*The Palaeobotanist 55(2006). 1-14*
*0031-0174/2006 $2.00*

# *Moscvostrobus* - a new genus of Carboniferous lycopods from the Moscow Region (Russia)

SERGE V. NAUGOLNYKH[1] AND OLGA A. ORLOVA[2]

[1]*Laboratory of Paleofloristics, Geological Institute, Russian Academy of Sciences, Pyzhevsky per. 7, Moscow 109017, Russia. Email: naugolnykh@rambler.ru*
[2]*Department of Paleontology, Geological Faculty, Moscow State University, Leninskie Gory, Moscow119992, Russia. Email: oorlova@geol.msu.ru*

(Received 27 February, 2005; revised version accepted 22 February, 2006)

**ABSTRACT**

Naugolnykh SV & Orlova OA 2006. *Moscvostrobus* - a new genus of Carboniferous lycopods from the Moscow Region (Russia). The Palaeobotanist 55(1-3): 1-14.

A new taxon of heterosporous lycopsid strobilus, *Moscvostrobus mirabile* gen. et sp. nov. is described from a clay shale of the Serpukhovian (Namurian, Lower Carboniferous) deposits in the Zaborie quarry, located near the town of Serpukhov, Moscow Region, Russia. The strobilus is preserved in natural connection to the leafy branch, attached to a shoot. The outer surface of the shoot has a thin longitudinal ribbing. Small subtriangular leaves are helically arranged on the shoot. The strobilus has a spherical shape, which is unusual for Carboniferous lycopods. The apex is round and base is wedge-shaped. Three lanceolate sporophylls with acuminate, flexuous tips are clearly seen in the upper part of the strobilus. The edges of the sporophylls are serrate in their upper part. Mega- and microsporangia are irregularly arranged. The microspores are of *Lycospora*-type. Megaspores are gulate. *Moscvostrobus mirabile* could be compared to strobili of the Lepidocarpaceae, but exact systematic position of the genus is still problematic.

**Key-words**—Carboniferous, Russian Platform, Lycophytes, Heterosporic plant.

## *मॉस्क्वोस्ट्रोबस* - मास्को क्षेत्र (रूस) से प्राप्त कार्बनी लाइकोपॉड्स का नवीन वंश

सर्गी वी. नौगोलनीख एवं ओल्गा ए. ओर्लोवा

**सारांश**

रूस के मास्को क्षेत्र में सेर्पुखोव कस्बे के निकट स्थापित ज़बोरी खान में सेर्पुखोविअँ (नेमुरियन, निम्न कार्बनी) निक्षेपों के मृत्तिका शेल से प्राप्त विषमजीवाणु लाइकोप्सिड शंकु, *मॉस्क्वोस्ट्रोबस मिराबाइल* नव वंश की नवप्रजाति का एक नवीन वर्गक वकर्णत किया गया है। प्ररोह से जुड़े शंकु प्राकृतिक संबंध रूपी घनी शाखा से परिरक्षित होते है। प्ररोह के बाह्य पृष्ठ पर पतले अनुदैर्ध्य सिरे हैं। छोटी उपत्रिकोणीय पतृतियाँ प्ररोह पर कुंडलिनुमा का व्यवस्थित हैं। शंकु की आकृति गोलाकार है, जो कि कार्बनी लाइकोपाड्स हेतु असामान्य है। शिखर गोला है तथा आधार फानाकार है। लंबाग्र, टेढ़ी-मेढ़ी नोंक सहित तीन भालाकार बीजाणुपर्ण शंकु के ऊपरी भाग में स्पष्ट रूप से देखे गए हैं। बीजाणुपर्णों के कोने उनके ऊपरी भाग में ?तेदार हैं। स्थूल एवं सूक्ष्म बीजाणुधानी असामान्य रूप से व्यवस्थित हैं।

सूक्ष्मबीजाणु *लायकोस्पोरा* तरह के हैं। स्थूलबीजाणु गुलेट हैं। लीपिडोकार्पेसीए के शंकुधारी से *मॉस्क्वोस्ट्रोबस मिराबाइल* की तुलना की जा सकती थी किंतु वंश की सही सुव्यवस्थित स्थिति अभी भी जटिल है।

**संकेत-शब्द**—कार्बनी, रूसी प्लेटफार्म, लायकोफाइटीस, विषमबीजाणु पौधा।

## INTRODUCTION

LYCOPODIOPSIDA was one of the most widely spread and dominant higher plant group during the Late Paleozoic. Representatives of Lycopodiopsida were especially important constituents of the equatorial Carboniferous vegetation. They were well adapted to the warm humid climatic conditions. These plants formed quite often monodominant communities and played an essential part in peat-accumulating process (DiMichele & Phillips, 1985).

Carboniferous lepidophytes (arborescent lycopods) are well studied, especially the anatomically preserved permineralised material of coal-balls known from coalfields in Europe and North America. General morphology and the anatomical structure of these plants have been examined in detail (Brack-Hanes & Thomas, 1983; DiMichele & Phillips, 1985, 1994;Long, 1967; Nemejc, 1954; Phillips & DiMichele, 1992, etc).

Although there is not much published information on lepidophytes from antitropical areas of that time of Angaraland and Gondwana (Anderson & Anderson, 1985; Gutierrez *et al.*, 1986; Lemoigne & Brown, 1980; Rayner, 1986), a notable contribution on Angaran lepidophytes was made by Meyen (1976).

The present paper deals with new strobilus *Moscvostrobus mirabile* gen. et sp. nov. The studied material was collected from the Zaborie quarry located near the town of Serpukhov, Moscow Region, Russia.

## GEOLOGY OF THE AREA

The Zaborie quarry is located in the southern part of Moscow Sineclise on the left bank of the Oka River near Myrniy Village (Fig. 1), south of the town of Serpukhov (54°54' N, 37°27' E). The Zaborie quarry had been extensively exploited for over 150 years and had been known as a rich source of Lower Carboniferous fossils, mostly marine invertebrates. In the late 1990s, the quarry was closed down, but its outcrops comprising about 30 meters of Serpukhovian Stage are still open for collecting geological samples.

The Zaborie quarry sequence represents a complete thickness of the Serpukhovian Stage and was proposed as a lectostratotype of the Serpukhovian (Gibshman, 2001; Kabanov, 2003). According to modern stratigraphic nomenclature, the Serpukhovian Stage is divided into two substages: Lower Serpukhovian and Upper Serpukhovian (Makhlina *et al.*, 1993). In Moscow Sineclise the Lower Serpukhovian deposits include Tarusian and the Steshevian Horizons. The Seventh pocket of the sequence is represented by facies of "Steshevian lagoon" i.e., black clays with thin layers of limestones and dolomites at the pocket base. Stratigraphically the Seventh pocket belongs to foraminifer zone *Eostaffellina decurta* (Gibshman, 2001), conodont zone *Lochriea nodosa* (Nikolaeva *et al.*, 2002).

The strobilus under analysis was found in the upper part of the Steshevian Horizon in the 39th layer of the Seventh pocket (Fig. 2).

Layer No 39 is 1.1 m thick and represented by dark-grey clayey schist, not disintegrating in water, rather similar to stiff paper. Small ichnofossils of *Zoophycos* Massalongo and *Teichichnus* Seilacher often occur in the layer. There are also isolated valves of brachiopods *Eomarginifera lobata* (Sow.) and graptolites (*Dictyonema* spp.). The specimen of *Moscvostrobus mirabile* was found right in the middle part of this layer.

## MATERIAL AND METHODS

The solitary specimen used in this study is a coalified strobilus, which is heavily deformed and laterally compressed. The strobilus is preserved in natural connection to the leafy shoot. In some places, where the coalified material broke into crumbs and separated, one could see external imprint of the strobilus surface.

A fragment of the coalified material (5 x 5 mm) was taken from basal part of the sporophylls left of the

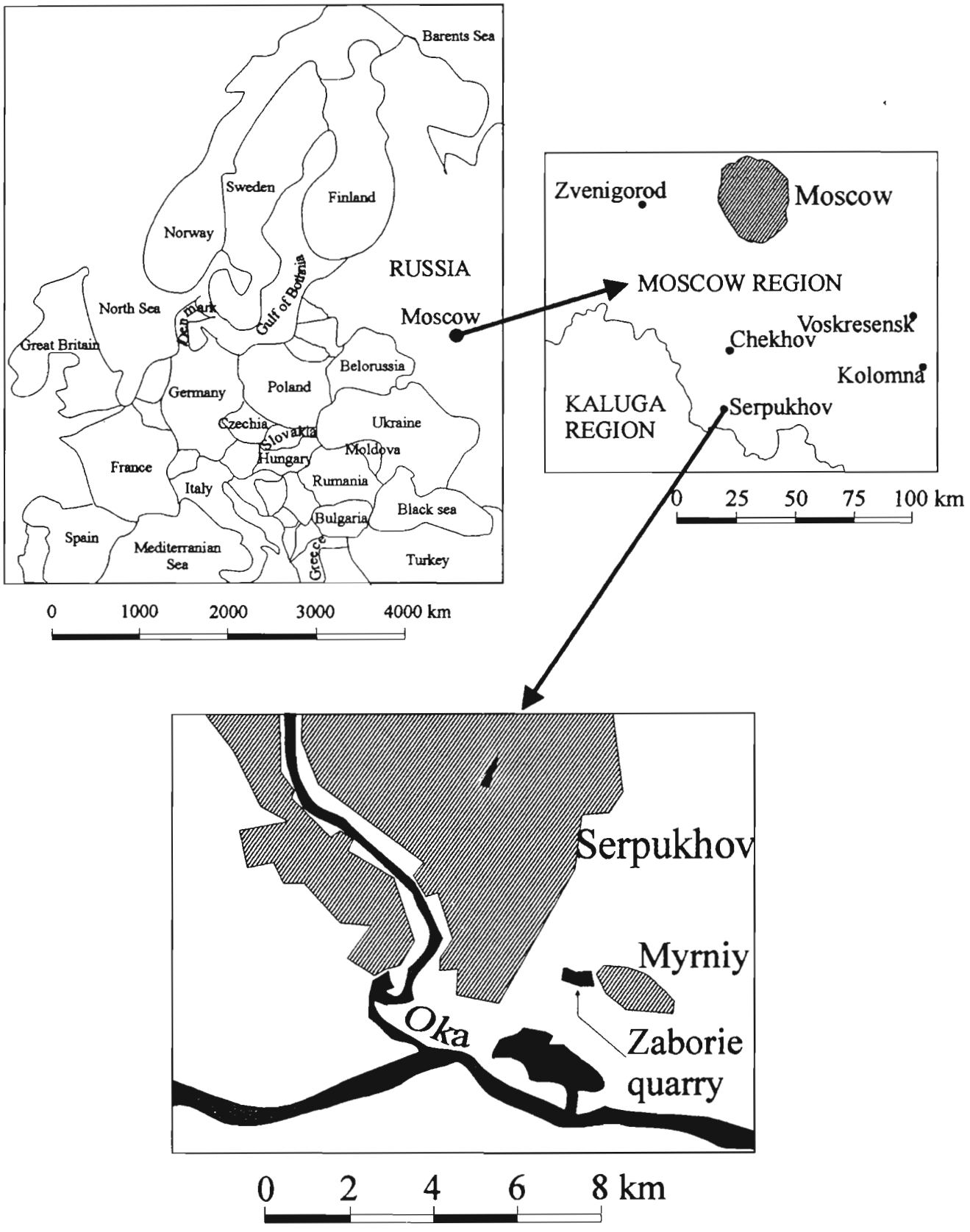


Fig. 1—Geographic position of the locality Zaborie quarry.

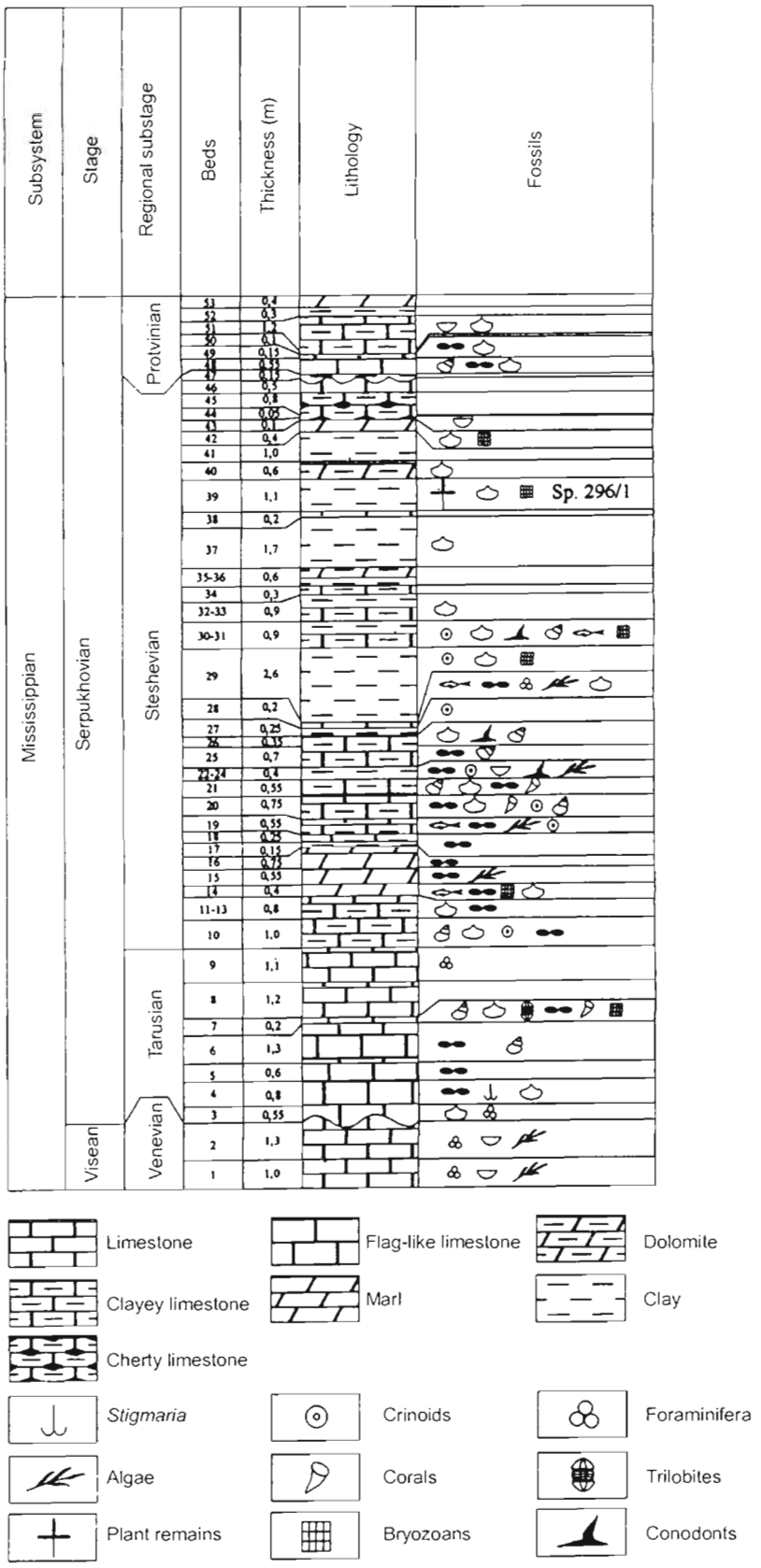


Fig. 2—Stratigraphic column and level of layer No. 39, where the specimen of *Moscvostrobus mirabile* was found.

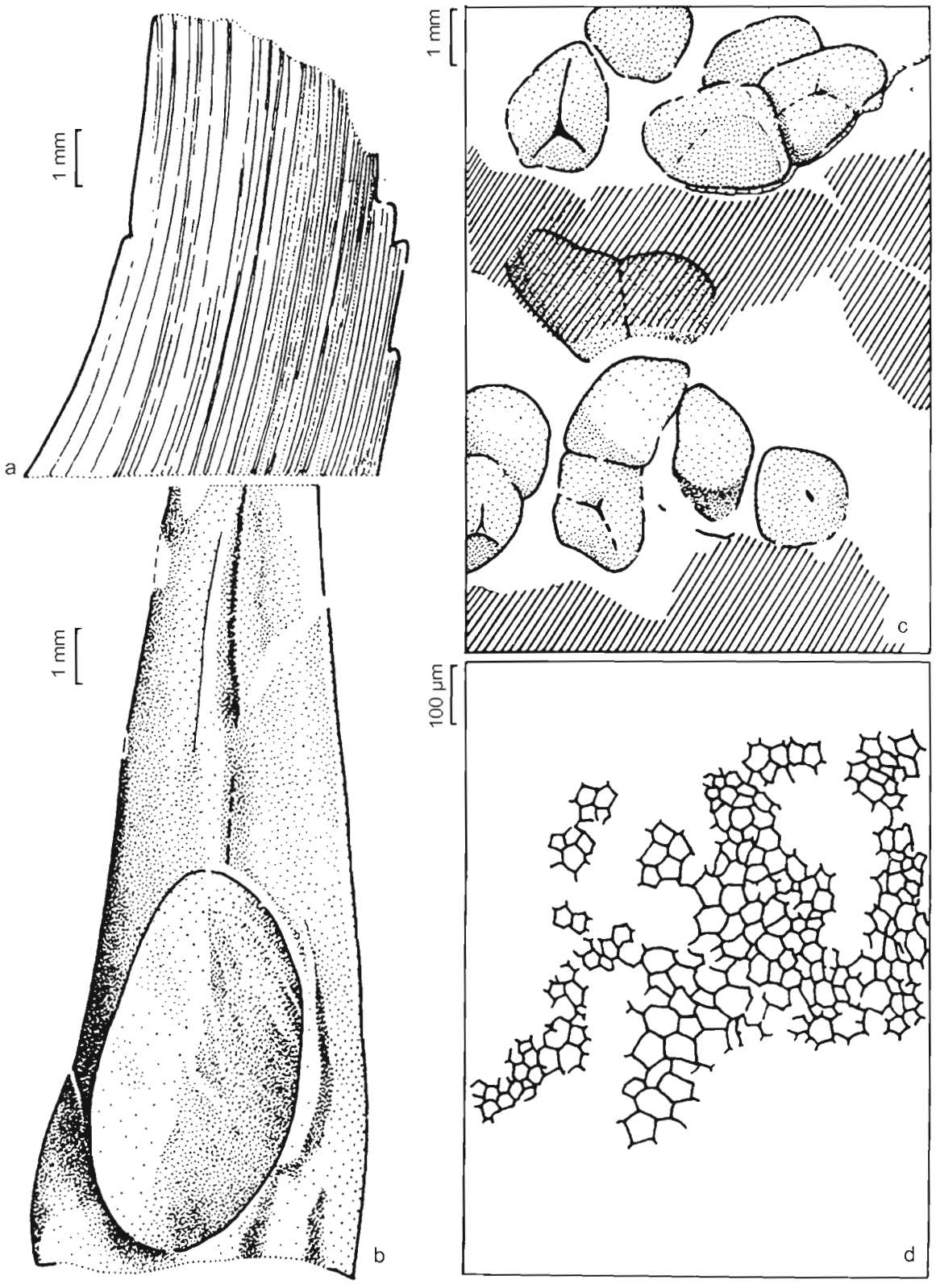


Fig. 3—*Moscvostrobus mirabile* specimen No. 296/1, (a) apical part of the sporophyll with serrated margin; (b) basal part of the sporophyll with the sporangium (based on Pl. 2.3); (c) the aggregation of megaspores into partially preserved megasporangia; (d) epidermal layer of adaxial surface of the megasporophyll.

axis of the strobilus, comprising a fragment of sporangium and part of the sterile foliar segment of the sporophyll. The fragment was macerated in the Schultz reagent. The cuticles obtained were washed in distilled water, dried and mounted on the stubs with acryl glue for study under SEM (Stereoscan 600). Line drawings of morphological features were made after tracing photographs (Fig. 3).

Authors used higher plant classification proposed by Meyen (1987).

## SYSTEMATICS

**Class—LYCOPODIOPSIDA** Bartling, 1831

**Order—ISOETALES** Prantl, 1874

**Family—INDETERMINATE**

**Genus—MOSCVOSTROBUS** gen. nov.

**Type species—*Moscvostrobus mirabile*** sp. nov.

(Pl. 1-3)

*Diagnosis*—Heterosporous lycopod strobilus of spherical shape; sporophylls longitudinally striated in sterile part. Distal parts of sterile sporophylls relatively large, lanceolate with acute apices. Sporophyll margin in apical part serrate. Ovoid sporangia adaxially attached to proximal part of sporophylls. Megasporangia contain more than one (normally three to four) megaspore tetrad of *Sublagenicula*-type. Microsporangia contain microspores of *Lycospora*-type. Mega- and microsporangia are disposed on the fertile axis irregularly to each other.

*Comparison*—The new genus differs from the most similar genera in its spherical shape, considerably large size and serrate apical margins of the sporophylls. Important features of some comparable Carboniferous lepidophytes are shown on Fig. 5.

*Etymology*—After Moscow City.

***Moscvostrobus mirabile*** sp. nov.

(Pl. 1-3; Figs 3, 4)

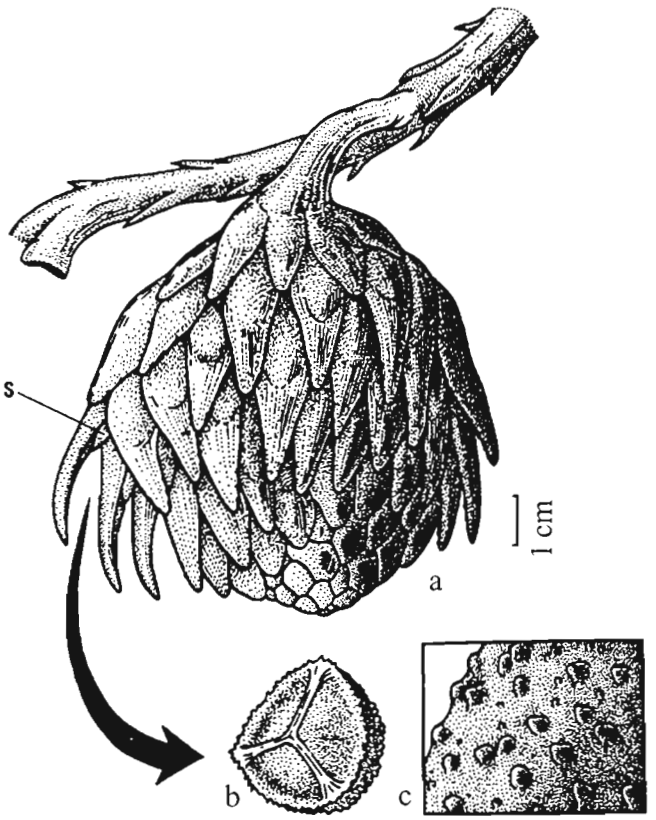


Fig. 4— (a) Reconstruction of general morphology of the strobilus *Moscvostrobus mirabile,* sporangium(S); (b) the microspore of *Lycospora*-type (not to scale); (c) the sculpture on distal surface of a microspore (not to scale).

*Diagnosis*—Strobilus large, spherical, laterally disposed on a branching stem. Basal part of strobilus cuneate, wedge-like; apical part round. Sterile part of lanceolate sporophylls relatively long and wide and apices serrated. Surface of sterile part of sporophylls longitudinally striated. Strobilus heterosporous. Sporangia located in proximal parts of sporophylls and adaxially attached to them. Sporangia on average 5-8 mm long and 3-5 mm wide. Each megasporangium containing more than one (three or four) megaspore tetrad of *Sublagenicula*-type. Microsporangia contain microspores of *Lycospora*-type. Megasporangia and microsporangia are disposed on the fertile axis irregularly.

*Description*—The fossil is a fragment of stem measuring 12 mm wide and 120 mm long. A large spherical strobilus is attached on a small pedicel (Pl. 1. 1). Outer surface of the stem has fine longitudinal ribs

| Genera | General shape of strobilus | Type of strobilus | Type of *in situ* spores | Age | Geographical distribution | Parent plant | Reference |
|---|---|---|---|---|---|---|---|
| *Lepidostrobus* (Brongniart) Brack-Hanes & Thomas, 1983 | Cylindrical | Microstrobilus | *Lycospora* | Carboniferous-Permian | Global | *Lepidodendron* | Bek & Opluštil, 2004 |
| *Flemingites* (Carruthers) Brack-Hanes & Thomas, 1983 | Cylindrical | Heterostrobilus | *Lagenicula or Lagenioisporites; Lycospora* | Carboniferous | USA, England, Russia, Germany, France | *Paralycopodites (=Anabathra)* | DiMichele & Phillips, 1994 |
| *Achlamydocarpon* Schumacher-Lambry, 1966 | Cylindrical | Megastrobilus, Microstrobilus | *Cystosporites, Granasporites* | Carboniferous | USA, Ukraine, Belgium, England | *Diaphorodendron, Synchysidendron, Hizemodendron* | Long, 1967; DiMichele & Phillips, 1994; Bateman *et al.*, 1992 |
| *Lepidocarpon* Scott, 1900 | Cylindrical | Megastrobilus | *Cystosporites* | Carboniferous | France, Czech Republic, England, USA | *Lepidofloyos* | Bateman *et al.*, 1992 |
| *Mazocarpon* Benson, 1918 (=compression *Sigillariostrobus*) | Cylindrical | Microstrobilus, Megastrobilus | *Crassispora, Laevigatosporites* or *Tuberculatisporites* | Carboniferous | England, Holland, USA | *Sigillaria* | DiMichele & Phillips, 1994 |
| *Omphalophloios* (White, 1898) Brousmiche-Delcambre *et al.*, 1995 | Fertile zone | Bisporangiate fertile zone | *Densosporites, Cristatisporites* | Late Carboniferous | Poland, Czech Republic, USA, Spain, England | *Bodeodendron* | Bek & Strakova, 1996 |
| *Chaloneria* Pigg & Rothwell, 1983 | Fertile zone | Bisporangiate fertile zone | *Endosporites, Valvisisporites* | Late Carboniferous | USA | *Chaloneria (=Polysporia)* | Pigg & Rothwell, 1983 |
| *Miadesmia* Benson, 1918 | Fertile zone | Monosporangiate fertile zone | unknown shape | Late Carboniferous | England | *Miadesmia* | Thomas, 1997 |
| *Carinostrobus* Baxter, 1971 | Cylindrical | Microstrobilus | *Acanthotriletes* or *Granulatisporites* | Late Carboniferous | USA | unknown | Baxter, 1971 |
| *Spencerites* Scott emend. Drabkova, Bek & Opluštil, 2004 | Fertile zone | Isosporangiate fertile zone | *Spencerites* | Late Carboniferous | England, Czech Republic, USA | *Spencerites* | Drabkova, Bek & Opluštil, 2004 |
| *Moscvostrobus* gen. nov. | Spherical | Heterostrobilus | *Lycospora, Sublagenicula* | Early Carboniferous | Russia | unknown | this paper |

Fig. 5—General features of important Carboniferous lepidophytes.


**PLATE 1**

| Equatorial view | | Polar view | | |
|---|---|---|---|---|
| Length (μm) | Width (μm) | Length (μm) | Width (μm) | Height of gula (μm) |
| 600 | 500 | 1700 | 1150 | 250 |
| 800 | 600 | 1100 | 750 | 238 |
| 800 | 450 | 500 | 275 | 50 |
| 750 | 600 | 450 | 250 | 50 |
| 1100 | 900 | 1000 | 750 | 150 |
| 2000 | 2000 | 2000 | 1800 | 300 |
| 2000 | 1800 | 2000 | 1500 | 300 |

Fig. 6—Sizes of megaspores extracted from *Moscvostrobus mirabile*.

and furrows, 0.5 mm wide. These ribs probably are peridermal in nature and could correspond to mechanical tissues. Partly preserved scale-like leaves, subtriangular in shape with wide bases are seen on some parts of the stem. General morphology of these leaves are similar to short subtriangular leaves of the Lower Carboniferous lepidophyte *Stansburya petersenii* Tidwell and Jennings, 1986. The stem is slightly curved. Two small branchlets lie laterally in distal and proximal parts of the stem. Proximal branchlet is the pedicel of the strobilus. These branchlets are at a distance of 9.5 cm from each other. The branchlets arise from the main stem at an angle of 60°.

The strobilus is 116 mm long, maximum width of the strobilus is near its upper part and measures 92 mm. Apex of the strobilus is round and basal part is cuneate wedge-like (Pl. 1.5). Maximum width of the pedicel is 6 mm.

Sporophylls are not clearly seen mostly because of considerable deformation of the strobilus. Nonetheless, three relatively better preserved sporophylls are observed at the upper right side of the strobilus (Pl. 1.2-4). The lowest sporophyll is preserved almost completely (Pl. 1.3). Sporophylls are lanceolate in shape with acute apices which slightly curve upwards. Sterile part of the sporophyll is 30 mm long and 10-11 mm wide. Margins of the sporophylls are serrate in the apical parts (Pl. 2.1, Fig. 3a). Surface of the sporophylls bears fine longitudinal ribs. Distance between neighbouring ribs averages 0.8 mm.

There is one relatively well preserved microsporangium located at the lower part of the strobilus near the base. Microsporangium is ovoid, 5 mm long x 1.3 mm wide and adaxially attached to the microsporophyll. It is connected with the fertile axis of the strobilus at right angle. There are numerous microspores inside the distal part of the sporangium; some spores form round aggregations, while others are isolated.

Microspores extracted from the macerated sporangium are circular in shape and usually up to 20-25 μm in diameter (Pl. 3.1, 3-6), but some spores are up to 40 μm in diameter (Pl. 3.2). Proximal surface of the spores bears a trilete scar; rays short, 1/4 of spore diameter (Pl. 3.1, 2). Proximal surface of the microspores is smooth (Pl. 3.1), more rarely it could be sculptured with small granules (Pl. 3.2). The microspores have 2-4 μm wide cingulum (Pl. 3.1, 5, 6). Distal surface is ornamented by small differently developed granules (Pl. 3.3-6) of 0.3-0.4 μm. Morphologically the microspores correspond to diagnosis of dispersed spore genus *Lycospora* (Schopf *et al.*) Somers, 1972. Diversity of the genus is quite high, even for spores extracted from one and the same sporangium (Balbach, 1966).

There is an imprint of megasporangium near the basal part of the strobilus. It is 6.5 mm long and 3 mm wide. One incomplete tetrad of pear-shaped megaspores is seen inside the megasporangium. Megaspores bear near-apical extension (subgula) 50 μm high. Megaspores are small, 500-800 μm long and 275-450 μm wide.

On the upper part of the strobilus there is a relatively distinct imprint of another round to ovoid, 6.5 mm long and 4.5 mm wide megasporangium. It contains

←

**PLATE 1**

*Moscvostrobus mirabile* gen. et sp. nov., Specimen No. 296/1.

1. General view. x 1.1.
2-4. Sporophyll morphology. x 3.
5. Structure of the strobilus basal part. x 3.

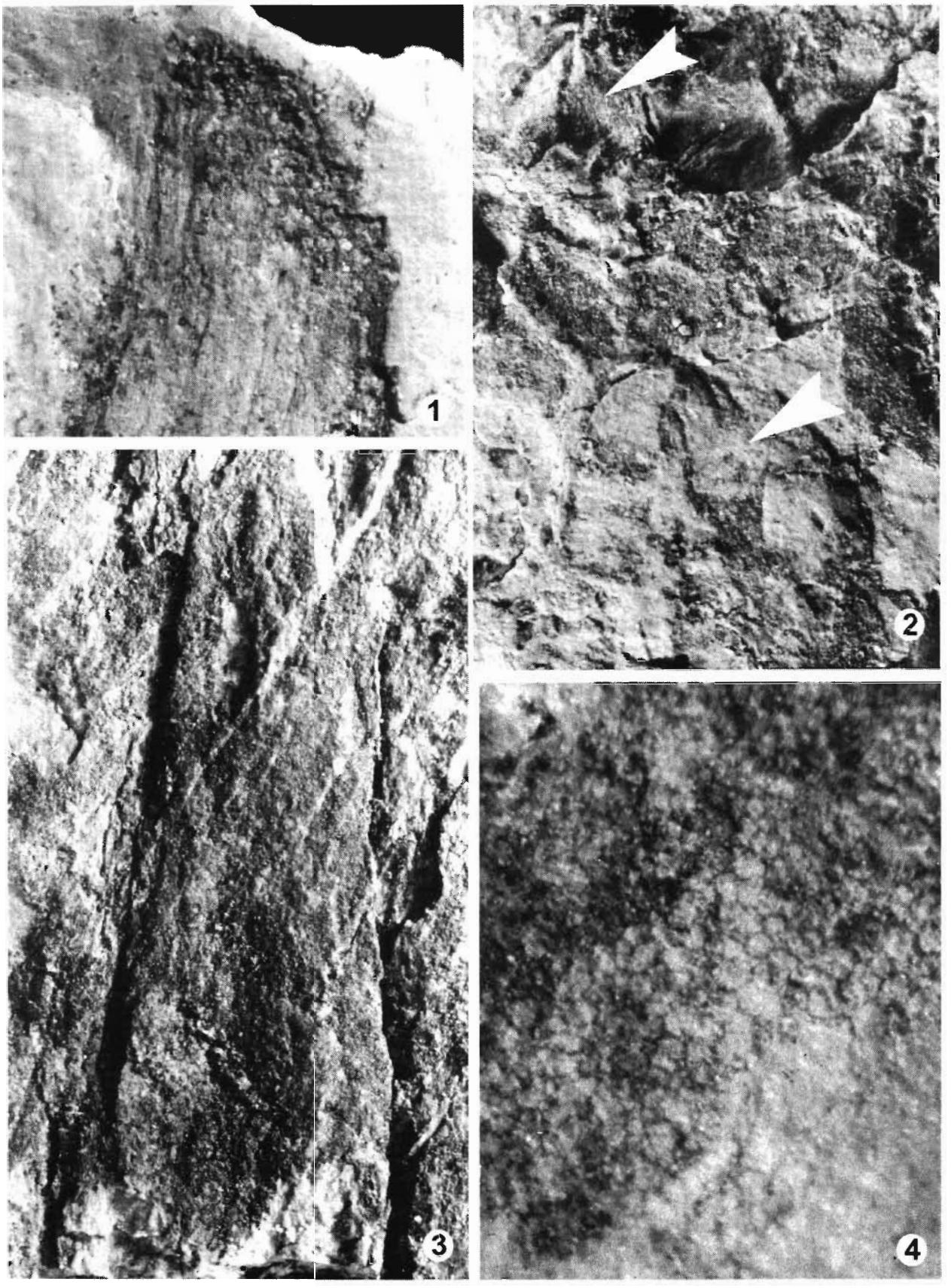


**PLATE 2**

larger megaspores measuring nearly 2000 μm in equatorial diameter. Megaspores are partly united into tetrads; partly disposed in ones or twos. Similar aggregation of the megaspores exists in the megasporangium of neighbouring sporophyll (Pl. 2.2, Fig. 3c). Outlines of the megaspores are round or subtriangular in equatorial view. Laesura is distinct with three rays. Length of the rays is almost equal to the spore radius. Curvatures are not well developed. The megaspore surface is smooth. According to the morphological features mentioned above, the megaspores could be assigned to *Sublagenicula* (Dybova-Jachowicz *et al.*) Oshurkova, 2001.

Impression of the megaspores and their tetrads of the same morphology were found in other parts of the strobilus. It may be noted that the megaspores widely vary in size (Fig. 6). Relatively small megaspores (450-500 μm) are characteristic of basal part of the strobilus, while larger megaspores (2000 μm) are found in the middle and apical parts.

*Holotype*—Specimen No. 296/1, Plates 1-3, Figures 3-4.

*Repository*—Department of Paleontology, Geological Faculty, Moscow State University, Moscow.

*Occurrence*—Russia, Moscow Region, in the vicinity of the town of Serpukhov, the Zaborie quarry; Lower Carboniferous, Serpukhovian Stage, Steshevian Horizon.

*Etymology*—From mirabilis (Latin), wonderful.

*Discussion*—In its general architecture and the structure of micro- and megaspores, *Moscvostrobus mirabile* is similar to several genera of the Lepidodendrales (Chaloner, 1953, 1967). Therefore this taxon could be attributed to Lepidodendrales or Isoetales *sensu lato* (according to Meyen, 1987). Using the system of lepidophyte families proposed by Thomas and Brack-Hanes (1984), *Moscvostrobus* could be compared to Lepidocarpaceae, but the systematic position of the genus at family level is still problematic. General shape of the sporophylls of *Moscvostrobus* is quite typical of Lepidocarpaceae. Close similarity exists in proportions and structure of sterile part of the sporophylls between *M. mirabile* and *Lepidostrobophyllum alatum* Boulter, 1968 but the latter species lacks apical serration. Microspores of *M. mirabile* are very similar to the microspores extracted from the type specimen of *Lepidostrobus ornatus* (Brongniart) Brack-Hanes & Thomas, 1983, though the species of *Lepidostrobus* have cylindrical shape of the strobili. There are many features common between microspores of *M. mirabile* and *Lepidostrobus binneyanus* Arber (Thomas, 1970, 1988), the species characteristic of European Westphalian B. But the proximal side of microspores of *L. binneyanus* has feebly developed granules (spores of this morphotype commonly assignable to *Lycospora perforata* Bharadwaj & Venkatachala, 1958). General shape, size and sculpture on proximal side of the microspores of *M. mirabile* compare closely to *Lycospora noctuina* extracted from the sporangia of *Lepidostrobus haslingdenensis* (Thomas & Dytko, 1980), but differ in the absence of papillae on equator in the former.

Several forms of *Lepidostrobus* figured in the monograph of Nemejc (1954), compare closely to *M. mirabile* having relatively broad sporophylls and ovoid-cylindric strobilus rather than narrow-cylindric shape of the strobili. The taxa *Lepidostrobus sternbergii* Corda emend. Bek and Opluštil (2004, pl. V. 4-6); *L. nemejcii* Bek and Opluštil (2004, pl. V. 7); *L. cernuus* Sternberg (1826, pl. IX, X); and some sporophylls of *Lepidostrobophyllum lanceolatum* Lindley & Hutton (1831-1833, pl. VIII, 7-9) also compare with present strobilus, but all of these forms have non-serrate margins in the apical part of the sporophyll. Beside, Nemejc based speciation of *Lepidostrobus* strobili only on the

←

**PLATE 2**

*Moscvostrobus mirabile* gen. et sp. nov., Specimen No. 296/1.

1, 3. Sporophyll morphology. x 10.

2. The aggregations of megaspores in partially distroyed megasporangia. x 10.

4. Epidermal structure of the adaxial surface of the megasporophyll. x 100.

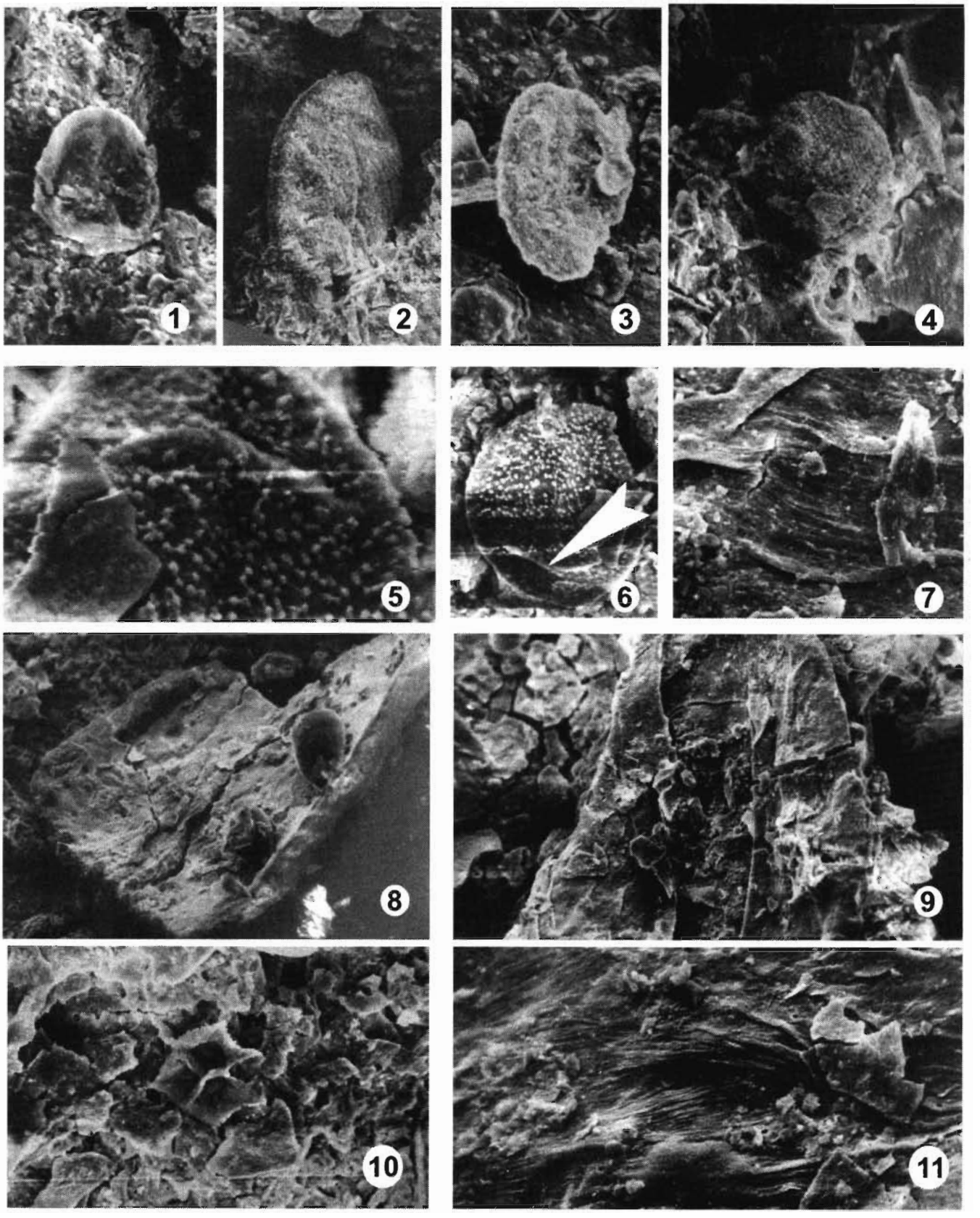


**PLATE 3**

cone morphology without considering *in situ* microspores. Bek and Opluštil (2004) re-examined Nemejc's material and transferred some specimens from *Lepidostrobus sternbergii* to *L. nemejcii* based on their spore characters.

Fertile stems of *Lepidodendropsis devoogdi* Jongmans, 1954 were described from the Lower Carboniferous deposits from Peru. Some of the stems bear megasporangia with megaspores preserved *in situ* (Jongmans, 1954, pl. 21. 22, 22a). Size and structure of the megasporangia resemble *M. mirabile*, but the sporophylls of *L. devoogdi* are not aggregated in compact strobili and formed fertile zones that sometime occurs on dichotomously branched stems.

***Acknowledgements***—*We are grateful to Dr A.L. Jurina (Moscow State University) for valuable comments. Dr H.K. Maheshwari (Lucknow, India) and Dr S.Opluštil (Prague, Czech Republic) are gratefully acknowledged for their constructive and important advice and reviewing the manuscript. The study was supported by the Grant of President of Russian Federation No. MD-1703.2005.5; Russian Fund for Basic Researches, Project 03-04-49351, State Grant for Scientific Schools of Russia, Project 372.2006.5, Program 25 of Basic Researches of the Presidium of the Russian Academy of "Factors of biosphere evolution".*

## REFERENCES

Anderson JM & Anderson HM 1985. Palaeoflora of Southern Africa. Prodromus of South African megafloras, Devonian to Lower Cretaceous. Rotterdam. A.A. Balkema. 423 pp.

Balbach MK 1966. Microspore variation in *Lepidostrobus* and comparison with *Lycospora*. Micropaleontology 12 : 334-342.

Bateman RM, DiMichele WA & Willard DA 1992. Experimental cladistic analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica : An essay on paleobotanical phylogenetics. Annales of Missouri Botanical Garden 79 : 500-559.

Baxter RW 1971. *Carinostrobus foresmani*, a new lycopod cone genus from the middle Pennsylvanian of Kansas. Palaeontographica B 134 : 124-130.

Bek J & Strakova M 1996. Carboniferous fertile branch *Sporangiostrobus feistmantelii* (O. Feistmantel) Nemejc and its miospores from the Kladno Basin, Bohemian Massif. Acta musei Nationalis Pragae. Series B. Historia Naturalis 51 : 37-51.

Bek J & Opluštil S 2004. Palaeoecological constraints of some *Lepidostrobus* cones and their parent plants from the Late Palaeozoic continental basins of the Czech Republic. Review of Palaeobotany and Palynology 131 : 49-89.

Benson MJ 1918. *Mazocarpon* of the structural *Sigillariostrobus*. Annales of Botany 32 : 569-590.

Bharadwaj DC & Venkatachala BS 1958. Miofloristic evidence on the boundary between the Carboniferous and Permian systems in Pfalz (W. Germany). Palaeobotanist 6 : 1-11.

Boulter MC 1968. A species of compressed lycopod sporophyll from the Upper Coal Measures of Somerset. Palaeontology 11 : 445-457.

Brack-Hanes SD & Thomas BA 1983. A re-examination of *Lepidostrobus* Brongniart. Botanical Journal of the Linnean Society 86 : 125-133.

Brousmiche-Delcambre C, Mercier D & Coquel R 1995. Implications stratigraphiques de la revision de la flore Carbonifere au Sud de Brianson. Comptes rendus de l'Academie des Sciences, Paris 320 (IIa) : 335-340.

Chaloner WG 1953. On the megaspores of four species of *Lepidostrobus*. Annals of Botany (N.S.) 17 : 264 pp.

Chaloner WG 1967. Lycophyta. *In*: Boureau ME (Editor)—Traite de Paleobotanique. II. Bryophyta, Psilophyta, Lycophyta. Masson & Cie. Paris : 434-845.

DiMichele WA & Phillips TL 1985. Arborescent lycopod reproduction and paleoecology in coal-swamp environment of a late Middle Pennsylvanian Age (Herrin Coal, Illinois, U.S.A.). Review of Palaeobotany and Palynology 44 : 1-26.

DiMichele WA & Phillips TL 1994. Paleobotanical and paleoecological constrains on models of peat formation in the Late Carboniferous of Euramerica. Palaeogeography Palaeoclimatology Palaeoecology 106 : 39-90.

←

**PLATE 3**

*Moscvostrobus mirabile* gen. et sp. nov., Specimen No. 296/1.

1-6. Microspores preserved *in situ*. 1, x 1500; 2, x 750. 3, 4, 6. proximal side of microspores. x 1500; a cingulum (marked by arrow on 6). 5. Distal side of microspores with the granules. x 2900.

7,10,11. 7. Epidermal structure of the sporophylls. x 1500. 10. Cuticle with stoma and partially preserved mesophyll tissues. x 750; 11. Fine longitudinal striation of cuticle of distal sporophyll part. x 1500.

8, 9. Fragments of sporangia. 8. Basal part of small, weakly developed sporangium. x 37; 9. Apical part of small, feebly developed sporangium. x 37.

Drabkova J, Bek J & Opluštil S 2004. The first compression fossils of *Spencerites* (Scott) emend., and its isospores, from the Bolsovian (Pennsylvanian) of the Kladno-Rakovnik and Radnice basins, Czech Republic. Review of Palaeobotany and Palynology 130 : 59-88.

Gibshman NB 2001. Foraminiferal biostratigraphy of the Serpukhovian Stage stratotype (Zaborie quarry, Moscow Basin). Newsletter on Carboniferous Stratigraphy 19 : 31-34.

Gutierrez PR, Cesari SN & Limarino CO 1986. *Bumbudendron versiforme*, a new lycophyte species from the Late Paleozoic of Argentina. Review of Palaeobotany and Palynology 46 : 377-386.

Jongmans WJ 1954. The Carboniferous flora of Peru. Bulletin of the British Museum (Natural History). Geology 2 : 191-223.

Kabanov PB 2003. The stratotype of the Serpukhovian Stage in the Zaborie quarry. Part 1. Lithofacies description. Stratigraphy. Geological Correlation 11 : 20-38 (in Russian).

Lemoigne Y & Brown JT 1980. Sur une flore a Glossopteridopsida et Lycopsida de Nabie (Sud-Ouest Africain). Geobios 13 : 541-553.

Lindley J & Hutton W 1831-1833. The fossil flora of Great Britain, on figures and descriptions of the vegetable remains found in a fossil state in this country. James Ridgway. London 218 pp.

Long AG 1967. Some specimens of *Mazocarpon*, *Achlamydocarpon* and *Cystosporites* from the Lower Carboniferous rocks of Berwickshire. Transactions of the Royal Society of Edinburgh 67 : 359-372.

Makhlina MK, Vdovenko MV, Alekseev AS, Byvsheva TV, Donakova LM, Zhulitova VE, Kononova LI, Umnova NI & Shik EM 1993. Lower Carboniferous of the Moscow Syneclise and Voronezh Anteclise. Nauka. Moscow : 3-98 (in Russian).

Meyen SV 1976. Carboniferous and Permian lepidophytes of Angaraland. Palaeontographica B 157: 112-157.

Meyen SV 1987. Fundamentals of Palaeobotany. Chapman and Hall. London. 432 pp.

Nemejc F 1954. Taxonomical studies on the strobili of the Lepidodendraceae of the coal districts of Central Bohemia. Acta Musei Nationalis Pragae. Vol. 10, B. No 5. Geologia et Palaeontologia 3 :1-84.

Nikolaeva SV, Gibshman NB, Kulagina EI, Barskov IS, Pazukhin VN 2002. Correlation of the Visean-Serpukhovian boundary in its type region (Moscow Basin) and a proposal of boundary markers (ammonoids, foraminifers, conodonts). Newsletter on Carboniferous Stratigraphy 20 : 16-21.

Oshurkova MV 2001. Carboniferous megaspores. Systematics, Biostratigraphic Significance. VSEGEI Press, St.-Petersburg. 112 pp. (in Russian).

Phillips TL & DiMichele WA 1992. Comparative ecology and life-history biology of arborescent lycopsids in Late Carboniferous swamps of Euramerica. Annals of Missouri Botanical Garden 79 : 560-588.

Pigg KB & Rothwell GW 1983. *Chaloneria* gen. nov.; heterosporous lycophytes from the Pennsylvanian of North America. Botanical Gazette 144 : 132-147.

Rayner RJ 1986. *Azaniadendron*, a new genus of lycopod from South Africa. Review of Palaeobotany and Palynology 47 : 129-143.

Schumacher-Lambry J 1966. Etude d'un cone de Lepidocarpaceae du houiller belge : *Achlamydocarpon belgicum* gen. et sp. nov. Bruxelles : Palais des Academies 27 pp.

Scott DH 1900. On the occurrence of a seed-like fructification in certain Palaeozoic lycopods. Annales of Botany 14 : 713-717.

Somers Y 1972. Revision du genre *Lycospora* W. et B. Microfossiles Organiques du Paleozoicque. 5. Spores. Centre National Recherche Scientifique. CIMP, Paris : 7-110.

Sternberg G 1826. Essai d'un Expose Geognostico-Botanique de la Flore du Monde primitif. Christophe Ernest Bench. Ratisbonne. 217 pp.

Thomas BA 1970. A new specimen of *Lepidostrobus binneyanus* from the Westphalian B of Yorkshire. Pollen et Spores 12 : 217-234.

Thomas BA 1988. The fine structure of the Carboniferous lycophyte microspore *Lycospora perforata* Bharadwaj and Venkatachala. Pollen et Spores 30 : 81-88.

Thomas BA 1997. Upper Carboniferous herbaceous lycopsids. Review of Palaeobotany and Palynology 95 : 129-153.

Thomas BA & Brack-Hanes SD 1984. A new approach to family groupings in the lycophytes. Taxon 33 : 247-255.

Thomas BA & Dytko A 1980. *Lepidostrobus haslingdenensis*: a new species from the Lancashire Millstone Grit. Geological Journal 15 : 137-142.

Tidwell WD & Jennings JR 1986. *Stansburya petersenii* gen. et sp. nov., an anatomically preserved lycopod from the Desert Limestone (Mississippian) of Utah. Palaeontographica B 198 : 1-11.