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Wulfenia **20** (2013): 1–16

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

The heterosporous lycopodiophyte *Pleuromeia rossica* Neuburg, 1960 from the Lower Triassic of the Volga River basin (Russia): organography and reconstruction according to the 'Whole-Plant' concept

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Summary: The article deals with the heterosporous lycopodiophyte *Pleuromeia rossica* Neuburg, 1960 from Lower Triassic deposits of the European part of Russia (the Volga River basin, Yaroslavl region, Rybinsk district). Morphology of stems, rhizophores, reproductive organs (cones, sporophylls) and micro- and megaspores preserved *in situ* is described in detail. A 'Whole-Plant' reconstruction of *P. rossica* is proposed. Taphonomical observations and palaeoecological considerations are discussed. It is shown that the lycopodiophyte *P. rossica* grew in semiarid climate nearby waters, where this plant was dominant. Phylogenetically, the Permian genera *Viatcheslavia* Zalessky and *Signacularia* Zalessky, the earliest representatives of the family Pleuromeiaceae, should be regarded as direct predecessors of *Pleuromeia*.

Keywords: Lycopodiophyta, Triassic, *Pleuromeia*, morphology, reconstruction, evolution

The lycopodiophyte *Pleuromeia rossica* Neuburg was established by Neuburg (1960) on the basis of the collection originated from the upper stream of the Volga River (European part of Russia). This plant can be regarded as a typical representative of heterosporous lycopodiophytes belonging to the family Pleuromeiaceae of the order Isoetales in the sense of the taxonomical concept of Meyen (1987).

Pleuromeia rossica was subject to the works of many palaeobotanists and palynologists, who studied its macromorphology (Neuburg 1960; Dobruskina 1974, 1982, 1985; Snigirevskaya 1989) or microspores and megaspores, which are preserved in sporangia *in situ* (Yaroshenko 1975, 1985; Lugardon et al. 1999, 2000; Utting et al. 2004). These data were used for broad phylogenetical and taxonomical considerations (Retallack 1997; Grauvogel-Stamm & Lugardon 2001). The present author published a general description of this plant in context of geology of the source strata based on some characters of weakly developed fossil palaeosoils (FPS-profiles; Naugolnykh 2004). Later this material was summarized in the large collective monograph by Kiselev (2012), unfortunately, published only in Russian without English equivalent.

The main aim of the present article is to consider *P. rossica* as a whole plant in strictly botanical terms and to use the 'Whole-Plant' concept for the description.

Materials and methods

The collection studied includes more than one hundred fossil remains of *P. rossica* represented by both imprints (impressions) and compressions (fossils with coalified plant tissues). Organographically, the collection contains stems, rhizophores, cones (strobili), isolated sporophylls and all these organs connected in different modes, i.e. stems with rhizophores in natural connection and cones attached to apical parts of the stems (see Table 1 below).

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Table 1. The material studied (collection GIN No. 4851).

Type of fossil remains	General amount	Collection numbers of specimens
1. Isolated stems	33	4851/104 (2 spec.); 4851/106 (3 spec.); 4851/110 (3 spec.); 4851/258 (8 spec.); 4851/259 (2 spec.); 4851/260 (1 spec.); 4851/263 (1 spec.); 4851/264 (1 spec.); 4851/265 (1 spec.); 4851/266 (1 spec.); 4851/270 (5 spec.); 4851/272 (2 spec.); 4851/274 (3 spec.)
2. Stems with rhizophores	3	4851/101 (1 spec.); 4851/106 (1 spec.); 4851/108 (1 spec.)
3. Stems with cones preserved in natural connection to each other	4	4851/98 (1 spec.); 4851/104 (1 spec.); 4851/107 (1 spec.); 4851/267 (1 spec.)
4. Isolated cones	9	4851/99 (1 spec.); 4851/100 (1 spec.); 4851/103 (1 spec.); 4851/104 (1 spec.); 4851/108 (1 spec.); 4851/109 (1 spec.); 4851/109 (1 spec.); 4851/110 (1 spec.); 4851/256 (1 spec.)
5. Isolated sporophylls	157	4851/106 (14 spec.); 4851/250 (23 spec.); 4851/251 (2 spec.); 4851/252 (1 spec.); 4851/253 (1 spec.); 4851/254 (2 spec.); 4851/255 (5 spec.); 4851/257 (1 spec.); 4851/258 (14 spec.); 4851/259 (11 spec.); 4851/261 (12 spec.); 4851/268 (3 spec.); 4851/269 (2 spec.); 4851/270 (6 spec.); 4851/272 (4 spec.); 4851/273 (9 spec.); 4851/274 (47 spec.)

All the material studied originated from the locality Tikhvinskoe, which is situated 5 km downstream from the City of Rybinsk, on the right bank of the river Volga, in the Rybinsk district of the Yaroslavl region (Fig. 1). Stratigraphically, the locality Tikhvinskoe belongs to the Parshinskoe pocket of the Rybinsk Formation of the Vetluzhskian Series of Lower Triassic (Kiselev 2012) and corresponds to the boundary level between the upper part of Induan Stage and the lower part of Olenekian Stage. The locality Tikhvinskoe is very well-known among geologists and palaeontologists as a palaeontological monument, which is a source for numerous and exceptionally well-preserved Lower Triassic fossils such as ostracods, conchostraceans, horseshoe crabs or limulids like *Limulitella volgensis* Ponomarenko (Ponomarenko 1985), insects (Ponomarenko 2008), fishes, tetrapods, which were mostly represented by amphibians like the labyrinthodonts *Thoosuchus jakovlevi* (Riabinin) and *Benthosuchus korobkovi* Ivakhnenko (Ivakhnenko 1972; Novikov & Sennikov 2003).

Most of the material used for the present research was collected by the author in 1989–2008. The collection is stored at the Geological Institute of Russian Academy of Sciences, Moscow (GIN, No. 4851). Sporophylls of *P. rossica* were macerated in concentrated nitric acid. Spores, which were obtained as a result of maceration procedure (both microspores and megaspores from different sporangia), were studied by means of SEM (Vega Tescan MV 2300).

Taphonomical and palaeoecological observations

Pleuromeia rossica is the totally predominant element of the fossil flora of the locality Tikhvinskoe. This plant is represented there practically by all organs (Figs 2–7). Fossil remains of *P. rossica* formed in this locality lens-like bodies enriched by stems, rhizophores and cones. On the one hand, the rhizophores very often have adventive roots preserved in natural attachment (Fig. 3 D), what shows clearly that the plant remains were buried nearby the place where the

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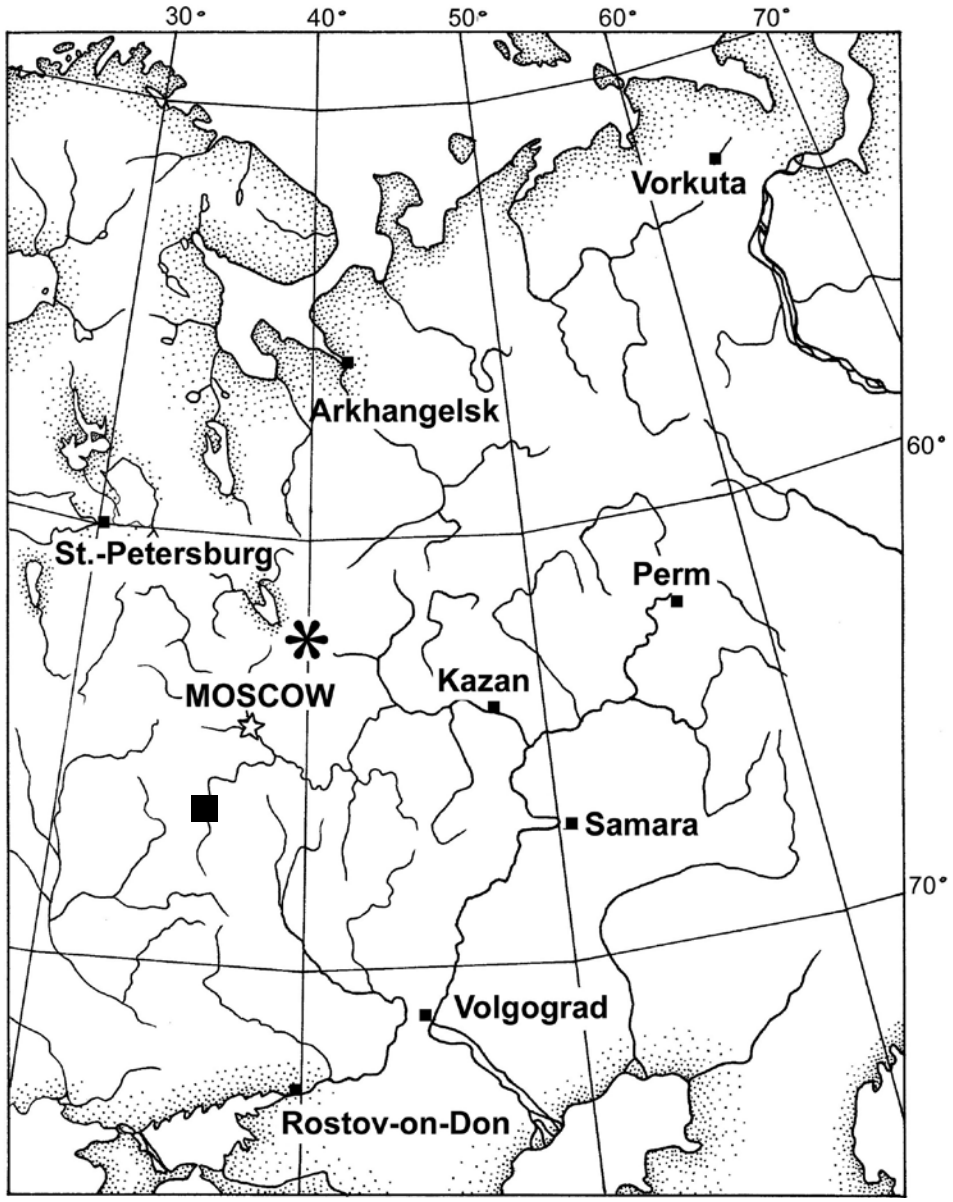

Figure 1. Geographical position of the locality Tikhvinskoe (marked by an asterisk).

parent plants grew in life. On the other hand, many observations show that the *P. rossica* stems in the locality Tikhvinskoe are orientated in one and the same direction (Fig. 2 B, D). Occasionally, microlayers abandoned with isolated sporophylls occur (Fig. 3 A). That points to relatively high hydrodynamics, which took place in time of forming the burials (phytoorictocoenoses) with *P. rossica.* Due to this hydrodynamics, probably linked to or produced by wind-driven waves or even tides in the shoreside area of a shallow lagoon or a large lake, the remains of *P. rossica* were more or less regularly orientated (Fig. 2 B, D), most probably along the lake shore.

Palaeoecologically, it seems that *P. rossica* formed monodominant or even monospecific wetland communities, which were also well-adapted for both temporary dry conditions and growing in semi-sunken position in shallow waters. Some of the present-day plants, which inhabit shores

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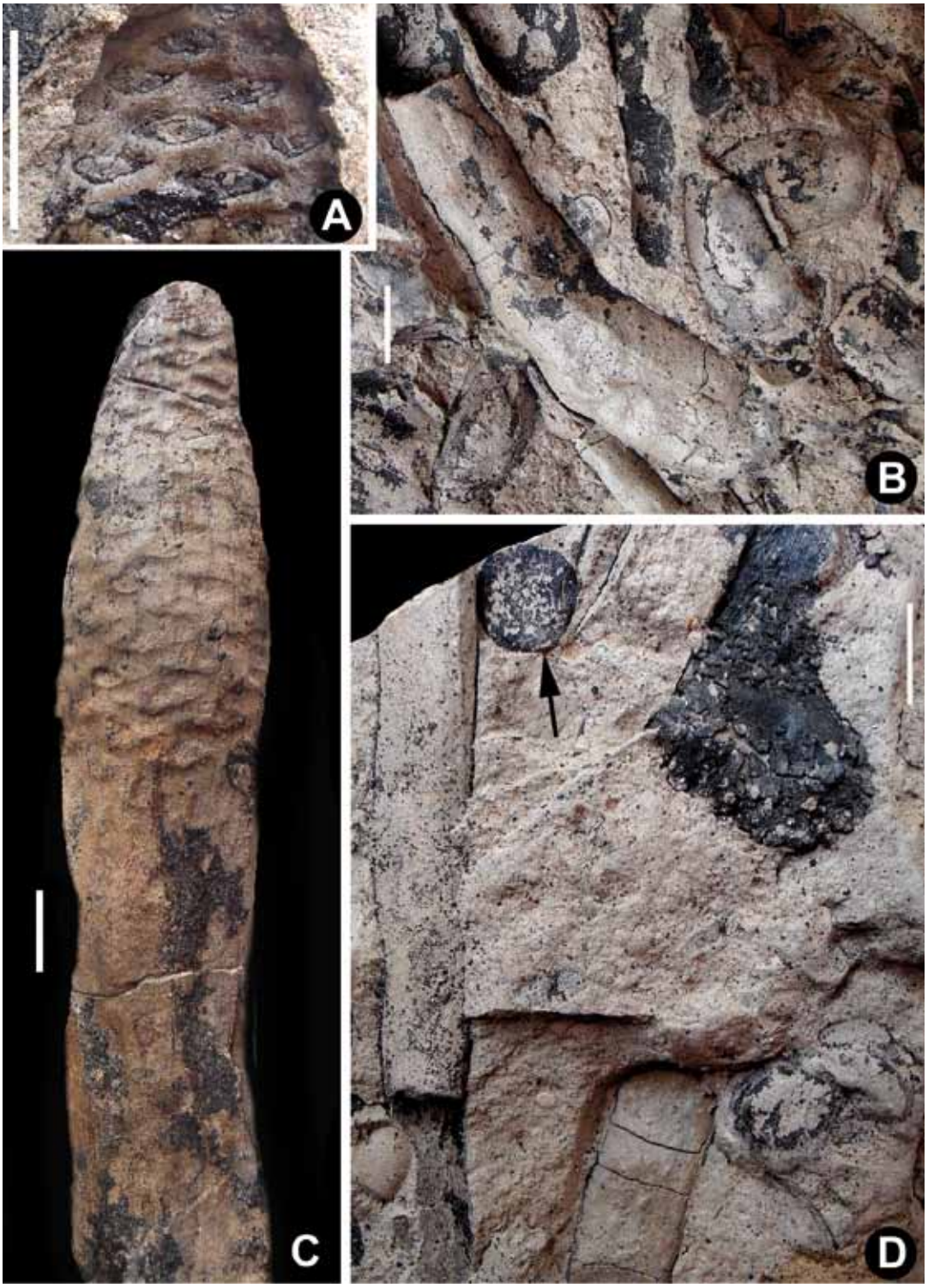

Figure 2. Morphology of the stems, rhizophores and sporophylls of *Pleuromeia rossica* Neuburg from Tikhvinskoe. A – axis of the well-developed strobilus, spec. 4851/110; B – stems and isolated sporophylls preserved in one taphonomical association, spec. 4851/258; C – an isolated axis with spirally arranged scars, left by dropped off sporophylls (in the upper part of the axis), spec. 4851/98; D – stem and rhizophore (upper right side of the picture), one isolated sporangium is marked by an arrow, spec. 4851/106. Scale bars = 1 cm.

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of playa lakes and temporary/seasonally wet lowlands in semiarid landscapes, have similar adaptations.

Apparently, *P. rossica* grew in wet shoreside habitats and formed monodominant communities. Such ecological type of a monodominant plant community is quite typical of such hygrophilous vegetation in both the geological past and the present-day world, but it is inhabited by taxonomically different plants. At the same time the number of xerophilous characters, such as unbranched, relatively thick, photosyntetically active stems, weak development or complete absence of well-developed phylloids, leads to the idea that this plant was well-adapted for semiarid, seasonally dry climate. *P. rossica* can be regarded as a halophyte (Neuburg 1960) or a plant, which existed in semiarid climate near water basins, which are basins of abnormal salinity as a rule. Such plants (halophytes) often form (and formed in the past) monodominant or even monospecific plant communities.

Monodominant pioneer palaeophytocoenoses, which were formed by several closely related species of *Pleuromeia* (Wang 1996; Retallack 1997; Grauvogel-Stamm 1999), were extremely widespread on all Pangea in Early Triassic. They were dominant in many Early Triassic floras of the Northern hemisphere and were also quite common in the Southern hemisphere (Retallack 1975, 1997). The same ecological strategy was suggested for *Viatcheslavia vorcutensis* Zalessky, which was a phylogenetical predecessor of *Pleuromeia* (Naugolnykh 1992, 2004). High ecological tolerance and xerophilous adaptations helped these plants to invade into the free niches in terrestrial ecosystems of Early Triassic immediately after the global Perm/Triassic ecosystem crisis.

Taxonomical considerations

The genus *Pleuromeia* Corda and its nearest relatives (some of which probably could be synonymous to *Pleuromeia*) was extremely widespread around Pangea in Early Triassic and partly Middle Triassic (see for discussion: Retallack 1975; Dobruskina 1985; Grauvogel-Stamm 1999). The species *Pleuromeia rossica* was assigned to the genus *Pleuromeia* in the protologue (Neuburg 1960), but several years later Dobruskina (1985) proposed a new genus *Lycomeia* Dobruskina for this species. The main reason for this taxonomical decision was the absence of phylloids or their scars of attachment on the stems of *P. rossica*; in other words, Dobruskina believed that the stems of *P. rossica* were naked. In subsequent works Dobruskina and co-authors used the name *Pleuromeia rossica* again (Lugardon et al. 1999, 2000).

I have already argued against the validity of the genus *Lycomeia* Dobruskina, mostly because of the fact that gerontic specimens of *P. rossica* do possess clearly visible leaf scars with a distinct ligula pit on the bark (e.g., Kiselev 2012, Plate 21, upper left). Moreover, there are several species of *Pleuromeia* (e.g., *P. jiaochengensis* Wang et Wang, *P. marginulata* Meng, *P. sanxiaensis* Meng from the Triassic deposits of China) with naked stems (see, for instance, reconstructions of these plants published by Grauvogel-Stamm & Lugardon 2001, Fig. 2). I believe that presence or absence of phylloids of *Pleuromeia* is a morphological character, apparently of ecological nature. In unfavorable ecological conditions *P. rossica* grew relatively fast but formed only short or middle sized photosynthetically active stems. Under such circumstances, the plant started to generate reproductive organs very early. In favorable conditions *P. rossica* formed higher stems, which could possess small, weakly developed phylloids, which normally were not preserved in fossil state because of their thin lamina, but left distinct leaf scars on the stems.

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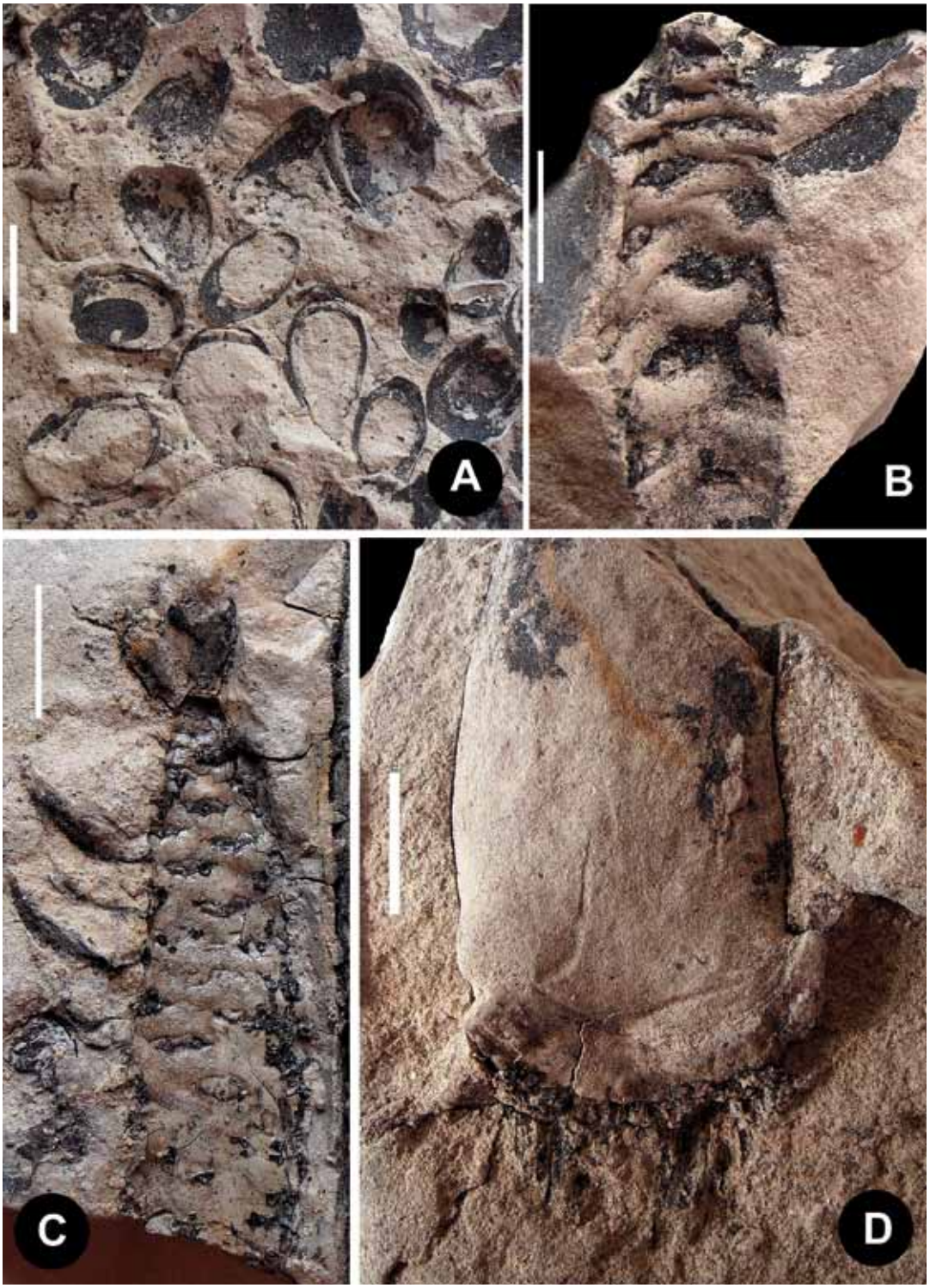

Figure 3. Morphology of isolated sporophylls, cones and rhizophore of *Pleuromeia rossica* Neuburg from Tikhvinskoe. A – numerous sporophylls, preserved on one sedimentation layer, spec. 4851/274; B – basal part of the cone with clear scars of dropped off sporophylls, spec. 4851/256; C – apical part of the strobilus with several sporophylls, preserved in natural connection to the axis, spec. 4851/108; D – rhizophore with partly preserved adventive roots, spec. 4851/101. Scale bars = 1 cm.

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Systematics and description

Division Lycopodiophyta D. H. Scott, 1900

Classis Lycopodiopsida Bartl., 1830

Order Isoetales Prantl, 1874

Family **Pleuromeiaceae Potonie, 1901**

***Pleuromeia* Corda, 1852**

***Pleuromeia rossica* Neuburg, 1960** (Figs 2–9)

Selected synonymy:

Pleuromeia rossica Neuburg: Neuburg 1960: 81–88, Figs 1–18, Plates I–VII; Dobruskina 1974: 114–117, Figs 3–5, Plate IX 1–8, 13–20; Grauvogel-Stamm 1999: Abb. 12–14; Lugardon et al. 1999: 438, Figs 1–9; Lugardon et al. 2000: 503–506, Figs 1–10; Naugolnykh 2004: Fig. 86 A, B; Naugolnykh 2012a: 92–95, Figs 21–24, Plates 20–21.

Lycomeia rossica (Neuburg) Dobruskina: Dobruskina 1985: 101.

Holotype. GIN No 2856/1; Lower Triassic, Vetluzhskian Series, Volga River basin, Yaroslavl region, Rybinsk district, Sheksna River 3 km upstream from its mouth.

Diagnosis. Plant with unbranched stems of middle size (up to 50–60 cm high and 2–3 cm wide). Stems are naked or with small, weakly developed phylloids disposed in its upper third. The basal part of the stem has a cormose rhizophore, with two or four lobes (four lobes originate by dividing of an initially two-lobed rhizophore). Thin adventive roots are attached to the rhizophore in unclear spiral order. Apically, the stem bears a terminal, heterosporous cone (strobilus) consisting of sporophylls. The upper part of the cone possesses microsporophylls, the lower part has megasporophylls. Sometimes microsporophylls and megasporophylls can be intercalated in the middle part of the cone. Sporophylls are disposed in spiral order on cone axis. Both microsporophylls and megasporophylls are obovate, with a round to ovoid adaxially disposed sporangium and have a ligula, located distally to the sporangium. Microspores are round, trilete, cavate, 30–40 µm in diameter. Megaspores are round to ovoid, up to 300–400 µm in diameter, cavate, with a lamellate sporoderm and a small trilete mark.

Description. *Pleuromeia rossica* was a relatively short herbaceous plant without secondary tissues. Average height of the stem is about 0.5 m. Normal thickness of the stem is 1–1.5 cm, but occasionally considerably thicker stems can be also found. Their diameter can reach 3 cm or even slightly more. Most of the stems are naked, but some well-developed or gerontic stems can bear widely disposed leaf scars left by dropped off phylloids (Kiselev 2012: Plate 21, upper left figure). The phylloids were attached to the stem in loose spiral phyllotaxis. They are most probably characteristic only of those plants of *P. rossica* which grew in favorable environmental conditions.

The widened base of *P. rossica* forms a cormose rhizophore of spherical or semispherical shape (Fig. 2 D, upper right; Fig. 3 D; Fig. 4 E; Fig. 6 D), with two or four extenuate lobe-like extensions, which were necessary for fixing the plant in soft swampy or sandy soil. The outer surface of the rhizophore has small round root scars (Fig. 2 D, upper right; Fig. 4 E; Fig. 6 D) up to 1 mm in diameter with a point-like center (200–300 µm in diameter) caused by central conducting tissues. The scars are disposed in unclear or occasionally slightly irregular spiral

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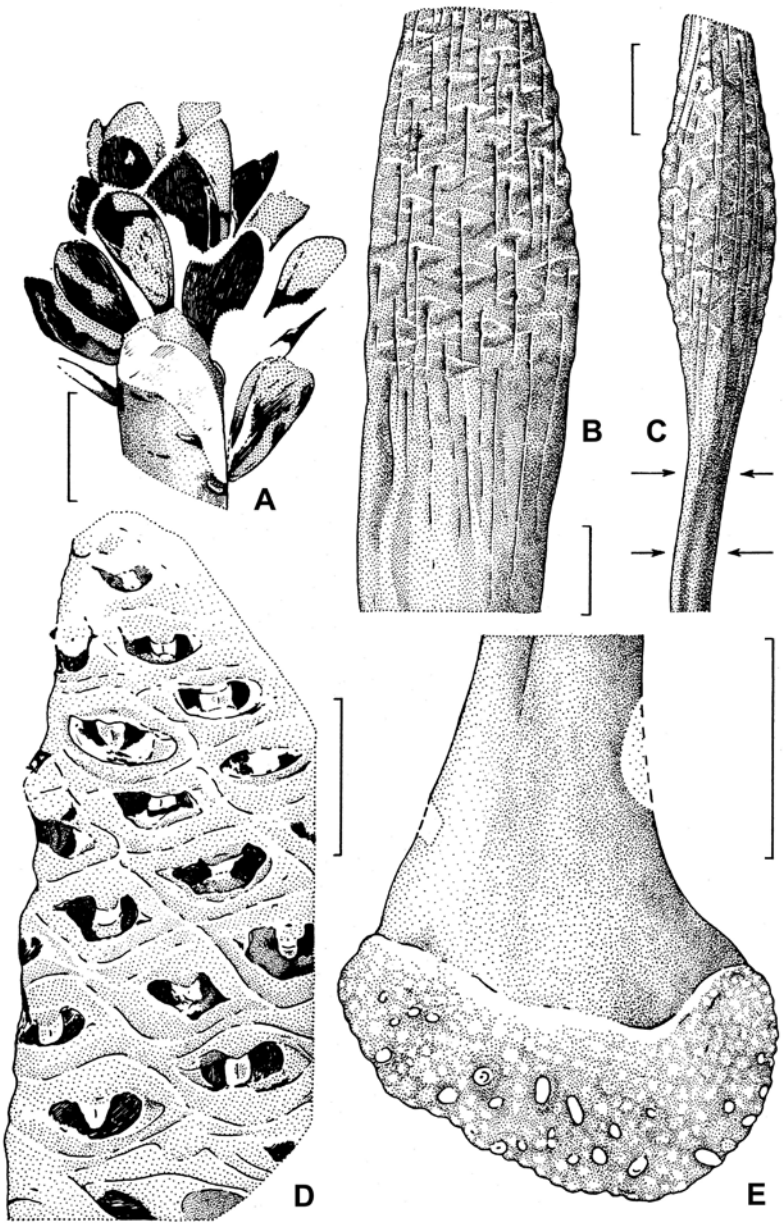

Figure 4. Morphology of strobilus, axes and rhizophore of *Pleuromeia rossica* Neuburg from Tikhvinskoe. A – strobilus with sporophylls, preserved in natural connection to the axis, spec. 4851/99; B, C – an isolated axis in two different projections, with spirally arranged scars, left by dropped off sporophylls (in the upper part of the axis), spec. 4851/98; D – axial part of the strobilus with scars of dropped off sporophylls, spec. 4851/100; E – rhizophore with root scars, spec. 4851/106. Scale bars = 1 cm.

order. Long and thin appendices (functional roots) were attached to the scars when the plant was alive. Remains of rhizophores with such roots in life position were found (Fig. 3 D; also see Naugolnykh 2004: 216, Fig. 86).

The apical part of the *P. rossica* stem bears a compact cone (strobilus). Its size and shape are somewhat different because of different age and extent of individual development. Relatively young, but already fertile plants of *P. rossica* have cones, 40–50 mm long and 30–40 mm wide

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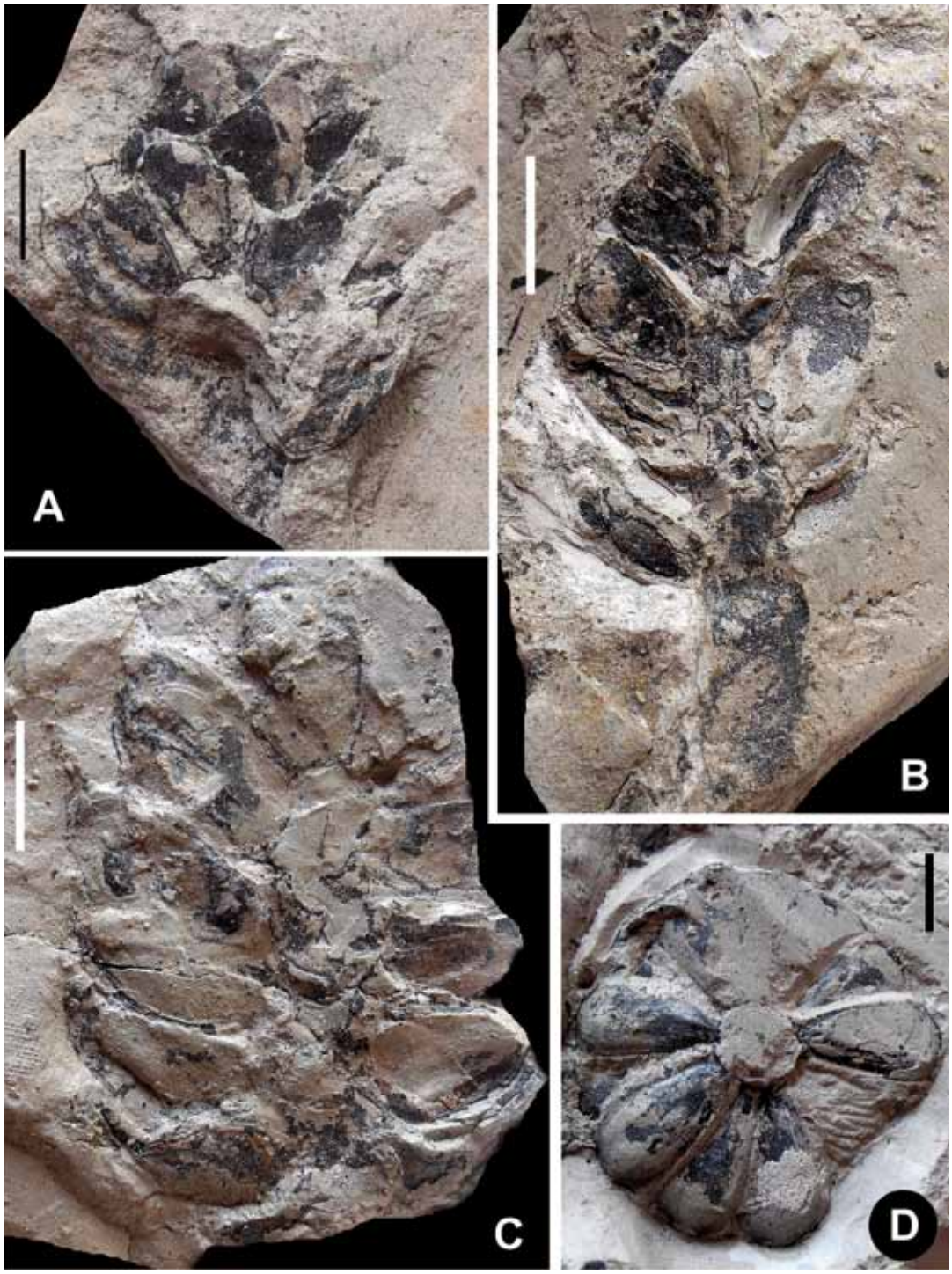

Figure 5. Morphology of the strobili of *Pleuromeia rossica* Neuburg from Tikhvinskoe. A – spec. 4851/99; B – spec. 4851/107; C – spec. 4851/103; D – spec. 4851/104. Scale bars = 1 cm.

(Fig. 4 A; Fig. 5 A, B; Fig. 6 B). Sporophylls are attached to the cone axis in dense spiral order. Diameter of the cone axis of young *P. rossica* plants is 7–10 mm (Fig. 3 B, C). Well-developed adult to gerontic specimens of *P. rossica* have cones of considerably larger size: up to 70–80 mm

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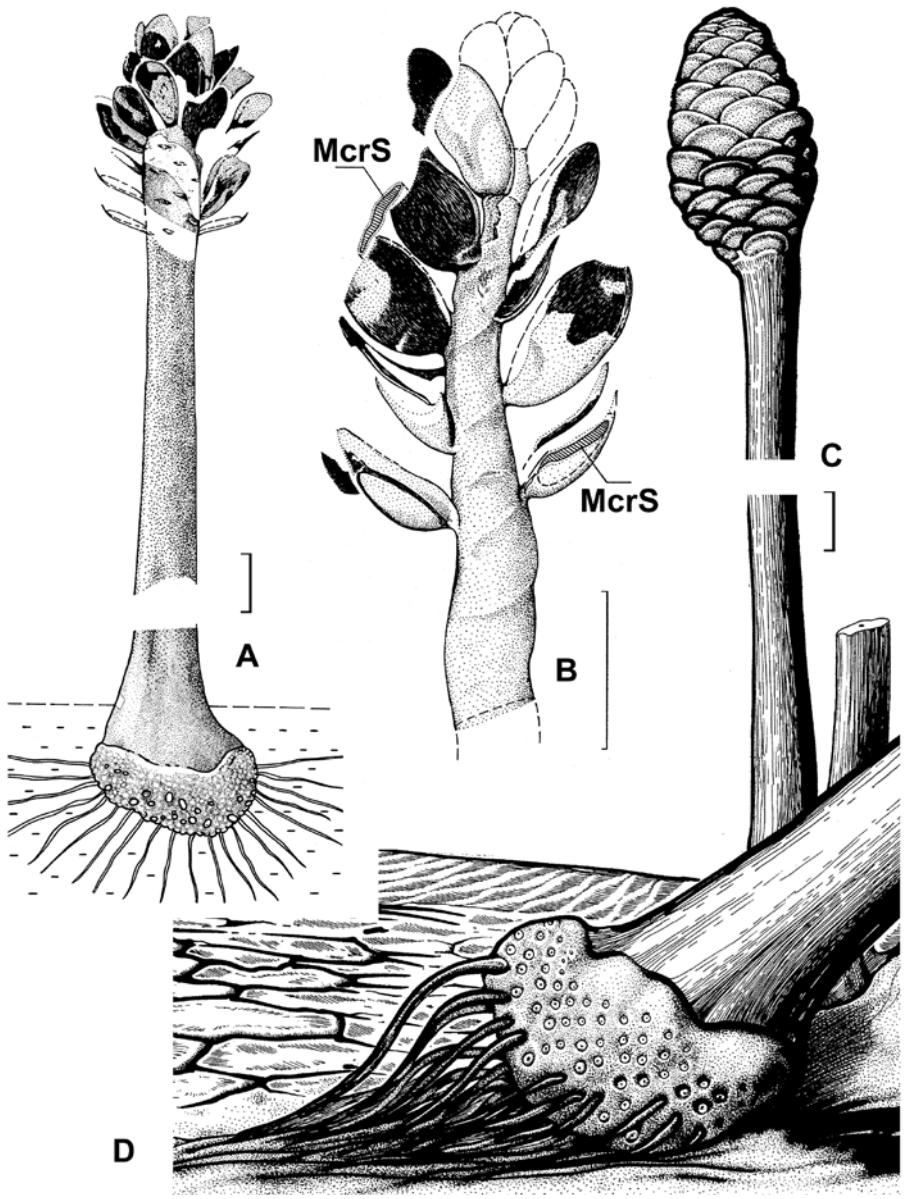

Figure 6. Morphology of strobili, axes and rhizophore of *Pleuromeia rossica* Neuburg from Tikhvinskoe. A – reconstruction based on spec. 4851/99 (strobilus), spec. 4851/259, 4851/260, 4851/262, 4851/263, 4851/264, 4851/265, 4856/266, 4851/270, 4851/271 (isolated stems) and spec. 4851/106 (rhizophore); B – apical part of the strobilus with microsporophylls (McrS) from which the *in situ* microspores were extracted (see here Fig. 8A), spec. 4851/107; C – reconstruction of the growth form of *P. rossica* Neuburg; D – rhizophore of *P. rossica* uncovered from substrate. Scale bars = 1 cm.

long and 50 mm wide (Fig. 3C; Fig. 5C, D; Fig. 7A–D). The cone axis of such individuals is much thicker and can reach 30 mm in diameter (Fig. 2A, C; Fig. 4B, D). As a rule, only fragments of such large cones occur in the locality Tikhvinskoe. After the reproductive season the sporophylls of *P. rossica* dropped off, separated from the cone axis by an abscission layer and left specific scars of semi-lunar outlines on the cone axis (Fig. 7A, B). Such dropped off sporophylls often formed mass burials on the surface of layers (Fig. 3A).

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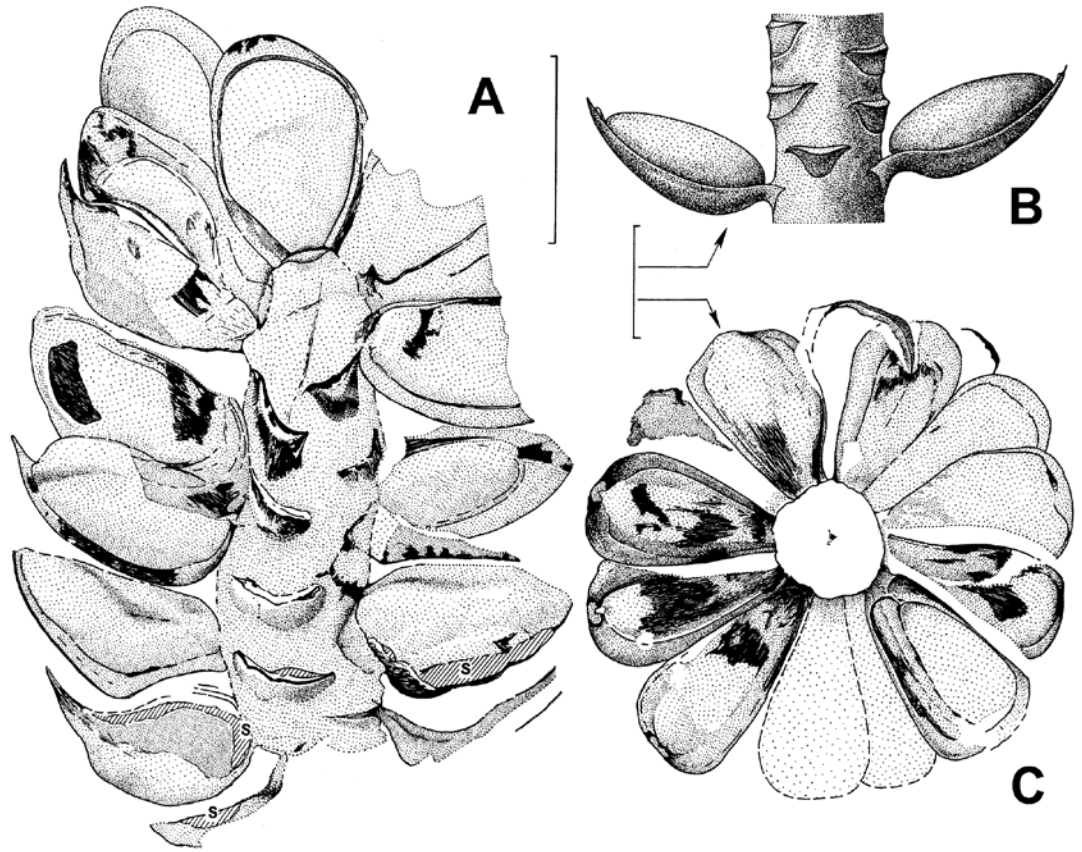

Figure 7. Morphology of strobili and stem of *Pleuromeia rossica* Neuburg from Tikhvinskoe. A – the basal part of the strobilus from which the *in situ* megaspores were extracted (see here Fig. 8 B–D), spec. 4851/103; B – reconstruction of an axis bearing two sporophylls with adaxially disposed sporangia, based on spec. 4851/103; C – cross section of the strobilus of spec. 451/104; D – co-occurrence of a strobilus and a stem, spec. 4851/104. Scale bars = 1 cm.

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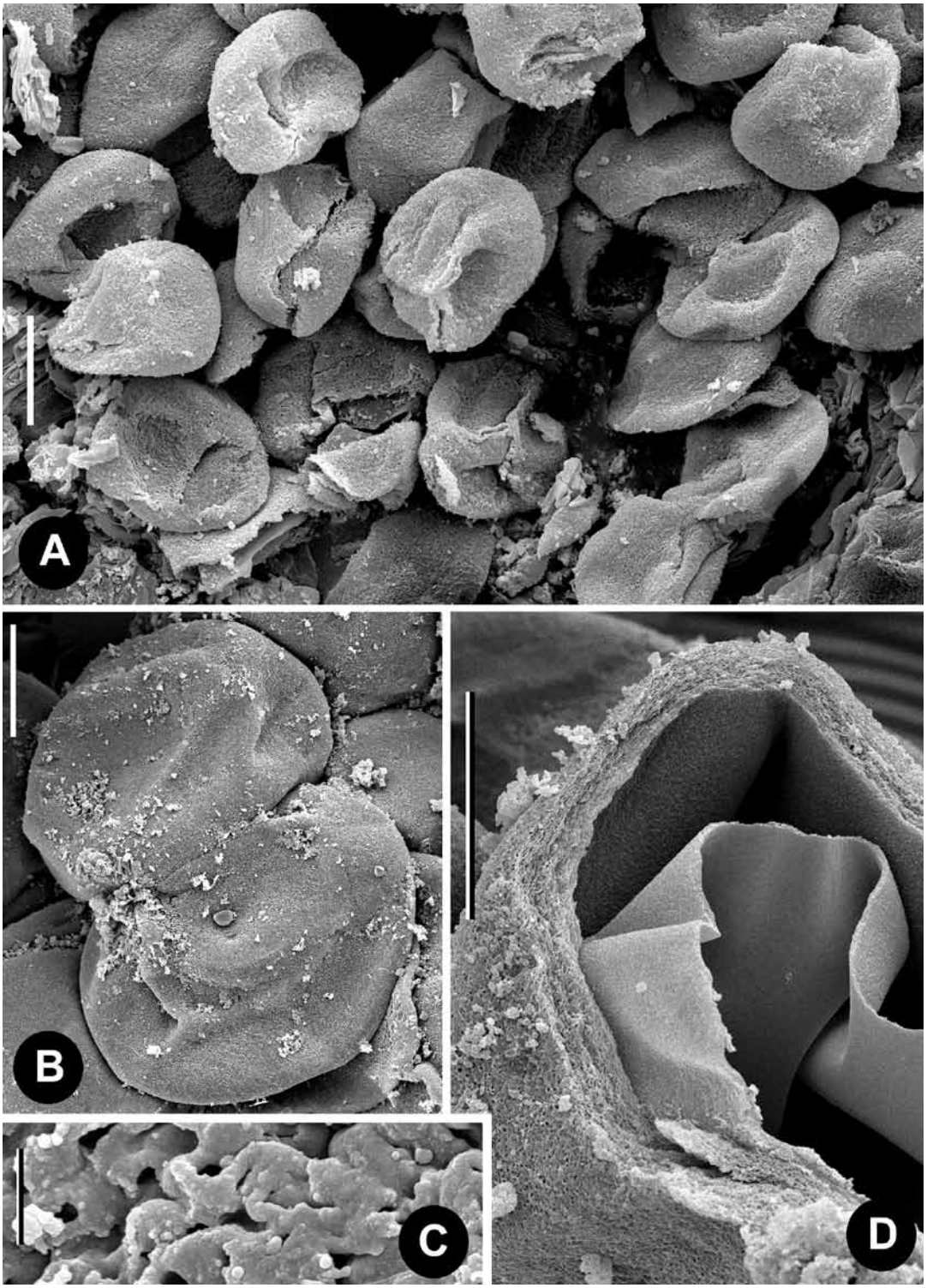

Figure 8. *In situ s*pores of *Pleuromeia rossica* Neuburg from Tikhvinskoe. A – microspores of *Densoisporites neuburgae* (Schulz) Balme, spec. 4851/107; B – two *in situ* megaspores of one tetrad, spec. 4851/103; C – ultrastructure of the megasporal sporoderm, spec. 4851/103; D – cross section through the megaspore, two layers (outer lamellate layer and inner dense layer) and the cavity between them can be seen clearly, spec. 4851/103. Scale bars: A = 20 µm; B = 100 µm; C = 2 µm; D = 50 µm.

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Sporophylls of *P. rossica* are obovate, with a round to obtuse apex, which often bears a small sinus in its medial part. Sporangia are round (Fig. 2 D, marked by an arrow) to ovoid (Fig. 7 A, B), repeating outlines of the sporophylls in a smaller size. The sporangia are attached to the sporophylls adaxially. Distally to the sporangium there is a ligular pit, also located on the adaxial surface of the sporophyll, but nearer to its apex.

Microspores of *P. rossica* were studied in detail (Lugardon et al. 1999). The microspores were assigned to a separate formal species *Densoisporites neuburgae* (Schulz) Balme. In common palynological practice the name *Densoisporites neuburgae* is used only for dispersed isolated microspores found in palynological preparations. If the microspores are extracted directly from the microsporangium, in other words, if they are found *in situ*, the name *P. rossica* is applied for both macrofossils and microspores. The microspores of *P. rossica* are very similar, but not identical to the microspores of *P. sternbergii* (Münster) Corda (Grauvogel-Stamm & Lugardon 2004).

The microspores of *P. rossica* are round, about 40 µm in diameter (Fig. 8 A). They have a distinct trilete scar (= trilete mark) on the proximal side of the microspore. Laesurae of trilete marks don't reach the equator of the microspore: their length is ⅔ of the microspore's radius. Sporoderm sculpture is scabrate. Sporoderm of the microspores has two well-formed layers with a cavity between (Yaroshenko 1975, 1985). Inner layer (nexine) forms the so-called corpus (= central body) of the microspore. Outer layer (sexine) consists of lamellae, which can be separated or, in contrast, conjoined into complex systems of lamellae (Lugardon et al. 1999). A very similar structure of sporoderm is characteristic of the microspores *Densoisporites polaznaensis* Naug. et Zavialova, belonging to the heterosporous lycopodiophyte *Viatcheslavia vorcutensis* Zalessky emend. Naug. (Naugolnykh & Zavialova 2004; Naugolnykh 2005). Now *Viatcheslavia* is believed to be one of the direct predecessors of *Pleuromeia* (see below 'Phylogeny' and Fig. 10).

Superficially, megaspores of *P. rossica* are similar to the microspores of the same plant, but differ in a considerably larger size and more smooth sporoderm (Fig. 8 B, D). The sporoderm surface of the megaspores of *P. rossica* has numerous micropores and sometimes is ornamented by small scabrae and pustulae (Fig. 8 C). A very similar ultra-relief is known for megaspores of the Upper Carboniferous (Stephanian) lycopodiopsid *Polysporia doubingeri* Grauvogel-Stamm et Langiaux (Grauvogel-Stamm & Langiaux 1995: Planche IV, Fig. 6a). Diameter of the megaspores of *P. rossica* is 300–400 µm, but occasionally even bigger megaspores occur. Exosporium is thick and consists of numerous lamellae (Lugardon et al. 2000. See this work for futher references on megaspores of Pleuromeiaceae). It is divided distally and marginally into a thick, loose outer part and a thin, dense inner part (Fig. 8 D). Both parts (layers) can often be divided by empty space, apparently homologous to the cavity in microspores.

Reconstruction of the whole plant of *Pleuromeia rossica*

Despite the great number of scientific contributions focused on *P. rossica*, no attempts to reconstruct the growth form or whole plant have been made for a long time. A first sketch of a reconstruction of *P. rossica* was published by the present author (Naugolnykh 2004: 216, Fig. 86 A, B). A reconsidered and more detailed version of this reconstruction is proposed here (Fig. 8 A, C, D; Fig. 9 A). All data on morphology, including parts preserved in natural connection to each other (Fig. 2 C, D; Fig. 3 B, D; Fig. 4 E; Fig. 5 B), were used for this reconstruction.

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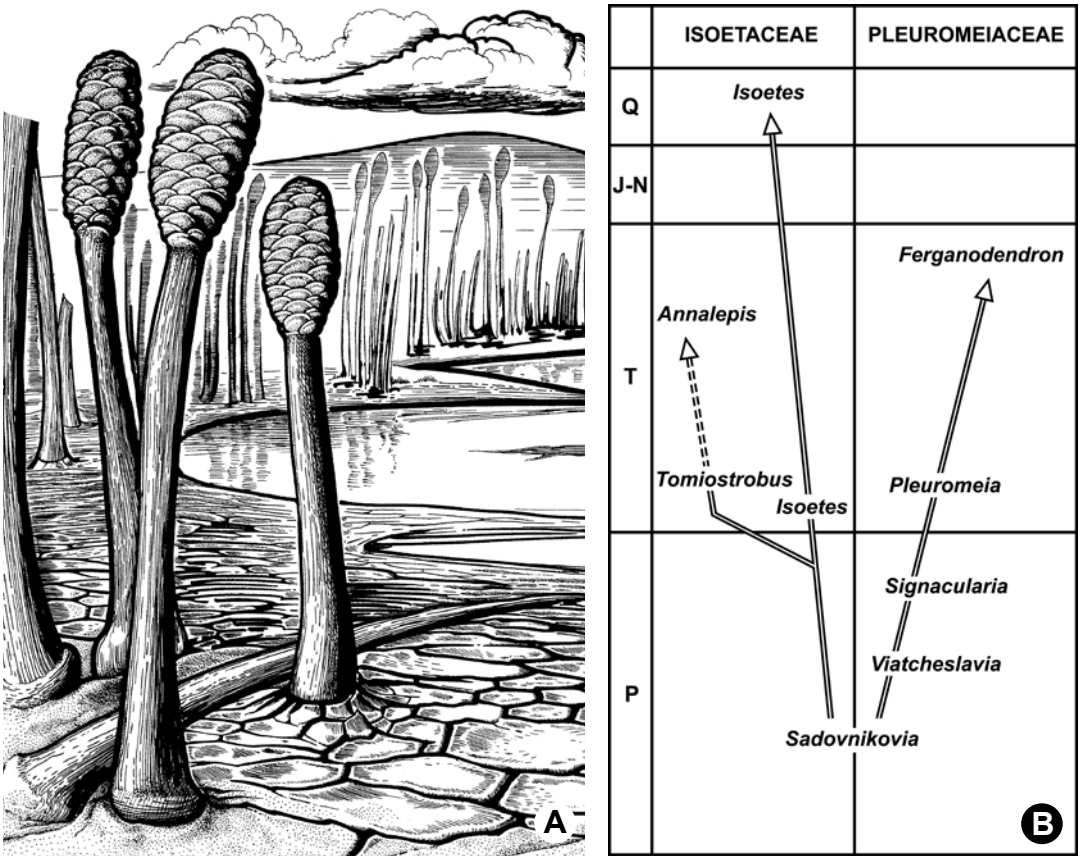

Figure 9. Reconstruction and phylogenetical relationship. A – Reconstruction of the whole plant of *Pleuromeia rossica* Neuburg. The plants are shown as elements of a monodominant community nearby waters, consisting of halophytes which grow in conditions of a semiarid climate. B – Phylogenetical relationship between the families Isoetaceae and Pleuromeiaceae based on Naugolnykh (2012b).

Phylogeny

The closest phylogenetical predecessor of the genus *Pleuromeia* is the genus *Signacularia* Zalessky (Zalessky 1929). The latter genus was reconsidered by Esaulova (1986) and Naugolnykh & Pukhonto (2007). *Signacularia* is typical of Kazanian Stage (or Wordian; Middle Permian) of Volga River basin and Cis-Urals. *Signacularia* can be regarded as an intermediate form between the older genus *Viatcheslavia*, which is typical of Ufimian (Roadian) Stage of Cis-Urals and the genus *Pleuromeia*. According to the author's viewpoint, the genus *Viatcheslavia* originated from the Lower Permian (Kungurian) genus *Sadovnikovia* Naug. which was a common ancestor of both sister-families, Isoetaceae and Pleuromeiaceae (Fig. 9 B). Further discussions can be found in Naugolnykh (2012b).

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: Wulfenia

Jahr/Year: 2013

Band/Volume: 20

Autor(en)/Author(s): Naugolnykh Serge V.

Artikel/Article: The heterosporous lycopodiophyte Pleuromeia rossica Neuburg, 1960 from the Lower Triassic of the Volga River basin (Russia): organography and reconstruction according to the "Whole-Plant" concept. 1-16