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Svalbardia from Givetian of Central Russia (Voronezh Region): leaf morphology and spores from sporangium

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ABSTRACT

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The new combination *Svalbardia furcihasta* (Krassilov *et al.*) Jurina, comb. nov. from Givetian of Voronezh region of Central Russia is described. Micro–and megaspores isolated from the sporangia of this plant, along with the taxa of dispersed miospores are discussed. The characters which are important for species diagnosis of the genus *Svalbardia* are discussed and the stratigraphic position of certain species of *Svalbardia* is clarified.

Key–words—*Svalbardia*, Givetian, Central Russia, Leaf morphology, Spores in situ, Dispersed miospores.

केन्द्रीय रूस (वोरोनेझ क्षेत्र) के गिवेशियन से प्राप्त *स्वालबर्डिया* : पर्ण आकारिकी एवं बीजाणुधानी से प्राप्त बीजाणु

अलेफ्टिना एल. जुरीना एवं मरीना जी. रसकाटोवा

सारांश

केन्द्रीय रूस में वोरोनेझ क्षेत्र के गिवेशियन से प्राप्त नव संयोजन *स्वालबर्डिया फुर्सीहास्ता* (क्रेसीलोव व अन्य) जुरीना का वर्णन किया गया है। इस पादप के स्पोरेंजिया से प्राप्त एकल सूक्ष्म एवं गुरूबीजाणुओं के साथ–साथ परिक्षिप्त सूक्ष्मबीजाणुओं के वर्गकों की चर्चा की गई है। *स्वालबर्डिया* वंश के लक्षणों के निदान, जो इनकी प्रजातियों के लिए महत्वपूर्ण है, पर चर्चा की गई है और *स्वालबर्डिया* की निश्चित प्रजाति की स्तरिकी स्थिति को स्पष्ट किया गया है।

सूचक शब्द—*स्वालबर्डिया*, गिवेशियन, केन्द्रीय रूस, पर्ण आकारिकी, बीजाणु स्वस्थाने, परिक्षिप्त सूक्ष्मबीजाणु।

INTRODUCTION

THE monotypic genus *Tanaitis* was proposed by the authors (Krassilov *et al.*, 1987) for the plant remains from the Upper Devonian of Pavlovsk Quarry in the Voronezh region (Central Russia). Its general appearance is arhaeopteridalean like. The fertile part and spores of *Tanaitis* are similar to any kind of *Archaeopteris* Dawson, 1871, and the terminal sterile appendages are more similar to the appendages of *Aneurophytales*. According to the authors, it was supposed to be an intermediate position of genus *Tanaitis* between the two orders of progymnosperms: *Archaeopteridales* and *Aneurophytales*. There was a short comparison between the fertile parts of the genera *Tanaitis*, *Rellimia* Leclercq & Bonamo, 1973, *Tetraxylopteris* Beck, 1957 and *Oocampsa* Andrews *et al.* 1975. Since then, the genus *Tanaitis,* was not discussed in the literature. Only Snigirevskaya (2000) briefly mentioned that the structure of generative organs of this genus may be identical with the generative organs of genus *Archaeopteris.*

The aim of our research is re–studying the common and detail structure of *Tanaitis* and its type species *T. furcihasta*: its leaf morphology, spores in situ, dispersed miospores from matrix rocks and the stratigraphic position of the remains. Generic and species membership of megaspores from the megasporangia of this plant was revised. During the present study it was found that the genus *Tanaitis* is synonym with genus *Svalbardia* Høeg, 1942. Identification of the main characteristics of species of the genus *Svalbardia* have also been undertaken.

Studying of *Svalbardia* is of great interest because it is a plant with unusual leaf morphology; however, it is rarely found in the Devonian sediments. There are currently only 11 known finds of *Svalbardia*: 7 in Europe (Norway, Denmark, Germany, Scotland, Latvia, Ukraine, the north of Russia), 2 in the Asian part of Russia (Kuzbass, the South of Western Siberia) and 2 in North America (U.S.A. and Canada). In Central Russia, *Svalbardia* was not previously observed. The species of *S. furcihasta* described here represents the first proof of *Svalbardia* in a new region and the locality of this genus. Every new find adds to the details of the structure as there is not yet complete understanding regarding the general structure of this genus.

CRITERIA FOR SUBSTITUTION OF THE GENERIC NAME TANAITIS KRASSILOV *et al.* 1987

Brief mention should be made of the terms used for description of the leaf structures. Till 1960 all

Fig. 1—Geographical position of Pavlovsk Quarry.

Fig. 2—Common prospect of Pavlovsk Quarry.

archaeopteridalean plants were described by terms: frond, pinna, pinnule. Carluccio *et al.* (1966), Beck (1970, 1971) showed that the anatomy of the rachis and pinna of the genus *Archaeopteris* is similar to the anatomy of a stem and it is characterized by radial vascular system; frond tends to flatten and terminal appendages arranged spirally. They concluded that the frond of *Archaeopteris* is not a typical compound leaf–frond and, most likely, the planated branch system. After these convincing anatomic researches it becomes possible to use the term "leaf" in the characteristic of terminal appendages of archaeopteridalean reminiscent of the frond. We follow this point of view.

As the main distinctive characters of the genus *Tanaitis* the following were specified (Krassilov *et al.*, 1987):

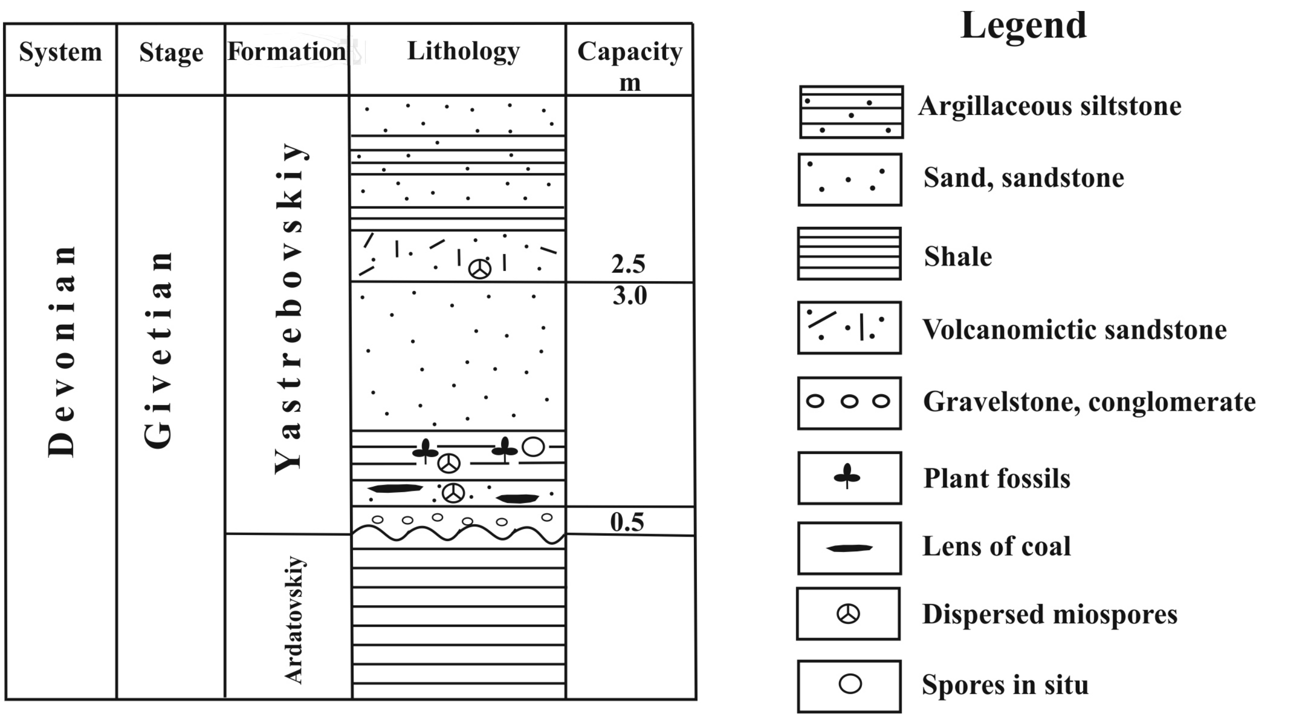

Fig. 3—Stratigraphic column of Yastrebovskaya Formation (West wall of Pavlovsk Quarry)

(1) three–dimensional system of branching with a spiral arrangement of branches; (2) proximal and distal parts of the branches bear sterile terminal appendages; (3) sterile terminal appendages unwebbed which are not dorsiventral; (4) fertile appendages consisting of single or couple of upright sporangia, being attached by a short pedicel to the acropetal part of a sporophyll; (5) mixed arrangement of the micro–and megasporangia on fertile branches; micro–and megaspores never mixed up in one sporangium (numbering of signs ours, according to a description order in the primary article).

The combination of the specified diagnostic characters is typical for the external morphology of the order *Archaeopteridales*. For the genus *Tanaitis*, only one of the essential characters of archaeopteridalean plants–eustele structure of axes is not specific. However, many palaeobotanists, based on a big rarity in the fossil preservation of anatomical structure of axes, interpreted the above features of the external structure, especially characters (1–2), (4–5) as indicating affiliation to *Archaeopteridales* (Andrews *et al.*, 1965; Beck, 1970, 1971; Bonamo, 1975; Carluccio *et al.*, 1966; Gensel & Andrews, 1984; Kenrick & Fairon–Demaret, 1991; Meyen, 1984, 1987; Schmalhausen, 1894; Scheckler, 1978; Snigirevskaya, 1995, 2000; Taylor *et al.*, 2009; Zimmermann, 1930). The order of *Archaeopteridales* is one of three in the class *Progymnospermopsida* which was founded by Beck (1960). According to the modern classification (Carluccio *et al.*, 1966; Bonamo, 1975; Matten, 1981; Meyen, 1987; Taylor *et al.*, 2009 and all) the order *Archaeopteridales* includes three genera, that are distinguished by external morphology; *Archaeopteris* Dawson, 1871; *Eddya* Beck, 1967 and *Svalbardia* Høeg, 1942. Regarding the last two genera there is no consensus. Some of the authors consider them as synonyms of the genus *Archaeopteri*s, but other consider them as independent genera. Following Carluccio *et al.*, (1966), Matten (1981), Schweitzer (1999) and many other researchers we consider the genus *Svalbardia* independent and accept it as a form–genus. The main characters in determining the genus, as indicated by these researchers that should be considered are the presence of unwebbed leaves, lobes or segments which are often arranged in different planes. We completely share this opinion and follow it regarding the establishment of the genus *Svalbardia* (Jurina & Raskatova, 2012). The genus *Eddya* (Beck, 1967) is characterized by a wedge–shaped, entire, flabelliform leaf lamina with a fanlike venation. It is believed that the plants of this genus represent a sporeling of *Archaeopteris* (Meyen, 1987). The genus *Eddya* is excluded from our analysis.

Generic characters, on which the genus *Tanaitis* was based, especially signs (1–2), (4–5), answer the Archaeopteridales characters. The described objects on the basis of sign 3 (sterile terminal appendages unwebbed without dorsiventral signs) belong to the genus *Svalbardia.* In establishing the genus *Tanaitis* (Krassilov *et al.*, 1987) the sign (3) described briefly. This genus was compared with other genera and sign (3) was paid not enough attention.

We consider the genus *Tanaitis* (Krassilov *et al.*, 1987) as a synonym of the genus *Svalbardia* (Høeg, 1942) and transfer the type species of the genus *Tanaitis* to the genus *Svalbardia* as *S. furcihasta* (Krassilov *et al.*) Jurina, comb. nov.

MATERIAL AND METHODS

The studied material is from the Devonian deposits of the Pavlovsk Quarry, located 15 km south–east from Pavlovsk in the Voronezh region, on the right bank of the Don River, in Central Russia (Figs 1, 2). *Tanaitis furcihasta*, now *Svalbardia furcihasta*, occurs in the Upper Devonian (Lower Frasnian), but the position in the section and connection with a certain formation were not specified (Krassilov *et al.*, 1987). M. Raskatova (1995) has refined the stratigraphic affiliation of *Svalbardia furcihasta* to Yastrebovskaya Formation, which belongs to the Lower Frasnian and has described the section of the Yastrebovskaya Formation in the western wall in the Pavlovsk Quarry in detail (Raskatova, 2004). In this outcrop the base of the section is represented by gravelstones or, rarely, conglomerates lying on the rocks of the Ardatovskaya Formation (Fig. 3). Above the gravelstones lies a pack of grey–brown sandstones up to 2.5–3.0 m thick with a few layers of clays and argillaceous siltstones. In the base of the pack of sandstones, the fossils of *Svalbardia furcihasta* occur. Fragments of plants are randomly oriented and confined to the surface of the sandstone strata. On some surface layers there are numerous plant detritus (about 5–7 cm), which form the curved, discontinuous lenses of coal. The coarse–grained sandstones contain particles of volcanic basic rocks. The total thickness of Yastrebovskaya Formation in this section is 4 m. As the Pavlovsk Quarry is presently quarried for granite, it is possible that this section is not completely preserved.

M. Raskatova (2004) has studied dispersed miospores from the layer which contained *Svalbardia furcihasta*. She has shown their conformity to miospores belonging to the palynological Subzone *Ancyrospora incisa–Geminospora micromanifesta* (IM) and the *Contagisporites optivus–Spelaeotriletes krestovnikovii* Zone which was placed at

PLATE 1 →

Sporangia and spores of *Svalbardia furcihasta* (Krassilov *et al.*) Jurina, comb. nov. from the Givetian of the Voronezh Region, LM, SEM.

1. Megasporangium with megaspores, SEM.
2. Fertile appendages showing megasporangia (arrow), LM.
3. Megasporangium, LM.
4. Megaspore from megasporangium (1), LM.
5. Fertile appendages showing microsporangia (arrow), LM.
6. Microsporangium, SEM.
7. Microsporangium (details of sculpture 6), SEM.
8. Microspore from microsporangium (details from 6), LM.

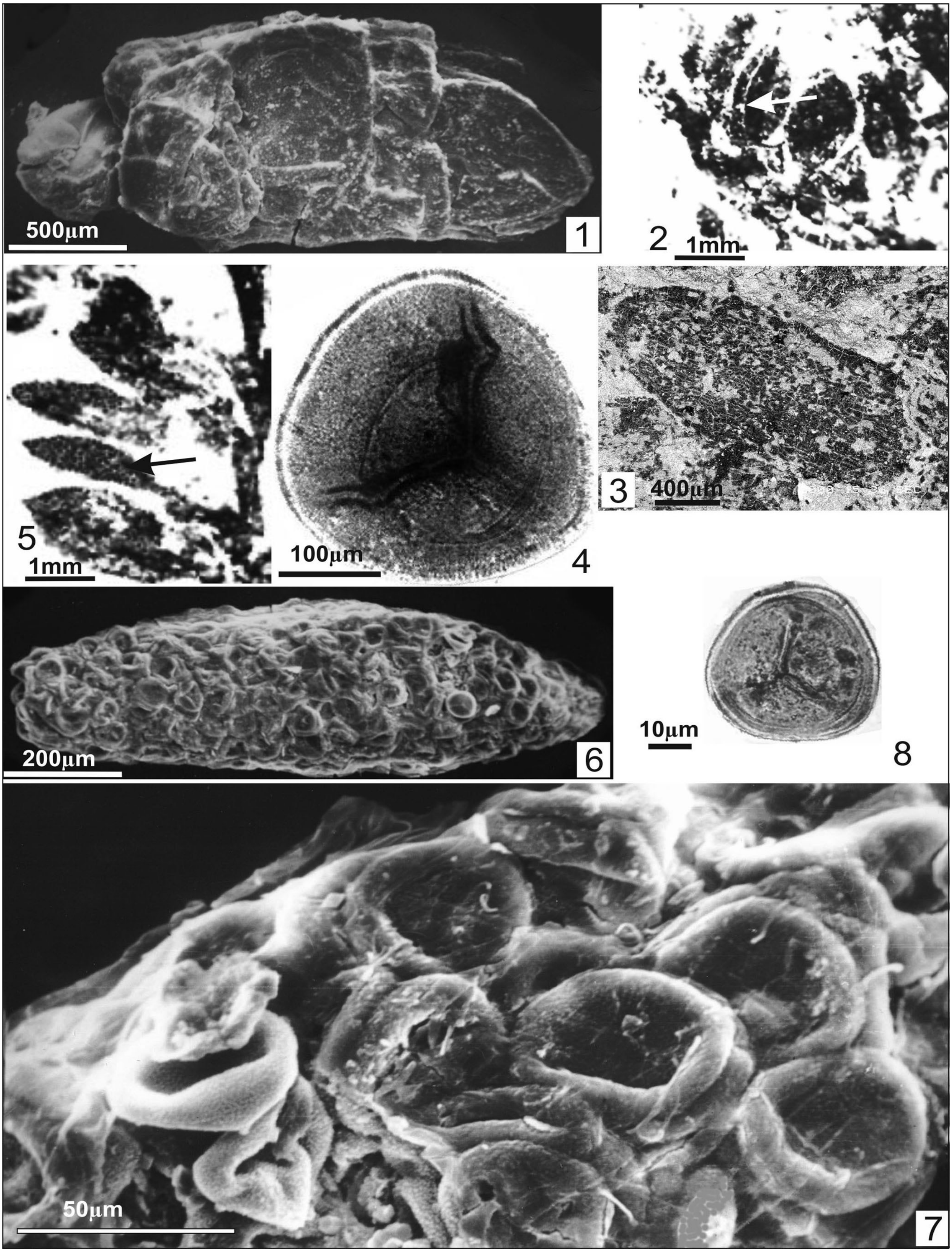

PLATE 1

the base of the Frasnian Stage in the spore zonation scheme of the East European Platform (Avkhimovich *et al.*, 1993). On this basis, Yastrebovskaya Formation and the genus *Svalbardia* were considered as a part of the Upper Devonian Frasnian Stage at that time. The Stratigraphic Committee of Russia proposes to draw the boundary between the Givetian and Frasnian Stages in Russia on the basis of the Upper Timanian Subhorizon of the East European Platform (Sobolev & Evdokimova, 2008). According to this resolution, the IM miospore Subzone moved to the Givetian Stage and characterizes its upper part. Therefore, the age of Yastrebovskaya Formation should now be considered Late Givetian (Fig. 3). Accordingly, the age of *Svalbardia furcihasta* from Yastrebovskaya Formation of the Pavlovsk Quarry also changes from the Frasnian to Givetian. This part of Yastrebovskaya Formation (miospore Subzone IM) could be correlated with the *Optivus–Triangulatus* Zone (OT) of the Old Red Sandstone continent (Richardson & McGregor, 1986) and with the lower part of *Triangulatus–Concinna* (TCo) Oppel Zone of the Ardenne–Rhenish region (Streel *et al.*, 1987). Subzones OT and TCo according to Richardson, McGregor, Streel *et al.* characterize the Upper part of the Givetian Stage and the Lower part of Frasnian Stage.

When there was a need to examine the original material again (this material was housed in the Institute of Biology and Pedology in Vladivostok, Russia, collection № NDP1, Krassilov *et al.*, 1987), we addressed the Institute to provide us with a collection of plants or its part. However, the answer of the staff of the Institute (e–mail <bugdaeva@ ibss.dvo.ru> 21.03.2008) was "during the great flood in Vladivostok, the entire collection was destroyed". Fortunately a small collection was kept in Voronezh State University. M Raskatova was one of the authors of the first description and had participated in collecting the fossil material in Pavlovsk Quarry in 1985. In her collection some fragments of the plants from the original collection, as well as the permanent and temporary preparations of spores were saved. The collection of microspores № P–1987 mc and megaspores–№ P–1987 mg is saved in the Laboratory of Micropaleontology of the Geological Department of Voronezh State University, Voronezh, Russia. These materials and the first publication of the plants from Pavlovsk Quarry formed the basis for this article.

Spores from the sporangia of *Svalbardia* and dispersed spores from the matrix rocks were studied with LM and TEM POLAM–312; photography was carried out by NIKON camera in the Laboratory of Micropaleontology of the Voronezh State University. Removing spores from the sporangia (independently of micro–or megasporangium) was carried out under a binocular microscope. Marked sporangium was processed with 76% alcohol to prevent crushing of the material. The sporangium was placed on medical glass with a hollow in the middle and filled with a Schultze mixture (HNO_3 + $KClO_3$). The glass was then transferred to a thermostat where a temperature of 70°C was maintained for 10 minutes for the oxidation of organic matter. Thereafter the sporangium was placed on a separate glass slide and washed in distilled water several times to remove the Schultze mixture. Opening of a sporangium was made by a needle under a binocular microscope. Micro–or megaspores recovered from the sporangia were removed with glass micropipettes and placed into a glycerin drop for photographing under a light microscope. To photograph the spores in a scanning electronic microscope, a fragment of film was stuck to a metal table and mega–or microspore was transferred on this film. Then the object was covered with a thin layer of a heavy metal and examined in the electron microscope. If it was required, the spores were turned over and covered with heavy metal again.

SYSTEMATICS

Class—PROGYMNOSPERMOPSIDA Beck, 1960

Order—ARCHAEOPTERIDALES W. Zimmermann, 1930

Genus—SVALBARDIA Høeg, 1942

Svalbardia: Høeg, 1942, p. 193; Lepekhina *et al.*, 1962, p.134; Carluccio *et al.*, 1966, p. 727; Stockmans, 1968, p. 23; Matten, 1981, p. 1383; Gensel & Andrews, 1984, p. 229; Meyen, 1987, p. 130.

Tanaitis: Krassilov *et al.*, 1987, p. 163.

Diagnosis—The branching system is with straight or slightly curved rachis of different orders; the rachis of the first order are long, straight, longitudinally grooved with lateral fertile and sterile branches, arranged spirally. Fertile branches are mainly located in the middle part of the branching system. Fertile branches paniculate, consist of a dissected sporophyll with columnar sporangia placed acropetally single or in groups

PLATE 2 →

Morphology and details of structure of mega–and microspores from sporangia of *Svalbardia furcihasta* (Krassilov, Raskatova & Istchenko) Jurina, comb. nov., SEM, LM

1. Masses of megaspores in megasporangium, LM.
2, 3. Megaspores from proximal view, showing inner body and thickened curvatures, SEM.
3. Megaspore from equatorial view (details of sculpture 2) SEM.
4. Megaspores from proximal view with shagreen sculpture, LM.
5. Megaspore (details of structure 2) sculpture in the region of a curvature, SEM.
6, 7. Tetrad of microspores, LM, SEM.
8. Microspore from microsporangium (detail from Pl. 1.6), SEM.
9. Microspore (details of structure 8), proximal view, SEM.

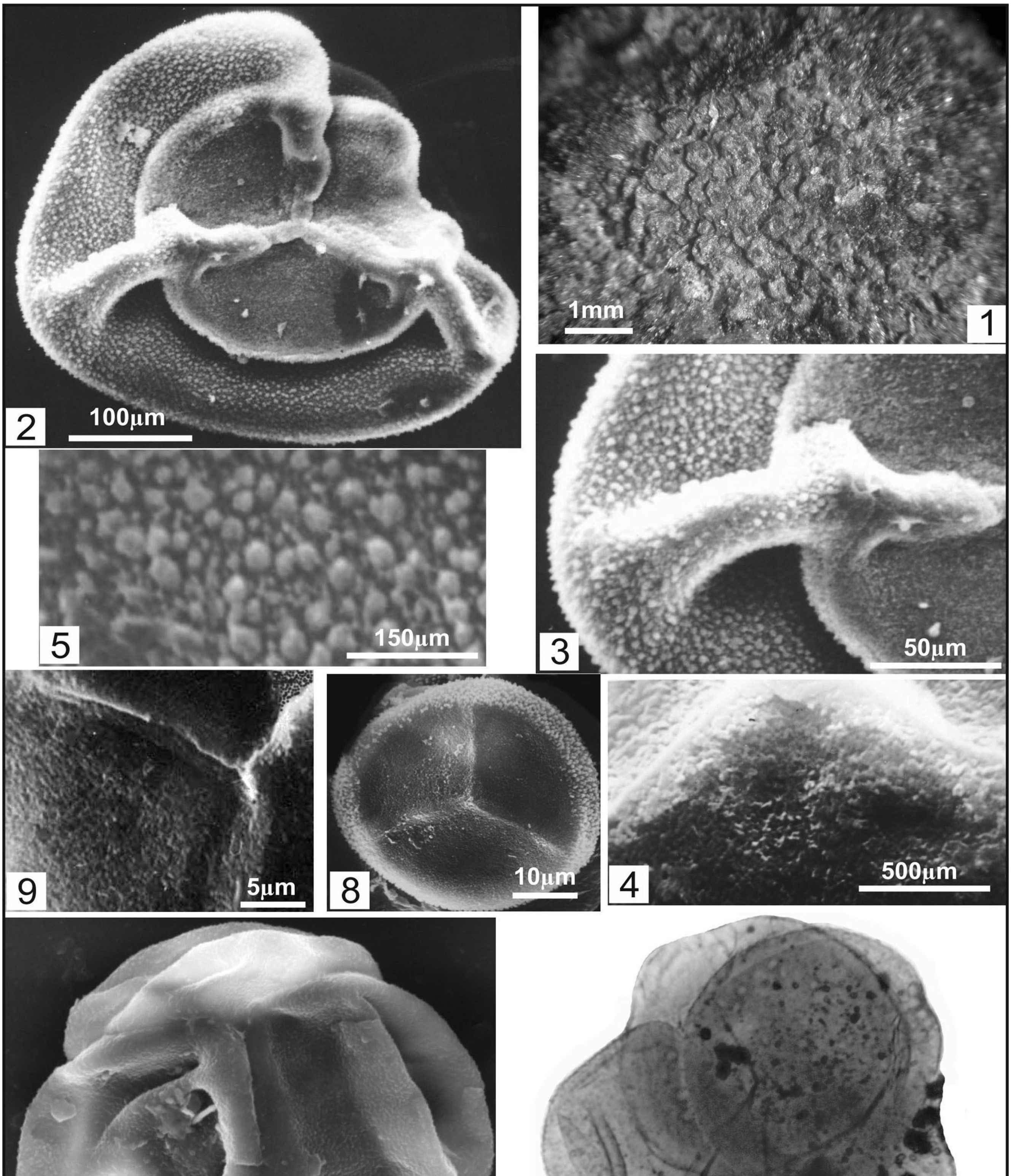

PLATE 2

and terminate with a bifurcate sterile apex. Vegetative units of the last order are represented by dichotomizing unwebbed leaf formations. They are located in more than one plane and dissected into long lobes or segments. Spores with distinct trilete marks and thin tuberculate ornamentation are connected in tetrads. Underground and basal parts are unknown.

Type Species—*Svalbardia polymorpha* Høeg, 1942; Middle Devonian (Givetian Stage); Norway (Spitsbergen).

Species composition. Seven species (Table 1). Givetian and Frasnian deposits of Eurasia; Upper Devonian deposits of Ukraine, U.S.A and Canada.

Svalbardia furcihasta (Krassilov *et al.*) Jurina, comb. nov.

Pl. 1–2; Fig. 4.

1987–*Tanaitis furcihasta* Krassilov *et al.*, 1987, p.164, Pl. I–VII.

Description—Description of sterile and fertile appendages of the plant as well as the epidermis has been done quite in detail in the protologue and does not need to be repeated. We will pay further attention to the structure of the leaves and the in situ spores, because some corrections are required.

Leaves are present in the form of fragmentary compressions that are attached to the axes or, more often isolated from the axes. The axes (about 2–6 mm of length and 2–3 mm of width) are longitudinally grooved and transversely wrinkled. Unwebbed leaves are spirally attached to the axes. Each axis has two leaves on each side or only on one side. The angle between an axis and a leaf is 30°. Sometimes the axis does not bear signs of attachment of leaves. The length of leaves is 1–1.5 mm consisting of twice or four times dichotomizing segments. The base of the leaf up to the first branching has a width about 1.1–1.25 mm, the terminal unit has a width of about 0.5–0.8 mm. Initial segments are straight, slightly curved, on the distal side with pointed hastate ends (Fig. 4 d–f, m, n, q–the present work; Krassilov *et al.*, 1987, Pl. III.4;). Generally segments are broken off or splited. They are unwebbed, branched twice, deeply incised into segments with distal broken ends. Width of the segments before the dichotomy is 1.5 mm, and after dichotomy is 0.6–0.75 mm. Segments of the leaves attached or lying freely diverge fan–like from the base, forming a common wedge–shaped form of leaves.

The fossil material contains a few whole units of dichotomy. They are often broken and lay in different planes or angles to the observer without signs of dorsiventral differentiation (Fig. 4b, c, k, o, p). It is suggested that segment branching is three–dimensional.

The main mass of sporangia are elliptical, pointed, about 2 mm long including a stalk about 0.3 mm. Two modes of their width are 1 mm and 0.6 mm. During a preliminary study of fertile branches it was noticed that the megasporangia are larger than microsporangia (Pl. 1.2; indicated by arrows). The larger sporangia contain megaspores, while the narrower ones contain microspores. Mega–and microspores in one sporangium are never observed. Megaspores are about 16 per megasporangium, 200–350 μm in size (Pl. 1.4; Pl. 2.2). The amb of megaspores is rounded–triangular, with an inner body about one half of the diameter (100–160 μm). Exoexine is attached to the intexine over the entire, or part of the proximal region but is separated in the equatorial plane and over the entire distal region. Trilete mark distinct, laesurae straight, accompanied by highly elevated lips (up to 10–13 μm), equal to the full radius of the megaspore. Sometimes, one or two rays of the trilete mark are shorter than the other, equal to the full radius of the inner body. The thick folds of the exoexine accompanying the laesurae are swollen into thickened nodes where they intersect the curvaturae and on the ends (Pl. 2.2–3). Contact areas are limited by curvature which more or less coincide with the contour of the inner body. The exine sculpture consists of thin, partially fused baculi or granula on the contact areas, which form the shagreen structure under light microscope (Pl. 2.4). Both equatorial and distal sides carry on a lot of granulas with different sizes (up to 10 μm) (Pl. 2.5). The surface between them is filled

Fig. 4—Drawings of *Svalbardia furcihasta* (Krassilov *et al.*) Jurina, comb. nov., based on photos of the part specimens from Krassilov *et al.*, 1987, Pl. I, fig. 1. Imprint or compression of plant material shown in black; conjectured position of missing material in dotted lines. A, B = axes with leaves or without; a, b–attached leaves; c–q–isolates leaves; b, c, k, o, p–leaves seen in various orientations.

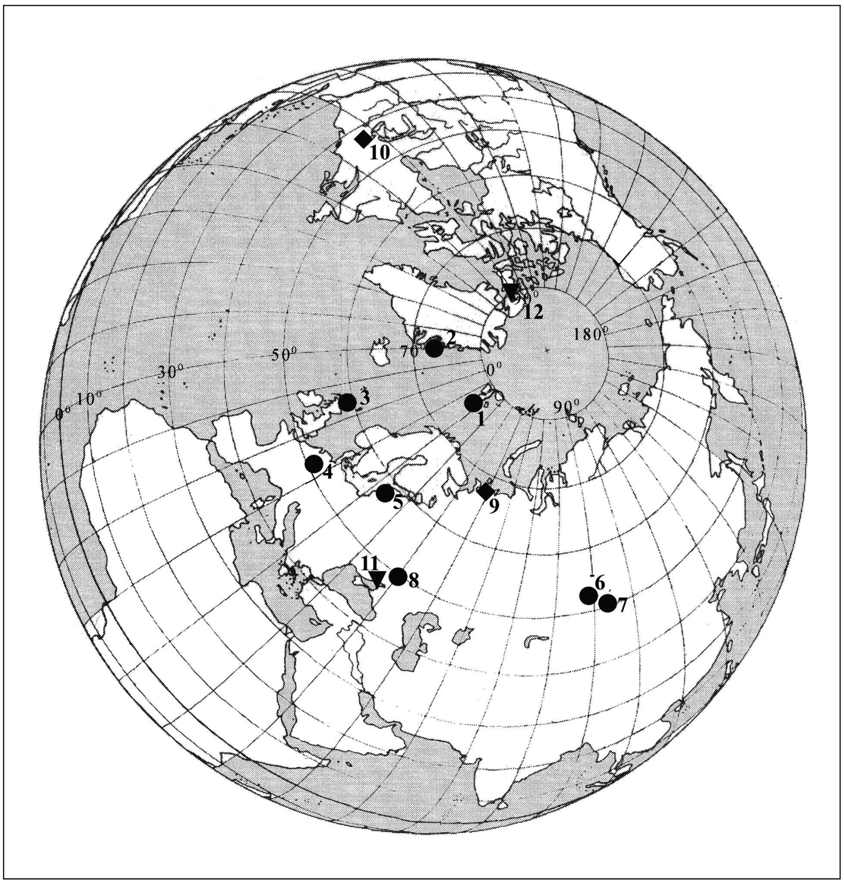

Fig. 5—Geographic localities of genus *Svalbardia*.

with small grains (1–2 µm high). Exine sculpture is changed in the curvaturae area: conate tuberculas extend up to 12–14 µm, become more peaked, and are located much more densely. Microspores contained in the microsporangium in clusters of tetrads or singly (Pl. 2.6–7). Microspores (Pl. 2.8) are radial, trilete, cavate. Amb rounded; in lateral profile the proximal surface is flattened or low pyramidal, the distal surface is hemispherical. Diameter of the spore is about 37–42 µm. Trilete rays are simple, straight, about 4/5 of the microspore radius. Exoexine is separated in the equatorial plane and over the distal region. Contact areas are covered with small grains forming scabrate ornamentation (Pl. 2.9). The sculpture on the equatorial and distal surfaces is the same and represented with conical tubercles and granules arranged more densely in the equatorial region and scattered on the distal surface. We studied the exine sculpture in SEM (x1500) and established that the sculpture of microspore is more complex: it consists of two layers, more or less of large tubercles. Conate tuberculas vary in size (0.1–3 µm in basal diameter and up from 0.5 to 3 µm high) and configuration. The upper part of conate tuberculas are pointed and sometimes curved. The base of these elements is indistinctly oval. The base of the elements are more densed in the equatorial region; between them there are a lot of small granules (0.5–1 µm), creating the overall effect of the density of sculptural elements.

Holotype–Krassilov *et al.*, 1987, Pl. I, fig. 2. (according to the article 33.4 of the International Code of Botanical Nomenclature (Vienna Code); McNeill *et al.*, 2006).

Remarks—Authors of the original description under “holotype” have given holotype № NDP1–1 and referred to the image on Plate I, fig. 1 (Krassilov *et al.*, 1987: 164). This fig. 1 shows a sample of the compression with only sterile branches. In the following text of the article reference is made to the holotype in different ways (Krassilov *et al.*, 1987; either Pl. I, fig. 1, or Pl. I, fig. 2) and as a result there is some confusion. It seems that the image of sterile and fertile branches on Pl. I, fig. 2, correspond more exactly to the holotype.

DISCUSSION

The stratigraphic distribution of the genus *Svalbardia* ranges from Givetian Stage of the Middle Devonian–Upper Devonian. 10–15 years ago many of the finds of this genus were dated under Frasnian Stage, and the age of some revised forms were updated as Givetian. The first concerns the type species *S. polymorpha* Høeg (Høeg, 1942), which was described from Spitsbergen (Norway, Fig. 5.1). The age of Members, from which some impressions of this species were collected was regarded as "upper Middle Devonian or lowermost Upper Devonian?"; Høeg 1942: 193. Since then, this interval was marked in all the publications related to this genus (Petrosjan & Radczenko, 1960; Lepekhina *et al.*, 1962; Chaloner, 1972; Carluccio *et al.*, 1966; Stockmans, 1968; Matten, 1981; Gensel & Andrews, 1984; Meyen, 1987; Jurina & Raskatova, 2012 and all).

Schweitzer (1999) visited the localities which Høeg described and studied their geological position and collected fossil plants. Schweitzer corrected the age of Mimerdalen Formation, consisting of two Members: Estheriahaugen and Fiskekløfta, as Middle–Late Givetian on the basis of the study of spore assemblages from these lithounits. Also he has noted, that the fishes of the genus *Asterolepis* Eichwald, 1840b are found in these units, but the genus *Bothriolepis* Eichwald, 1840a is never marked there. According to Schweitzer, few sterile prints of *Svalbardia polymorpha* were present in the Estheriahaugen Member. Abundant sterile and fertile prints of this species were noted in the Fiskekløfta Member. The holotype *S. polymorpha* and other specimens of this species were found in the Fiskekløfta Member by Høeg (1942). We propose to consider, according to Schweitzer, the age of the genus *Svalbardia* and its type species in Spitsbergen as Givetian instead of Upper Devonian (or the Lowermost Upper Devonian?). The axes of *Svalbardia* sp. and asterolepid plates (Marshall & Stephenson, 1997) are recorded from the Givetian sediments in the East Coast of Greenland (Fig. 5.2). Stratigraphic position of *Svalbardia* in Greenland is similar to that in Spitsbergen. Both the localities are situated in the eightieth Northern latitudes (25° W 73° N and 15° E 79° N respectively). *Svalbardia scotica* Chaloner (Chaloner, 1972) was described from the Givetian Formation of Bu Ness Group in the North of Scotland (Fair Isle, 2° W 59° N, Fig. 5.3). *Svalbardia boyi* Kräusel & Weyland (Kräusel & Weyland, 1960) was recovered from the Givetian sediments of Oberer Plattenkalk of Bergisch–Gladbach in the West of Germany (7° E 51° N, Fig. 5.4). We also described *S. banksii* Matten (Jurina & Raskatova, 2012) from the Givetian Stage (Lode Formation) in Lode clay pit, Latvia (23° E 57º N, Fig. 5.5). The holotype of this species (Matten, 1981) is found in the only locality from the Frasnian deposits of Delaware River Flags, Oneonta Formation; New York State, U.S.A. (77° W 43° N, Fig. 5.10).

From Russia four localities with *Svalbardia* are known: three of them are Givetian and one is Frasnian. *Svalbardia osmanica* Petrosjan & Radczenko (Petrosjan & Radczenko, 1960) is described from Falenovye layers of Kuzbass (88° E 53° N, Fig. 5.6) whose age was considered as the earliest Frasnian. Subsequently, Stepanov (1975) indicated that the layers with *S. osmanica*, were stratigraphically lower than the Falenovye layers. The boundary between the Givetian and Frasnian Stages in Kuzbass was proposed to be drawn on Falenovye limestones and the underlying strata was considered as the Givetian Stage according to the Stratigraphic Committee of Russia (Sobolev & Evdokimova, 2008). Thus, *S. osmanica* should be attributed to the Givetian. *S. polymorpha* Høeg (Lepekhina *et al.*, 1962) was recorded from the Givetian Stage (Ilemorovskaya Formation) in the south of Central Siberia in Tuva (92° E 51° N, Fig. 5.7). The third Givetian locality of the genus *Svalbardia* in Russia was recorded in Yastrebovskaya Formation (40° E 50° N, Fig. 5.8). From this locality we have described *S. furcihasta* (Krassilov *et al.*) Jurina, comb. nov. in this article. The only Frasnian locality of the genus *Svalbardia* with *S. osmanica* (Petrosjan & Radczenko, 1960) in Russia was from the Ustbezmoshitskaya Formation, Northern Timan (48° E 67° N, Fig. 5.9).

The geological age of *S. fissilis* (Schmalhausen) Matten is much different from other species. This species was described by Schmalhausen (1894) from the Famennian deposits of Ukraine, Donbass (38° E 48° N, Fig. 5.11) and also noted in the Upper Devonian sediments (details not specified) of Canadian Arctic (Andrews *et al.*, 1965; 80° W 80° N, Fig. 5.12). Stepanov (1975) pointed to the Givetian finding of *S. fissilis* in Russia (Kuzbass).

Høeg (1942) described the genus *Svalbardia* as a monotype and did not clearly distinguish the generic and specific characters. Over the past few decades a lot of new information about this genus and its species has been generated. Characters of the genus *Svalbardia* by external morphology were discussed above. We have not considered the structure of fertile parts of this plant because fertile and vegetative parts of the genera *Svalbardia* and *Archaeopteris* have much in common (Petrosjan & Radczenko, 1960; Carluccio *et al.*, 1966; Beck, 1971; Matten, 1981).

Table 1 shows that it is difficult or almost impossible to distinguish the main determining species character of the genus *Svalbardia*. For the differentiation of species we propose to use a combination of two or three characters: the length of leaf, the width of leaf segments and the structure of petiole if it is present. Such characters, as the number of segments in the leaf and the proportions of segments should be attributed to that of "additional category" assisting in the determination of species. In some cases, the characteristic of form segments has a special significance. On this basis we distinguish two species (Table 1). Some characters are not determinative for the species category, for example, the form of leaf. There are no clear differences in the form of leaf between most of the species, which varies from wedge to fan–shaped.

Let us review some examples. The longest leaves (up to 3.2 cm) belong to *S. banksii*. Leaves of *S. osmanica*, *S. fissilis* and *S. furcihasta* are much shorter than that of *S. banksii* and nearly equal in length (1–1.5 cm). These three species can be distinguished by the width of segments: *S. osmanica* has wide segments (2–5 mm), *S. furcihasta*–considerably narrower (0.5–0.7 mm) and *S. fissilis* has filiform segments.

Features/ Species	GENUS SVALBARDIA HØEG 1942						
	S. polymorpha Høeg 1942	*S. osmanica* Petrosjan & Radczenko 1960	*S. boyi* Kräusel & Weyland 1960	*S. scotica* Chaloner 1972	*S. banksii* Matten 1981	*S. fissilis* (Schmal-hausen, 1894) Matten 1981	*S. furcihasta* (Krassilov *et al.*, 1987) comb. nov.
the form of leaves	wedge–shaped	oblique–wedge–shaped	wedge–shaped, fan–shaped	wedge–shaped	wedge–shaped	wedge–shaped	wedge–shaped
the length of leaves, cm	2, 5	1–1.5	1–2.7	2	up to 3.2	1–1, 4[x]	1–1.5 [x]
the number of segments	8	8	3	4	4–8	2–4, seldom 8	4
the width of segments, mm	filiform	2–5	—	3	0.8–1.3	filiform	0.5–0.7 [x]
the proportion of segments	equal	unequal	unequal, central is longer	equal	equal	unequal	equal
the form of segments	linear	linear, curved [x]	linear [x]	linear	linear	setiform	hastate
petiole	thin	wide, deccurent	—	—	thin, straight	—	—
geological age, region	Givetian; Norway, Russia (Siberia)	Givetian; Russia (Kuzbass); Frasnian; Russia	Givetian; Germany	Givetian; Scotland	Givetian; Latvia; Frasnian; U.S.A.	Famennian; Ukraine; Upper Devonian; Canada	Givetian; Central Russia

Table 1—Comparison of the important characters of *Svalbardia* species. Legend: [x] the character is not indicated in original description; — the character is absent.

Filiform segments of two species *S. polymorpha* and *S. fissilis* are identical but their quantity in a leaf is different: 8 in the first species and 2–4 (rarely 8) in the second one. These two species differ in the length of leaves. *S. boyi* has the smallest quantity of segments in a leaf (3), but all segments are different in length with the central one being longer. The proportions of segments and their quantity are the specific characters of *S. boyi*. For *S. osmanica* the segments are also of unequal length, but this character is not important for this species. The leaf of *S. polymorpha, S. scotica, S. banksii, S. furcihasta* is dissected into equal segments. The majority of species do not differ in the type of segments: linear or slightly curved. For *S. furcihasta* and *S. fissilis* the type of segments is important because *S. furcihasta* has hastate type of segments and *S. fissilis*–setiform segments.

Usually the petiole is not noticeable in the genus *Svalbardia.* The most complete description of petiole was given for *S. osmanica* by Petrosjan and Radczenko (1960). They described the length and width of the petiole and its deccurent base. The deccurent base of the petiole is an important character of this species (the widest segments are 2–5 mm). The thin petiole is specified only for *S. polymorpha* and *S. banksii*. We believe that it is necessary to pay more attention on the structure of petiole.

Identity of in situ spores of genus Svalbardia —Høeg (1942) first identified spores from the sporangia of the type species *S. polymorpha* from Spitsbergen. He singled out some spores from the syntypes, briefly described them, but did not give any name. According to their size (60–70 µm) they belong to the microspores. Høeg also noted that similar spores are present in the matrix of the rocks. Vigran (1964) studied spores belonging to *Svalbardia*, in preparations indicated by Høeg which are stored in the Paleontological Museum at Oslo. Study of the spores was made under LM. She established *Lycospora svalbardiae* Vigran as a new species and included in it *in situ* spores of *S. polymorpha* and dispersed spores of similar morphology and sizes (65–83 μm). As the holotype, she proposed dispersed spore and as the paratype, a spore from the sporangium of *Svalbardia polymorpha*. From our point of view, according to her illustrations and those of Høeg (1942), *Lycospora svalbardiae* is quite similar to *Geminospora* species. Allen (1965) transferred the spores of *Lycospora svalbardiae* Vigran in another genus and described them as *Geminospora svalbardiae* (Vigran) Allen. Balme (1995) in the annotated catalogue of fossil in situ spores agreed with the proposals of the above researchers to refer the microspores of *Svalbardia polymorpha* to the genus *Geminospora* Balme, 1962 and marked their similarity to *G. micromanifestus* (Naumova) Medianik, which are similar to the microspores of *Archaeopteris* species. For the megaspore *Svalbardia furcihasta* (then *Tanaitis furcihasta*) Krassilov *et al.* (1987), Balme (1995) assigned the genus *Biharisporites* Potonié, 1956. He proposed to refer the microspores to the genus *Geminospora*, based on the SEM illustrations in Krassilov *et al.*, where an intexine is not visible. Schweitzer (1999, Taf. 5, Figs 6–8) pictured (without description) three specimens of dispersed spores *Geminospora lemurata* Balme, emend. Playford from the Mimerdalen Formation, which according to his opinion, belonged to *Svalbardia polymorpha* Høeg.

Spores from the sporangia of *Svalbardia furcihasta* were first described and represented by Krassilov *et al.* (1987). Megaspores, from the brevity of description, have been wrongly attributed to the formal taxon *Biharisporites* Potonié. Later Raskatova (1995) studied and described these spores in LM and SEM and concluded that the megaspores correspond to the formal taxon *Contagisporites optivus* (Tschibr.) Owens, while microspores compared with the formal taxon *Geminospora* Balme emend. Owens.

The present study of the spores extracted from the sporangia of *Svalbardia furcihasta* showed that they are well preserved and it is possible to compare them with the formal taxa of dispersed miospores. We confirm the finding of Raskatova (1995) that the megaspores, in the presence of the inner body and distinct curvaturae, the character of the exine sculpture can be compared with the taxon *Contagisporites optivus* (Tschibrikova) Owens, 1971. Given the size and features of the structure of microspores (trilete mark, the character of the exine sculpture), they can be compared with the taxon *Geminospora lemurata* Balme, emend. Playford, 1983.

We have reviewed in situ spores belonging to two species of the genus *Svalbardia*: *S. polymorpha* and *S. furcihasta* and come to the conclusion that almost all researchers have attributed the microspores of these two species to the genus *Geminospora*, but to different species. The megaspores related only to *S. furcihasta* (Krassilov *et al.*, 1987 and this work), are presented by genus *Contagisporites* Owens, 1971. *Svalbardia furcihasta* is heterosporous, but heterospory of *S. polymorpha* cannot be confirmed.

Megaspores from the reproductive organs of *Svalbardia furcihasta* have the greatest morphological similarity with the megaspores of *Biharisporites* from the sporangia of *Archaeopteris halliana* (Goeppert) Dawson (Phillips *et al.*, 1972; pl. 43, fig. 28; pl. 44, fig. 44), with size variations over wide intervals. There is also a great similarity to the megaspores of the species of *Biharisporites*, from the sporangia of *Archaeopteris latifolia* Arnold (Pettitt, 1965; pl. 2, fig. 6) and to megaspores *Contagisporites* from the sporangia of *Archaeopteris* sp. 2 (Telnova & Meyer–Melikian, 1993), which are two times larger (up to 600 μm), than the megaspores of *Svalbardia furcihasta*. There are also similarities with the megaspores of *Biharisporites* from the sporangium of *Archaeopteris* sp. (Medianik, 1982) and separate sporangium (Raskatova, 2000). All of these megaspores have wide elevated, ridge–like curvaturae. The thick folds of exine accompanying the laesurae are also swollen into thickened nodes where they intersect the curvaturae. These features in the structure of in situ megaspores of various species of *Archaeopteris* allow to speak about the great similarity with the in situ megaspores of *Svalbardia furcihasta* and about the relationship of this plant with Archaeopteridaleans. In situ megaspores *Contagisporites optivus* from the sporangium of *Svalbardia furcihasta* are similar to the dispersed miospores *C. optivus* from containing rocks. However, they differ in small insignificant details (Raskatova, 1995).

Microspores of *Svalbardia furcihasta* are attributed to the genus *Geminospora* as well as many microspores of some species of *Archaeopteris* and have almost identical morphological characteristics. Microspores are radial, trilete and cavate. The layers of exine are separated in the equatorial plane and over the entire distal hemispherical surface. The sculpture is represented by tubercules of various configurations and sizes. It is developed on the equatorial and distal surfaces, and normally reduced or absent on the contact areas. The differences between the microspores of Archaeopteridaleans consist in the nature of the ornamentation of exine and the degree of separation of exine layers.

Preliminary data of ultrastructure studies of microspores of *Geminospora* from the sporangia of *Svalbardia furcihasta* by N Zavialova (personal communication), have revealed a two–layer sporoderm, of which the outer layer repeatedly exceeds the thickness of the inner layer. There is a cava between the layers in the distal and equatorial areas. The structural elements of the outer layer are represented by granules. An inner layer is formed by flattened lamellae. Such type of ultrastructure was observed previously in other representatives of Archaeopteridaleans (Pettitt, 1966; Telnova & Meyer–Melikian, 1993).

CONCLUSION

Genus *Svalbardia* represented by *S. furcihasta* (Krassilov *et al.*) Jurina, comb. nov. with dissected unwebbed leaves and terminal hastate segments is described for the first time from the Givetian Formation of the European part of Central Russia.

Basic localities of the genus *Svalbardia* (8 of 12 well–known) are Givetian, as the analysis of the stratigraphic distribution of the genus has shown. Most localities are concentrated in the sixties northern latitudes in Eurasia. Six of the seven well–known species of the genus *Svalbardia* (*S. polymorpha, S. scotica, S. boyi, S. banksii, S. furcihasta, S. osmanica*) are from these Givetian localities. Two Frasnian localities are distributed between the two continents: Europe and North America. In these localities, *S. osmanica* and *S. banksii*, which are also known from Givetian occur. *S. fissilis* was described only in two localities from the Upper Devonian in Europe and Canada.

We have observed that the length of leaf, the width of leaf segment and the structure of petiole are the most important characters of *Svalbardia* species. Number of segments in a leaf, proportions and forms of segments can often be significant for the characteristic of species.

S. fissilis (Schmalhausen) Matten takes a special place among other species of *Svalbardia.* This peculiarity is in the unusual structure of the leaf and the estimated phylogenetic value. Schmalhausen (1894, Taf. I, Figs. 1, 3, 4b, 5a, 5b) observed the dissected leaf of this species on which individual segments are connected by leaf tissue from bottom to the top. We believe that this fact indicates the concrescence of leaf segments. Matten (1981) noted that an ancient *Svalbardia* may be the archaeopterid precursor. It is quite possible that this role belongs to *S. fissilis.* As noted above, the stratigraphic distribution of this species does not include the Givetian age.

Our study of *Svalbardia furcihasta* (Krassilov *et al.*, 1987) Jurina comb. nov. have enabled us to come to the conclusion that this representative of the genus *Svalbardia* is the apparent exemplar of Archaeopteridaleans. This is confirmed by the fertile structure of this species, noted above (Krassilov *et al.*, 1987), similar to those in the genus *Archaeopteris;* presence of in situ spores: megaspores *Contagisporites optivus*, microspores *Geminospora lemurata*, type of in situ microspore wall ultrastructure, which is known for many archaeopteridalean species.

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