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Sporophyll morphology and reconstruction of the heterosporous lycopod *Tomiostrobus radiatus* Neuburg emend. from the Lower Triassic of Siberia (Russia)

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ABSTRACT

Naugolnykh SV 2012. Sporophyll morphology and reconstruction of the heterosporous lycopod *Tomiostrobus radiatus* Neuburg emend. from the Lower Triassic of Siberia (Russia). The Palaeobotanist 61(2): 387-405.

The paper deals with the taxon *Tomiostrobus radiatus* Neuburg emend., a heterosporous isoetopsid lycopod from the Babiy Kamen Locality of Lower Triassic of Siberia (Russia). Morphological diversity of the *T. radiatus* sporophylls is described in detail. Interpretation of structure and function of the sporophylls, and analysis of their morphological peculiarities are given. Arguments for attributing the lycopod *T. radiatus* to the Isoetaceae family have been provided. The reconstruction of *T. radiatus* is proposed. Origin and evolution of the families Isoetaceae and Pleuromeiaceae are also discussed.

Key-words—Triassic, Siberia, lycopods, *Tomiostrobus*, Isoetaceae, *Isoetes*.

बीजाणुपर्ण आकृतिविज्ञान तथा साइबेरिया (रुस) के निम्न तृतीयक से प्राप्त विषमबीजाणु लाइकोपॉड *टॉमिओस्ट्रोबस रेडिएटस* न्यूबर्ग इमेंड नवम के वृद्धि प्ररुप की पुनर्संरचना

सर्ज वी नौगॉल्नीख

सारांश

यह शोध-पत्र साइबेरिया (रुस) के निम्न ट्राइऐसिक, बेबीय कमेन उपबस्ती से प्राप्त विषम बीजाणु आइसोएटॉप्सिड लाइकोपॉड, *टॉमिओस्ट्रोबस रेडिएटस* न्यूबर्ग इमेंड नवम जाति से संबद्ध है। *टी.रेडिएटस* बीजाणुपर्ण की आकारिकीय विविधता विस्तृत रुप से वर्णित की गई है। संरचना की व्याख्या एवं बीजाणुपर्ण के प्रकार्य तथा उनकी आकारिकीय विशिष्टताओं को बताया गया है। लाइकोपॉड *टी.रेडिएटस* को आइसोइटेसी परिवार का मानने हेतु तर्क दिए गए हैं। *टी.रेडिएटस* की संपूर्ण पादप पुनर्संरचना प्रस्तावित है। आइसोइटेसी एवं प्लूरोमाएसी परिवारों के उद्भव एवं विकास की भी चर्चा की गई है।

संकेत-शब्द—ट्राइऐसिक, साइबेरिया, लाइकोपॉड, *टॉमिओस्ट्रोबस*, आइसोइटेसी, *आइसोइटेस* ।

INTRODUCTION

The present-day lycopods are represented by non-arborescent forms only, which are assigned to the families Lycopodiaceae, Selaginellaceae and Isoetaceae. There are many challenges in systematics and phylogeny of some of the groups of spore plants, specially regarding the origin of modern lycopod families. The questions related with the appearance and origin of the modern lycopod families are still unanswered. The complexity of the issues related to analysis of the initial phases of evolution of the modern lycopod families arises from superficial interpretation of some fossil lycopod representatives. Nevertheless, these taxa play an essential role for proper understanding of the evolution of this plant group. Absence of well-documented morphological features of such key-taxa does not enable them to compare properly with the recent taxa for consideration of the potential phylogenetic descendants.

The present study deals with the Early Triassic lycopod *Tomiostrobus radiatus* Neuburg, its systematic position, detailed characteristics of sporophylls and reconstruction. Special attention is given to the phylogenetic role of this plant in the origin of the family Isoetaceae, which can be regarded in the modern plant world as a typical example of the "living fossils".

MATERIAL

The material under examination was collected in 2001 from the Babiy Kamen ("Women's Stone") Section, located in the Kuznetsk coal basin, on the right bank of Tom River (Fig. 1) and was provided to the present author by D.E. Scherbakov, who is a researcher of the Palaeontological Institute of Russian Academy of Sciences (Moscow). The Babiy Kamen Section is well-known as a classic outcrop of the Lower Triassic (Induan) deposits and has yielded fossil plants, represented by both macrofossils and palynomorphs.

The sporophylls of *Tomiostrobus radiatus* were collected from the dark-grey to black siltstones belonging to Tarakhanikha packet of the lower part of the Ostashinskaya Formation of the Maltsevka Series. Besides the fossil plants, these deposits also contain numerous shells of conchostraceans, as well as some insects.

The collection includes more than eighty extremely well preserved fossil plant remains. Most of the plant macrofossils are sporophylls of the isoetopsid lycopod taxon *Tomiostrobus radiatus* Neuburg, initially described on the basis of the material found in the Babiy Kamen Locality. The plant fossils are mostly preserved as impressions on fine-grained dark-grey siltstone, however, several fossils are partly preserved as compressions having limonitizied tissues.

The sporophylls of *Tomiostrobus radiatus* from this collection can be grouped into several categories according to mode of their preservation. The first category includes

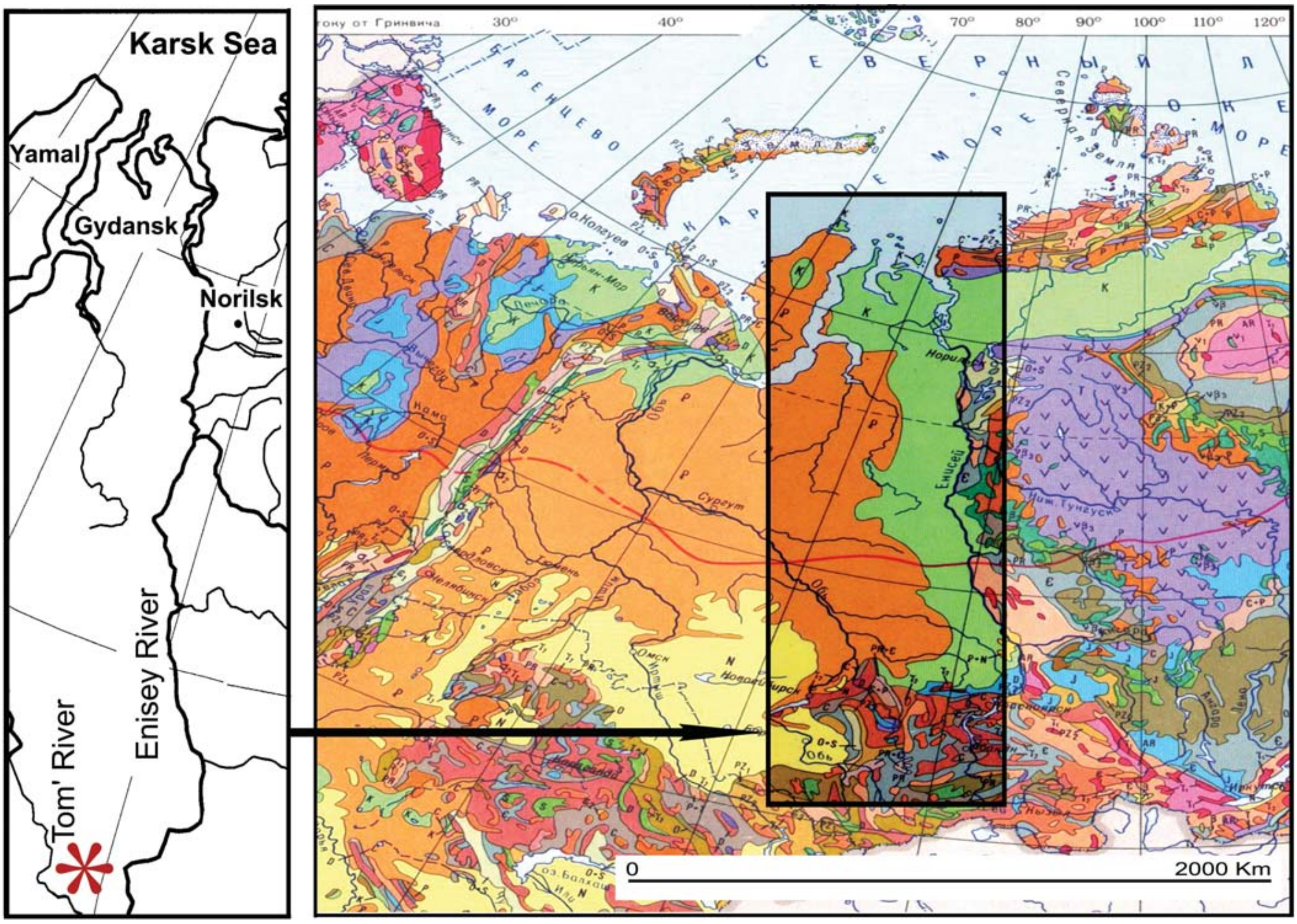

Fig. 1—Geographical position of the Babiy Kamen Locality. The locality is marked by asterisk. Geological map modified after: http://jurassic.ucoz.ru.

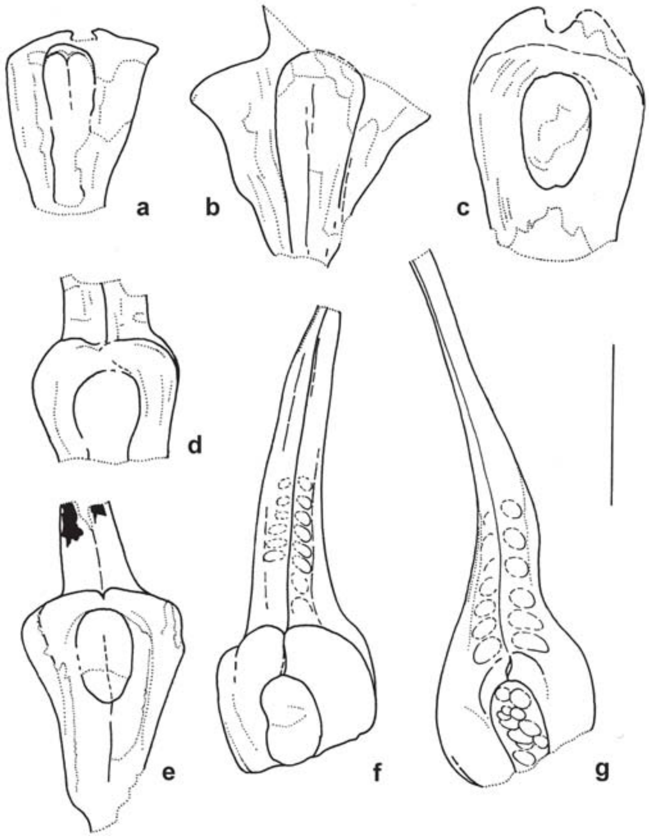

Fig. 2—*Tomiostrobus radiatus* Neuburg, sporophyll diversity: a – 4851/113; b – 4851/114; c – 4851/115a; d – 4851/115b; e – 4851/127; f – 4851/119a; g – 4851/128. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

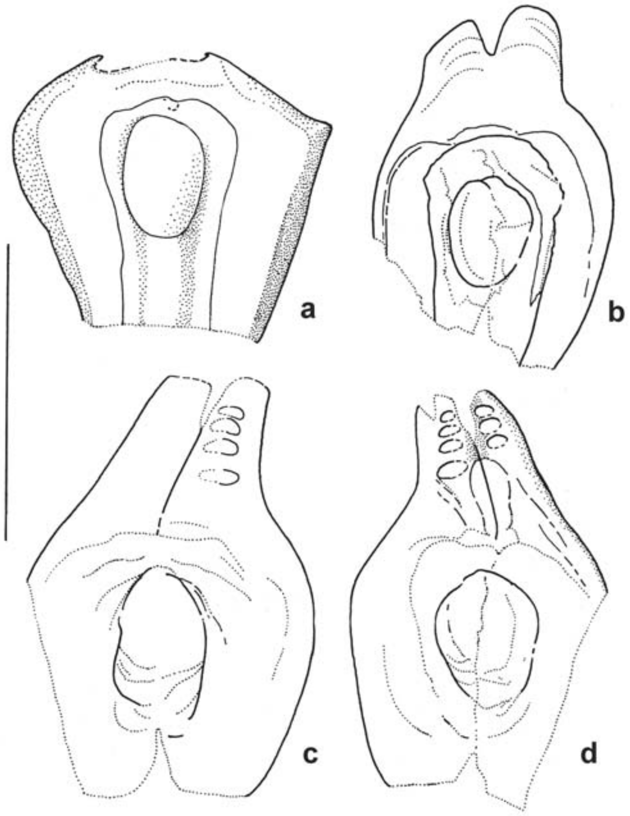

Fig. 3—*Tomiostrobus radiatus* Neuburg, sporophyll diversity: a – 4851/122; b – 4851/118; c – 4851/116; d – 4851/121. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

virtually completely preserved sporophylls or their imprints with the observed fertile (proximal) and sterile (distal) parts. The second category includes proximal (fertile) parts of sporophylls without distal segments, which were most probably detached naturally as generally happens with the extant representatives of the genus *Isoetes* L. (see the "Discussion" part below). The third category includes the proximal (fertile) parts of the *Tomiostrobus radiatus* sporophylls, also without distal (sterile) segment, but in this case the distal segment was lost as a result of mechanical damage of the specimens. Isolated distal segments of the sporophylls are assigned to the fourth category.

The approach of monotopic site analysis as suggested by Meyen (1966) is applied in the present study as a methodological basis for description of the *Tomiostrobus radiatus* sporophylls. This approach was based on the multisubjective study of plant macrofossils collected from one and the same locality (from one and the same layer or depositional surface), presumably all these macrofossils represent the same natural community or population (in case of monospecies locality). The monotopic site approach enables to estimate the main modes of intraspecific variability of the most important diagnostic features. This approach has been found to be very effective and productive both for the systematics and taxonomy, not only for the palaeobotanical but also for the palaeozoological studies (Serezhnikova, 2008). Some of the sporophylls are photographed in different modes for an adequate demonstration of their morphological features.

MORPHOLOGY OF THE SPOROPHYLLS OF *TOMIOSTROBUS RADIATUS* NEUBURG

Despite a very high morphological variability, the sporophylls of *Tomiostrobus radiatus* of the present collection have been assigned to one and the same natural or "botanical' species. Using typological basis/approach for *Tomiostrobus radiatus* taxonomy (based on the structure of sporophylls), one can divide these sporophylls into several formal morphotaxa, but this way can hardly be accepted as biologically valuable. The observed differences can be explained as reflections of (1) a different position of the sporophylls on protocorm; (2) a different age (or onthogenetic stage) of the

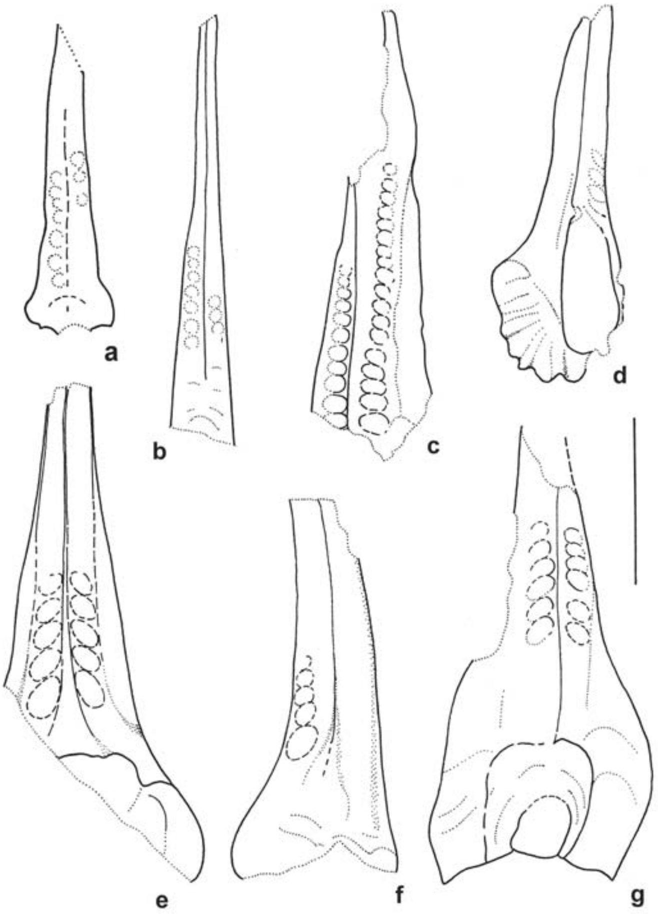

Fig. 4—*Tomiostrobus radiatus* Neuburg, sporophyll diversity: a – 4851/123; b – 4851/124; c – 4851/126; e – 4851/127; f – 4851/119a; g – 4851/128. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

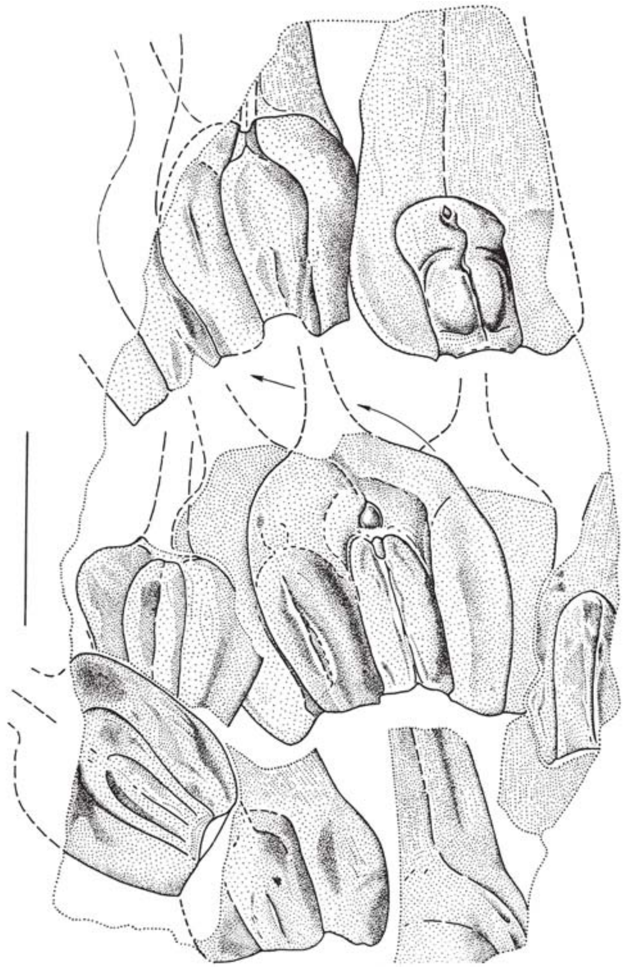

Fig. 5—*Tomiostrobus radiatus* Neuburg, several sporophylls belonged to one and the same parent plant; 4851/161. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

parent plants; (3) a natural intraspecific or intra-population variability of the parent plants and natural variability of their parts/different organs.

All general linear parameters of the sporophyll morphology have been measured (Fig. 10). If the linear size of the sporophyll part could not be stated, the cell of the Fig. 10 has been left blank with (-) mark. All the measurements are given in millimeters. The individual number of the specimen has been mentioned repeatedly if the specimen includes several sporophylls.

Sporophylls of *Tomiostrobus radiatus* have two distinctive parts: basal (proximal) fertile part and apical (distal) sterile part (Figs 2-6; Pls 1-5, 6.1, 6). The proximal part of the sporophyll is ovoid, elongate in shape. Adaxial surface of the proximal part bears a sporangium, slightly submerged into the sporophyll and partly covered by fine narrow limb-like filmy tissue – velum. Average size of the sporangium is 4 x 6 mm. Ligula is situated on the adaxial surface of the sporophyll placed distally in relation to the sporangium. The ligula is observed in very few specimens only (Figs 2g, 5, Pl. 4.1). Proximal part of the sporophyll distally continues very gradually into the distal (sterile) part (distal segment). The distal segment is narrow and possesses long, acute apex (Figs 2f, 2g, 4a-g, 6; Pl. 1.4-5,8-9, Pl. 2.1-4, Pl. 3.3, 4, Pl. 5.1, 2). A distal single vein runs through all the distal segments. This vein approaches the distal segment from the proximal part of the sporophyll, but here the vein is covered by the sporangium. Hence, if the sporophyll is exposed by its adaxial surface in the proximal part, the vein cannot be observed. An interesting peculiarity of the sporophyll of *Tomiostrobus radiatus* is the presence of the so-called rib-like extenuation (Sadovnikov, 1982). Similar structures are known for some representatives of the present-day heterosporous lycopods, for example, *Selaginella scandens* (P. Beauv.) Spring (Lotsy, 1909, Fig. 339, 6). However, Dobruskina (1985) rejected the possibility of recognizing this rib-like extenuation of *Tomiostrobus* and

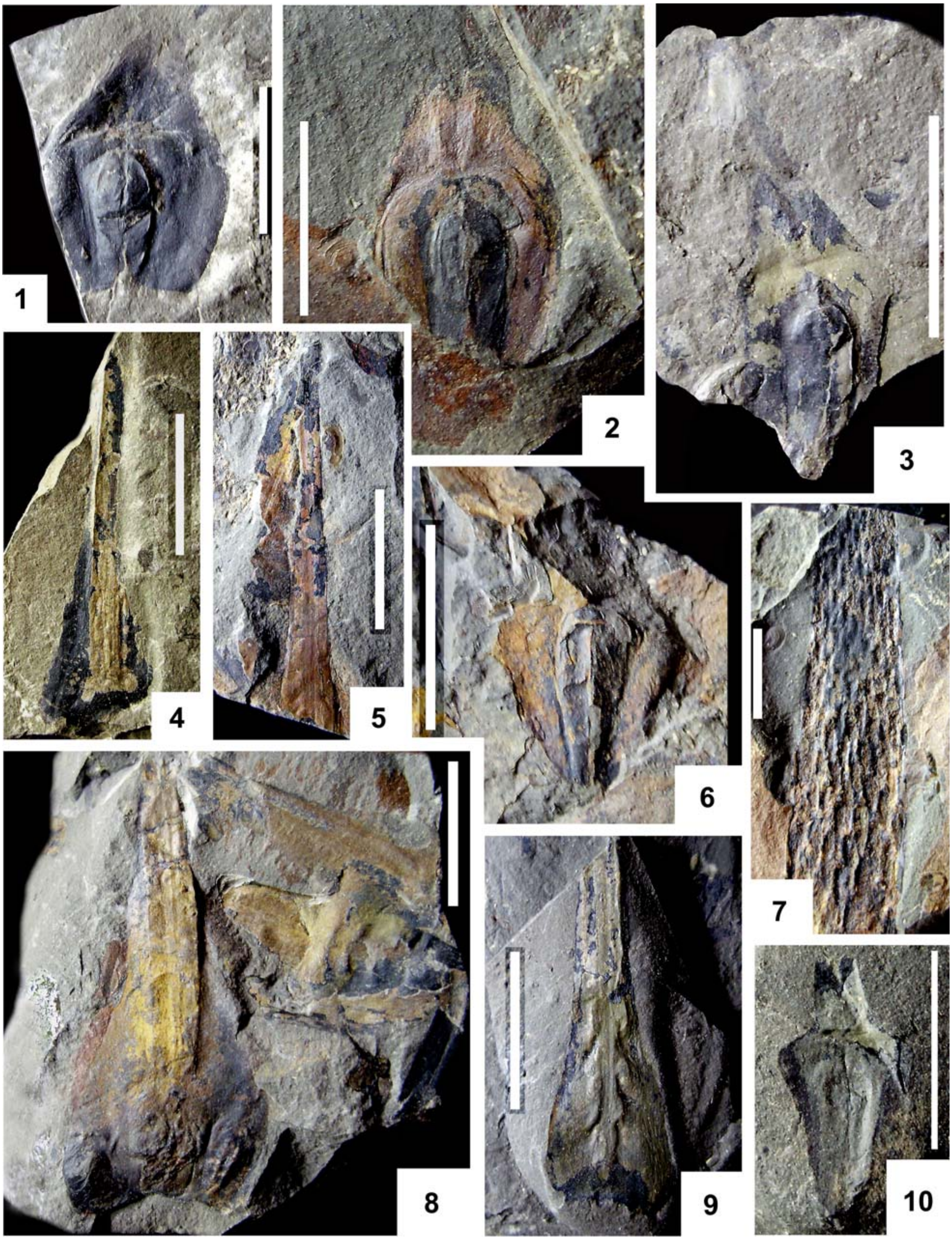

PLATE 1

Tomiostrobus radiatus Neuburg, morphology of sporophylls (1-6, 8-10) and axial part of the protocorm (7); 1 – 4851/115a; 2 – 4851/114; 3 – 4851/158; 4 – 4851/132a; 5 – 4851/124; 6 – 4851/118; 7 – 4851/134; 8 – 4851/128; 9 – 4851/132a; 10 – 4851/120. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

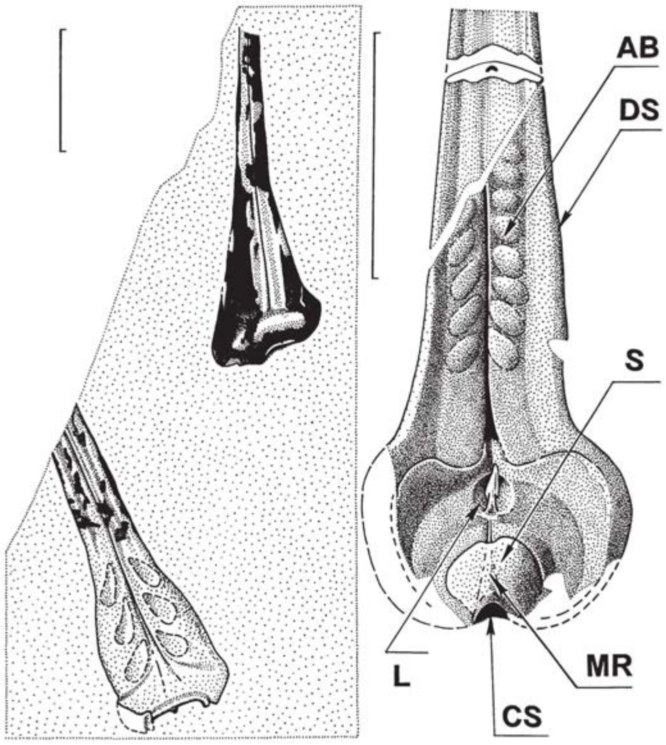

Fig. 6—*Tomiostrobus radiatus* Neuburg, sporophyll diversity: left fig. – 4851/132a; right fig. – interpretation of the sporophyll morphology based on the specimen 4851/130. AB – air bladders (=air chambers); DS – distal segment; S – sporangium; L – ligula; CS – central conducting strand; MR – median rib. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

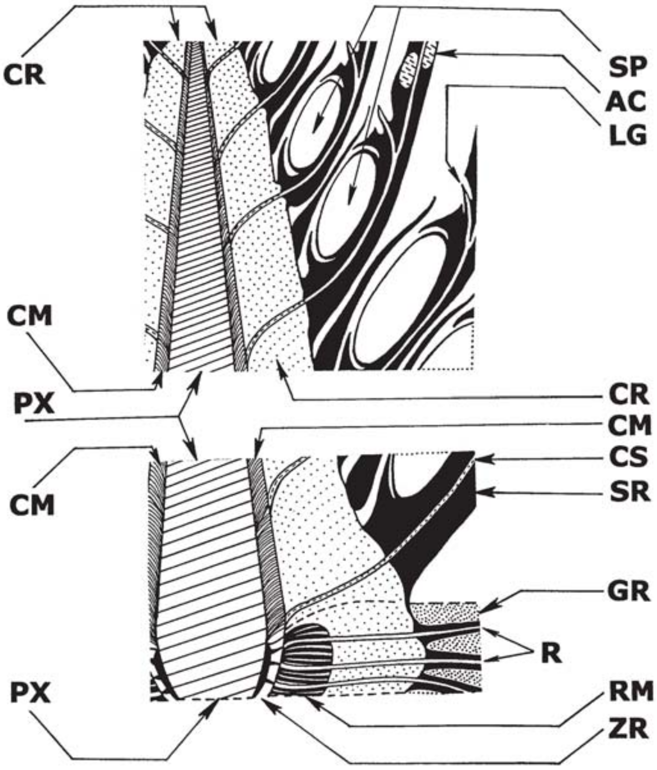

Fig. 7—*Tomiostrobus radiatus* Neuburg, putative interpretation of the whole plant morphology. CR – outer cortex; SP – sporangia; AC – air bladders (=air chambers); LG – ligula; CM – inner cortex; PX – axial conducting tissues; CS – central conducting strand in sporophylls; SR – sporophyll; GR – ground, substrate; R – roots; RM – rhizophore meristem; ZR – rhizophore cortex.

situated directly above the conductive strand, but the degree of development of this extension is distinct for different ontogenetic stages of the sporophyll growth. It can also vary considerably in different specimens belonging to one and the same plant population. Such a high variability of this feature in the same population (monotopic site, according to the terminology of Meyen, 1987) doesn't enable the usage of this rib-like elevation as a taxonomically important feature.

The distal segments of *Tomiostrobus radiatus* bear well represented ovoid cyst-like bodies oriented across the sporophyll. These bodies are separated from each other by shallow furrows (when there is positive relief of the sporophyll) or by flattened ribs (when there is negative relief of the sporophyll on its impression).

Relatively broad ribs and furrows are oriented across the leaves (phylloids) and the distal segments of the sporophylls. These ribs and furrows are also characteristic of many representatives of fossil isoetalean and *Pleuromeia*-like lycopods, e.g. *Pleuromeia sternbergii* (Muenster) Corda (Magdefrau, 1931). The ribs and furrows of the leaves have been interpreted as surface structures corresponding to the air chambers located inside the leaf mesophyll tissues. These air chambers are homologous to the air chambers characteristic of many recent species of *Isoetes* L.

Grauvogel-Stamm and Lugardon (2001) opined that the distal part of sporophylls of *Annalepis zeillerii* Fliche was oriented at the right angle to the proximal part of the sporophyll. They have the same opinion regarding the morphology of the sporophylls of *Tomiostrobus*, but I disagree with such interpretation. Not a single specimen of *Tomiostrobus radiatus* in this collection has a cross fold characteristic of the sporophylls of *Annalepis*. Moreover, all the best-preserved sporophylls of *Tomiostrobus radiatus* demonstrate a very gradual transition between the fertile proximal part of the sporophyll (part bearing a sporangium) and the sterile part of the sporophyll (terminal segment). The presence of relatively large sporophylls with detached distal parts show that after the sporangia got mature the distal parts of the sporophylls became dry, curved and then fell, as is shown in the reconstruction (Figs 7, 8). It may also be stated that the young and well-developed sporophylls of *Tomiostrobus radiatus* were straight or slightly curved, like the sporophylls of extant *Isoetes*.

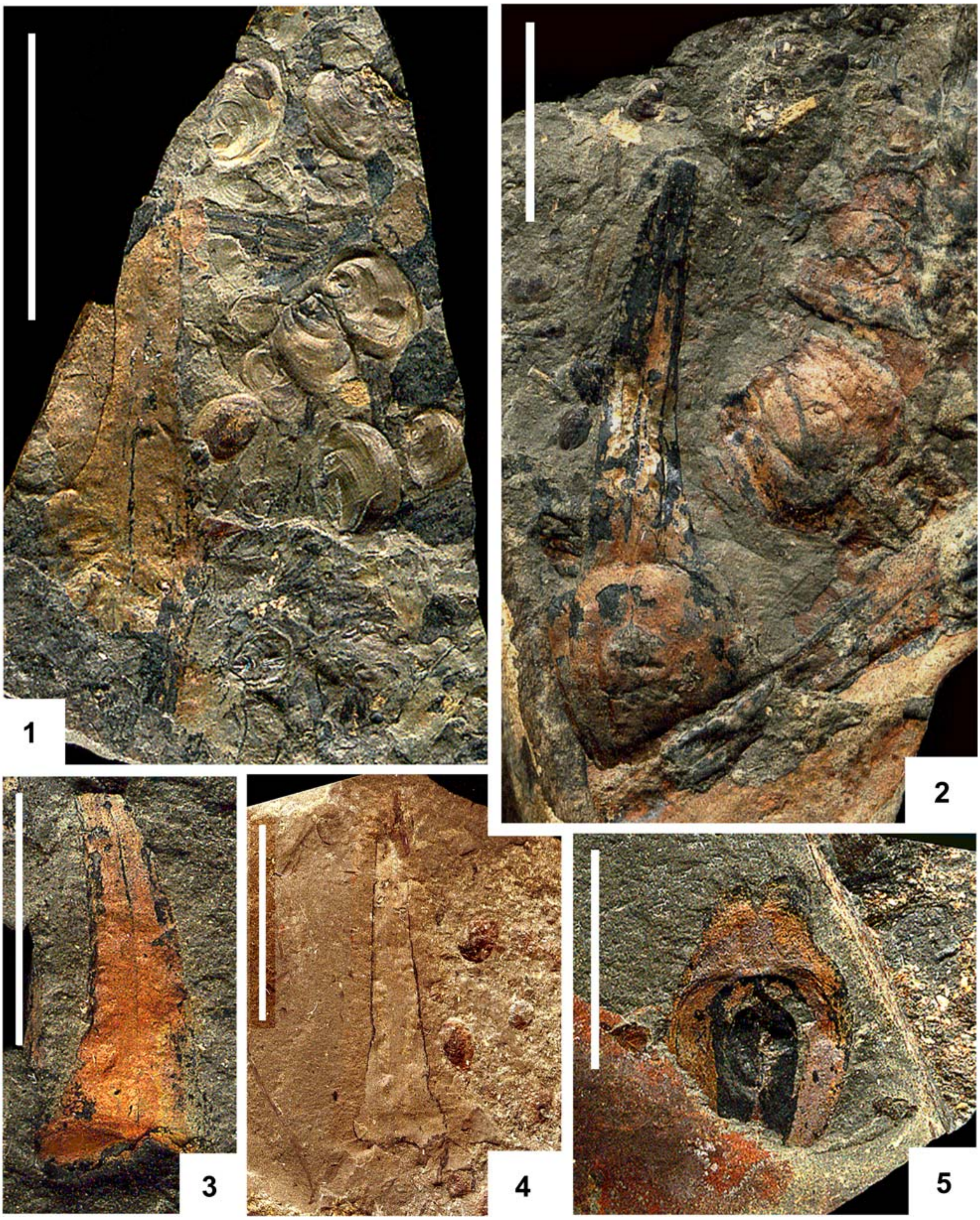

PLATE 2

Tomiostrobus radiatus Neuburg, morphology of sporophylls; 1 – 4851/126; 2 – 4851/121; 3 – 4851/119a; 4 – 4851/123; 5 – 4851/114. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

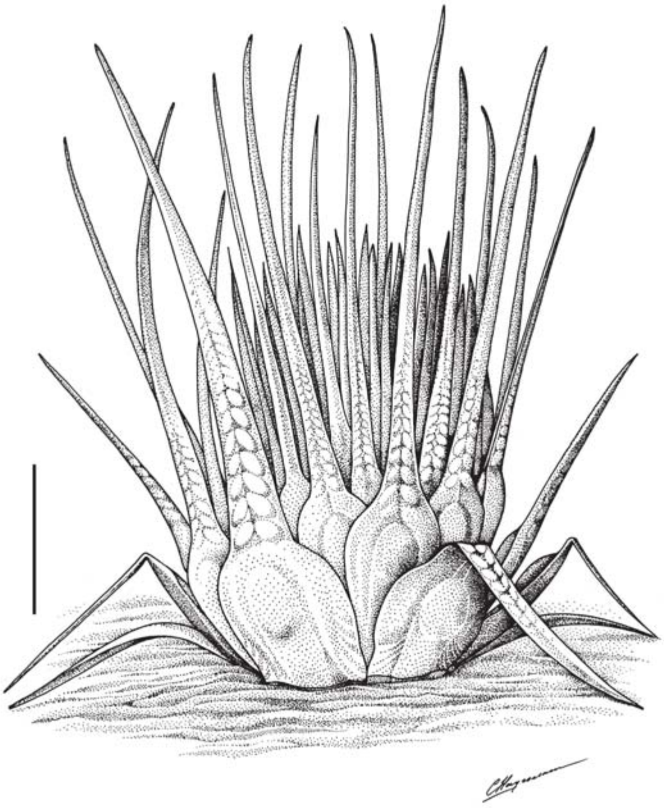

Fig. 8—*Tomiostrobus radiatus* Neuburg: reconstruction of the whole plant. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

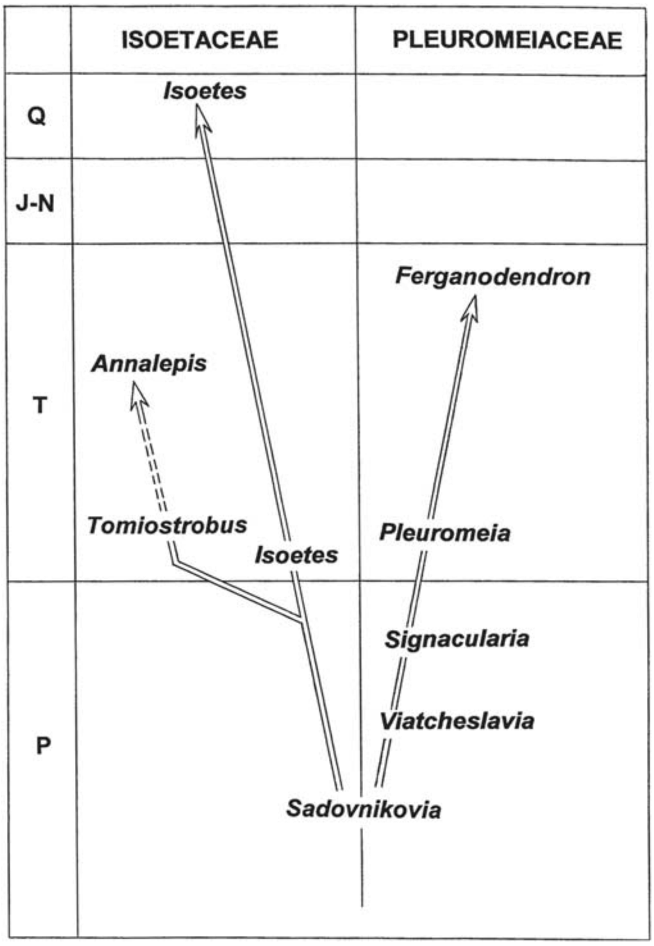

Fig. 9—General phylogeny of the families Pleuromeiaceae and Isoetaceae.

Another important problem related with the interpretation of *Tomiostrobus*, *Annalepis* and other closely related lycopods and, in large scale, linked with the reconstruction of their growth form, is the issue of comprehension of form and function of their stem or protocorm. The stem of the *Pleuromeia*-like lycopods is well-developed, has mechanical function, and most probably is involved in photosynthesis. In contrast, the stem of *Tomiostrobus* and *Annalepis* is transformed into short stem or protocorm, which has a different function. The main function of the protocorm is to firmly fasten the plant with the substrate. Besides, during the dry seasons the protocorm could also have provided extra water and food supplements to the plant.

The reconstruction of *Annalepis zeillerii* Fliche, proposed by Grauvogel-Stamm and Lugardon 2001 (Fig. 7) shows a plant with a well-developed stem bearing massive apical cone (strobilus). The cone axis has been reconstructed purely hypothetically. This reconstruction is not acceptable since the present study indicates that the sporophylls of this plant are attached to the protocorm and not to the apical part of the stem. Accordingly, the scars present on the protocorm are the remnants of the sporophylls of *Annalepis zeillerii*, and not of the leaves, as was initially assumed by Grauvogel-Stamm and Lugardon. Therefore, the plant itself was geotropic, not geliotropic and superficially resembled the extant genus *Welwitschia*, but without hypertrophied leaves. Ecologically, representatives of *Annalepis* and *Lepacyclotes* were close to the present-day phreatophytes or succulents. This idea is also supported by the presence of the well-developed roots, typical of *Annalepis*. These roots were attached to the base of the cormose rhizophore of *Annalepis*.

DISCUSSION

The genus *Tomiostrobus* Neuburg, 1936 was initially established for isolated sporophylls, erroneously misinterpreted as seed scales of conifers (Araucariaceae). *Tomiostrobus* together with the superficially similar genera, *Araucarites* and *Pseudoaraucarites* has been attributed to the conifers for a long time (Neuburg, 1936; Vladimirovich *et al.*, 1967; Fefilova, 1983). Some of the sporophylls of *Tomiostrobus* are quite similar to the isolated seed scales of *Araucaria*.

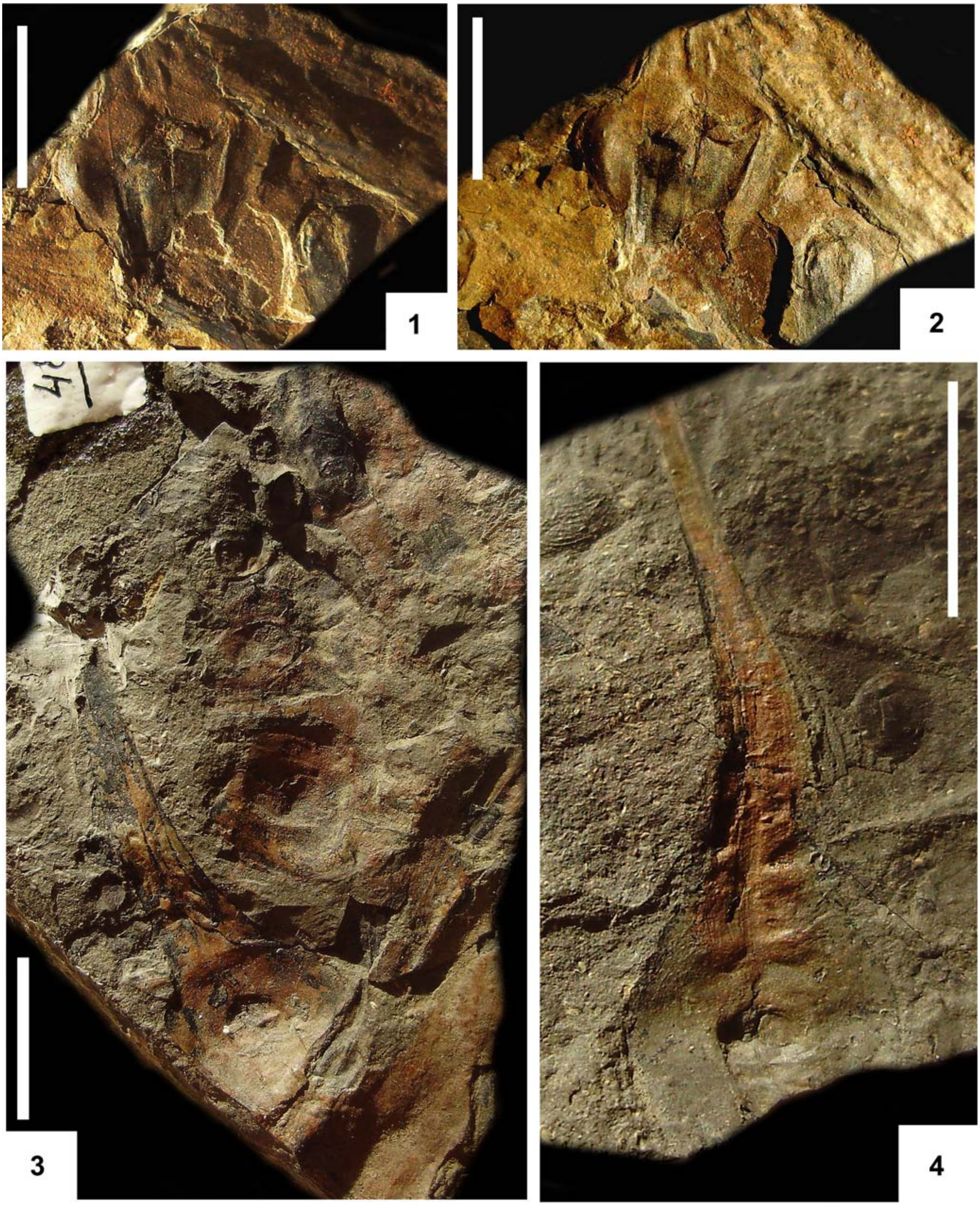

PLATE 3

Tomiostrobus radiatus Neuburg, morphology of sporophylls; 1, 2 – 4851/155; 3 – 4851/121; 4 – 4851/128. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

1	2	3	4	5	6
1	4851/113	10,5	9	-	-
2	4851/114	11	8	-	-
3	4851/115a, b	10	9,5	6	>>7
4	4851/116	7	10	-	-
5	4851/117	9	10,5	5	>22
6	4851/118	8,5	9	-	-
7	4851/119a, b	8	>>1	5	20
8	4851/120	6,5	10	2,5	>4
9	4851/121	11	10	4	22
10	4851/121	9	8	-	-
11	4851/122	8	10,5	-	-
12	4851/123	6	3	4	18
13	4851/124	-	-	5	25
14	4851/125	-	-	5	>21
15	4851/126	6	7	3	>10
16	4851/127	>8	>8	5,5	>22
17	4851/128	13	12	7	>17
18	4851/128	9,5	10	5	>>7
19	4851/128	-	-	3	13
20	4851/129b	5	6,5	-	-
21	4851/129b	7	6	-	-
22	4851/129a	7	5	5	13
23	4851/129a	11	7	8	27
24	4851/129a	9	>5	5	>14
25	4851/130	9	5	6	>12
26	4851/130	-	-	6	>26
27	4851/131	8	3	6	24
28	4851/132a, b	7	3	6	24
29	4851/132a, b	8	3	7	>17
30	4851/132a	8	5	3	>19
31	4851/133	13	10	11	>>8
32	4851/136	11	5,5	8	>>13
33	4851/137	10	7	-	-
34	4851/138	9	9	4	>15
35	4851/138	-	-	4	16
36	4851/139	9	8	3	>>2
37	4851/139	5	7	-	-
38	4851/139	-	-	2	10
39	4851/140	10	15	4,5	>15
40	4851/140	7	4	5	18
41	4851/140	7	5	5	>10
42	4851/140	-	-	4,5	>14
43	4851/140	11	13	5,5	>9
44	4851/141	9	11	7	>>6
45	4851/141	6	9	-	-
46	4851/141	8	6	-	-
47	4851/141	11	12	-	-
48	4851/141	9	>10	-	-
49	4851/141	5	8	-	-
50	4851/142	13	12	-	-
51	4851/143	10	5	6	>7
52	4851/143	9	9	-	-
53	4851/143	-	-	2	18
54	4851/144	10	10	4	>17
55	4851/145	4	9	1,5	>2,5
56	4851/146	8	>4	6	>15
57	4851/146	4	3	3	>15
58	4851/146	-	-	2	>10
59	4851/146	9	10	-	-
60	4851/146	-	-	1,5	10
61	4851/147	11	11	-	-
62	4851/147	7	5	5	>8
63	4851/149	4	8	1,5	>>2
64	4851/150	9	10	-	-

65	4851/151	7	5	-	-
66	4851/152	6	7	2	>>3
67	4851/153	12	10	6	>>11
68	4851/153	6	12	-	-
69	4851/153	-	-	2	>>7
70	4851/153	8	7	-	-
71	4851/153	7	5	6	>>10
72	4851/154	7	11	-	-
73	4851/154	8	5	4,5	>>13
74	4851/154	7	4	5	>>9
75	4851/154	-	-	2	>>9
76	4851/155	10	5	6	>>9
77	4851/155	10	9,5	5	>>2
78	4851/155	10	9	-	-
79	4851/156	-	-	2	>10
80	4851/157	10	8	8	>>9
81	4851/157	>5	>3	5	16
82	4851/157	-	-	5	>20
83	4851/157	-	-	2	>11
84	4851/158	8	4	4	>16
85	4851/158	7	9	4	>5
86	4851/159	>6	8	>5	>9
87	4851/160	3,5	6	-	-
88	4851/161	10	11	6	>>7
89	4851/161	9	10	-	-
90	4851/161	12	10,5	-	-
91	4851/161	10	8	-	-
92	4851/161	9	9	-	-

Fig. 10—1-Serial numbers; 2-specimen numbers; 3-maximal width of proximal (fertile) part of sporophyll (mm); 4-length of proximal (fertile) part of sporophyll (mm); 5-maximal width of distal (sterile) part of sporophyll (mm); 6-length of distal (sterile) part of sporophyll (mm).

While studying the type-species *Tomiostrobus radiatus*, Meyen (1987) found a ligula on the sporophylls of *Tomiostrobus*. He also extracted microspores from the coalified sporangia of *Tomiostrobus.* This proved that *Tomiostrobus* belonged to the lycopods and not to the gymnosperms (Sadovnikov, 2005).

The spores extracted from the sporangia of *Tomiostrobus radiatus* were studied in detail using both optical microscopy and SEM by Yaroshenko (1988), who showed that these spores, if found in isolated state, could be assigned to the genus *Aratrisporites* Leshik emend. Playford & Dettmann (in Yaroshenko, 1988). The spores were monolete and cavate. Juvenile spores measured 15 x 20 µm in size (Pls. 5.3, 4, 6; Pl. 6.2-5), whereas, well-developed spores measured 40 x 65 µm in size, with a distinct ornamentation of sporoderm (Yaroshenko, 1988). Similar spores have been described later from the Lower Triassic of the Pechora syneclise (Yaroshenko & Golubeva, 1989).

Sadovnikov believed that the sporophylls of *Tomiostrobus radiatus* belonged to pleuromeioid plants (Pleuromeiaceae) and noted that the barks of *Pleuromeia*-like morphology were found both on the upper and lower layers of the sediments with numerous sporophylls and "cones" of *Tomiostrobus radiatus.* Since the genus *Pleuromeia* itself was not found in this locality, Sadovnikov suggested that these pleuromeioid barks belonged to *Tomiostrobus* (Sadovnikov, 1982). He also found *Tomiostrobus* to be more closely related to the genus *Pleuromeia* Corda. Sadovnikov (1982) did not compare *Tomiostrobus* and *Annalepis.*

Varied shapes of the sporophylls and their distal segments ("acute apices" or "acute-points", as mentioned by Sadovnikov, 1982), together with the "degree of protrusion" of the sporophyll margins, were used as characters for distinguishing the different species of *Tomiostrobus.*

A representative specimen having numerous sporophylls of *Tomiostrobus* "*bulbosus*" Sadovnikov, kept in the State Darwin Museum (Moscow) was studied. This specimen shows that the shape of the sporophylls, as well as their proportions can vary in high degree even in one and the same population. Both the long narrow sporophylls and relatively short wide sporophylls of different proportions do occur together. Such a high variability of morphological characters can also be observed in the monotopic "population" of the sporophylls of *Tomiostrobus radiatus*, which was characterized above. This fact prompts us to express serious doubts about the validity of the species established by Sadovnikov, i.e. *Tomiostrobus belozerovii* Sadovnikov, *T. fusiformis* Sadovnikov and *T. bulbosus* Sadovnikov. I believe, that all these three species originally described by Sadovnikov as new species of *Tomiostrobus* are junior synonyms of *Tomiostrobus radiatus* (see for additional comments: Naugolnykh & Mogutcheva, 2006).

RECONSTRUCTION OF *TOMIOSTROBUS RADIATUS* NEUBURG

The reconstruction of the general habit (growth form) of *Tomiostrobus radiatus* has been attempted considering three parameters (1) morphological interpretation and reconstruction of the sporophylls; (2) determination of the sporophyll position on the protocorm and (3) reconstruction of the protocorm itself. Most of the remains of *T. radiatus* in the collection studied are represented by isolated sporophylls, with the exception of two specimens demonstrating life disposition of the sporophylls in relation to each other. The reconstruction has been attempted in an analytical way (Naugolnykh, 2008b).

The first stage of reconstruction was less complicated, due to the presence of completely preserved sporophylls in the collection. Their morphological interpretation was relatively simple and was fulfilled without serious doubts (Figs 2f, g, 4g; Pl. 1.8; Pl. 2.2; Pl. 3.3, 4; Pl. 5.1.2). For fragmentally specimens, additional information about main modes of variability of the sporophylls was used (Fig. 10).

Generalized scheme of structure of the sporophyll is shown on the right hand side of Fig. 6. This scheme is mostly based on specimen 4851/130. The sporophyll has a well-developed distal segment (DS) very similar to the distal segments of recent *Isoetes* (Pl. 7). There are numerous air chambers or air bladders (AB) located at the basal and middle parts of the distal segment in the mesophyll tissues of the sporophyll. These air chambers are obliquely oriented to the midvein (=central vein) of the sporophyll. The margins of the air chambers are situated close to the margins of the sporophyll and inclined towards the proximal (fertile) part of the sporophyll. The sporophyll itself was slightly U-shaped in the cross section, with protruded abaxial surface.

The sporophylls, which occupied different positions on the protocorm, had a wide proximal (fertile) part of slightly different shape. The outer sporophylls were larger in size and had wider proximal parts. The inner (apical) sporophylls were of smaller size, narrower and more elongate as compared to the sporophylls of the proximal parts.

It is presumed that *Tomiostrobus radiatus* had no sterile leaves (phylloids). The sporophylls, which had no definite sporangium (Fig. 6, left; Pl. 1.4, 9; Pl. 2.4) were aborted or undeveloped, and most probably were situated closer to the protocorm apex. Such sporophylls were of smaller size, as a rule.

The sporangium (S) was located at the proximal part of the sporophyll at its adaxial surface. It had ovoid outline and was prolonged along the sporophyll axis. The margins of sporangium were covered by filmy velum, the remains of which form a narrow (not wider than 0.5 mm) limb disposed all around. The ligular pit with the ligula (L) was situated distally in 0.2-0.4 mm in relation to the sporangium. The median rib (MR) was located at the place of attachment of sporangium to the sporophylls, above the conducting strand. The median rib is often well preserved on the impressions, but when the plant was alive, this structure was very indistinct. The central conducting strand (CS) entered the base of the sporophyll and then ran through the whole sporophyll from its basal part, through fertile proximal part up to the apex of the distal segment.

The sporophylls of *Tomiostrobus radiatus* were attached to the protocorm in a spiral order. The protocorm consisted of a relatively narrow conducting cylinder (Fig. 7; Pl. 1.7) with a well-developed wide cortical layer. Closest sporophylls were partly covered by each other, subsequently covering the middle part of the adjacent sporophyll with their margins. This kind of subsequent covering of sporophylls is also a characteristic feature of *Annalepis zeillerii* (Grauvogel-Stamm & Lugardon, 2001).

As soon as the sporangia became mature, the outer sporophylls could have slightly curved from the protocorm to release spores from the sporangia. Such curved sporophylls with adult sporangia are characteristic of many extant lycopods. Examination of the well-preserved large sporophylls present in the collection with detached distal segments (detachment obviously had happened before the plant was buried in sediment), revealed that the distal segments of the adult sporophylls could have curved, then dried off and detached in a natural way, exactly as it happens in some of the species of recent *Isoetes* (Hickey; in Grauvogel-Stamm & Lugardon, 2001, p. 136).

The adult plant of *Tomiostrobus radiatus* consisted of a dense cluster of the sporophylls spirally attached to the protocorm (Fig. 8). The sporophylls had long upward oriented acute distal segments. The plant was 10-15 cm high and 8-12 cm wide. An exact number of the sporophylls on the protocorm is still unknown, but the comparison of the material in hand with the morphologically similar Early Triassic isoetalean lycopods, i.e. *Isoetes bestonii* Retallack and *I. innae* Naugolnykh & Mogutcheva, for which the completely preserved plants with the sporophylls in organic connection to the protocorm are known, allows us to suggest that the number of the sporophylls in the individual plant of *Tomiostrobus radiatus* was no less than fifty.

The general habit of the *Tomiostrobus radiatus* plant was quite similar to that of the related lycopod *Isoetes innae*, but it differs from *I. innae* in the absence of scale-like sporophylls attached to the apical part of the protocorm. Such scale-like sporophylls are typical of *I. innae*, and are also known for several recent species of *Isoetes*, resembling sporophylls of *Lepayclotes* and *Annalepis* (Grauvogel-Stamm & Lugardon, 2001).

PALAEOECOLOGY

The fossils of *Tomiostrobus radiatus* form the mono-species thanatocoenosis in clastic volcano-genetic sediments. Considering these taphonomic conditions, it is suggested that the parent plant of *Tomiostrobus radiatus*, as well as the

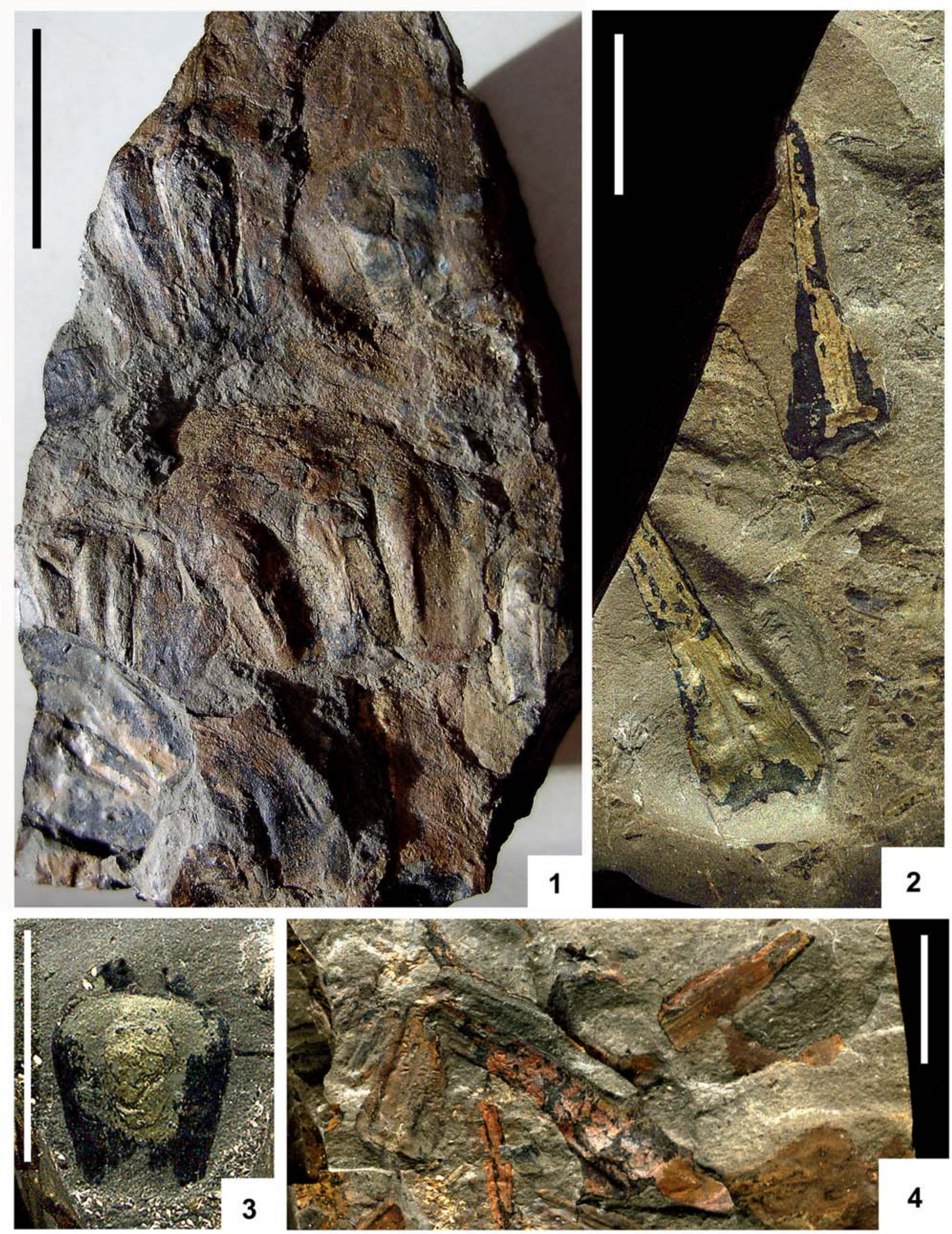

PLATE 4

Tomiostrobus radiatus Neuburg, morphology of sporophylls; 1 – 4851/161; 2 – 4851/132a; 3 – 4851/116; 4 – 4851/157. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm.

closely related species *Isoetes bestonii* (Retallack, 1997) and *I. innae*, formed pioneer communities with very loose covering, which most probably existed along the shores of low bioproductive (oligotrophic) ephemeral lakes and ponds.

Generally speaking, the genera *Pleuromeia, Tomiostrobus, Viatcheslavia, Sadovnikovia* and *Signacularia* were ecologically very similar. All of them belonged to pioneer plant communities, and were characterized by high edaphic and climatic tolerance, but at the same time they were well-adapted to dry/arid climatic conditions. This group of lycopods became extinct before the end of Triassic while competing with the other plant groups that predominated in the Mesozoic (marattialean and osmundalean ferns, corystosperms, caytonialeans, cycadophytes, ginkgophytes and conifers). Only a few representatives of this group belonging to the genus *Isoetes* had survived as "living fossils" (Ash & Pigg, 1991; Hickey, 1986; Hill, 1987; Taylor & Hickey, 1992; Pfeiffer, 1922; Pigg, 1992; Skog *et al.*, 1992).

It is a well known fact that the boundary between the Palaeozoic and the Mesozoic corresponds to the onset of the lycopods of the family Pleuromeiaceae and the synchronous decrease in taxonomical diversity among other higher plants (Wang, 1989, 1996; Retallack, 1975, 1997). A great change in taxonomical composition of fossil floras also took place at the Permian/Triassic boundary in Siberia (Mogutcheva & Naugolnykh, 2010). This change is marked by the extinction of typical Palaeozoic plants (equisetophytes of the family Tchernoviaceae) and by the appearance of numerous Mesozoic elements. The time interval of *Tomiostrobus radiatus* is precisely near the boundary layer, above the typical Permian flora and just below the Korvunchanka flora, which is characterized by usual Early Mesozoic plants: *Lobifolia, Cladophlebis, Scytophyllum, Williamsoniella, Leuthardtia, Yuccites* and *Glossophyllum* (Mogutcheva, 1973). These *Tomiostrobus radiatus*-dominated communities may be interpreted as the pioneer vegetation covering terrestrial ecosystems just after the Permian/Triassic ecosystem crisis in Early Triassic high latitude floras of North Asia.

PHYLOGENETIC CONCLUSIONS

Two alternative morphogenetic trends reflecting an adaptive process were already formed in the early phase of evolution of the lycopod families Pleuromeiaceae and Isoetaceae. In the Early Permian, the representatives of these two families were united in one relatively homogenous group. In the Late Permian, this group was differentiated and divided into two independent evolutionary lines choosing geliotropic or geotropic morphotype as the basis for further idioadaptive transformations.

Geliotropic plants of the lycopod group formed relatively dense monospecific communities in the near-water habitats in conditions of intensive natural selection and evolved in direction to get the selective preferences using relatively high stems, but without the possibility to form secondary tissues, in contrast to the Carboniferous arborescent lycopods of the order of Lepidodendrales (=Lepidocarpales Meyen, 1987). High intensity of natural selection can be due to general aridization of the climate, which took place at the end of the Permian period and the beginning of the Triassic period. This aridization was especially strong in low latitudes. Arid climatic conditions have decreased a number of relatively comfortable periodically wet habitats in the low latitudes, and because of this the plants had to survive in the communities with high competition.

The lycopods of geliotropic specialization formed the family Pleuromeiaceae. The possible ancestor of this family was the genus *Sadovnikovia* Naugolnykh from the Lower Permian (Kungurian) deposits of the Cis-Urals. The genus *Viatcheslavia* Zalessky (Late Permian, Ufimian of the Cis-Urals) originated from the genus *Sadovnikovia*. Later, in Kazanian, the genus *Signacularia* Zalessky originated from the genus *Viatcheslavia* (Zalessky, 1937; Naugolnykh & Pukhonto, 2007). The numerous species of the genus *Pleuromeia* appeared in the Early Triassic and this genus became virtually cosmopolitan. Only a few representatives of the pleuromeians and their close relatives were preserved up to the Late Triassic, for example, the genus *Ferganodendron* Dobruskina was established on the material from the Middle(?)-Upper Triassic deposits of the Madygen Locality of Kirgizstan, Middle Asia (Dobruskina, 1974).

It should be noted that the sporophyll aggregations of the genera *Pleuromeia* and *Viatcheslavia* were shaped in a different way, though we have kept both these genera in one and the same family Pleuromeiaceae (Naugolnykh, 2007).

The sporophylls in *Pleuromeia* were aggregated into a compact terminal strobilus (cone) whereas in *Viatcheslavia* they formed subsequent fertile zones segregated by wide zones of sterile leaves (Naugolnykh & Zavialova, 2004, Fig. 3). Considering the present-day lycopods as an example for methodological basis of systematics, we can see that even the genus *Huperzia* of the family Lycopodiaceae is represented by the plants both with the fertile zones and terminal strobili. Therefore, I sincerely believe, that the genera *Pleuromeia, Viatcheslavia* and *Signacularia* be united and put into one family Pleuromeiaceae sionce these have more or less natural (="botanical") taxonomical status.

Geotropic representatives of heterosporous lycopods in the Late Permian and Early Triassic formed less dense communities. These plants, as a rule, preferred higher latitudes and grew in conditions of weak evolutionary competition in habitats located along the low biologically productive oligotrophic lakes and ponds. The short protocorm was a more useful and practical organ for the geotropic lycopods in this palaeoclimatic and palaeogeographic situation, in contrast to relatively long stems of the representatives of the family Pleuromeiaceae. I think that the protocorm of geotropic

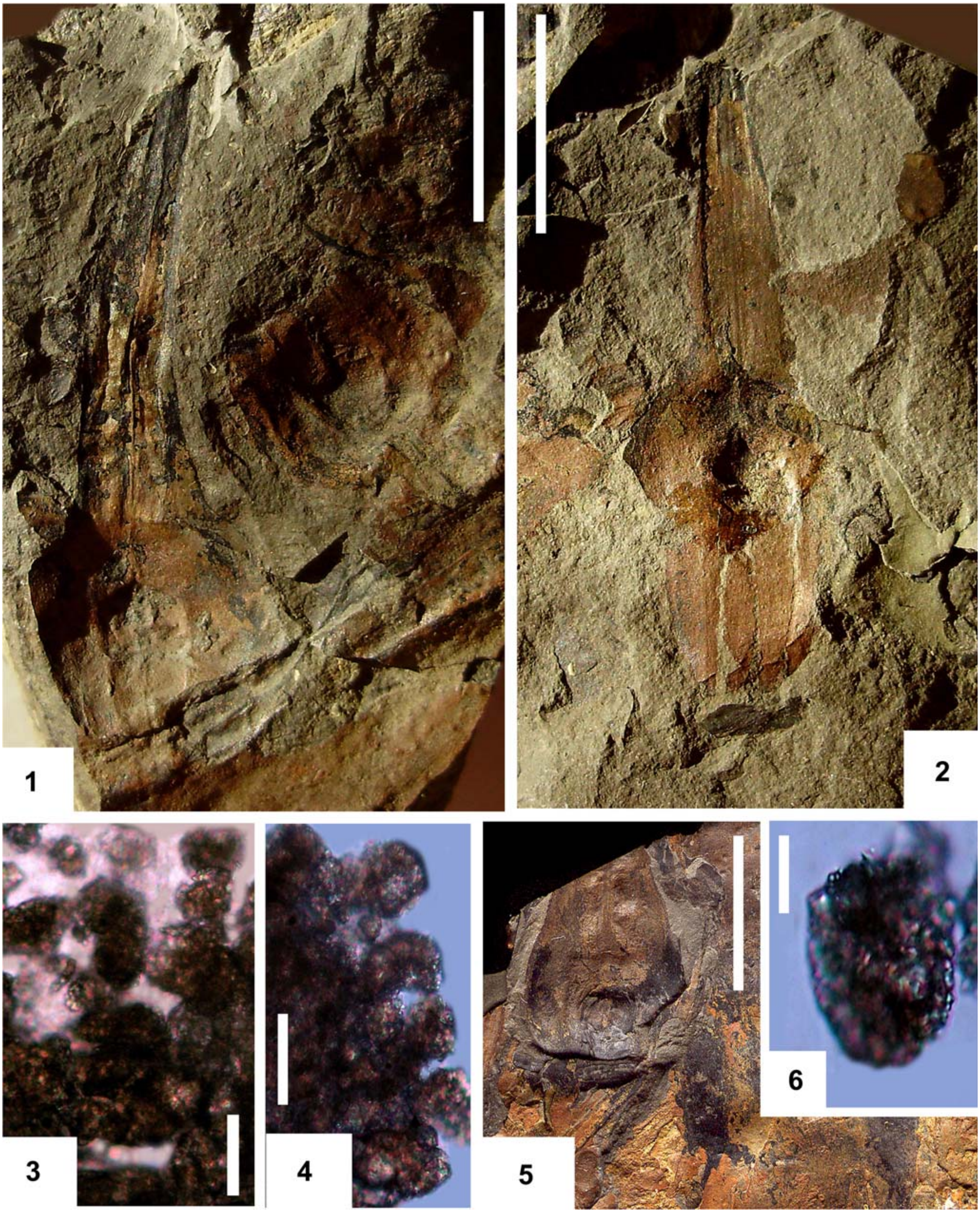

PLATE 5

Tomiostrobus radiatus Neuburg, morphology of sporophylls (1, 2, 5) and spores in situ (3, 4, 6); 1 – 4851/121; 2 – 4851/140; 3, 4, 6 – 4851/153 (macromorphology of this sporophyll see on Plate VI, fig. 1); 5 – 4851/133. Lower Triassic, Induan Stage. Babiy Kamen Locality. Scale – 1 cm (for figs 1, 2, 5); 20 μm (for figs 3, 4), 10 mkm (for fig. 6).

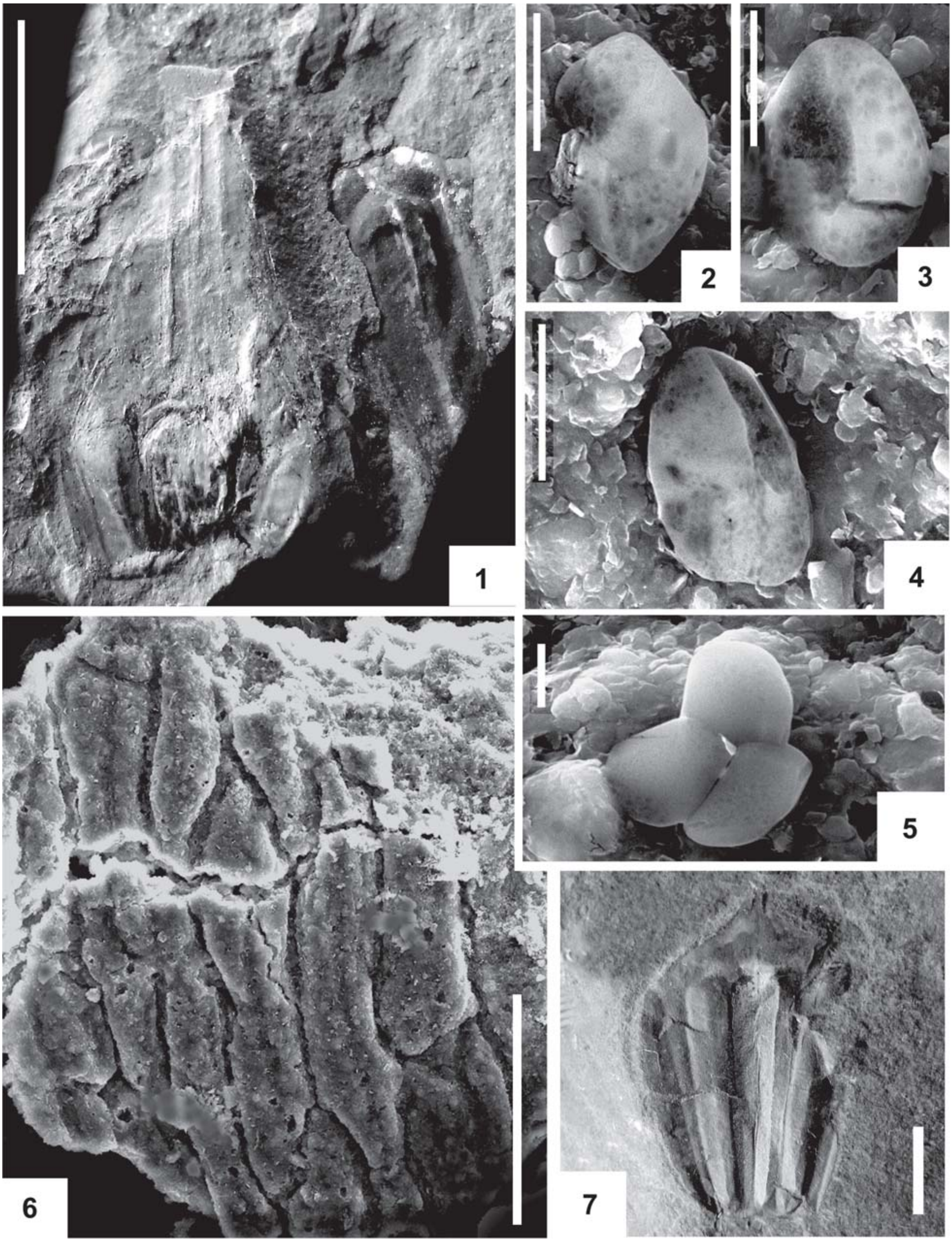

PLATE 6

Tomiostrobus radiatus Neuburg, morphology of sporophylls (1), spores in situ (2-5), cuticle (6), and morphology of *Annalepis kryshtofovichii* (Volynetz) Naugolnykh, comb. nov. (7); 1-6 – 4851/153; 7 – 4685/290 (Volynets collection). Lower Triassic, Induan Stage. Babiy Kamen Locality (1-6), Middle Triassic, Primorie (7). Scale – 1 cm (for figs 1, 7); 100 µm (for fig. 6); 10 mkm (for figs 2-5).

lycopods was not photosynthetically active and all the functions related to photosynthetic and respiration were carried out by the sporophylls with the well-developed distal segments. Common sterile leaves or the phylloids most probably were absent in the plants of this group, which was separated as an independent family Isoetaceae as early as the Early Triassic.

The most ancient true representatives of the family Isoetaceae are now known from the Lower Triassic of Australia (Retallack, 1997) and from the Tunguska Basin, Siberia (Naugolnykh & Mogutcheva, 2006). The genera *Tomiostrobus* and *Annalepis* should also be assigned to this family (Wang, 1991; Naugolnykh, 2008a).

The genus *Annalepis* Flische is widely known from the Triassic deposits in Western and Central Europe (Flische, 1910; Kelber, 1990; Kelber & Hansch, 1995; Grauvogel-Stamm, Lugardon, 2001). The sporophyll of *Annalepis* was described (but incorrectly oriented with the apex downwards as a result of misinterpretation of this fossil as a part of bennettitalean cone *Williamsoniella*) from the Ambinskian Formation (Upper Triassic, Norian) of the Russian Far-East (Volynets, 2008, Plate II, figs. 3, 4). A new combination for this plant is suggested below: *Annalepis kryshtofovichii* (Volynets) Naugolnykh, com. nov. Pl. 6.7, Holotype: 4685/290, figured by Volynets, 2008, Plate II, Figs 3, 4; see also here the photograph of the holotype after reinvestigation made by the present author: Plate VII, Fig. 7. Basionym: *Williamsoniella kryshtofovichii* Volynetz, 2008, p. 160, Plate II, Figs. 3, 4.

One more geotropic heterosporous lycopod quite similar to *Annalepis* was described from the Triassic of North America by another specific name *Lepacyclotes circularis* Bock (Bock, 1969).

Grauvogel-Stamm and Lugardon (2001) while reviewing morphology, systematics and diversity of the representatives of the genera *Pleuromeia* and *Annalepis* concluded that during the Triassic period these genera had prevailed among lycopods, and were closely interconnected to each other. The genus *Annalepis* was indicated as a possible ancestor of the family Isoetaceae. The genus *Isoetites* (nom. illeg; see for further comments and details: Chaloner, 1967) was used by Grauvogel-Stamm and Lugardon not as a nomenclatural variant for the fossil *Isoetes*, but as a putative intermediate genus between *Annalepis* and *Isoetes.*

According to Snigirevskaya (1989) the sporophylls of *Pleuromeia* could have borne a long distal segment, which dried out and detached as soon as the sporangium became an adult. However, after studying a large collection of the sporophylls of *Pleuromeia rossica*, including the sporophylls of different sizes and ontogenetic stages of development, isolated and aggregated in cones (strobili) it was found that there is no real evidence for the existence of such terminal segment. No distal segments on the sporophylls of *Pleuromeia rossica* were shown on the whole-plant reconstruction of *Pleuromeia rossica* (Naugolnykh, 2008a, b). Grauvogel-Stamm and Lugardon (2001) also doubted the presence of the terminal distal segments of the sporophylls in *Pleuromeia*. They opined that the genera *Pleuromeia* and *Annalepis* were very close to each other and even taxonomically connected by their generic boundaries through such short forms as *Pleuromeia sanxianensis* Meng of 5 cm hight. More than half of this plant is its strobilus. However, even such forms (with the strongly reduced stem) have sporophylls of ovoid shape with round apex, always characteristic of true *Pleuromeia.* In other words, such reduction of the sporophyte of *Pleuromeia sanxianensis* doesn’t lead to transformation of the stem into the true protocorm typical of *Isoetes* and its close relatives, such as *Annalepis, Lepacyclotes* and *Tomiostrobus.*

The families Isoetaceae and Pleuromeiaceae as they are understood in the present paper (Fig. 9) are well-segregated both in macromorphology and microspore structure. The microspores of Pleuromeiaceae are cavate, always with a distinct trilete mark, having more or less smooth surface in the proximal side. Distal side of the spores bears small spines or glabrae and scabrae. The microspores of representatives of the family Isoetaceae are mostly monolete. The sporoderm of the microspores of Isoetaceae is strongly sculptured both on the proximal and distal surfaces. These spores can be easily recognized even if they are isolated. Such isolated isoetalean microspores refer to the genus *Aratrisporites* (Yaroshenko, 1988). Examination of ultrastructure of different representatives of the families Pleuromeiaceae and Isoetaceae points to the common origin of both families (Grauvogel-Stamm & Lugardon, 2001; Naugolnykh & Zavialova, 2004). Both these families are separated from other groups of lycopods in their sporoderm ultrastructure.

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REFERENCES

Ash SR & Pigg KB 1991. New Jurassic *Isoetites* (Isoetales) from the Wallowa Terrane in Hells Canyon, Oregon and Idaho. American Journal of Botany 78: 1636-1642.

PLATE 7

Isoetes lacustris L., recent plant; Herbarium of the Laboratory of Palaeofloristics, Geological Institute of Russian Academy of Sciences. Scale – 1 cm.

Bock W 1969. The American Triassic flora and global distribution. Geology of Central Resources 3-4: 1-406.

Chaloner WG 1967. Lycophyta. E. Boureau (ed.). Traite de Paleobotanique. Paris: Masson et Cie. P. 437-802.

Dobruskina IA 1974. Triassic lepidophytes. Paleontological journal (Moscow) 3: 111-124.

Dobruskina IA 1985. Questions of systematics of Triassic lycopods. Paleontological journal (Moscow) 3: 90-104.

Fefilova LA 1983. Fossil plants from the stratotype of the Byzovskaya Formation from the Middle Pechora Basin. Annals of Institute of Geology of the Komi Filial of the USSR Academy of Sciences 43: 46-54.

Flische P 1910. Flore fossile du Trias en Lorraine et Franche-Comte. Paris et Nancy: Berger-Levrault. 297 p.

Grauvogel-Stamm L & Lugardon B 2001. The Triassic Lycopsids *Pleuromeia* and *Annalepis*: Relationships, evolution and origin. American Fern Journal 91: 115-149.

Hickey JR 1986. The early evolutionary and morphological diversity of *Isoetes*, with descriptions of two new Neotropical species. Systematic Botany 11: 309-321.

Hill RS 1987. Tertiary *Isoetes* from Tasmania. Alcheringa 12: 157-162.

Kelber K-P 1990. Die versunkene Pflanzenwelt aus den Deltasumpfen Mainfrankens vor 230 Millionen Jahren. Makrofloren aus dem Germanischen Unterkeuper. Beringeria1 : 1-67.

Kelber K-P & Hansch W 1995. Keuperpflanzen. Die Entraetsehung einer uber 200 Millionen Jahre alten Flora. Museo 11: 1-157.

Lotsy JP 1909. Vortrage uber botanische Stemmesgeschichte. Zweiter Band: Cormophyta Zoidogamia. Jena. Gustav Fischer Verlag. 902 pp.

Magdefrau K 1931. Zur Morphologie und phylogenetischen Bedeutung der fossilien Pflanzengattung *Pleuromeia*. Beihefte Botanische Centralblatter 48: 119-140.

Meyen SV 1966. Cordaiteans of the Upper Paleozoic of North Eurasia (morphology, epidermal structure, systematics and stratigraphical significance). Moscow. Nauka. 184 p. (in Russian).

Meyen SV 1987. Fundamentals of Palaeobotany. London: Chapman & Hall. 432 p.

Mogutcheva NK 1973. Lower Triassic flora of the Tunguska Basin. Moscow: Nedra. 160 p.

Mogutcheva NK & Naugolnykh SV 2010. *Gagariostrobus cylindricus* (Prynada) Mogutcheva and the Permian–Triassic Ecosystem Flora Reorganization in the Tunguska Basin. Stratigraphy and Geological Correlation 18: 31-41.

Naugolnykh SV 2007. Permian floras of the Urals. Moscow: Geos. 322 pp. (Transactions of the Geological institute of RAS, Vol. 524).

Naugolnykh SV 2008a. The Great Break in history of the plant world. Mineral Observer. Mineralogical Almanac 13c: 36-50.

Naugolnykh SV 2008b. Reconstructions of fossil plants. Mnogogrannaya Geologia. Vol. II. Sanct-Petersbourg: VNIIOceanology. P. 47-56 (in Russian).

Naugolnykh SV & Mogutcheva NK 2006. A new representative of lycopods (Lycopodiopsida) from the Lower Triassic of the Tungusca syneclise (Siberian platform). News of Palaeontology and Stratigraphy. Supplement to "Geology and Geophysics" 8: 81-93.

Naugolnykh SV & Pukhonto SK 2007. Morphology and systematic position of the Permian lycopod *Signacularia* Zalessky, 1929. VM-Novitates, News from the V.I. Vernadsky Geological Museum 14: 20 pp.

Naugolnykh SV & Zavialova NE 2004. *Densoisporites polaznaensis* sp. nov.: with comments on its relation to *Viatcheslavia vorcutensis* Zalessky. Palaeobotanist 53: 21-33.

Neuburg MF 1936. On the stratigraphy of the coal-bearing deposits of the Kuznetsk Basin. Izvestia Akademii Nauk SSSR. Ser. Geologicheskaya 4: 469-510.

Pfeiffer NE 1922. Monograph of the Isoetaceae. Annals of the Missouri Botanical Garden 9: 79-232.

Pigg KB 1992. Evolution of isoetalean lycopsids. Annals of the Missouri Botanical Garden 79: 589-612.

Retallack GJ 1975. The life and times of a Triassic lycopod. Alcheringa 1: 3-29.

Retallack GJ 1997. Earliest Triassic origin of *Isoetes* and quillwort evolutionary radiation. Journal of Paleontology 71: 500-521.

Sadovnikov GN 1982. Morphology, systematics and distribution of the genus *Tomiostrobus*. Paleontological journal (Moscow) 1: 100-109.

Sadovnikov GN 2005. Six steps together. In memorium to Sergei Viktorovich Meyen (to 70th anniversary). Transactions of International Palaeobotanical Conference. Vol. 3. Moscow: Geos. P. 56-59 (in Russian).

Serezhnikova EA 2008. Attaching adaptation of sedentary organisms from the Vendian of the Southern-Eastern White Sea area and Siberian platform. Moscow: Paleontological Institute of RAS preprint. 24 p. (in Russian).

Skog JE, Dilcher DL & Potter FW 1992. A new species of *Isoetes* from the mid-Cretaceous Dakota Group of Kansas and Nebraska. American Fern Journal 82: 151-161.

Snigirevskaya NS 1989. Once more about status of the genus *Pleuromeia* Corda. Questions of palaeofloristics and stratigraphy. Leningrad: Nauka. P. 74-88 (in Russian).

Taylor CW & Hickey RJ 1992. Habitat, evolution and speciation in *Isoetes*. Annals of the Missouri Botanical Garden 79: 613-622.

Volynets EB 2008. ***Williamsoniella kryshtofovichii.*** Triassic and Jurassic of the Sikhote-Alin. Book 2. Vocanogenetic-sedimentary complex, palaeobiogeography. Vladivostok: Dalnauka. P. 160 (in Rusian).

Vladimirovich VP, Lebedev VM, Popov UN, Radczeko GP & Schvedov NA 1967. Stratigraphy of Triassic deposits of the Middle Siberia. Stratigraphy of Mesozoic and Palaeozoic of the Middle Siberia. Moscow: Nauka. P. 7-30 (in Russian).

Wang Z-Q 1989. Gigantic palaeobotanical events in North China. Acta Palaeontologica Sinica 28: 314-343.

Wang Z-Q 1991. Advances on the Permo-Triassic lycopsids in north China. I. An *Isoetes* from the mid-Triassic in northern Shanxi Province. Palaeontographica. Abt. B 222: 1-30.

Wang Z-Q 1996. Recovery of vegetation from the terminal Permian mass extinction in North China. Review of Palaeobotany and Palynology 91: 121-142.

Yaroshenko OP 1988. Microspores from the sporangium of the lycopod *Tomiostrobus radiatus* Neuburg (Lower Triassic, Kuzbass). Palynology in USSR. Articles of Soviet palynologists for VII International Congress, Brisben, Australia. Novosibirsk: Nauka. P. 77-79. (in Russian).

Yaroshenko OP & Golubeva LP 1989. New species of spores from the Lower Triassic of the Pechora syneclise. Paleontological journal (Moscow) 4: 101-108.

Zalessky, 1937. Sur la distinction de l'etage Bardien dans le Permien de l'Oural et sur sa flore fossile. Problems of Paleontology 2-3: 37-101.