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Sphenophylls from the Permian deposits of the Pechora Cis-Urals (Russia)

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Summary: The present paper deals with the newly reconsidered species *Sphenophyllum comiense* Tschirkova, which is characterized on the basis of representative collections of leafy shoots and isolated leaf-whorls. A new species *Sphenophyllum dianthoides* sp. nov. is described on the basis of specimens collected from the Permian deposits of the Pechora Cis-Urals (Russia). General thoughts on the growth-forms and palaeoecology of plants studied are discussed.

Keywords: sphenophylls, taxonomy, new taxa, Permian, Angaraland, Pechora basin, *Sphenophyllum*

Sphenophylls were wide-spread plants of the Late Palaeozoic world, but their stratigraphical and palaeophytogeographical distribution was not the same in different geological epochs. The highest diversity of sphenophylls occurred in the Late Carboniferous in the Euramerian palaeofloristic realm, where these plants were represented by a great number of well-defined and botanically well-understood species, such as *Sphenophyllum angustifolium* Germar, *S. cuneifolium* Sternberg, *S. emarginatum* Brongniart, *S. majus* Brongniart, *S. myriophyllum* Crepin, *S. longifolium* Germar, *S. verticillatum* Schlotheim, *S. tenuifolium* Fontaine & White, *S. oblongifolium* (Germar & Kaulfuss) Unger, *S. thonii* Mahr, and some others. The last two species are also typical of the Lower Permian deposits of Euramerica (Storch 1965; Remy & Remy 1959; Stschegolev 1991).

Sphenophylls of the Cathaysian flora are mostly characteristic of the Permian deposits of China and adjacent regions, but several Carboniferous species are also known, for example, the Euramerian species *S. tenerrimum* Ettingshausen was reported from the Lower Carboniferous Huadu flora of Southern China (Naugolnykh & Jin 2014). Younger Permian sphenophylls of the Cathaysia palaeofloristic realm include *S. apiciserratum* Yao et al., *S. fimbriatum* Halle, *S. oblongifolium* (Germar & Kaulfuss) Unger, *S. rotundatum* Halle, *S. sinense* Hong & Guang-Long, *S. sinocoreanum* Yabe, *S. thonii* Mahr, *Paratrizygia koboensis* (Kobatake) Asama, *S. meridionale* Yao et al. and *S. minor* Gu & Zhi (Halle 1927; Yao et al. 2000), closely associated with the strobili of the genus *Bowmanites* Binney (Sze 1955).

The Gondwana flora includes less taxonomically rich sphenophylls, among them *Trizygia speciosa* Royle is widely distributed (Pant & Mehra 1963), but some other species are also reported from the Permian deposits of Australia (Rigby 1966; McLoughlin 1992).

The Angara flora yielded a number of formally described species of *Sphenophyllum* (for overview see Neuburg (1948) and Storch (1983)), but some of them could be at least partly synonymous with some Euramerian species of that genus. For instance, the Angaran species *S. denticulatum* Zalessky has many features in common with *S. majus* Brongniart; *S. kemerovoense*

Gorelova (Betekhtina et al. 1988, Plate XXIX fig. 8) probably is conspecific with Euramerian *S. oblongifolium* (Germar & Kaulfuss) Unger. A general list of the Angaran sphenophylls includes *S. alatum* Chachlov, *S. biarmicum* Zalessky emend. Naugolnykh, *S. bilobum* Chachlov, *S. boreale* (Mogutcheva) Stur, *S. chachlovii* Stur, *S. comiense* Tschirkova emend. nov. (see the emended diagnosis and description below), *S. denticulatum* Zalessky, *S. dianthoides* Naugolnykh sp. nov. (see the diagnosis and description below), *S. duplex* Chachlov, *S. kemerovoense* Gorelova, *S. meyenii* Zimina, *S. originale* Chachlov, *S. osipoviense* Zimina, *S. primitivum* Gor, *S. prokopievskiense* Gorelova, *S. spiralicum* Chachlov, *S. subrotundatum* Neuburg, *S. stoukenbergii* Schmalhausen (other orthographical variants of this name: *stouckenbergii* or *stuckebergii* (Zalessky 1927; Boureau 1964) from more correct transliteration of the last name of Professor A.A. Stuckenberg) and *S. tomiense* (Gorelova & Radczenko) Boureau.

Information about the reproductive organs of the Angaran sphenophylls is rather scarce. Only one species of the sphenophyll strobili *Bowmanites biarmensis* Naugolnykh linked with the foliage *Sphenophyllum biarmicum* Zalessky has been described up to the present time (Naugolnykh 1998, 2003, 2007).

The present paper deals with *Sphenophyllum comiense* Tschirkova emend. Naug., emend. nov. and *Sphenophyllum dianthoides* Naugolnykh sp. nov. from the Permian deposits of the Pechora Cis-Urals.

The material studied originated from the Middle Permian (Ufimian and Kazanian) deposits of the Pechora Cis-Urals, northern part of European Russia (Fig. 1A, B). Pukhonto (1998) gave detailed information about the regional stratigraphy. For more adequate and effective illustrating of morphological features of the plant studied, some of the most important specimens are shown in different magnification and in differently directed light. The main terms used for the description are explained on Fig. 1C.

Systematics and description

Class Sphenophyllopsida Engler, 1892

Order Sphenophyllales Campbell, 1905

Family Sphenophyllaceae Warm., 1891 (= Bowmanitaceae S. Meyen, 1978)

Sphenophyllum Brongniart, 1828

***Sphenophyllum comiense* Tschirkova, emend. Naugolnykh, emend. nov. (Fig. 2A, D; Fig. 3A–G; Fig. 4A–E; Fig. 5A–E; Fig. 6A–C; Fig. 7; Fig. 8; Fig. 9A–E; Fig. 10A, B).**

Selected synonymy:

Sphenophyllum comiense Tschirkova (Zalessky & Tschirkova 1938, p. 15–16, figs. 7–10; Neuburg 1964, p. 11–13, Plate I, figs 1–5, Plate V, fig. 7; Dedeev 1990, Plate XXII, fig. 5; Naugolnykh 2007, fig. 46, A–C, Plate XII, fig. 7).

Holotype was not designated in the protologue.

Lectotype was selected by Neuburg (1964); figured by Zalessky & Tschirkova (1938, p. 15, fig. 9); left bank of the Vorkuta River, upstream of the Ajachjaga River mouth. outcrop 49; see here Fig. 6B.

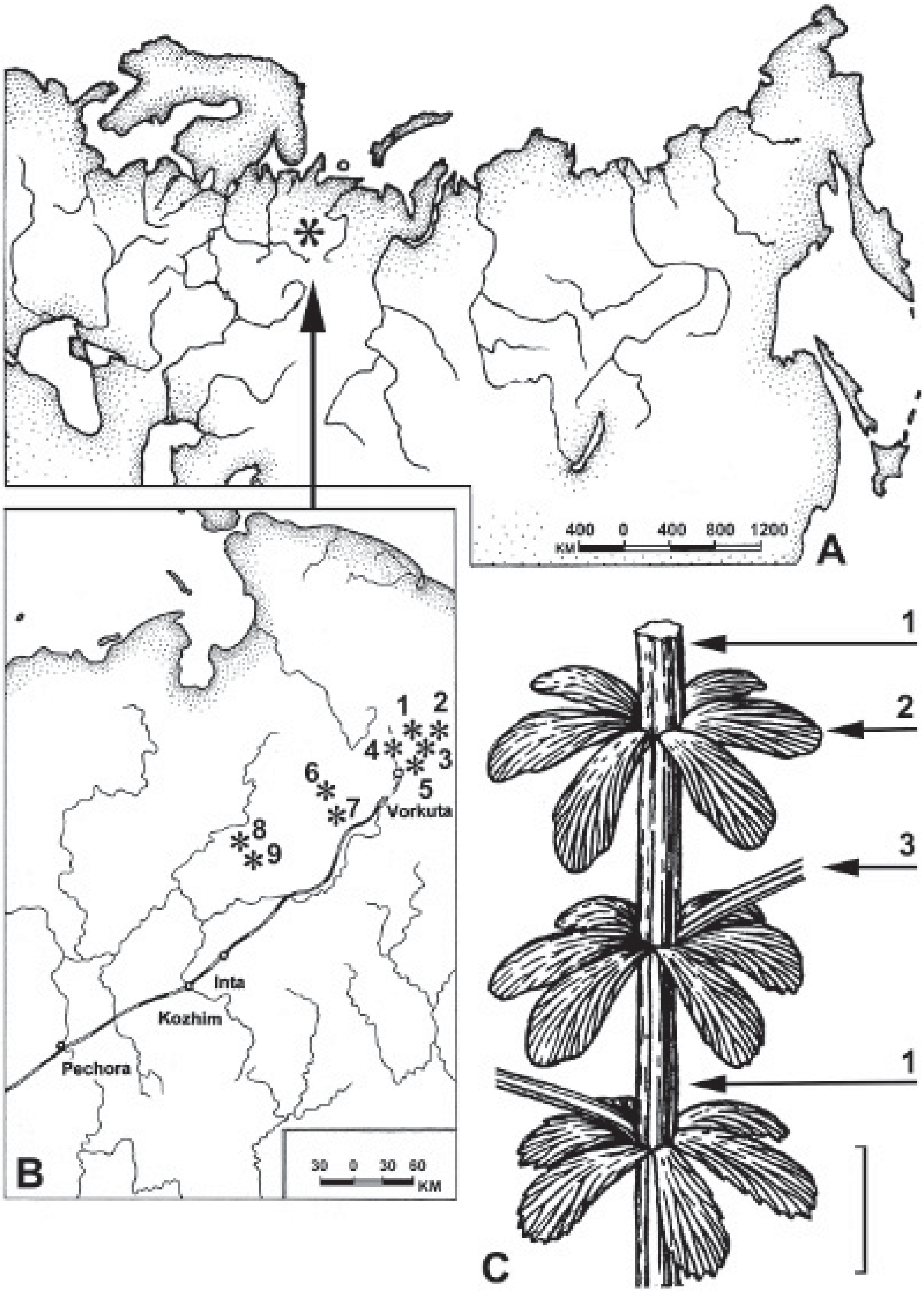

Figure 1. Geographical position of the localities studied (A, B) and terminological system (C). A – position of the studied area; B – location of the studied boreholes and outcrops: 1 – KhK-157; 2 – KhK-1155; 3 – Vorkuta-49; 4 – K-1348; 5 – Vorkuta-37; 6 – SDK-466; 7 – UK-47; 8 – SDK-72; 9 – SDK393, SDK-466; C – morphological terminology, which is used in the present paper: 1 – axis of penultimate order, 2 – leaf-whorl with the leaves attached to the node, 3 – lateral axis (ultimate axis or axis of last order). Scale bar for C = 1 cm.

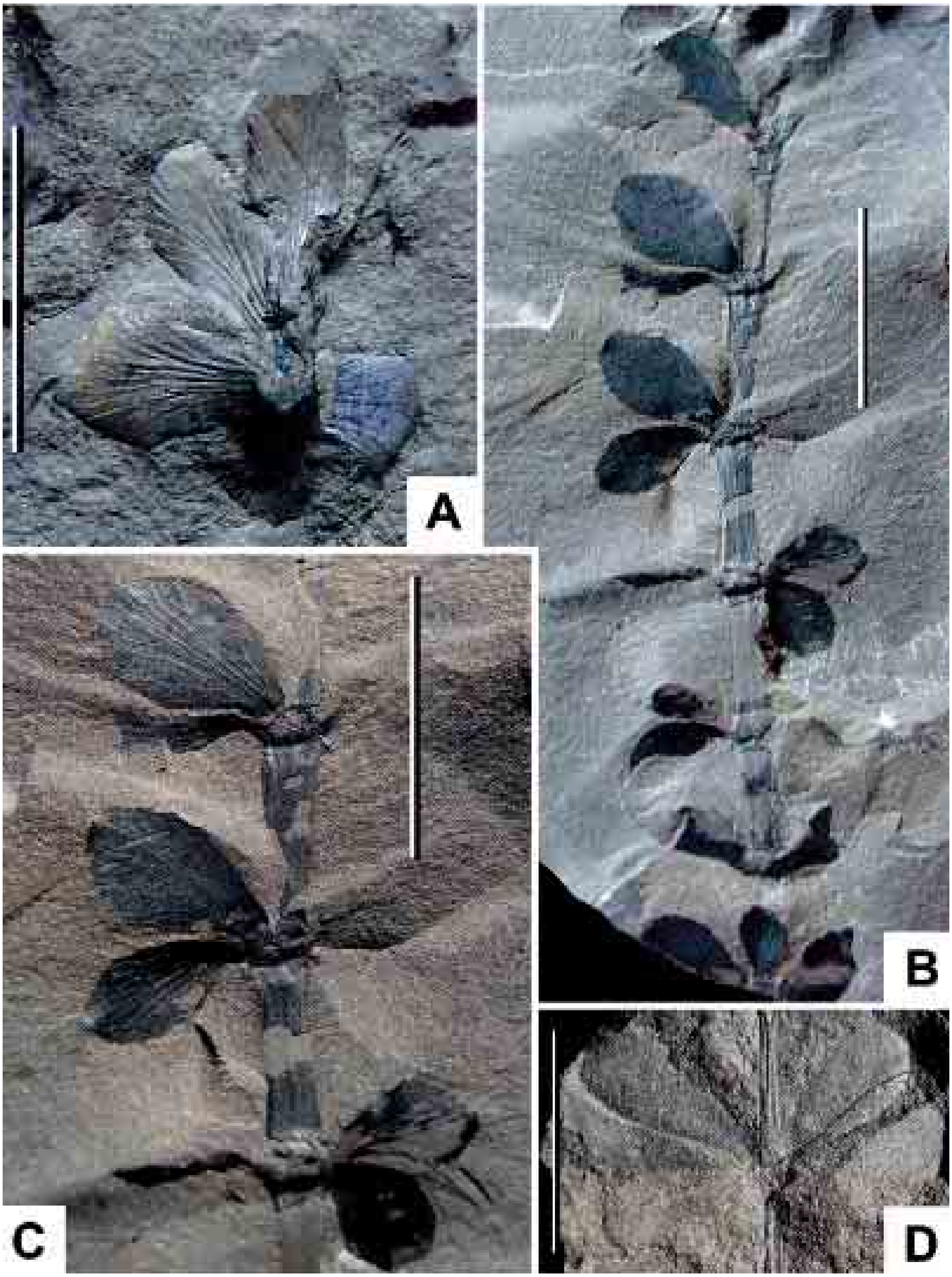

Figure 2. Permian sphenophylls of the Pechora Cis-Urals; *Sphenophyllum comiense* Tschirkova, emend. Naug., emend. nov. A – isolated leaf-whorl, spec. GIN 4851/281; B – leafy shoot; note increasing size of the leaves towards the shoot apex, spec. GIN 4851/287; C – two neighboring leaf-whorls with the obovate leaves, spec. GIN 4851/287, detail of B; D – leaf-whorl, spec. GIN 4851/294. Localities: Vorkuta River, left bank near the Ajachjaga River mouth, Ajachjaginskaya Subformation, outcrop 49, packet S (A, D); KhK-157 borehole, depth 460.0 m (B, C). Scale bars = 1 cm.

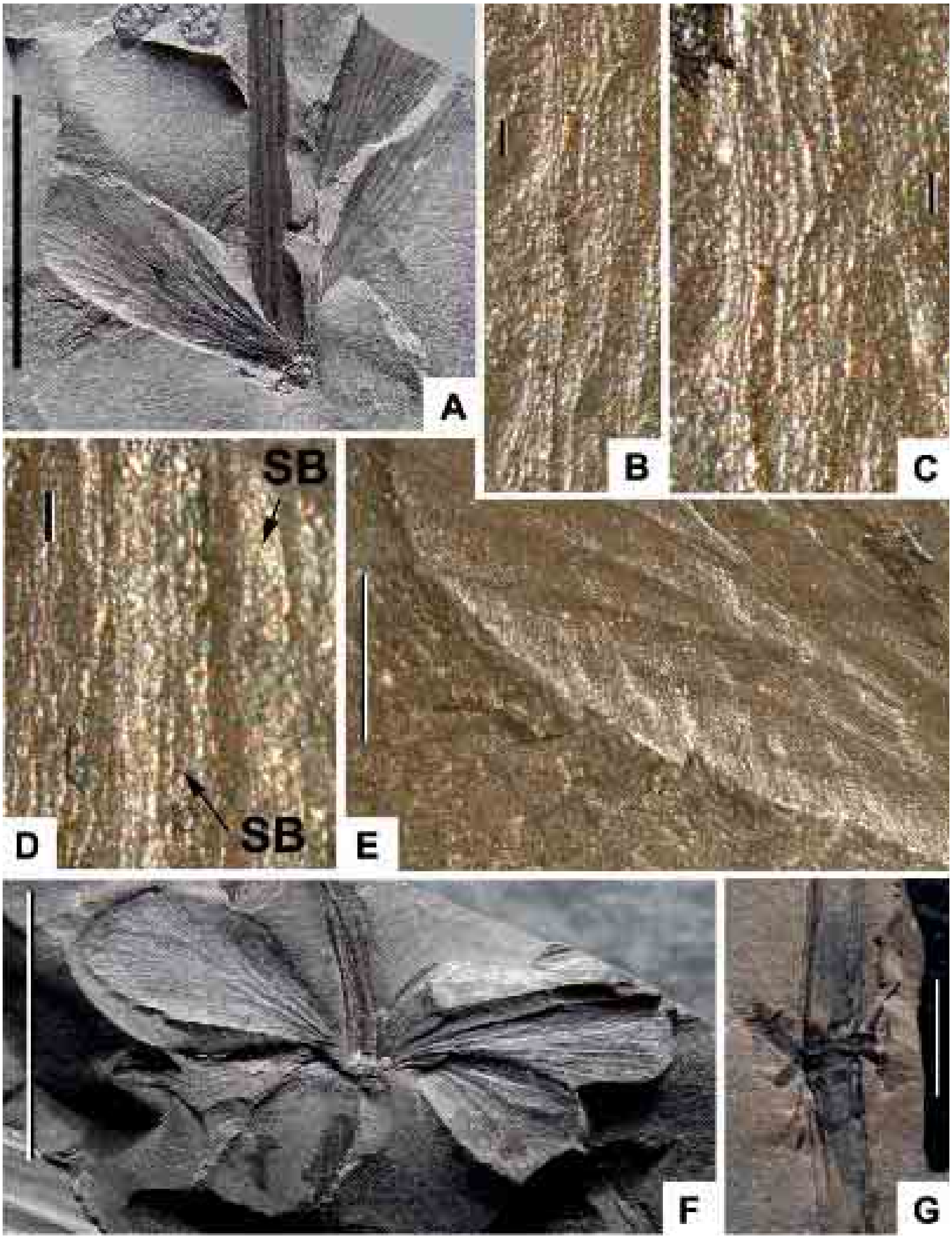

Figure 3. Permian sphenophylls of the Pechora Cis-Urals; *Sphenophyllum comiense* Tschirkova, emend. Naug., emend. nov. A – stem with a leaf-whorl, the left leaf was studied microscopically for obtaining data on epidermal/cuticular structure (see here Fig. 3B–E), spec. GIN 4851/289B; B–D – epidermal structure of the leaf, figured on Fig. 6A, left, SB – stomatal bands, spec. GIN 4851/289B; E – marginal part of the leaf, note longitudinal position of the epidermal cells along the veins, spec/ GIN 4851/289B; F – bilaterally symmetrical pseudotrizygoid leaf-whorl, note two branch initials at the leaf axils, spec. GIN 4851/289A; G – the node bearing the modified spine-like leaves, spec. GIN 4851/286. Localities: KhK-1155 borehole, depth 51.6 m (A–F); KhK-157 borehole, depth 460.0 m. Scale bars = 1 cm (A, F, G); 100 μm (B–D); 1 mm (E).

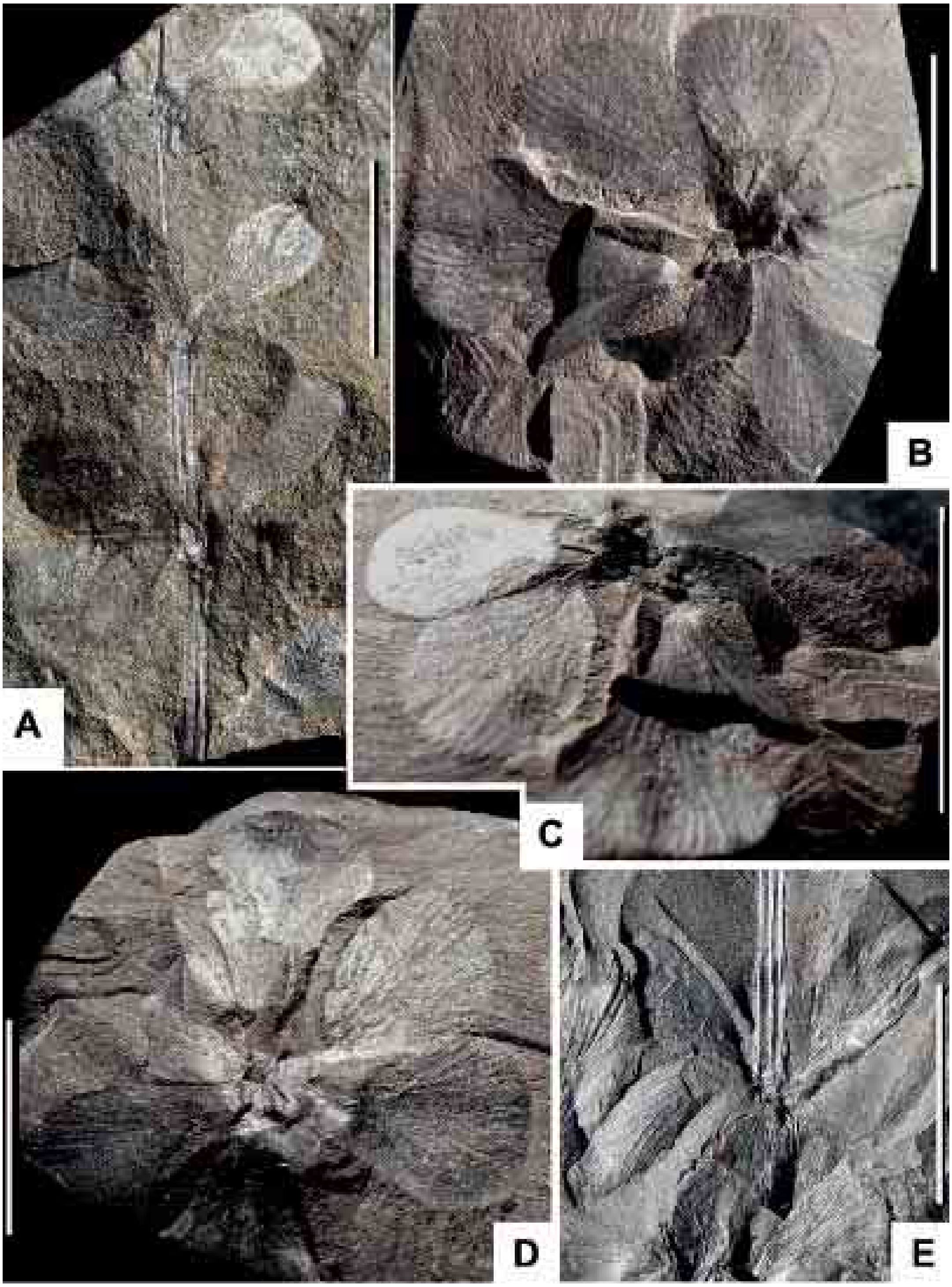

Figure 4. Permian sphenophylls of the Pechora Cis-Urals; *Sphenophyllum comiense* Tschirkova, emend. Naug., emend. nov. A – the leafy stem, spec. GIN 4851/297; B–D – the leaf-whorl with the short round leaves with obtuse apices, spec. GIN 4851/282; E – the stem with the isometric radially symmetrical leaf-whorl, GIN 4851/280. Localities: Vorkuta River, left bank near the Ajachjaga River mouth, Ajachjaginskaya Subformation, outcrop 49, packet S (A); K-1348 borehole (B–D); KhK-1155 borehole, depth 51.6 m. Scale bars = 1 cm.

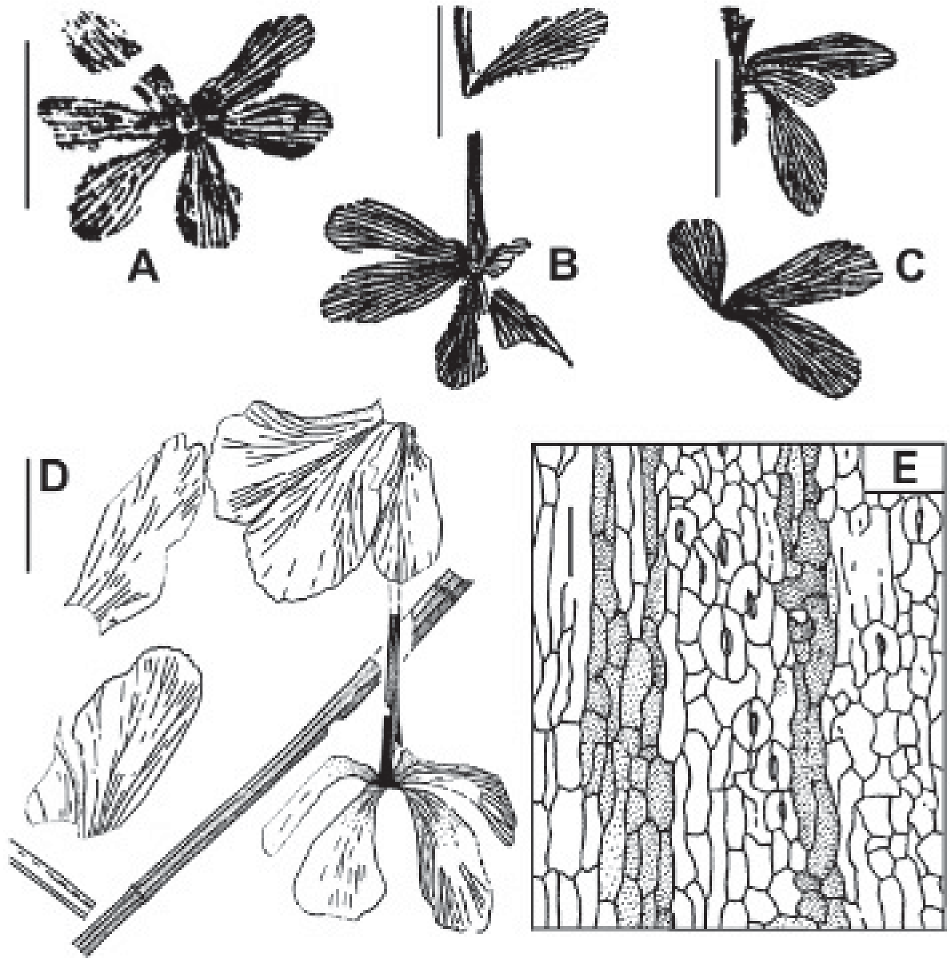

Figure 5. Permian sphenophylls of the Pechora Cis-Urals; *Sphenophyllum comiense* Tschirkova, emend. Naug., emend. nov. (A–E). A–C – canonic illustrations of *Sphenophyllum comiense*, published in Zalessky & Tschirkova (1938); B – lectotype, selected by Neuburg (1964); D – the leafy stems, preserved together (after Naugolnykh 2007, p. 116, fig. 46), spec. GIN 4851/298; E – epidermal structure of the leaf *Sphenophyllum comiense*, spec. GIN 4851/289B. Localities: Vorkuta River, left bank near the Ajachjaga River mouth, Ajachjaginskaya Subformation, outcrop 49, packet S (A–C); Vorkuta River, outcrop 37 (D); KhK-1155, depth 51.6 m (E). Scale bars = 1 cm (A–D); 50 μm (E).

Emended diagnosis. Sphenophylls with long stems branched at least two times. Axes of first order are thick, sometimes robust. Penultimate and ultimate axes are thin, slender. All axes have six longitudinal ribs. Leaves are obovate, with round apex and fun-shaped venation. Leaves vary from almost round short to cuneate long. Veins run to both leaf apex and lateral margins. Veins dichotomize up to three times. Small lobes can be present on leaf margin. Epidermal cells form costal fields with prolonged cells with stronger cutinization of periclinal and anticlinal walls and intercostal fields with more isometric but still prolonged cells. Stomata disposed in intercostal fields. All stomata are orientated along veins by their apertures. Stomata with two relatively large subsidiary cells and small guard cells, orientated in same direction along veins.

Description. The collection studied includes several types of organs attributed to this species: leafy stems with more than one normal leaf-whorl (Fig. 2B, C; Fig. 4A; Fig. 6A; Fig. 7; Fig. 10;

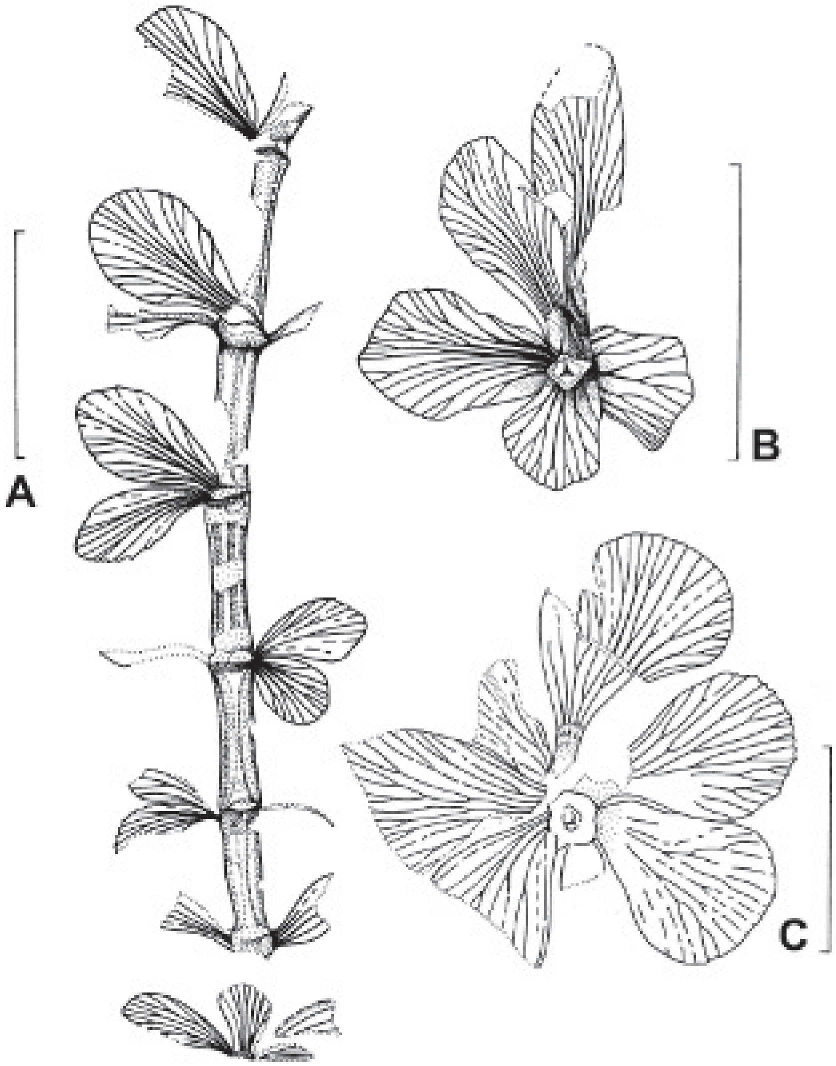

Figure 6. Permian sphenophylls of the Pechora Cis-Urals; *Sphenophyllum comiense* Tschirkova, emend. Naug., emend. nov. A – the leafy stem, line tracing after Fig. 2B, spec. GIN 4851/287; B – the leaf-whorl with prolonged leaves, line tracing after Fig. 2A, spec. GIN 4851/281; C – the leaf-whorl with short, almost round leaves, line tracing after Fig. 4B–D, spec. GIN 4851/282. Localities: KhK-157 borehole, depth 157.46 m (A); 49-141 borehole (B); K-1348 borehole (C). Scale bars = 1 cm.

etc), isolated leaf-whorls (Fig. 2A; Fig. 4B–D; Fig. 6B, C) or small fragments of stems with only one preserved leaf-whorl (Fig. 9B), stems with modified hook-like or spine-like leaves (Fig. 3G) and defoliated stems (Fig. 9C; Fig. 10A). Practically all the specimens attributed to this species show the characters, which link all the morphotypes between each other through the intermediate forms.

This species has three-dimensionally branched leafy shoot systems consisting of the main stem, which probably stood vertically, and lateral shoots with photosynthetic function (Fig. 7; Fig. 8; Fig. 10B). All the stems are covered by six distinct longitudinal ribs. Normally, only three of them can be seen on fossils. The stems are widening in the nodes. As a rule, the main stem lacks leaves, but lateral branches always have leaves. They are arranged in whorls consisting of six leaves.

Figure 7. *Sphenophyllum comiense* Tschirkova, emend. Naug., emend. nov., general macromorphology, spec. GIN 4851/289, line tracing. Locality: KhK-1155 borehole, depth 51.6 m. Scale bar = 1 cm.

The leaves are obovate, with attenuate to cuneate base and round apex, but general proportions of the leaves can widely vary from almost round and more or less isometrical (Fig. 4B–D; Fig. 6C), short obovate (Fig. 2B, C; Fig. 6A) to long and narrow almost subtriangular (Fig. 2A, D; Fig. 3A, F; Fig. 4A, E; Fig. 5D; Fig. 6B; Fig. 7; Fig. 9A, E; Fig. 10B). The leaves of one and the same whorl can be of different length and in this case they form a bilaterally symmetrical pseudotrizygoid whorl (Fig. 3F). Size of the leaves decreases towards the stem apex, but in some cases the size of the leaves also can decrease distant from the stem apex (Fig. 2B, C; Fig. 6A). The leaves normally are entirely margined (Fig. 2A–D; Fig. 4A; etc.), but they also can bear small but distinct marginal lobes, which are well-developed in apical area of the leaf (Fig. 3A, left). The lobes are loosely arranged and normally are disposed in the places where the veins came out to the leaf margin. There are some leaves, initially attributed to the species *S. thonii* Mahr (Neuburg 1964,

Figure 8. *Sphenophyllum comiense* Tschirkova, emend. Naug., emend. nov., reconstruction of a leafy shoot, after spec. GIN 4851/289. Scale bar = 1 cm.

Plate II, fig. 4–6, Plate III, fig. 1, 1a, etc.) with long apical lobes. I believe that these leaves also belong to the same parent plant as *S. comiense*, judging from their basic similarity and the fact that both morphotypes do occur on one and the same leafy stem (Neuburg 1964, Plate II, fig. 1, 1a).

Venation is fun-shaped. It is very difficult to state how many veins come into the leaf base from the stem, because the leaf blade is very thick at the base and the veins can not be seen clearly there. But judging from the most well-preserved specimens (Fig. 2C; Fig. 3A, F; Fig. 6A), we can suppose that only one initial thick vein runs into the leaf base. This vein immediately dichotomizes once and then again to give rise to four veins which run further to the leaf blade and dichotomize again up to two or even three times. The veins run to the apical area of the leaf as well as to the lateral margins, what is a typical feature of the species group '*Sphenophyllum thonii*' (see below detailed comparison).

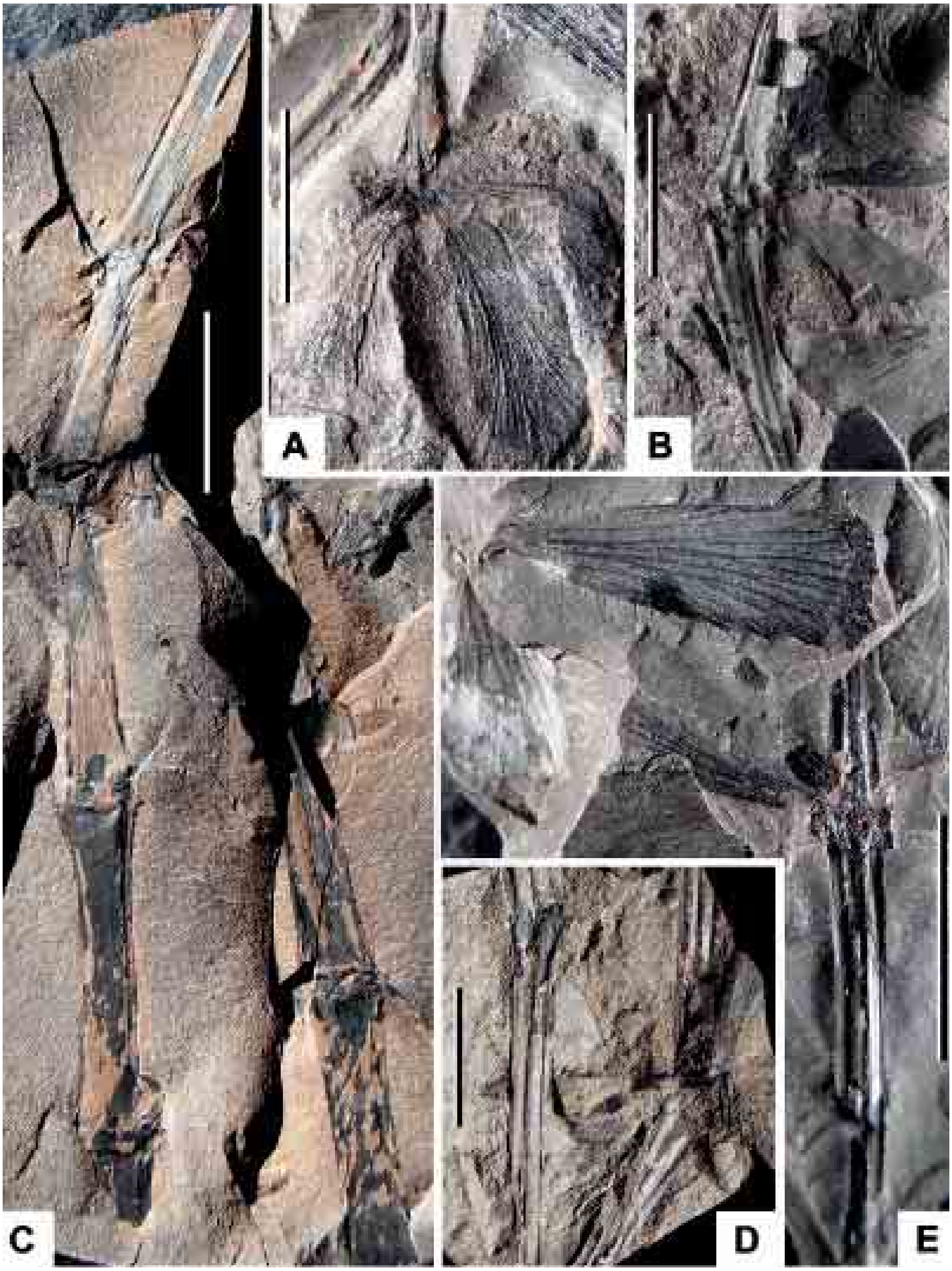

Figure 9. Permian sphenophylls of the Pechora Cis-Urals; *Sphenophyllum comiense* Tschirkova, emend. Naug., emend. nov. A – radially symmetrical leaf-whorl, spec. GIN 4851/298; B – the stem with the leaf-whorl, spec. GIN 4851/279; C – partly defoliated stems, spec. GIN 4851/286; D – two stems with well-pronounced longitudinal ribs, spec. GIN 4851/295; E – the leafy stems with long and narrow leaves, spec. GIN 4851/289A. Localities: Vorkuta river, outcrop 37 (A); SDK-466 borehole, depth 413.2 m (B); KhK-157 borehole, depth 460.0 m (C); Vorkuta River, left bank near the Ajachjaga River mouth, Ajachjaginskaya Subformation, outcrop 49, packet S (D); KhK-1155 borehole, depth 51.6 m (E). Scale bars = 1 cm.

Figure 10. *Sphenophyllum comiense* Tschirkova, emend. Naug., emend. nov. A – two defoliated stems with widened nodes, spec. GIN 4851/277; B – general macromorphology of branching stem with the lateral leafy shoots. Localities: SDK-466 borehole, depth 413.2 m (A); KhK-1155 borehole, depth 51.6 m (B). Scale bars = 1 cm.

There is one partly mineralized leaf in the collection studied. This leaf shows some patterns of epidermal cell arrangement (Fig. 3B–E; Fig. 5E). Most of the epidermal cells are prolonged along the leaf veins (Fig. 3E), but costal cells are somewhat longer. The stomata are disposed in the space between veins (in the intercostal fields) and form more or less regular stomatal bands

(Fig. 3D; Fig. 5E). Stomata unsunken, with two large subsidiary cells. Stomatal apertures are orientated along the veins.

Comparison and remarks. *Sphenophyllum comiense* belongs to the often cited '*thonii*-group'. Sphenophylls of that group are typical of Lower Permian deposits in Euramerica (*Sphenophyllum thonii* Mahr), Permian deposits of Cathaysia (*S. fimbriatum* Halle, *S. rotundatum* Halle, *S. sinense* Hong & Guang-Long, *S. sinocoreanum* Yabe) and Angaraland (*S. comiense* Tschirkova emend. nov., *S. biarmicum* Zalessky emend. Naugolnykh, *S. stoukenbergii* Schmalhausen). There is no doubt that all these species are closely related. Most of them are valid and should be considered as separate species.

In the Angara flora the most ancient species of this group is *S. biarmicum*, which is typical of the Kungurian (uppermost Lower Permian) deposits of the Middle and Southern Urals (Zalessky 1937; Naugolnykh 1998, 2003, 2007). Morphologically this species is very diverse. It unites both the radially symmetrical leaf-whorls and the plagiotropic, bilaterally symmetrical, pseudotrizygoid leaf-whorls, which can have hypertrophically overdeveloped leaves of uncommonly large size up to 6 cm long.

Sphenophyllum biarmicum gave rise to the slightly younger species *S. comiense*, which is typical of the Ufimian and Kazanian (Middle Permian) deposits of northern regions of the European part of Russia (Zalessky & Tschirkova 1938; Neuburg 1964; Dedeev 1990). This species differs from *S. biarmicum* in a smaller size of leaves and less developed pseudotrizygoid whorls. *S. comiense* appeared in the end of Kungurian, flourished in Ufimian and still existed in Early Kazanian, but in the very beginning of Kazanian it gave rise to one more species, namely *S. stoukenbergii* Schmalhausen, which is characteristic of the Kazanian deposits of the Volga River and Kama River basins (Esaulova 1987).

Statistically, the typical representative of *S. stoukenbergii* has longer and narrower leaves than *S. biarmicum* and *S. comiense*, but morphological characteristics of *S. stoukenbergii* should be studied more detailed for a further proper comparison of these three species.

Palaeoecology. The material available allows us to suggest some thoughts on the life habit and palaeoecology of *S. comiense*. Obviously, it was not a tall plant, it was non-arborescent, with a vertically orientated main stem and the lateral branches diverging from it in three-dimensional pattern (Fig. 8). Frequent occurrence of several leafy stems together with the well-preserved leaves in life position show that this plant grew nearby the same place where it was buried (Fig. 5D; Fig. 7; Fig. 9C–E; Fig. 10A, B). Most probably the living plant grew in submerged position in shallow waters of ponds with low hydrodynamics and belonged to hydrophilous plant communities. This species also had modified spine-like leaves and marginal and apical lobes adapted for attaching and fixing this plant on stems of neighboring plants.

Material. Fifteen specimens of good and excellent preservation. Deposited at Geological Institute of Russian Academy of Sciences, Moscow.

Distribution. Uppermost Kungurian, Ufimian, Lower Kazanian.

Sphenophyllum dianthoides **Naugolnykh, sp. nov. (Fig. 11A–G; Fig. 12A–C)**

Etymology. After generic name *Dianthus*, because of superficial similarity between leaves of the new species and flowers of the present-day angiosperm *Dianthus*.

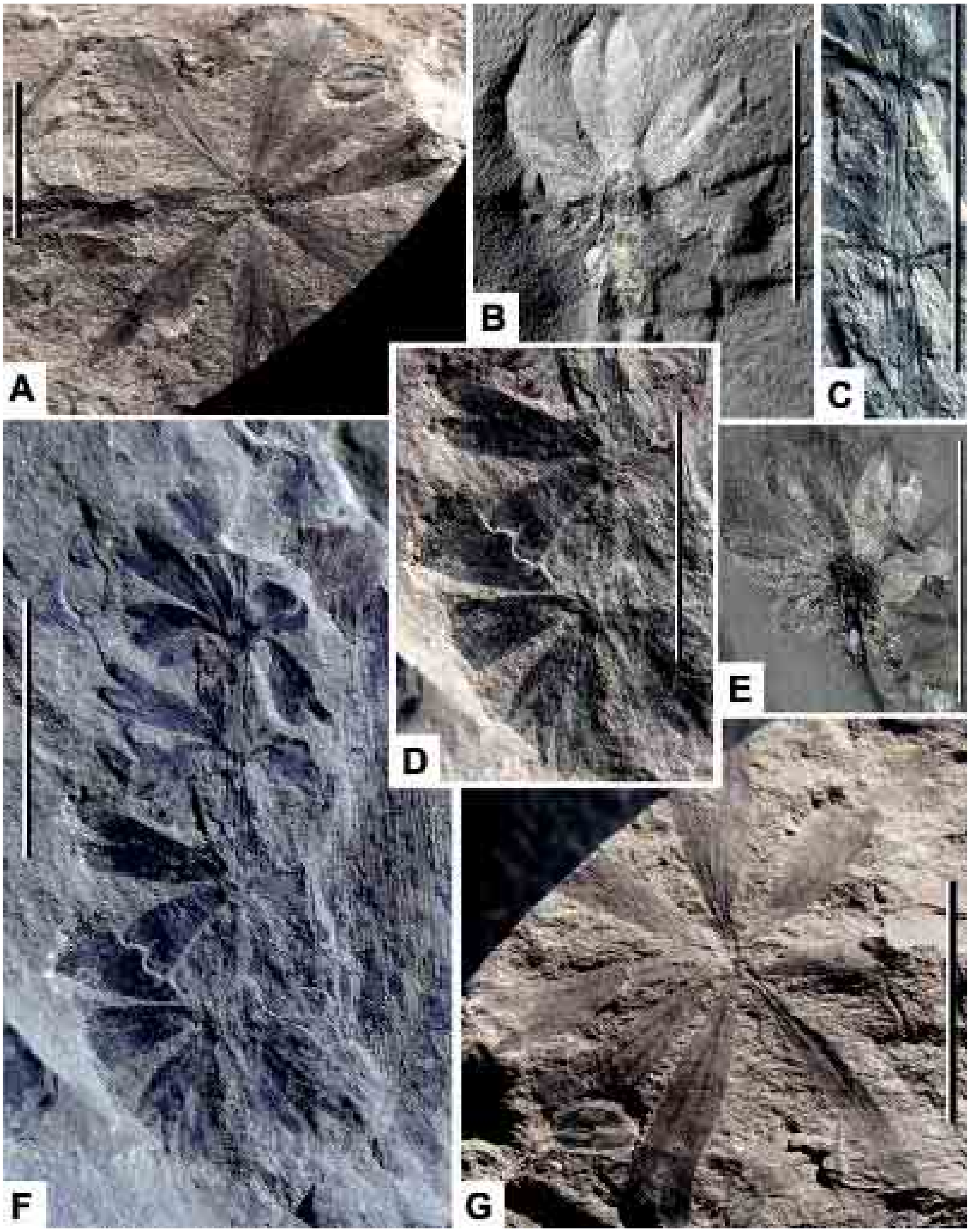

Figure 11. *Sphenophyllum dianthoides* Naug., sp. nov. A, G – isolated leaf-whorl, spec. GIN 4851/290; B, E – isolated leaf-whorl, spec. GIN 4851/283; C, D, F – leafy shoot, holotype GIN 4851/291. Localities: SDK-393 borehole, depth 139.8 m (A, G); 8-133-5 outcrop (B, E); SDK-72 borehole, depth 268.0 m (C, D, F). Scale bars = 1 cm.

Holotype. GIN 4851/291 (Fig. 11C, D, F; Fig. 12A–C); SDK-72 borehole, depth 268.0 m; Middle Permian, Kazanian. Deposited at Geological Institute of Russian Academy of Sciences, Moscow.

Diagnosis. Axes narrow, dissected to nodes and internodes, with six longitudinal ribs. Nodes bear leaf-whorls, each consisted of six leaves. Leaves with cuneate bases, leaf lamina is dissected by main sinus into two main lobes, each of which is dissected at least once again by sinuses of next order. Veins are dichotomizing one or two times. Apical part of leaf has apical lobes with acute apices. One vein runs into every apical lobe.

Description. The collection studied includes three specimens (holotype 4851/291; syntypes 4851/290, 4851/283), attributed to this species. All of them basically have one and the same morphological characteristics, but with some insignificant differences which can be explained as reflecting the intraspecific variations.

The holotype (Fig. 11C, D, F; Fig. 12A) is a representative part of a leafy shoot with four almost completely preserved leaf-whorls and one apical leaf-whorl, which is represented by only one leaf. The stem is relatively thin (1 mm in diameter). The stem most probably was slender when the plant was alive. The stem bears clear longitudinal ribs (Fig. 11C), three of them are on exposed surface of the stem, so the complete amount of the ribs was originally six. On the holotype (Fig. 11F; Fig. 12A) four completely preserved internodes, with lengths of 6, 5, 4.5 and 3 mm from basal part to the apex can be observed. The nodes bear leaf-whorls of somewhat asymmetrical (pseudotrizygoid) shape. Each leaf-whorl has six leaves. The leaf of subtriangular shape is dissected by main sinus into two main lobes. The leaf base is cuneate. The main lobes of well-developed leaves also can be dissected into lobes of second order. Lobe apices are cuneate.

Comparison. The new species differs from the similar species *S. longifolium* (Germar) Gutbier (for comparison see: Remy & Remy 1959: 90, 91, Abb. 70) in a less number of terminal lobes and the lanceolate shape of the leaves and from another similar species *S. oblongifolium* (Germar & Kaulfuss) Unger in a less pronounced bilateral symmetry of the leaf-whorls (for comparison see: Barthel 1976, Tafel 19, figs 2, 3, Tafel 24, figs 1, 4) and in thicker venation.

Material. One representative fragment of the leafy stem selected as holotype and two isolated leaf-whorls. Deposited at Geological Institute of Russian Academy of Sciences, Moscow.

Distribution. Middle Permian of the Pechora Cis-Urals.

Conclusions

Permian sphenophylls of the Pechora Cis-Urals and Pechora coal basin are represented by at least two species, established on the leafy shoots: *Sphenophyllum comiense* Tschirkova and *S. dianthoides* sp. nov. Both species are quite different from each other and belong to two different lineages in the evolution of the genus *Sphenophyllum. S. comiense* derived from the '*S. thonii* group', e.g. *S. biarmicum* Zalessky. *S. dianthoides* originated from the Euramerian cluster of *S. longifolium* (Germar) Geinitz – *S. oblongifolium* (Germar & Kaulfuss) Unger and can be regarded as a relict representative (persisting taxon or 'living fossil') of that sphenophyll lineage. Palaeoecologically, *S. comiense* grew in hydrophilous plant communities and was a non-arborescent, partly submerged plant, also having additional adaptations such as modified spine-like leaves and probably marginal and apical lobes for attaching and fixing on stems of other plants.

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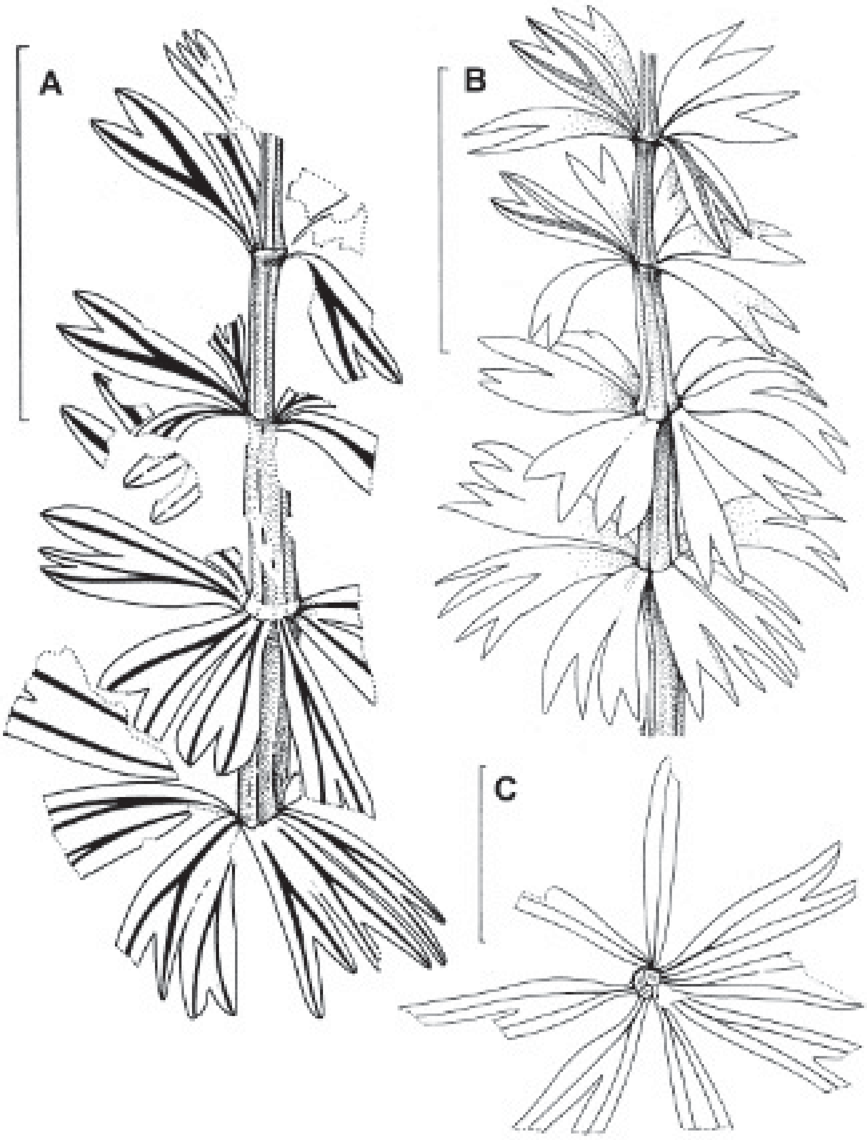

Figure 12. *Sphenophyllum dianthoides* Naug., sp. nov. A – the leafy shoot, spec. GIN 4851/291; B – reconstruction of the leafy shoot based on spec. GIN 4851/291, figured on Figs 14F and 15A, the venation is shown only for three leaves; C – isolated leaf-whorl, spec. GIN 4851/290. Localities: SDK-72 borehole, depth 268.0 m (A); SDK-393 brehole, depth 139.8 m (C). Scale bars = 1 cm.

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