

Morphology and Taxonomy of *Sphenophyllum biarmicum* Zalesky, 1937 from the Lower Permian of the Cis-Urals

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Received August 28, 2001

Abstract—The morphology and systematic position of *Sphenophyllum biarmicum* Zalesky are discussed. *Gangamopteris fimbriata* Zalesky, *G. tenuinervis* Zalesky, and *Sphenophyllum comiense* Tschirkova are considered to be synonyms of *S. biarmicum*. The paleoecology of the species is discussed, and its whole-plant-concept reconstruction is proposed.

Key words: sphenophylls, *Sphenophyllum*, Permian, paleoecology.

INTRODUCTION

In sciences dealing with the organic world's diversity, a great amount of newly established taxa is often considered as a criterion of effective investigations. However, paleontological systematics (in particular, paleobotanical systematics) is overburdened with numerous taxa, introduced on the basis of very fragmentary material or minor differences from the related taxa of the same taxonomical rank. This leads to the inflation of names of taxa, which is especially conspicuous at the specific and generic levels (Meyen, 1990).

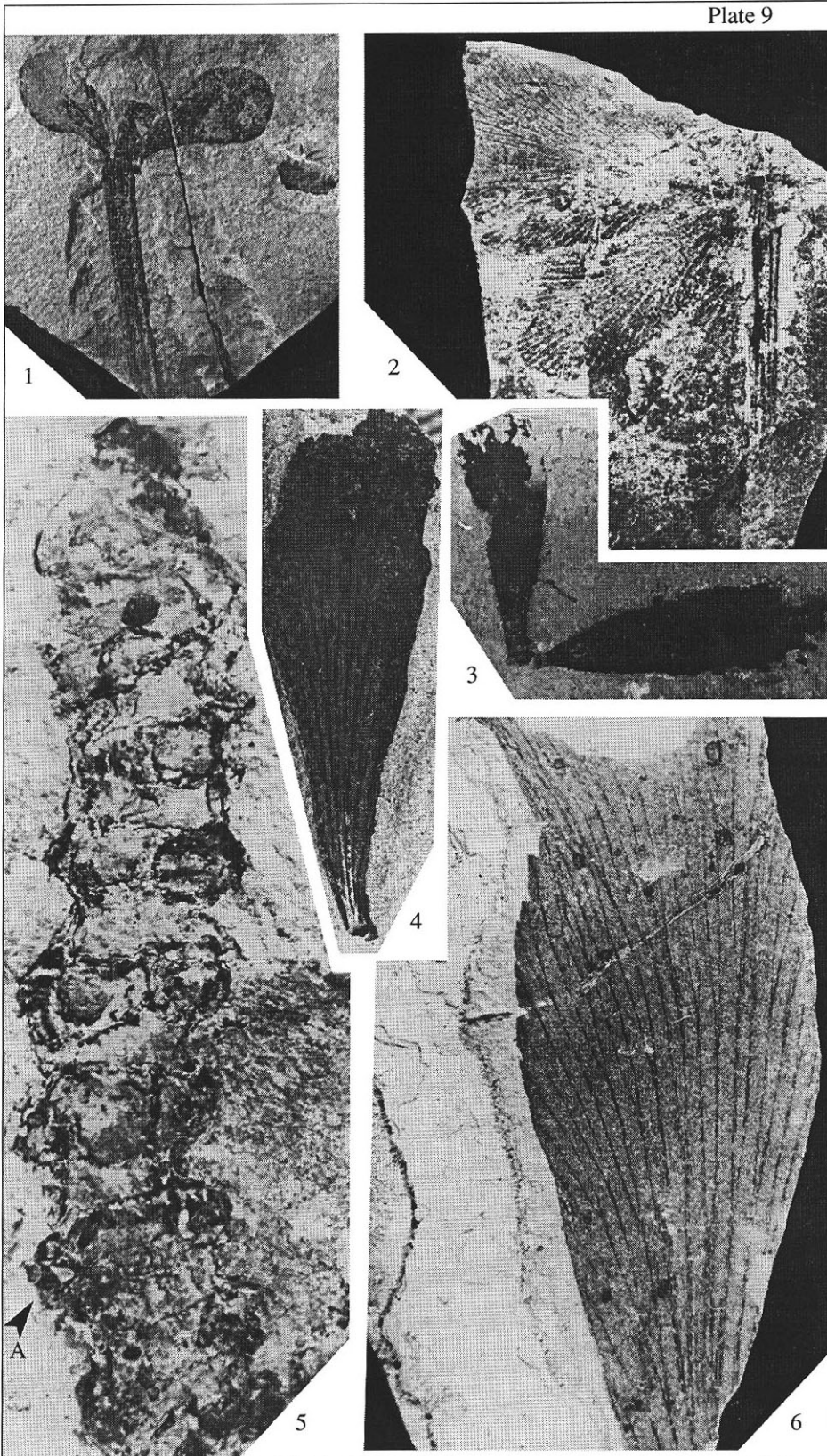
The revision, including redescription of earlier introduced taxa and placement (if necessary) of earlier synonyms into the synonymy of the species having priority, is the only means against the unjustified creation of taxa. However, within recent years such works have rarely appeared in paleobotanical literature. The opinion about the overestimated diversity of many Late Paleozoic floras of Angaraland is quite common in the scientific community. Species are often differentiated on the basis of insignificant features, which fully fit into the intraspecific variability.

A widely distributed species from the Kungurian of western Subangaraland (southern and central Cis-Urals and the Pechora Basin), *Sphenophyllum biarmicum* Zalesky, is redescribed in the present paper. Binomens earlier considered as separate species and specimens described in open nomenclature are treated as synonyms of the species. The systematics and paleoecology are discussed, and the whole-plant-concept reconstruction is proposed.

In recent decades numerous papers have appeared that are focused on the vegetative organs of sphenophylls (Doubinger and Vetter, 1953, 1954; Remy and Remy, 1959; Remy, 1962; Schabillon, 1970; Batenburg, 1977, 1981, 1982; Storch and Barthel, 1980; Storch, 1983; Riggs and Rothwell, 1985; Tidwell *et al.*, 1988;

Chen Qi-shi, 1988; Zodrow, 1989; Zhang Hong and Schen Guang-long, 1990; Yao *et al.*, 2000), their epidermal morphology (Pant and Srivastava, 1983; Barthel, 1997), anatomy (Snigirevskaya, 1959; Darrah, 1968; Baxter, 1972; Good and Taylor, 1972), sporangio-phores (Baxter, 1950; Sze, 1955; Remy, 1960, 1961; Remy and Remy, 1961; Snigirevskaya, 1962; Hetterschheid and Batenburg, 1984; Kerp, 1984; Riggs and Rothwell, 1985; Zodrow and Gao Zhifeng, 1991; Cuneo *et al.*, 1993), in situ spores (Taylor, 1985), and general ecology of this plant group (Shchegolev, 1991).

The systematic position and rank of sphenophylls were treated in different ways. Krishtofovich (1957) assigned the genera *Sphenophyllum* Brongn. 1822 and "*Tristachya*" *Raciborskii* to the order Sphenophyllales of the subdivision Sphenopsida, division Psilogenae. In *Osnovy ...* (1963) the order Sphenophyllales was assigned to the class Equisetinae of the division Arthropsidea (=Sphenopsida); the families Sphenophyllaceae Potonie 1897, Cheirostrobaceae D. Scott 1907, and "*Tristachyaceae*" Lilpop 1937 were included in the order Sphenophyllales (*Osnovy paleontologii*, 1963). Takhtajan (1986) included these families into the order Sphenophyllales, class Sphenophyllopsiada of the division Equisetophyta of his system of the higher plants. Many reviews of Late Paleozoic plants do not consider the families of the order Sphenophyllales. Thus, Lemoigne (1988) only enumerated the genera of this order, *Sphenophyllum* Koenig 1925, *Trizygia* Royle 1839, *Parasphenophyllum* Asama 1970, *Paratrizygia* Asama 1970, and *Lilpopia* Conert et Schaarschmidt 1970 (= "*Tristachya*" Lilpop 1937, nom. illeg.). Taylor and Taylor (1993) considered (within the order Sphenophyllales) the genera *Sphenophyllum* and *Bowmanites* Binney 1871, *Peltastrobis* Baxter 1950, *Sentistrobis* Riggs et Rothwell 1985, *Cheirostrobis* Scott 1897, and *Lilpopia* and noted the distinctiveness of the latter. The Upper Devonian genus *Eviostachya* Stockmans 1948 is



considered to be close to the order Sphenophyllales (Stockmans, 1948; Leclercq, 1957). Meyen (1987) assigned all sphenophylls to the order Bowmaniales of the subclass Bowmanitidae, class Equisetopsida. The present author adopts the traditional conception of the systematics of sphenophylls, including the existence of the family Lilpopiaceae (Takhtajan, 1986).

There are two distinct groups of sphenophylls with considerably different sporangiophores. The more numerous group embraces plants with compact strobili of the *Bowmanites* (= *Sphenophyllostachys* Seward 1898) type and derivative forms assigned to *Sentistrobus*, *Peltastrobus*, and some other genera (*Anastachys* Remy 1955, *Aspidiostachys* Remy 1955, *Bifurcosphenophyllum* Lotsy 1909, *Koinostachys* Remy 1955, *Monosphenophyllum* Lotsy 1909, and *Tetrasphenophyllum* Lotsy 1909). However, some paleobotanists do not accept the existence of these latter genera. Another group comprises plants with specific fertile zones of the *Lilpopia* type.

Sphenophyllum biarmicum Zalessky emend. Naugolnykh, emend. nov. belongs to the first group and should be considered within the family Sphenophyllaceae (= Bowmanitaceae s.s.), since it possessed compact terminal strobili characteristic of *Bowmanites biarmensis* Naug. (Naugolnykh, 1998; see also the present paper, Pl. 7, fig. 5, Pl. 8, figs. 1, 6). However, the long terminal lobes and veins in lateral leaf margins make leaves of *Sphenophyllum biarmicum* similar to the leaves of the *Lilpopia* group. This similarity could be explained by the parallel development of both families in the Late Carboniferous–Early Permian time.

MATERIAL

A representative sampling (over 30 specimens) has been studied. The majority of the specimens have been collected by the author (Geological Institute of the Russian Academy of Sciences, GIN, nos. 3773(11) and 4856). The originals and syntypes to the papers by Vladimirovich (1985, 1986) housed at the Central Geological Museum (TsNIGR, St. Petersburg), nos. 12230 and 12339, have also been studied.

SYSTEMATIC PALEOBOTANY

Sphenophyllum biarmicum Zalessky emend. Naugolnykh, emend. nov.

Plate 7, figs. 1–4, 6; Plate 8, figs. 2–5, 7

Sphenophyllum biarmicum Zalessky: Zalessky, 1937, pp. 44–46, figs. 7, 8; Vladimirovich, 1985, pl. V, figs. 8b, 9b, 11b, 13b, 14; Vladimirovich, 1986, pl. 139, fig. 2; Naugolnykh, 1998, pp. 35–37, pl. I, fig. 4; pl. III, figs. 4, 5; pl. VI, fig. 3; pl. VII, fig. 6; text-figs. 12b, A–C, E, F; text-figs. 13, B, D.

Gangamopteris fimbriata Zalessky: Zalessky, 1937, fig. 7.

Gangamopteris tenuinervis Zalessky: Zalessky, 1939, pp. 347–348, fig. 26.

Sphenophyllum comiense Tschirkova: Zalessky and Tschirkova, 1938, pp. 15–16, figs. 7–10; Neuburg, 1964, pl. I, figs. 1–5; pl. V, fig. 7; Pukhonto, 1998, pl. 1, fig. 6.

?*Sphenophyllum thonii* Mahr: Neuburg, 1964, p. 13–20, pl. II, figs. 1–6; pl. III, figs. 1–4; pl. IV, figs. 1–7; pl. V, figs. 1–6.

Sphenophyllum cf. *thonii* Mahr: Vladimirovich, 1985, pl. V, figs. 10, 12.

Trizygia biarmica (Zalessky): (*Osnovy* ..., 1963, text-fig. 4).

Sphenophyllum sp. SVN-1: Naugolnykh, 1998, pp. 37–38, text-figs. 13A, 14A–14C.

Sphenophyllum sp. SVN-2 (aff. *thonii* Mahr): Naugolnykh, 1998, p. 38, text-fig. 17A.

Lectotype. It was figured by Zalessky (1937, text-fig. 7) and came from the Krutaya Katushka locality: Lek Formation, Filippovo Horizon, Kungurian Stage, Lower Permian; central Cis-Urals. The lectotype was chosen by Naugolnykh (1998).

Emended diagnosis. Vegetative organs of sphenophylls. Leaves heterophyllous, varying from well-developed ovoid to reduced and specialized hook-like. Fully developed leaves have entire margins, small marginal teeth or even long terminal lobes. Venation open, fan-shaped, dichotomizing up to four times. Leaf whorls symmetrical or, rarely, asymmetrical anisomorphic (pseudotrizygoid). Branching pattern of stems three-dimensional. Strobilus of *Bowmanites biarmensis* Naug. type, with ten whorls of sporangiophores (sporophylls). Bracts scalelike, relatively short, with terminal spines. Terminal part of the strobilus conical. Sporangiphore bears at least two ovoid sporangia.

Description (Figs. 1, 2, 3c–3e, 3g, 4, 5). Since the leaf macromorphology of *S. biarmicum* is well studied, it is only briefly described below.

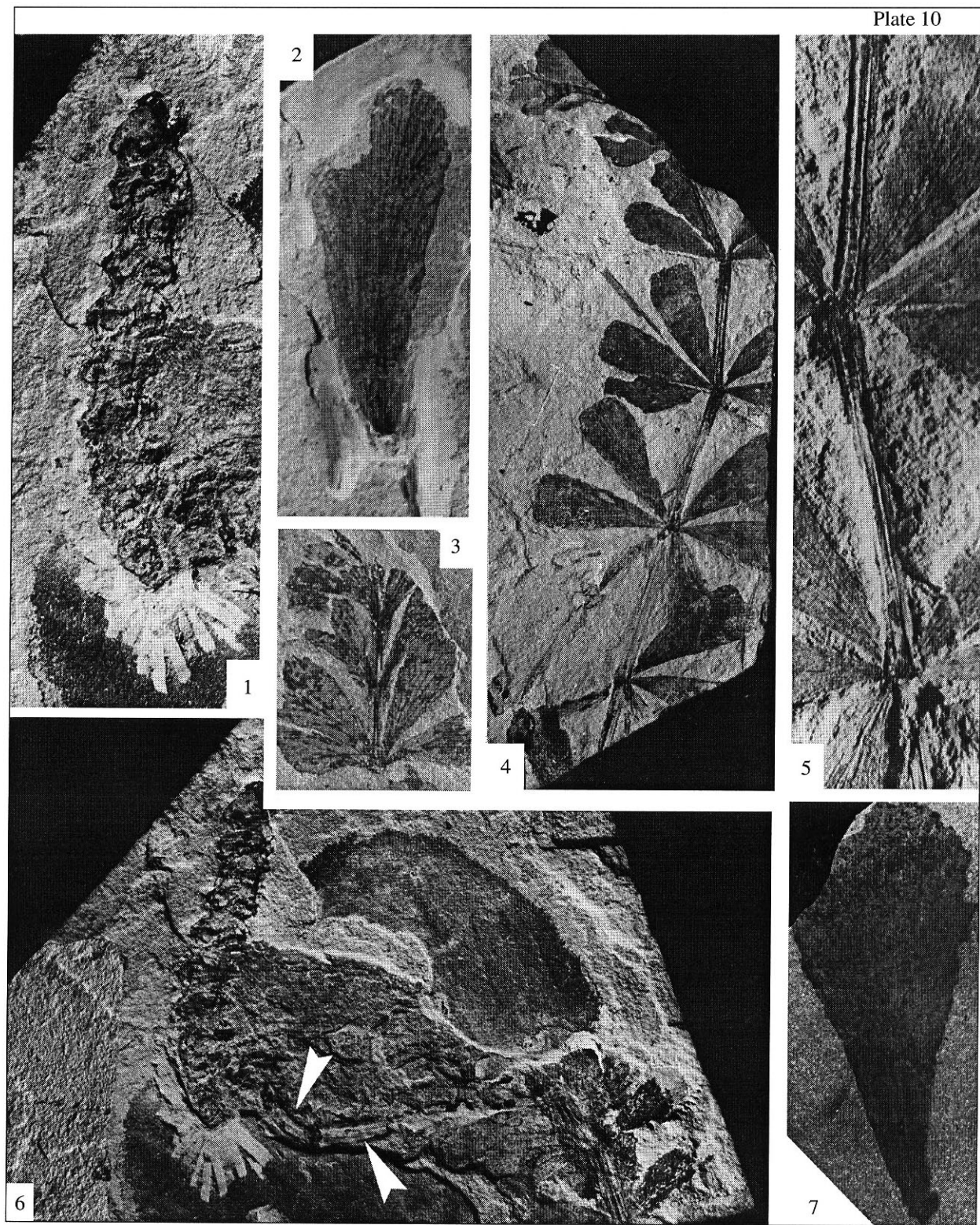
Leaves are entire-margined or with small marginal teeth. Occasionally, leaves with hypertrophied teeth continuing into long marginal lobes occur (see below). A single vein enters into each tooth. The leaf base is cuneiform and attenuated. The veins dichotomize up to five times in the leaf axis and up to two or three times in lateral regions of the leaves. The venation is fan-shaped. The veins diverge and enter in both the lateral leaf margins and in the leaf apex. An apical notch may be present on the leaves of juvenile shoots or subapical regions of shoots, shaping cordate leaf outlines.

This description shows that even normal leaves of *S. biarmicum* are characterized by fairly high macromorphological variability. This concerns general leaf proportions, leaf margins, and the leaf apex. Nevertheless, the presence of gradual transitions within each

Explanation of Plate 9

Figs. 1–4, 6. *Sphenophyllum biarmicum* Zalessky, emend. nov., (1) GIN, no. 3773(11)/229(90), $\times 1.2$; (2) GIN, no. 3773(11)/265(91), $\times 1.5$; (3) GIN, no. 3773/447, $\times 1.5$; (4) 3737/146, $\times 2$; (6) GIN, no. 3773(11)/309(91), $\times 1.7$. Localities Chekarda-1, bed 10 (1, 2, 4, 6), Krutaya Katushka (3).

Fig. 5. *Bowmanites biarmensis* Naug., holotype GIN, no. 3773(11)/217(90), $\times 4$, Chekarda-1 locality, bed 10; (A) two sporangia, preserved in the axil of a scalelike bract.



Explanation of Plate 10

Figs. 1, 6. *Bowmanites biarmensis* Naug., GIN, no. 3773(11)/217(90), (1) $\times 1.5$, (2) arrows indicate a shoot devoid of leaves to which the strobile is attached, $\times 1$. Chekarda-1 locality, bed 10.

Figs. 2-5, 7. *Sphenophyllum biarmicum* Zalessky, emend. nov.: (2) GIN, no. 3773(11)/275(91), $\times 2$; (3) GIN, no. 3737/175, $\times 3$; (4) GIN, no. 3737/14, $\times 1$; (5) GIN, no. 3737/14, $\times 2.5$; (7) GIN, no. 3773(11)/115(89), $\times 3$. Chekarda-1 locality, bed 10.

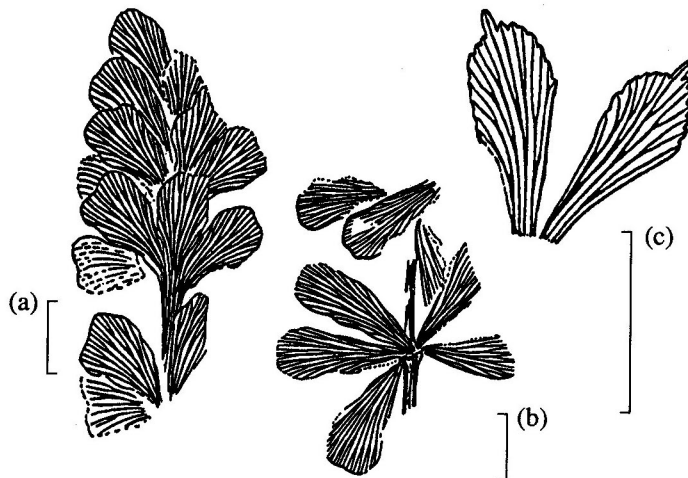


Fig. 1. *Sphenophyllum biarmicum* Zalessky, emend. nov. (a) and (c) from unpublished materials by Zalessky, found by the present author in the V.I. Vernadsky State Geological Museum, Moscow (Naugolnykh, 1998): (a) shoot apex with five leaf whorls, Krasnaya Glinka locality (collected by G.T. Mauer, 1936, after Zalessky, published for the first time); (b) lectotype, shoot fragment with an almost completely preserved lower leaf whorl, Krasnaya Glinka locality (Zalessky, 1937, text-fig. 8); (c) two leaves from the same whorl, primarily determined as *S. stouckenbergii*, Chekarda-2 locality (collected by Mauer, 1934, after Zalessky, published for the first time); Scale bar 1 cm.

feature enables their assignment to the intraspecific variability.

Vladimirovich (1985, pl. V, fig. 12, specimen no. 49/12399; Fig. 2b, present paper) defined as *Sphenophyllum* cf. *thonii* Mahr a small shoot fragment having a node with four leaves (two of them are relatively well-preserved) and two more leaves of the next leaf whorl. This specimen, however, significantly differs from typical *S. thonii* by the very narrow leaves, greater terminal teeth, and looser venation. The shoot morphology, leaf venation, and leaf proportions of the specimen are identical to those of other members of *Sphenophyllum* that were also found in the locality and confidently assigned to *S. biarmicum*.

One of the most interesting specimens from Vladimirovich's collection (Fig. 2f), she decided, was *S. biarmicum*. A single leaf, which had a partly preserved rounded terminal part with smooth margins (like in normal leaves of *S. biarmicum*), was made available for study by Vladimirovich (1985, pl. 5, fig. 9, specimen, no. 45/12399). After additional treatment, I have revealed the morphology of the apices of two more leaves, on which well-developed terminal teeth are situated. The teeth of the lower leaf even formed long terminal lobes. Therefore, leaves with a smooth subapical margin and leaves with well-developed terminal teeth may occur even within one shoot and one whorl. A similar specimen with both entire-margined and dentate leaves located on the same shoot was figured by Neuburg (1964, pl. II, figs. 1–3, 3a).

The branching pattern of *S. biarmicum*, with the formation of secondary shoots bearing relatively short internodes, is seen in one more specimen, figured but not described by Vladimirovich (1985, pl. V, fig. 15, specimen, no. 50/12399; Fig. 2g, present article). The

secondary shoots are situated in normal leaf axils of the main shoot. The leaves are entire-margined. Although most of these leaves are slightly smaller than in other specimens of the sampling, their width-to-length ratio is greater.

One important aspect of leaf polymorphism in *S. biarmicum* is related to the presence of both radial and bilateral anisomorphic (pseudotrizygoid) leaf whorls. Radial whorls apparently were typical of vertical shoots; and anisomorphic whorls were borne on inclined or even subhorizontal shoots, since this position provided optimal exposure to sunlight for bilateral leaf whorls. Shoots with radial whorls of leaves are shown in Figs. 1a, 1b, 2e–2g, and those with anisomorphic pseudotrizygoid whorls are shown in Fig. 2c (see also Naugolnykh, 1998, text-fig. 13A).

A representative shoot fragment of three branching orders is stored in the author's collection (Fig. 3c). A lateral shoot (second order) is attached to the main shoot (first order) slightly above the nodal line. The fragment is 110 mm long. The length of the preserved part of the main shoot is 62 mm, the maximal thickness is 8 mm, and minimal thickness is 5 mm. Three nodes and four internodes are preserved on the main shoot. The lengths of two entirely preserved internodes are 19.5 and 18 mm, respectively. As in many sphenophylls, the shoot widens in the nodes and gradually tapers toward the middle of the internodes. The length of the preserved region of the secondary shoot is 56 mm. The maximal and minimal thickness of the shoot is 4 and 3 mm, respectively. Seven nodes and seven complete internodes are preserved on this secondary shoot, which also widens in the nodes. The lengths of the internodes are 2.5, 2.5, 5, 5.5, 10, 11, and

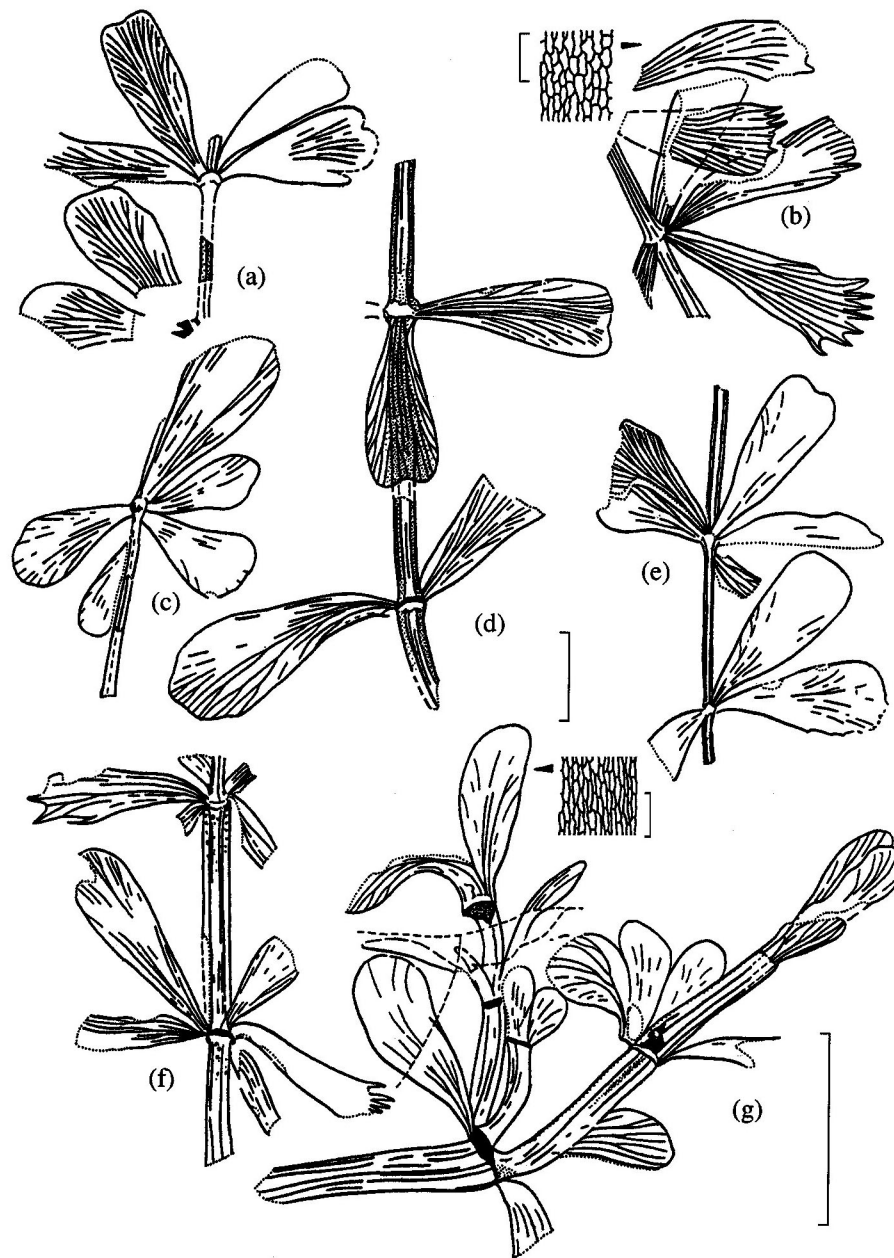


Fig. 2. *Sphenophyllum biarmicum* Zalessky, emend. nov., leaf variability: (a) TsNIGR, no. 46/12399, shoot fragment with two whorls, the upper leaf from the upper whorl with an apical notch; (b) TsNIGR, no. 49/12399, shoot fragment primarily determined as *S. cf. thonii* Mahr, all leaves with long terminal lobes, which are variously developed. With dissecting microscope, the upper leaf shows a surface microstructure, formed by rectangular cells with slightly sinuous walls; (c) TsNIGR, no. 44/12399, anysophyllous (pseudotrizygoid) leaf whorls; (d) TsNIGR, no. 47/12399, fragment of well-developed shoot with two leaf whorls; (e) TsNIGR, no. 32/12230, shoot fragment with two preserved leaf whorls, entire-margined leaves with rounded, obtuse bilobed apices; (f) TsNIGR, no. 45/12399, shoot fragment with two leaf whorls, leaves with well-defined terminal lobes and leaves with rounded entire-margined apices are present in the same shoot; (g) TsNIGR, no. 50/12399, the most complete specimen showing two orders of branching. Localities Chekarda-1, beds 7, 10 (a, c, e), Krasnaya Glinka (b, d, f, g); specimens shown in (a, e) were collected by V.P. Gorskii, 1965 and (b–d, f, g) are collected by E.F. Tschirkova, 1938. Scale bar 1 cm (macromorphology) and 0.1 (microstructure).

13 mm; the internode length regularly increases in the distal direction. Within the fifth internode (from the base of the secondary shoot) there is a large scar of a tertiary shoot. The scar is oval and transversely elongated, 2.5 mm long, and 1 mm wide. Judging from the

scar sizes, the tertiary shoot was thinner than the secondary shoot and was arranged in another plane. Therefore, the shoots branched in there rather than in one plane, as one could conclude from the flattened and diagenetically deformed shoot remains.

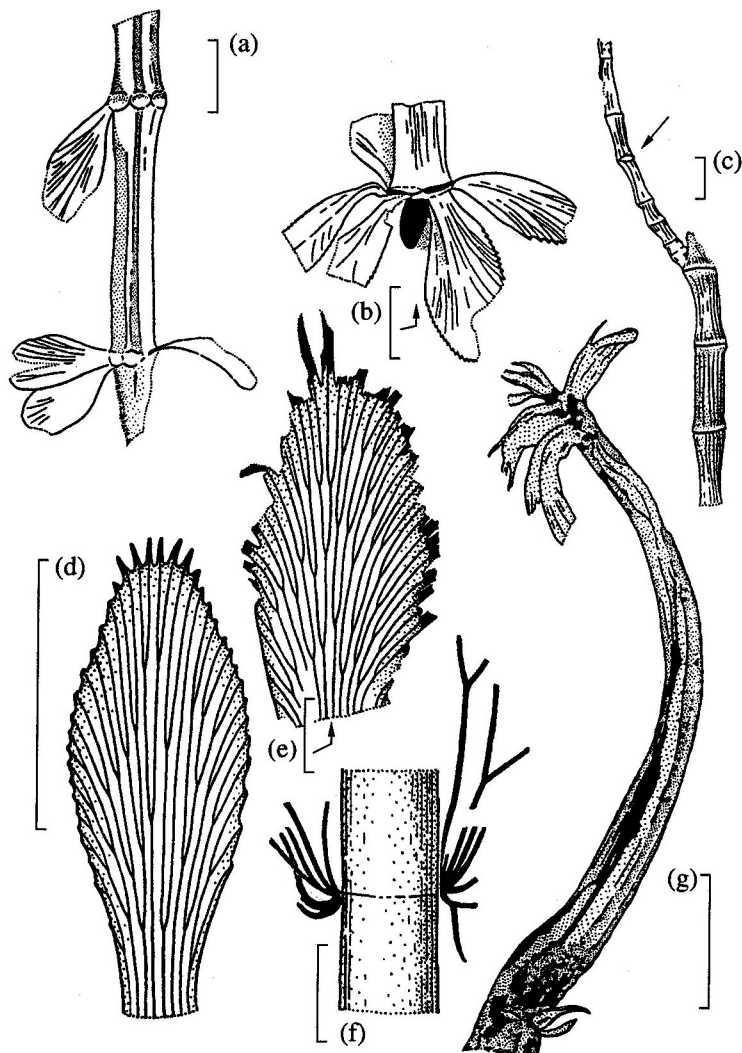


Fig. 3. *Sphenophyllum biarmicum* Zalessky, emend. nov. and allied forms from the Permian of western Angaraland: (a, b, f) *S. stouckenbergii* Schmalhausen (Schmalhausen, 1887), the Kazanian Stage, town of Chistopol', Kama River, Tatarstan; (c–e, g) *S. biarmicum*; (c) shoot fragment with three branching orders, arrow indicates the attachment scar of a branch of the third order, GIN, no. 3773(11)/302(91); (d) leaf with long terminal lobes, reconstructed on the basis of GIN, nos. 3773(11)/268(91), 3773/447, 3773(11)/309(91), and others; (e) anomalously large leaf with small marginal teeth and at least two large lobes on the apex, GIN, no. 3773(11)/309(91); (f) fragment of subterranean stolon with roots; (g) shoot apex with modified leaves, the upper whorl bears deeply dissected leaves with long terminal lobes, two hook-shaped leaves are present in the lower node, GIN, no. 3773(11)/240(91). Localities Chekarda-1, beds 10 (c–e) and 7 (g), Chistopol'. Scale bar 1 cm.

In spite of the absence of leaves, the shoot could be assigned to *Sphenophyllum* based on the increase of the shoot thickness in the nodes; feature is very characteristic of sphenophylls. Since all sphenophyll remains from these deposits can be assigned to the polymorphic species *S. biarmicum*, this specimen is also somewhat tentatively assigned to this species.

Two nodes with modified leaves are seen on another shoot, also assigned to *S. biarmicum*. The leaves of the upper whorl resemble the leaves with long terminal lobes that earlier were determined as *S. af. thonii*. However, the lower whorl bears two hook-shaped spinelike leaves, which possibly served to cling to other plants

(Fig. 3g). The lengths of these hook-shaped leaves are 3 and 2.5 mm, and the maximal width is 1 mm. The length of the only preserved internode is 46.6 mm, its maximal width is 5 mm, and its minimal width is 2 mm.

Comparison. The relationships between *S. biarmicum* and other similar species (*S. thonii* Mahr, *S. comiense* Tschirk., and *S. stouckenbergii* Schmalh.) should be discussed in detail. *S. fimbriatum* Halle (1927) and *S. sinense* Zhang Hong et Schen Guanglong (1990) also belong to the same group of species.

S. biarmicum is very close to the equatorial *S. thonii*, known from many Late Carboniferous (Stephanian) and Early Permian (Autunian) localities of Europe,

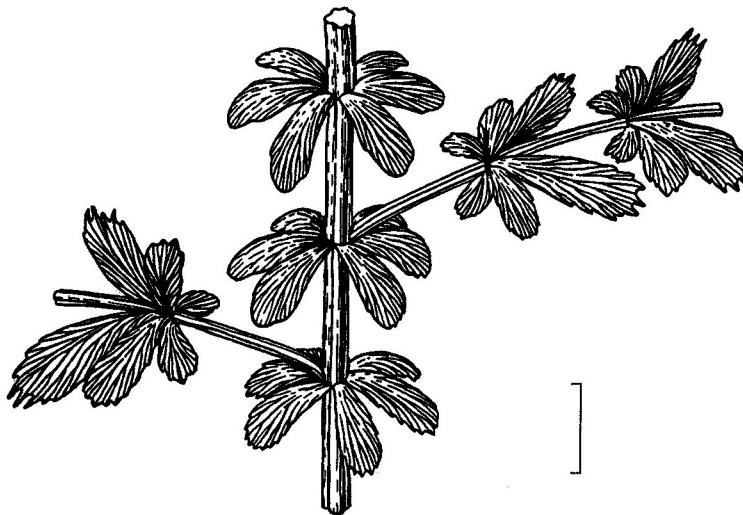


Fig. 4. *Sphenophyllum biarmicum* Zalessky, emend. nov., coarrangement of shoots with anyzophyllous bilateral leaf whorls and long terminal lobes (arranged horizontally) and shoot with izophyllous radially symmetrical whorls (arranged vertically); Early Permian, Kungurian Stage; Central Cis-Urals. Scale bar 1 cm.

North America, and China. The presence of the latter species in the Upper Permian deposits of China and some regions of Gondwana indicates its migration from the original habitat to higher latitudes. *S. biarmicum* is an evolutionary descendent of *S. thonii*, which migrated to western Angaraland during the second half of the Early Permian. Considerably narrower leaf proportions and more simple venation of *S. biarmicum* are the main differences between these species.

The differentiation between *S. biarmicum* and *S. comiense* is a more complicated task. The latter is considered to be a characteristic species of the upper part of the Vorkuta Series (Lekvorkuta Formation and its analogues) and lower part of the Pechora Series (Inta Formation) of the Pechora Cis-Urals. The leafed shoots of *S. comiense* described and figured by Tschirkova and other leaves and shoots of this species (Fefilova and Pukhonto, 1983; Pukhonto, 1998) are very similar to the leaf remains of *S. biarmicum* Zal. The only difference, the smaller size of *S. comiense* leaves, could be explained by the more severe climate of that time in the north of the Cis-Ural foredeep in comparison with the hot arid or semiarid climate of the central Cis-Urals during Kungurian time.

I included *S. comiense* into the extended synonymy of *S. biarmicum* with a question mark in order to indicate the supposed taxonomical identity of these plants. Nevertheless, one can continue to use the name *S. comiense* for microphyllous sphenophylls from the Pechora Cis-Urals that migrated to this region from the central Cis-Urals in the Kungurian and adapted to wetter and cooler climatic conditions. These remains could be segregated as a new variety or ecological morph of *S. biarmicum*. However, the rare usage of such varieties

in stratigraphical and paleobotanical practice makes their establishment inexpedient.

The species *S. biarmicum* and *S. stouckenbergii* are difficult to differentiate because of their obvious phylogenetical relationships. *S. stouckenbergii* is a direct descendent of *S. biarmicum*, vegetated during the Kazanian (Late or Middle Permian according to the modern stratigraphic nomenclature) on the Russian Platform. Judging from the figures of the type specimens of *S. stouckenbergii* (Schmalhausen, 1887; Figs. 3a, 3b, present paper) and the detailed redescription by Esaulova (1987), *S. stouckenbergii* differs from *S. biarmicum* by the shorter leaves. Detailed comparison of these species will be possible after a detailed study of their microstructure and generative organs.

Remarks. A leaf fragment without the leaf base was described by Zalessky (1934) from the Kungurian of the central Cis-Urals as a new species, *Gangamopteris fimbriata* Zal. The description was accompanied by a single drawing of a broadly lanceolate leaf with well-developed terminal teeth and fan-shaped venation. Oblique anastomoses between veins were described and drawn. Later, Zalessky (1939) introduced one more species of the same genus, *G. tenuinervis* Zal., on the basis of a single specimen, very similar to *G. fimbriata* in morphology and preservation, but lacking terminal teeth.

Two leaves, very similar to *G. fimbriata* and *G. tenuinervis*, are present in the author's collection and were described as *Sphenophyllum* sp. SVN-1 (Naugolnykh, 1998). In one of these unusually large hypertrophied leaves, one of the terminal lobes is superposed on the leaf margin to match the lobe venation and leaf margin resulting in the appearance of false anastomoses. Primarily, the unusually large sizes and the presence of well-developed terminal teeth and lobes prevented the

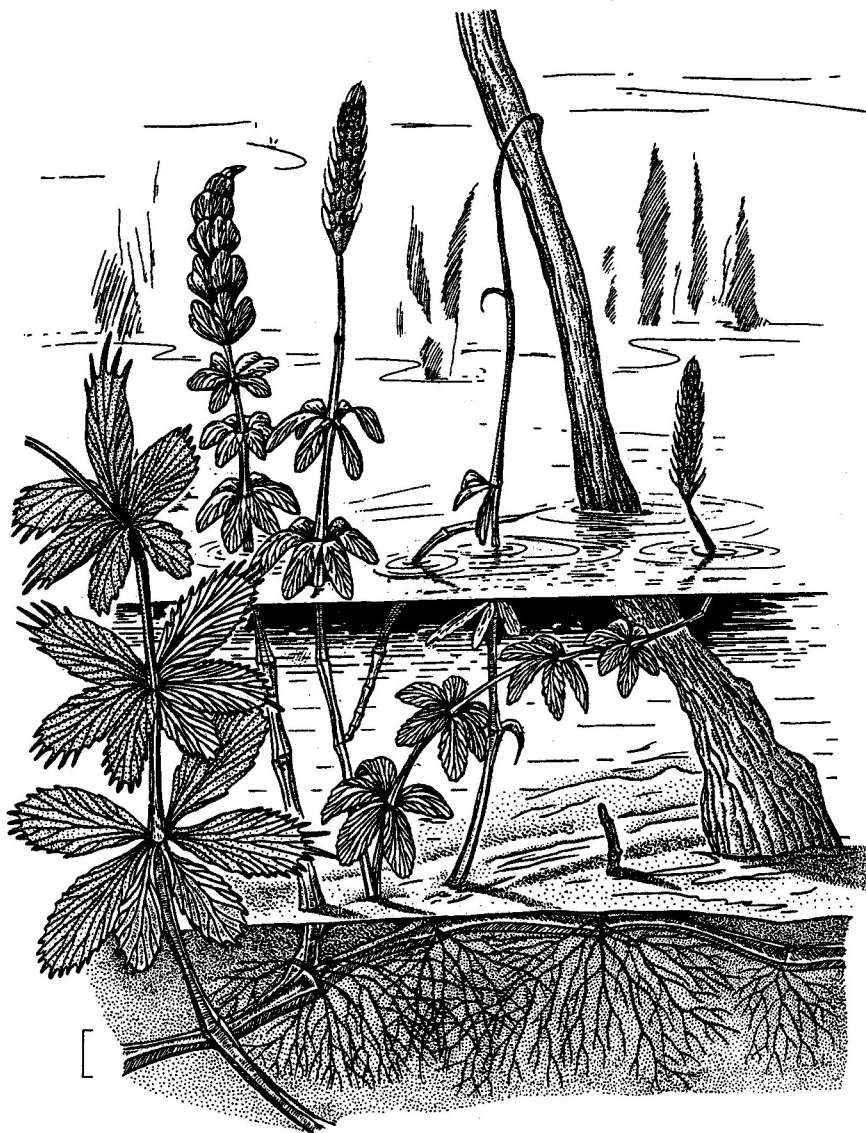


Fig. 5. *Sphenophyllum biarmicum* Zalessky, emend. nov., plant reconstruction, to the left a shoot with large anisophyllous leaf whorls and long terminal lobes; Early Permian, Kungurian Stage; central Cis-Urals. Scale bar 1 cm.

assignment of the leaves to *Sphenophyllum biarmicum*, characteristic of the same deposits. The study of a more representative sampling in which leaves with a significant size variation (up to 3.5 times) were present on the same shoot and even in the nearest nodes (Fig. 3g) has made doubtful the importance of leaf size for the taxonomy of the Permian *Sphenophyllum*. In this paper, these leaves are also assigned to *S. biarmicum*, whereas *Gangamopteris fimbriata* and *G. tenuinervis* are treated as junior synonyms of *S. biarmicum*.

Vegetative organs of sphenophylls are extremely polymorphous because of their heterophylly widespread in this plant group. Nevertheless, homomorphic species with a quite constant leaf and shoot morphology were also reported within the genus content. *Sphenophyllum biarmicum* Zal., very typical of the

Kungurian Cis-Urals, was also included in this group for a long time. However, detailed study of the topotypical leaf sampling of this species (see above) and similar species from the same deposits revealed the presence of heterophylly in *S. biarmicum*. In addition to normal leaves, hypertrophied leaves with long terminal lobes, reduced spinelike leaves, and specialized narrow band-shaped leaves were found. Leaves of different types occasionally were found to be attached to the same shoots.

Occurrence. Kungurian Stage of the Cis-Urals.

Material. Thirty-four specimens from the Lek and Koshelevo formations (Kungurian Stage) of the central Cis-Urals. References to the localities are given in the figure and plate captions; for geographical details see Naugolnykh (1998).

ECOLOGY

To date, the ecology of sphenophylls has remained a moot point. Some scientists consider these plants or, at least, part of the group, to be hydrophytes or hygrophytes (Tschegolev, 1991; Barthel, 1997). Other paleobotanists incline to treat sphenophylls as liana-like plants (Reed, 1949; Magdefrau, 1956; Snigirevskaya, 1959). The third group of scientists assigns sphenophylls to herbaceous synusia or underbrush of Carboniferous and, partly, Permian forests (Taylor and Taylor, 1993). The sphenophyll ecology was reviewed by Storch (1966) and Tschegolev (1991).

Ecologically, *Sphenophyllum biarmicum* certainly vegetated in wet conditions and obviously was partly submerged. This conclusion is proved by the finds of several shoots preserved in a hypautochthonous position with natural co-orientation of shoots and leaves (for example, Zalessky, 1937). The hydrophyllly or hygrophylly of this plant is additionally supported by its heterophyllly and, especially, by the presence of anizophyllly, i.e., trizigoid leaf whorls on thin and long lateral shoots. Such a morphological adaptation is effective in the case of constant coarrangement of leaves and shoots, namely, when they are submerged in water, not moved by wind, and not effected by other terrestrial agents (weather change, precipitation, and so on), which is especially dangerous for thin and long leafed shoots. These modified anizophyllous shoots apparently were arranged horizontally, near the water surface, whereas shoots with isophyllous whorls rose from the substrate vertically (Fig. 4). Generative organs should be elevated over the water surface for effective spore dissemination. Very similar adaptations are known in many modern aquatic plants, e.g., *Potamogeton* L. However, the presence of modified leaves in *S. biarmicum*, similar to hooks or attachment organs of liana-like plants, allows one to suppose that the shoots may cling to stems or trunks of other plants, as is reconstructed in Fig. 5.

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