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Higher plants and miospore assemblage of Burtnieki Regional Stage (Givetian) of South Estonia

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ABSTRACT

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The flora of Joosu Quarry (Estonia) is additionally studied from the deposits of Abava Member of Givetian Burtnieki Regional Stage. Its systematic composition has been expanded to four species instead of the previously known single species. The predominance of representatives of *Pseudosporochnus* and presence of single lycopsid is reported. The diagnostic features of *Pseudosporochnus* species are revealed and the specific composition of this genus is inspected. Spores from sporangia of *Pseudosporochnus* for the first time along with the miospore assemblage from the deposits of Abava Member, containing plants are allocated and illustrated. The age of Abava Member deposits is determined by macroflora as the possible Lower Givetian. Dispersed miospores allowed us to take Abava Member to the *Geminospora extensa* (EX) Zone which corresponds to the modern view the lower and middle parts of Givetian.

Key–words—Higher plants, Pseudosporochnids, Spores from sporangia, Dispersed miospores, Givetian, Estonia.

दक्षिणी ऐस्टोनिया में बर्टनीकी आंचलिक स्टेज (जिवेटियन काल) की उच्चतर वनस्पतियां एवं सूक्ष्मबीजाणु समुच्चय

एलफटिना एल. जुरीना एवं मरीना जी. रस्काटोवा

सारांश

जिवेटियन कालीन बर्टनीकी आंचलिक स्टेज के अबावा सदस्य के निक्षेपों से प्राप्त जोसु खदान (ऐस्टोनिया) अतिरिक्त रूप से अध्ययन की गई हैं। इसका क्रमबद्ध संघटन पहले से ज्ञात एकल जाति के बजाय चार जातियों तक विस्तृत है। *प्स्युडोस्पोसेकनस* निरूपकों की पूर्वप्रभाविता तथा एकल लायकोप्सिड की विद्यमानता वर्णित की गई है। *प्स्युडोस्पोसेकनस* जाति के नैदानिक लक्षण प्रकट किए गए हैं तथा इस वंश के विशिष्ट संघटन जांचे गए हैं। वनस्पति सन्निहित अबावा सदस्य के निक्षेपों से प्राप्त सूक्ष्मबीजाणु समुच्चय के साथ पहली बार *प्स्युडोस्पोसेकनस* के स्पोरान्जिया से बीजाणु नियत एवं चित्रित किए गए हैं। अबावा सदस्य निक्षेपों का काल स्थूल वनस्पतिजात से यथा संभव निम्न जिवेटियन निर्धारित किया गया है। परिक्षिप्त सूक्ष्मबीजाणुओं ने अबावा सदस्य को *जेमिनोस्पोरा एक्सटेन्सा* (ई एक्स) अंचल में नियत करने पर सुझाया जो जिवेटियन के अधो एवं मध्य भागों के आधुनिक परिदृश्य के अनुरूप हैं।

सूचक शब्द—उच्चतर वनस्पतियां, प्स्युड़ोस्पोरोकनिड्स, स्पोरोन्जिया से बीजाणु, परिक्षप्ति सूक्ष्मबीजाणु, जिवेटियन, ऐस्टोनिया।

INTRODUCTION

GIVETIAN plants and miospores were not known in the territory of Estonia, until the end of twentieth century, except one locality with remains of flora in Burtnieki Regional Stage in Joosu Quarry. In this locality *Pseudosporochnus estonicus* was described by Kalamees (1988), however the position of this plant in the section and its belonging to the certain member was also not indicated. Dispersed miospores from the Burtnieki Regional Stage deposits in the territory of Estonia are unknown.

The aims of this research are: (1) to study more plants from Joosu Quarry and establish their general systematic composition; (2) allocation of dispersed miospores and finding the spores in sporangia of plants; (3) determination of the age of the deposits on the basis of macroflora and miospores studied.

We have given special attention to the revision of the species composition of the genus *Pseudosporochnus* Potonié & Bernard, 1904 and also to the complicated problem of identification of diagnostic and specific features. Studying the stratigraphic and geographic distribution of *Pseudosporochnus* is of great interest because it is rarely found in the Devonian of Western Europe. Now–a–days in this region only four districts, namely Czechia, Belgium, Scotland and Estonia have reported this genus. Detailed study of macroflora and miospores of Estonia will reveal the age of the rocks containing these remains and their complete correlation with the coeval deposits in other regions.

MATERIAL AND METHODS

The material was collected by Mark–Kurik from Givetian of South Estonia from the Joosu Quarry, located 50 km to the south of Tartu on a left bank of the River Vohandu (Figs 1, 2). This material was studied in the Moscow State University. The collection has more than 30 fragments impressions and counter–impressions of vegetative and fertile axes of plants. It is housed in the Department of Palaeontology, Faculty of Geology, Moscow State University, Moscow, Russia, № 349.

Fig. 1—Geographic position of Joosu Quarry.

Identification of the plants is based on comparison with collections from Stur (1881, Taf. II, fig. 2), which first described and depicted fertile specimens *P. verticillatus* from the Middle Devonian of Czechia, and are stored in the National Museum in Prague and Museum of Karlov University. Much attention was paid to research of the lectotype and paratypes of *Pseudosporochnus verticillatus* and holotype of *P. chlupáči*. The lycopsid collection from Devonian of Libya, housed at Laboratoire de Paléobotanique Université Pierre et Marie Curie, Paris was also studied. Museum collections from Czechia and Libya have served as a significant additional material for this research.

Dispersed miospores were extracted from the matrix rocks, using the latest methods (Vidal, 1988; Raevskaya & Shurekova, 2011). Spores from sporangia are winkled out according to the method described in Jurina & Raskatova (2014). Spores were studied with LM and SEM POLAM–312; photography was carried out by NIKON camera. The collection of miospores N J–014–7 m and spores from sporangia (N J–014–7–0 mc, N J–014–7–1 mc) is housed in the Laboratory of Micropalaeontology of Geological Department of Voronezh State University, Voronezh, Russia.

STRATIGRAPHIC COLUMN IN JOOSU QUARRY

The section in Joosu Quarry was fully described by Kuršs (1992) and was a stratotype, proposed for the first time in Joosu Formation which was placed in the upper part of Givetian Burtnieki Regional Stage (Kuršs, 1992). For the lower part of Burtnieki Regional Stage, allocation of a separate formation was not supposed. Mark–Kurik & Nemliher (2003) indicated that the fish fauna and lithological content of Joosu show that it can be considered as the upper part of the Abava beds–the third or upper part of Burtnieki Regional Stage. These layers were named as Abava Member and were placed it in the upper part (not specified precisely) of Givetian Burtnieki Regional Stage of stratigraphic scheme (Mark–Kurik & Põldvere, 2012). In this work we consider, that the studied plants belong to Abava Member of Burtnieki Regional Stage. A section described by Kuršs was taken and used it in the modified and simplified forms. Kuršs (1992) picked out 4 layers with ikhtiofauna, consistently alternating with the remains of other 6 layers of macroflora in the section. The conditional badges and their position in a section were shown but a systematic structure of palaeontologic objects was missing. We have numbered each layer, keeping the sequence of stratigraphic positions, specified by Kuršs (1992) and tried to find out the systematic structures of some layers according to other references (Fig. 3).

In this section Kuršs (1992) has marked out three geologic layers of varying thickness and various palaeontologic remains. The lowermost layer (4 m thick) consists of greenish–grey and variegated claystone. It marks the first interlayer with fossil fishes, as concretion with fish remains

Fig. 2—General view of outcrops and deposits of Abava Member talus; in the foreground paleoikhtiolog E Mark–Kurik and her daughter.

in the core. Above in the section two interlayers (the 2nd and the 3rd) have shells of the conchostraceans, which were named by following workers: *Asmussia* Pacht, 1849 (Tallinn *et al.*, 1970) or *Glyptoasmussia* by Novojilov & Varentsov, 1956 (Mark–Kurik & Nemliher, 2003) were observed. Tasch (1969) showed that *Glyptoasmussia* is synonymous of the genus *Asmussia*, and we also use the name *Asmussia*. Plant macroremains in the lowermost layer are not marked. The middle layer consists of grey and dark grey fine–dispersed claystone (up to 11 m), where three interlayers with fish and all macroflora of Joosu Quarry were marked. The arthodire *Watsonosteus* Miles & Westoll, 1962 and the antiarch *Microbrachius* Traquair, 1888 were seen in the 5th and 11th interlayers. The 8th interlayer includes phosphatic concretions containing parts of squamation and other skeletal remains of different fishes namely psammosteids and sarcopterygians (Mark–Kurik & Nemliher, 2003). It was difficult to establish the correspondence of plants and miospores in one of the six stratigraphic levels specified in the section by Kuršs (1992) because a lot of remains yielded in talus (Mark–Kurik & Nemliher, 2003, p. 2; Personal communications from Mark–

Kurik). The colour of the rock with impressions of plants was studied and saw that the larger part impressions come from the dark claystone and the smaller part–come from the light claystone. Some of them are characterized by intermediate shades of claystone colour. There is a probability that these two localities with macroflora may have been located close to each other. These localities probably correspond to the 7th interlayer with flora according Kuršs (1992) which have been designated with two parallel signs of macroflora at the same level. Probably, these two localities were placed along the strike of the claystones 7th interlayer. We have identified locality with the dark claystone as a 7a (the numbers of collection of macroflora are: 349/1–349/30) and light claystone as a 7b (349/31–349/40). Macroflora from the 7a locality consists of: *Pseudosporochnus verticillatus* (Krejči) Obrhel, *P. chlupáči* Obrhel, *P. estonicus* Kalamees. The systematic composition of dispersed miospores is: *Punctatisporites atavus* (Naum.) Ahmed., *P. solidus* (Naum.) Byvsch., *Lophotriletes fastuosus* Naum., *Cyclogranisporites plicatus* Allen, *Microreticulatisporites minor* (Naum.) Oshurk., *Convolutispora subtilis* Owens, *Retusotriletes laevis* Tchibr., *R. simplex* Naum., *R.* sp., *Chelinospora concinna* Allen, *Apiculiretusispora* cf. *plicata* (Allen) Streel, *Reticulatisporites perlotus* (Naum.) Obukh., *Cymbosporites magnificus* (McGregor) McGregor & Camfield, *Geminospora extensa* (Naum.) Gao, *G. tuberculata* (Kedo) Allen, *G. decora* (Naum.) Arkh., *G. mutabilis* (Kedo) Owens, *G. pustulata* (Naum.) Zbuk., *G. rugosa* (Naum.) Obukh., *G. notata* (Naum.) Obukh., *G. micromanifesta* (Naum.) Owens = *G. lemurata* Balme, *G. compta* (Naum.) Owens, *G. treverica* Riegel, *G. antaxios* (Tchibr.) Owens, *G.* sp., *Cristatisporites* (?) *violabilis* (Tchibr.) M. Rask., *Tholisporites variabilis* (Naum.) Oshurk. var. *insignis* Sen., T. sp., *Stenozonotriletes stenolomus* (Naum.) Kedo, *Ambitisporites simplex* (Naum.) Oshurk.

Macroflora from the 7b locality consists of: *Precyclostigma* sp., *Pseudosporochnus estonicus* Kalamees. Miospore assemblage is represented by small single forms, viz. *Punctatisporites atavus* (Naum.) Ahmed., *P. solidus* (Naum.) Byvsch., *Microreticulatisporites minor* (Naum.) Oshurk., *Retusotriletes* sp.

Position in Joosu section of *Pseudosporochnus estonicus*, described by Kalamees (1988), is unknown, perhaps this plant is disposed from these two localities. The typical material is now lost.

The section ends with the third layer (2 m thick) consisting of the cross–bedded sandstones, siltstones and claystones devoid of fauna and flora. The total thickness of Abava Member of Joosu Quarry is 17 m.

PALAEONTOLOGICAL SECTIONS

I. Lycopsids: characteristics and features of the stratigraphic distribution of the genus Precyclostigma

The genus *Precyclostigma* which is still not marked amongst the European, Asian and American Devonian floras has been recorded from noted in the Devonian deposits of Joosu Quarry (Estonia, Burtnieki Regional Stage, Abava Member).

This genus was first described by Lejal–Nicol (1975a) from the Tadrart Formation (Middle Siegenian): base of Emsian and, according to the modern stratigraphic scheme as Middle Pragian to base of Emsian in North Africa (Murzuk, Libya, Murzuk). Devonian sediments in the Murzuk Basin are divided into three formations: the Tadrart, Ouan Kasa and Aouinet–Ouenine, each of which contains a considerable floral element. The Lower Tadrart Formation lies unconformably on the Lower Silurian. The age of this formation is set by correlation with the formations of the Sahara, containing marine fauna (Klitzsch *et al.*, 1973; Lejal–Nicol, 1975a, b). Ouan Kasa Formation lies conformably on the Tadrart Formation and in accordance with the findings of spiriferidians, rhynchonellides and trilobites (the compositions of which are not specified) refers to the Emsian (Lejal–Nicol, 1975a, b). Upper Aouinet–Ouenine Formation lies in accordance with Ouan Kasa Formation and dates like Middle–Upper Devonian. This conclusion is based on spiriferidians (Lejal–Nicol, 1975a, b; Lejal–Nicol & Massa, 1980). According to us the age of formations is reasonably very unconvincing. First of all, the relative position of fauna and flora, in sections of each formation are not shown; the levels with fossils aren't allocated and systematic structures of fauna and flora are not described. In establishing the Early Devonian age to these sediments the presence of "spiriferidian, rhynchonellidian and trilobites" (Lejal–Nicol, 1975a, p. 55) is not evidence–based.

Flora of the three formations is represented by a large compositional variability, consisting of more than 15 genera of lycopsids (Lejal–Nicol, 1975a; Lejal–Nicol & Massa, 1980). Genus *Precyclostigma* is seen in each formation. The

PLATE 1

The plant remains of vegetative units from Burtnieki Regional Stage of Estonia, *Precyclostigma* sp. (1); *Pseudosporochnus verticillatus* (Kreiči) Obrhel (3, 5, 7, 8); *Pseudosporochnus estonicus* Kalamees (2, 4, 6), LM; Abava Member: locality 7a (6, 7), locality 7b (1–5, 8).

1. Specimen 349/36, axis with leaf scars, in centre of axis impression of conducting cylinder. x 2.
2. Specimen 349/39, dichotomizing ultimate unit at wide angle. x 2.5.
3. Specimen 349/32, digitate branching of axis. x 1.
4. Specimen 349/37, twice dichotomizing axis. x 2.
5. Specimen 349/9, dichotomy of axis at wide angle. x 1.
6. Specimen 349/38, small bulb base of axis. x 2.
7. Specimen 349/1, cluster form of lateral branching system. x 2.
8. Specimen 349/35, axis with nests of sclereid. x 2.5.

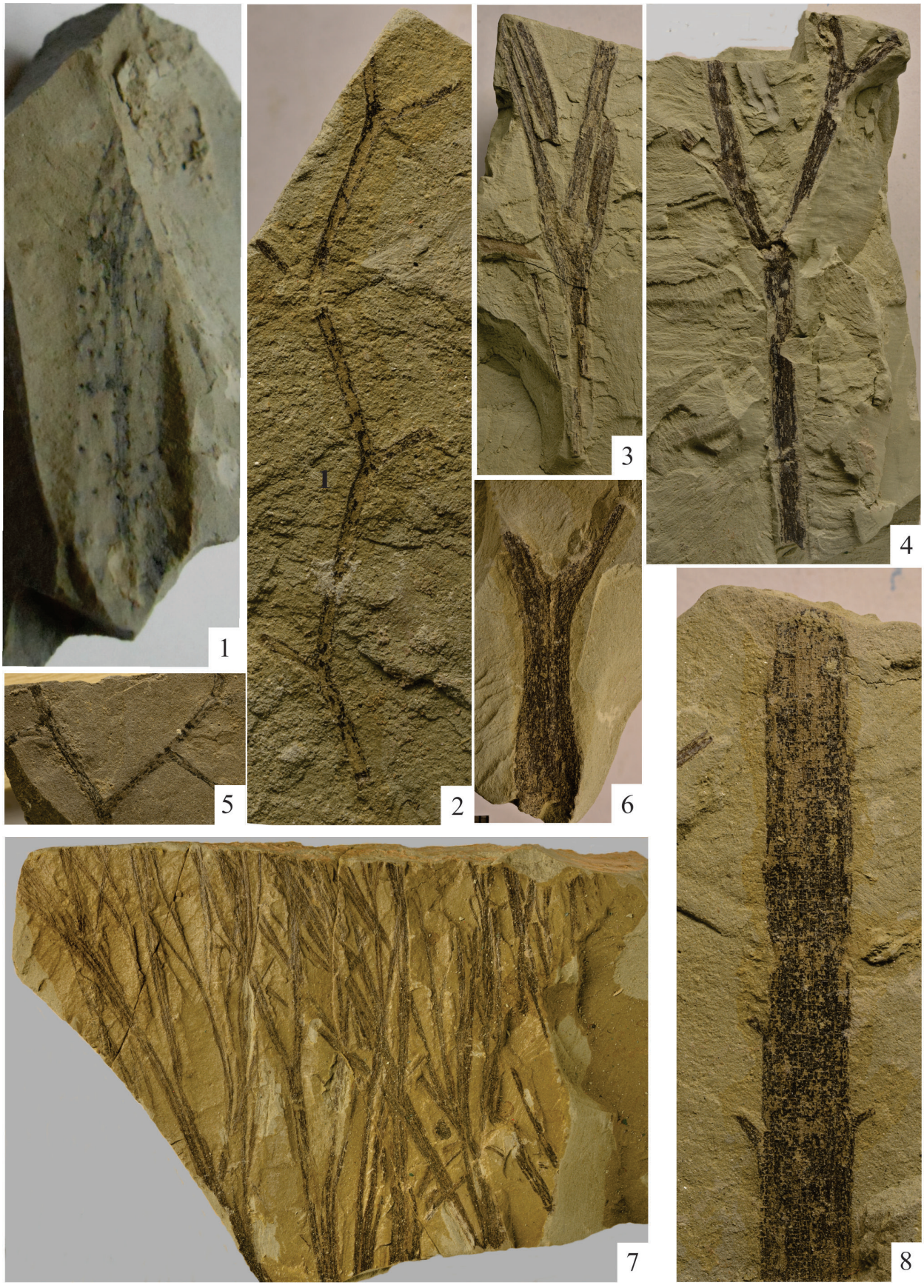


PLATE 1

presence of generas such as *Archaeosigillaria* Kidston, 1901; *Lepidodendropsis* Lutz, 1933; *Prelepidodendron* Danzé–Corsin, 1960; *Pseudolepidodendropsis* Schweitzer, 1969; *Abacodendron* Radczenko, 1956; *Tomiodendron* (Radczenko) emend. Meyen, 1972 and many others in the Lower Devonian sediments, seems doubtful. It is noted by Meyen (1976: p. 121): "The generic affinities of the African plants for the inclusion in *Tomiodendron* nov., seems rather doubtful", and also emphasized that many of these genera are in need of total revision. According to the world paleobotanical literature, genera of plants of the Murzuk Basin are found in North America, Europe, Kazakhstan, China, in the Middle Devonian (mainly Givetian)–Lower Carboniferous sediments. However Lejal–Nicol has not analyzed the stratigraphic distribution of genera and species of plants. It appears that the age of the Tadrart, Ouan Kasa, Aouinet–Ouenine formations of Libya, may be determined as the Middle–Late Devonian, based on the generic composition of plants. Unfortunately, the Libyan Murzuk Basin flora has not been discussed in the literature up till present.

The position of the genus *Precyclostigma* amongst the higher systematic categories of lycopsids is not clear. Lejal–Nicol (1975a) placed the genus *Precyclostigma* in the family *Sublepidodendraceae* together with 8 other previously known genera. The main features indicated for this family by Schweitzer (1969), are not marked in the *Precyclostigma* species. These features include the absence of a tree shape plant, leaf cushions, similar to the true lepidodendroids cushions and the reproductive organs. Therefore it is not necessary to include the genus *Precyclostigma* in Sublepidodendraceae, and we should not compare this genus with other members of this family, as it was previously done by Lejal–Nicol, (1975a, b). It appears that the absence of many important features gives sufficient reasons to place the genus *Precyclostigma* in lycopsids incertae sedis.

LYCOPSIDS INCERTAE SEDIS

Genus—PRECYCLOSTIGMA Lejal–Nicol, 1975

Precyclostigma: Lejal–Nicol, 1975a, p. 72; 1975b, p. 75; 1980, p. 234.

Diagnosis—The leaf cushions are absent or reduced to leaf scars with long tapered tips; the cortex is smooth and slightly ribbed. The leaf scars are ovate or rounded with cicatricle in the centre; they are arranged vertically or at a low spiral. Parichnos and ligule are absent. Leaves and reproductive organs are unknown.

Species composition—Two species: *P. tadrartense* Lejal–Nicol, 1975; *P. caudata* Lejal–Nicol, 1975.

Type Species—P. tadrartense Lejal–Nicol, 1975, Lower (?)–Upper Devonian; Africa, Libya.

Stratigraphic and geographic distribution—Africa, Libya, Murzuk Basin; Lower Devonian (?)–Upper Devonian; Europe, Estonia, Burtnieki Regional Stage, Givetian.

Precyclostigma sp.

Pl. 1.1

Description—Fragment of an axis with a parallel smooth edges is 53 mm long. The width of the axis (11–12 mm) and is constant along the entire visible length. The rounded leaf scars with a diameter 0.5–0.6 mm located at a low spiral (angle 5–7°). 11–12 rows of scars are observed separated by 4–6 mm; the distance between scars is 3–4 mm. The rounded distinct cicatricle (diameter 0.08–0.09 mm) is placed in the centre of the leaf scar. A long narrow strand with width 1.8–1.9 mm is located in the central part of the axis which is observed along the entire length; it apparently represents the impression of a conducting cylinder.

Material—1 specimen (impression and part of counter–impression). Estonia, Joosu Quarry; Burtnieki Regional Stage (Givetian), Abava Member.

II. Briefly about the morphology and structure of pseudosporochnid plants

Plants of extinct class *Cladoxylopsida* Pichi–Sermolli, 1959 have a large distribution in the Middle Devonian. They belong to the basal group of fernlike plants with missing

PLATE 2 →

Fertile units and spores "in situ" of *Pseudosporochnus* from Burtnieki Regional Stage of Estonia, *P. verticillatus* (Kreiči) Obrhel (3, 5, 6, 7); *P. estonicus* Kalamees (1, 2, 4, 7); *Retusotriletes laevis* Tchibrikova (8, 9,13); *Retusotriletes sp*. (10–12); Abava Member, locality 7a.

1. Specimen 349/4, single club–shaped upright sporangia. x 5, LM.
2. Specimen 349/5, single club–shaped upright sporangia. x 5, LM.
3. Specimen 349/6, sporangia with gradual separation from segment. x 8, LM.
4. Specimen 349/4, enlarged sporangium without spores from Fig. 1 (arrow). x 10, LM.
5. Specimen 349/30, enlarged sporangium with spores from Fig. 6 (arrow). x 10, LM.
6. Specimen 349/30, sporangia with gradual separation from segment. x 5, LM.
7. Specimen 349/3, sporangia of *P. verticillatus* in the left part of the image (arrow indicates the sporangium with spores), *P. estonicus* in right. x 2, LM.

8, 9, 13. Specimen 349/30, *Retusotriletes laevis*–spores from sporangium of *Pseudosporochnus verticillatus*, proximal view; 8–distinct curvature, x 600, SEM; 9–detail of curvature, x 800, SEM; 13–proximal view, showing destroyed exine and distinct curvature. x 600, SEM.

10–12. Specimen 349/3, *Retusotriletes* sp.–spores from sporangium of *P. verticillatus*, proximal view. x 600, SEM.

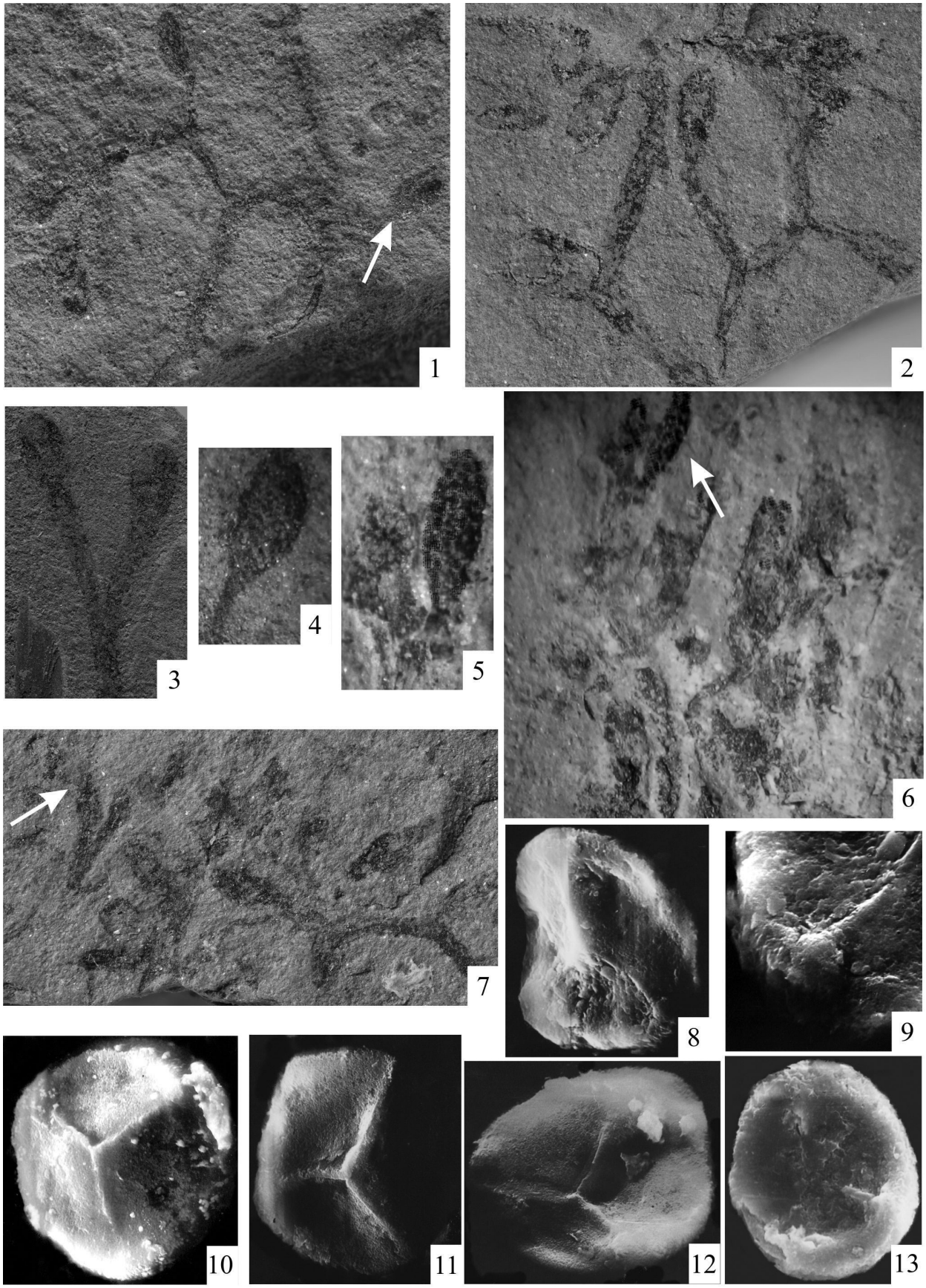


PLATE 2

leaves. The function of leaves is performed by bilaterally symmetrical or three–dimensional of branching systems. Significant components among cladoxylopsids were representatives of *Pseudosporochnales*, which together with lycopsids and progymnosperms constituted the terrestrial ecosystems from Emsian to Early Mississippian (Soria & Meyer–Berthaud, 2005). Presently four genera are included in the *Pseudosporochnales*: *Pseudosporochnus* Potonié & Bernard, 1904; *Calamophyton* Kräusel & Weyland, 1926; *Wattieza* Stockmans, 1968; *Lorophyton* Fairon–Demaret & Li, 1993. The morphology and, to a lesser extent, anatomy is studied for these genera (Soria & Meyer–Berthaud, 2003; Wang & Berry, 2006).

It has been over 100 years since the establishment of a type genus *Pseudosporochnus* of *Pseudosporochnales*. Two species were known until the middle of last century: *P. verticillatus* (Krejči) Obrhel, 1959 and *P. chlupáči* Obrhel, 1959, from the Middle Devonian of Czechia (Krejči, 1881; Stur, 1881; Potonié & Bernard, 1903–1904; Kräusel & Weyland, 1933) and Belgium (Leclercq, 1940). Characteristics of the genus was extremely poor at that time. By the end of the twentieth century, and especially at the beginning of twenty–first, the characteristics of this genus have become more or less complete with the new findings.

First of all, the anatomical structure of the stem for the belgian Middle Devonian *P. nodosus* Leclercq & Banks, 1962 was studied and was shown that this genus belonged to cladoxylalean (Leclercq & Banks, 1962; Leclercq & Lele, 1968). This made a complete picture about the genus *Pseudosporochnus* and its distinctive features from other genera of *Pseudosporochnales* (Fairon–Demaret & Li, 1993; Soria & Meyer–Berthaud, 2003, 2005; Taylor *et al.,* 2009). Under the new model *Pseudosporochnus* is a tree about 6 meters high (Meyer–Berthaud & Decombeix, 2009; Meyer–Berthaud *et al.*, 2010).

Class—CLADOXYLOPSIDA Pichi–Sermolli, 1959

Order—PSEUDOSPOROCHNALES Hirmer, 1927

Genus—PSEUDOSPOROCHNUS Potonié & Bernard, 1904

Chondrites: Krejci, 1881, p. 69.

Sporochnus: Stur, 1881, p. 342.

Pseudosporochnus: Potonié & Bernard, 1904, p. 25; Hirmer, 1927, p. 162; Lang, 1927, p. 453; Kräusel & Weyland, 1933, p. 12; Obrhel, 1961, p. 12; Leclercq & Banks, 1962, p. 3; Jurina, 1969, p. 63; Kalamees, 1988, p. 84; Fairon–Demaret & Li, 1993, p. 17; Soria & Meyer–Berthaud, 2005, p. 873; Taylor *et al.*, 2009, p. 389; Meyer–Berthaud, Soria & Decombeix, 2010, p. 63.

Diagnosis—Trees about 6 m high, with straight, vertical and robust main branch, digitate crown of branches at the top of the plant and bulbulian base in the bottom. The branches form the lateral branch systems that divide dichotomously. Among the vegetative units the ultimate fertile units are arranged. Ultimate units show a planated morphology and are rarely three–dimensional, fertile and vegetative units are identical. Sporangia are terminal, upright, single or paired, clearly or less clearly separate from the ultimate segment. On all parts of the plants rounded bodies are observed which represented the nests of sclereid. The anatomical structure is represented by dissected vascular system of the various configurations of the primary xylem.

Comparison—Genus *Pseudosporochnus* differs from other genera of *Pseudosporochnales* in a structure of terminal branching system. The system is characterized by the terminal dichotomously divided flattened units with the upright sporangia on the ends of the unmodified fertile units, located among sterile.

Type Species—*Pseudosporochnus verticillatus* (Krejči) Obrhel, 1959; Middle Devonian (Givetian); Czechia.

Species composition—Five species: *P. verticillatus* (Krejči) Obrhel, 1959; *P. chlupáči* Obrhel, 1959; *P. nodosus* Leclercq & Banks, 1962; *P. estonicus* Kalamees, 1988; *P. hueberi* (Matten) Stein & Hueber, 1989.

PLATE 3

Dispersed miospores from Burtnieki Regional Stage, Abava Member, locality 7a of Estonia, specimen N–J–014–7; 1–13 x 400; 15–22 x 450; LM.

1. *Geminospora pustulata* (Naum.) Zbuk.
2. *Reticulatisporites perlotus* (Naum.) Obukh.
3. *Tholisporites variabilis* (Naum.) Oshurk. var. *insignis* Sen.
4. *Tholisporites* sp.
5. *Retusotriletes laevis* Tchibr. Miospore close to spores from sporangium of *P. verticillatus* (specimen 349/30).
6. *Apiculiretusispora* cf. *plicata* (Allen) Streel
7. *Retusotriletes simplex* Naum.
8. *Retusotriletes* sp.
9. *Geminospora decora* (Naum.) Arkh.
10. *Geminospora* sp.
11. *Geminospora* sp.
12. *Ambitisporites simplex* (Naum.) Oshurk.
13. *Geminospora mutabilis* (Kedo) Owens
14. *Geminospora compta* (Naum.) Owens
15. *Geminospora treverica* Riegel
16. *Cristatisporites* (?) *violabilis* (Tchibr.) M.Rask.
17, 18. *Geminospora notata* (Naum.) Obukh.
19. *Geminospora rugosa* (Naum.) Obukh.
20. *Geminospora micromanifesta* (Naum.) Owens
21. *Geminospora antaxios* (Tchibr.) Owens
22. *Geminospora* cf. *micromanifesta* (Naum.) Owens

PLATE 3

The problem of species composition of the genus *Pseudosporochnus*

Till date 9 species of *Pseudosporochnus* are described in the literature with varying degrees of detail: *P. verticillatus* (Krejči) Obrhel, 1959; *P. chlupáči* Obrhel, 1959; *P. nodosus* Leclercq & Banks, 1962*; P. ukrainica* Ischenko, 1965; *P. ambrockense* Mustafa, 1978*; P. heteroramis* Schweitzer & Cai, 1987; *P. estonicus* Kalamees, 1988; *P. hueberi* (Matten) Stein & Hueber, 1989; *P. vogtii* (Høeg) Schweitzer, 1999. 6 of them are known only from external morphology (*P. verticillatus, P. chlupáči, P. ukrainica, P. heteroramis, P. estonicus, P. vogtii*), 1 species (*P. hueberi*), is known only from anatomy, 2 species (*P. nodosus, P. ambrockense*) are known from their external and internal structure. *P. nodosus* from the Middle Devonian of Belgium is the most complete pseudosporochnid, which has an external morphology, anatomical structure and the overall appearance of the plant (Leclercq & Banks, 1962).

In the 9 mentioned species of *Pseudosporochnus* some researchers views are not included in this genus. Most palaeobotanists clearly accept the following species: *P.verticillatus, P. chlupáči, P. nodosus* (Jurina, 1969; Kalamees, 1988; Fairon–Demaret & Li, 1993; Soria & Meyer–Berthaud, 2005; Taylor *et al.*, 2009). Some discrepancies were concerned to the name of the type species only, which were resolved with the researches by Obrhel (1959. 1961).

Krejči (1881) has briefly described, but has not depicted, fossil plants from the Middle Devonian of the Central Bohemia under the name *Chondrites verticillatus*, relating them to algae. Stur (1881) has repeatedly described the same plants, depicted them and placed in the extant genus of algae *Sporochnus* as *S. krejčii.* Potonié & Bernard (1904) have studied the Bohemian flora on the same collections and have established that the majority of plants belong to the vascular plants. They had installed the scalariform tracheids and tracheids with rounded (bordered?) pores for the specimens of *Sporochnus krejčii* and a new genus was created *Pseudosporochnus*. The species name now is *P. krejčii* (Stur) P.& B. Up to sixties of the last century some researchers used this name (Hirmer, 1927; Lang, 1927; Kräusel & Weyland, 1933; Leclercq, 1940 & all). Obrhel (1959, 1961) first pointed out that the specific name of *verticillatus* used Krejči (1881: 69) has priority over the name *krejčii*, assigned to the same species by Stur (1881: 342). He created a nomenclature combination of *Pseudosporochnus verticillatus* (Krejči) Obrhel and noted that the type species (for Obrhel genotype) of genus *Pseudosporochnus* should be called as a *P. verticillatus* (Krejči, 1881). This name will be followed by all palaeobotanists in the future.

The new species *P. ukrainica* from the Late Givetian of Donbass (Ukraine) were described by Ischenko (1965). Only the vegetative axes dichotomously branched with filiform ultimate segments was used by her. Species from Donbass does not even have features of the genus *Pseudosporochnus*, therefore, we must assume the erroneous reference of *P. ukrainica* in the species composition of the genus *Pseudosporochnus* (Jurina, 1969; Kalamees, 1988).

P. ambrockense was installed in the Upper Eifelian sediments of Germany. Unfortunately, the original description of this species was not available to us. Information about this plant is taken from the article of Fairon–Demaret & Li (1993), in which they described two cladoxylopsids: *Lorophyton goense* and *Pseudosporochnus ambrockense*. *P. ambrockense* which have a number of features that are not typical to the genus *Pseudosporochnus*: systems of branching are only entirely sterile or only fertile (*Pseudosporochnus* is characterized by the arrangement of reproductive units among vegetative); sporangia are paired, pendent with twisted tips (sporangia of *Pseudosporochnus* are single and upright); the terminal units are three–dimensional (*Pseudosporochnus* has planated terminal units). These characteristics raised doubts in the relationship of *P. ambrockense* with genus *Pseudosporochnus. P. ambrockense* which were not considered in the genus *Pseudosporochnus* by us.

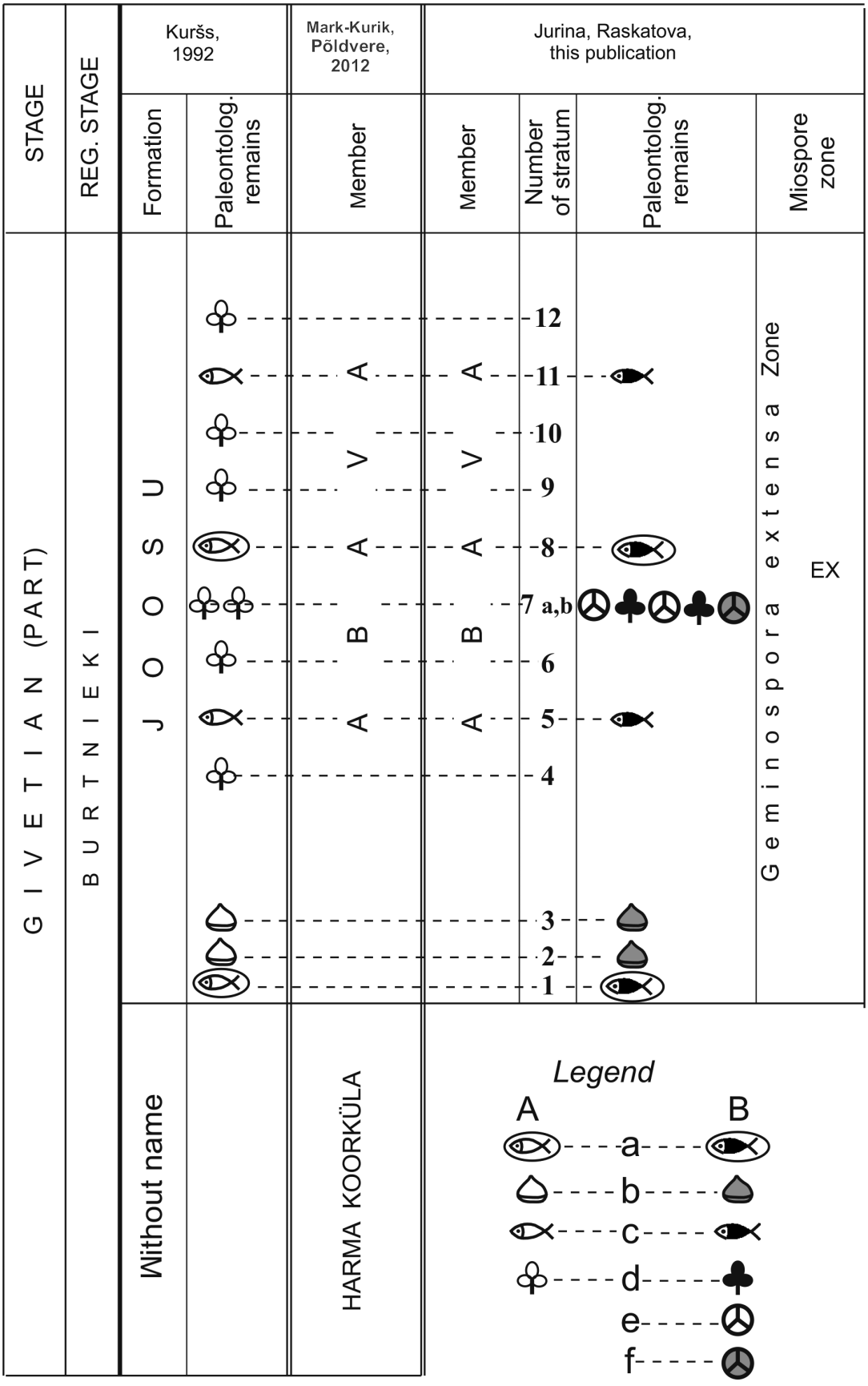
Schweitzer & Cai (1987) described a new species *P. heteroramis* that was presented with sterile impressions from Givetian of South China. The two types of branching of main axis were distinguishing features which identified them from other species which represented with irregularly dichotomous or hand shaped in the lower part and pseudoverticillate in the upper part. The lateral branching systems consist of units branching distally onece. Fertile organs were not preserved. Comparison with other species of this genus has not been conducted. It appears that the described features *P. heteroramis* do not match the characteristics of the genus *Pseudosporochnus.* Most likely, these impressions from South China should be attributed to some another genera. Fairon–Demaret & Li (1993: 17) did not include this species in the genus, and preferred "to leave it apart".

P. estonicus (Kalamees, 1988) from Givetian of Estonia is a valid species. It has the features of the genus *Pseudosporochnus* and new species (Table 1), but, unfortunately, it is probably unknown to present researchers.

Schweitzer (1999) reinvestigated the original specimens of *Hyenia* (*Hyeniopsis*) *vogtii* Høeg from the Devonian of Spitsbergen, described by Høeg (1942). He came to the conclusion that the structure of the vegetative lateral organs is closer to the genus *Pseudosporochnus* than to the genus

→

Fig. 3—The correlation and age of regional stratigraphic units in the Joosu Clay Quarry (Estonia). Legend: a–fish remains in core; b–conchostaceans; c–fish remains; d–plant macroremains; e–dispersed miospores; f–miospores from sporagia; A–taxonomic composition is not indicated; B–taxonomic composition is given in this publication.


STAGE
REG. STAGE
Kuršs, 1992
Formation
Paleontolog. remains
Mark-Kurik, Põldvere, 2012
Member
Jurina, Raskatova, this publication
Member
Number of stratum
Paleontolog. remains
Miospore zone
GIVETIAN (PART)
BURTNIEKI
JOOSU
A
V
A
B
A
B
A
A
A
12
11
10
9
8
7 a,b
6
5
4
3
2
1
Geminospora extensa Zone
EX
Without name
HARMA KOORKÜLA
Legend
A
B
a
b
c
d
e
f

Hyenia and created a new combination: *Pseudosporochnus vogtii* (Høeg) Schweitzer. The position of the three–dimensional branching system of terminal lateral units Schweitzer did not discuss. The pictures of terminal units of *P. vogtii* (Schweitzer, 1999, Abb. 38 a, b) illustrate three–dimensionality, which causes doubts in a relationship of this plant with genus *Pseudosporochnus*. Schweitzer (1999) also noted that the assignment of the species *vogtii* to the genus *Pseudosporochnus* has no clear proof for the absence of reproductive system and anatomical structure.

P. hueberi was found in the Lower Frasnian deposits of North America and was presented by permineralized specimens (Stein & Hueber, 1989). Tissue of this plant is only primary xylem and has many anastomosing xylem primary segments. General anatomical structure of *P hueberi*, according to the authors of the species is similar to *P. nodosus* and convinces us of the correctness of referring it to the genus *Pseudosporochnus.*

ANALYSIS OF DIAGNOSTIC FEATURES OF THE EXTERNAL STRUCTURE OF PSEUDOSPOROCHNUS SPECIES

Criteria for the selection of species of the genus *Pseudosporochnus* is discussed rarely in literature. Earlier (Jurina, 1969) briefly marked only few features as a species features without discussing them to the concrete representatives. Review of the literature data and the detailed study of the collections from Czechia (*P. verticillatus, P. chlupáči*), from Central Kazakhstan (*P. nodosus)* and from Estonia (*P. verticillatus, P. chlupáči, P. estonicus*) allowed us to identify more distinct the characteristics of the species of this genus. Ten features, which are often used in the description have been chosen for the comparative analysis (Table 1).

The first five features relate to the characteristics of the sporangia and are fundamental in identifying of species. Most

Genus *Pseudosporochnus* Potonié & Bernard, 1903-1904

Species / Features	***P. verticillatus*** **(Krejči) Obrhel, 1959**	***P. chlupáči*** **Obrhel, 1959**	***P. nodosus*** **Leclercq & Banks, 1962**	***P. estonicus*** **Kalamees, 1988**
The sporangium of terminal segment	single	single	pair	single
The sporangium separation from segment	gradual	clear [x]	clear	clear
The form of sporangia	club-shaped	globular	elliptic [x]	oblong-oval
The size of sporangia, mm	1,2 - 0,35	1-1 [x]	2-3 – 0,8	average 3,12 – 1,32
The degree of elongation	3,4 [x]	1 [x]	2,5, seldom 3 [x]	2,35
The form of the lateral branching system	cluster, narrowly-triangular [x]	equilateral-triangular[x]	lanceolate	broadly-triangular
The angle branching of vegetative units°	5-10 [x]	15-50, more often 15- 40 [x]	20-40 [x]	50-80
The angle branching of fertile units°	5-7, seldom 15 [x]	30-45 [x]	20-35 [x]	60-90
The number of dichotomies vegetative units	3, seldom 4 [x]	4, seldom 5[x]	3	3-4 [x]
The number of dichotomies fertile units	2, more often 3 [x]	3-4 [x]	3	4-6

Table 1—Comparison of the importance characters of *Pseudosporochnus* species. Legend: [x]the character is not indicated in original description.

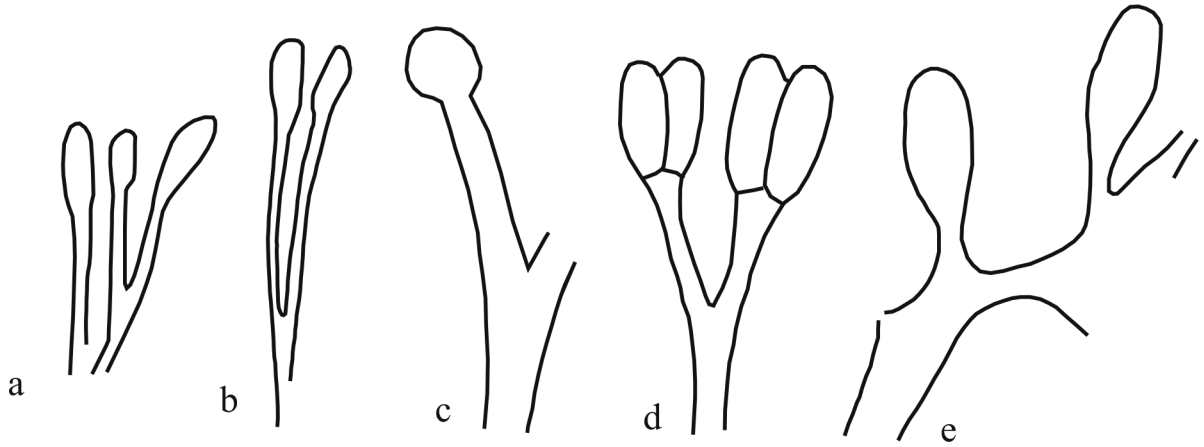


Fig. 4—Drawings of form sporangia species of the genus *Pseudosporochnus* (all figures are based on the data of pictures and drawings of different researchers; the magnification for all figures the same x 10): a, b–*P. verticillatus* (a–Leclercq, 1940, Pl. VIII, fig. 49; b–Leclercq & Banks, 1962, Pl. 4, fig. 23); c–*P. chlupáči* (Obrhel, 1961, Taf. V); d–*P. nodosus* (Leclercq & Banks, 1962, text fig. 2); e–*P. estonicus* (Kalamees, 1988, text fig. 1).

important are: the nature of the sporangium of the terminal segment (single or pair), the method of separation of the sporangium from the segment and the degree of elongation of the sporangium.

It is necessary to make explanations about the number of sporangia on the terminal segment of the *Pseudosporochnus verticillatus*. Stur (1881, Taf. II, fig. 2) was first who described and depicted fertile specimens *P. verticillatus* from the Middle Devonian of Czechia. He noted that thin hair–like terminal ends of the lateral axes terminate with club–shaped fruit bodies (Stur, 1881: 347, "keulenförmigen Früchten"). These fruit bodies are single and appear gradually from the hair–like part of the ends. Potonié & Bernard (1904) have briefly described the same specimens of *P. verticillatus*, and suggested that the swollen terminal ends of the axes were equivalented to the sporangia. Since then, the subsequent researchers, using data of Stur and Potonié & Bernard, regarded them as the real sporangia. Leclercq (1940, Pl. VIII, fig. 49) described and depicted sporangia of *P. verticillatus* from the Middle Devonian of Belgium as a single elongated swollen terminal ends of axes (Fig. 4). She extracted the spores from these bodies. Leclercq & Banks (1962) interpreted in two ways the character of the terminal segments of *P. verticillatus*. The sporangium belonging to this species that was sent to them from Czechia, is depicted and described as a single (Leclercq & Banks 1962, Pl. 4, fig. 23; p. 25: "Sporangia of *P. verticillatus* are borne single on a short pedicel"). Comparing *P. nodosus* and *P. verticillatus*, they also noted the position of the pair of sporangia *P. verticillatus* (Leclercq & Banks 1962: 24," Both species bear sporangia in terminal pairs"). Some researchers (Jurina, 1969; Kalamees, 1988 and all) initially took the second view of Leclercq and Banks (1962) for paired sporangia at the end of the terminal units. Subsequent study of the lectotype and isotypes of *P. verticillatus*, from the National Museum and the Charles University Museum in Prague, have convinced us that the sporangia of *P. verticillatus* are single (Fig. 4).

Sporangia of *P. verticillatus, P.chlupáči* and *P. estonicus* are single. The last two species differ from *P. verticillatus* with clear and not gradual separation of the body of the sporangium from the axis. Distinctive feature of the last two species is the form of sporangium: globular to *P. chlupáči* and oblong–oval to *P. estonicus* should be noted that the form of the sporangium is not always possible to distinguish between species. Sporangia described as club–shaped (*P. verticillatus*), elliptic (*P. nodosus*) and oblong–oval (*P. estonicus*) are close to each other. The sizes of sporangia allow to distinguish species, but usually referred to the spread of numbers is not very intuitive. It is therefore proposed to apply coefficient–degree of elongation (proportion of length to width of sporangia). This coefficient is almost never used in descriptions of species. However, this coefficient differs among the above–mentioned species, and from our point of view, immediately gives an idea of the shape of sporangium: globular or elongated, and how much elongated (Table 1).

The following five signs are important to establish specimens of *Pseudosporochnus* that are represented with sterile axes of the plants. The form of the side branch system in the species varies from narrow–to the widely–triangular. It is determined by the angles of branching like the sterile and fertile units that are within the same species close to each other. So narrowly–triangular shape to *P. verticillatus* is formed by branching angles of 5–10° units of both types and broadly–triangular form to *P. nodosus* is characterized by the angles from 50 to 80–90°. The number of dichotomies is not an indicative sign. It is almost the same to all species and changes both at sterile units, and at fertile from 3 to 4. These two features can be only auxiliary.

Description of the studied species of *Pseudosporochnus* does not provide, (as in the previous literature they repeatedly

described in great details), that it is specified in corresponding sections of this article and in Table 1, by us. We do not reveal some new morphological data except spores produced from the sporangia that is allocated to a separate section.

SPORES FROM SPORANGIA

Spores from sporangia of the genus *Pseudosporochnus* are almost unknown. In the previous literature, there are two short mentions about spores "in situ" of this genus without establishment of their latin names and without their descriptions. Kräusel & Weyland (1933) have described the tiny oblong oval spores (4–7 µm in diameter) taken from the mixed sporangia placed close to impressions of *P. verticillatus,* from the Middle Devonian of Czechia belonging, in their opinion, to this species. Except the sizes, they haven't specified other data about these spores. Leclercq (1940) recovered spores from the sporangia with swollen ends of the Givetian plant *P. verticillatus* from Belgium. Spores were dark red in colour with smooth wall, 6–9 µm in size. Pictures, description and the names of the spore's species were not given by the researchers.

We have attempted to extract the spores from the sporangia of the two species of the genus *Pseudosporochnus: P. estonicus* and *P. verticillatus*. Sporangium of *P. estonicus* (specimen 349/4 it is specified by the arrow) (Pl. 2.2,4) did not contain spores although in some distance from the fragments of the fertile parts of the plant a lot of small (10–12 µm) miospores simple in their morphology have been found in clusters. The sporangia *P. verticillatus* (specimen 349/6) (Pl. 2.3) also did not contain spores. In the sporangia of two specimens of the specimen *P. verticillatus* (specimens 349/30, 349/3) (Pl. 2.5,6,7) spores have been found. The sporangium of the specimen 349/30 (Pl.2.5) contained a large number of spores of well (Pl. 2.8,9) and poorly (Pl. 2.13) preserved spores ranging in size from 10–12 to 15–17 µm. The spores were contained in the sporangium in the total mass. Their spores are trilete and radial. Amb broadly rounded subtriangular. Exine laevigate or with very fine infrastructure, 0.5 µm thick. Trilete mark is distinct. Laesura are simple, straight, varying in length between 1/3 and 3/4 of the spore radius. Ends of the laesura are joined by distinct curvature which may mark a slight change in thickness of the exine. Some specimens of spores show the distinct curvature of one or two ends of the trilete mark. Wall slightly sculptured, may appear insignificantly thicker (by about 0.2 µm) at the equator inter–radially because of confluence of curvatural ridge with the equator in that region. Walls are commonly thinner to the contact areas than elsewhere. The sporangium of the specimen 349/3 (Pl. 2.7, arrow indicates the sporangium with spores) contained spores with good and satisfactory preservation from 13 to 18 µm in size (Pl. 2.10–12). Spores are radial, trilete. Amb is circular. Laesura are distinct, simple, varies in length. Ends of rays are connected by curvature that may be confined to the proximal face. Curvature may be indistinct. Slight perforation is present on the contact areas of some specimens.

The present study of the spores extracted from the sporangia of *P. verticillatus* showed that they are well preserved microspores and it is possible to compare them with the formal taxa of dispersed miospores. Given the size and features of the structure of spores (trilete marked with distinct curvature, the character of the exine) from sporangium (349/30) can be compared with the formal taxon *Retusotriletes laevigatus* Tchibr. Microspores from sporangium (349/3) can be compared with the taxon *Retusotriletes* sp.

GEOLOGIC AGE OF ABAVA MEMBER DEPOSITS ACCORDING FAUNA AND FLORA IN JOOSU QUARRY

Fishes

The small complex of ikhtiofauna represented with placoderms *Watsonosteus* and *Microbrachius*, is set in Joosu Quarry in Abava Member. This assemblage is compared to the assemblage of fishes of the same mineralogically similar layers in the nearby close located localities along Vohandu River (Mark–Kurik & Nemliher, 2003). Stratigraphically important fishes were found in this locality: *Psammolepis abavica* Mark–Kurik, *Watsonosteus* sp., *Microbrachius* sp. First two forms have been mentioned as the key–fossils of the Abava level of the Middle Givetian (Mark–Kurik, 2000; Mark–Kurik & Põldvere, 2012). Abava Member is correlated with Scottish units of John o' Groats Sandstones and Eday Flagstones, in which placoderms *Microbrachius* and *Watsonosteus* are found (Ahlberg *et al.,* 1999; Mark–Kurik & Nemliher, 2003). Nodular phosphatic concretions from the middle layer of Joosu section with squamation and other skeletal remains of different fishes (psammosteids, sarcopterigians), as Mark–Kurik & Nemliher (2003) indicated, are unknown from other localities in Estonia but occur in Scotland. Mark–Kurik & Nemliher (2003) have marked the possible correlation of Abava Member with Givetian Moroch Formation of the Polotsk Regional Stage of Belarus, which contains the antiarch *Microbrachius*. These researchers have placed the Abava Member with fossil fishes in the middle of Givetian Stage.

Conchostraceans

Conchostraceans of genus *Asmussia* without specific name were found in two interlayers of Joosu section. Some species of this genus are marked in Givetian deposits of Tuva and other regions of Russian Federation. Other species were fixed in Paleozoic deposits of Russain Federation: Tuva, Khakassia, Eastern Siberia, the Arctic (Novojilov, 1960). The age of deposits with remains of this genus may be determined not older than Givetian. It is important to note that the presence

in the sediments Conchostraceans suggests the existence of shallow lagoons, with numerous banks.

Dispersed miospores

Dispersed miospores of Abava Member were installed in Joosu Quarry from two localities: 7a and 7b. Systematic composition of miospore assemblage from 7a locality is more variable (27 species), than composition from 7b locality (4 species). Assemblage from 7b locality is represented by single and small forms with simple and rugulate exine ornamentation. 4 species from 7b are also known in 7a. Therefore, we combine these two assemblages into a single one, which corresponds to the 7a miospore assemblage, consisting of 27 species, listed above. This assemblage is characterized by the domination (up to 65–70%) of small miospore (10–18 μm), belonging to the genera: *Punctatisporites, Cyclogranisporites, Lophotriletes, Retusotriletes*. Miospores of the genus *Geminospora* make up the third part of the assemblage (about 38%). They demonstrate the variability of sculptures from the typical forms with acutely tuberous forms like *Geminospora tuberculata* (Kedo) Allen (5–7%) to the species with roundly tuberous sculpture of the exine like *Geminospora micromanifesta* (Naum.) Owens (=*Geminospora lemurata* Balme) (25–30%). Large miospore with size more than 60 μm with zone and bifurcate processes in the studied assemblage are absent. On the whole the miospore assemblage from Joosu Quarry is characterized by the appearance of the genus *Geminospora* and the development of species include: *G. extensa, G. tuberculata, G. decora, G. mutabilis, G. compta, G. treverica, G. pustulata, G. micromanifesta, G. rugosa, G. notata, G. antaxios* (Pl. 3). Its composition corresponds to the characteristic of *Geminospora extensa* (EX) Zone, allocated for the Givetian Stage of the East European Platform (EEP) (Avkhimovitch *et al*., 1993). This Zone has been conformed to the Starooskol Superhorizon including Vorobiev, Ardatov and Mullin Regional Stage. According to the decisions of the Stratigraphic Committee of Russia (Sobolev & Evdokimova, 2008) the EX miospore Zone corresponds to the Lower and Middle Givetian. The EX Zone is divided into three Subzones: *Cymbosporites magnificus–Hymenozonotriletes tichonovitschi* (MT) (Vorobiev Regional Stage), *Vallatisporites celeber–Cristatisporites* (?) *violabilis* (CV) (Ardatov Regional Stage), *Cristatisporites triangulatus–Corystisporites serratus* (TS) (Mullin Regional Stage). We assume that Abava Member miospore assemblage from Joosu Quarry most likely characterizes the lower MT and middle CV Subzones of EX Zone. Index species *Cymbosporites magnificus* of subzone MT and index species *Cristatisporites* (?) *violabilis* of Subzone CV are present in the Joosu Assemblage. Both indexes species of Subzone TS are absent.

Miospore assemblage of Abava Member from Estonia is close to miospore assemblage of Salatzskaya Formation of Givetian from Latvia, allocated by Ozolinja (1963). However, the assemblage from Latvia is characterized by poor species composition (11 species). Species of genera: *Punctatisporites, Lophotriletes, Microreticulatisporites, Geminospora* (morphon *G. lemurata*), *Tholisporites* (*T. variabilis=Archaeozonotriletes variabilis*) and *Ambitisporites* (A. *simplex*) are common for assemblages of Estonia and Latvia. Some of miospore species of Salatzskaya Formation are represented by small miospores with a simple or reticulate ornamentation of the exine like in the Joosu Assemblage. Detailed comparison with miospores of Salatzskaya Formation is difficult because the representations of the miospores from Latvia are provided only drawn.

The studied assemblage can be correlated with the miospore assemblage from Givetian deposits of Belarus. The studying of dispersed miospores in Belarus and the establishment of their stratigraphic significance a large group of researchers has been carried out (Obukhovskaya TG *et al*., 2005, 2014; Obukhovskaya VYu *et al*., 2015). They allocated the EX miospore Zone composed of 2 Subzones: *Geminospora vulgata–Retispora archaeolepidophyta* (VA), *Cristatisporites triangulatus–Corrystisporites serratus* (TS), corresponding to the lower and middle parts of Givetian Stage. We hold to the three–membered division of the same Zone, according to Avkhimovitch *et al.* (1993). Presence of a relatively large percent of cavate miospore genus *Geminospora* in Abava Member and the absence in it indexes species of the TS Subzone *triangulatus–serratu*s for Belarus allows us to note the possible identity of the Abava Member miospore assemblage and lower VA Subzone of EX Zone in Belarus.

Miospore assemblage of *Geminospora extensa* (EX) Zone from Joosu Quarry is comparable with assemblage of *Aneurospora extensa* (EX) Zone from Central Poland (Turnau & Racki, 1999). This Zone is subdivided into three subzones: Ex 1, Ex 2, Ex 3, corresponding to the lower and middle parts of the Givetian Stage. From our point of view, EX miospore Zone of Poland is similar to EX Zone of EEP but the boundaries of Subzones in these two regions do not coincide. The miospore assemblage from Joosu Quarry studied by us can be compared with the assemblage from the Ex 2 Subzone in Poland. Both these assemblages are characterized by the presence of the genus *Geminospora* (especially index species *extensa*), the appearance species of the genus *Chelinospora* (including the marker of the lower boundary of the Subzone Ex 2–*Chelinospora concinna*) and the genus *Retusotriletes*.

The general comparison of miospore assemblage from Abava Member of Estonia with assemblages from Salatzskaya Formation of Latvia, the EX Zone of Belarus and the EX Zone of Poland shows the presence of many general characteristic forms. This confirms our conclusion about reference of miospore assemblage from Joosu to the *Geminospora extensa* (EX) miospore Zone of EEP, corresponding to the lower and middle parts of Givetian Stage.

Macroflora

We relied on the following facts when establishing the age of the layers containing macroflora: (1) the general systematic composition of the macroflora from 7a and 7b localities: *Precyclostigma* sp., *Pseudosporochnus verticillatus*, *P. chlupáči*, *P. estonicus;* (2) the stratigraphic position of the same name *Pseudosporochnus* species in different regions of Western Europe, the sequence of their appearance in time and the quantitative species composition into complexes (Fig. 5); (3) the age of the Abava Member deposits according the fish remains and dispersed miospores from South Estonia.

Genus *Pseudosporochnus* in Western Europe is marked only in the Middle Devonian. The localities of this genus are situated in the sixties Northern latitude between about 60° and 50°N. Czechia is the main area of growth of these plants. In the Central Bohemia 7 localities with *P. verticillatus* in the upper part of the Givetian kačak beds and 3 localities–in the lower part of Givetian roblin beds are known (Obrhel, 1959, 1961; Jurina *et al*., 2009). In these localities *P. verticillatus* is represented by several tens of vegetative and fertile specimens. *P. chlupáči* is noted in the same Givetian layers of the Central Bohemia, but only in three localities and in smaller quantities (3 specimens). The single specimen of *P. verticillatus* from the Eifelian choteč deposits (Obrhel, 1960) raises doubts in generic and specific definition that was already discussed by us earlier (Jurina, 1988).

In Belgium genus *Pseudosporochnus* is marked only in two localities. Leclercq (1940) has described the vegetative and fertile specimens of *P. verticillatus* from Mousset locality of Upper Couvinien. Leclercq & Banks (1962) have described numerous specimens of *P. nodosus* (more than 500) from Lower Givetian in Goé Quarry. Lessuise & Fairon–Demaret (1980) have shown that localities of Goé and Mousset with flora belong to one stratigraphic level of the Lower Givetian–Gi b.

In the Middle Devonian deposits of Germany the doubtful specimen of ?*P. verticillatus* was specified without description and drawing (Kräusel & Weyland; 1948; Obrhel, 1961). This locality was not taken into account among localities of *Pseudosporochnus* in Western Europe.

The most Northern locality of *Pseudosporochnus* in Western Europe is the locality Orkney in Scotland (≈ 59° N). Lang (1927) has described one vegetative specimen of *P. verticillatus* from this locality and has indicated its stratigraphic position as Stromness beds, the Achanarras Zone. Now Stromness layers are subdivided into Eifelian Lower Stromness beds and Givetian Upper Stromness beds (Ahlberg *et al.*, 1999; Mark–Kurik & Põldvere, 2012). The presence of the plant in these layers is not specified. It is difficult to define the exact stratigraphic provision of the Scottish plant. Most likely it comes from the Upper Eifelian.

The most Eastern locality of *Pseudosporochnus* in Europe is Joosu Quarry in Estonia (58° N). Kalamees (1988) described 200 vegetative and fertile specimens only of *P. estonicus* from this quarry, from undivided Givetian Burtnieki deposits. In this research article we showed more various systematic composition of flora of this quarry from Burtnieki Regional Stage: the predominant pseudosporochnid ferns: *Pseudosporochnus verticillatus, P. chlupáči, P. estonicus*, and also single lycopsid *Precyclostigma* sp.

Summing up the data on distribution of species *Pseudosporochnus* in Western Europe, we note that the age of the deposits in two districts is dated to Lower Givetian and in the third district–most likely, as Upper Eifelian. In Czechia and Belgium *Pseudosporochnus* from Givetian is known for a big variety of species (four), on a large number of specimens (from several tens to 500) and in a large number of localities (in Bohemia over 10). The greatest similarity was observed at comparison the flora of Joosu and Czechia which appears in the identity of the species and the quantitative compositions of plants. In both areas, the predominant number of the specimens *is P. verticillatus* and the species *P. chlupáči* is single. Similarity of Lower Givetian flora (Gi b) from Belgium (Mousset) and Joosu is expressed in presence of a common species of *P. verticillatus* in all these districts. These data give the basis to establish the Early Givetian age of Abava Member in Joosu Quarry by macroflora. On establishing the age of the deposits, and being a single lycopsid member *Precyclostigma* sp. was not taken into account by us. This is very rarely occurring plant, only in Libya and Estonia. The stratigraphic range of distribution of this genus needs to be tested.

CONCLUSION

Burtnieki Regional Stage (composed of three members) of Estonia, traditionally refers to the Givetian. Fishes, conchostraceans and plant remains were marked in the upper third member of Abava Member. Abava Member is correlated with the Middle Givetian of Western Europe on the fishes. Conchostraceans allowed to determine the age in a very wide stratigraphic range. Macroflora was only recorded in the Givetian deposits, without determining the age of rocks. The question about more detailed age of deposits did not arise (Kalamees, 1988: Mark–Kurik, 2000; Mark–Kurik & Nemliher, 2003; Mark–Kurik & Põldvere, 2012).

We studied the new plant material from Abava Member of Joosu Quarry of Estonia. We include Abava Member in Givetian Burtnieki Regional Stage as well as previous researchers and thus the new data on macroflora and spores allowed us to set up more detailed geological age of this member. The miospore assemblage from Abava Member was reported for the first time in Estonia by us. Studied assemblage (27 species) can be attributed to the *Geminospora extensa* Zone (EX), which is characterized

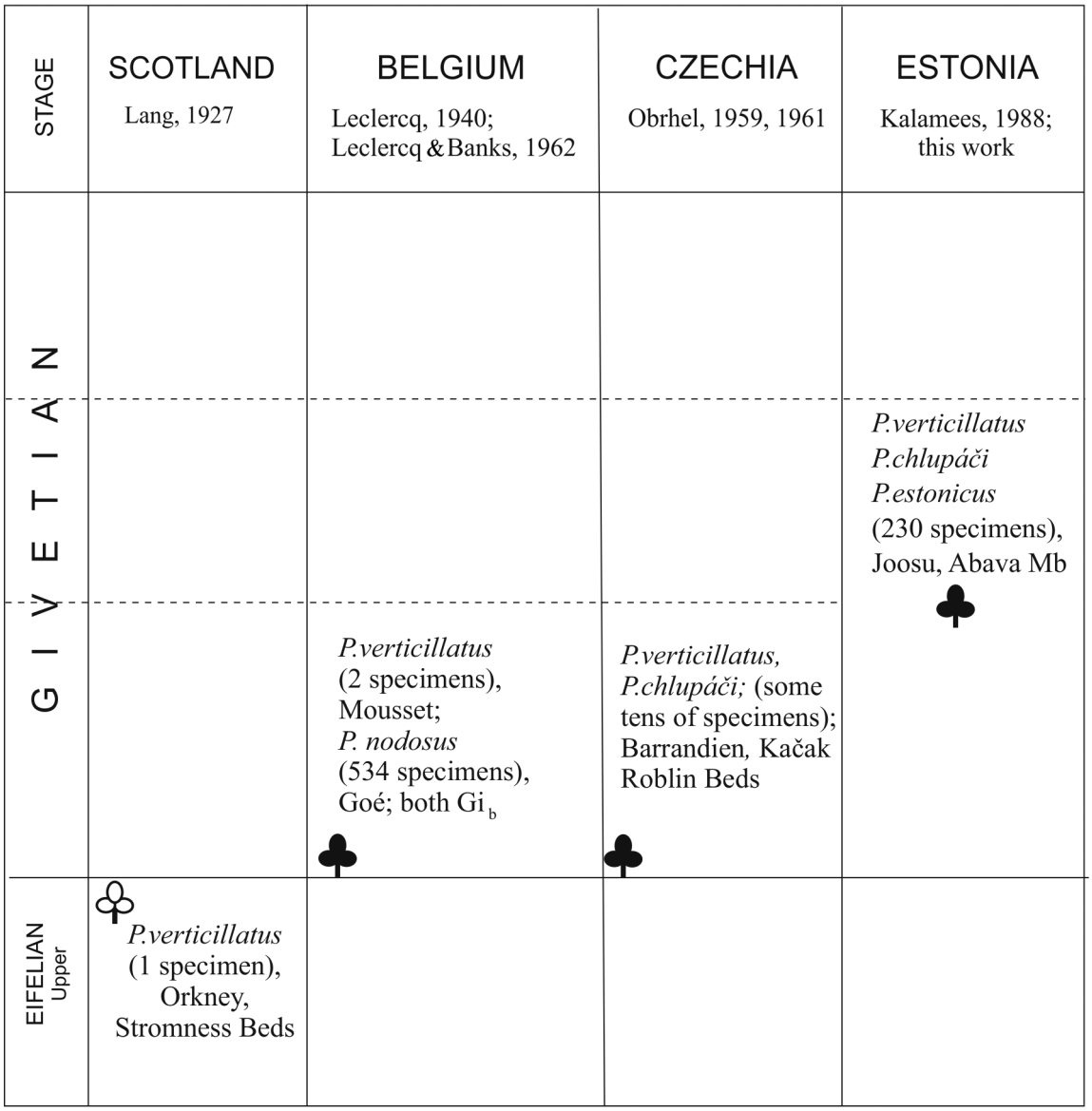


Fig. 5—Stratigraphic position of districts with *Pseudosporochnus* in the Middle Devonian in Western Europe. Legend: in black–position is clear, in light–position is doubtful.

the lower and middle part of Givetian. Spores extracted from the sporangia *Pseudosporochnus verticillatus* was also described and depicted for the first time. They are related to the dispersed morphon *Retusotriletes laevis* Tchibr. and *Retusotriletes* sp. The systematic composition of macroflora was greatly expanded. It is represented by four taxa, three of which are reported from Estonia for the first time: lycopsid *Precyclostigma* sp.; pseudosporochnid ferns: *Pseudosporochnus verticillatus* (Krejči) Obrhel, *P. chlupáči* Obrhel. The latter two species are indicated to the Early Givetian age of Abava Member.

Summarizing the data on the age of the fish, macroflora and dispersed miospores of Abava Member Burtniecki Regional Stage from Joosu Quarry of Estonia we assume that geologic age corresponds to the Early and Middle Givetian.

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