



Taxonomic significance of morphological characters of spores in the family Ophioglossaceae (Psilotopsida)

Natalia Olejnik^{a,*}, Zbigniew Celka^a, Piotr Szkudlarz^a, Myroslav V. Shevera^b

^a Department of Plant Taxonomy, Faculty of Biology, Adam Mickiewicz University in Poznań, Umultowska 89, 61-614 Poznań, Poland

^b Department of Systematics and Floristic of Vascular Plants, M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine

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ABSTRACT

Primary and secondary ornamentation of spores of ferns of the family Ophioglossaceae are important characters, used in the taxonomy of this group. Considering the small number of published data on those characters in the Ophioglossaceae from Central and Eastern Europe, this study aimed (1) to describe morphological characters of spores of *Botrychium* and *Ophioglossum* species and to assess their taxonomic significance; (2) to analyse variation in spore size between and within species of these genera, based on specimens from various habitats and geographic locations; and (3) to create a key to species identification based on the diagnostic characters of the spore ornamentation. We examined spores of 6 species from 16 localities in Central and Eastern Europe. Results of cluster analysis based on morphological characters of spores indicate that the species form well-defined groups, partly reflecting the systematics of the Ophioglossaceae. A comparison of our results with data from North-West Europe and North America shows differences in some species. The broad range of variation in the size of spores from European populations, in comparison with American ones, may be linked with polyploidy of the studied species. Our findings will help in identification of spores of the family Ophioglossaceae in palynological and palaeobotanical studies.

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1. Introduction

Pteridophytes are divided into 4 classes: Psilotopsida, Equisetopsida, Marattiopsida, and Polypodiopsida (Smith et al., 2006, 2008). The Psilotopsida are most often subdivided into 2 families, Ophioglossaceae and Psilotaceae, less often into 5, including additionally the Botrychiaceae, Helminthostachyaceae, and Tmesipteridaceae (Smith et al., 2006; Mabberley, 2009; Christenhusz et al., 2011). Depending on classification, the Ophioglossaceae include 4–9 genera: *Botrychium* s.s., *Sceptridium*, *Botrypus*, *Japanobotrychium*, *Cheiroglossa*, *Ophioderma*, *Ophioglossum*, *Helminthostachys*, and *Mankyua* (Kato, 1987; Hauk et al., 2003; Smith et al., 2006, 2008; Mabberley, 2009; Christenhusz et al., 2011).

In Europe the family Ophioglossaceae is represented by 11 species of 2 genera: *Botrychium lunaria* (L.) Swartz, *B. matricariifolium* (Retz.) A. Braun ex Koch, *B. virginianum* (L.) Swartz, *B. simplex* E. Hitchc., *B. boreale* Milde, *B. lanceolatum* (S. G. Gmelin) Ångström, *Ophioglossum vulgatum* L., *O. lusitanicum* L., *O. azoricum* C. Presl., and *O. polyphyllum* A. Braun (Valentine and Moore, 1993). In Central and Eastern Europe, 8 species of this group are found (Mosyakin and Fedoronchuk, 1999;

Didukh and Protopopova, 2000; Mirek et al., 2002; Danihelka et al., 2012; Novikov, 2014; floraweb.de; ibot.sav.sk/checklist).

On the global scale, the genus *Botrychium* Swartz is rich in species (28), as compared to other genera of the family Ophioglossaceae. They include diploids, tetraploids, and hexaploids. Fertile tetraploids result from hybridization between species of this genus. So far no hybrids of *Botrychium* with other genera of this family have been reported (Hauk, 1995). Plants of this genus are relatively small-sized, as their sporophytes are about 1–40 cm high. Trophophores are pinnately divided into lobes of various shapes, either thin or fleshy. Sporophores are variously divided, and their shape somewhat reflects the shape of the trophophores. Sporangia spherical and thick-walled, opening through a horizontal slit.

The genus *Ophioglossum* L. comprises about 30 species. Trophophores and sporophores are not pinnate. Trophophores are single, oblong-ovate or elliptic, on average up to about 20 cm long, margin entire. The base is narrower, slightly decurrent into a petiole, embracing the sporophore. Sporophores are single, with 2 rows of 10–40 sporangia each (Smith et al., 2006).

Morphological characters (including those of spores) of the members of Ophioglossaceae are used in the systematics of this family (e.g. Clausen, 1938; Tryon and Tryon, 1982). Both studied genera have more than 1000 spores per sporangium and are eusporangiate (Smith et al., 2008; Mehlreter et al., 2010). Many researchers emphasize that

* Corresponding author.

E-mail addresses: nmw.olejnik@gmail.com (N. Olejnik), zelka@amu.edu.pl (Z. Celka), szkudl@amu.edu.pl (P. Szkudlarz), shevera.myroslav@gmail.com (M.V. Shevera).

spore ornamentation is highly valuable in taxonomic studies, especially at the species and genus level (Johns, 2000; Regalado and Sánchez, 2002; Wei and Dong, 2012; Wang et al., 2015). There are some publications on spore morphology in single or many species of this family (e.g. Nakamura and Shibasaki, 1959; Bobrov et al., 1983; Burrows, 1999; Goswami, 2007; Zenkteler, 2012; Meza Torres et al., 2015), but no studies investigated the variation in spore size of species from various geographic regions and habitat types. Also keys to species identification of the Ophioglossaceae are rarely based on spore characters and most often lead to spore types and spore groups (see Mc Vaugh, 1935; Sahashi, 1979, 1980; Stafford and Paul, 2009).

Our study was aimed (i) to describe morphological characters of spores of *Botrychium* and *Ophioglossum* species found in Central and Eastern Europe, and to assess their significance; (ii) to analyse the variation in spore size between and within species of the same genus coming from populations from various geographic regions and habitat types; and (iii) to create a key to species identification on the basis of spores ornamentation of the Ophioglossaceae from Central and Eastern Europe.

2. Material and methods

2.1. Plant material

The spores used in this study originate from herbarium specimens from the Herbarium of the Department of Plant Taxonomy of Adam Mickiewicz University in Poznań (POZ), Herbarium of the M. G. Kholodny Institute of Botany of the NAS of Ukraine in Kiev (KW), and from material collected specifically for this study (Table 1). The analyses do not include *Botrychium lanceolatum*, which is extinct in Poland (Michalik, 2014), in herbarium materials no specimens with spores were found, and the species is absent from other countries of Central and Eastern Europe. For comparison, we used specimens of *Psilotum nudum* (L.) P. Beauv., from the Botanical Garden in Poznań, and results of measurements and micrographs of spores of this species are also included in this paper. From each population, a random sample of 30 spores was examined. The analysis of variation in spore size between populations from various geographic regions and habitat types, was conducted for *B. lunaria* and *O. vulgatum*.

2.2. Description of spore morphology

The spores were studied using light microscopy (LM) and scanning electron microscopy (SEM). LM was used to measure spore size: polar and equatorial diameters of spores (Fig. 1). SEM images allowed us to

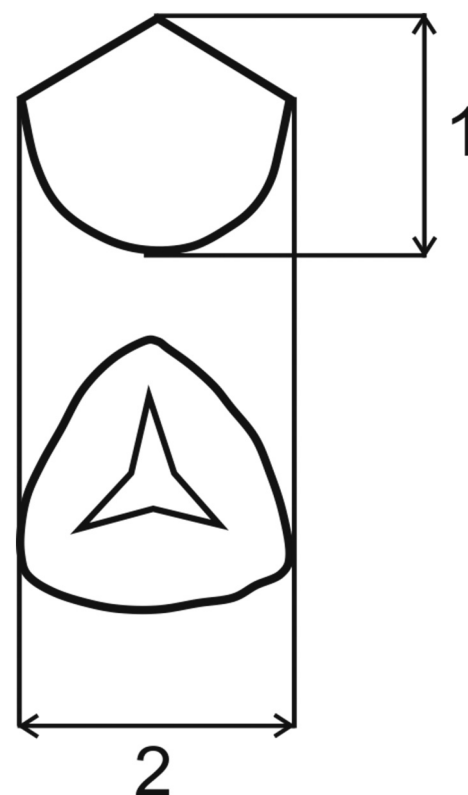


Fig. 1. Schematic diagram of spore measurements (after Nakamura and Shibasaki, 1959): 1 – polar diameter (equatorial view); 2 – equatorial diameter (proximal view).

describe the spore surface (exine). We examined primary and secondary ornamentation. Primary ornamentation was defined as the sculpture of spore surface, while secondary ornamentation consisted of tiny structures, smaller than 1 μm , found on larger elements of spore sculpture. When describing the spores, we used terms from the *Glossary of pollen and spore terminology* (Punt et al., 2007) and the commonly known terms used in palynological publications (Nakamura and Shibasaki, 1959; Lellinger, 2002; Stafford and Paul, 2009).

2.3. Taxonomic analysis

On the basis of our study of spore morphology, we selected the characters that can be considered crucial. These are multistate qualitative

Table 1
Origin of spore samples of ferns of the family Ophioglossaceae.

Species	Locality, habitat	Collection date	Collector ^a
<i>Botrychium simplex</i>	Wierzchowo, West Pomerania, Poland; escarpment above the lake	05.07.1905	C. Kolhshoff (POZ)
<i>Botrychium matricariifolium</i>	Taczanów Forest District, Wielkopolska region, Poland; broad-leaved forest	13.06.2013	Z. Celka, N. Olejnik
<i>Botrychium virginianum</i>	Koltiv, Lviv Oblast, Ukraine; beech forest	07.07.1936	J. Małdalski (KW)
<i>Botrychium multifidum</i>	Maśluchy, Lublin region, Poland; grassland dominated by <i>Nardus stricta</i>	22.08.2013	Z. Celka, N. Olejnik
<i>Botrychium multifidum</i>	Sianki, Podkarpacie region, Poland; partly overgrown grassland in a former timber store	20.08.2013	Z. Celka, N. Olejnik
<i>Botrychium lunaria</i>	Bobrowiec in Tatra Mts; Małopolska region, Poland; subalpine grassland	12.07.2013	N. Olejnik
<i>Botrychium lunaria</i>	Stupy, Kujawy region, Poland; meadow dominated by <i>Molinia caerulea</i>	18.06.2013	Z. Celka, N. Olejnik
<i>Botrychium lunaria</i>	Dziewicza Góra, Wielkopolska region, Poland; ash forest	02.07.2013	Z. Celka, N. Olejnik
<i>Botrychium lunaria</i>	Śnieżka (Sněžka) Massif in Karkonosze (Krkonosé) Mts.; Lower Silesia, Poland; subalpine grassland in a place where a chalet was burnt	23.07.2013	Z. Celka, N. Olejnik
<i>Botrychium lunaria</i>	Sitno, West Pomerania, Poland; xerothermic grassland	12.06.2013	Z. Celka, N. Olejnik
<i>Botrychium lunaria</i>	Shepit, Chernivtsi Oblast, Ukraine; alpine meadows	05.07.1968	O. Pidgirnyak (KW)
<i>Ophioglossum vulgatum</i>	Porąbka, Małopolska region, Poland; meadow	18.06.2014	N. Olejnik
<i>Ophioglossum vulgatum</i>	Imielenko, Wielkopolska region, Poland; sedge bed	01.08.2013	Z. Celka, N. Olejnik
<i>Ophioglossum vulgatum</i>	Skorzęcin, Wielkopolska region, Poland; meadow	19.06.2013	Z. Celka, N. Olejnik
<i>Ophioglossum vulgatum</i>	Zabudnik, Biebrza National Park, Podlasie region, Poland; meadow	23.08.2013	Z. Celka, N. Olejnik
<i>Psilotum nudum</i>	Botanical Garden of Adam Mickiewicz University in Poznań, Poland	16.06.2015	N. Olejnik

^a If spores were extracted from herbarium specimens, the collector's name is followed by the herbarium acronym in brackets; KW – Herbarium of the M. G. Kholodny Institute of Botany in Kiev; POZ – Herbarium of the Department of Plant Taxonomy of Adam Mickiewicz University in Poznań.

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