SPORE ULTRASTRUCTURE OF *SELAGINELLITES LEONARDII* AND DIVERSITY OF SELAGINELLALEAN SPORES

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With 2 tables and 3 plates

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Abstract

The morphology and ultrastructure of spores of *Selaginellites leonardii* Kustatscher et al. 2010 from the Anisian (Middle Triassic) of the Dolomites is studied. The microspores are assignable to *Uvaesporites* Döring, 1965. Distally and equatorially they are covered with verrucae fused into rugae; proximally they are smooth or finely granulate. The sporoderm includes two layers, which appear homogeneous; the outer layer greatly varies in thickness at the expense of the sculptural elements, is much thicker and slightly less electron dense than the inner layer. The microspores were probably originally acavate, with an homogeneous sporoderm. Although a multi-layered sporoderm forming a cavum is the most common type occurring in selaginellalean microspores, acavate sporoderms are also known with a very high ratio between sporopollenin units and the spaces between them. The megaspores are rounded to rounded-triangular, with a very dense two-layered sporoderm, with the outer layer many times as thick as the inner layer. We suppose that originally the megaspore sporoderm was granular, formed by fused spheroid units, and could belong to the irregularly granular type or to the laterally fused type of selaginellalean sporoderms. The occurrence of various spore types in the Selaginellales is known from the Carboniferous until the present day. Available data on the sporoderm ultrastructure in the Selaginellales and Isoetales, similarities and dissimilarities between the two groups are discussed in light of the newly obtained information.

Keywords. *Selaginellites, in situ* spores, sporoderm ultrastructure, *Uvaesporites*, Middle Triassic, Dolomites.

1. Introduction

The genus *Selaginellites* was defined by Zeiller (1906) for fossil herbaceous lycophytes resembling the living genus *Selaginella* Palisot de Beauvois, 1804. *Selaginellites* is restricted to heterosporous species, whereas *Lycopodites* Lindley et Hutton, 1833 (fossil representatives of the extant *Lycopodium* Linnaeus, 1753) includes isosporous taxa, but also taxa of which it is unknown if they are hetero- or isosporous (Zeiller, 1906; Halle, 1907; Seward, 1910; Andrews, 1961).

The oldest *Selaginellites* fossils have been found in Carboniferous sediments; they are often based on sterile fragments only (Thomas, 1992), because fertile remains are rare (but known already from the Carboniferous, e.g., *Selaginellites fraipontii* (Leclercq) Schlanker et Leisman, 1969). Leaves are organized generally in four ranks with two ranks being smaller in size, like in living *Selaginella*. Some authors (e.g., Schimper, 1869; Lee, 1951; Pal, 1984; Schweitzer et al., 1997) consider these dimorphic (anisophyllous)

leaves typical of *Selaginellites* even if no spores have been found. Others, however, do not consider the presence of anisophyllous leaves enough evidence to distinguish between *Selaginellites* and *Lycopodites* (Halle, 1907; Thomas, 1992).

There is some debate as to whether fossil species should be assigned to the extant genus *Selaginella* or kept apart in the fossil genus *Selaginellites* (e.g. Thomas, 1992; Schweitzer et al., 1997). One of the main differences between *Selaginella* and *Selaginellites* is the higher amount of megaspores per sporangium in the fossil material (16-24 against 4 in extant *Selaginella*; Zeiller, 1906; Halle, 1907), although there are some living species with more than four megaspores per sporangium (Thomas, 1992, and references therein).

From the Triassic only few lycophytes were attributed to the genera *Selaginella* or *Selaginellites*: *Selaginella anasazia* Ash, 1972 from the Upper Triassic of Arizona, *Selaginellites polaris* Lundblad, 1948 from the Triassic of East Greenland, *Selaginellites hallei* Lundblad, 1950 from the Rhaetian of Sweden and *Selaginellites yunnanensis* Hsü, 1950 from the Rhaetian of China. Megaspores and microspores are known only in two of them: *Selaginellites hallei* and *Selaginellites polaris*.

The Triassic was an important moment during the evolution of this particular genus, and also a time of high abundance and diversity of lycophytes. With the disappearance of the arborescent Lepidodendrales during the Permian, various "pseudoherbaceous" or herbaceous forms radiated in the Early-Middle Triassic (Taylor et al., 2009). These genera are, however, not closely related but belong to various groups, such as Lycopodiales (e.g. *Lycopodites*), Selaginellales (e.g. *Selaginellites* Zeiller, 1906), Pleuromeiales (e.g., *Pleuromeia* Corda ex Giebel, 1853, *Chinlea* Daugherty, 1941, *Takhtajanodoxa* Snigirevskaya, 1980, and *Cyclomeia* White, 1981) and Isoetales (e.g. *Isoetes* Linnaeus, 1753 / *Isoetites* Münster, 1842, Lepacyclotes Emmons, 1856, and **Tomiostrobus** Neuburg, 1936 sensu Retallack, 1997).

Recently, a new species was described (*Selaginellites leonardii* Kustatscher et al., 2010) from an Anisian (Middle Triassic) fossil locality in the NW-Dolomites (Kühwiesenkopf). The present paper supplements this description with additional information on the spore morphology and provides new data on the sporoderm ultrastructure. We believe these data will help to understand better the genus in general and its evolution into the extant *Selaginella*.

2. Selaginellalean spore morphology

Microspores

The morphology of selaginellalean spores underwent many changes through geological times and they were represented by more than one type of microspores and megaspores in each epoch. Modern spores are also quite diverse in terms of morphology.

The most ancient, Carboniferous, members are known to have produced trilete, zonate, labrate, and distally hilate (or with a few distal foveolae, depending on morphological interpretation) microspores ascribed to *Cirratriradites* Wilson et Coe, 1940 and trilete, cingulate or cinguli-zonate spores attributed to *Densosporites* (Berry) Butterworth et al., 1964. Spore dimensions range from 36 to 80 µm. *Cirratriradites* spores were extracted from *Selaginella gutbieri* (Göeppert) Thomas, 1997 and *S.* cf. *leptostachys* (Bek et al., 2001). Taylor & Taylor (1990), who studied with SEM and TEM *Cirratriradites* type of microspores extracted from *S. fraipontii*, suggested similarities between these fossil microspores and those from modern *Isoetes* and *Selaginella*, such as the presence of a paraexospore (a layer external to and largely free from the exospore, but with a similar ontogeny and staining characteristics, as defined by Tryon & Lugardon, 1991) and proximal multilamellate zones. Although multilamellate zones are usually considered an isoetalean feature, they are also known in the Selaginellaceae. Taylor & Taylor (1990) considered their microspores to be closer to *Selaginella*, namely, *S. selaginioides* (Linnaeus) Link, 1841. The sporoderm of the dispersed spore *Densosporites meyeriae* Telnova, 2004 probably consists of one homogeneous layer only (though the author mentioned lamellae in the sporoderm, they are not visible in the published section). No traces of a cavum are seen, thus questioning the paracavate nature of this spore type, hypothesized on LM basis (Telnova, 2004). Spores of *Cirratriradites* were found *in situ* only in selaginellalean strobili, spores of *Densosporites* were also found in the Chaloneriaceae (Balme, 1995).

The Permian *Selaginella harrisiana* Townrow, 1968 yields circular, paracavate (zonate, cingulate?), trilete, endopapillate, distally spinose microspores, of 43-58 µm diameter attributed to the genus *Indotriradites* Tiwari emend. Foster, 1979 (Townrow, 1968). Such microspores are also known from the Permian lycopsid of uncertain affinity *Azaniodendron fer-*

tile Rayner, 1986 (Balme, 1995). No information is available about its sporoderm ultrastructure.

Triassic *in situ* microspores are represented by two types. The first one is subcircular, cavate, endo-tri-papillate, scabrate, 40 µm in diameter and assigned to the genus *Densoisporites* (Weyland et Krieger) Dettmann, 1963. These spores are known *in situ* from the Pleuromeiaceae, and also as *sporae dispersae* in pre- and post-Triassic deposits (e.g., Guy-Ohlson, 1979; Retallack et al., 2006). Triassic *Densoisporites* extracted from *Pleuromeia rossica* Neuburg, 1936 (= *Lycomeia rossica* (Neuburg) Dobruskina, 1985) shows a lamellate sporoderm with multilamellate zones around the proximal pole (Lugardon et al., 1999). A similar structure was revealed in Permian *Densoisporites* associated with another pleuromeiaceous plant, *Viatcheslavia vorcutensis* Zalessky 1936 (Naugolnykh & Zavialova, 2004). The ultrastructure of the dispersed microspores *D. psilatus* (de Jersey) Raine & de Jersey, 1988 and *D. microrugulatus* Brenner, 1963 (now synonymized with *D. velatus* Weyland et Krieger, 1953) was documented from the Triassic by Raine et al. (1988) and interpreted as a lycopsid sporoderm ultrastructure. Consequently, though some information on the *Densoisporites* ultrastructure is available, we still do not know if and how selaginellalean *Densoisporites* differ from pleuromeiaceous *Densoisporites* in its sporoderm ultrastructure.

Uvaesporites Döring, 1965 includes subcircular, cingulate, distally rugulo-verrucate spores, 29-50 µm in size. So far, *Uvaesporites* spores were never found *in situ*, only associated with selaginellalean macroremains. Ultrastructural information about this spore type was related to end-Permian dispersed spores (Looy et al., 2005). The sporoderm is complex, consisting of several sublayers, interpreted as a faint solid inner exospore, wavy and more electron dense outer exospore and three layers of paraexospore: the outer thicker solid layer forms sculptural elements, the middle thinner layer is composed of thin interwoven filaments, and the inner layer is composed of elements similar to those of the outer layer, but smaller in size. Additionally, Collinson (1991) reported *Lundbladispora* Balme, 1963 emend. Playford, 1965 as selaginellalean microspores, while Balme (1995) attributed the same *in situ* spores to the genus *Densoisporites*. The ultrastructure of dispersed end-Permian *Lundbladispora* resembles closely those of *Densoisporites*, although the presence or absence of multilamellate zones is not proved (Looy et al., 2005).

Microspores of *Foveosporites* Balme, 1957 (convexotriangular, trilete, distally foveolate and proximally smooth, 38-52 µm in diameter) are known from Cretaceous deposits. So far, *in situ* such a spore type is only known from selaginellalean macroremains.

Microspores of modern *Selaginella* are 18-60 µm in diameter, tetrahedral-globose, or slightly flattened, often with an equatorial flange and a trilete aperture with the arms varying in length between 1/2 and almost 7/8 of the spore radius. The surface is variable: often finely to coarsely echinate, sometimes rugulate, cristate, baculate, striate, papillate, or with large spherules. The exospore is plain, verrucate, or spinulose, usually overlain by either perispore or paraexospore; sometimes one of them or both may be lacking (Tryon & Lugardon, 1991).

Modern analogues can be found for most microspore types known from fossil Selaginellaceae. Moreover, the microspore diversity of modern *Selaginella* is much higher (e.g., their sculpture) than that so far known of *in situ* microspores of fossil Selaginellaceae. On the other hand, dispersed assemblages from various geological periods, starting from the Carboniferous or even Late Devonian, contain plenty of spores which are comparable with microspores of modern *Selaginella* in their ornamentation and could, thus, have a selaginellalean origin, but so far have not been found *in situ*. In addition, some types of microspores are recorded *in situ* in both selaginellalean and isoetalean remains, as well as from lycopsid macroremains of unclear position (Table 1).

Megaspores

Three types of megaspores were extracted from Carboniferous selaginellalean macroremains. The most commonly occurring type, *Triangulatisporites* (Potonié et Kremp) Karkzewska, 1976, includes subtriangular trilete, labrate megaspores, although the main spore body of permineralised specimens may appear spherical. These spores are paracavate and zonate: they are characterized by an equatorial flange which usually appears as a flattened wing. Both hemispheres are covered with a more or less developed reticulum (Cottnam et al., 2000; Bek et al., 2001). Taylor (1994) described the sporoderm of *Triangulatisporites* from *Selaginellites fraipontii* as a complex of interconnected units forming a fine 3D reticulum sharing common features with modern members of

Geological age	microspore/megaspore	Isoetalean	Lycopod taxon of unclear affinity
Carboniferous	*Cirratriradites/ Triangulatisporites*	-/-	-/-
Carboniferous	*?/Bentzisporites*	-/-	-/-
Carboniferous	*Densosporites/ Setosisporites*	Chaloneriaceae/-	-/*Bothrodendrostrobus*, *?Barsostrobus*
Permian	*Indotriradites/ Bacutriletes*	-/-	*Azaniodendron/ Synlycostrobus tyrmensis* (from Jurassic/Cretaceous)
Triassic	*Densoisporites/ Banksisporites*	Pleuromeiaceae/ Pleuromeiaceae	*Bisporangiostrobus/-*
Triassic and Triassic/Jurassic	*Uvaesporites/ Banksisporites*	- /Pleuromeiaceae	-/-
Cretaceous	*Foveosporites/ Minerisporites* (?)	-/Isoetaceae	-/*Limnoniobe*

Table 1. Occurrence of micro- and megaspores known from selaginellalean remains *in situ* in non-selaginellalean taxa (compiled from Balme, 1995 and including our data)

the Selaginellaceae and Isoetaceae. Nevertheless, *in situ Triangulatisporites* finds are so far restricted to selaginellalean macroremains. Cottman et al. (2000) studied dispersed *Triangulatisporites* from several Carboniferous localities and *in situ* megaspores of the same type extracted from *Selaginellites gutbieri* and showed the diversity of the sporoderm ultrastructure: they described some sporoderms as particulate and others as more laminate.

The second Carboniferous type is *Setosisporites* (Ibrahim) Potonié et Kremp, 1954 emend. Dybova-Jachowicz et al., 1979 (circular, labrate, trilete, distally with bifurcating spines, proximally smooth, 300-400 µm in diameter). The sporoderms of dispersed Carboniferous *S. hirsutus* (Loose) Ibrahim, 1933 and *S. brevispinosus* (Zerndt) Brzozowska, 1969 are two-layered; the outer layer is much thicker than the inner, very dense, indistinctly stratified toward the inner hollow (Kempf, 1973). The third type is *Bentzisporites* Potonié et Kremp, 1954, which is 315-400 µm in dia-

meter, convexotriangular, cingulate, curvaturate, labrate, trilete, subverrucate and endopapillate. *Triangulatisporites* and *Bentzisporites* were found *in situ* only in selaginellalean strobili, while *Setosisporites* was also found in lycopsid macroremains of unclear systematic position (Balme, 1995).

Megaspores of the Permian *Selaginella harrisiana* belong to the *Bacutriletes* (van der Hammen) Potonié, 1956 type, which is described as circular, cavate, trilete, endopapillate, baculate, and 180-320 µm in diameter (Townrow, 1968). Such megaspores were also recorded in *Synlycostrobus tyrmensis* Krassilov, 1978, a lycopsid of uncertain affinity (Krassilov, 1978). Electron microscopical data are available on dispersed *Bacutriletes*: *B. ferulus* Koppelhus et Batten, 1989 and *B. majorinus* Koppelhus et Batten, 1989 were studied with SEM (Koppelhus & Batten, 1989), TEM studies were made on Lower Cretaceous *B. triangulatus* Taylor et Taylor, 1988 and *Bacutriletes* spp. (Taylor & Taylor, 1988), *B. guttula* Archangelsky

et Villar de Seoane, 1991 (Archangelsky & Villar de Seoane, 1991).

Megaspores of *Banksisporites* Dettmann, 1961 emend. Banerji et al., 1978, described as circular, trilete, cavate, labrate, scabrate, 392-421 µm in diameter, are found *in situ* in selaginellalean strobili in sediments of Triassic-Jurassic age. *Selaginellites hallei* from the Rhaetian of Sweden (Lundblad, 1950) yields putatively immature, spheroidal, trilete, smooth-granulate, cavate megaspores of 330-425 µm diameter, attributed to *Triletes pinguis* Harris, 1935 (now *Banksisporites pinguis* (Harris) Dettmann, 1961). Unfortunately, no information was given on its ultrastructure. TEM data are available from dispersed *B. dejerseyi* Scott et Playford, 1985, *B. viriosus* Scott et Playford, 1985 (Hemsley & Scott, 1989) and Upper Keuper *B. pinguis* (Harris) Dettmann, 1961 (Kempf, 1971).

Cretaceous *Selaginella dawsonii* (Seward) Watson, 1969 yields megaspores supposedly assignable to *Minerisporites* Potonié, 1956 (Watson, 1969). The megaspores are convexo-triangular, paracavate, labrate, distally coarsely vermiculate, with verrucate contact faces, 284-305 µm in diameter. Such a spore type is also known in *Limnoniobe* Krassilov, 1982. However, much more often, this type was reported from the Isoetaceae. A considerable bulk of information is obtained with application of electron microscopes, albeit on dispersed specimens. SEM data were obtained on Cretaceous *M. labiosus* Baldoni et Taylor, 1985 (Baldoni & Taylor, 1985), *M. dissimilis* Tschudy, 1976 and *M. marginatus* (Dijkstra) Potonié, 1956 (Kovach & Dilcher, 1988) and *M. aequatus* Villar de Seoane et Archangelsky, 2008 (Villar de Seoane & Archangelsky, 2008). SEM and TEM data were obtained on Lower Cretaceous *M. elegans* Archangelsky et Villar de Seoane, 1989, *M. patagonicus* Archangelsky et Villar de Seoane, 1989 (Archangelsky & Villar de Seoane, 1989), *M. laceratus* Archangelsky et Villar de Seoane, 1990 (Archangelsky & Villar de Seoane, 1990), Maastrichtian *M. succrassulus* Tschudy, 1976 (Bergad, 1978), and Upper Paleocene and Paleocene/Eocene of *M. glossoferus* (Dijkstra) Tschudy, 1976, *M. mirabilis* (Miner) Potonié, 1956, and *M. mirabillissimus* (Dijkstra) Potonié, 1966 (Batten & Collinson, 2001). Sporoderms of all studied megaspores are rather similar and show a multilamellate ultrastructure common in Isoetales, with considerable spaces between lamellae. In addition, monolete spores (comparable with the typically isoetalean microspore *Aratrisporites* Leschik, 1955) were reported associated with dispersed

megaspores, e.g., those found in hollows of the surface of *M. mirabilis* (Miner) Potonié, 1956 (Batten & Collinson, 2001). Keeping in mind that most indices point to an isoetalean affinity of *Minerisporites*, ultrastructural study of the megaspores of *S. dawsonii* would be very pertinent to find out if any differences between such megaspores of selaginellalean and isoetalean affinities exist at ultrastructural level.

Several genera of dispersed megaspores (or some of their species) have not been so far reported *in situ* but are considered as supposedly selaginellalean in affinity because of their ultrastructure: *Thylakosporites retiarius* (Hughes) Potonié, 1956, *Trileites persimilis* Erdtman, 1947 ex Potonié, 1956, *Hughesisporites patagonicus* Archangelsky, 1963, *Erlansonisporites* Potonié, 1956 (see e.g. Takahashi et al., 2001), *Horstisporites* Potonié, 1956, *Rugotriletes* van der Hammer, 1955 ex Potonié, 1956, *Ricinospora* Bergad, 1978, and *Cabochonicus* Batten et Ferguson, 1987 (Kovach, 1994).

Megaspores of modern species of *Selaginella* are 200-1033 µm in diameter, tetrahedral-globose, often with an equatorial flange, trilete, with the arms reaching 2/3 of the radius or equal to it. The surface is often reticulate, sometimes rugate, baculate, verrucate, scabrate, or granulate. The exospore consists of two layers, the outer usually with distinctive zones. A perispore is lacking (Tryon & Lugardon, 1991).

Selaginellalean megaspores are very diverse and represented by more than one morphological type in each geological period. The number of dispersed megaspore genera showing presumably selaginellalean features is much greater than the number of selaginellalean megaspores so far found *in situ*. With new *in situ* finds, our concept of selaginellalean megaspores will be corrected. Several types of megaspores are known from both selaginellalean and isoetalean macroremains (Table 1), posing two problems: unclear affiliation of dispersed megaspores of spore types known in both groups (such as *Setosisporites*, *Banksisporites*, and *Minerisporites*), and a possibility that spores so far known only in one of the groups can be later found in macroremains of the other. In this relation, accumulation of data on *in situ* megaspores is important as ultrastructural information may differentiate between selaginellalean and isoetalean megaspores.

Both selaginellalean microspores and megaspores are very diverse, and there are enough grounds to believe that a considerable portion of this diversity has

been still undiscovered. More studies on *in situ* material with application of SEM and TEM will help us to understand better the morphological diversity of one of the oldest groups of higher plants (Table 2). The comparison between selaginellalean and isoetalean spores from various epochs is important in order to reveal characters allowing to differentiate between the two groups on the basis of spore morphology and ultrastructure as well as to estimate their similarities. The diagnostics of dispersed spores as members of one of the two groups also should be mentioned.

The present study deals with *in situ* spores of Triassic *Selaginellites leonardii*. Data on their morphology and ultrastructure contribute to these aims.

3. Material and Methods

The strobili of *Selaginellites leonardii* belong to the rich flora from Kühwiesenkopf / Monte Prà della Vacca section in the Dolomites (for more information see Broglio Loriga et al., 2002; Kustatscher, 2004; Kustatscher et al., 2006, 2010), stored nowadays at the Museum of Nature South Tyrol (BZ, Italy). The well-known section (Bechstädt & Brandner, 1970; De Zanche et al., 1993; Senowbari-Daryan et al., 1993) has been dated by brachiopods (Bechstädt & Brandner, 1970), foraminifers (Fugagnoli & Posenato, 2004), ammonoids and palynomorphs (Kustatscher et al., 2006; Kustatscher & Roghi, 2006) to the middle - late Pelsonian (upper Anisian, Middle Triassic).

The strobili have been studied with a dissecting microscope and *in situ* spore preparations were made (for more details see also Batten, 1999). For this purpose, small sporophyll fragments were macerated in Schulze's reagent (KClO3 and 30% HNO3) and neutralized with 5% ammonia. The sporangia were separated with the aid of needles, and monads or groups of spores (depending on their maturity) were extracted, mounted in glycerine jelly and sealed with paraplast.

In transmitted light, the spores were studied with a ZEISS AXIOPLAN-2 and a Leica DFC-420 digital camera, under 100x oil immersion objective at the Paleontological Institute of the Russian Academy of Sciences, Moscow. In addition, some microspores were studied with help of a Leica DM6000 fluorescent microscope using a Leica DC300F camera, HBO 103 W/2 Mercury Lamp reflected light source and A filtercube (BP340-380, LP 425) at the Institute of Molecular Genetics (Moscow). Slides were observed under 63x

oil objective. Image-Pro AMS has been used as acquisition software. To calculate an EDF (extended depth of field) composite image, a stack of 30 slices was produced using motorized Z-drive function of the microscope, and the composite image calculated in Image-Pro (Pl. 1, fig. 6).

Several groups and individual microspores were mounted on scanning electron microscopy (SEM) stubs and coated with platinum/palladium and viewed on a CAMSCAN SEM at Lomonosov Moscow State University, at 20 kV accelerating voltage.

For transmission electron microscopy (TEM), megaspores and microspores were removed from temporary light-microscopical slides and embedded following the method of Meyer-Melikian & Zavialova (1996). Ultrathin sections of 50 nm thick were made with an LKB ultra-microtome, the sections were viewed unstained on Jeol 100 B and Jeol 400 TEM and photographed. The accelerating voltage was 80 kV.

Although the terminology developed by Tryon & Lugardon (1991) is most desirable to describe strata in sporoderms, the definitions imply sufficient data on the position, ultrastructure, electron density, and ontogenesis of particular strata of the sporoderm. No ontogenetic information can be deduced for the fossil sporoderms at hand, and the preservation is far from ideal: at least some ultrastructural information is probably lost. Therefore, we refrain from designating the sublayers revealed as exospore or paraexospore and use instead such neutral terms as outer and inner layers of the sporoderm.

4. The strobilus

So far only two strobilus fragments (up to 17 mm long and 3 mm wide) of *Selaginellites leonardii* Kustatscher et al., 2010 have been found. They are not in organic connection but preserved on slightly different horizons on the same rock sample (collection number PAL536). The sporophylls are helically to decussately arranged in four irregular vertical rows of microsporophylls and megasporophylls (Kustatscher et al., 2010, pl. 1, figs. 1-3). The sporophylls are ovate (1.5-2 x 1-1.2 mm) and entire margined, with a long, acuminate apex (about 2 mm long).

Maceration of the sporophylls resulted in small cuticle fragments with isodiametric cells and slightly immature micro- and megasporangia. Additionally, megaspores were found dispersed in the sediment at the apex of one strobilus.

Geological age	Spore type	Data on sporoderm ultrastructure, if available, with the interpretation of sporoderm layers, which can be preserved in fossil state	Parent plant, references
Microspores			
Carboniferous	*Cirratriradites*	Thin exospore and paraexospore of three sublayers. Multilamellate zones are present	*S. crassicinctus = S. fraipontii*, Taylor & Taylor 1990
Triassic	*Uvaesporites*	Supposed exospore of two homogeneous layers. Multilamellate zones are not found.	*S. leonardii*, present paper
Modern	Spores are trilete, tetrahedral-globose, often with an equatorial flange; the surface is often echinate, sometimes rugulate, cristate, baculate, striate, papillate, or with large spherules.	The exospore consists of inner lamellate and outer amorphous layers. It can either include multilamellate zones or be pierced with numerous radial canals. In some species, paraexospore and/or perispore may be present enveloping the exospore.	General characteristic of the modern genus *Selaginella*, Tryon &Lugardon, 1990
Megaspores			
Carboniferous	*Triangulatisporites*	Exospore of highly interconnected network of wall units, which are thickest and least compressed in the center.	*S. crassicinctus= S. fraipontii*, Taylor 1994
Triassic	*?*	Supposed exospore of two layers: thin inner layer and thicker outer layer of granular elements.	*S. leonardii*, present paper
Modern	Spores are trilete, tetrahedral-globose, often with an equatorial flange; the surface is often reticulate, sometimes rugate, baculate, verrucate, scabrate, or granulate.	The exospore of two layers: an inner compact layer and a much larger, outer labyrinth or gridlike layer, often heavily infiltrated with silica. The perispore is absent.	General characteristic of the modern genus *Selaginella*, Tryon & Lugardon, 1990

Table 2. Available ultrastructural data on *in situ* selaginellalean spores compared with modern Selaginella
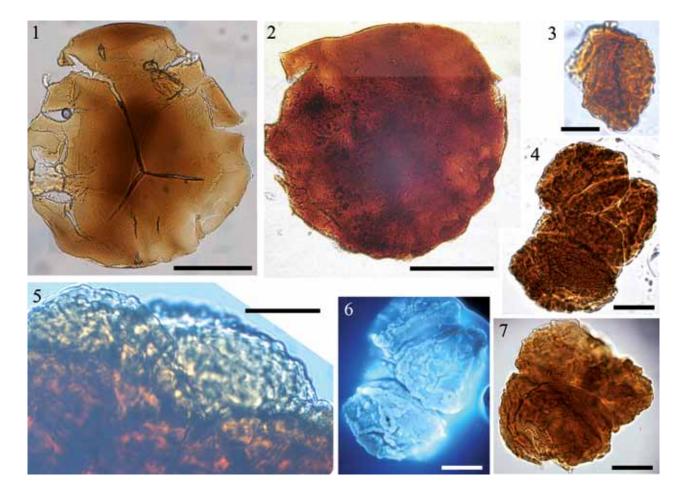
Plate 1 (LM)
1. Megaspore with a trilete scar. 2. Megaspore, no proximal scar is visible. 3. Microspore, equatorial view. 4. Group of microspores, distal sculpturing is distinct. 5. Group of microspores under higher magnification, note uneven contours of microspores. 6. Microspore tetrad, fluorescence microscopy. 7. The same tetrad as in fig. 4. Scale bar (1, 2) 100 µm, (3-7) 20 µm.

5. Microspore morphology and ultrastructure

Microspores are in clusters as well as in damaged tetrads and monads, significantly varying in sizes (Pl. 1, figs. 3, 4-7; Pl. 2, figs. 1, 3). The spores are rounded-triangular and most probably trilete (no monad preserved in polar position was found). The distal and equatorial surfaces of the microspores are rugulate: covered with verrucae mostly fused into ridges elevated at a various height over the surface of the spores (Pl. 1, figs. 4, 6, 7; Pl. 2, figs. 1, 2, 4). The specimens greatly vary in the development of the sculptural elements. The proximal sporoderm is smooth or covered with small granules (Pl. 2, fig. 2). In general morphology and sculpturing, the microspores are assignable to the dispersed genus *Uvaesporites*. The sporoderm is two-layered, both layers look homogeneous, the outer layer is slightly less electron dense than the inner layer (Pl. 3, figs. 3, 4, 6). The outer layer greatly varies in thickness at the expense of the sculptural elements: equatorial areas are thickest, and proximal areas are thinnest (Pl. 3, fig. 4). The sculptural elements more often appear in sections as elongate appendages, stretched along the rest of the sporoderm (Pl. 3, fig. 6). No cavum between the outer and inner layers or within the outer layer was found, but some

gaps were detected between sculptural elements and the rest of the sporoderm. The inner layer is more or less constant in thickness, about 0.22-0.26 µm.

In the microspores of modern *Selaginella* the sporoderm layer enveloping the exospores varies: it may form a perispore, an paraexospore, or may be missing (Tryon & Lugardon, 1991), and the perispore is rarely preserved in fossil state. Thus, the two layers of the sporoderm most probably can be either two sublayers of the exospore or correspond to exospore and paraexospore. We consider the former theory more probable, since the paraexospore is usually largely detached from the exospore, and that is not the case of the outer layer of the sporoderm under study.

6. Megaspore morphology and ultrastructure

Megaspores are irregularly rounded or rounded-triangular, 265-303 x 306-336 µm in size (about 283 x 320 µm on average). Most specimens do not show a tetrad scar (Pl. 1, fig. 2); the only specimen that retains it shows an open trilete scar, occupying more than a half of the radius (Pl. 1, fig. 1). The megaspores are deep brown (Pl. 1, fig. 2) or uneven in colour (Pl. 1, fig. 1), with numerous traces of corrosion and mechanical damage.

No inner hollow of the spore is visible in optical sections. No unequivocal cavum is visible, but a torn specimen (Pl. 1, fig. 1) shows a space between the layers of the sporoderm that, however, can be of mechanical origin. Since we are not sure that all general morphological characteristics are preserved, we refrain from assigning the megaspores to a particular genus of *sporae dispersae*. The sporoderm is very dense, two-layered. The outer layer varies in thickness from 4.9 µm to 11.3 µm, pierced with numerous minute alveolae, 0.01-0.05 µm in diameter (Pl. 3, figs. 1, 2, 5, 7-9). In some places, globular units of about 0.4 µm also pierced with alveolae are vaguely recognizable (Pl. 3, figs. 1, 5, 7). The inner layer is of constant thickness, 0.17-0.23 µm, appearing homogeneous (Pl. 3, fig. 2). No definite cavum was revealed. In places, gaps in the outer layer were observed (Pl. 3, fig. 5). The inner hollow looks like a narrow slit (Pl. 3, fig. 2).

The uneven coloring of the megaspores, traces of corrosion and the fact that the inner hollow which once contained the gametophyte now is indistinguishable in transmitted light allow us to suspect that the megaspores are too much secondarily changed

to reveal the original sporoderm ultrastructure in ultrathin sections. Our TEM observations confirmed this suspicion. In our opinion, the minute alveolae numerous in the outer layer of the sporoderm are secondary changes not reflecting its original ultrastructure. This is supported by the fact that they are also present at the contact between the inner sporoderm layer and the megaspore hollow (Pl. 3, fig. 2). Besides, one of the authors (N.Z.) observed very similar minute alveolae in places in the sporoderm of *Biharisporites capillatus* Fuglewicz et Prejbisz, 1981, a megaspore from much older deposits and supposedly produced by an unrelated plant group (Turnau et al., 2009, pl. IV, fig. 5); in case of *Biharisporites*, it was also concluded that such alveolae did not reflect the typical ultrastructure of the sporoderm (Turnau et al., 2009). On the other hand, the areas of the sporoderm where globular units are distinguishable, are altered in a less degree than the majority of the sporoderm, in our opinion. The outer layer of the sporoderm might have been composed of such globular units fusing with each other and more or less elongated around the inner layer of the sporoderm. A few gaps observed in the sporoderm are most probably traces of mechanical damage: one of them is situated in the outer layer, cuts the inner layer, and reaches the inner hollow of the spore (Pl. 3, fig. 5). Dealing with such degree of preservation, we cannot decide about the presence or absence of a cavum. However, if our guess about globular units constituting the outer layer of the sporoderm is correct, such an ultrastructural type quite easily allows sporoderm splitting.

In modern *Selaginella* megaspores, the exospore consists of two layers: a thin and usually lamellate inner exospore and a much thicker outer exospore containing the aperture (Tryon & Lugardon, 1991). The inner layer under study appears homogeneous, and the ultrastructure of the aperture has remained unknown; however, the relative development of the two layers (thin inner layer and much thicker outer layer) implies that they may represent inner exospore and outer exospore.

7. Discussion

New finds of *in situ* spores have contributed to the knowledge on selaginellalean spores characterizing this group of plants during various periods of its geological history. Keeping in mind the diversity of
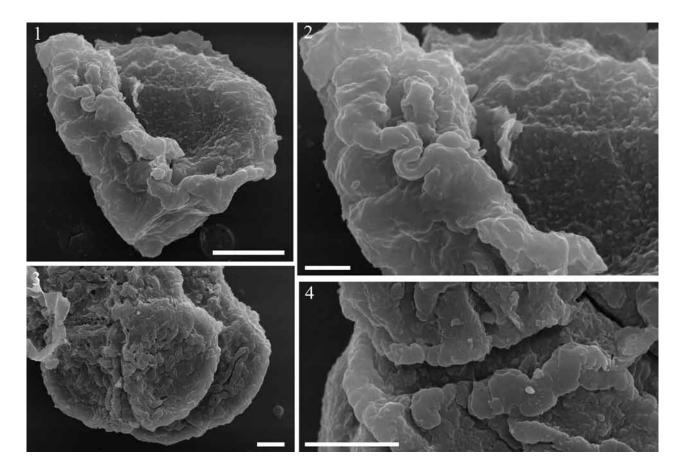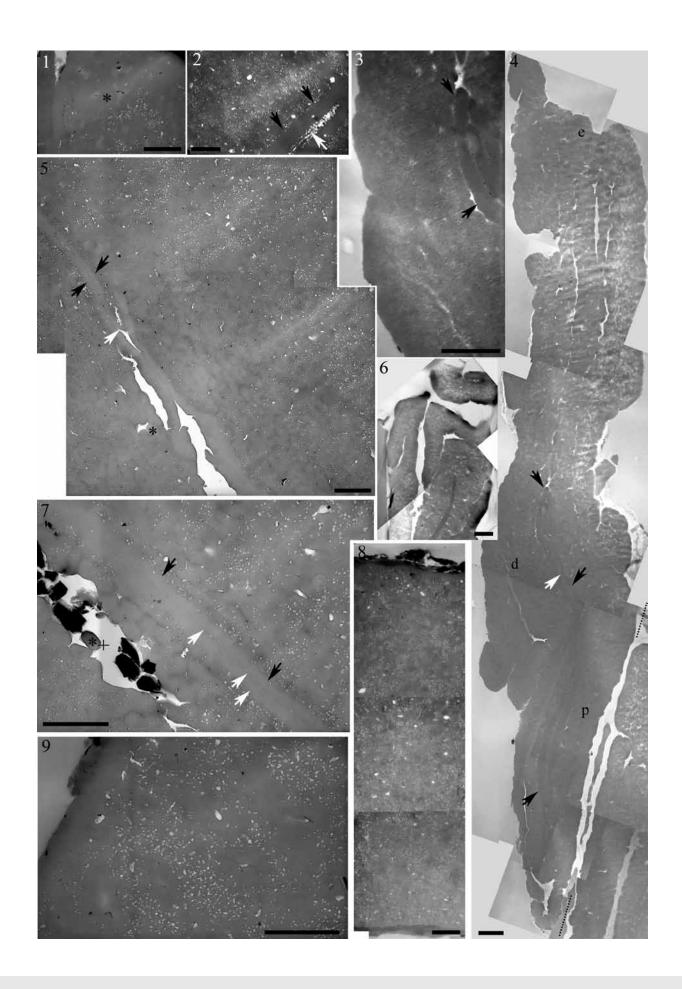
Plate 2 (SEM)
1. Individual microspore in lateral position. 2. Blowing-up of fig. 1 showing rugulate sculpturing of the equatorial to distal area and finely granulate sculpturing of the proximal area. 3. Cluster of several microspores showing rugulate distal sculpturing. 4. Enlargement of distal and equatorial sculpturing. Scale bar (1, 3, 4) 10 μm, (2) 3 μm.

Plate 3 (TEM)
1, 2, 5, 7-9. Ultrathin sections of megaspore sporoderm. 3, 4, 6. Ultrathin sections of microspore sporoderm. 1. Area of the section (closer to the surface of the megaspore), supposedly showing a region of the outer sporoderm with less alternated ultrastructure; nonetheless, minute alveolae are present. 2. Area of the section showing outer (to the left) and inner (to the right) layers of the sporoderm, the inner hollow of the megaspore is visible between the proximal and distal portions of the inner layer; minute alveolae are present in the outer layer and at the contact between the inner layer and the inner hollow. 3. Blowing up of fig. 4 showing outer and inner layer of microspore sporoderm. 4. Composite image of ultrathin section of microspore sporoderm. 5. An area of the section showing gaps in the sporoderm. Note outer and inner layers of the sporoderm. 6. Area of section of microspore sporoderm, elongated sculptural elements are cut. 7. Area of the section showing inner layer of the sporoderm and the outer layer of the megaspore sporoderm that in part pertains its supposed original globular ultrastructure. Note the globular units between the gap filled with black mineral stuff and the inner layer of the sporoderm. The inner hollow of the megaspore is traceable only as a darker contour between proximal and distal portions of the inner layer. 8. Area of section of megaspore sporoderm in the equatorial region, the most common appearance of megaspore sporoderm. 9. Minute alveolae piecing the megaspore sporoderm, an area of the outer layer shown situated close to the surface. Legend: black arrows - inner layer of sporoderm; white arrows - inner hollow of spore; asterixes - supposed globular units in megaspore sporoderm; p - proximal area of sporoderm; d – distal area of sporoderm; e – equatorial area of sporoderm; dotted line – boundary between two members of microspore tetrad. Scale bar (1-9) 1 μm.

spores in hundreds of modern species of *Selaginella* and the diversity of supposed selaginellalean spores from dispersed palynological assemblages that have never been reported from strobili, our concept about selaginellalean spores will become much more ramified with accumulation of additional data on *in situ* spores.

Spores of *Uvaesporites*, a dispersed genus suitable for microspores of *S. leonardii*, were already reported *in situ* from *Selaginellites hallei*, the macromorphologically most similar Triassic *Selaginellites* species to *S. leonardii* (Lundblad, 1950). Microspores of *S. hallei* are slightly smaller than those of *S. leonardii* (29-50 μm against 45-62.5 μm), but fall partly within its variability range. Although Lundblad (1950) interpreted the sculpturing of *S. hallei* as damaged (because of taphonomy or maceration), microspores of both species show a similar rugulate sculpturing. Unfortunately, no data about the ultrastructure of microspores of *S. hallei* are available. End-Permian dispersed *Uvaesporites* spores have a complex sporoderm that differs strongly in ultrastructure from microspores of *S. leonardii*: the sporoderm of the Permian spores was interpreted as consisting of an exospore and a complex paraexospore, whereas the two layers of the sporoderm of the Triassic microspores more probably both represent exosporal layers. To date, *Uvaesporites* was only reported from Selaginellales, but the ultrastructure of the Permian *Uvaesporites* does not exclude an isoetalean affinity. No *Uvaesporites* is so far known *in situ* from Permian strobili (either selaginellalean or isoetalean). Indeed, all these indices imply that the Permian *Uvaesporites* may be of isoetalean rather than selaginellalean origin. Similar spores are found *in situ* in both groups (Table 1). Future studies of the sporoderm ultrastructure will show if any differences exist between selaginellalean and isoetalean spores similar in gross morphology.

Although a sporoderm that includes several layers and easily allows splitting under forming a cavum is the most common type in selaginellalean microspores, acavate and much denser sporoderms are also known, where the ratio between sporopollenin units and spaces between them is very high. For example, dispersed Carboniferous *Densosporites* probably has a homogeneous sporoderm (Telnova, 2004). Taylor & Taylor (1989) studying dispersed the Lower Cretaceous megaspore *Erlansonisporites sparassis* (Murray) Potonié, 1956 of supposed selaginellalean affinity, found in their surface reticulum small trilete spores, which could have been produced by the same parent plant. The proximally smooth and distally verrucate

spores are two-layered; both layers appear homogeneous. Although the preservation of our material forces us to be cautious in our conclusions, we consider the microspores acavate and with a homogeneous sporoderm. Of interest is that though *Uvaesporites* type was not reported *in situ* from younger than Jurassic strobili, it seems to exist in some modern species. Thus, modern *Selaginella gracillima* (Kunze) Spring ex Salomon, 1883 has microspores that, as one can judge by illustrations, fit the genus *Uvaesporites*, if found as fossil *sporae dispersae* (Tryon & Lugardon, 1991, fig. 231.3).

Non-selaginellalean lycophytes are also abundant in Lower-lower Middle Triassic sediments, but strobili are only known for a few of them, and even less have preserved *in situ* spores. Thus, only *Aratrisporites*, *Lundbladispora*, and *Densoisporites* are known *in situ*. The microspores of *S. leonardii* differ from these types in general morphology and from *Densoisporites* (on which ultrastructural information is available) also in sporoderm ultrastructure. The intriguing question if Triassic *Densoisporites* of selaginellalean affinity differs in its ultrastructure from contemporaneous *Densoisporites* of isoetalean affinity is pending till *in situ* spores of the former will be studied by TEM.

There are classifications of extant selaginellalean megaspore sporoderms, proposed by Morbelli (1977), Minaki (1984) and Taylor (1989). The first two authors distinguished granular and spongy types; Minaki subdivided the granular type into irregular and ordered types, and the spongy type into two types. Taylor (1989) distinguished an ordered granular type and two spongy types: laterally and laminar fused. The laterally fused type is composed of anastomosing rod-like or spherical elements (so, in part it corresponds to an irregular granular type), and the laminar type is composed of wider sheet-like elements, often forming closed vesicles. These types can be used to reveal selaginellalean ultrastructure in fossil sporoderms. We incline that, when unaltered, the sporoderm of megaspores *S. leonardii* was granular, formed by fused spheroid units. In terms of the above classifications, it belongs to irregular granular type or to laterally fused type. Most dispersed megaspores of presumed selaginellalean affinity can be incorporated into this group, e.g., *Banksisporites* and *Bacutriletes* (other Triassic *in situ* finds of megaspores).

In dimensions, megaspores of *S. leonardii* are slightly smaller than those of *S. hallei* (270-340 x 300-410 μm against 330-425 μm) but fall partly within its variability range (Lundblad, 1950). The megaspore surfaces of both species lack distinct

sculptural elements, but megaspores of *S. hallei* are distinctly labrate, and their sporoderm is thicker than that in *S. leonardii* (about 15 μm against about 5.1-11.5 μm). The megaspores of *S. hallei* were assigned by Lundblad (1950) to *Triletes pinguis* Harris, 1935, which is now *Banksisporites pinguis* (Harris) Dettmann, 1961. Ultrastructural data on dispersed megaspores of this species from the Upper Keuper of Denmark were obtained by Kempf (1971). The sporoderm is two-layered. The outer layer is 15-20 μm thick, composed of numerous, irregularly distributed, more or less spherical particles (0.3-0.5 μm in diameter against about 0.4 μm of *S. leonardii*), partly fused and interconnected, with considerable spaces between them; the porosity of this layer does not seem to vary over the distance from the sporoderm surface. Such a sporoderm can be incorporated in the irregular granular type, the same type we have chosen for *S. leonardii*. However, the sporoderm of *S. leonardii* is so much denser and some of the units we managed to distinguish seem to be aligned along the inner layer. The inner layer in *B. pinguis* seems nearly homogeneous and reaching about 1-2 μm proximally (comparable with *S. leonardii*), but transforms into a loose lamellate net more than 10 μm in thickness distally (nothing comparable was observed in *S. leonardii*). Unlike *S. leonardii*, a cavum is clearly seen in *B. pinguis* (Kempf, 1971). Dettmann (1961, pl. 1, fig. 5) published a microtome section viewed in transmitted light of *B. pinguis* from the Triassic of Tasmania showing a cavate nature of the spore.

Kovach (1994) pointed out that the differences in sporoderm ultrastructure between two living groups of heterosporous lycopsids are less obvious than in their gross morphology. The sporoderms are composed of anastomosing sporopollenin elements, which range from rod-like to granular and form a porous network. Rod-like elements of living *Isoetes* tend to orient parallel to the surface of the spore and the sporoderm has a high porosity; sporopollenin elements of *Selaginella* are oriented more randomly and the sporoderm has lower porosity than in *Isoetes*: the sporopollenin elements tend to have less open space between them. Using these criteria, Kovach (1989) succeeded at differentiating between Cretaceous megaspores of the Selaginellales and Isoetales. However, Taylor (1994) dealing with older megaspores failed: isoetalean coats were very dense and fell into selaginellalean group. Although the general criterium (by higher/lower porosity) for differentiation between Isoetales and Selaginellales does not work for pre-Cretaceous specimens, some fossil sporoderms can

be considered selaginellalean with much confidence because of their similarity to certain ultrastructural types of modern species. Thus, very characteristically looking labyrinthine structure (e.g. *Selaginella erythropus* (Mart.) Spring, 1840, Tryon & Lugardon, 1991, fig. 231.83) and highly ordered grid-like structure (e.g. *S. marginata* (von Humboldt & Bonpland ex von Willdenow) Spring, 1838, Morbelli and Rowley, 1996, fig. 14; *S. sulcata* (Desvaux ex Poir.) Spring ex Mart., 1837, Morbelli et al., 2001, fig. 36D) were repeatedly observed in dispersed fossil megaspores: e.g. *Horstisporites harrisii* (Murray) R. Potonié illustrates the former type (Bergad, 1978, pl. 3, fig. 6) and *Erlansonisporites sparassis* (Taylor & Taylor, 1988, pl. 2, fig. 7), and *Richinospora cryptoreticulata* Bergad, 1978 (Bergad, 1978, pl. 5, figs. 1, 3) show the latter structure.

However, other types are not as easy to differentiate from the isoetalean ultrastructure, and this problem is still pending. Further ultrastructural studies will contribute to differentiation between these two groups or, alternatively, might show clearly overlapping characteristics. The current rarity of TEM studies on *in situ* selaginellalean spores by comparison to those accomplished on dispersed material should be underlined (Table 2), as well as the greater importance of the former for differentiation between the Selaginellales and Isoetales on the basis of sporoderm ultrastructure.

Outlining non-selaginellalean Triassic lycophytes, a greater number of *in situ* finds of megaspores can be mentioned compared to microspores. These *in situ* megaspores can be ascribed to *Dijkstraisporites* Potonié, 1956, *Minerisporites*, and *Tenellisporites* Potonié, 1956, *Horstisporites*, and *Maiturisporites* Maheshwari et Banerji, 1975. Megaspores of two species of *Banksisporites* were extracted from *Cylostrobus* strobili (one of them, B. pinguis, is the same species as was extracted from *Selaginellites hallei*). Some of the above-mentioned spore types are known in the Selaginellaceae as well; some (e.g. *Minerisporites* and *Horstisporites*) being found as *sporae dispersae* although in younger deposits, were considered by different authors as megaspores of selaginellalean (Archangelsky & Villar de Seoane, 1989) or isoetalean (Batten & Collinson, 2001) affinity.

Although the ultrastructural characteristics ascribed to the Selaginellales and Isoetales are often merging and certain types of megaspores are known from both groups, megaspores of the species under study show an ultrastructure that is quite dissimilar from typical isoetalean ultrastructure and corre-

sponds quite well to one of the known types of sela-
ginellalean ultrastructure.

8. Conclusions

This study further elucidates the diversity in spo-
re morphology and ultrastructure in one of the most
long-living groups of higher plants and documents
for the first time the ultrastructure of its *in situ* spo-
res dated to the Middle Triassic. The microspores are
supposedly acavate and have a two-layered homo-
geneous sporoderm; similar sporoderms are rare but
not a unique case among selaginellalean microspores.
Further ultrastructural studies on the Triassic materi-
al seem very promising, in particular, to estimate how
typical selaginellalean the ultrastructure revealed in
the microspores of *Selaginellites leonardii* is. *In situ*
finds of Permian *Uvaesporites* might resolve the si-
gnificance of the ultrastructural differences revealed
between Permian *Uvaesporites* and *in situ* microspo-
res of *S. leonardii*. The sporoderm ultrastructure of
the megaspores is interpreted as belonging to the
irregular granular or laterally fused types, which are
common among megaspores of presumed selaginel-
lalean affinity, including Triassic megaspores.

References

Andrews, H. N. (1961): Studies in Palaeobotany. - 487
   pp., Wiley and Sons Ed., New York and London.
Archangelsky, S., Villar de Seoane, L. V. (1989): Ultra-
   estructura de dos nuevas megasporas cretacicas de
   Santa Cruz, Argentina. - Boletín Asociación Latino-
   americana Paleobotánica y Palinologia, 12: 13-25.
Archangelsky, S., Villar de Seoane, L. V. (1990): Mor-
   fologia y estructura de megasporas cretacicas de
   Patagonia. Republica Argentina. - Revista Espanola
   de Micropaleontologia, 22 (3): 419-450.
Archangelsky, S., Villar de Seoane, L. V. (1991): Notas
   sobre la flora fosil de la Zona de Tico, provincia de
   Santa Cruz: XI. Morfologia y estructura de tres me-
   gasporas. Ameghiniana (Rev. Asoc. Paleontol. Ar-
   gent.) 28(3-4): 353-364.
Baldoni, A. M., Taylor, T. N. (1985): Megasporas Creta-
   cicas dea la formacion Springhill et El Subsuelo de
   Argentina y Chile austral. – Ameghiniana, 21(2-4):
   151-167.
Balme, B.E., 1995. Fossil *in situ* spores and pollen
   grains: An annotated catalogue. - Rev. Palaeobot.
   Palynol., 87: 1-323.
Batten, D. J. (1999): Small palynomorphs. - In: Jones,
   T. P., Rowe, N. P. (eds.): Fossil plants and spores. –
   Modern Techniques, 15-19, The Geological Society,
   London.
Batten, D. J., Collinson, M. E. (2001): Revision of spe-
   cies of *Minerisporites*, Azolla and associated plant
   microfossils from deposits of the Upper Palaeocene
   and Palaeocene/Eocene transition in the Nether-
   lands, Belgium and the USA. - Rev. Palaeobot. Paly-
   nol., 115: 1-32.
Bechstädt, T., Brandner, R. (1970): Das Anis zwischen
   St. Vigil und dem Höhlensteintal (Pragser-und
   Olanger Dolomiten, Südtirol). - In: Mostler, H. (ed):
   Beiträge zur Mikrofazies und Stratigraphie von Tirol
   und Vorarlberg, 9-103, Festband des Geologischen
   Institutes, 300-Jahr-Feier Universität Innsbruck,
   Wagner, Innsbruck.
Bek, J., Oplustil, S., Drabkova, J. (2001): The species of
   Selaginella cones and their spores from the Bohe-
   mian Carboniferous continental basins of the Czech
   Republic. - Rev. Palaeobot. Palynol., 114: 57-81.
Bergad, R. D. (1978): Ultrastructural studies of se-
   lected North American Cretaceous megaspores of
   Minerisporites, *Erlansonisporites*, *Horstisporites*
   and Richinospora, n. gen. - Palynology, 2: 39-51.

Bernard, S., Benzerara, K., Beyssac, O., Brown, G. E. Jr., Grauvogel-Stamm, L., Duringer, P. (2009): Ultrastructural and chemical study of modern and fossil sporoderms by Scanning Transmission X-ray Microscopy (STXM). - Rev. Palaeobot. Palynol., 156: 248-261.

Broglio Loriga, C., Fugagnoli, A., van Konijnenburg-van Cittert, J. H. A., Kustatscher, E., Posenato, R., Wachtler, M. (2002): The Anisian macroflora from the Northern Dolomites (Monte Prà della Vacca/Kühwiesenkopf, Braies): a first report. – Riv. Ital. Paleont. Stratigr., 108: 381-390.

Collinson, M. E. (1991): Diversification of modern heterosporous pteridophytes. - In Blackmore, S., Barner, S. H. (eds.): Pollen and Spores. Systematic Association Special Volume, 44: 119-150, Clarence Press, Oxford.

Cottman, C. F., Hemsley A. R., Rössler R., Collinson M. E., Brain, A. P. R. (2000): Diversity of exine structure in Upper Carboniferous (Westphalian) selaginellaceous megaspores. - Rev. Palaeobot. Palynol., 109: 33-44.

Dettmann, M. E. (1961): Lower Mesozoic megaspores from Tasmania and South Australia. - Micropaleontology, 7 (1), 71-86.

De Zanche, V., Gianolla, P., Mietto, P., Siorpaes, C., Vail, P. R. (1993): Triassic sequence stratigraphy in the Dolomites (Italy). - Mem. Sci. Geol., 45: 1 – 27.

Fugagnoli, A., Posenato, R. (2004): Middle Triassic (Anisian) benthic Foraminifera from the Monte Prà della Vacca/Kühwiesenkopf section (Dont Fm, Braies Dolomites, Northern Italy). – Boll. Soc. Paleontol. Ital., 43 (3): 347-360.

Guy-Ohlson, D. (1979): A new species of *Densoisporites* (Weyland & Krieger) Dettman in the Jurassic of southern Sweden. - Grana, 18(2): 129-131.

Halle, T. G. (1907): Einige krautartige Lycopodiaceen paläozoischen und mesozoischen Alters. – Kungl. Svensk. Vetenskapsakad. Handl., 7 (5): 1-17.

Hemsley A. R., Scott, A. (1989): The ultrastructure of four Australian Triassic megaspores. - Pollen et Spores, 31: 133-154.

Kempf, E. K. (1971): Electron microscopy of Mesozoic megaspores from Denmark. - Grana, 11: 151-163.

Kempf, E. K. (1973): Transmission electron microscopy of fossil spores. - Paleontology, 16: 787-797.

Koppelhus, E.B., Batten, D.J. (1989): Late Cretaceous megaspores from southern Sweden: morphology and paleoenvironmental significance. - Palynology, 13: 91-120.

Kovach, W. L., (1989): Quantitative method for the study of lycopod megaspore ultrastructure. - Rev. Paleobot. Palynol., 57: 233-246.

Kovach, W. L. (1994): A review of Mesozoic megaspore ultrastructure. – In: Kurmann, M. H., Doyle, J. A. (eds.): Ultrastructure of fossil spores and pollen, p. 23-38.

Kovach, W. L., Dilcher. D. L. (1988): Megaspores and other dispersed plant remains from the Dakota Formation (Cenomanian) of Kansas, U.S.A. - Palynology, 12: 89-119.

Krassilov, V. A. (1978): Mesozoic lycopods and ferns from the Bureja basin. – Palaeontographica, Abt. B., 166 (1-3): 16-29.

Kustatscher, E. (2004): Macroflore terrestri del Triassico Medio delle Dolomiti e loro inquadramento bio-cronostratigrafico e paleoclimatico mediante palinomorpfi. - 220 pp., unpublished PhD Thesis. University of Ferrara, Ferrara.

Kustatscher, E., Manfrin, S., Mietto, P., Posenato, R., Roghi, G. (2006): New biostratigraphic data on Anisian (Middle Triassic) palynomorphs from the Dolomites (Italy). - Rev. Paleobot. Palynol., 140: 79–90.

Kustatscher, E., Roghi, G. (2006): Anisian palynomorphs from the Dont Formation of Kühwiesenkopf / Monte Prà della Vacca section (Braies Dolomites, Italy). - Micropalaeontology, 52 (3): 223-244.

Kustatscher E., Wachtler, M., van Konijnenburg-van Cittert J.H.A. (2010): Lycophytes from the Middle Triassic (Anisian) locality Kühwiesenkopf (Monte Prà della Vacca) in the Dolomites (Northern Italy). – Palaeontology, 53(3): in press.

Lee, H. H., (1951): On some *Selaginellites* remains from the Tatung Coal series. - Science Record, 4 (2): 193-196.

Looy, C. V., Collinson, M. E., Van Konijnenburg-Van Cittert, J. H. A., Visscher, H., Brain, A. P. R. (2005): The ultrastructure and botanical affinity of end-Permian spore tetrads. - Int. J.Plant Sci., 166(5): 875-887.

Lugardon, B., Grauvogel-Stamm, L., Dobruskina, I. (1999): The microspores of *Pleuromeia rossica* Neuburg (Lycopsida, Triassic): comparative ultrastructure and phylogenetic implications. - Compt. Rend. Acad. Scienc., ser. II, fasc. A, Scienc. Terr. Plan., 329 (6): 435–442.

Lugardon, B., Grauvogel-Stamm, L., Dobruskina, I., (2000): Comparative ultrastructure of the megaspores of the Triassic lycopsid *Pleuromeia rossica* Neuburg. – Compt. Rend. Acad. Scienc., ser. II, fasc. A, Scienc. Terr. Plan., 330 (7), 501–508.

Lundblad, B. (1950): On a fossil *Selaginella* from the Rhaetic Hyllinge, Scania. - Svenska Botaniisk Tidskrift, 44 (3), 475-487.

Meyer-Melikian, N.R., Zavialova, N.E. (1996): Disperse distal-sulcate pollen grains from the Lower Jurassic of Western Siberia. - Botanich Zhurn., 81(6): 10-22 [In Russian].

Minaki, M., (1984): Macrospore morphology and taxonomy of *Selaginella*. - Pollen et Spores, 26: 421-480.

Morbelli, M. A. (1977): Esporas de las especies argentinas de *Selaginella* (Selaginellaceae-Pteridophyta). - Obra Cent. Mus. La Plata, 3: 121-150.

Morbelli, M. A., Rowley, J. R., 1996. Application of confocal microscopy to exospore ultrastructure of megaspores of *Selaginella convoluta* and *S. marginata.* - J. Plant Res., 109: 33-44.

Morbelli, M. A., Rowley, J. R., Claugher, D. (2001): Spore wall structure in *Selaginella* (Lycophyta) species growing in Argentina. - Bol. Soc. Argent. Bot., 36(3-4): 315-368.

Naugolnykh, S. V., Zavialova, N. E. (2004): *Densoisporites polaznensis* sp. nov.: with comments on its relation to *Viatcheslavia vorcutensis* Zalessky. - The Paleobotanist, 53: 21-33.

Pal, P.K. (1984): Morphotaxonomy of heterophyllous Lycopsid shoot from the Rajmahl Hills, India. - The Palaeobotanist, 32 (3): 321-325.

Raine, J.I., N.J. De Jersey, and K.G.Ryan (1988): Ultrastructure and lycopsid affinity of *Densoisporites psilatus* (de Jersey) comb. nov. from the Triassic of New Zealand and Queensland. - Mem. Ass. Australas. Palaeontols, 5: 79-88.

Retallack, G.J., 1997. Earliest Triassic origin of *Isoetes* and Quillwort evolutionary radiation. – Jour. Palaeont., 71(3): 500-521.

Retallack, G. J., Metzger, C. A., Graver, T., Jahren, A. H., Smith, R. M. H., Sheldon, N. D. (2006): Middle-Late Permian mass extinction on land. – Geol. Soc. Amer. Bull., 118: 1398-1411.

Schimper, W. P. (1869): Traité de Paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel. - 738 pp., I. J. B. Baillère et Fils éd., Paris.

Schweitzer, H.-J., van Konijnenburg-Van Cittert, J. H. A., van de Burgh, J. (1997): The Rhaeto-Jurassic flora of Iran and Afghanistan. 10. Bryophyta, Lycophyta, Sphenophyta, Pterophyta-Eusporangiatae and -Protoleptosporangiatae. - Palaeontographica, Abt. B., 243: 103-192.

Senowbari-Daryan, B., Zühlke, R., Bechstädt, T., Flügel, E. (1993): Anisian (Middle Triassic) Buildups of the Northern Dolomites (Italy): The Recovery of Reef Communities after the Perm/Triassic Crisis. - Facies, 28: 181-256.

Seward, A. C. (1910): Fossil Plants II – A Textbook for students of Botany and Geology. - 624 pp., Cambridge University Press, Cambridge.

Skog, J. E., Hill, C. R. (1992): The Mesozoic herbaceous lycopsids. - Annals of the Missouri Botanical Garden, 79 (3): 648-675.

Srivastava, G. K., Srivastava, P. C., Shukula, P. K. (1993): Antiquity and diversification of *Isoetes* through the ages. – In: Srivastava, P. C. (ed.): Vistas in Palaeobotany and Plant Morphology: Evolution and Environmental Perspectives, Prof. D.D. Pant Memorial Volume, U.P. Offset, Lucknow, India.

Takahashi, M., Crane P.R., Ando, H. (2001): Fossil Megaspores of Marsileales and Selaginellales from the Upper Coniacian to Lower Santonian (Upper Cretaceous) of the Tamagawa Formation (Kuji Group) in Northeastern Japan. – Int. Journ. Plant Scienc., 162(2): 431-439.

Taylor, T. N., Taylor, E. J., Krings, M. (2009): The Biology and Evolution of plants. - 1230 pp., Elsevier, Amsterdam.

Taylor, W. A. (1989): Megaspore wall organization in *Selaginella*. - Pollen et Spores, 31: 251-288.

Taylor, W. A. (1994): Tests and application of a method of quantitative analysis of fossil and extant lycopsid megaspore walls. – In: Kurmann, M. H., Doyle, J. A. (eds.): Ultrastructure of Fossil spores and Pollen. pp. 39-52, Royal Botanical Garden, Kew.

Taylor, W. A., Taylor, T. N. 1988. Ultrastructural analysis of selected Cretaceous megaspores from Argentina. - J. Micropaleontol. 7: 73-87.

Taylor, W. A., Taylor, T. N. (1990): Persistent ultrastructural features in microspores of heterosporous lycophytes. – Grana, 29: 219-228.

Telnova, O. P. (2004): New species of spores from the Devonian deposits of southern Timan Region. - Bull. Moscow Society of Naturalists, Biol., 109(1): 63-70 [in Russian].

Thomas, B. A. (1992): Paleozoic herbaceous lycopsids and the beginnings of extant *Lycopodium* sens. lat. and *Selaginella* sens. lat. – Ann. Miss. Bot. Garden, 79: 624-631.

Townrow, J.A. (1968): A fossil *Selaginella* from the Permian of New South Wales. - J. Linn. Soc. London Bot., 61: 13-23.

Tryon, A. F., Lugardon, B. (1991): Spores of Pterido-phyta: surface, wall structure and diversity based on electron microscope studies. - Springer. New York.

Turnau, E., Zavialova, N., Prejbisz, A. (2009): Wall ul-trastructure in some dispersed megaspores and seed-megaspores from the Middle Devonian of northern Poland. - Rev. Palaeobot. Palynol., 156: 14–33.

Villar de Seoane, V., Archangelsky, S. (2008): Taxonomy and biostratigraphy of Cretaceous megaspores from Patagonia, Argentina. – Cretac. Res., 29: 354–372.

Watson, J. (1969): A revision of the English Wealden flora. I. Charales - Ginkgoales. - Bull. Mus. Nat. Hist. Geol., 17: 207–254.

Zeiller, R. (1906): Bassin houiller et Permien de Blanzy et du Creusot. II. Flore fossile. Études Gîtes Miné-raux de la France. - 265 pp., Ministère des Travaux Publics, Paris.