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New Species of *Sphenobaiera* Florin (Ginkgoales) from the Lower Cretaceous of Transbaikalia

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Abstract—Two new species of *Sphenobaiera* from the Baisa locality and Chernovskoe coal mine (Lower Cretaceous, Transbaikalia) are described. The cuticle of these plants inhabiting different environments differs significantly. Leaves of *S. starukhiniae* sp. nov. have a very thin cuticle, almost not sunken, open, nonprotected stomata, while the leaves of *S. vitimica* sp. nov. have relatively thick and strong cuticle, well-developed papillae overhang the sunken stomata. Guard cells of both species usually have fine radial striations. Apparently, the first plant dwelt in wet habitats, and the second, in the areas with a temporary shortage of water. This reconstruction is confirmed by sedimentological data, coal-bearing sediments (where *S. starukhiniae* sp. nov. was found) formed in swampy areas, carbonate deposits (*S. vitimica* sp. nov. was collected in marls of the Baisa locality), in the droughty one. It is not improbable that the cuticular features revealed of these two species contributed to more efficient water exchange and allowed plants to exist in these different environments.

Key words: *Sphenobaiera*, Ginkgoales, Lower Cretaceous, Transbaikalia, cuticular analysis.

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INTRODUCTION

The genus *Sphenobaiera* Florin is widely represented in Mesozoic floras of Eurasia (Florin, 1936; Harris et al., 1974; *Mesozoic Gymnosperms* ..., 1980; *Phytostratigraphy* ..., 1985; Samylina, 1988; Lydon et al., 2003; Sun et al., 2003; etc.). The type species *S. spectabilis* (Nath.) Florin is the oldest, comes from the Rhaetian of southern Sweden (Florin, 1936); the latest record was described as *Sphenobaiera* sp. from the Upper Cretaceous of the Arkagala Basin (Samylina, 1988).

This genus was established by Florin (1936). The shape and size of leaves of *Sphenobaiera* vary considerably (Doludenko and Rasskazova, 1972; Krassilov, 1972; *Phytostratigraphy ...,* 1985; Wang et al., 2005); therefore, the cuticular study is of great significance for the revelation of the taxonomic position of plant remains.

The assignment of *Sphenobaiera* to Ginkgoales is undoubted, whereas its position within the order remains questionable. Samylina (1970), noting the peculiarity of this genus, in particular, the structure of the leaf epidermis, erected the family Sphenobaieraceae. Krassilov (1972) reconstructed the relationship between leaves of *Sphenobaiera* and the ovule of *Karkenia* Archangelsky and, on this basis, proposed a new family, Karkeniaceae. Recently, this point of view was supported by studies of the cuticular ultrastructure of *S. huangii* (Sze) Hsü (Wang et al., 2005).

Samylina (1986), who studied with a scanning electron microscope morphology and epidermal structure of leaves of ten species of *Sphenobaiera*, including the type species *S. spectabilis*, noted that their stomata are uniform and well distinguished from the stomata of other gymnosperms. She pointed out that, in projection, the stomata of *Sphenobaiera* are strongly and smoothly convex in the middle part and abruptly narrow at the poles. In contrast to the stomata of *Ginkgo*, the stomata of this genus are usually very large, with a well-developed median cuticular thickening, which usually has a radial striation. According to Samylina, striation results from the radial orientation of microfibrils of guard cells. In the description of *Sphenobaiera ikorfatensis* (Seward) Florin from both the type locality Ikorfat in western Greenland (Lydon et al., 2003) and the Huolinhe Formation of China (Sun et al., 2003), such a thin striated cutinization was included as a distinctive feature in the diagnosis of the species. According to these authors, “the nature of such formation is not fully understood” (Lydon et al., 2003, p. 417). Most likely, it is typical for all *Sphenobaiera,* but because of its thinness and delicacy, it is not always preserved. For example, the radial striation on the stomata of *Sphenobaiera* from the Chernovskoe coal mine (Transbaikalia) occur rather rare; in general, it is often disrupted. The same is true of the Chinese species *S. huangii*, fine radial striation on guard cells of which is not always pronounced (Wang et al., 2005).

In modern plants, the radial orientation of cellulose microfibrils in the membranes of guard cells (radial micelles) plays an important role in the mechanism of stomatal movements, especially in opening of the stomatal aperture (Raven et al., 1986). These radial micelles allow the guard cells to lengthen and, at the same time, prevent expansion. An increase in turgor pressure causes the external (dorsal) walls of guard cells to move externally relative to their common walls. During this process, the radial micelles force the movement of the wall bordering the stomatal aperture, and the aperture opens (Raven et al., 1986, pp. 165).

In Late Mesozoic floras of Transbaikalia, *Sphenobaiera* appeared only in the Barremian–Aptian time. The most abundant remains occur in the Chernovskoe coal mine near the city of Chita (Tignya Formation, dated based on paleobotanical data as the Barremian–Aptian). Fossil plants were collected from the roof and underclay of the upper coal seams and directly from the coal. We revealed that representatives of the genera *Sphenobaiera* and *Pseudotorellia* Florin (*P. transbaikalica* Bugd.) were coal-forming plants. In addition, the flora includes *Equisetum* sp., *Coniopteris onychioides* Vassil. et K.-M., *Cladophlebis pseudolobifolia* Vachr., *Sphenopteris transbaicalica* Pryn., *Sphenopteris* sp., *Ginkgoites* ex gr. *huttonii* (Stern.) Black, *Karkenia* sp., *Phoenicopsis* ex gr. *angustifolia* Heer, *Pityophyllum* sp., *Desmiophyllum* sp., *Stenorachis* sp.

In some beds of this locality, ferns predominate, while others -are dominated by ginkgoaleans, conifers, and leaves with parallel venation of uncertain affinity. In cases when these leaves retained phytoleim and it was possible to study the cuticle, it was revealed that this leaves belong to *Pseudotorellia, Sphenobaiera*, and *Phoenicopsis* Heer.

In lacustrine marls in the Baisa locality (Zaza Formation, Barremian–Aptian), the following plants have been found: *Equisetum* sp., *Coniopteris* aff. *setacea* Vachr., *Neozamites verchojanensis* Vachr., *Nilssoniopteris* sp. nov., *Vitimia doludenkoi* Vachr., *Baiera* sp., *Ginkgoites* sp., *Sphenobaiera vitimica* sp. nov., *Pseudotorellia* sp., *Karkenia* sp., *Czekanowskia vachrameevii* Kirichkova et Samylina, *Phoenicopsis* sp. A, *Brachyphyllum* sp., *Pagiophyllum* sp., *Elatocladus manchurica* Pryn., *Pityolepis* aff. *oblonga* Samyl., *Pityophyllum* ex gr. *solmsii* Sew., *P.* ex gr. *nordenskioldii* (Heer) Nathorst, *Pityospermum turgense* Pryn., *P. witimii* (Reis) Prynada, *Schizolepis kryshtofovichii* Prynada, *Nageiopsis transbaikalica* Srebr., *Podozamites baissicus* Bugd., *Swedenborgia transbaikalica* Bugd., *Pseudolarix erensis* Krassil., *Samaropsis aurita* Krassil., *Pityanthus* sp., *Pityocladus* sp., and *Carpolithes* sp. (Bugdaeva, 1989). A group of plants combined in proangiosperms occupies a prominent place in this assemblage. These are *Baisia hirsuta* Krassil., *Eoantha zherikhinii* Krassil., *E. ornata* Krassil., *Prognetella minuta* Krassil. et Bugd., *Loricanthus resinifer* Krassil. et Bugd., *Preflosella nathania* Krassil., *Baissianthus ramosus* Krassil. et Bugd., *Praeherba spathulata* Krassil. et Bugd., *Vitimantha crypta* Krassil. et Bugd. (Krassilov and Bugdaeva, 1982, 2000; Krassilov, 1986, 1997;). In addition, this locality has yielded remains of angiosperms: leaf of *Dicotylophyllum pussilum* Vachr., fruit, and pollen of *Asteropollis asteroides* Hedlund et Norris (Vachrameev and Kotova, 1977).

The burials of the Baisa locality are dominated by conifers (*Pityophyllum* ex gr. *solmsii* and *Podozamites baissicus*) and proangiosperms (mostly *Baisia hirsuta*). Ginkgoaleans are rather rare, but they often occur as a whole leaves. A similar type of preservation is evidence about their really sparse participation in the lakeside plant communities. In the coeval Yixian Formation of Northeastern China *Sphenobaiera* is also extremely rare (Sun et al., 2001). Such a decline of ginkgoaleans in lakeside communities sharply contrasts with their dominance in swamp phytocenoses. The ferns are in a similar situation, their role is great in the floras of the coeval coal-bearing deposits, while in the Baisa locality their importance sharply drops.

MATERIAL AND METHODS

The material comes from the Early Cretaceous Baisa locality and Chernovskoe coal mine (Central Transbaikalia). In the former, two almost complete leaves and leaf fragments have been found in beds 15 and 31 (bed nos. follow Martinson, 1961); the latter has yielded one almost complete leaf and ten incomplete leaves.

The phytoleim was skimmed from specimens by a needle, passed through the nitric acid and alkali, washed with distilled water, and then analyzed in preparations for light (LM) and scanning electron (SEM) microscopes. Photographs were taken by the author using an Axioscop 40 microscope, with a Axiocam HRc camera and by N.N. Naryshkina with the aid of a SEM EVO 40 (Institute of Biology and Soil Science, Far East Branch, Russian Academy of Sciences: IBSS).

SYSTEMATIC PALEOBOTANY

Order Ginkgoales

Family Karkeniaceae Krassilov, 1972

Genus *Sphenobaiera* Florin, 1936

***Sphenobaiera vitimica* Bugdaeva, sp. nov.**

Plate 2, figs. 1–10

E t y m o l o g y. From the Vitim River.

H o l o t y p e. IBSS, no. ZB 31/140; leaf; western Transbaikalia, upper reaches of the Vitim River, right

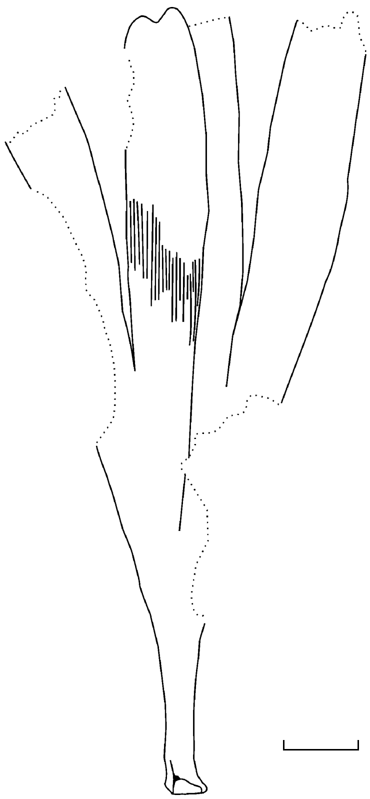


Fig. 1. *Sphenobaiera vitimica* sp. nov. holotype IBSS, no. ZB 31/140, leaf. Scale bar, 1 cm.

bank, Baisa locality; Zaza Formation, Lower Cretaceous (Figs. 1, 2a, Pl. 2, figs. 1–10).

D i a g n o s i s. Wedge-shaped leaf, 11 cm long, divided into two lobes. Each lobe divided into two lanceolate retuse lobes. Number of veins 15 or 16 per 10 mm. Lamina gradually descending into flat indistinct petiole with rounded abscission line. Leaf amphistomatic, lower cuticle thicker than upper cuticle. Upper cuticle composed of indistinct bands of cells. Cell ranging from irregularly rectangular to, less frequently, triangular, pentagonal, or fusiform with acuminate endings. Anticlinal walls thin, straight, and slightly undulate. Both well-developed (usually 40 × 60 μm) and underdeveloped (20–28 × 28–48 μm) stomata frequent. Stomata longitudinally or, less frequently, obliquely oriented. Subsidiary cells (five to eight) and ordinary epidermal cells equally cutinized. Proximal walls with large papillae, rarely without them. Subsidiary cells of underdeveloped stomata lacking papillae. Dark rounded cells frequent, surrounded by 5–7 cells identical to ordinary epidermal cells. Resin bodies of narrow elongated fusiform shape. Lower cuticle consisting of alternating stomatal and nonstomatal bands. Nonstomatal bands composed of one or two rows of elongate irregularly rectangular and oblong polygonal cells. Periclinal wall of almost all epidermal cells with cuticular thickening or papilla in central part. Anticlinal walls straight, slightly undulate, or, less frequently, finely sinuous. Stomata in intercostal zone arranged in two or, less frequently, one or three long rows. Stomata approximately 45–52 × 70–75 μm in size. Stomata sunken, obliquely and longitudinally orientated relative to veins, often contiguous or separated be one cell. Subsidiary cells five to seven. Papillose thickenings, overhanging stomatal aperture, developed on subsidiary cells, proximal papillae occasionally fused. Radial walls strongly cutinized. Stomata with radial striate cutinization. In intercostal zone, epidermal cells irregularly polygonal or, less frequently, elongated. Each cell having central papilla or cuticular dome with indistinct outlines.

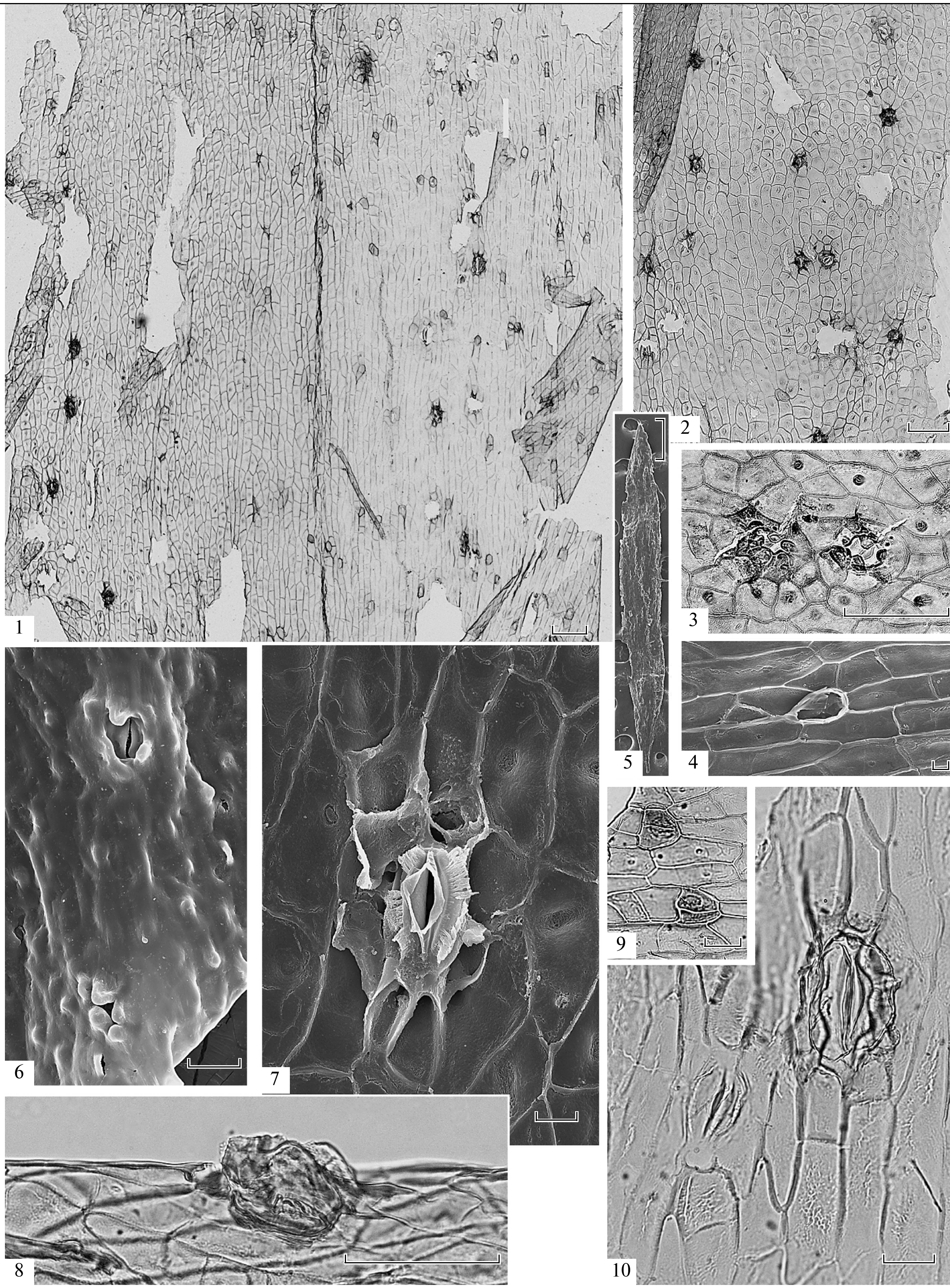
D e s c r i p t i o n (Figs. 1, 2a). The leaf is wedge-shaped, 11 cm long, divided into two lobes 7 cm long. Each lobe is divided into two lanceolate retuse lobes 5 cm long; each lobe has an apical emargination, ranging from 1 to 2 mm in depth. The lobes are lanceolate, their greatest width is in the upper part, and the apices of the lobes are sharply rounded. Density of veins is 15–16 per 10 mm. Each lobe is 12 mm wide. The lamina gradually descends into an indistinct flat petiole 4 mm wide. The petiole is slightly expanded at the base, with a rounded abscission line (Figs. 1, 2a).

The leaf is amphistomatic; the lower cuticle is thicker than the upper cuticle (Pl. 2, fig. 1). The lower cuticle is composed of indistinct bands of cells (Pl. 2, fig. 2). The costal and intercostal zones are poorly pronounced. The cell shape ranges from irregularly tetragonal to (less frequently) triangular, pentagonal, or fusiform with acuminate endings. The anticlinal walls are thin, straight, and slightly undulate. The cells are 14–16 (rarely 24) μm wide × 47–70 (rarely 120) μm long. The papillae occur extremely rarely on their periclinal walls. Both well-developed stomata (usually 40 × 60 μm) and underdeveloped stomata (20–28 × 28–48 μm) are common, but less frequent, than in the epidermis of the lower leaf surface. They are oriented

E x p l a n a t i o n o f P l a t e 2

Figs. 1–10. *Sphenobaiera vitimica* sp. nov., holotype IBSS, no. ZB 31/140: (1) fragments of the lower (left) and upper (right) cuticle; on the latter, rounded dark cells are visible; (2–4, 6–10) lower epidermis of leaf: (2) distribution of stomata in the stomatal zone; (3) geminated stomata; (4) rounded hair base; (5) resin body; (6) two stomata, one of which is covered with papillae, external view; (7) stoma, external view, remains of radial cutinization are visible on guard cells; (8) papillae covering the stomatal aperture, external view; (9) rounded hair bases on two cutinized cells; (10) two stomata, one is well-developed with papillae, second is smaller and lacks papillae. Scale bar: (1, 4, 7) 10 μm, (2, 3) 100 μm, (5) 200 μm, (6) 30 μm; (8) 50 μm; (9, 10) 20 μm. (1–3, 8–10) LM, (4–7) SEM.

Plate 2




(a)
(b)
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longitudinally, less frequently obliquely (Pl. 2, fig. 10). Subsidiary cells (from 5 to 8) and ordinary epidermal cells are equally cutinized; however, the inner anticlinal walls are deeply cutinized, forming thickened rim of the pit. The proximal walls usually have large papillae, sometimes, lack them (Pl. 2, figs. 3, 6, 8). Subsidiary cells of underdeveloped stomata lack papillae (Pl. 2, fig. 10). The rounded hair bases, developing on two or three ordinary epidermal cells, are rare (Pl. 2, fig. 9). Dark rounded cells, approximately 16 × 28 μm, are abundant, surrounded by five to seven cells and identical to ordinary epidermal cells. Perhaps, these are abortive maternal cells of stomata (Pl. 2, figs. 1, 4). Abundant resin bodies of narrow spindle shape, 170–280 × 900–2400 μm in size were macerated (Pl. 2, fig. 5).

The epidermis of the lower leaf surface consists of alternating stomatal and nonstomatal bands. Nonstomatal bands consist of one or two rows of elongate irregularly rectangular and oblong polygonal cells, on average 54 × 28.5 μm in size. The periclinal wall of almost all epidermal cells has a papilla or cuticular thickening in the central part. The anticlinal walls are straight, slightly undulate, or, less frequently, finely sinuous. The stomata in the intercostal zone are arranged mostly in two or, less frequently, one or three long rows; they are approximately 45–52 × 70–75 μm in size. The stomata are sunken, obliquely and longitudinally orientated relative to the veins, often contiguous (Pl. 2, fig. 3) or having one common cell. The number of subsidiary cells is from five to seven. They vary in cutinization; some subsidiary cells are as cutinized as ordinary epidermal cells, some are cutinized to a greater extent. Papillose thickenings, overhanging stomatal aperture, are developed on subsidiary cells; the proximal papillae are occasionally fused (Pl. 2, figs. 3, 6, 8, 10). The radial walls are strongly cutinized. Radial striate cutinization is preserved on the stomata (Pl. 2, fig. 7). The stomata on the upper cuticle are scarce, less frequent than on the lower cuticle, or absent. The underdeveloped stomata on the lower cuticle are markedly less frequent. Epidermal cells of the intercostal zone are irregularly polygonal or, less frequently, elongated; 37–62.5 × 27.5–42.5 μm in size. Each cell bears a central papilla or cuticular dome with indistinct outline (Pl. 2, figs. 6, 7). Each papilla stands out in relief of the inner surface as a small rounded pit (Pl. 2, fig. 7). At the leaf margin, there is a relatively wide (12–15 cells) band of elongated wedge-shaped and rectangular cells, with straight and slightly sinuous walls, sometimes, with nodular thickenings of the walls.

C o m p a r i s o n. In the epidermal structure, the leaf from the Baisa locality stands out among other leaves of this genus. It is primarily distinguished by the large number of abortive maternal cells of the stomata, the presence of both well-developed large stomata with papillae and underdeveloped much smaller stomata without papillae. In addition, the lower cuticle is very papillate, while the upper cuticle lacks papillae.

Krassilov (1972) described *Sphenobaiera ikorfatensis* (Seward) Florin forma *papillata* Samylina from the Barremian–Aptian Chemchukin Formation of the Bureya Basin, which is similar to *S. vitimica* sp. nov. in the amphistomatic leaf, the presence of papillae on the ordinary epidermal cells and dark-colored oval cells surrounded by 5–7 ordinary cells, interpreted as abortive stomata (Krassilov, 1972). However, the new species has a four-lobed leaf blade, while, in species from Bureya, it is bilobed; in *S. ikorfatensis* forma *papillata*, the number of stomata on the lower and upper surfaces are approximately equal, the stomata are larger, guard cells of stomata are very slightly sunken, open, cutinized around the oblong aperture, whereas, in *S. vitimica* sp. nov., the papillae partially or completely close the stomatal aperture in the well-developed stomata.

R e m a r k s. Lydon et al. (2003) described the lectotype of *Sphenobaiera ikorfatensis* (Sew.) Fl. from the Lower Cretaceous Ikorfat locality in western Greenland. These authors cited unpublished theses of Hall (1987), who proposed to group all species of *Sphenobaiera* into two main types: (1) with thinly cutinized subsidiary cells and exposed guard cells (as in *S. ikorfatensis*), (2) with thickly cutinized, frequently papillate subsidiary cells overhanging the guard cells. An example of *S. vitimica*, in which well-developed stomata with strong papillae are combined with underdeveloped, open stomata without papillae, suggests that this division is premature.

When describing *S. ikorfatensis* from the Lower Cretaceous Huolinhe Formation in Inner Mongolia, China, Sun et al. (2003) attached particular biogeographic importance to this species. According to these authors, the study of the lectotype of *S. ikorfatensis*, in particular, using a scanning electron microscope, revealed the presence of papillae on the periclinal cell walls. Therefore, they believed that the forma *papillata*, described from the Aldan Basin (Samylina, 1956), has no taxonomic status.

The leaves of *S. vitimica* sp. nov. have a thick cuticle and stomata protected by papillae, which are evidence of adaptation to changing conditions, possibly, water deficit. The plants were found in the marl beds. It is

Fig. 2. Leaves of (a) *Sphenobaiera vitimica* sp. nov., holotype IBSS, no. ZB 31/140; (b–h) *Sphenobaiera starukhiniae* sp. nov.: (b) specimen IBSS, no. ZBCH-7571, leaf bedding; (c) specimen IBSS, no. ZBCH-7575; (d) specimen IBSS, no. ZBCH-7570; (e) specimen IBSS, no. ZBCH-7559; (f) holotype IBSS, no. ZBCH-7557; (g) specimen IBSS, no. ZBCH-7563; (h) specimen IBSS, no. ZBCH-7568. Scale bar, 1 cm

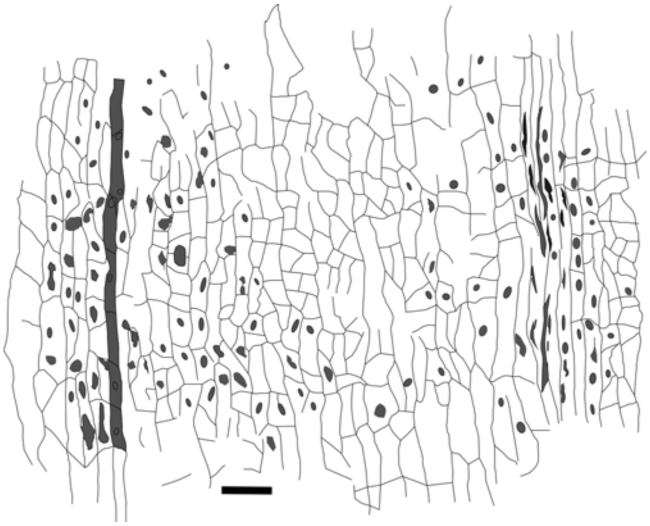


Fig. 3. *Sphenobaiera starukhiniae* sp. nov., holotype IBSS, no. ZBCH-7557, cuticle of the upper leaf surface. Scale bar, 100 μm.

known that carbonate rocks formed in the areas of semiarid climate, sufficiently hot for water evaporation.

M a t e r i a l. In addition to the holotype, an almost complete leaf (specimen IBSS, no. ZB 15/5) and leaf fragments from the Baisa locality.

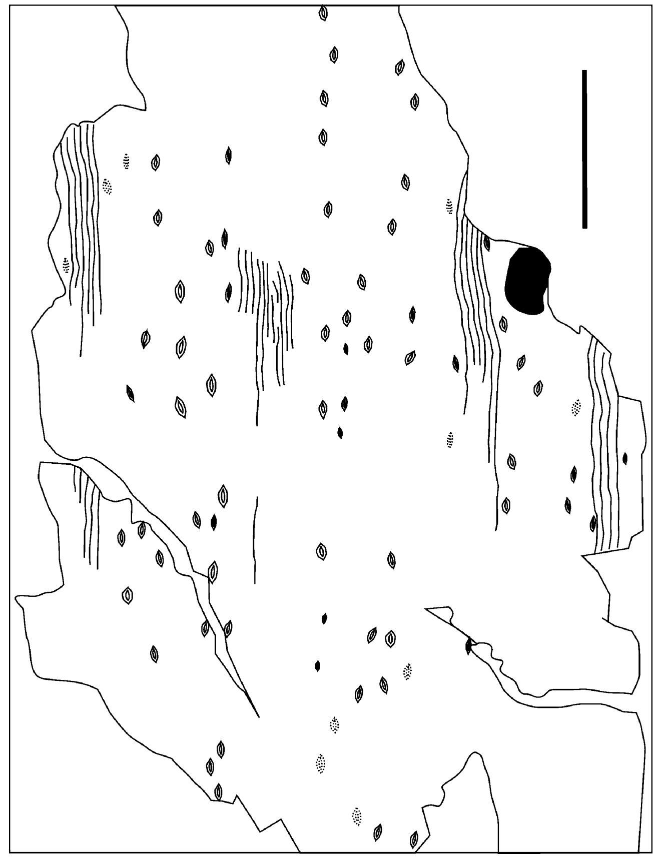


Fig. 4. *Sphenobaiera starukhiniae* sp. nov., holotype IBSS, no. ZBCH-7557, cuticle of the lower leaf surface, orientation and distribution of stomata in stomatal zone are shown. Scale bar, 500 μm.

***Sphenobaiera starukhiniae* Bugdaeva, sp. nov.**

Plate 3, figs. 1–6

E t y m o l o g y. In honor of the geologist Lyudmila Petrovna Starukhina.

H o l o t y p e. IBSS, no. ZBCh-7557; Chernovskoe coal mine, central Transbaikalia; Lower Cretaceous, Tignya Formation (Pl. 3, figs. 1–6; Fig. 2f).

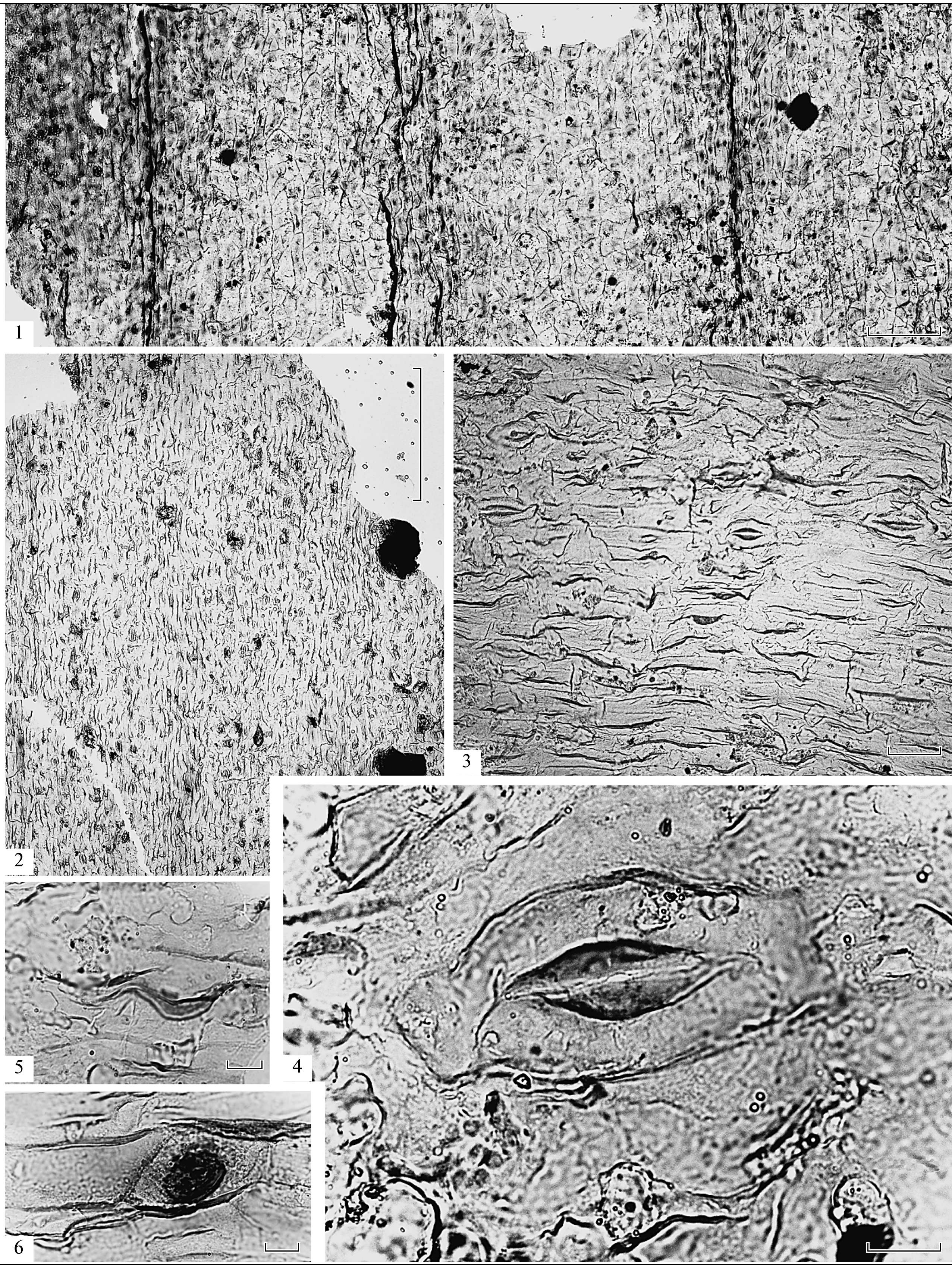
D i a g n o s i s. Wedge-shaped leaves, at least 6 cm long. Longest leaves more than 10 cm long. Leaf divided into two segments, each of which, in turn, into two lobes. Lobes lanceolate to linear, maximum width near middle. Density of veins 14 per 10 mm. Leaf hypostomatic, lower cuticle thicker than upper cuticle. In costal zones, cells of upper epidermis elongate, narrow, and irregularly rectangular. Cells often cutinized and distinguished by dark color, cutin ridges, or elongated cutin thickenings. Cell sizes 20–28 × 125 μm. Cells in intercostal zones trapeziform, irregularly tetragonal, isodiametric, triangular, or fusiform. Cells adjoining costal zones having papilla or cuticular ridge. Cell sizes 40 × 48–60 μm. Lower epidermis divided into costal and intercostal zones, consisting of irregularly tetragonal cells with extremely thin, straight, or, scarcely, undulate anticlinal walls, arranged in rows. Periclinal walls of epidermal cells very thin, slightly curved, convex. Almost each cell with longitudinal cutinized ridge, which occasionally relatively high and very narrow in projection or curved and crescent in section. Stomata in each intercostal zone arranged in four or five vague discontinuous rows, mostly obliquely or, less frequently, longitudinally orientated relative to veins. Subsidiary cells (five to seven, usually six) and ordinary epidermal cells equally cutinized. Stomata very slightly sunken, mostly without trichomes. Guard cells cutinized along elongated aperture.

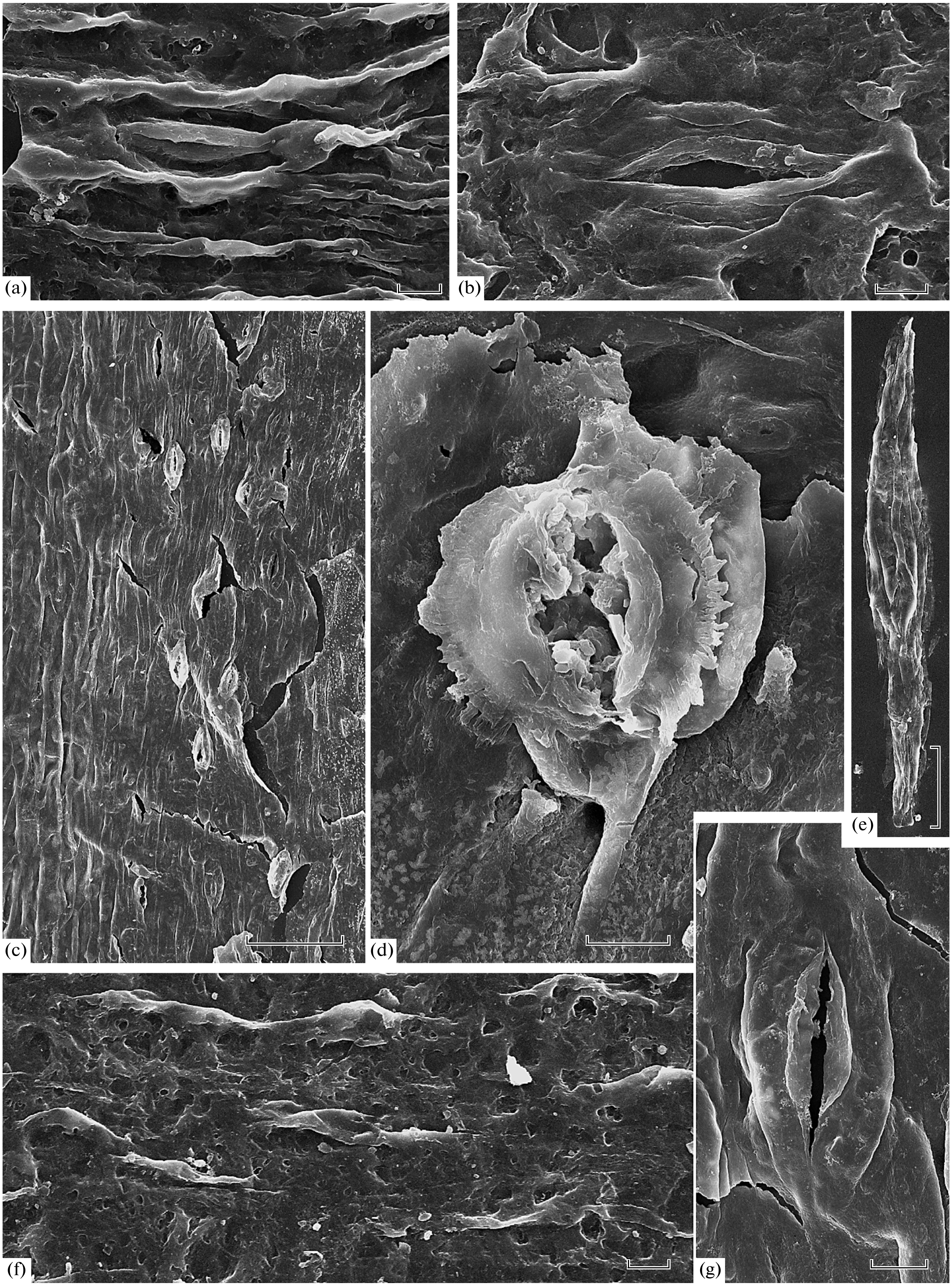
D e s c r i p t i o n (Figs. 2a–2h, 3, 4, 5a–5g). The leaves are wedge-shaped. The longest best preserved

E x p l a n a t i o n o f P l a t e 3

Figs. 1–6. *Sphenobaiera starukhiniae* sp. nov., holotype IBSS, no. ZBCH-7557, LM: (1) three costal and four intercostal zones of the upper epidermis; (2) lower cuticle, dark traces of fungal lesions are visible; (3) lower cuticle, arrangement of stomata in stomatal zone is seen; (4) stoma of the lower cuticle; (5) cuticular ridge on the epidermal cell of the lower epidermis; (6) rounded hair base on the periclinal wall of cell of the lower epidermis. Scale bar: (1) 200 μm; (2) 500 μm; (3–6) 10 μm.

Plate 3

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specimen is 10 cm long. The lamina is divided into two segments, each of which is in turn divided into two lobes from 4 to 8 cm long. The lobes are lanceolate to linear, with the maximum width near the middle. The apices of lobes are rounded. The density of veins is 14 per 10 mm. The width of each lobe ranges from 0.5 to 1 cm.

The leaf is hypostomatic, the lower cuticle is thicker than the upper cuticle. Cells of the upper epidermis are various in shape (Pl. 3, fig. 1; Fig. 3). In the costal zones, corresponding to veins, cells are elongate, narrow, and irregularly rectangular, 20–28 μm wide and from 90 (minimum) to 170 (maximum) μm long (on average about 125 μm long). The costal zones are about 170–180 μm wide. They are often more cutinized and distinguished by dark color, cutin ridges, or elongated cutin thickenings (Fig. 3). The intercostal zones are about 820 μm wide. Cells composing the intercostal zone vary in shape from trapeziform, irregularly tetragonal, isodiametric, triangular, to fusiform. Cells adjoining the costal zones have a papilla or cuticular ridge. The bases of hairs are rare. The papillae on the cells of the central part of the intercostal zone are relatively rare. The cells are mostly 40 × 48–60 μm in size, although some cell are about 24 (minimum) or 65 μm (maximum) wide, and from 40 μm (minimum) to 80 μm (maximum) long. The outer surface has a distinct relief; in addition to narrow, longitudinally extending ridges, there are many rough structures, pits, and grooves.

The lower epidermis is divided into costal and intercostal zones (Pl. 3, fig. 2; Fig. 4). The costal zones are from 95 to 160 μm wide. They are composed of irregularly tetragonal cells with extremely thin, straight or, scarcely, undulate anticlinal walls. The cells are arranged in rows. The cells are about 16–18 μm wide; the length is very difficult to estimate because of trichomes, folds, and extremely thin walls; it is probably about 70 μm. The intercostal zones are from 300 to 570 μm wide. The anticlinal walls of epidermal cells are very thin, slightly curved, convex, from 16 to 20 μm wide, about 70 μm long. Almost each cell has a longitudinal cutinized ridge, which is occasionally relatively high and very narrow in projection, or curved and crescent in section (Pl. 3, fig. 5; Fig. 5f). Cutinized cells with the base of a broken off hair are rare (Pl. 3, fig. 6). The stomata in each intercostal zone are arranged in four or five vague discontinuous rows, which are orientated obliquely or, less frequently, longitudinally relative to the veins (Pl. 3, figs. 2, 3). Contiguous stomata have not been recorded. The stomatal pit is bordered by a cutin rib (Pl. 3, fig. 4; Figs. 5a, 5b). The dimensions of stomata are 28–35 × 50–60 μm. Subsidiary cells (five to seven, usually six) and ordinary epidermal cells are equally cutinized. The stomata are very slightly sunken, mostly lack trichomes, rarely have rounded papillae on subsidiary cells (Figs. 5a–5d, 5g). Guard cells are cutinized along elongated aperture. Only three of all observed stomata have preserved radial striation on cutin thickenings (Fig. 5d). Some stomata are considerably narrower and smaller than others; they also differ in the less cutinized guard cells. Perhaps, these are immature stomata (Fig. 5g).

Comparison. *Sphenobaiera consimilis* Kiritchk. and *S. lenaensis* Kiritchk. from the lower part of the Batylykh Formation (Berriasian–Barremian), *S. subtilis* Kiritchk. from the upper part of the Ekseny-akh Formation (Aptian) of the Lena River Basin have hypostomatic leaves, like the new species (*Phtostratigraphy* ..., 1985). However, as distinct from *S. starukhiniae* sp. nov., the lower epidermis of *S. consimilis* consists of hardly discernible stomatal and nonstomatal zones and the periclinal walls of ordinary epidermal cells have papillae. The walls of subsidiary cells of the stomata of leaves of *S. consimilis* facing the stomatal aperture are sometimes strongly cutinized and, in this case, they have papillae. Subsidiary cells of the stomata of *S. lenaensis* have large, thickly cutinized papillae overhanging the stomatal aperture. Ordinary epidermal cells of the upper epidermis of *S. subtilis* are much smaller than in *S. starukhiniae* sp. nov. In addition, the longitudinally oriented stomata of *S. subtilis* form 2–4 indistinct discontinuous rows in the stomatal band, while the new species has more rows. The stomatal bands of *S. subtilis* are composed by isodiametric cells with straight anticlinal walls and distinct papillae, while cells of stomatal bands of *S. starukhiniae* sp. nov. are more elongated and have peculiar ridges. Subsidiary cells of the stomata of *S. subtilis* have thickly cutinized papillae overhanging the stomatal aperture; this feature was not observed in the new species.

The hypostomatic leaves are characteristic of *Sphenobaiera czekanowskiana* (Heer) Florin from the Ust'-Balei locality of the Early–Middle Jurassic Cheremkhovo Formation in the Irkutsk Basin (Doludenko and Rasskazova, 1972). These authors point out that, on the upper epidermis, individual stomata occur. *S. czekanowskiana* differs from *S. starukhiniae* sp. nov. in the fact that each subsidiary cell of its stomata has a small papilla located in the center of the cell or displaced toward the stomatal aperture. In addition, the stomata of *S. czekanowskiana* scattered randomly between the veins or in one or

Fig. 5. *Sphenobaiera starukhiniae* sp. nov., holotype IBSS, no. ZBCH-7557, cuticle of the lower leaf surface, SEM: (a, b) stomatal complexes, external view; (c) distribution of stomata in the stomatal zone; (d) stomata with remains of radial fibrils; (e) resin body; (f) external surface complicated by ridges and roughness; (g) stoma without radial fibrils. Scale bar: (a, b, d, f, g) 10 μm; (c, e) 100 μm.

three short vague rows in the stomatal band. The stomata of the new species are arranged in 3–7 more or less distinct rows in the stomatal band. Cells of the lower epidermis of *S. czekanowskiana* are wider, each ordinary epidermal cell has a small rounded and sometimes hollow papilla; in *S. starukhiniae* sp. nov., the majority of cells have a crest.

Remarks. A photograph of the external leaf surface of *S. ikorfatensis* is presented by Lydon et al. (2003). The authors noted the presence of many grooves, striations, and holes, none of which show apparent sensitivity to the position of the veins or stomata. They assumed that these marks represent insect rasping and bites, or fungal lesion. The latter seems to them more likely in view of abundant fungal spores adhering to the external surface, which are regarded as fossil rather than Recent spores. In addition to ridges and protrusions, the external leaf surface of *S. starukhiniae* sp. nov. is complicated by tubercles, pits, and coarse structures. Although it was revealed that the cuticle of *S. starukhiniae* sp. nov. has many fungal lesions (dark rounded bodies in Pl. 3, fig. 2), they seem to play a minor role in the complications of its relief. First, the overwhelming majority of fungal lesions on the leaves of *S. starukhiniae* sp. nov. are confined to the lower cuticle, while the surface is rough on both upper and lower cuticles; second, insect injuries and fungal lesions are restricted to local areas, whereas the relief described is observed on both surfaces of all leaves.

The cuticle of the new species is extremely thin. The stomata on the lower epidermis lack protective formations. Perhaps, these features reflect paleoenvironments, in which this plant existed, swampy area with constant regime of excessive water. It is not inconceivable that fogs usually occurred over the marsh, where plant remains accumulated to produce coal, as often happens at present. For this reason, plants did not develop adaptations to droughts and water retention during dry periods.

Material. In addition to the holotype, the Chernovskoe coal mine has yielded ten incomplete leaves from the roof and bottom of the upper coal seam, dispersed cuticles macerated from coal samples.

CONCLUSIONS

The cuticle of two species of the genus *Sphenobaiera*, which grew in different environments, is significantly different. The species *S. starukhiniae* sp. nov. has an extremely thin cuticle, slightly sunken, open nonprotected stomata, whereas *S. vitimica* sp. nov. has a rather thick and strong cuticle, the stomata are sunken and protected by solid papillae. Apparently, the first plant dwelt in moist habitats, and the second, in the areas with a temporary shortage of water. It is evident that *Sphenobaiera* from the Chernovskoe coal mine was not short of water supply. Many of its leaves are invaded by fungi, which mostly colonized the lower epidermis. Wet conditions are favorable for the life activity of fungi. This reconstruction is confirmed by sedimentological data. Coal-bearing sediments (in which *S. starukhiniae* was found) formed in swampy areas, while carbonate deposits (*S. vitimica* was collected from marls in the Baisa locality) accumulated under semiarid conditions. The two localities differ essentially in floral composition: the Chernovskoe assemblage is dominated by ferns and ginkgoaleans; in the Baisa locality, conifers and proangiosperms prevail. Interestingly, representatives of one genus show remarkable plasticity in adaptation to different environments. It is not improbable that this adaptability is associated with the radial striation on guard cells. So far, only *Sphenobaiera* among Mesozoic gymnosperms have shown this feature. Perhaps it favored more efficient water exchange.

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REFERENCES

1. E. V. Bugdaeva, “Correlation of the Lower Cretaceous Deposits of Isolated Basins of Transbaikalia Based on Flora,” Tr. Inst. Geol. Geofiz. Sib. Otd. Akad. Nauk SSSR, No. 722 (Stage and Zone Scales of the Boreal Mesozoic of the USSR), 162–168 (1989).
2. M. P. Doludenko and E. S. Rasskazova, “Ginkgoales and Czekanowskiales of the Irkutsk Basin,” Tr. Geol. Inst. Akad. Nauk SSSR, No. 230 (Mesozoic Plants (Ginkgoales and Czekanowskiales) of Eastern Siberia), 7–43 (1972).
3. R. Florin, “Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters: II. Allgemeiner Teil,” Palaeontographica Abt. B **82** (1–4), 1–72 (1936).
4. N. A. Hall, “A Taxonomic Revision of Some Mesozoic Ginkgoales, Czekanowskiales and Related Gymnosperms” in *PhD Theses* (Unpublished) (Univ. Manchester, 1987).
5. T. M. Harris, W. Millington, and J. Miller, *The Yorkshire Jurassic Flora: IV* (Brit. Mus. Nat. Hist., London, 1974).
6. V. A. Krassilov, *The Mesozoic Flora of the Bureya River (Ginkgoales and Czekanowskiales)* (Nauka, Moscow, 1972) [in Russian].

7. V. A. Krassilov, "New Floral Structure from the Lower Cretaceous of Lake Baikal Area," Rev. Palaeobot. Palynol. **47**, 9–16 (1986).

8. V. A. Krassilov, *Angiosperm Origins: Morphological and Ecological Aspects* (Pensoft, Sofia, 1997).

9. V. A. Krassilov and E. V. Bugdaeva, "Achene-Like Fossils from the Lower Cretaceous of the Lake Baikal Area," Rev. Palaeobot. Palynol. **36**, 279–295 (1982).

10. V. A. Krassilov and E. V. Bugdaeva, "Gnetophyte Assemblage from the Early Cretaceous of Transbaikalia," Palaeontographica B **253**, 139–151 (2000).

11. S. J. Lydon, J. Watson, and N. A. Harrison, "The Lectotype of *Sphenobaiera ikorfatensis* (Seward) Florin, a Ginkgophyte from the Lower Cretaceous of Western Greenland," Palaeontology **46** (2), 413–421 (2003).

12. G. G. Martinson, *Mesozoic and Cenozoic Mollusks from Continental Deposits of the Siberian Platform, Transbaikalia, and Mongolia* (Akad. Nauk SSSR, Moscow, 1961) [in Russian].

13. *Mesozoic Gymnosperm Plants of the USSR: Reference Guide* (Nauka, Moscow, 1980) [in Russian].

14. *Phytostratigraphy and Flora of Jurassic and Lower Cretaceous Deposits of the Lena Basin* (Nedra, Leningrad, 1985) [in Russian].

15. P. Raven, R. Evert, and S. Eichhorn, *Biology of Plants*, 4th ed. (Worth Publ., New York, 1986), Vol. 2.

16. V. A. Samylina, "Epidermal Structure of Leaves of the Genus *Sphenobaiera*," Dokl. Akad. Nauk, **106** (3), 537–539 (1956).

17. V. A. Samylina, "Ginkgoales and Czekanowskiales (Some Results and Tasks of Research)," Paleontol. Zh., No. 3, 114–123 (1970).

18. V. A. Samylina, "Comparative and Stomatographic Study of Ginkgoales and Czekanowskiales: First Results of Use of Electron Scanning Microscope," in *Problems of Paleobotany*, Ed. by. A. L. Takhtajan (Nauka, Leningrad, 1986), pp. 119–126 [in Russian].

19. V. A. Samylina, *Arkagala Stratoflora of Northeastern Asia* (Nauka, Leningrad, 1988) [in Russian].

20. Ge Sun, S. J. Lydon, and J. Watson, "*Sphenobaiera ikorfatensis* (Seward) Florin from the Lower Cretaceous of Huolinhe, Eastern Inner Mongolia, China," Palaeontology **46** (2), 423–430 (2003).

21. Ge Sun, Sh.-L. Zheng, D. L. Dilcher, Y.-D. Wang, and Sh.-W. Mei, *Early Angiosperms and Their Associated Plants from Western Liaoning, China* (Shanghai Sci. Techn. Educ. Publ. House, Shanghai, 2001).

22. V. A. Vachrameev and I. Z. Kotova, "Early Angiosperms and Associated Plants from the Lower Cretaceous of Transbaikalia," Paleontol. Zh., No. 4, 101–109 (1977).

23. Y.-D. Wang, G. Guignard, F. Thevenard, et al., "Cuticular Anatomy of *Sphenobaiera huangii* (Ginkgoales) from the Lower Jurassic of Hubei, China," Am. J. Bot. **92**, 709–721 (2005).