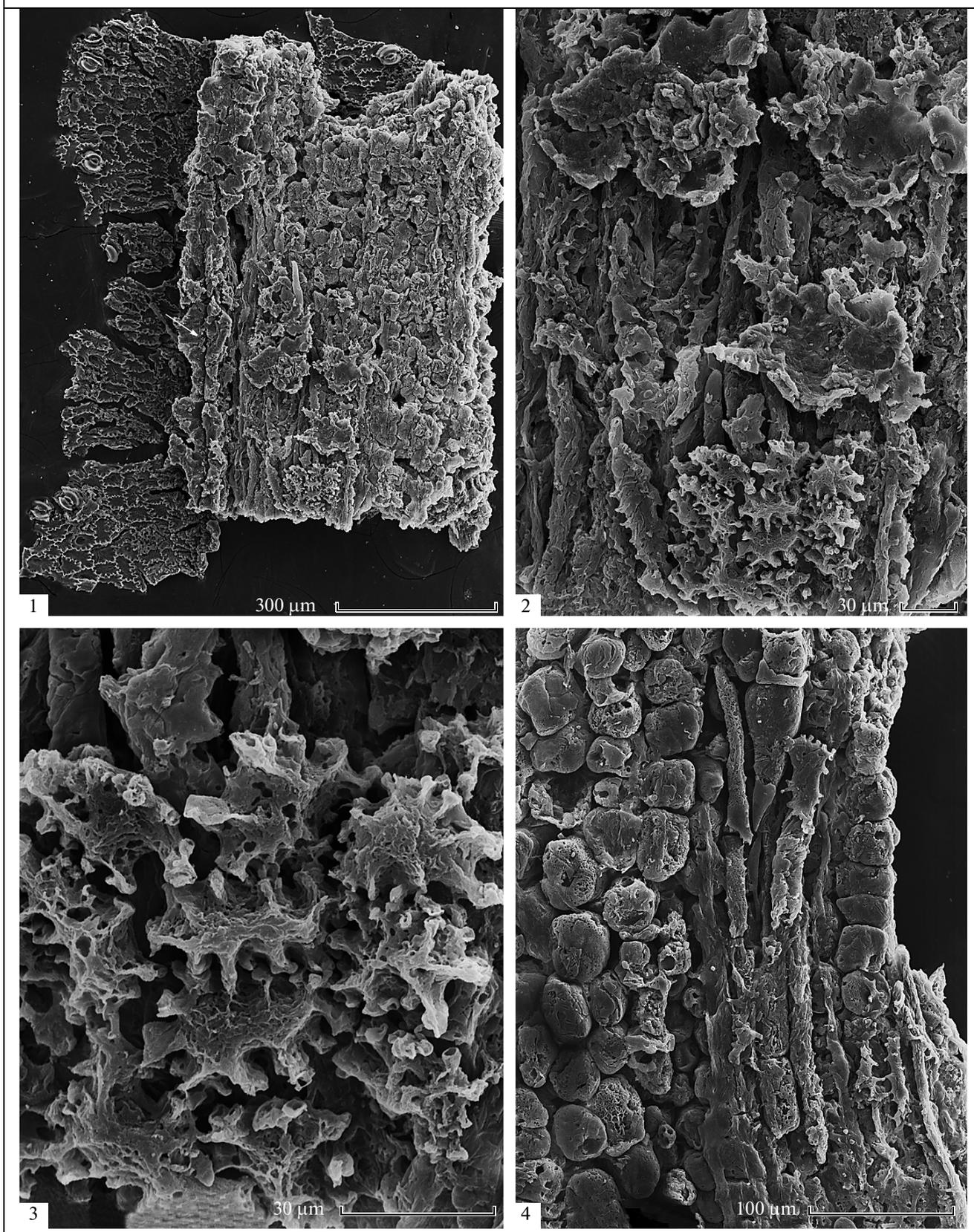
Explanation of Plate 22

Figs. 1–4. *Sympterophyllum sympinnatum* gen. et sp. nov., LM: (1, 3, 4) holotype no. 5137/30: (1) leaf fragment; (3) fragment of cuticle of the lower epidermis, syndetocheilic stomatal apparatuses and bicellular trichome base are visible; (4) fragment of cuticle of the lower epidermis, syndetocheilic stomatal apparatuses and unicellular trichome base are visible; (2) no. 5137/31, leaf fragment.

Plate 22







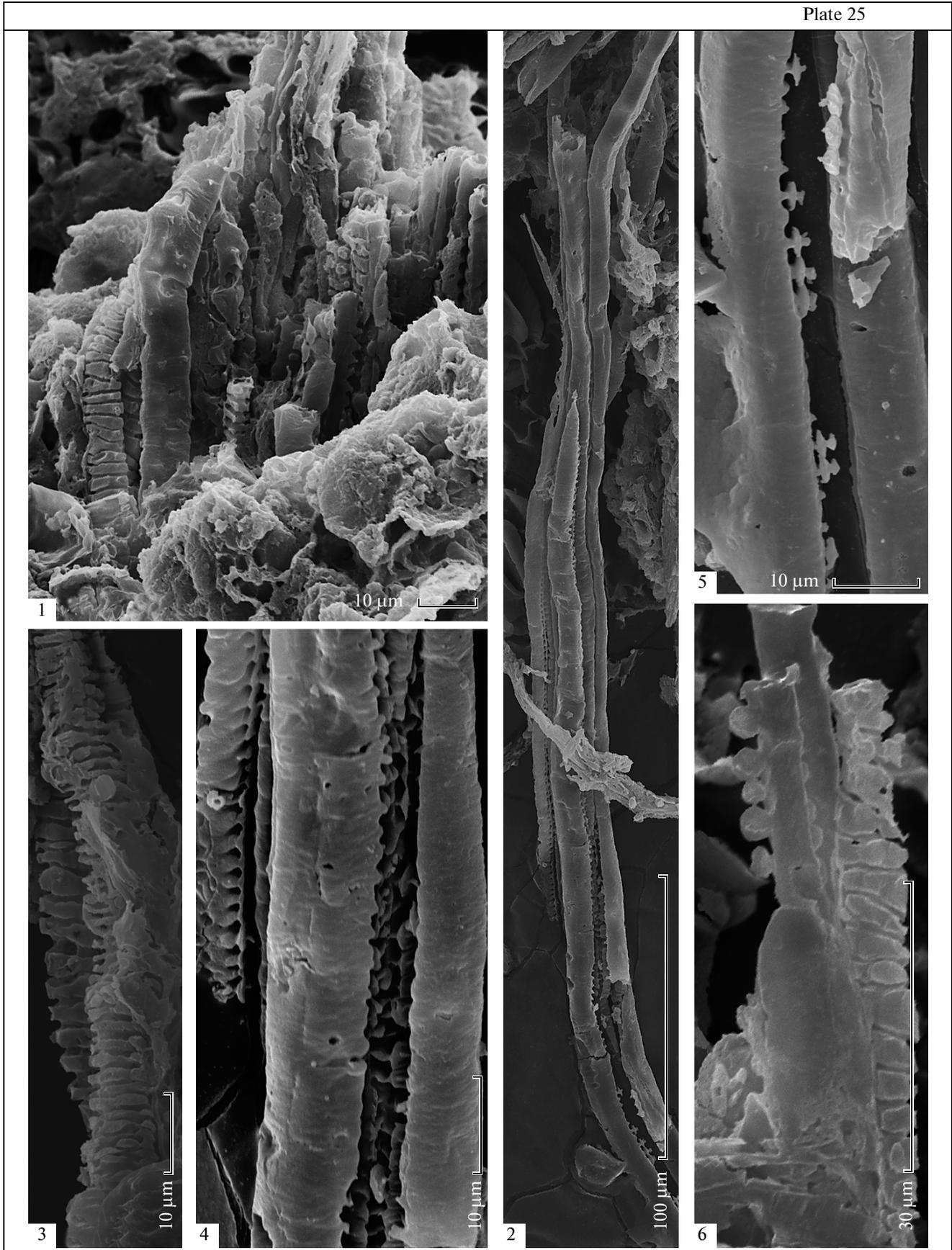
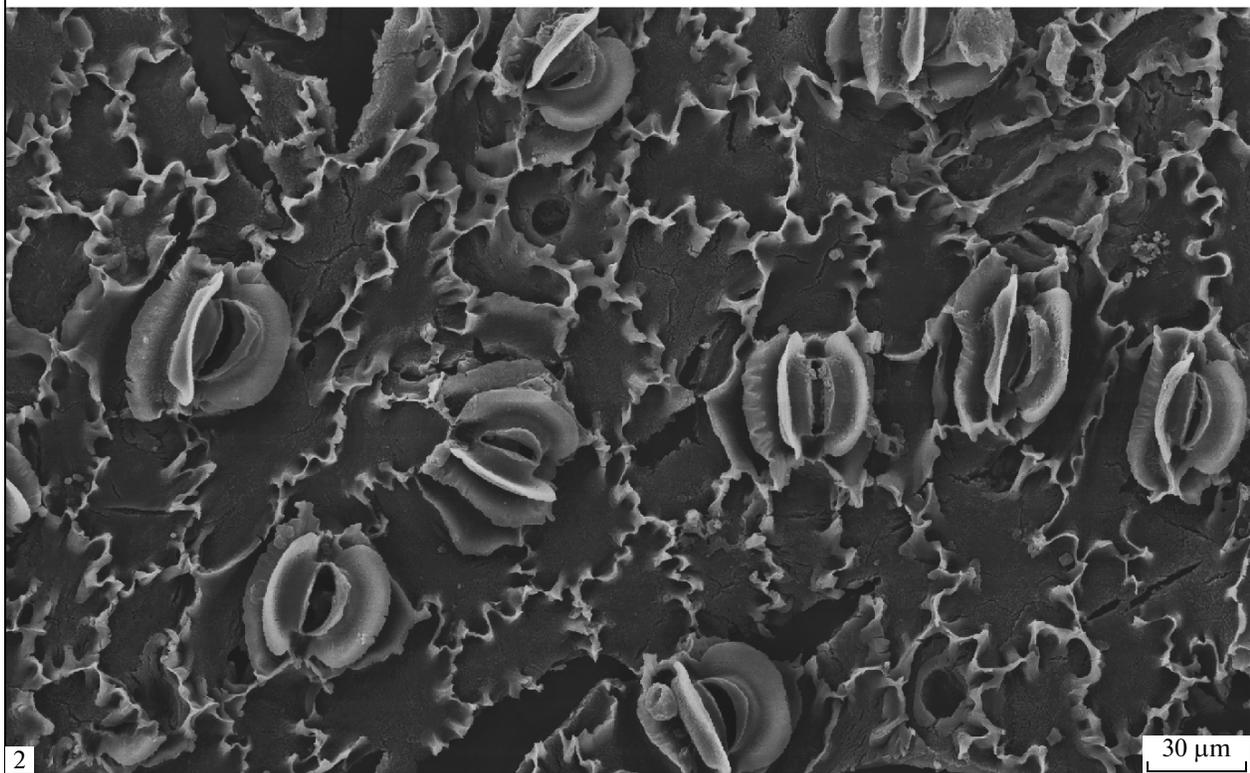
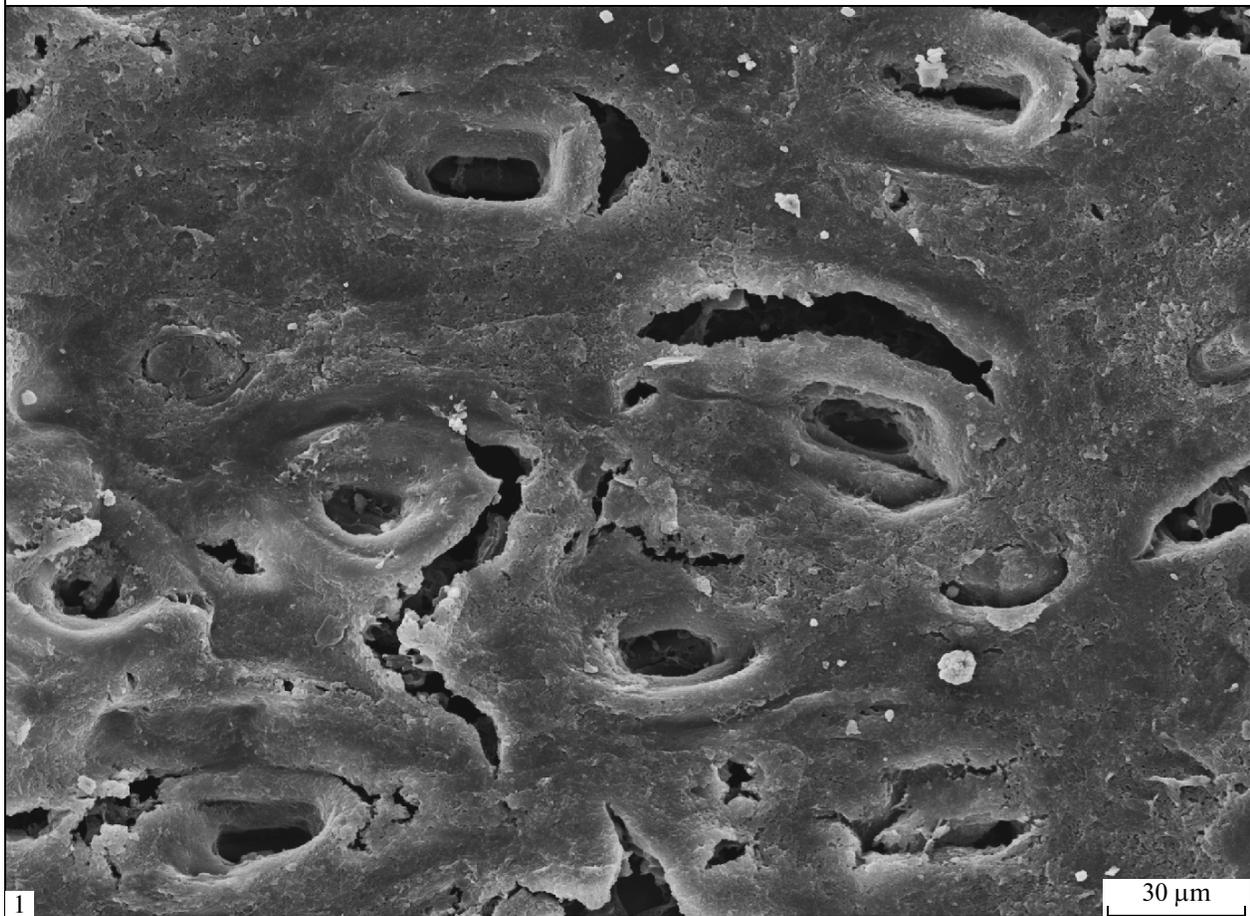
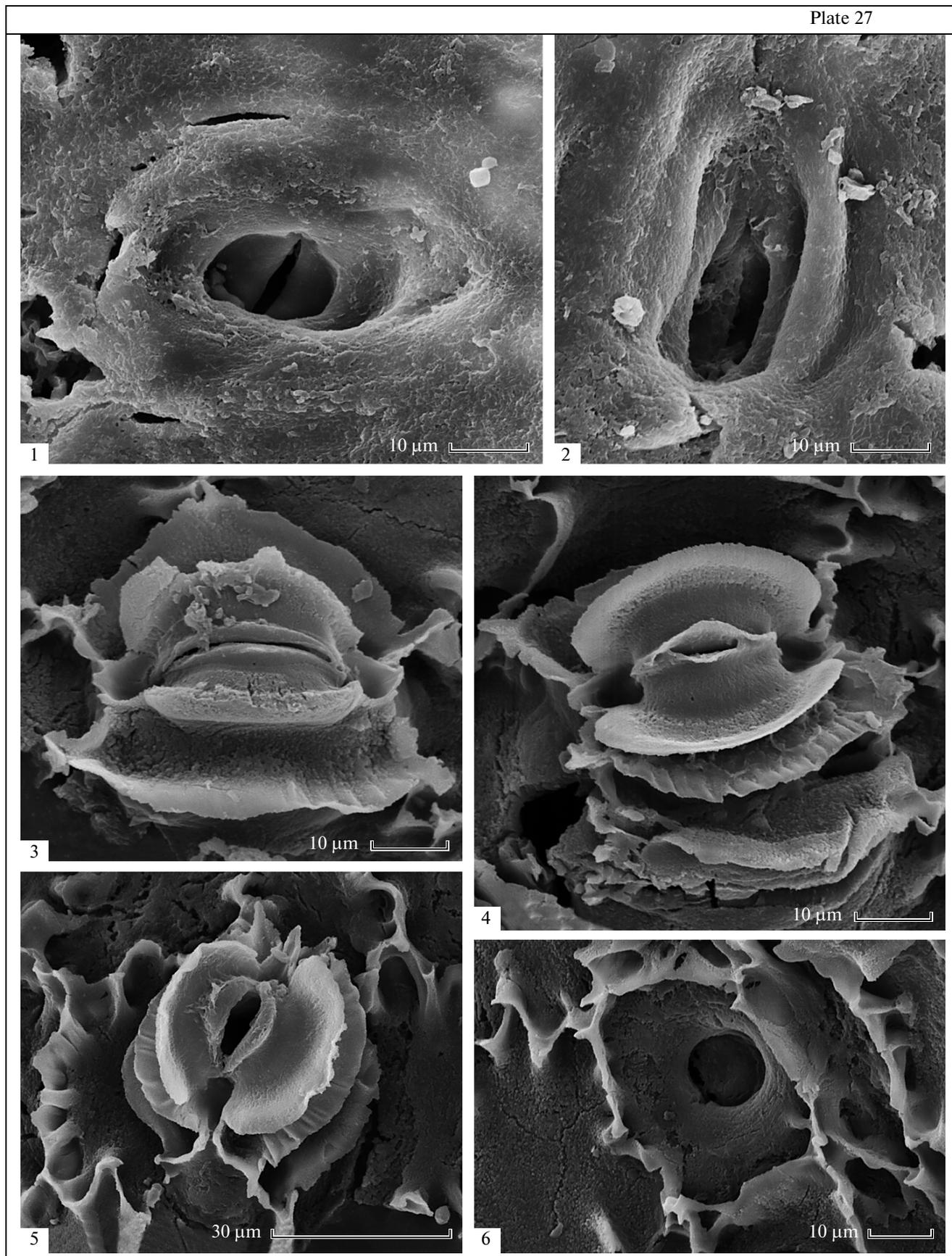
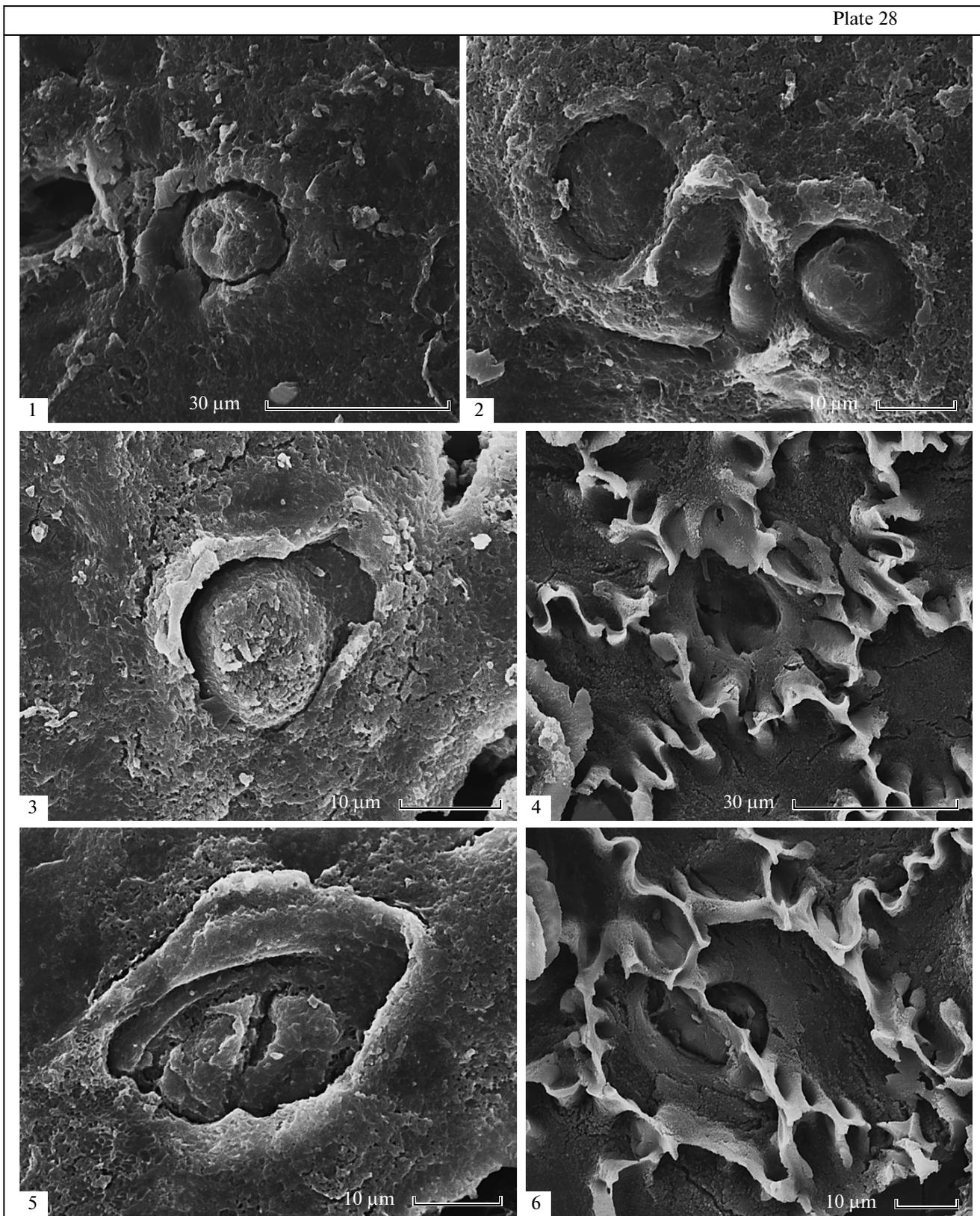
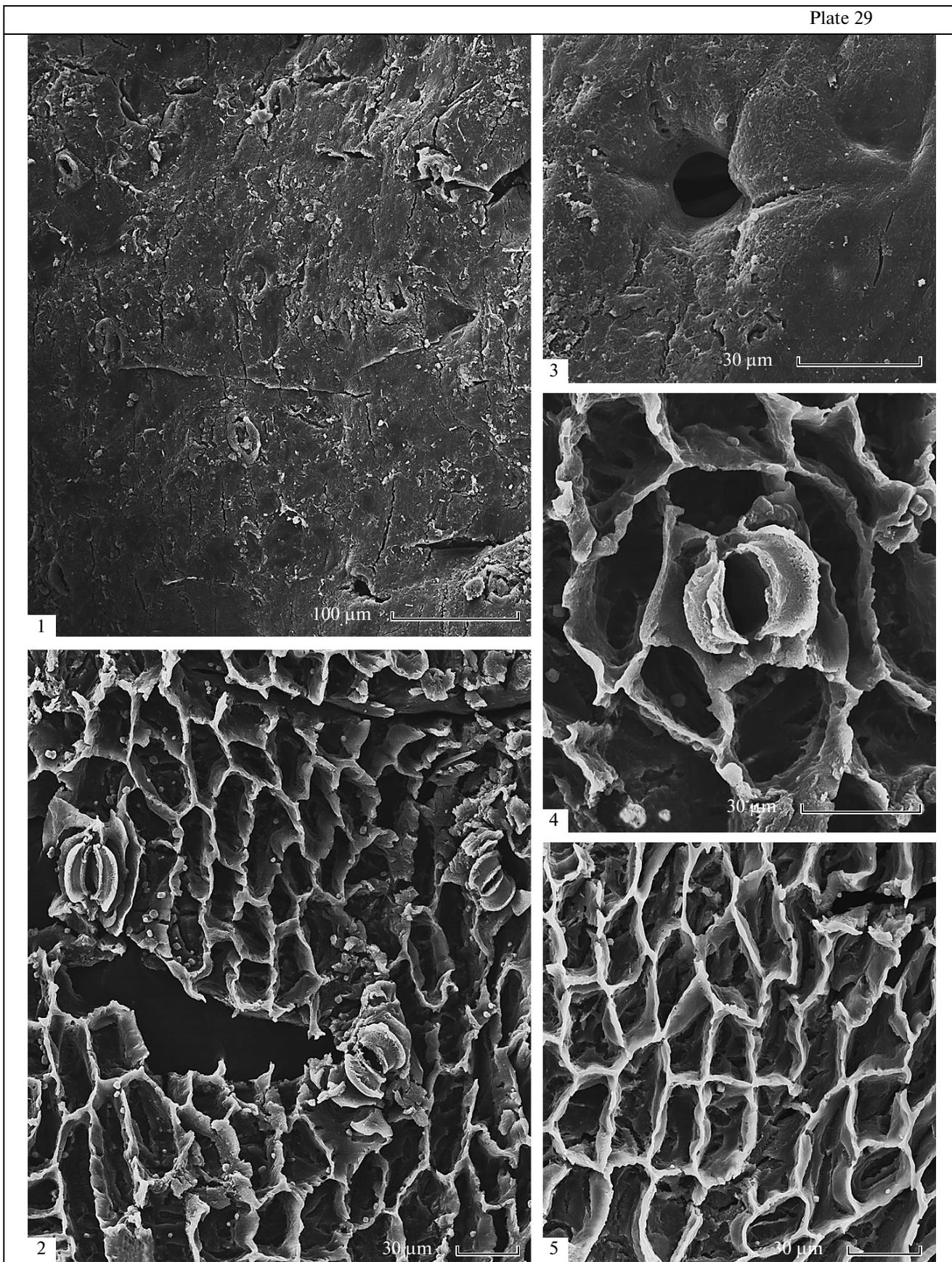


Plate 26









Explanation of Plate 23

Figs. 1–6. *Sympterophyllum sympinnatum* gen. et sp. nov., holotype no. 5137/30, SEM: (1) fragment of lower surface of a leaf, bases of fused segments, attached to the rachis, are visible (sutures are noted by arrows); (2) detail of fig. 1, wide stomatal zone is visible; (3) detail of fig. 2, numerous stomatal cavities and trichome bases are visible; (4) common cuticular wall between two adjacent segments; (5) suture between two segments on the lower leaf surface, marginal narrow nonstomatal zones are visible; (6) suture between two segments on the lower leaf surface.

Explanation of Plate 24

Figs. 1–4. *Sympterophyllum sympinnatum* gen. et sp. nov., holotype no. 5137/30, SEM: (1) leaf blade fragment in the contact area of two segments, on the left from suture, leaf tissues were removed (cuticle of marginal part of segment is visible), on the right from the suture, leaf tissues remain; suture between two segments is noted by arrow; (2) detail of fig. 1, upper surface of a leaf with removed cuticle; epidermal cells are preserved in the lower part, fibers are visible in the middle part; (3) detail of fig. 2, casts of epidermal cells from the upper surface of leaf blade; (4) fragment of the upper leaf surface, cells of mesophyll and fibers above vascular bundles are visible.

Explanation of Plate 25

Figs. 1–6. *Sympterophyllum sympinnatum* gen. et sp. nov., holotype no. 5137/30, SEM: (1) tracheid casts in the vascular bundle of segment; (2) fragment of vascular bundle, tracheids are preserved as casts; (3) tracheid casts in the vascular bundle of segment, impressions of inner thickenings are visible; (4) detail of fig. 2, tracheid casts in the vascular bundle of segment, casts of scalariform bordered pits are visible; (5) detail of fig. 2, tracheid casts in the vascular bundle of segment, casts of bordered pit chambers are visible; (6) tracheid casts, impressions of inner thickenings and bordered pit chambers are visible.

Explanation of Plate 26

Figs. 1 and 2. *Sympterophyllum sympinnatum* gen. et sp. nov., holotype no. 5137/30, SEM: (1) fragment of stomatal zone (outer surface of cuticle), stomatal pits and trichome bases are visible; (2) fragment of stomatal zone (inner surface of cuticle), variously orientated syndetoheilic stomatal apparatuses and trichome bases are visible.

Explanation of Plate 27

Figs. 1–6. *Sympterophyllum sympinnatum* gen. et sp. nov., holotype no. 5137/30, SEM: (1, 2) stomatal pits (outer surface of cuticle) show ledges, successively formed of neighboring and subsidiary cells; guard cells are visible on the bottom; (3) stomatal apparatus, possessing only subsidiary cells; (4) stomatal apparatus, one of subsidiary cells formed a neighboring cell; (5) stomatal apparatus, both subsidiary cells formed neighboring cells; (6) unicellular trichome base, view from the inner surface.

Explanation of Plate 28

Figs. 1–6. *Sympterophyllum sympinnatum* gen. et sp. nov., holotype no. 5137/30, SEM: (1, 2) unicellular trichome bases, view from the outer surface of cuticle; (3) bicellular trichome base, view from the outer surface of cuticle; (4) paired unicellular trichome bases, view from the outer surface of cuticle; (5) unicellular trichome base, view from the inner surface of cuticle; (6) bicellular trichome base, view from the inner surface of cuticle.

Explanation of Plate 29

Figs. 1–5. *Sympterophyllum sympinnatum* gen. et sp. nov., holotype no. 5137/30, SEM: (1) outer surface of cuticle on the lower part of rachis with scattered stomatal apparatuses; (2) inner surface of the lower cuticle of rachis, stomatal apparatuses are visible; (3) stomatal pit, view from the outer surface of cuticle on the lower side of rachis; (4) stomatal apparatus; (5) the fragment of inner surface of rachis cuticle, nearly straight anticlinal walls of cells are visible.

DISCUSSION

Coherent coalescence of leaf segments, which is so characteristic for the Late Paleozoic and Mesozoic Ginkgoopsida (Meyen, 1987), was found in bennettitaleans for the first time. But unlike Gigantonomiales, which had leaf blade with intercalary growth (Meyen, 1987), coherent leaves of the new genus would have marginal growth. Thus, we do not see in this case any direct parallelism.

In the whole, the details of leaf segments anatomical structure in the new genus are similar to those known in *Otozamites kerae*. The distinction is that, that in segments of *O. kerae*, continuous hypodermal tissue was developed, whereas in the new genus this tissue is absent.

From the ecological point of view, the origin of such a morphotype on the basis of *Pterophyllum*-type leaves can be explained by transition to shadowy wet habitats; that may be by implication suggested by purely developed palisade mesophyll, the absence of continuous layer of hypodermal tissue and fleshiness of segments. The presence of trichome bases on the lower surface of leaf and deeply sunken stomata suggest well developed protection of leaf from the water loss. Such a leaf xeromorphism, expressed in sunken stomatal apparatuses and developed trichomes, may be explained by the fact that these plants grew in windy areas.

Relatively small participation of vascular and mechanical tissues, and absence of hypodermal tissue

in segments, probably, were partially recompensed by turgor pressure in the parenchyma cells. Probably, the coalescence of segments was caused by purpose to strengthen the whole leaf construction. Taking into account the locality taphonomical features, the possible ecological niche of the plant, possessing studied leaves, may be shadowy river banks.

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