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UPPER CARBONIFEROUS SEED FERN (PTERIDOSPERMOPHYTA) POLLEN ORGANS FROM SILESIA (POLAND) AND RELATED EVOLUTION CONSIDERATIONS

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[*Renaultia schwerini*, Pterophytina]

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ABSTRACT

Grzegorz Pacyna and Danuta Zdebska. *Upper Carboniferous seed fern (Pteridospermophyta) pollen organs from Silesia (Poland) and related evolution considerations.* Monogr. Bot., Vol. 100, 81 pp., 2010.

Extinct seed ferns (Pteridospermophyta) fill a key position in the evolutionary tree of seed plants. Their reproductive structures enable to recognition of the interrelationship within seed ferns and other seed plants descending from them. Seed fern reproductive structures from Poland are very rarely found and very poorly known, especially the pollen organs to which this paper is dedicated. A new genus and species *Silesiatheca formosa* Pacyna & Zdebska, gen. et sp. nov. of lyginopteridalean aggregated synangia was recognized based on specimens preserved within sideritic nodules from Sosnowiec. The genus *Codonotheca* is recognized from European Carboniferous for the first time. The least evolutionarily advanced species of *Codonotheca* – *Codonotheca silesiaca* Pacyna & Zdebska sp. nov., is described based on specimens with weakly expressed radial symmetry and slight fusion of the sporangia. This species matches the hitherto hypothetical simplest species of *Codonotheca* very well, constituting the initial form for all the more compound pollen organs of Medullosales. For the first time in the European Carboniferous the North American species *Aulacotheca campbellii* (White, 1900) Halle, 1933 is recognized. A new emended diagnosis for the typical species *Boulayatheca fertilis* (Kidston, 1914) Taylor & Kurmann, 1985 is proposed, based on specimens from Poland. Two new species of genus *Boulayatheca* Taylor & Kurmann, 1985 are recognized. *Boulayatheca ciliata* Pacyna & Zdebska, sp. nov. with a synangium surface covered with hairs (a feature hitherto unknown in the *Boulayatheca* genus) and *Boulayatheca saganii* Pacyna & Zdebska, sp. nov. with a markedly elongated synangium. Occurrence of *Whittleseya* Newberry, 1853a emend. Halle, 1933 typical species – *Whittleseya elegans* Newberry, 1853a was confirmed in Lower Silesia based on new specimens. Some specimens referred to earlier in the literature as *W. elegans* were ascribed here to the new species *W. silesiaca* Pacyna & Zdebska, sp. nov., which differs from typical species in synangium shape and sporangia clustering into groups. The new species *Whittleseya campanulata* Pacyna & Zdebska, sp. nov. has a large synangium and sporangia clustering into groups. Heterogeneity within the genus *Whittleseya* is recognized, where some species, including those new described here, probably formed compound synangia. The aggregated synangia of Medullosales are recognized in thecompression state of preservation for the first time they are the base for establishing a new genus and species *Kotasotheca annaeadamii* Pacyna & Zdebska, gen. et sp. nov. The genus *Dolerotheca* Halle, 1933 was recognized in the Polish Carboniferous for the first time and a new species *Dolerotheca migierii* Pacyna & Zdebska, sp. nov. was described. T.N. Taylor's model of evolution of medullosalean pollen organs was confirmed, and the new taxa described were included within it.

Key words: seed ferns, pollen organs, Medullosales, Lyginopteridales, Upper Carboniferous, sideritic nodules, Lower Silesian Coal Basin, Upper Silesian Coal Basin, Poland.

1. INTRODUCTION

Extinct seed ferns (Pteridospermophyta) fill a key position in the evolutionary tree of seed plants (Hilton & Bateman 2006). They give rise to Cycadophytina and Magnoliophytina (Doyle 2006; Taylor & Taylor 2009; Taylor *et al.* 2009). This is the reason for renewed interest in them by paleobotanists. Seed fern reproductive structures enable recognition of the interrelationships within seed ferns and other seed plants descending from them.

Seed fern reproductive structures from Poland are very rarely found and very poorly known (Kotasowa & Migier 1995; Pacyna 2003), especially the pollen organs to which this paper is dedicated. Four species have been described so far. Two species of medullosalean pollen organs – *Potoniea adiantiformis* (Gothan 1913) and *Whittleseya elegans* (Potonie 1904; Gothan 1923a) and two species of lyginopteridalean pollen organs *Paracalathiops stachei* (Remy 1953) and *Simplotheca silesiaca.* The genus *Simplotheca* has been proposed based on specimens from Lower Silesia (Remy & Remy 1955a). All the pollen organs in Lyginopteridales and Medullosales from Palaeozoic Poland described so far have been compiled in Table 1, most of these should be revised.

Table 1
Seed fern pollen organs described so far from Poland territory

* – papers with taxon illustrated, ^ – papers with taxon described as new from Poland, USCB – Upper Silesian Coal Basin, LSCB – Lower Silesian Coal Basin

Taxa	Localities	Horizon	Age	References
Aphlebiocarpus schutzei	LSCB, Intra-Sudetic Depression, Thorez mine, Chwalibóg, Krakus shaft	Wałbrzych Formation	Namurian	Stur (1885), Zimmermann (1958), Migier (1972)
Alcicornopteris convoluta	LSCB, Intra-Sudetic Depression, Wałbrzych	Szczawno Formation	Upper Visean	Zimmermann (1958), Kotasowa & Migier (1995, 2001)
Alcicornopteris zeilleri	LSCB, Intra-Sudetic Depression, Wałbrzych	Szczawno Formation	Upper Visean	Zimmermann (1958), Kotasowa & Migier (1995)
Aulacotheca	Poland	-	Carboniferous	Kotasowa & Migier (2001)
Calathiops sp.	LSCB, Intra-Sudetic Depression, Bardo Mountains, Paprotnia, Czerwieńczyce, Mokrzeszów, Lubiechów	Mergelinge Schichten, Paprotnia beds	Upper Devonian, Visean, Upper Visean	Goppert (1865), Gothan & Zimmermann (1937*), Górecka (1958), Zimmermann (1958, 1962), Migier (1972)
Calymmotheca	LSCB, Wałbrzych, Stary Zdrój	Wałbrzych Formation	Namurian A	Behrend (1909)
	USCB, Beuthen, Heinitz mine, borehole Przeciszów XIX	Muldengruppe	Middle Westphalian	Gothan (1913*)

Table 1 cont.

Diplotheca stellata	LSCB, Intra-Sudetic Depression, Kamienna Góra, Wałbrzych	Szczawno Formation, Wałbrzych Formation	Upper Visean, Namurian A	Zimmermann & Gothan (1932*), Zimmermann (1956, 1958, 1960*), Sagan (1965*), Kotasowa & Migier (1995)
Paracalathiops stachei	LSCB, Wałbrzych or Nowa Ruda area, Krakus shaft; borehole Chełm I	Wałbrzych Formation	Namurian A	Remy (1953^*), Zimmermann (1958), Karczewska (1969), Kotasowa & Migier (1995)
Potoniea adiantiformis [=*Potoniea adiantoides*]	LSCB, Wałbrzych Depression, Chrobry mine	Biały Kamień Formation, Zacler Formation	Namurian C – Westphalian B	Zimmermann (1962), Kotasowa & Migier (1995)
	USCB, Zabrze, Luise mine	Untere Muldengruppe	Middle Westphalian	Gothan (1913*), Migier (1972)
Simplotheca silesiaca	LSCB, Rudolf mine	Wałbrzych Formation	Namurian A	Remy & Remy (1955a^*)
Pollen organs associated with *Sphenopteris adiantoides* leaves	LSCB, Wałbrzych	Wałbrzych Formation	Namurian A	Gothan (1923a*); Zimmermann (1960*)
Pollen organs associated with *Sphenopteris bermudensiformis* leaves	LSCB, Intra-Sudetic Depression, Kamienna Góra, Wałbrzych	Wałbrzych Formation	Upper Visean, Namurian A	Zimmermann & Gothan (1932), Zimmermann (1958, 1960*), Sagan (1965*)
Pollen organs associated with *Sphenopteris dicksonioides* leaves	LSCB, Dzikowiec, Fortuna mine	Wałbrzych Beds	Namurian A	Gothan (1923a*)
Pollen organs associated with *Sphenopteris divaricata-linki* leaves	LSCB	Wałbrzych Formation	Namurian A	Zimmermann (1960*)
Pollen organs connected with *Sphenopteris* (*Lyginopteris*) *völkeli* leaves	LSCB	Wałbrzych Formation	Namurian A	Wolf *et al.* (1977*)
Schützia anomala	LSCB, North-Sudetic Basin, Radogoszcz, Zgorzelec area	Świerzawa Formation	Rothliegenden, Stephanian – Lower Permian	Weiss (1879), Mastalerz (1990), Kotasowa & Migier (2001), Lipiarski & Sarnecka (2001)
Telangium bifidum [=*Rhodea lipoldi*]	LSCB, Intra-Sudetic Depression	Szczawno Formation, Wałbrzych Formation	Upper Visean, Namurian	Zimmermann (1958)
Telangium (*Calymmotheca*)	LSCB	Wałbrzych Beds	Namurian A	Gothan (1923a*)
Whittleseya elegans	LSCB	Biały Kamień Formation, Zacler Formation	Westphalian A and B	Potonie (1904), Gothan (1923b), Zimmermann (1962), Migier (1972), Kotasowa & Migier (1995)

2. MATERIALS AND METHODS

The pollen organ specimens described here are from the Lower Silesia Coal Basin (abbreviated as LSCB) and the Upper Silesia Coal Basin (abbreviated as USCB) (Fig. 1). Specimens from LSCB are preserved as coalfield compressions and derived from the Zacler Formation (Westphalian) near Wałbrzych. These specimens were collected in the 20th century by Franz Zimmermann and Eufrozyn Sagan and became part of the District Museum in Wałbrzych collection (abbreviated as MW). The specimens from USCB are derived from two localities. Coalified compressions from a bore hole near Oświęcim were collected by Anna Kotasowa, while the remaining specimens from a new locality in Sosnowiec (Załęże Beds, Langsettian) were collected by us during 1998-2004 excavations (Pacyna & Zdebska 2001, 2002). These specimens are preserved three-dimensionally within sideritic nodules. Sideritic nodules were discovered on a spoil heap at the Porąbka-Klimontów mine. From the macrofloristic ground age of sideritic nodules from Sosnowiec have been estimated as Langsettian (Pacyna 2002a, b; Pacyna & Zdebska 2002; Pacyna 2004).

The specimens from USCB are deposited in the Paleobotanical Museum, Institute of Botany, Jagiellonian University under collection numbers MP IB UJ S/100 and S/101, which are indicated in the diagnosis and plate explanations. The stratigraphical derivation of the specimens is shown in Tables 2 and 3.

Table 2
Lithostratigraphical and chronostratigraphical correlation for Carboniferous strata in Lower Silesian Coal Basin (LSCB) (acc. to Kotasowa & Migier 1983, 1995; Górecka-Nowak & Majewska 2002, modified).
Stratigraphical location of described specimens are marked with an asterisk (*)

Chronostratigraphical divisions of LSCB				**Lithostratigraphical division of LSCB**
North American division	West European division			
Permian	Lower Permian	Autunian		Ludwikowice Formation
Pennsylvanian	Upper Carboniferous	Stephanian	C	
			B	Glinik Formation
			A	
		Westphalian	D (Asturian)	
			C* (Bolsovian)	Zacler Formation*
			B* (Duckmantian)	
			A* (Langsettian)	
		Namurian	C	Biały Kamień Formation
			B	
			A	Wałbrzych Formation
Mississippian	Lower Carboniferous	Visean	Upper	Szczawno Formation

Table 3

Lithostratigraphical, chronostratigraphical and biostratigraphical (floristic assemblages) correlation for Carboniferous strata in Upper Silesian Coal Basin (USCB) (acc. to Kotasowa 1995; Kotasowa & Migier 1983, 1995). Stratigraphical location of described specimens are marked with an asterisk (*)

Lithostratigraphical divisions of USCB				Floristic assemblages	**Chronostratigraphical divisions of USCB**				
					West European division				North American division
Sediments type	Western area	Central and Eastern area							
Continental sediments		Kwaczała Arkose		**XIII**			Steph	Upper Carboniferous	Pennsylvanian
		Cracow Sandstone Series*	Libiąż beds	**XII**	Asturian	D	Westphalian		
			Łaziska Beds*	**XI**	Bolsovian	C			
				X	Duckmantian*	B*			
		Mudstone Series*	Orzesze Beds*	**IX**					
	Załęże Beds		Załęże Beds*	**VIII**	Langsettian*	A*			
	Ruda Beds	Upper Silesian Sandstone Series	Ruda Beds	**VII**	Yeadonian	C	Namurian		
	Anticlinal Beds		Anticlinal Beds =Zabrze Beds	**VI**	Kinderscoutian	B			
	Jejkowice Beds			**V**	Arnsbergian	A			Mississippian
Paralic sediments	Poruba Beds	Paralic Series	Grodziec Beds	**IV**					
	Jaklovec Beds								
	Grodziec Beds		Flora Beds	**III**	Pendleian				
	Petrkovice Beds		Sarnów Beds	**II**					
Diastrophic marine sediments	Kyjovice Beds		Malinowice Beds Zalas Beds	**I**	Brigantian	Upper	Visean	Lower Carboniferous	
	Hradec Beds								
	Morawice Beds								
Limestone series									

The specimens were freed from sediment remains covering them by degagement (Fairon-Demaret *et. al.* 1999). Details of the specimens were observed using a Leica stereomicroscope. Digital photographs of the specimens were taken with a Nikon Digital Camera. All photographs were saved in JPG format and assembled for publication without further modifications using Corel PHOTO-PAINT 9. The specimens are highly coalified, and thus it was impossible to obtain any information on their anatomy and prepollen grains.

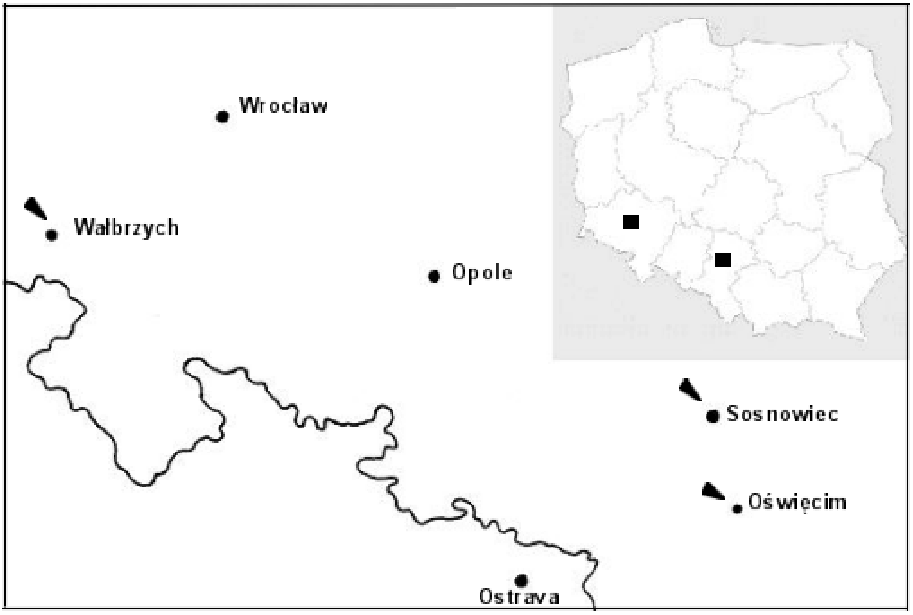

Fig. 1. Map showing locations where described specimens were found (arrows).

3. SYSTEMATIC DESCRIPTION

Pollen organs of the Palaeozoic lyginopteridalean and medullosalean seed ferns have features making them different, as well as shared, they let for comparing them (Millay & Taylor 1979; Stidd 1981; Taylor 1981, 1988; Taylor & Millay 1981a; Taylor & Taylor 1993; Matten & Finne 1994).

Pollen organs from both orders are synangiate and grew on three-part split shoots. Oldest, primitive organs of Lyginopteridales, e.g., *Geminitheca* and *Pullaritheca* constitute the exception, they are built from nonsynagiate concentrations of the sporangia (Smith 1959; Millay & Taylor 1979).

In synangia there are some amount of sterile tissue. In many medulosalean seed ferns sporangia are placed in it, however, at Lyginopteridales the tissue is found only at synangia bases. It was missing at nonsynagiate species.

Differences appear in the vascularization of synangia. Nonsynangiate Lyginopteridales have sporangia without vascular bundle, synangiate species have sporangia with vascular bundle reaching to the base of every sporangium. In Medullosales vascular bundle is found in dorsal sporangial wall.

In most species from both orders sporangia in the synangia have usually created the concentric ring built of one layer of the sporangia. Within Lyginopteridales *Telangium scottii, Crossotheca* and *Feraxotheca* are an exception (Danze 1960; Millay & Taylor 1977, 1978, 1979). They were bilaterally symmetrical, though built of one layer of the sporangia. In the order Medullosales genus *Parasporotheca* (Dennis & Eggert 1978) and it may be *Whittleseya* (Newberry 1853a, b) were symmetrical bilaterally. In the *Potoniea* genus

(Stidd 1978) appeared compound synangia built from concentric rings of synangia every built around 4–6 sporangia.

Dehiscence of sporangia by the oblong crack of ventral walls is universal for both orders. Nonsynangiate Lyginopteridales were an exception. They did not have the clearly marked place of dehiscence of the sporangium.

Subphyllum CYCADOPHYTINA

Class **Pteridospermophyta** Olivier & Scott 1905 sensu Taylor *et al.* 2009
[= Lyginopteropsida sensu Szweykowska & Szweykowski 1997, non
Lagenostomopsida Cleal 1993]
Order **Lyginopteridales** sensu Taylor *et al.* 2009 [= Lagenostomales Seward 1917 sensu
Cleal 1993]
Family **Lyginopteridaceae**

There is no good systematic division to the family level, including all dispersed organs, for the order Lyginopteridales (Meyer-Berthaud 1989; Snigirevskaya 2000). The order Lagenostomales according to Cleal (1993), is divided into families based only on ovules.

Synangiate lyginopteridalean seed fern pollen organs could be divided into two groups (Rowe 1992). Simple synangia consisted of a simple band or ring (with or without a hollow central cavity) of sporangia. They could be less or more fused, and rise from the stalk or basal cushion of sterile tissue. In this type, the external walls of the sporangia are the external wall of the synangium, e.g., *Canipa, Crossotheca, Dichotangium, Simplotheca, Schuetzia, Telangium, Telangiopsis* and *Zimmermannitheca* (Benson 1935; Remy & Remy 1955b, 1959; Danze 1956, 1960; Cridland & Darrah 1968; Skog *et al.* 1969; Eggert & Taylor 1971; Jennings 1976; Millay & Taylor 1977, 1978, 1979; Stubbfield *et al.* 1982; Brousmiche 1982, 1986; Stidd *et al.* 1985; Meyer-Berthaud & Galtier 1986; Orloga *et al.* 2009).

These simple synangia could unite into aggregate synangia, e.g., *Dichotangium, Phacelotheca* and *Schopfiangium* (Stidd *et al.* 1985; Meyer-Berthaud & Galtier 1986; Rowe 1988). Another type of aggregate synangia is rarely found, e.g., *Melissiotheca* (Meyer-Berthaud 1986) and *Cornutheca* (Rowe 1992). In this type, the synangium consists of many sporangia (up to a hundred) irregularly embedded at its base in an extensive parenchymatous cushion. This cushion may form an outer wall enclosing the sporangia with its outer surface covered with capitatae glands. In *Melissiotheca,* the parenchymatous cushion is divided into lobes and is therefore considered to be an aggregate synangium (Meyer-Berthaud 1986).

Silesiatheca Pacyna & Zdebska, *gen. nov.* Plate 1, Figs 1-4

Type species. *Silesiatheca formosa* Pacyna & Zdebska, *sp. nov.*

Diagnosis. Monopodially branching system of axis bearing terminal aggregated synangia. Each aggregated synangium consisted of a whorl of 4–5 ovate synangia. Each synangium consisted of 3–5 sporangia. The synangia stalked without a sterile basal cushion. The synangia in a whorl are located in one plane, slightly bent toward the axis carrying them.

Etymology. *Silesia* – referring to the occurrence of this genus in Silesia, Greek *theca* – referring to a container with pollen.

Silesiatheca formosa Pacyna & Zdebska, *sp. nov.* Plate 1, Figs 1-4

2007a *Telangiopsis* sp. from Sosnowiec; Pacyna, p. 104.

Diagnosis. Monopodially branching system of axis bearing terminal aggregated synangia. Axis 0.5 mm wide. Each aggregated synangium consisted of a whorl of 4–5 ovate synangia. Each synangium consisted of 3–5 sporangia. The synangia are ovate, 0.5–1.0 mm long, 0.3–0.5 mm wide, stalked, and without a sterile basal cushion. The synangia in a whorl are located in one plane, slightly bent toward the axis carrying them. The sporangia are elongated, 0.1–0.2 mm wide, and they stretch out along the entire length of the synangia.

Age. Upper Carboniferous (Pennsylvanian), Langsettian (Westphalian A).

Type horizon. Mudstone Series, Załęże Beds.

Type locality. Upper Silesia, Dąbrowa Górnicza area, Sosnowiec–Zagórze, Porąbka-Klimontów mine.

Holotype. S/101/P5, Pl. 1, Figs 1-4.

Referred specimen. S/100/P6.

Etymology. Lat. *formosa* – beautiful, in allusion to the well preserved specimens and morphology of this species.

Description. Monopodially branching system of axis bearing terminal aggregated synangia. Axis 0.5 mm wide. Each aggregated synangium consisted of a whorl of 4–5 ovate synangia. Each synangium consisted of 3–5 sporangia (Pl. 1, Figs 1 and 4). The synangia are ovate, 0.5–1.0 mm long, 0.3–0.5 mm wide. The synangia in a whorl are located in one plane, slightly bent toward the axis carrying them, and grow straight from the axis without a sterile basal cushion (Pl. 1, Fig. 3). The sporangia are elongated, 0.1–0.2 mm wide, and stretch out along the entire length of the synangia. Laminar pinnae are found at the base of branching system but are in the worst condition (Pl.1, Fig. 2). Pinnae is dissected with rounded pinnules. Prepollen grains not preserved.

Discussion. The new genus and species described here is typical for Lyginopteridales (MILLAY & TAYLOR 1977, 1979). However, it is distinguishable from all previously described species because the whorl consists not of sporangia but of synangia (EGGERT &TAYLOR 1971; THOMAS & CRAMPTON 1971; MILLAY & TAYLOR 1979; STUBBFIELD *et al*. 1982; PACYNA 2007a, b). We are dealing here with a simple aggregated synangium, in which the synangia are united but not fused. Such an organ could have arisen from organs similar to *Telangiopsis* or *Crossotheca* (DANZE 1960; EGGERT & TAYLOR 1971; JENNINGS 1976; STUBBFIELD *et al*. 1982) by a reduction of sterile tissue at the base of the synangium a multiplication of the number of sporangia per whorl, and a fusion of sporangia into synangia. It is an example of the convergence amongst Lyginopteridales towards the important evolutionary Medullosales trend consisting in increasing the amount of sporangia in the synangium. These, however, are a different trend from that which resulted in the formation of aggregated sporangia in such genera as *Dichotangium, Phacelotheca* lub *Schopfiangium*. In

Phacelotheca, the synangium consists of 8 sporangia on a single axis (Meyer-Berthaud & Galtier 1986), while in *Dichotangium* and *Schopfiangium* the numerous sporangia have arisen from a parenchymatous cushion divided into lobes (Stidd *et al.* 1985; Rowe 1988).

A further advanced *Silesiatheca* feature is a monopodially branching system of axis bearing terminal aggregated synangia. The axis is clearly flattened, rather than three-dimensional, and is like a pinnated fern sporophyll (Pl. 1, Fig. 3). This resemblance is worth emphasizing, because, as which some abovementioned pollen organs, some authors report doubts as to the lyginopteridalean affinity. These authors believe that they are fern sporophylls (e.g., some species of *Crossotheca* – Danze 1956, 1960, Meyen 1987, Brousmiche 1982, 1986; *Canipa* – Thomas & Crampton 1971). Unfortunately, prepollen grains isolated from these primitive pollen organs did not differ in practice from fern spores. Here, the opinion expressed and supported by many arguments in previously quoted papers by the Taylor team was accepted, that they were pollen organs of Lyginopteridales.

Order **Medullosales** [=Trigonocarpales]

Family **Medullosaceae** [= Trigonocarpaceae Seward, 1917; including Whittleseyinae Halle 1933 and Neuralethospermaceae Laveine 1967]

The order Medullosales is a well defined monophyletic clade. For a list of synapomorphies, see Kenrick & Crane (1997).

There is no good systematic division to the family level of the order, including all dispersed organs. The Medullosaceae family is based on anatomically preserved stems (Stidd 1991). The Whittleseyinae (included genera: *Whittleseya, Goldenbergia, Boulaya, Aulacotheca, Codonotheca* and *Dolerotheca*) and Potonieinae (genus *Potoniea* only) families were created by Halle (1933) based only on pollen organs. Many new pollen organ genera with preserved anatomical datails have been created since that time (Taylor *et al.* 2009). Cleal (1993) dividied the Medullosales order (which should, according to him, be named Trigonocarpales) into two families: Trigonocarpaceae (corresponding to Medullosaceae) and Potonieaceae. He noticed, however, that only the Potonieaceae family is well defined, and that the Trigonocarpaceae [= Medullosaceae] family including all other genera of the Medullosales. According to current practice families should be based on natural genera, and not only organ or form genera.

Medullosalean seed ferns pollen organs are highly diversified as for morphology, anatomy and prepollen grains type (Stidd *et al.* 1977; Millay & Taylor 1979; Stidd 1981; Taylor & Millay 1981b; Taylor 1981, 1988; Taylor & Taylor 1993; Serbet *et al.* 2006). A dozen or so genera have been described, mostly from coal balls with preserved anatomical details. Some genera, e.g., *Boulayatheca,* were founded on specimens preserved within sideritic nodules (Halle 1933). Genera described from coalified specimens are poorly known.

All the described genera could be divided into three types of morphological construction, each successively more advanced evolutionarily.

Simple synangia – e.g., *Aulacotheca, Boulayatheca, Codonotheca, Goldenbergia, Halletheca, Murielatheca* consist of ring of more or less fused sporangia.

Aggregate synangia – e.g., *Parasporotheca, Kotasotheca* Pacyna & Zdebska, gen. et sp. nov. consist of a dozen or so microsynangia (each microsynangium consisting of a few or a dozen or so sporangia) aggregated but not fused.

Compound synangia – e.g., *Dolerotheca, Potoniea* consist of hundreds of microsynangia (each consisted of a few sporangia) tightly fused to form a bell shaped organ (Millay & Taylor 1979).

Genus ***Codonotheca*** (Sellards, 1903) Pacyna & Zdebska, *emend. nov.*

1903 *Codonotheca* Sellards, 1903; Sellards, p. 87-95.
1925 *Codonotheca* Sellards, 1903; Noe, p. 15, 18, pl. 43, figs. 1-3.
1933 *Codonotheca* Sellards, 1903; Halle, p. 40-42.
1948 *Codonotheca* Sellards, 1903; Schopf, p. 681-724, pl. 111, figs. 1-2.
1994 *Codonotheca* Sellards, 1903; Drinnan & Crane, p. 243.

Emended diagnosis. Pollen organ elongated, stalked, consisting of 4–12 elongated sporangia, more or less proximally fused. Each sporangium is flanked on either side by a strand of resistant tissue (?sclerenchyma). The surface of the pollen organ is covered with hairs in some species.

Type species. *Codonotheca caduca* Sellards, 1903 emend. Drinnan & Crane, 1994.

Included species. *Codonotheca corymbiata* Stidd & Leisman, 1986, *Codonotheca*? *pusilla* Nathorst, 1914, *Codonotheca silesiaca* Pacyna & Zdebska, sp. nov.

Discussion. Genus *Codonotheca* with type species *C. caduca* was introduced by Sellards in 1903 based on specimens preserved within sideritic nodules from Mazon Creek, and additional details were added by Sellards (1907) (see also Drinnan & Crane 1994). Sellards (1903) did not differentiate genus and species diagnosis this is the reason that a new emended diagnosis has been proposed here. This new diagnosis includes new information gathered from the new species *Codonotheca silesiaca* Pacyna & Zdebska, sp. nov. described here. Subsequently, *Codonotheca* specimens from Mazon Creek concretions have been illustrated and discussed by Noe (1925), Halle (1933), Schopf (1948), Darrah (1970), Millay and Taylor (1979) and Stidd (1981). Based on a dozen or so specimens preserved within Mazon Creek concretions deposited in paleobotanical collections of the Field Museum of Natural History, Drinnan and Crane (1994) emended the *C. caduca* diagnosis and described new details.

Another species of *Codonotheca* was described by Nathorst (1914) from the Lower Carboniferous of Spitsbergen (Mitterhuk des Bellsundes) as *Codonotheca*? *pusilla*, but the single specimen that has been examined has not been found to contain any spores, and nothing is known of its structure. Halle (1933) considered referral of this species to *Codontheca* as doubtful.

Stidd and Leisman (1986) have described yet another species of *Codonotheca* – *Codonotheca corymbiata* from the Upper Pennsylvanian (Upper Stephanian) of Kansas. *Codonotheca corymbiata* has only four sporangia per synangium (Stidd 1981; Taylor & Taylor 1993; Drinnan & Crane 1994). The sporangia are more fused together than in *C. caduca.* This is probably due to the younger geological age of *Codonotheca corymbiata* species.

Codonotheca silesiaca Pacyna & Zdebska, *sp. nov.* Plate 2, Figs 1-6; Fig. 2A

2007a *Codonotheca* sp.; Pacyna, p. 105.

Diagnosis. Pollen organ consisted of about 12 elongated sporangia, 20–25 mm long, 1.0–1.5 mm wide. Sporangia are proximally slightly fused, distally markedly extended to form a brushlike structure. Sporangial tips slightly adpressed to each other. Each sporangium is flanked on either side by a strand of resistant tissue (?sclerenchyma). The sporangial surface is smooth without hairs.

Age. Upper Carboniferous (Pennsylvanian), Langsettian (Westphalian A).

Horizon. Mudstone Series, Załęże Beds.

Type locality. Upper Silesia, Dąbrowa Górnicza area, Sosnowiec–Zagórze, Porąbka-Klimontów mine.

Holotype. S/100/867, Pl. 2, Figs 1-2; Fig. 2A.

Referred specimens. S/100/868, S/100/869, S/100/870, S/100/871.

Ethymology. Referring to the occurrence of this species in the Silesia.

Description. Pollen organ consisted of elongated sporangia, 20−25 mm long, 1.0−1.5 mm wide. About 12 sporangia per synangium (Pl. 2, Figs 1-6). Sporangia are proximally slightly fused (but they don't form swollen, sterile, proximal portion as in *C. caduca*). Sporangia form misshapen ring, distally markedly extend to form brushlike structure, but sporangial tips slightly adpress to each other (Pl. 2, Figs 1-2, 5-6). Each sporangium flanked on either side by a strand of resistant tissue, likely sclerenchyma. Sporangial surface is smooth without hairs (Pl. 2, Figs 1-4). Prepollen grains have not been found.

Discussion. *Codonotheca silesiaca* Pacyna & Zdebska, sp. nov. differs from *C. caduca* and *C. corymbiata* in the following features: sporangia are less fused in proximal portion, radial symmetry of synangium is less marked, number of sporangia per synangium is higher (*C. silesiaca* − 12, *C. caduca* – 6, *C. corymbiata* − 4).

Hairs on the surface of pollen organ have not been observed. This feature contrasts with *C. caduca*. The surface of *C. caduca* pollen organ is often covered with densely-spaced hairs (Schopf 1948; Drinnan & Crane 1994; Pacyna 2007a). The surface of pollen organ covered with hairs is characteristic of Medullosales, but some genera like *Boulayatheca* and *Halletheca* are not covered with hairs (Halle 1933; Taylor 1971).

The new species *C. silesiaca* matches the so far hypothetical simplest species of *Codonotheca*, constituting the initial form for all more compound Medullosales pollen organs very well. The sporangia are numerous, clustered, radial symmetry is less marked the sporangia are proximally only slightly fused, swollen, sterile, proximal portion is absent. The absence of hairs on the sporangia is no surprise, because they are particularly characteristic of the most advanced forms, e.g., *Dolerotheca*.

The poorly visible radial symmetry at the base of the *C. silesiaca* organ may indicate, that the radial symmetry of the medullosalean pollen organs is of a secondary nature and it came into existence through the strong closing up of the sporangia which were at first arranged pinately on axis (cf. Schopf 1948 versus Taylor & Taylor 1993).

The question is, how to explain the temporary tied paradox where *C. silesiaca,* about the very primitive structure, is relatively young geologically (Westphalian A) and occurs together with such an advanced genus as *Dolerotheca* (*D. migierii*). Meanwhile, the majority of primitive medullosalean pollen organs come from the Early Namurian, e.g., *Boulaya praelonga* and several primitive species of *Aulacotheca. Codonotheca silesiaca* Pacyna & Zdebska, sp. nov. may be a relic of primitive forms which survived until the Westphalian stage, which may also show that evolution in different Medullosales lines proceeded at the different paces. The primitive genus *Codonotheca* survived until the Late Stephanian (*C. corymbiata*), being subject to alight morphological alteration – the sporangia underwent bigger fusion. This tendency towards more and more fusion of the sporangia manifests itself in the entire evolution of this genus, from *C. silesiaca* (Westphalian A), whose sporangia are almost not integrated at the base, through *C. caduca* (Westphalian D) with partly integrated sporangia, to *C. corymbiata* (Upper Stephanian), whose sporangia are even more integrated for.

Genus ***Aulacotheca*** Halle, 1933

1933 *Aulacotheca* Halle, 1933; Halle, p. 28-40, Pl. 7-8.
1941 *Aulacotheca* Halle, 1933; Hemingway, p. 197-201, Pl. 5.
1953 *Aulacotheca* Halle, 1933; Stockmans & Williere, p. 331-337, pl. 31, 32, 36, 48.
1961 *Aulacotheca* Halle, 1933; Stockmans & Williere, p. 84-89, pl. 9-10.
1969 *Aulacotheca* Halle, 1933; Eggert & Kryder, p. 414-419.
1978 *Aulacotheca* Halle, 1933; Gillespie *et al*., p. 112.
1979 *Aulacotheca* Halle, 1933; Millay & Taylor, p. 341-344.
1984 *Aulacotheca* Halle, 1933; Mickle & Leary, p. 343-357.
1994 *Aulacotheca* Halle, 1933; Drinnan & Crane, p. 239.
2000 *Aulacotheca* Halle, 1933; Goubet *et al*., p. 31-34.

Diagnosis (after Halle 1933, p. 40). Seed-like synangiate pollen organs of clavate to cylindrical shape; apex more or less rounded, base gradually tapering; surface with a few (6−9) marked longitudinal ridges and furrows; synanagium formed of a single whorl of long and narrow concrescent sporangia which correspond in number and position to the longitudinal ridges, extend longitudinally from base to apex and enclose a central empty space; spores in the flattened state elliptical, with 1−3 longitudinal lines, their longer diameter more than 0.1 mm.

Type species. *Aulacotheca elongata* (Kidston, 1886) Halle, 1933.

Included species. *A. campbellii* (White, 1900) Halle, 1933; *A. collicola* Mickle & Leary, 1984; *A. dixiana* Hemingway, 1941 *nomen dubium*; *A. hallei* Hemingway, 1941; *A. hemingwayi* Halle, 1933; *A. idelbergeri* Halle, 1933; *A. iowensis* Eggert & Kryder, 1969; *A. parva* Stockmans & Williere, 1953.

Discussion. The genus *Aulacotheca* was proposed by Halle (1933), with type species *Aulacotheca elongata*. Halle has also described the species *A. hemingwayi* and *Aulacotheca* (?) *idelbergeri.* Later, Hemingway (1941) have described specimens of this genus (species *A. hemingwayi* and two new species *A. hallei* and *A. dixiana*) from the United Kingdom. Belgian specimens of *Aulacotheca* (species *A. elongata, A. hallei, A. hemingwayi, A. idelbergeri*, new species *A. parva*) were described by Stockamns and Williere (1952-1953, 1961). From North America three new species have been described: *Aulacotheca campbellii* (White 1900), *A. iowensis* (Eggert & Kryder 1969) and *A. collicola* (Mickle & Leary 1984). For synonymy of species belonging to genus *Aulacotheca* (see Table 4).

The pollen organs of *Aulacotheca* are among the geologically oldest in Medullosales. The genus is well described based on many well preserved specimens, species of *Aulacotheca* are easily recognizable (see Table 5). For these reasons, *Aulacotheca* is a key genus in understanding the evolution of medullosan seed ferns pollen organs (e.g., Millay & Taylor 1979). The synangia of *Aulacotheca* are interpreted as a radially symmetrical hollow

Table 4
Synonymy of species belonging to genus *Aulacotheca*

Authors	Species				
	Aulacotheca campbellii	***Aulacotheca collicola***	***Aulacotheca dixiana***	***Aulacotheca elongata***	***Aulacotheca hallei***
Kidston (1886)				*Rhabdocarpus elongatus* pars	
White (1900)	*Whittleseya campbellii*				
Crookall (1930) in Crookall (1955-1976)				*Holcospermum elongatum* pars	
Halle (1933)	*Aulacotheca campbellii*			*Aulacotheca elongata*	
Carpentier (1934)			*Boulaya praelonga*		
Hemingway (1941)			*Aulacotheca dixiana*	*Aulacotheca elongata*	*Aulacotheca hallei*
Stockmans & Williere (1952-1953)			*Aulacotheca dixiana*	*Aulacotheca elongata*	*Aulacotheca hallei*
Stockmans & Williere (1961)			*Aulacotheca dixiana*	*Aulacotheca elongata*	*Aulacotheca hallei*
Eggert & Kryder (1969)	*Aulacotheca campbellii*		*Aulacotheca dixiana*	*Aulacotheca elongata*	*Aulacotheca hallei*
Crookall (1955-1976)			*Boulaya praelonga*	*Aulacotheca elongata*	*Aulacotheca hallei*
Millay & Taylor (1979)	*Aulacotheca campbellii*		*Aulacotheca dixiana*	*Aulacotheca elongata*	*Aulacotheca hallei*
Mickle & Leary (1984)	*Aulacotheca campbellii*	*Aulacotheca collicola*	*Aulacotheca dixiana*	*Aulacotheca elongata*	*Aulacotheca hallei*
Pacyna & Zdebska, this paper	*Aulacotheca campbellii*	*Aulacotheca collicola*	*nomen dubium*	*Aulacotheca elongata*	*Aulacotheca hallei*

Authors	Species				
	Aulacotheca hemingwayi	***Aulacotheca idelbergeri***	***Aulacotheca iowensis***	***Aulacotheca oblonga***	***Aulacotheca parva***
Kidston (1890)	*Rhabdocarpus elongatus pars*				
Crookall (1930) in Crookall (1955-1976)	*Holcospermum elongatum pars*				
Halle (1933)	*Aulacotheca hemingwayi*	*Aulacotheca* (?) *idelbergeri*			
Walton (1940)				*Aulacotheca oblonga*	
Hemingway (1941)	*Aulacotheca hemingwayi*	*Aulacotheca idelbergeri*			
Stockmans & Williere (1953)	*Aulacotheca hemingwayi*	*Aulacotheca idelbergeri*			*Aulacotheca parva*
Stockmans & Williere (1961)	*Aulacotheca hemingwayi*	*Aulacotheca idelbergeri*			*Aulacotheca parva*
Eggert & Kryder (1969)	*Aulacotheca hemingwayi*	*Aulacotheca idelbergeri*	*Aulacotheca iowensis*		
Crookall (1955-1976)	*Aulacotheca hemingwayi*				
Millay & Taylor (1979)	*Aulacotheca hemingwayi*	*Aulacotheca idelbergeri*	*Aulacotheca iowensis*		*Aulacotheca parva*
Mickle & Leary (1984)	*Aulacotheca hemingwayi*	*Aulacotheca idelbergeri*	*Aulacotheca iowensis*		*Aulacotheca parva*
Pacyna & Zdebska, this paper	*Aulacotheca hemingwayi*	*Aulacotheca idelbergeri*	*Aulacotheca iowensis*	*nomen dubium*	*Aulacotheca parva*

Table 5
Comparison between the *Aulacotheca* species

Features of species	***A. campbellii*** (White, 1900) Halle, 1933	***A. collicola*** Mickle & Leary, 1984	***A. dixiana*** Hemingway, 1941	***A. elongata*** (Kidston, 1886) Halle 1933
Synangium length (mm)	11−22	11−17	22−25	15
Synangium width (mm)	2.0−5.0	2.5−4.0	4	3.5
Number of sporangia	6	4−6	9 (?)	9
Prepollen length (μm)	135	141−230	150	187−230, 140−150
Prepollen width (μm)	176	89−160	170	119−179, 90−100
Sporangial distal tips	not preserved	rounded-acute, indistinct	rounded, indistinct	rounded, indistinct
Longitudinal striations	present	present	present	present
Ridges	broad, distinct	broad, low, distinct	indistinct	broad, low, indistinct
Prepollen type	*Monoletes*	*Monoletes*	*Monoletes*	*Monoletes*
Localities	USA, Michigan, Virginia	USA	United Kingdom	Scotland, Belgium, USA: Virginia
Age	Early-Middle Pennsylvanian (Westphalian)	Early Pennsylvanian (Early Westphalian)	Late Carboniferous	Early Pennsylvanian (Namurian C, Westphalian A-B)
References	White (1900), Halle (1933), Eggert & Kryder (1969), Millay & Taylor (1979), Mickle & Leary (1984)	Mickle & Leary (1984)	Hemingway (1941), Eggert & Kryder (1969), Millay & Taylor (1979), Mickle & Leary (1984)	Halle (1933), Eggert & Kryder (1969), Millay & Taylor (1979), Mickle & Leary (1984)
Features of species	***A. hallei*** Hemingway, 1941	***A. hemingwayi*** Halle, 1933	***A. idelbergeri*** Halle, 1933	***A. iowensis*** Eggert & Kryder, 1969
Synangium length (mm)	16	18−30	30−35	5
Synangium width (mm)	3.5	4.5−5.5	6−7	1.5
Number of sporangia	6 (?)	9	6−8 (?)	3−4
Prepollen length (μm)	113	170−220	-	88−165
Prepollen width (μm)	73	120−170	-	44−121
Sporangial distal tips	-	pointed, distinct	pointed, distinct	indistinct
Longitudinal striations	-	-	-	-
Ridges	-	narrow, prominent	narrow, prominent	curved, indistinct
Prepollen type	*Monoletes*	*Monoletes*	-	*Monoletes*
Localities	United Kingdom, Belgium	United Kingdom, Belgium, Germany, Turkey, USA: Virginia	Germany, Belgium	USA
Age	Late Carboniferous, Westphalian A-B	Early-Late Carboniferous, Namurian C, Westphalian A	Namurian – Westphalian A	Middle Pennsylvanian (Late Westphalian)
References	Hemingway (1941), Eggert & Kryder (1969), Millay & Taylor (1979), Mickle & Leary (1984)	Halle (1933), Eggert & Kryder (1969), Millay & Taylor (1979), Mickle & Leary (1984)	Halle (1933), Eggert & Kryder (1969), Millay & Taylor (1979), Mickle & Leary (1984)	Eggert & Kryder (1969), Millay & Taylor (1979), Mickle & Leary (1984)

Table 5 cont.
Comparison between the *Aulacotheca* species

Features of species	***A. parva*** Stockmans & Williere, 1953	***Aulacotheca* sp.** Mickle & Leary, 1984	***Aulacotheca* – *Cardioneuropteris asiatica*** (Laveine 1997)
Synangium length (mm)	7.5–14.5	21–33	10
Synangium width (mm)	1.6–4.5	3.8–5.5	3
Number of sporangia	5–6	4–6	4–6
Prepollen length (μm)	-	-	-
Prepollen width (μm)	-	-	-
Sporangial distal tips	indistinct	mucronate, distinct	acute
Longitudinal striations	present	present	-
Ridges	narrow, distinct	broad, low, indistinct	-
Prepollen type	-	-	-
Localities	Belgium	USA	Kazakhstan, Karaganda
Age	Namurian	Early Pennsylvanian (Early Westphalian)	Uppermost Visean
References	Stockmans & Williere (1953), Millay & Taylor (1979), Mickle & Leary (1984)	Mickle & Leary (1984)	Goganova *et al.* (1993)

ring of elongated laterally fused sporangia with dehiscence slits directed inside. In at least one species (*A. iowensis*), the synangia were aggregated (Eggert & Kryder 1969).

Distribution. Genus *Aulacotheca* is well represented in the fossil record. Six species of *Aulacotheca* have been found in Europe: *A. elongata, A. hemingwayi, A. idelbergeri* (Halle 1933), *A. hallei*, *A. dixiana* (Hemingway 1941) and *A. parva* (Stockmans & Williere 1952-1953), which range in age from Namurian to Westphalian B. The genus *Aulacotheca* is rarer in North America than in Europe six species have been described: *Aulacotheca campbellii*, *A. hemingwayi* and *A. elongata* (Jongmans 1937 and Tidwell 1967), *A. iowensis* (Eggert & Kryder 1969), *A. collicola* (Mickle & Leary 1984), *Aulacotheca* sp. (Mickle & Leary 1984) and *Aulacotheca* sp. (Goubet *et. al.* 2000). Genus *Aulacotheca* have also been found in Kazakhstan (Laveine 1997).

Aulacotheca campbellii (White, 1900) Halle, 1933 Plate 3, Figs 1-2

1900 *Whittleseya campbellii* sp. nov. White, 1900; White, p. 905-907, pl. 190, fig. 9-11.
1933 *Whittleseya campbellii* White, 1900 1933; Halle, p. 20, 39.
1937 *Aulacotheca campbellii* (White, 1900) Halle, 1933; Jongmans, p. 399, 403.
1949 *Aulacotheca campbellii* (White, 1900) Halle, 1933; Arnold, p. 207, pl. 24, figs. 4-6.
1967 *Aulacotheca campbellii* (White, 1900) Halle, 1933; Tidwell, p. 3-66.
1969 *Aulacotheca campbellii* (White, 1900) Halle, 1933; Eggert & Kryder, p. 414-419.
1978 *Aulacotheca campbellii* (White, 1900) Halle, 1933; Gillespie *et al.*, p. 115, 128, pl. 47, figs 4, 6.
1979 *Aulacotheca campbellii* (White, 1900) Halle, 1933; Millay & Taylor, p. 342.
1984 *Aulacotheca campbellii* (White, 1900) Halle, 1933; Mickle & Leary, p. 343-357.
2002 *Aulacotheca campbellii* (White, 1900) Halle, 1933; Blake *et al*., p. 289-290, pl. 14, fig. 6, pl. 15, fig. 3.
2007a *Aulacotheca campbellii* (White, 1900) Halle, 1933; Pacyna, p. 105.

Referred specimens. LSCB: MW 948 – Wałbrzych area, spoil heap of B. Chrobry mine, collected by E. Sagan in 1957 – 10 well preserved specimens on shale slab, Zacler Formation, Duckmantian (Westphalian B).

Description. Synangium elongated, clavate-cylindrical in shape, sometimes very slightly cuneate, base markedly gradually tapering, apex only slightly contracted (Pl. 3, Figs 1-2). Synangium 15–22 mm long, 3.0–4.5 mm wide. Lateral borders parallel or nearly parallel from a point one-fourth of the way from the base to apex. Some specimens have borders slightly arched laterally. Apex truncated, rounded, and indistinctly toothed (Pl. 3, Fig. 2). At the apex, lateral borders slightly contracted. Sporangium surface longitudinally ridged with a few (3–5) marked parallel longitudinal ridges and furrows (Pl. 3, Fig. 2). Ridges are very well visible from synangium base to apex. At apex, ridges are contracted. Longitudinal ridges corresponds in number and position to the sporangia. Sporangial distal tips indistinct. Stalks not preserved. Prepollen grains also not preserved.

Discussion. White in 1900 proposed the species *Aulacotheca campbellii* (under the generic name *Whittleseya*). He considered specimens to be leaves in origin, but despite this his description is very thoughtful and acurrate. White (1900) did not designate a holotype specimen. The specimens illustrated by him in Plate 190, Figs 9-11 should be considered as syntypes. Halle (1933, p. 20, 39) first recognized this species as belonging to the genus *Aulacotheca*.

Species of *Aulacotheca* are differentiated based on: synangium dimensions, number of sporangia and corresponding ridges, shape of sporangial distal tips, and prepollen grains features, if preserved (see Table 5). The specimens from Wałbrzych described here conform to the features of *A. campbellii* species. Dimensions fits very well, the number of sporangia is also the same as in White's specimens. Ridges are broad and distinct, which is also characteristic for *A. campbellii* (Mickle & Leary 1984). The morphologically similar species *A. hemingwayi* has bigger synangia (18–30 mm long) on average and narrow and prominent ridges. The described specimens are slightly younger (Duckmantian) than specimens from the USA (Namurian C – Langsettian).

Distribution. The specimens of *A. campbellii* from Wałbrzych are the first recognition of this species outside North America. There are two species of *Aulacotheca* – *A. hemingwayi* and *A. elongata,* that have been found in North America and Europe, third common species have been recognized here (see Table 5). The *A. campbellii* species is well represented in North America – specimens have been found in Michigan, Virginia, Utah and Pennsylvania (White 1900; Jongmans 1937; Arnold 1949; Tidwell 1967; Gillespie *et al*. 1978; Blake *et al*. 2002), and they range from early to middle Pennsylvanian in age. The late stratigraphical apperance (Duckmantian) of this species in Poland compared to North America (Namurian C – Langsettian) may suggest that that species evolved in North America and next migrated to Europe (see Laveine 1997 for a similar scenario for medullosalean foliage *Neuropteris*).

Genus ***Boulayatheca*** Taylor & Kurmann, 1985 [= *Boulaya* Carpentier, 1925; non *Boulaya* Cardot, 1912]

1912 non *Boulaya* Cardot, 1912; Cardot, p. 1-3.
1914 *Whittleseya* (?) Newberry, 1853a; Kidston, p. 166.
1914 *Whittleseya* (?) Newberry, 1853a; Carpentier, p. 363-367, Pl. 10.
1925 *Boulaya* Carpentier gen. nov.; Carpentier, p. 149, pl. 6, fig. 1.
1933 *Boulaya* Carpentier, 1925 emend. Halle, 1933; Halle, p. 24-28, Pl. 6, figs 4-8.
1941 *Boulaya* Carpentier, 1925; Gothan 1941, p. 278-282.
1953 *Boulaya* Carpentier, 1925; Stockmans & Williere, p. 337.

1961 *Boulaya* Carpentier, 1925; Stockmans & Williere, p. 89-91, 110, fig. 33, pl. 10, fig. 2.
1964 *Boulaya* Carpentier, 1925; Delevoryas, p. 60-63.
1979 *Boulaya* Carpentier, 1925; Millay & Taylor, p. 344.
1984 *Boulaya* Carpentier, 1925; Kurmann & Taylor, p. 109-116, Pl. 1-2.
1985 *Boulayatheca* nom. nov. Taylor & Kurmann, 1985; Taylor & Kurmann, p. 666-667.
1994 *Boulayatheca* Taylor & Kurmann, 1985; Drinnan & Crane, p. 243.
2000 *Boulayatheca* Taylor & Kurmann, 1985; Goubet *et al.,* p. 33-34.

Diagnosis (after Halle 1933, p. 28)**.** Pollen organ clavate-pyriform in shape, roundedly triangular in transverse section, contracted and somewhat rounded at the irregulary dentate apex, finely longitudinally striated but not ribbed; with a central empty space enclosed by a thick wall containing a spore-bearing zone; spores of the bilateral type, in the flattened state elliptical, with one to three longitudinal lines, very large (0.2−0.23 mm long in *Boulayatheca fertilis*).

Type species. *Boulayatheca fertilis* (Kidston, 1914) Taylor & Kurmann, 1985.

Included species. *Boulayatheca hallei* (Gothan, 1941) Pacyna & Zdebska emend. et comb. nov.; *Boulayatheca ciliata* Pacyna & Zdebska, sp. nov.; *Boulayatheca saganii* Pacyna & Zdebska, sp. nov.; *Boulaya praelonga* Carpentier 1934 nomen dubium.

Discussion. The genus *Boulaya* was proposed by CARPENTIER in 1925 without formal diagnosis and without combination with a specific epithet. The new genus was created to accommodate specimens described earlier by KIDSTON (1914) and CARPENTIER (1914) as *Whittleseya* (?) *fertilis*.

HALLE (1933) validated the genus *Boulaya,* and proposed a combination *Boulaya fertilis* for type species (but ascribed binomen to Carpentier's authorship).

Then, CARPENTIER (1934) described another species of *Boulaya* – *B. praelonga* and concurred with Halle on the resolution of genus circumstance.

TAYLOR and KURMANN (1985) recognized that *Boulaya* Carpentier 1925 is a later homonym of *Boulaya* Cardot 1912, a generic name applied to a moss included in family Leskeaceae. According to Article 64.1 of the International Code of Botanical Nomenclature (2006) the generic name *Boulaya* Carpentier 1925 was rejected as being illegitimate and replaced by TAYLOR and KURMANN (1985) with a new generic name *Boulayatheca.* The new name combination for type species *Boulayatheca fertilis* was also proposed in this paper. TAYLOR and KURMANN (1985) neglected to take into account other species ascribed to genus *Boulaya* (*Boulaya hallei* and *B. praelonga*), however. The new combined name *Boulayatheca hallei* (Gothan 1941) Pacyna & Zdebska emend. et comb. nov. for *Boulaya hallei* is proposed in this paper. *Boulaya praelonga* is considered to be the *nomen dubium* in this paper (see Tables 6 and 7).

Distribution. Genus *Boulayatheca* is known from the early Westphalian in Europe only (see Table 7).

Boulayatheca fertilis (Kidston, 1914) Taylor & Kurmann, 1985 Pacyna & Zdebska, *emend. nov.*

Plate 4, Figs 1-2

1914 *Whittleseya* (?) *fertilis* sp. nov. Kidston, 1914; Kidston, p. 166-169, pl. 15, figs 1-10.
1914 *Whittleseya* (?) *fertilis* Kidston, 1914; Carpentier, p. 363-367, pl. 10, figs 4-5.
1925 *Boulaya* gen. nov. Carpentier, 1925 (sine nom. spec.); Carpentier, p. 149, pl 6, fig. 1.
1933 *Boulaya fertilis* (Kidston, 1914) Halle, 1933; Halle, p. 24-28, Pl. 6, figs 4-8.
1941 *Boulaya fertilis* (Kidston, 1914) Halle, 1933; Gothan 1941, p. 278-282.
1953 *Boulaya fertilis* (Kidston, 1914) Halle, 1933; Stockmans & Williere, p. 337.

1961 *Boulaya fertilis* (Kidston, 1914) Halle, 1933; Stockmans & Williere, p. 89-90, 110, fig. 33, pl. 10, fig. 2.
1964 *Boulaya fertilis* (Kidston, 1914) Halle, 1933; Delevoryas, p. 60-63.
1979 *Boulaya fertilis* (Kidston, 1914) Halle, 1933; Millay & Taylor, p. 344.
1984 *Boulaya fertilis* (Kidston, 1914) Halle, 1933; Kurmann & Taylor, p. 109-116, Pl. 1-2.
1985 *Boulayatheca fertilis* comb. nov. (Kidston, 1914) Taylor & Kurmann, 1985; Taylor & Kurmann, p. 666- 667.
2007a *Boulayatheca fertilis* (Kidston, 1914) Taylor & Kurmann, 1985; Pacyna, p. 105.

Emended diagnosis. Synangium (14—24 mm long and 7—10 mm wide) clavate-pyriform in shape, consisted of ring of sporangia, roundedly triangular in transverse section, contracted and somewhat rounded at the irregulary dentate apex, number of teeth from six to eight. Synangium finely longitudinally striated but not ribbed with a central empty space which is roundedly triangular in transverse section and enclosed by a thick wall containing sporangia. Prepollen grains *Monoletes*, 210—280 μm long, 150—180 μm wide.

Type specimens. Kidston (1914) did not designate holotype all specimens described by him are syntypes.

Referred specimens. LSCB: MW 946 — Wałbrzych, spoil heap of B. Chrobry mine, collected by E. Sagan in 1957 — two specimens on one shale slab, only mould, Zacler Formation, Duckamantian (Westphalian B); MW 947 — Wałbrzych, spoil heap of B. Chrobry mine, collected by E. Sagan in 1957 — two specimens on one shale slab, only one complete, only casts, Zacler Formation, Duckmantian (Westphalian B); MW 947a – one specimen, only cast, probably the same geological provenence, MW 931 — Wałbrzych, spoil heap of B. Chrobry mine, collected by E. Sagan – one specimen mould and cast, Zacler Formation, Duckmantian (Westphalian B).

Description. Synangium elongated, pyriform, markedly expanded distally (Pl. 4, Figs 1-2) consists of ring of sporangia which surround a central hollow cavity inside. Stalk not preserved. Synangium is 17—23 mm long, in most proximal part 2 mm wide, in most distal part 7—10 mm wide. Mould has central convexity which corresponds with concavity on cast this is the remainder of the central hollow cavity preserved after compression. Central

Table 6
Synonymy of species belonging to genus *Boulayatheca* Taylor & Kurmann, 1985
[= *Boulaya* Carpentier, 1925]

Authors	**Species**		
	Boulaya fertilis	***Boulaya hallei***	***Boulaya praelonga***
Kidston (1914)	*Whittleseya* (?) *fertilis*		
Carpentier (1914)	*Whittleseya* (?) *fertilis*		
Carpentier (1925)	*Boulaya* sine nom. spec.		
Halle (1933)	*Boulaya fertilis*		
Carpentier (1934)	*Boulaya fertilis*		*Boulaya praelonga*
Gothan (1941)	*Boulaya fertilis*	*Boulaya hallei*	
Hemingway (1941)			*Aulacotheca dixiana*
Stockmans & Williere (1953)	*Boulaya fertilis*		*Boulaya praelonga*
Stockmans & Williere (1961)	*Boulaya fertilis*	*Boulaya hallei*	*Boulaya* (?) *praelonga*
Crookall (1955-1976)	*Boulaya fertilis*		*Boulaya praelonga*
Millay & Taylor (1979)	*Boulaya fertilis*	*Boulaya hallei*	
Kurmann & Taylor (1984)	*Boulaya fertilis*		
Taylor & Kurmann (1985)	*Boulayatheca fertilis*		
Pacyna & Zdebska, this paper	*Boulayatheca fertilis*	*Boulayatheca hallei* comb. nov.	*nomen dubium*

Table 7
Comparison between the *Boulayatheca* species

Features of species	***Boulayatheca ciliata*** Pacyna & Zdebska, sp. nov.	***Boulayatheca fertilis*** (Kidston, 1914) Taylor & Kurmann, 1985	***Boulayatheca hallei*** (Gothan, 1941) emend. et comb. nov.	***Boulaya praelonga*** Carpentier 1934	***Boulayatheca saganii*** Pacyna & Zdebska, sp. nov.
Synangium length (mm)	23	14−24	7−12	21−25	16−22
Synangium width (mm)	11	6−10	3−5	4−5	5−8
Number of sporangia	2−4−6(?)	12−16(?)	5−7(?)	?	at least 6
Sporangial distal tips	lobate	acute	lobate, obtuse	?	rounded
Prepollen type and dimensions	not preserved	*Monoletes*, 210−280 μm × 150−180 μm	not preserved	not preserved	not preserved
Longitudinal striations	present, distinct	present, distinct	present, distinct	present, distinct, also ridges	present, distinct
Hairs on surface	present	absent	absent	absent	absent
Localities	Poland, Upper Silesia	United Kingdom, France, Germany, Holland, Belgium, Poland, Lower Silesia	France, Belgium	England, Belgium, France	Poland, Lower Silesia
Age	Westphalian A	Westphalian B	Westphalian A	Namurian B, Westphalian A	Westphalian
References	Pacyna & Wojciechowski (2004), Pacyna (2007a), Pacyna & Zdebska, this paper	Kidston (1914), Carpentier (1914), Halle (1933), Stockmans & Williere (1961), Crookall (1955-1976), Millay & Taylor (1979), Kurmann & Taylor (1984), Taylor & Kurmann (1985)	Carpentier (1914), Gothan, (1941), Millay & Taylor (1979)	Carpentier (1934), Stockmans & Williere, (1953, 1961), Crookall (1955-1976)	this paper

concavity is very well visible, deep, runnig parallel lengthwise to synangium. Central concavity is in most proximal part 1 mm wide, in most distal part to 3–4 mm wide (Pl. 4, Fig. 2). Synangium surface covered with longitudinal striation. Striae are 0.5 mm wide and consisted of alternating ridges and grooves. Ridges covered with strips of coalfield tissue (Pl. 4, Fig. 2). Distal margin of synangium sligthly contracted. Distal ends of sporangia, at least 6 in number, are more acuted than rounded, 1 mm wide. Hairs on the surface of the pollen organ have not been found. Prepollen grains not presereved.

Discussion. Kidston, following the custom of the time, did not announce his differential diagnosis of the new species he had described (at the time still in combination with the genus *Whittleseya*), but gave only a thorough description (KIDSTON 1914, p. 166-167). HALLE (1933), when revising the genus *Boulaya,* did not propose a separate diagnosis for the typical species. CROOKALL (1955-1976, p. 873) gave a very good, shortened description of this species based mainly on the KIDSTON (1914) description, but did not take the new interpretations carried out by HALLE (1933) into account. So *Boulayatheca fertilis* remains without a formal diagnosis, despite what TAYLOR and KURMANN (1985) have written, therefore, a new emended diagnosis is proposed here.

The Wałbrzych specimens match the previously mentioned specimens of *Boulayatheca fertilis* (KIDSTON 1914; CARPENTIER 1914; HALLE 1933; STOCKMANS & WILLIERE 1961; PACYNA 2007a) very well, both morphologically and in dimensions. The elongated pear-shaped shape is typical of this species, the specimens from Wałbrzych are almost identical in this respect with the specimens described earlier. HALLE (1933), emphasises the appearance of the central convexity/concavity, which is the remains of the central hollow cavity inside the organ. This feature, the result of partial compaction of specimens, is very well visible in the Wałbrzych specimens. The distinct striation of organs along the entire length is the next feature stressed by Halle in the description of this species. This striation is very well visible on the specimens from Wałbrzych. CROOKALL (1955-1976) and CLEAL and THOMAS (1994) give the following dimensions for the *B. fertilis*: length 14–24 mm, breadth 8–9 mm. The specimens from Wałbrzych are located within the variability of the given length, but their breadth demonstrates the greater variability 7–10 mm (Table 7).

Unfortunately, prepollen grains have not been preserved in the material from Wałbrzych. Prepollen grains are very big in the species *B. fertilis* (0.2–0.23 mm long), and visible even under the a magnifying glass (compare HALLE 1933, Pl. 6, Fig. 6; TAYLOR 1978). Prepollen grains are not always preserved *in situ* in the microsynangia of seed ferns. The majority of *B. fertilis* specimens examined by HALLE (1933), coming from Great Britain, had no preserved prepollen grains. HALLE (1933) believed that the organs were empty during fossilization or that diagenetic processes destroyed grains.

Distribution. United Kingdom, Ten-foot Ironstone Measures, Clayscroft Openwork, Coseley near Dudley, North Staffordshire, Westphalian B (KIDSTON 1914; HALLE 1933; CROOKALL 1955-1976; KURMANN & TAYLOR 1984). France, Nord (Denain), Fosse nr 8 des Mines de Bethune (Pas-de-Calais), 3 fosse Casimir-Perier and Fosse Turenne, Mines d'Anzin, Anzin, fosse d'Haveluy; Westphalian (CARPENTIER 1914; HALLE 1933). Germany, Westphalian (HALLE 1933). Holland, Grube Emma, Westphalian B (HALLE 1933). Belgium, zone de Beyne, Bassin de Liege, Veine Maldaccord, siege Homvent des Charbonnages de Werister a Beyne-Heusay; Middle Westphalian A (STOCKMANS & WILLIERE 1961). Poland, Lower Silesia, Wałbrzych, B. Chrobry mine; Westphalian B (this paper).

Boulayatheca ciliata Pacyna & Zdebska, *sp. nov*.   Plate 4, Figs 3-6, Plate 5, Figs 1-5; Fig. 2E

2004 *Boulayatheca fertilis*? (Kidston, 1914) Taylor & Kurmann, 1985; Pacyna & Wojciechowski, p. 143-147.
2007a *Boulayatheca* cf. *fertilis* (Kidston, 1914) Taylor & Kurmann, 1985; Pacyna, p. 106.

Diagnosis. Synangium elongated, pyriform in shape, markedly expanded distally, 23 mm long, in most proximal part 5 mm wide, in most distal part to 11 mm wide, consists of ring of sporangia which surround a central hollow cavity inside. Synangium roundedly triangular in transverse section, slightly contracted and somewhat rounded at the irregulary dentate apex, teeth (presumable free distal tips of sporangia) are lobate, 2 mm wide, contracted distally. The central hollow cavity is roundedly triangular in transverse section and enclosed by a thick wall containing sporangia. Synangium finely longitudinally striated. Striae are 0.5 mm wide, runnig parallel lengthwise to the synangium margin. Synangium covered with hairs, at least 10 per 1 mm^2. Hairs are thin, needle-shaped, to 0.2 mm long, expanded to base.

Age. Upper Carboniferous (Pennsylvanian), Westphalian A (Langsettian).

Horizon. Mudstone Series, Załęże Beds.

Type locality. Upper Silesia, Dąbrowa Górnicza area, Sosnowiec–Zagórze, Porąbka-Klimontów mine.

Holotype. S/100/P2, Pl. 4, figs 3-4; Fig. 2E.

Referred specimens. S/100/P4, S/100/P7.

Etymology. Lat. *ciliate* – covered with hairs, alluding to covering synangium surface with hairs.

Description. Synangium elongated, pyriform in shape, markedly expanded distally, consists of ring of sporangia (individual sporangium hardly distinguish) which surround a central hollow cavity inside (Pl. 4, Figs 3-6, Pl. 5, Figs 1-2). Stalk not preserved. The synangium is 23 mm long, in most proximal part 5 mm wide, in most distal part to 10 mm wide. The mould has a central convexity which corresponds to the concavity on the cast this is the remainder of the central hollow cavity preserved after compression. Central concavity is very well visible, deep, run parallel lengthwise to synangium margin. Central concavity is in most proximal part 2 mm wide, in most distal part to 5 mm wide (Pl. 5, Figs 1-2). Synangium surface covered with longitudinal striation. Striae are 0.5 mm wide and consist of alternating ridges and grooves. Ridges covered with strips of coalfield tissue. Distal margin of synangium rounded, slightly contracted with presumable free distal tips of sporangia visible. Free distal tips of sporangia are lobate, 2 (proximally) to 1 (distally) mm wide. Only two well preserved sporangial tips are visible. Synangium covered with hairs, at least 10 per 1 mm^2. Hairs are thin, needle-shaped, to 0.2 mm long, expanded to base (Pl. 5, Figs 3-4). Bases of hairs are visible on the surface of synangium as dark spots 0.2 mm in diameter (Pl. 5, Fig. 5). Prepollen grains not preserved.

Discussion. Specimens correspond very well in terms of morphological structure to the diagnosis of the *Boulayatheca* genus in the HALLE (1933) interpretation. The elongated pear-shaped shape is typical for that genus. HALLE (1933), emphasizes the appearance of the central convexity/concavity which is the remains of the central hollow cavity inside the organ. This feature, the result of partial compaction of specimens, is very clearly visible on the Sosnowiec specimens (Pl. 5, Figs 1-2). Furthermore, the duality of this structure on one of the specimens (holotype) from Sosnowiec confirms the accuracy of Halle's interpretation that the organ in cross section (as well as the empty channel inside it) had the shape of a triangle with rounded angles. The distinct striation of organs along the entire length is the next feature Halle stressed in his description of the *Boulayatheca* genus. This striation is very well visible on the specimens from Sosnowiec. Striation is not very distinct in the morphologically similar *Schopfitheca* genus, and this enables clear distinction between these genera (Drinnan & Crane 1994).

Specimens of the new species correspond to the morphological structure of *Boulayatheca fertilis*, although they are wider (*B. ciliata* sp. nov. – breadth of 11 mm, *B. fertilis* – breadth 8–9 mm, Cleal & Thomas 1994) and, most importantly, are covered with well preserved hairs this feature was previously unknown in this genus (Pl. 5, Figs 3-5, Pacyna & Wojciechowski 2004; Pacyna 2007a, b). The *Boulayatheca* genus was recognised devoid of structures of this type (Millay & Taylor 1979). The appearance of hairs on the surface of the organ is the most important autapomorphic feature of the new species and enables determination of this material as a new species.

The genus *Schopfitheca,* described from Mazon Creek nodules, is morphologically similar to *Boulayatheca,* but has distinct hairs appearing more densely than on the Sosnowiec specimens. These specimens cannot, however, be referred to as genus *Schopfitheca* because they clearly differ in morphological structure from that genus. The *Schopfitheca* genus is more oval in shape, rather than pear-shaped (compare holotype specimen – Delevoryas 1964, Pl. 12, Figs 1-2), has no distinct striation, lacks the central convexity/concavity, since it was only in part empty in the most distal section (Drinnan & Crane 1994). Pollen organs hairs have only not been described in two genera of medullosalean – *Boulayatheca* and *Halletheca* – all other genera have well preserved hairs (Taylor 1971; Millay & Taylor 1979; Taylor & Millay 1981; Mapes 1982). It is possible to suppose that this is a feature both universal and typical of medullosalean pollen organs, and that perhaps it was not described in the *Boulayatheca* genus previously on account of the poor preservation of the specimens.

Two species are still known from the *Boulayatheca* genus in which described the material differs, and both originate from the Upper Carboniferous of Western Europe. *B. praelonga* (Carpentier 1934) which has similar dimensions to *Boulayatheca ciliata* Pacyna & Zdebska, sp. nov. (21–25 mm of the length, 4–5 mm of the breadth), but is clavate and does not broaden clearly to the distal end. *B. hallei* (Gothan 1941; Stockmans &Williere 1961) is smaller (8–10 mm of the length, 3–5 mm of the breadth) and is bell-shaped.

Boulayatheca saganii Pacyna & Zdebska, *sp. nov.* Plate 5, Fig. 6, Plate 6, Figs 1-2

2007a *Boulayatheca* sp.; Pacyna, p. 106.

Diagnosis. Synangium elongated, rod-shaped, slightly pyriform, markedly expanded distally, 16–22 mm long, in most proximal part 1 mm wide, in most distal part 5–8 mm wide, consisting of a ring of sporangia which surround a central hollow cavity inside. Synangium roundedly triangular in transverse section, slightly contracted and somewhat rounded at the dentate apex, teeth (presumable free distal tips of sporangia) are lobate, not contracted distally, 1 mm wide, number of teeth at least six. The central hollow cavity is roundedly triangular in transverse section and enclosed by a wall containing sporangia. Synangium finely longitudinally striated. Striae are 0.5 mm wide, running parallel lengthwise to the synangium margin.

Age. Westphalian.

Horizon. Zacler Formation.

Type locality. Lower Silesia, Wałbrzych, B. Chrobry mine.

Type specimens. MW 944, Wałbrzych, B. Chrobry mine, collected by E. Sagan in 1957, tens of specimens on one shale slab, specimen 944/1 designated here as holotype, the other specimens on this slab designated here as paratypes (Pl. 5, Fig. 6, Pl. 6, Figs 1-2).

Etymology. To honour Eufrozyn Sagan – collector of many of the specimens described here.

Description. Synangium elongated, rod-shaped, slightly pyriform, markedly expanded distally (Pl. 5, Fig. 6, Pl. 6, Figs 1-2), consists of ring of sporangia which surround a central hollow cavity inside. Synangium is 16−22 mm long, in most proximal part 1 mm wide, in most distal part 5−8 mm wide. The mould has a central convexity which corresponds to the concavity on the cast, this is the remainder of the central hollow cavity preserved after compression. The central concavity is very well visible, deep, running parallel lengthwise to the synangium margin. The central concavity is in most proximal part 1−2 mm wide, in most distal part to 3 mm wide (Pl. 6, Figs 1-2). Synangium surface covered with longitudinal striation. Striae are 0.5 mm wide and consist of alternating ridges and grooves. Ridges covered with strips of coalfield tissue. Distal margin of synangium rounded, slightly contracted with presumable free distal tips of sporangia visible. Free distal tips of sporangia are lobate, 1 mm wide, not contracted distally. At least six free distal tips of sporangia are visible. Hairs not found. Prepollen grains not preserved.

Discussion. The new species described here was referred to genus *Boulayatheca* because it has features typical of that genus: clavate-pyriform shape, central concavity parallel to edges of the organ, striation appear, ridges typical of the *Aulacotheca* genus do not appear, tips of the sporangia are visible on the distal edge (Pacyna 2007a, b).

Boulayatheca saganii Pacyna & Zdebska, sp. nov. is distinguished from *B. fertilis* by the ends of the sporangia being more rounded than acute, smaller dimensions of synangium, and a more elongated shape it is also less pear-shaped than *B. fertilis*. *Boulayatheca saganii* sp. nov. may be distingiushed from *B. praelonga* (Carpentier 1934). *B. praelonga* is longer and narrower, clavate, and it does not widen clearly to the distal end. *B. hallei* (Gothan 1941; Stockmans & Williere 1961) is smaller (8−10 mm of the length, 3−5 mm of the breadth) and is bell-shaped. From *B. ciliata* sp. nov. it differs by dimensions, smaller ends of the sporangia, and lack of hairs (Table 7).

Boulayatheca hallei (Gothan, 1941) Pacyna & Zdebska, *emend. et comb. nov.*

1914 *Whittleseya* (?) *fertilis* Kidston, 1914; Carpentier, p. 363-367, pl. 10, figs 1-3.
1928 microsporophylls of *Lonchopteris rugosa*; Carpentier, p. 387, pl. 34, fig. 2.
1941 *Boulaya hallei* sp. nov. Gothan 1941; Gothan, p. 278-282, Taf. 22, fig. 4.
1961 *Boulaya hallei* Gothan, 1941; Stockmans & Williere, p. 90-91, 110, fig. 33, pl. 9, figs 1-8.
1979 *Boulaya hallei* (Kidston, 1914) Halle, 1933; Millay & Taylor, p. 342.

Emended diagnosis. Synangium elongated (7–12 mm long and 3–5 mm wide) clavate-pyriform in shape, often notably pyriform to ovate in shape, consisting of ring of sporangia, roundedly triangular in transverse section, contracted and somewhat rounded at the irregularly dentate apex, number of teeth from four, five to seven. Teeth are lobate, obtuse and very large proportionately to synangium size, but not as big as in other *Boulayatheca* species. Synangium finely longitudinally striated but not ribbed, with a central empty space which is roundedly triangular in transverse section and enclosed by a thick wall containing sporangia. This empty space is preserved as a central convexity running parallel lengthwise to the synangium margin.

Age. Westphalian.

Type locality. France, Houiller du Nord, Fosse nr 8 des Mines de Bethune (Pas-de-Calais).

Type specimens. GOTHAN (1941) did not designate a holotype specimen the specimens illustrated by him are syntypes.

Discussion. The specimens referred by GOTHAN (1941) to the new species *Boulaya hallei*, were first described and illustrated by CARPENTIER (1914, Pl. 10, Figs 1-3) under the name *Whittleseya* (?) *fertilis*. In his paper, GOTHAN (1941, Taf. 22, Figs 4) reproduced the specimen illustrated earlier by Carpentier, turned ca. 30° ahead. This fact remained unnoticed in the paleobotanical literature because Gothan wrote that the photograph dated from the Carpentier's work of 1928. All the specimens described and illustrated in CARPENTIER (1914) were quoted as *Boulayatheca* [= *Boulaya fertilis*] (TAYLOR & KURMANN 1985). In fact, the only specimens described in CARPENTIER (1914) on Pl. 10 Figs 4-5 are conspecific with KIDSTON (1914) specimens, and can be referred to *B. fertilis*. Specimens which should be referred to *B. hallei* previously were also probably described by CARPENTIER (1913) with specimens which should ranked among the *B. fertilis*. In his paper from 1928 Carpentier again appealed to specimens from his paper in 1914 (Pl. 10, Fig. 1), reproduced the photograph, and determined the discussed pollen organs as microsporophylls of *Lonchopteris rugosa*.

GOTHAN (1941) created the name *Boulaya hallei* for the specimens determined by CARPENTIER (1928) as microsporophylls of *Lonchopteris rugosa*, and also discussed earlier works by CARPENTIER (1913, 1914, 1925) associated with this material. In the GOTHAN (1941) paper, there is an absence of formal diagnosis and proper description of the new species. Yet the species looks well defined and is simple to distinguish from other *Boulayatheca* species, including the new species described here. STOCKMANS and WILLIERE (1961) described several dozen specimens referred to *B. hallei.*

Since TAYLOR and KURMANN (1985), during the genus name change from *Boulaya* on *Boulayatheca*, only proposed a new combination for typical species, not taking the *Boulaya hallei* into account this new combination is proposed here.

Distribution. France, Nord, Mines de Bethune, westfal (CARPENTIER 1928). Belgium, Zone de Genk, Bassin du Centre (Massif du Comble Nord), Bassin du Charleroi (Massif du Centre), Bassin du Liege (Veine Castagnette), Trieu-Kaisin, Massif du Gouffre; Late Westphalian A (STOCKMANS & WILLIERE 1961).

Comments on genus *Boulayatheca*. The question of synonymy of *Boulaya praelonga* with *Aulacotheca dixiana.* The species *Boulaya praelonga* was described validly, with a diagnosis and illustrated by CARPENTIER in 1934, on the basis of specimens coming from Westphalian of France (Nord, Mines d'Anzin). Later, very similar specimens were found by Dix in England (Nafferton Coal Group, High Shilford Colliery, Northumberland, Westphalian A). She described these specimens first, without determining the genus and species affinity. She also interpreted leaves found in specimens as connected with pollen organs (Dix 1932, 1933). Hemingway (1941) clarified the matter, according to him the leaves and pollen organs were only imposed on themselves. He described these pollen organs as a new species, *Aulacotheca dixiana*, being unaware that Carpentier had most probably previously described conspecific taxon from France – *Boulaya praelonga*.

Both Carpentier's (1934) and Hemingway's (1941) specimens, apart from the delicate oblong stripes, also have quite distinct ridges, and an indistinct shape varying between genera *Aulacotheca* and *Boulayatheca*. Which genus should they be referred to? Stockmans and Williere (1953), describing similar specimens from Namurian B of Belgium, noted this problem and therefore used the name in open nomenclature as *Boulaya* (?) *praelonga*. It is worthwhile adding that it is the only species of *Boulayatheca* which is Namurian in age all remaining species are Westphalian in age, however, *Aulacotheca* is known from Namurian to Westphalian.

Crookall (1955-1976) analysed this problem and admitted that Carpentier was right, and regarded the species described by Hemingway as a synonym.

Next, Millay and Taylor (1979) and Mickle and Leary (1984) regarded *Aulacotheca dixiana* as valid. If indeed the species should be ranked among the *Aulacotheca* genus, its correct name should be *Aulacotheca praelonga*, because this species name has priority, assuming the specimens of Carpentier and Hemingway are in fact conspecific. The quality of photographs in Carpentier's and Hemingway's papers is not the highest, and so an inspection of the original materials is necessary for settling the real generical membership of the species discussed here. Until then, these species should be recognized as *nomina dubia*. It is worth mentioning they are clearly distinguished from the *Aulacotheca* and *Boulayatheca* species described here. From their creators' perspective, both species were taken into account in descriptions and tables for comparative purposes with the material described here (Tables 5 and 7).

Genus ***Whittleseya*** Newberry, 1853a emend. Halle, 1933

1853a *Whittleseya* Newberry, 1853a; Newberry, p. 106.
1853b *Whittleseya* Newberry, 1853a; Newberry, fig. p. 116.
1900 *Whittleseya* Newberry, 1853a; White, p. 904-907.
1901 *Whittleseya* Newberry, 1853a; White, p. 98-110.
1904 *Whittleseya* Newberry, 1853a; Potonie p. 1-4.
1914 *Whittleseya* Newberry, 1853a; Kidston, p. 166.
1917 *Whittleseya* Newberry, 1853a; Seward, p. 124-131.
1933 *Whittleseya* Newberry, 1853a; Halle, p. 17-24, pl. 4, 5, 6, fig. 1-3, text-fig. 5.
1944 *Whittleseya* Newberry, 1853a; Bell, p. 83-84.
1961 *Whittleseya* Newberry, 1853a; Stockmans & Williere 1961, p. 97-98.
1979 *Whittleseya* Newberry, 1853a; Millay & Taylor, p. 342-348.
1994 *Whittleseya* Newberry, 1853a; Drinnan & Crane, p. 255.
2000 *Whittleseya* Newberry, 1853a; Goubet *et. al*., p. 33-34, fig. 15.4.
2005 *Whittleseya* Newberry, 1853a; Dilcher, Lott & Axsmith, p. 163.

Diagnosis (after Halle 1933, p. 23-24)**.** Synangia hollow and probably campanulate in natural state, leaf-like and broadly cuneate-spathulate when flattened; apex non-contracted, broadly truncate and dentate; surface with numerous marked longitudinal ridges running out into the apical teeth; wall of the campanulate body formed of a single whorl of long and narrow concrescent sporangia, which correspond to the external ribs, embedded in vegetative tissue and extend longitudinally from base to apex; spores of the bilateral type, with one to three longitudinal lines, elliptical in the flattened state very large (0.20–0.25 mm long in *W. elegans*).

Type species. *Whittleseya elegans* Newberry, 1853a.

Included species. *W. brevifolia* White, 1901; *W. crassifolia* Lesquereux, 1879; *W. dawsoniana* White, 1901; *W. desiderata* White, 1901; *W. microphylla* Lesquereux, 1884; *W. undulata* Lesquereux, 1879; *W. silesiaca* Pacyna & Zdebska, sp. nov., *W. campanulata* Pacyna & Zdebska, sp. nov.

Whittleseya elegans Newberry, 1853a Plate 7, Fig. 1

1853a *Whittleseya elegans* Newberry, 1853a; Newberry, p. 106.
1853b *Whittleseya elegans* Newberry, 1853a; Newberry, fig. p. 116.
1900 *Whittleseya elegans* Newberry, 1853a; White, p. 904.
1900 *Whittleseya elegans* var. *minor* White 1901; White, p. 904.
1901 *Whittleseya elegans* Newberry, 1853a; White, p. 98-110, pl. 7, fig. 5.
1904 *Whittleseya elegans* Newberry, 1853a; Potonie p. 1-4, fig. 1-3.
1914 *Whittleseya elegans* Newberry, 1853a; Kidston, p. 166, pl. 15, fig. 11.
1917 *Whittleseya elegans* Newberry, 1853a; Seward, p. 128-131, figs 428 A, C, 429 A, B.
1933 *Whittleseya elegans* Newberry, 1853a; Halle, p. 20-23, pl. 4, 5, 6, fig. 1-3, text-fig. 5.
1961 *Whittleseya elegans* Newberry, 1853a; Stockmans & Williere 1961, p. 97.
1961 *Whittleseya delphinae* Stockmans & Williere 1961; Stockmans & Williere 1961, p. 97-98, pl. 8, fig. 1.
1979 *Whittleseya elegans* Newberry, 1853a; Millay & Taylor, p. 342-348, fig. 17f.
2005 *Whittleseya elegans* Newberry, 1853a; Dilcher, Lott & Axsmith, p. 163, pl. 137, fig. 1-9, fig. 5.1.6.
2007a *Whittleseya elegans* Newberry, 1853a; Pacyna, p. 106.

Referred specimens. LSCB: S/101/1 – Wałbrzych, collected by E. Sagan – one well preserved specimen and badly preserved remains of several others, Upper Carboniferous; MW 943 – Wałbrzych, spoil heap of B. Chrobry mine, collected by E. Sagan in 1957 – one specimen on shale slab, Zacler Formation, Duckmantian (Westphalian B); MW 945 (F. Zimmermann collection number 738a) – Wałbrzych, Hangendzug Georg Schacht, collected by F. Zimmermann – one incomplete specimen on shale slab, Zacler Formation, Westphalian; MW 949 – Gorce, spoil heap of Klara shaft, collected by E. Sagan in 1963 – two badly preserved specimens on one shale slab, Zacler Formation, Langsettian (Westphalian A).

Description. Pollen organ cuneate-spathulate in shape, 23–40 mm long, 16–22 wide. Sporangia, about 20 in number, narrow, parallel, strongly marked, very well visible, poorly parallel or wavily striped (Pl. 7, Fig. 1). Sporangia do not cluster into groups in the distal part of the organ they are parallel, proximally they become lightly narrow and run towards the stalk. Sporangial distal tips (teeth) acute, distinct, triangular. Base of the organ contracted, widely rounded. Apex of the organ rather straight, broadly truncated, very poorly rounded off, perpendicular to sides of the organ. Stalk not preserved, prepollen grains also.

Discussion. NEWBERRY (1853a, b) did not differentiate generic and specific diagnosis for *Whittleseya elegans.* In his paper HALLE (1933) concentrated exclusively on the typical species *W. elegans*. In reference to POTONIE (1904) he considered that the majority of remaining species from the *Whittleseya* genus should be regarded as synonyms of *W. elegans* (opinion not resulting from the POTONIE (1904) work nor shared by the authors of this work). In detail he discussed the status of *W. campbellii* [= *Aulacotheca campbellii*] and *Whittleseya*? *fertilis* [= *Boulayatheca fertilis*], showing that they should not be referred to genus *Whittleseya* (Table 8). The emended diagnosis of the *Whittleseya* genus of the Halle's authorship, quoted earlier, could, in principle also describe the typical species *W. elegans*.

The specimens described here match well with both the size and the morphological structure of *W. elegans* (HALLE 1933; MILLAY & TAYLOR 1979; PACYNA 2007a, b) (Table 9). Peculiarly, the specimens described have a characteristic cuneate-spathulate shape and well visible narrow, self parallel sporangia which are terminate in sharpened teeth at the organ apex. Well preserved specimens have average dimensions as for this species, while bigger specimens are only fragmentarily preserved. Oblong striation of the sporangia in *W. elegans* was noticed for the first time by THOMAS (1912) on material from Great Britain. HALLE (1933) described this feature in detail, based on macerated specimens. This feature is well evident on two specimens from the Lower Silesia: on MW 945 the stripes are clearly parallel, on MW 943 – wavy.

On the basis of materials from Middle Westphalian of Belgium, STOCKMANS and WILLIERE (1961) described a new species *Whittleseya delphinae*. They only had a badly weathered shale slate with a few *Whittleseya* specimens at their disposal, which became the base for the description of the new species. The material was found in an old opencast mine in Massif du Comble Nord. All specimens were almost identical, while sizes demonstrated minute changeability. The only essential feature quoted in discussion by these authors as distinguishing *Whittleseya delphinae* from *W. elegans* is the smaller size of the Belgian species (Table 9). All remaining features are within the morphological variability of *W. elegans*. And so it seems that species *W. delphinae* is a younger synonym of *W. elegans*. STOCKMANS and WILLIERE (1961) also suggested that the specimens from Lower Silesia, illustrated by POTONIE (1904, Figs 3-4), should be referred to *Whittleseya delphinae*. According to authors' of this paper, the specimen illustrated by POTONIE (1904) on Figure 2 should be referred to *W. elegans*, and the specimen illustrated on Figure 4 to the new species described here *W. silesiaca*.

The morphologically distinct (much wider) specimens illustrated by LESQUEREUX (1879, Pl. 4, Fig. 1) and DILCHER *et al.* (2005, Pl. 137, fig. 3) referred to *W. elegans* are probably strongly flattened specimens of this species on which the part of the back wall of the organ is visible.

Distribution. Species *Whittleseya elegans* was described on the basis of specimens from the USA, from Ohio (NEWBERRY 1853a, b; HALLE 1933). It was next discovered in Great Britain (THOMAS 1912; KIDSTON 1914) and in Poland in Lower Silesia (POTONIE 1904; GOTHAN 1923a; ZIMMERMANN 1962; MIGIER 1972; KOTASOWA & MIGIER 1995). All specimens are Early and Middle Westphalian in age. Part of the material from Lower Silesia previously referred to *W. elegans*, is the basis for the description of the new species *W. silesiaca* here (Table 9).

Whittleseya silesiaca Pacyna & Zdebska, *sp. nov.* Plate 7, Figs 2-5

1904 *Whittleseya elegans* Newberry, 1853a; Potonie p. 1-4, fig. 4.
2007a *Whittleseya* cf. *elegans* Newberry, 1853a; Pacyna, p. 106-107.

Diagnosis. Pollen organ cuneate-campanulate, 28−32 mm long, 27−29 mm wide. Sporangia number from 15 to 25, narrow, parallel to each other, strongly marked, prominent, very visible, clearly longitudinally striped on the surface. Sporangia in the distal part of

Table 8
Synonymy of species belonging to genus *Whittleseya*

Authors	Species							
	Whittleseya brevifolia	**_Whittleseya campbelli_**	**_Whittleseya concinna_**	**_Whittleseya crassifolia_**	**_Whittleseya dawsoniana_**	**_Whittleseya delphinae_**	**_Whittleseya desiderata_**	**_Whittleseya elegans_**
Newberry (1853a, b)								*Whittleseya elegans*
Lesquereux (1879, 1880, 1884)				*Whittleseya crassifolia* Lesquereux, 1879				*Whittleseya elegans*
White (1900)		*Whittleseya campbelli*						*Whittleseya elegans*
White (1901)	*Whittleseya brevifolia*	*Whittleseya campbelli*		*Whittleseya crassifolia*	*Whittleseya Dawsoniana*		*Whittleseya desiderata*	*Whittleseya elegans*
Potonie (1904)	*Whittleseya brevifolia*	*Whittleseya campbelli*		*Whittleseya crassifolia*	*Whittleseya Dawsoniana*		*Whittleseya desiderata*	*Whittleseya elegans*
Matthew (1910) in Bell (1944)			*Whittleseya concinna* var. *lata* var. *arcta*					
Kidston (1914)								*Whittleseya elegans*
Halle (1933)		*Aulacotheca campbellii*						*Whittleseya elegans*
Bell (1944)	*Whittleseya brevifolia*		=*Whittleseya brevifolia*				*Whittleseya desiderata*	
Stockmans & Williere (1961)						*Whittleseya delphinae*		*Whittleseya elegans*
Millay & Taylor (1979)		*Aulacotheca campbelli*						*Whittleseya elegans*
Pacyna & Zdebska, this paper	*Whittleseya brevifolia*	*Aulacotheca campbelli*	=*Whittleseya brevifolia*	*Whittleseya crassifolia*	*Whittleseya dawsoniana*	*Whittleseya elegans*	*Whittleseya desiderata*	*Whittleseya elegans*
Lesquereux (1879, 1880, 1884)			*Whittleseya integrifolia* Lesquereux, 1880			*Whittleseya microphylla* Lesquereux, 1884	*Whittleseya undulata* Lesquereux, 1879	
White (1900)	*Whittleseya elegans* var. *minor*			*Whittleseya Lescuriana*		*Whittleseya microphylla*		

Table 8 cont.

Authors	**Species**							
	Whittleseya brevifolia	***Whittleseya campbelli***	***Whittleseya concinna***	***Whittleseya crassifolia***	***Whittleseya dawsoniana***	***Whittleseya delphinae***	***Whittleseya desiderata***	***Whittleseya elegans***
White (1901)				*Whittleseya Lescuriana*		*Whittleseya microphylla*	*Whittleseya undulata*	
Potonie (1904)			=*Whittleseya carssifolia*	*nomen nudum*		*Whittleseya microphylla*	*Whittleseya undulata*	
Kidston (1914)		*Whittleseya* (?) *fertilis*						
Halle (1933)		*Boulaya fertilis*						
Stockmans (1950) in Stockmans & Williere (1961)					*Whittleseya media*			
Stockmans & Williere (1953)					*Whittleseya media*			
Stockmans & Williere (1961)		*Boulaya fertilis*			*Givesia media*			
Millay & Taylor (1979)		*Boulaya fertilis*			*Givesia media*			
Taylor & Kurmann (1985)		*Boulayatheca fertilis*						
Pacyna & Zdebska, this paper	*Whittleseya elegans* var. *minor*	*Boulayatheca fertilis*	=*Whittleseya carssifolia*	*nomen nudum*	*Givesia media*	*Whittleseya*? *microphylla*	*Whittleseya*? *undulata*	

Table 9
Comparison between the *Whittleseya* species

Features of species	***Whittleseya brevifolia*** White, 1901	***Whittleseya campanulata*** Pacyna & Zdebska, sp. nov.	***Whittleseya crassifolia*** Lesquereux, 1879	***Whittleseya dawsoniana*** White, 1901	***Whittleseya delphinae*** Stockmans & Williere, 1961
Synangium length (mm)	7–14	35	80	13	31
Synangium width (mm)	9–7	47	60	17	21
Synangium shape	fan-shaped, very widely triangular	campanulate	-	very wide, wider than longer	bell-shaped (similar to the bowl)

Number of sporangia	20−25	ca. 30−40	-	10−12	15−20, essentially ca. 40
Longitudinal ridges (ribs) corresponding to sporangia	narrow, distant at 0.5 mm from each other, little distinct, more or less marked, time forked by the base	flat, distinct, parallel, 1 mm wide, additionally gently parallel striped	badly presreved	very wide, (1.5−1.75 mm), not forked, forming very wide and very low, flattened ribs	parallel, straight or arcuately bent, 0.75−1 mm wide
Sporangial distal tips (teeth)	blunt, very short	short (0.5 mm), rounded	a serration miss (perhaps not preserved?)	short, wide, blunt	short, pointed
Prepollen type and dimensions (µm)	not known	not known	not known	not known	not known
Localities	Canada: New Scotland	Poland: Lower Silesia	USA: Tuscaloosa, Alabama?, Pennsylvania	Canada: New Brunswick	Belgium
Age	Early Westphalian A	Upper Carboniferous	Upper Carboniferous	Early Westphalian	Westphalian A
References	White (1901), Potonie (1904), Bell (1944)	this paper	Lesquereux (1879), Potonie (1904)	White (1901), Potonie (1904)	Stockmans & Williere (1961)
Features of species	***Whittleseya desiderata*** White, 1901	***Whittleseya elegans*** Newberry, 1853a	***Whittleseya microphylla*** Lesquereux, 1884	***Whittleseya silesiaca*** Pacyna & Zdebska, sp. nov.	***Whittleseya undulata*** Lesquereux, 1879
Synangium length (mm)	8−14	50	25 (from what half stalk)	28−32	45
Synangium width (mm)	5–10	30	8	27−29	10
Synangium shape	elongate, slightly cuneate	cuneate-spathulate	cuneate, triangular	cuneate-campanulate	strongly elongated, apex irregular, undulating
Number of sporangia	18−24	Very numerous	-	ca. 15−25	5−6 (?)
Longitudinal ridges (ribs) corresponding to sporangia	poorly rounded, distinct, regular, running, moved away for 0.5 mm from each other, once forked under the big angle by the base	narrow, parallel, strongly marked, very well visible	difficult to distinguish, thick	narrow, parallel, strongly marked, prominent, very well visible, additionally clearly parallel striped	distinct, wide, few (?)
Sporangial distal tips (teeth)	acute, 0.5 mm long	acute, distinct, triangular	poorly visible	rounded, truncate	diminutive, poorly visible
Prepollen type and dimensions (µm)	not known	*Monoletes* 200−250 × 140−160	not known	not known	not known
Localities	Canada: New Scotland	USA: Ohio; Poland: Lower Silesia; United Kingdom	USA: Washington County, Arkansas	Poland: Lower Silesia	USA: Tuscaloosa, Alabama(?), Pennsylvania
Age	Early Westphalian A	Early-Middle Westphalian	Middle Westphalian	Westphalian A	Middle Westphalian
References	White (1901), Potonie (1904), Bell (1944)	White (1900, 1901), Potonie (1904), Halle (1933), Millay & Taylor (1979)	Lesquereux (1884), White (1901), Potonie (1904)	this paper	Lesquereux (1879), White (1901)

the organ parallel, slightly narrowing proximally and converging toward the base of the stalk. Distal ends of sporangia (teeth), rounded, truncate. Sporangia (5–10 in number) are combined in approximately 5 clusters, each probably corresponding to one synangium. Base of the organ tapered. Apex of the organ slightly rounded, perpendicular to the sides of the organ.

Age. Upper Carboniferous, Langsettian (Westphalian A).

Horizon. Zacler Formation.

Type locality. Lower Silesia, Wałbrzych area.

Type specimens. MP IB UJ 101/1 (2 complete and 3 incomplete specimens on one shale slab), holotype – completely preserved specimen (number 101/1/1), paratype – almost completely preserved specimen (number 101/1/2), the remaining three incomplete specimens – specimens assigned to this species (Pl. 7, Figs 3-4).

Referred specimens. MW 950 – Gorce area, spoil heap of Klara shaft, collected by E. Sagan in 1963 – five almost complete and two fragmentary pollen organs on one shale slab, all specimens not well preserved; MW 952 – the same provenance – mould and cast of one specimen.

Etymology. *silesiaca* – referring to the occurrence of this species in Lower Silesia.

Description. Pollen organ cuneate-campanulate in shape, length 28–32 mm and width 27–29 mm. Sporangia number from 15 to 25, narrow, closely adjacent to each other, parallel, strongly marked, prominent, very visible, clearly longitudinally striped on the surface (Pl. 7, Figs 2-5). Sporangia in the distal part of the organ parallel, slightly narrowing proximally and converging toward the base of the stalk (Pl. 7, Fig. 4). Distal ends of sporangia (teeth), rounded, truncate (Pl. 7, Fig. 5). Sporangia (5–10 in number) are combined in approximately 5 clusters, each probably corresponding to one synangium (Pl. 7, Fig. 3). And so the whole organ is a cluster of synangia. Base of the organ tapered. Stalk not preserved. Apex of the organ slightly rounded, perpendicular to the sides of the organ. Prepollen grains not preserved.

Discussion. The specimens referred to here as a new species *W. silesiaca* sp. nov. were previously labeled in the literature as *W. elegans* (Potonie 1904, Fig. 4; Pacyna 2007a, b). Stockmans & Williere (1961), however, expressed doubts as to the correctness of this assignment and proposed the allocation of specimens from the Lower Silesia illustrated by Potonie (1904, Fig. 3 and 4) to the species *Whittleseya delphinae* which they had created. According to us, *Whittleseya delphinae* should be considered a synonym of *W. elegans* (see the above discussion of *W. elegans*). The specimens from Lower Silesia illustrated by Potonie (1904) in Figure 3 should be attributed to *W. silesiaca* sp. nov., and the specimens in Figures 1, 2 and 4 to *W. elegans*.

The new species *W. silesiaca*, established on the basis of several specimens, demonstrates less variability in dimension than *W. elegans*, where the smallest specimens are smaller than *W. silesiaca* sp. nov., and the largest reach 50 mm in length and 30 mm wide (Millay & Taylor 1979; Pacyna 2007a, b).

The most important distinctive feature of this new species in comparison with *W. elegans*, however, is the shape of the organ, which in *W. elegans* is cuneate-spathulate (Millay & Taylor 1979), and in *W. silesiaca* sp. nov. cuneate-campanulate.

The clusters of sporangia in groups of 5–10 are another typical characteristic of this species, and this feature is also clearly evident in *W. campanulata* sp. nov., as well as presumably in *W. dawsoniana* and *W. undulata* (White 1901, Pl. 7). This may indicate that, at least in some species of *Whittleseya,* we are dealing with compound rather than simple synangia. This fact has not been recorded in the literature. In *W. silesiaca* sp. nov., five clusters of sporangia may be observed, whereas in *W. campanulata* Pacyna & Zdebska, sp. nov., described below, there are ten.

The sporangia of *W. silesiaca* sp. nov. are clearly, strongly striped longitudinally, and this feature is also visible but less pronounced in *W. elegans* (Seward 1917; Halle 1933) and *W. campanulata* sp. nov. In the remaining species of *Whittleseya*, this has not been described. However, it can be observed in White's figures (White 1901) in at least two more species: *W. desiderata* and *W. brevifolia*.

Distribution. Only LSCB – Wałbrzych, Gorce.

Whittleseya campanulata Pacyna & Zdebska, *sp. nov.* Plate 8, Figs 1-2

2007a *Whittleseya* sp.; Pacyna, p. 107.

Diagnosis. Pollen organ campanulate 35 mm long, 47 mm wide. Sporangia number 30–40, flat, clearly visible, arranged parallel to each other, 1 mm wide, in addition slightly longitudinally striped. Sporangia in the distal part of the organ parallel, slightly narrowing proximally and converging toward the base of the stalk. Distal ends of sporangia (teeth), short (0.5 mm long) rounded. Sporangia (5–10 in number) are combined in approximately 10 clusters, each probably corresponding to one synangium. Base of the organ broad, set on a considerably extended stalk apex. Apex of the organ slightly rounded, perpendicular to the sides of the organ.

Age. Upper Carboniferous, Westphalian A-C.

Horizon. Zacler Beds.

Type locality. Lower Silesia, Gorce area, Victoria mine, Witold shaft.

Holotype. MW 2a, b (1 specimen, mould and cast). The holotype is the only known specimen of this species, Pl. 8, Figs 1-2.

Etymology. Lat. *campanulate* – bell-shaped, the name refers to the shape of the synangium.

Description. Pollen organ campanulate, 35 mm long, 47 mm wide. Sporangia number 30–40, flat, clearly visible, arranged parallel to each other, 1 mm wide, in addition slightly longitudinally striped. Sporangia in the distal part of the organ parallel, slightly narrowing proximally and converging toward the base of the stalk. Distal ends of sporangia (teeth), short (up to 0.5 mm long), rounded. Sporangia (5–10) are combined in about 10 clusters likely to correspond to individual synangia (Pl. 8, Figs 1-2). Thus, the whole organ is a cluster of synangia. Base of the organ broad, set on a considerably extended stalk apex. Apex of the organ slightly rounded, perpendicular to the sides of the organ. Prepollen grains not preserved.

Discussion. This species is clearly distinguishable from previously described species in the *Whittleseya* genus (Table 9). In particular, its large dimensions are notable – only *W. elegans* is of similar size, and is clearly distinguishable in shape from *W. campanulata* sp. nov. The proportions of these two species are different: *W. elegans* is narrower and more elongated; *W. campanulata* shorter and very wide (Millay & Taylor 1979).

The clusters of sporangia in groups of 5–10 are another typical characteristic of this species, and this feature is also clearly evident in *W. silesiaca* sp. nov., as well as presumably in *W. dawsoniana* and *W. undulata* (White 1901, Pl. 7). This may indicate that, at least in some species of *Whittleseya*, we are dealing with compound rather than simple synangia. This has been previously overlooked in the literature.

The sporangia of *W. campanulata* sp. nov. are gently striped longitudinally, and this feature is also much more strongly visible but less pronounced in *W. elegans* (Seward 1917; Halle 1933) and *W. silesiaca* sp. nov. In the remaining species of *Whittleseya*, this has not been described. It is, however, evident in White's figures (White 1901) in at least two species: *W. desiderata* and *W. brevifolia*.

Another distinguishing characteristic of this species is the considerably extended apex of the stalk. The stalk is known only in some species of the genus *Whittleseya* (*W. desiderata*, *W. elegans*, *W. microphylla* and *W. undualata*), and in none of these species is the apex so clearly extended (White 1901). With the exception of *W. elegans*, in which the apex of the stalk is slightly extended, in the remaining species the stalk does not extend at its apex.

Comments on genus *Whittleseya*. The genus *Whittleseya* (type species *W. elegans*) was established by Newberry (1853a, b) and originally interpreted as representing Gingkoales leaves. The leaf interpretation of the organ was accepted by White (1900, 1901) and Potonie (1904). This interpretation was, however, questioned by Thomas (1912) and Kidston (1914), who described a new species – *Whittleseya? fertilis* [= *Boulayatheca fertilis*], claiming that within the specimens there were numerous well-preserved spores. The interpretation of the organs as prepollen grains producing and not leaves was presented by Seward (1917). But it was Halle (1933), based on maceration of numerous specimens, who clearly showed that it was a pollen organ formed of fused sporangia. Halle (1933) showed that the ridges visible on the surface of the organ were not leaf nerves, but very thin, and highly elongated sporangia entirely filled with prepollen grains. He interpreted the organ as a hollow campanulate synangium, comprised of long and narrow, tubular, fused sporangia embedded in a significant amount of sterile tissue. The sporangia were arranged in a single whorl, corresponded to the ridges on the outer surface of the organ, and stretched from the base to the apex of the organ. Halle (1933) cited the following arguments in support of its interpretation: During maceration of the flattened specimens, both organ walls (front and back) separated from one another; longer maceration led to the disintegration of the organ into isolated sporangia filled with spores corresponding to the visible ridges on the surface. In the coalification between the two organ sides, however, Halle found no evidence to suggest that they could not be fused. In some of the specimens between the walls of the organ there was a mineral deposit, indicating that during the plant's life there was an empty space here. Halle considered the idea that the body could be composed of two adjacent layers, with a small empty space between them, but on the basis of the construction of other pollen organs that had radial symmetry, he acknowledged that in the genus *Whittleseya* it could be similar, and that the organ was composed of a whorl of fused sporangia.

Schopf (1948) criticized Halle's interpretation. He worked on *Dolerotheca* specimens preserved in coal balls, in which the sporangia (in the smallest structural subdivision, since these organs were multiple compounds of such subdivisions propagated radially from the centre of the organ) occurred in two rows connected by sterile tissue. He believed that the shale that Halle found between the layers of the organ was, in fact, between layers of two belts of sporangia and got into the area of the dehiscing sporangia (in fact it is not known how *Whittleseya* sporangia dehisced). Schopf (1948) suggested *Whittleseya* should be interpreted as a flattened organ composed of two belts of sporangia connected by sterile tissue, somewhat like a (double) belt of *Dolerotheca* sporangia.

Similarly, Taylor and Millay (1979) inspired by Schopf's ideas, questioned the validity of Halle's interpretation. Their reasoning, however, went in a slightly different direction. They agreed with Schopf's interpretation that the synangia were flattened. They agreed with Halle (1933), that the synangia consisted of two rows of sporangia arranged in pairs opposite each other on both sides of the body. They suggested that the sporangia dehised at the distal ends to the interior of the organ. They concluded that, due to the very large surface area exposed to drying, the organ had neither the shape of a hollow campanulum nor flattened synangia. (In addition, the organ's surface was not covered with hairs to protect against drying, nor did it have thickened walls). They suggested that the synangia were indeed flat, but formed a cluster somewhat similar to „a pack of cards' growing out of a common stalk. In this way, they also explained the numerous incidences of specimens on one surface of the shale; they came simply from the decay of one numerous aggregation. They also indicated the weaknesses in their proposed reconstruction: If the flattened synangia formed an aggregation, the stalk should have undergone flattening, whereas the fragments of stalks found attached to the organs were not flattened. If they formed a concentration that was to prevent them from drying out too much, the individual synangia should be interlocked with dense hairs. These hairs occur in *Parasporotheca*, for example, whose synangia were flattened, grew thickly alongside each other and were linked by hairs. In *Whittleseya* there are no such hairs.

The *W. elegans* material from Lower Silesia fits both the reconstruction of the organ by Halle (1933) and Millay and Taylor (1979). However, the characteristic spathulate shape, flattening of the organs rather than those arising from compactional deformation and the manner of convergence of the sporangia (slight narrowing) toward the stalk rather points to the interpretation of Millay and Taylor. At the same time, *W. campanulata* sp. nov. confirms Halle's (1933) interpretation. The *W. campanulata* sp. nov. organ was a compound synangium in which individual synangia fused to form a ring; this is due to the strongly campanulate shape of the organ, the manner in which the sporangia converge (pronounced bending of the tapered sporangia) to the apex and the preserved trace of the base of the stalk. The base of *W. campanulata* sp. nov.'s stalk clearly broadened, perhaps after the organ dropped out, a hole remained at the place where the stalk had been attached. *W. silesiaca* sp. nov. probably also formed a compound, campanulate synangium. The sporangia in this species clearly taper towards the stalk, and the organ gives the impression of a flattened bell. Both *W. silesiaca* and *W. elegans* form relatively large accumulations in the material from Lower Silesia. *W. campanulata* sp. nov. is represented by one specimen.

A new feature observed in the material from Lower Silesia is the clustering of sporangia in groups of 5–10. This feature has not previously been described in any species of the genus *Whittleseya*. Judging by Halle's description and illustrations, it has certainly not occurred in the typical species *W. elegans*. Presumably it is evident in White's figures (1901) in at least two species: *W. dawsoni* and *W. undulata.* White, however, only provided drawings of the specimens, and to confirm the presence of this trait in these species it would be necessary to review the original material. The more so that *W. undulata* may not belong to the genus *Whittleseya* at all, but rather to the genus *Aulacotheca*. *W. undulata* has the elongated clavate shape typical of *Aulacotheca*. What is interpreted here in *W. undulata* as supposedly clusters of sporangia may in fact be sporangia, and the supposed sporangia only stripes.

The clustering of sporangia may indicate that, at least in some species of *Whittleseya*, we are dealing with compound rather than simple synangia. Thus, it would be a much more heterogeneous genus, perhaps even grouping representatives from several natural genera. The previously discussed diversification in the construction of the synangium (flat – bell-shaped) may also indicate this. Unfortunately, due to the preservation of all the members of this genus as compressions (and this state of preservation blurs many important features), for the time being it seems advisable not to divide the genus *Whittleseya* into a greater number of genera.

The longitudinal striations of the sporangia were recognized by HALLE (1933) as an artifact resulting from the flattening of the specimens. The two new species here described, and the *W. elegans* from Lower Silesia demonstrate such striations, visible and very regular. It seems that this feature is not caused by the compaction of specimens, but was a natural feature of these organs in life. Longitudinal striations on sporangia occur in many types of Medullosales pollen organs, including the above-described *Aulacotheca* and *Boulayatheca*. The universality of this feature may indicate that it is not only the result of the manner of preservation. All the more so because it is confirmed not only in highly flattened compression specimens, but is also three-dimensionally preserved within sideritic concretions (KIDSTON 1914; this paper).

Kotasotheca Pacyna & Zdebska, *gen. nov.* Plate 9, Figs 1-2

2007a aff. *"Parasporotheca"*; Pacyna, p. 107.

Type species. *Kotasotheca annaeadamii sp. nov*.

Generic diagnosis. Synangium scoop-shaped, proximally almost circular in cross section, in the distal direction more and more arched, the apex is lightly turned up outside, synangium triangular in the flattened state. Synangium constructed of a single layer propagating in a fan-like form from base to apex of the organ and slightly expanding distally, long and narrow fused sporangia separated by sterile tissue. The ribs visible on the surface of the organ correspond to sporangia, and these ribs are gently longitudinally striped. The distal ends of the sporangia are slightly protruding, rounded.

Kotasotheca annaeadamii Pacyna & Zdebska, *sp. nov.* Plate 9, Figs 1-2; Fig. 2C

2007a aff. *"Parasporotheca"* sp.; Pacyna, p. 107.

Specific diagnosis. Synangium scoop-shaped, proximally almost circular in cross section, in the distal direction more and more arched, the apex is lightly turned up outside, synangium triangular in the flattened state. Synangium length 24 mm, width 24 mm. Synangium constructed of a single layer propagating in a fan-like form from base to apex of the organ and slightly expanding distally, long and narrow (1 mm wide) fused sporangia separated by sterile tissue. The number of sporangia in the entire synangium is around 20. The ribs visible on the surface of the organ correspond to sporangia, and these ribs are gently longitudinally striped. The distal ends of the sporangia are slightly protruding, rounded.

Age. Upper Carboniferous (Pennsylvanian), Duckmantian (Westphalian B).

Type horiozon. Mudstone Series, Orzesze or Łaziska Beds.

Type locality. Upper Silesia, Oświęcim, Piast mine.

Type specimens. MP IB UJ 101/2, (fragment of the drill core, depth 102.0 m), in core breaks at different planes, four specimens can be observed: 101/2/1 – designated as the holotype, 101/2/2 and 101/2/3 are designated as paratypes; Pl. 9, Figs 1-2; Fig. 2C.

Etymology. In honour of Anna Kotasowa and Adam Kotas – eminent experts in the flora and geology of the Polish Carboniferous; generic name from the surname Kotas and gr. *theca* – cover – often applied to the end of seed fern pollen organ names; species name from the forenames: Anna and Adam.

Description. Synangium flat, scoop-shaped, proximally almost circular in cross section, in the distal direction more and more arched, the apex is lightly turned up outside. Synangium in the flattened state triangular (Pl. 9, Fig. 1-2). Synangium length 24 mm, width 24 mm. Synangium constructed of a single layer propagating in a fan-like form from base to apex of the organ and slightly expanding distally, long and narrow (1 mm wide) fused sporangia separated by a clear layer of sterile tissue (Pl. 9, Fig. 2). Number of sporangia in synangium ca. 20. The ribs visible on the surface of the organ correspond to sporangia, and these ribs are gently longitudinally striped. The ridges on the sporangia are straight, sometimes wavy. Distal ends of the sporangia slightly protruding, rounded (Pl. 9, Figs 1-2). Organ's surface without hair. Dehiscence splits not visible. Prepollen grains not preserved.

Discussion. So far, Medullosales pollen organs with such morphology have not been observed in the compression/impression state (Pacyna 2007a, b). Particularly striking, in spite of the flattening of the specimens, is the preserved scoop-like, arched shape of the synangia (triangular with edges folded inside). Two of the three specimens are preserved this shape, the third is completely flattened, but its triangular shape completely confirms the morphology of the preserved three-dimensional specimens. Moreover, in their organization (elongated, thin sporangia extending from the base to the apex of the organ, visible on the surface of the organ in the form of stripes) *Kotasotheca* gen. nov. are very similar to *Whittleseya*. However, in *Kotasotheca* gen. nov. the sporangia slightly expand distally, which does not occur in *Whittleseya*. In addition the free ends of the sporangia in *Whittleseya* clearly protrude and may be sharpened or rounded, where in *Kotasotheca* gen. nov. the ends of the sporangia are very clearly rounded and very slightly protruding.

The only genus morphologically similar to *Kotasotheca* gen. nov., *Parasporotheca*, was described in coal balls from the USA Upper Pennsylvanian (Dennis & Eggert 1978). This organ aroused particular interest (Millay & Taylor 1979; Taylor & Taylor 1993) because the synangia lack the radial symmetry (typical for almost all Medullosales pollen organs). As with *Kotasotheca* gen. nov., in *Parasporotheca* the elongated sporangia spread in a fan-like manner from the base to form an arched, scoop-like synangium. The number of sporangia in *Kotasotheca* (ca. 20) and in *Parasporotheca* (14–20) is similar. Individual sporangia in *Parasporotheca* are smaller than in *Kotasotheca*, and measure 0.5 × 0.8 mm; the dimensions of the *Parasporotheca* synangium are not known. In *Parasporotheca*, as in most other medullosalean pollen organs, sporangia cavities alternate with elongated lacunae in the ground tissue. Such lacunae have not been observed in *Kotasotheca*, while between the sporangia in *Kotasotheca* there are clear, thick bands of coalified tissue, indicating that there was a relatively large amount of tissue, perhaps in addition to the parenchyma there were also sclerenchymatous fibers, which are common in anatomically preserved medullosalean pollen organs. At the same time, in *Parasporotheca* the sporangia were surrounded by a thin layer of ground tissue. In the basal third of the synangium, the ventral surface was made up of fibers; in the distal direction, where there were synangium dehiscence slits, the sporangia walls consisted of thin-walled cells. In *Parasporotheca*, each sporangium has a single vascular bundle leading from the outer (dorsal) side of the synangium.

Parasporotheca synangia did not occur singularly, but formed a massive aggregation. The aggregation of synangia found by Dennis and Eggert (1978) was flattened and incomplete, and measured 20 cm long and 3 cm wide. They found no presence of any common ground tissue which would connect individual synangia, thus the grouping of synangia was not part of a compound pollen organ, as is the case in *Bernaultia* (see below discussion of the genus *Dolerotheca*). The synangia were, however, interlocked with peg-like hairs occurring on their outer surface. No hairs have been detected in *Kotasotheca* gen. nov. Dennis and Eggert (1978) consider it likely that individual synangia dried out and became detached from the aggregation, and therefore might have been preserved individually. For *Kotasotheca* gen. nov., it is not possible to conclude on the basis of the available material whether the synangia formed aggregations; however, the discovery of three specimens next to each other may indicate such a possibility. Here, the same feature – the occurrence on one slab of rock of accumulations of synangia – appears as in *Whittleseya*. Dehiscence in *Parasporotheca* did not require the disaggregation of the synangial mass, since numerous examples have been found of dehiscent synangia in close contact with neighboring synangia.

Dennis and Eggert (1978) suggested that each laminate synangium in *Parasporotheca* could have arisen from a laminar system of fertile telomes that underwent lateral fusion. Other Medullosales pollen organs give the impression of initially having radial symmetry (Millay & Taylor 1979). Dennis and Eggert (1978) suggest further that the radial forms may also be derived from laminar fertile telome systems and formed by the fusion of the two lateral margins of the synangia similar to *Parasporotheca*. At the same time, Millay and Taylor (1979) believe that all medullosalean pollen organs primarily have radial organization (radial symmetry) and not laminar (bilateral symmetry). They suggested the following alternative hypothesis explaining the emergence of synangia such as in *Parasoprotheca* or *Kotasotheca* described here. According to this hypothesis the laminate synangium of *Parasporotheca* is basically radial, although a small area of the enlarging cone-shaped synangium fails to develop. This area of abortive sporangia could have formed a slit in the wall (side) of the synangium and allowed the synangia to open out into the various curved arches. To support their claim, Millay and Taylor (1979) also cite that *Parasporotheca* synangia appear increasingly radial in the direction of the base. Similarly, *Kotasotheca* gen. nov. synangia become clearly radial towards the base, which may support Millay and Taylor's hypothesis (Millay & Taylor 1979).

In *Parasporotheca* sporangia, large bisaccate prepollen grains of the genus *Parasporites* has been found. Although ultrastructurally the exine of the pollen is similar to *Monoletes*, Stidd (1981) suggested on the basis of the generic difference of the prepollen grains that *Parasporotheca* may not belong to Medullosaceae, although it presumably represents the order Medullosales. Dennis and Eggert (1978) originally suggested the affiliation of *Parasporotheca* to *Sutcliffia*. Unfortunately, *Kotasotheca* gen. nov. prepollen grains have not been preserved.

Stidd (1981) derived *Parasporotheca* from the *Codonotheca* pollen organ type in which the sporangia grow together laterally (note that the genus *Codonotheca* was frequently interpreted as bilaterally symmetrical, which could confirm the interpretation of the emergence of *Parasporotheca* proposed by Dennis and Eggert (1978), see above discussion of the genus *Codonotheca*). According to him, *Whittleseya* arose similarly, although in this case the sporangia formed a closed ring.

Based on the differences mentioned above, the material from Upper Silesia cannot be classified as the species *Parasporotheca leismanii*. Differences in size, morphology and the preservation of the synangia, including in particular the lack of prepollen grains preservation and the absence of hairs, do not allow affiliation to the genus *Parasporotheca* as a new species. In *Kotasotheca* gen. nov., there is also the characteristic eversion of the apex of the synangia to the outside, which has not been observed in *Parasporotheca*. In any event, the morphology indicates a close relationship between these two genera.

Genus ***Dolerotheca*** Halle, 1933

Type species. *Dolerotheca fertilis* (Renault, 1896) Halle, 1933

Included species. *Dolerotheca berthieri* (Renault, 1896) Halle, 1933; *Dolerotheca cebennensis* (Grand'Eury, 1890) Schopf, 1950; *Dolerotheca formosa* Schopf, 1948; *Dolerotheca migierii* Pacyna & Zdebska, sp. nov.; *Dolerotheca pennsylvanica* (Dawson ex White, 1903) Schopf, 1950; *Dolerotheca reedana* Schopf, 1948; *Dolerotheca schopfii* Baxter, 1949; *Dolerotheca sclerotica* Baxter, 1949; *Dolerotheca warrenae* (Eggert & Rothwell, 1979) Stidd, 1990; *Dolerotheca villosa* Schopf, 1948 (Table 10).

Discussion. The genus *Dolerotheca* has a long and complicated taxonomic history. The early history of the genus is compiled in papers by Halle (1933) and Schopf (1948) (Table 10). The generic name *Dolerotheca* was proposed by Halle (1933) for pollen organs previously classified as genus *Dolerophyllum*. Halle (1933) did not provide a separate diagnosis for the proposed genus, but only an extensive description. He quoted the diagnosis of the typical species *Dolerotheca fertilis* by the originator of this species Renault (1896). Halle found some of Renault's original specimens and illustrated them with photographs because he noted that Renault drawings were somewhat idealized.

Schopf (1948) described the *Dolerotheca* material from North America. He had at his disposal well-preserved specimens in coal balls. He established three new species: *Dolerotheca formosa*, *D. villosa* and *D. reedana*. He also discussed the taxonomic problems with the genus *Dolerotheca*. In the same work, Schopf (1948) suggested that the genus *Daubreeia* (some specimens) and the species *Doleropteris pennsylvanicum* preserved as compressions should be transferred to the genus *Dolerotheca*. He worked on this problem in his next paper (Schopf 1950), where he proposed a new combination – *Dolerotheca pennsylvanica*. In this paper, too, he transferred the species *Discostachys cebennensis* to the genus *Dolerotheca* as *Dolerotheca* (?) *cebennensis.*

Based on specimens from U.S. coal balls, Baxter (1949) described two new species of the genus *Dolerotheca*: *D. sclerotica* and *D. schopfii.*

Table 10
Synonymy of species belonging to genus *Dolerotheca*

Authors	Species				
	Dolerophyllum berthieri	***Dolerotheca cebennensis***	***Dolerotheca fertilis***	***Dolerotheca formosa***	***Dolerotheca pennsylvanica***
Grand'Eury (1890)		*Androstachys cebennnensis* *Discostachys cebennnensis*			
Renault (1893-1896)	*Dolerophyllum berthieri*		*Dolerophyllum fertile*		
White (1903) in Schopf (1950)					*Doleropteris pennsylvanicum*
Halle (1933)	*Dolerotheca fertilis*	*Dolerotheca fertilis*	*Dolerotheca fertilis*		
Schopf (1948)	*Dolerotheca berthieri*	*Discostachys cebennnensis*	*Dolerotheca fertilis*	*Dolerotheca formosa*	*Doleropteris pennsylvanicum*
Baxter (1949)				*Dolerotheca formosa*	
Schopf (1950)		*Dolerotheca* (?) *cebennensis*	*Dolerotheca fertilis*	*Dolerotheca formosa*	*Dolerotheca pennsylvanica*
Eggert & Rothwell (1979)				*Dolerotheca formosa*	
Rothwell & Eggert (1986)			*Dolerotheca fertilis*	*Bernaultia formosa*	
Stidd (1990)		*Dolerotheca cebennensis*	*Dolerotheca fertilis*	*Dolerotheca formosa*	*Dolerotheca pennsylvanica*
Pacyna & Zdebska, this paper	*Dolerotheca berthieri*	*Dolerotheca cebennensis*	*Dolerotheca fertilis*	*Dolerotheca formosa*	*Dolerotheca pennsylvanica*

Authors	Species				
	Dolerotheca reedana	***Dolerotheca schopfii***	***Dolerotheca sclerotica***	***Dolerotheca warrenae***	***Dolerotheca villosa***
Schopf (1948)	*Dolerotheca reedana*				*Dolerotheca villosa*
Baxter (1949)	*Dolerotheca reedana*	*Dolerotheca schopfii*	*Dolerotheca sclerotica*		*Dolerotheca villosa*
Schopf (1950)	*Dolerotheca reedana*	*Dolerotheca schopfii*	*Dolerotheca sclerotica*		*Dolerotheca villosa*
Eggert & Rothwell (1979)				*Stewartiotheca warrenae*	
Rothwell & Eggert (1986)	*Dolerotheca reedana*	*Bernaultia sclerotica*	*Bernaultia sclerotica*	*Stewartiotheca warrenae*	*Dolerotheca villosa*
Stidd 1990	*Dolerotheca reedana*	*Dolerotheca schopfii*	*Dolerotheca sclerotica*	*Dolerotheca warrenae*	*Dolerotheca villosa*
Pacyna & Zdebska, this paper	*Dolerotheca reedana*	*Dolerotheca schopfii*	*Dolerotheca sclerotica*	*Dolerotheca warrenae*	*Dolerotheca villosa*

ROTHWELL and EGGERT (1986) obtained all Renault's original specimens, even those which Halle did not see. They illustrated these specimens and concluded that they were small fragments of a considerable volume of several genera of pollen organs. They also could not determine whether the differences between the specimens were due to the taphonomy or real taxonomic differences. Therefore, they suggested that the name *Dolerotheca* sensu Renault and Halle be limited to the fragmentarily preserved synangia of unclear morphological and anatomical structure. For the species *Dolerotheca formosa*, they proposed a new genus *Bernaultia*. They also attributed the species *Dolerotheca sclerotica* described by BAXTER (1949) to *Bernaultia*. The species *D. schopfii* established by BAXTER (1949) was considered to be a synonym of *Bernaultia sclerotica*. And in addition to the genus *Dolerotheca,* apart the typical species *D. fertilis*, they referred the species *D. villosa* and *D. reedana*, that is, specimens with and without preserved anatomical structures. ROTHWELL and EGGERT (1986) gave the following diagnosis for *Dolerotheca*: "Campanulate medullosan pollen organs with tubular sporangia embedded in ground tissue, and for which the external morphology and internal organization cannot be determined."

STIDD (1990, p. 80) was sharply critical of the taxonomic changes proposed by ROTHWELL and EGGERT (1986), found the separation of the genus *Bernaultia* to be unfounded, and indicated several errors in the interpretation of the construction of *Bernaultia* and *Dolerotheca* proposed by these authors. He held that the genus *Dolerotheca*, in Halle's sense (HALLE 1933), was valid for specimens with and without preserved anatomical details. The following species of *Dolerotheca* are valid according to STIDD (1990): *D. fertilis, D. reedana, D. villosa, D. sclerotica, D. schopfii, D. formosa, D. pennsylvanica* and *D. cebennensis*. STIDD (1990) recognized *Stewartiotheca warrenae* (EGGERT & ROTHWELL 1979) as a synonym of *Dolerotheca* and proposed a new combination – *Dolerotheca warrenae*.

DRINNAN and CRANE (1994), describing medullosalean pollen organs from Mazon Creek, also criticized Rothwell and Eggert's proposals (ROTHWELL & EGGERT 1986), indicating the excessively broad view of the species recognized by them as invalid. They referred well-preserved coalified specimens to the genus *Dolerotheca*. The diagnosis of the genus *Dolerotheca* by ROTHWELL and EGGERT (1986) cannot be accepted here. But the understanding of the genus *Dolerotheca* proposed by HALLE (1933), STIDD (1990) and DRINNAN and CRANE (1994) is adopted here. On the basis of these papers, it can be concluded that the material from Sosnowiec represents a new species of the genus *Dolerotheca*.

Distribution. The genus *Dolerotheca* was described on the basis of Upper Carboniferous materials from France (RENAULT 1893-1896). However, most specimens of this genus preserved either as compressions or with anatomical detail come from the Upper Carboniferous of the USA (HALLE 1933; SCHOPF 1948; RAMANUJAM *et al.* 1974) (Table 11). The genus *Dolerotheca* has not previously been described in Poland (Table 1). In the sideritic nodules from Sosnowiec only one specimen was found.

Dolerotheca migierii Pacyna & Zdebska, *sp. nov.* Plate 10, Figs 1-2; Fig. 2F

2007a *Dolerotheca* sp.; Pacyna, p. 107.

Diagnosis. Campanulate pollen organ (synangium), at least 31 mm in diameter, with tubular sporangia embedded in ground tissue. Sporangia are visible on the basal surface of the organ in the form of round spots 0.1−0.25 mm in diameter. Around trace of the

Table 11
Comparison between the *Dolerotheca* species

Features of species	***Dolerotheca berthieri*** (Renault, 1896) Halle, 1933	***Dolerotheca cebennensis*** (Grand'Eury, 1890) Schopf, 1950	***Dolerotheca fertilis*** (Renault, 1896) Halle, 1933	***Dolerotheca formosa*** Schopf, 1948	***Dolerotheca migierii*** Pacyna & Zdebska, sp. nov.
Preservation mode	compression / impression	compression / impression	with anatomical structure preserved	with anatomical structure preserved	compression / impression within sideritic nodule
Synangium diameter (mm)	55 × 40	40	-	40−45	31
Sporangium diameter (mm)	0.5−1.0		1.0	0.6−1.0	0.1−0.25
Sporangium length (mm)	-	-	12−15−20	4−12	-
Number of sporangia	-	-	-	1200	a few hundred
Prepollen type and dimensions (μm)	*Monoletes*, 460 μm, 410 × 280 μm	-	*Monoletes*, 300 (330)−460 μm	300−350 × 200−250 μm	-
Localities	France	France	France, Loire	USA, Illinois, Ohio	Poland, Upper Silesia
Age	Upper Carboniferous (Stephanian)	Upper Carboniferous	Upper Carboniferous (Stephanian A-B), Permian	Upper Pennsylvanian	Upper Carboniferous (Westphalian A)
References	Renault (1896), Halle (1933), Schopf (1948)	Grand'Eury (1890), Halle (1933), Schopf (1948, 1950), Stidd (1990)	Renault (1896), Halle (1933), Schopf (1948, 1950), Rothwell & Eggert (1986), Stidd (1990)	Schopf (1948), Baxter (1949), Schopf (1950), Eggert & Rothwell (1979), Rothwell & Eggert (1986), Stidd (1990)	this paper
Features of species	***Dolerotheca pennsylvanica*** (Dawson ex White, 1903) Schopf, 1950	***Dolerotheca reedana*** Schopf, 1948	***Dolerotheca schopfii*** Baxter, 1949	***Dolerotheca sclerotica*** Baxter, 1949	***Dolerotheca warrenae*** (Eggert & Rothwell, 1979) Stidd, 1990
Preservation mode	compression / impression	with anatomical structure preserved	with anatomical structure preserved	with anatomical structure preserved	with anatomical structure preserved
Synangium diameter (mm)	30−40	15−20	-	25−35	8 × 10
Sporangium diameter (mm)	-	0.35−0.5	1.0	0.6	0.5
Sporangium length (mm)	-	6	-	-	-
Number of sporangia	a few hundred	-	-	300−700	-

Prepollen type and dimensions (µm)	-	*Monoletes*, 260−325 × 165−250 µm	-	470−200 µm	264 × 183 µm
Localities	USA, West Virginia, Appalachians	USA, Illinois	USA, Kansas, Oklahoma, Iowa, Illinois, Ohio	USA, Kansas, Oklahoma, Iowa, Illinois, Ohio	USA¸ Illinois
Age	Upper Pennsylvanian	Middle Pennsylvanian	Middle Pennsylvanian	Middle Pennsylvanian	Upper Pennsylvanian
References	White (1903) in Schopf (1950), Schopf (1948, 1950), Gillespie *et al.* (1978), Stidd (1990), Blake *et al.* (1999) in Blake *et al.* (2002)	Schopf (1948), Baxter (1949), Schopf (1950), Rothwell & Eggert (1986), Stidd (1990)	Baxter (1949), Schopf (1950), Rothwell & Eggert (1986), Stidd (1990)	Baxter (1949), Schopf (1950), Rothwell & Eggert (1986), Stidd (1990)	Eggert & Rothwell (1979), Rothwell & Eggert (1986), Stidd (1990)
Features of species	***Dolerotheca villosa*** Schopf, 1948	***Dolerotheca* sp.** Schopf 1948	***Dolerotheca* sp. 1** Drinnan & Crane 1994	***Dolerotheca* sp. 2** Drinnan & Crane 1994	***Dolerotheca* sp. 3** Drinnan & Crane 1994
Preservation mode	with anatomical structure preserved	compression / impression within sideritic nodule	compression / impression within sideritic nodule	compression / impression within sideritic nodule	compression / impression within sideritic nodule
Synangium diameter (mm)	10	28	16.5–25	25–35	23
Sporangium diameter (mm)	0.3−0.4	-	-	-	-
Sporangium length (mm)	5−6	-	-	-	-
Number of sporangia	-	-	-	-	-
Prepollen type and dimensions (µm)	*Monoletes*, 130−150 × 100−120 µm	450 × 390 µm	*Monoletes*, 269−319 × 157−230 µm	*Monoletes*, 299−337 × 224−262 µm	*Monoletes*, 342−453 × 240−327 µm
Localities	USA, Illinois	USA, Illinois, Carterville	USA, Illinois, Mazon Creek	USA, Illinois, Mazon Creek	USA, Illinois, Mazon Creek
Age	Upper Pennsylvanian	Westphalian D	Westphalian D	Westphalian D	Westphalian D
References	Schopf (1948, 1950), Baxter (1949), Rothwell & Eggert (1986), Stidd (1990)	Schopf (1948)	Drinnan & Crane (1994)	Drinnan & Crane (1994)	Drinnan & Crane (1994)

stalk, sporangia arranged very densely, chaotically, toward the edge of the organ sporangia slightly increasing in size, and are slightly elongated radially, somewhat loosely arranged, forming a rows separated through strips of tissue (probably sclerenchyma). Stalk attachment 7 mm in diameter, settled centrally.

Age. Upper Carboniferous (Pennsylvanian), Langsettian (Westphalian A).

Horizon. Mudstone Series, Załęże Beds.

Type locality. Upper Silesia, Dąbrowa Górnicza area, Sosnowiec–Zagórze, Porąbka-Klimontów mine.

Holotype. S/100/P12, the holotype is the only known specimen of this species; Pl. 10, Figs 1-2; Fig. 2F.

Etymology. In honour of Dr. Teresa Migier – author of many papers on the floras of the Polish Carboniferous .

Description. Synangium campanulate in life, preserved within a sideritic nodule as a flattened disc with a diameter of at least 31 mm, where the maximum compaction affected the middle part of the organ, the edges partly preserved the original three-dimensional shape. Synangium visible from the basal side (Pl. 10, Figs 1-2). Stalk attachment is 7 mm in diameter, settled centrally (Pl. 10, Fig. 2). The entire surface of the organ covered with convex spots 0.1−0.25 mm in diameter, which are sporangia visible from above. Around trace of the stalk, sporangia arranged very densely, chaotically, toward the edge of the organ sporangia slightly increasing in size, and are slightly elongated radially, somewhat loosely arranged, forming a series of rows separated through strips of tissue (probably sclerenchyma) (Pl. 10, Fig. 1). Some sporangia at the edges of the organ partially visible from the side. There are no lacunae between the sporangia.

Discussion. The specimen is designated as genus *Dolerotheca* due to the flattened campanulate organ and the traces of numerous sporangia separated by bands of sclerenchyma (PACYNA 2007a, b) visible on the surface. The sporangia do not form clusters of 4, as in the morphologically similar genus *Potoniea*, but radiate from the stalk to form rows (at least in the distal portion of the organ), which is typical of the genus *Dolerotheca*. The specimen differs in morphology from those described previously, both those with preserved anatomy and coalified species of the genus *Dolerotheca* (Table 11), and therefore a new species is established on this basis.

The specimen described, due to its manner of preservation, may mainly be compared with species of *Dolerotheca* preserved as compressions. In the earlier literature, specimens preserved in this way received species names distinct from those anatomically preserved (e.g., HALLE 1933); in modern papers they are usually, though not always, labeled as *Dolerotheca* sp. (e.g., SCHOPF 1948; DRINNAN & CRANE 1994, but see GILLESPIE *et al.* 1978 and BLAKE *et al.* 2002). The typical species *D. fertilis* has preserved anatomical structure. HALLE (1933) also included coalified specimens, although with reservations.

Dolerotheca migierii sp. nov. is not similar to any of the coalified specimens of *Dolerotheca* described by SCHOPF (1948) and DRINNAN and CRANE (1994). It does not have the strip of ground outside tissue the synangium described by SCHOPF (1948) in the specimen he studied, and the dimensions of the entire synangium are also different, smaller in Schopf's specimen. The species described by DRINNAN and CRANE (1994) are smaller and have far larger sporangia.

Dolerotheca migierii sp. nov. most closely resembles the anatomically preserved *D. formosa*. There, too, the sporangia are densely arranged at the stalk, and there is no sclerenchymatous banding separating them; the farther from the stalk attachment, the slightly larger the sporangia, and there are also sclerenchymatous strips, but these are poorly marked. The absence of lacunae between the sporangia of *D. migierii* sp. nov. recall *Dolerotheca sclerotica* with preserved anatomical structure. *D. migierii* sp. nov. is not similar to the compressions of *D. fertilis* sensu Halle, 1933, because there the sporangia are larger, there are fewer of them, and they form distinct rows. *D. migierii* sp. nov. is not similar to *D. pennsylvanica*, in which the sporangia are larger and arranged in very distinct rows.

The specimen from Sosnowiec cannot be classified as morphologically similar to *Dolerotheca* genus *Potoniea* (Zeiller 1899; Laveine 1971; Stidd 1978; Gastaldo 1982; Schultka 1995). In genus *Potoniea*, the sporangia do not form rows, and are not arranged chaotically, but are clearly clustered in fours, in addition to which such sporangia protrude from the compression on the edge of the organ, especially in specimens preserved „sideways". It is worth noting that the genus *Potoniea* was described initially (Zeiller 1899) and for a long time (Schultka 1995) known only in the compressed state, but Stidd (1978) found it in coal balls (species *Potoniea illinoiensis*), thanks to this characteristic arrangement of sporangia in 4s.

4. SUMMARY OF RESULTS

The evolution of seed fern pollen organs and the location of the genera and species here described from the Polish Carboniferous

Seed ferns (the most primitive order Lyginopteridales) derive most likely from the progymnosperms of the order Aneurophytales. This is indicated by the occurrence of a secondary outward growth of shoots, a bifid wall of microspores, and the terminal location of the sporangia on the richly branched axes in both these groups. Aneurophytales are homosporous, but perhaps this group also held heterosporous forms like *Chauleria cirrosa* (Andrews *et al.* 1974). Its systematic position is, however, uncertain (Taylor & Taylor 1993).

Aneurophytales sporangia were elongated, with pointed tips, and dehisce lengthwise. They were formed terminally on dichotomously dividing branches in different planes and gathered in clusters up to 9 mm in length. The sporangium wall was not differentiated into layers. The spores were small and spherical with a tetrad mark (Matten & Finne 1994).

Lyginopteridales pollen organs share common characteristics with Aneurophytales sporangia: elongated sporangia with pointy tips, dehiscing lengthwise and created terminally on dichotomously divided axes. They differed from Aneurophytales sporangia in that they formed synangia and could have variously thickened walls of sporangia (Matten & Finne 1994).

The specialized pollen organs of Medullosales derive from Lyginopteridales (Millay & Taylor 1979). Figure 2 (this paper) illustrates these pollen organs and their evolutionary trends among Medullosales.

The changes in the evolution of Lyginopteridales and Medullosales pollen organs were: the position of the whole pollen organs in relation to other parts of the plant, the course of the vascular bundle in the synangia, the degree of fusion and number of sporangia in the synangia, their size and manner of branching stems carrying synangia and the microspore morphology (MILLAY & TAYLOR 1979; TAYLOR & MILLAY 1981a; GALTIER 1988; TAYLOR 1988; TAYLOR & TAYLOR 1993; MATTEN & FINNE 1994).

The pollen organs within the oldest Lyginopteridales order evolved from clusters of microsporangia not forming synangia as in the genera *Geminitheca* and *Pullaritheca* (SMITH 1959; ROTHWELL & WIGHT 1989), but by simple synangia like *Telangium* and *Feraxotheca* (MILLAY & TAYLOR 1977), to aggregated synangia as in genera *Dichotangium*, *Phacelotheca* and *Schopfiangium* (STIDD *et al.* 1985; MEYER-BERTHAUD & GALTIER 1986; ROWE 1988). Medullosales pollen organs were the most varied; there were simple, aggregated and compound synangia.

The way in which sporangia in the synangium fuse is very diverse within the two orders. Among Lyginopteridales, the easiest way is the absence of fusion, as in *Geminitheca* and *Pullaritheca* (SMITH 1959; ROTHWELL & WRIGHT 1989). Many species have basally fused sporangia like *Telangium schweizeri* – the oldest known synangium in this order (the highest Irish Devonian) (MATTEN & FINNE 1994). Geologically younger species, such as *Telangium scottii* (JENNINGS 1976; GALTIER 1988), have the sporangia fused along half their length. Among Medullosales, the sporangia are fused along half the length, e.g., *Codonotheca* (SELLARDS 1903), but there is a widespread trend towards almost total merging, e.g., *Aulacotheca* (HALLE 1933).

Lyginopteridales had relatively small pollen organs of the order of several millimeters. Medullosales are characterized by much larger pollen organs, typically a few centimeters in size. In both orders, the more primitive organs are smaller; specialisation is associated with increased size and amount of sterile tissue around the synangium.

In Lyginopteridales which do not make synangia, there is no sterile tissue accompanying the sporangia. Synangia-forming species usually have sterile tissue at the base of the organ. The greatest quantity of sterile tissue occurs in Medullosales. Embedding sporangia in a thick primary fibrous tissue is characteristic of this order.

The number of sporangia in the pollen organ was variable within these orders. Evolutionarily more advanced species formed more sporangia in the pollen organ. Among Lyginopteridales, in *Telangium schweizeri* there were eight sporangia in the synangium (MATTEN & FINNE 1994). In species forming aggregated synangia, the number of sporangia was very variable, from two in a simple synangium like *Phacelotheca pilosa* (MEYER-BERTHAUD & GALTIER 1986) to 100 sporangia in a pollen organ like that in *Melissiotheca longiana* (MEYER-BERTHAUD 1986). The number of sporangia in the pollen organ was similarly variable among representatives of the Medullosales. A synangium could form only two sporangia, as in *Goldenbergia glomerata* (HALLE 1933), or up to 100 or more as in *Potoniea* and *Dolerotheca* (STIDD 1978, 1990).

Prepollen grains in the sporangia of both orders are completely different, and enable investigators to distinguish between taxa in these orders. Lyginopteridales prepollen grains are usually small, radial and trilete; an exception is *Telangium scottii*, where the grains are elliptical. Medullosales prepollen grains are large, oval and monolete. The exception is *Potoniea* (STIDD 1978), whose grains are similar to Lyginopteridales grains, i.e., radial and trilete.

In the evolution of the pollen organs in the Lyginopteridales order, there were also changes in the construction of the sporangia walls of the synangia, their symmetry, and their occurrence on the plant (Millay & Taylor 1979; Taylor & Millay 1981a; Galtier 1988; Taylor 1988; Taylor & Taylor 1993).

One presumed primitive feature of the sporangia wall is its uniform thickness. This feature occurs in genera which do not form synangia, such as *Geminitheca* (Smith 1959). The sporangium wall in species which form synangia, as in *Telangium schweitzeri*, is dorsally thickened, and remains thin on the ventral side where dehiscing occurred. Therefore, *Telangium schweitzeri*, which is one of the oldest known pollen organs, has an advanced state of this trait, while the younger *Geminitheca* retained the original state of this trait (Matten & Finne 1994).

All the Lower Carboniferous Lyginopteridales species pollen organs include an empty central area surrounded by sporangia. The advanced state is the reduction of the central empty area in the synangium. This was found in the Upper Carboniferous *Feraxotheca* (Millay & Taylor 1977, 1978) and *Crossotheca* (Danze 1956, 1960; Cridland & Darrah 1968; Stubbfield *et al.* 1982; Brousmiche 1982, 1986). The sporangia in these species' synangium lie laterally adjacent on their ventral side.

There are three models of symmetry for Lyginopteridales pollen organs. The synangia of *Telangium schweitzeri, T. scottii* and *Dichotangium quadrothecum* were bilaterally symmetrical (Rowe 1988; Matten & Finne 1994). The synangia of *Crossotheca* (Danze 1956, 1960; Cridland & Darrah 1968; Stubbfield *et al.* 1982) and *Feraxotheca* (Millay & Taylor 1977, 1978) could be bilaterally symmetrical, but this depended on the number of sporangia within the synangium; when there were more of them, the symmetry became radial (Stubbfield *et al.* 1982). *Telangium* (Jennings 1976), *Canipa* (Skog *et al.* 1969), and *Phacelotheca* (Meyer-Berthaud & Galtier 1986) had synangia with radial symmetry. The *Melissiotheca* pollen organ was asymmetrical, and the sterile base of the organ was divided into two or more lobes without a clear shape.

Millay and Taylor (1979) presented a hypothetical model of the most primitive seed fern pollen organ. They imagine it as a dichotomous, tree-dimensional branching bearing terminal sporangia. The sporangia are believed to be elongated, thin-walled, with a lengthwise central dehiscing area; the organ created trilete microspores.

Meyer-Berthaud (1989) agrees with the Millay and Taylor (1979) model. She believes that there were two main types of fertile leaves among the early gymnosperms producing sporangia: a trifid leaf (known only from the Lower Carboniferous), in which there was a central fertile section leaving the trisection of the main axis of the leaf, and a bifid leaf (known from the Lower and Upper Carboniferous), which is considered to be derived from the trifid leaf. Meyer-Berthaud (1989) believes that diversification in the morphology of the synangia proceeded very rapidly during the early Carboniferous. She also believes that Millay and Taylor's hypothetical model (Millay & Taylor 1979) of the most primitive seed fern pollen organ not only applies to Lyginopteridales, but also to the primitive pollen organs of other early seed ferns, including the orders Buteoxylonales and Calamopityales.

Matten and Finne (1994) proposed a modification of Millay and Taylor's model (Millay & Taylor 1979). Namely, they included pollen organs that did not create synangia, such as *Geminitheca* and *Pullaritheca* in Lyginopteridales, and believed such forms to be the most primitive gymnosperm pollen organs.

The new genus and species *Silesiatheca formosa* described in this paper represents a previously unknown stage in the evolution of the radial Lyginopteridales pollen organs. In this genus, the whorl clusters not isolated sporangia, but synangia, each composed of

3–5 sporangia, which are aggregated synangia. Such a situation could arise from organs like *Telangiopsis* or *Crossotheca* by reduction of sterile tissue at the base of the synangium and increasing the number of sporangia in the whorl, which gathered groups of 4–5 units (Danze 1956, 1960; Cridland & Darrah 1968; Eggert & Taylor 1971; Stubbfield *et al.* 1982; Pacyna 2007a, b). Such a structure could provide evolutionary success by producing more prepollen grains in one organ during the short pollination period. This is an example of convergence among Lyginopteridales towards a particularly strong evolutionary trend in Medullosales, depending on increasing, and to a very large number, the quantity of sporangia in a synangium. Another advanced feature of *Silesiatheca* is the monopodial branched axis and its aggregated synangia.

Lyginopteridales disappear at the end of the Carboniferous. It is likely that Medullosales, Callistophytales, Peltaspermales and Corystospermales originate from them (Taylor & Taylor 1993).

The structure of the Medullosales pollen organs also manifested clear evolutionary trends in all genera in this order: a tendency to increase the number of sporangia in their synangium; fusion of sporangia; and protection against drying by the appearance of hairs on the surface of the sporangia (Taylor & Millay 1979; Stidd 1981; Taylor 1988; Taylor & Taylor 1993) (Fig. 2).

Even in the most primitive initial genus of *Codonotheca*, evolutionary trends typical of the order appeared: the quantity and fusion of the sporangia lengthwise, the appearance of hairs on their surfaces to protect them from drying out (in *C. silesiaca* there are no hairs, but they are present in *C. caduca* and *C. corymbiata*). The number of sporangia in the synangium becomes constant. It is still variable in the oldest *C. silesiaca* – up to 12, and then in the geologically younger it is constant, in *C. caduca* – 6, in *C. corymbiata* – 4. In the genus *Codonotheca*, the symmetry of the radial pollen organs also stabilizes, still poorly expressed in *C. silesiaca*, but pronounced in the later species of this genus. Only *Parasporotheca* and the newly created genus *Kotasotheca,* and perhaps some species of *Whittleseya* have bilateral symmetry. Most likely, this symmetry is secondary. It arose originally radially as a factor protecting against excessive drying of the relatively very large synangia bells (Millay & Taylor 1979; Taylor 1988; Taylor & Taylor 1993) (Fig. 2).

Appearance of hairs on the surface of the synangia also occurs in the evolution of the genus *Boulayatheca*. The newly described species of *B. ciliata* has hairs on the surface of the synangium; this feature was not known in previously described, somewhat older geologically species in this genus (Halle 1933; Kurmann & Taylor 1984).

Increasing the number of sporangia in the synangium during the evolution of Medullosales proceeded in the following way: in species creating simple synangia, the number of sporangia in the whorl increased, and with time these simple synangia gathered in groups to form aggregated synangia. Such aggregated synangia produced more prepollen grains, and also protected against drying by growing hairs on the surface of the synangium, which held individual simple synangia together. This can be seen perfectly in the genus *Parasporotheca* (Dennis & Eggert 1978). With time, the synangia forming aggregated synangia became more tightly linked to each other forming a huge compound synangium (Millay & Taylor 1979; Taylor 1988; Taylor & Taylor 1993). The new species *Dolerotheca migierii* described in the paper is an example of the most advanced, complex Medullosales pollen organs, which are characterized by a particularly large number of sporangia in a synangium (Fig. 2F).

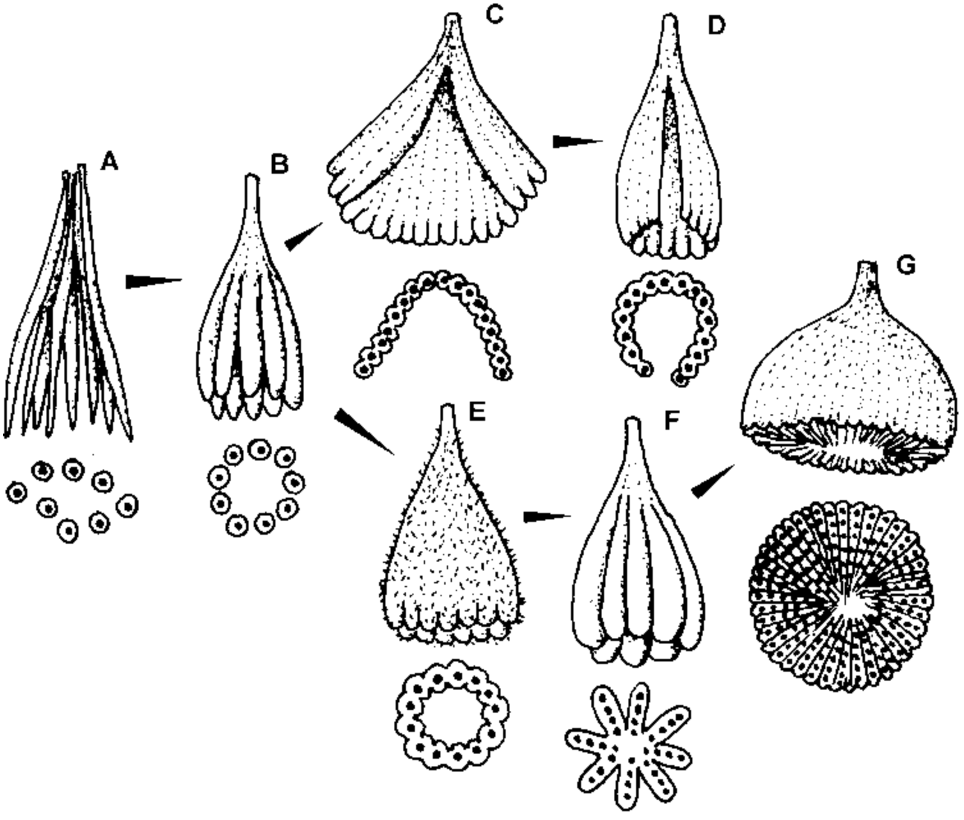

Fig. 2. Presumable evolutionary trends among Medullosales pollen organs including newly described taxa: A – ***Codonotheca silesiaca*** sp. nov. – about the poorly expressed radial symmetry, B – *Codonotheca caduca* – sporangia proximally slightly fused, organ radially symmetrical, C – ***Kotasotheca annaeadamii*** gen. et sp. nov. – sporangia form a widely open ring, D – *Parasporotheca leismanii* – sporangia form a slightly open ring, E – ***Boulayatheca ciliata*** sp. nov. – sporangia form closed ring, F – *Sullitheca dactylifera* – a number of the sporangia in synangium rise, they are plicated, G – ***Dolerotheca migierii*** sp. nov. – the number of sporangia increases, they are arranged very densely, between sporangia sclerenchymal strips appear (based on Taylor 1988; Taylor & Taylor 1993; Taylor *et. al.* 2009, modified).

What was the evolutionary meaning of the origins and development of such complicated, large, and complex structures to produce pollen? It was surely to produce a very large number of prepollen grains during the pollination season. Medullosales seeds were large, sometimes very large and heavy, reaching up to 10 cm in length (Gastaldo 1978). Plants formed single-species aggregations (Laveine 1967, 1997). The prepollen was transferred to the female organ by the wind, but also by insects (Labandeira 1998). Known specimens of *Dolerotheca formosa* are preserved in coal balls with traces of feeding by the Paleodictyopterida group of insects, and so the pollen-carrying agents could have been insects (Schopf 1948; Labandeira 1998). Such large pollen organs, probably constructed of soft tissues (although there were also bands of sclerenchyma in them), could have been a source of food for these insects and thus lured them.

Much evidence suggests that even in the Carboniferous, Medullosales gave rise to Cycadales and Bennettitales (Taylor & Taylor 1993).

5. CONCLUSIONS

A new genus and species of lyginopteridalean aggregated synangia has been recognized

- ***Silesiatheca formosa*** Pacyna & Zdebska, gen. et sp. nov. from the sideritic nodules from Sosnowiec.

Ten species of medullosalean microsynangia were recognized, including one new genus and seven new species:

- the most primitive species is the microsynangium ***Codonotheca*** – ***Codonotheca silesiaca*** Pacyna & Zdebska, sp. nov. with weakly expressed radial symmetry and slight fusion of the sporangia, whose existence is postulated in the evolutionary trees of Medullosales (Fig. 2A), is the first record of *Codonotheca* in the European Carboniferous ;
- for the first time in the European Carboniferous the microsynangium species ***Aulacotheca campbellii*** (White, 1900) Halle, 1933 previously known only from North America was recognized;
- genus ***Boulayatheca*** Taylor & Kurmann, 1985 was emended;
- a new, emended diagnosis has been proposed for the typical species ***Boulayatheca fertilis*** (Kidston, 1914) Taylor & Kurmann, 1985, based on specimens from Poland (first record in Poland);
- two new species of the genus *Boulayatheca* Taylor & Kurmann, 1985 have been described – ***Boulayatheca ciliata*** Pacyna & Zdebska, sp. nov. – characterized by having hairs on the surface of the synangium (a feature previously unknown in genus *Boulayatheca*) (Fig. 2E) and ***Boulayatheca saganii*** Pacyna & Zdebska, sp. nov. with a highly elongated synangium;
- a new emended diagnosis for the species *Boulaya hallei* Gothan 1941 has been proposed and a new combination with the correct generic name – ***Boulayatheca hallei*** (Gothan, 1941) Pacyna & Zdebska, emend. et comb nov.;
- the presence in Lower Silesia of the typical species for the genus ***Whittleseya*** Newberry, 1853 emend. (***Whittleseya elegans*** Newberry, 1853a emend. Halle, 1933) has been confirmed on the basis of new specimens;
- some of the specimens previously classified as *Whittleseya elegans* Newberry, 1853, have been described as a new species ***Whittleseya silesiaca*** Pacyna & Zdebska, sp. nov, which differs from the typical species by the shape of the synangium and the clustering of sporangia in groups;
- a new species ***Whittleseya campanulata*** Pacyna & Zdebska, sp. nov. has been described, with a relatively large synangium and sporangia clustered in groups;
- the history and taxonomy of the genus *Whittleseya* Newberry, 1853a emend. Halle 1933 has been discussed in detail, indicated the presence of heterogeneity within the genus, which is thought to be formed with a ring of numerous, highly elongated sporangia (as in the typical species *W. elegans*), the new established species suggest that some of them can form compound synangia where microsynangia (comprising several sporangia each) were closely fused to form a compact organ, the new species described here of this genus were compared in detail with those previously described, and alternative reconstructions of the synangium were discussed;
- for the first time, aggregated synangia of Medullosales constructed of several microsynangia (each microsynangium consisting of over a dozen sporangia) gathered together but not fused were recognized in compression state of preservation; thus far,

they have only been known in coal balls; based on specimens from Oświęcim, a new genus and species – ***Kotasotheca annaeadamii*** Pacyna & Zdebska, gen. et sp. nov. – were established (Fig. 2C);

- for the first time in the Polish Carboniferous the genus ***Dolerotheca*** Halle, 1933 has been discovered and the new species ***Dolerotheca migierii*** Pacyna & Zdebska, sp. nov. from the nodules from Sosnowiec have been described (Fig. 2F).

The model for the evolution of medullosalean pollen organs proposed by T.N. Taylor (TAYLOR 1988; TAYLOR & TAYLOR 1993; TAYLOR *et al.* 2009) has been confirmed, and the new taxa described have been placed within it (Fig. 2).

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7. ORGANY PYŁKOWE PAPROCI NASIENNYCH (PTERIDOSPERMOPHYTA) Z GÓRNEGO KARBONU ŚLĄSKA (POLSKA) I ŁĄCZĄCE SIĘ Z NIMI ROZWAŻANIA EWOLUCYJNE – streszczenie

Wymarłe paprocie nasienne (Pteridospermophyta) zajmują kluczową pozycję w ewolucji roślin nasiennych, z których wyprowadza się nagozalążkowe wielkolistne (Cycadophytina) oraz okrytozalążkowe (Magnoliophytina).

Organy rozrodcze paproci nasiennych pozwalają prześledzić pokrewieństwa w tej grupie, jak i wnioskować o powstaniu wywodzących się z nich innych grup roślin nasiennych. W karbonie Polski są rzadko znajdowane i bardzo słabo poznane, zwłaszcza słabo znane są męskie organy pyłkowe.

W pracy opisano nowe organy pyłkowe z rzędów Lyginopteridales i Medullosales z górnego karbonu Dolnego i Górnego Śląska. Z rzędu Lyginopteridales opisano nowy rodzaj i gatunek mikrosynangiów – *Silesiatheca formosa* gen. et sp. nov. z langsetu Sosnowca. Są to połączone synangia zbudowane z okółka u nasady zrośniętych synangiów wyrastających z monopodialanej osi.

Z rzędu Medullosales najliczniejsze są zróżnicowane taksonomicznie proste synangia zbudowane z radialnego okółka, silnie wydłużonych, zrośniętych mikrosporangiów. Wśród nich najprymitywniejszy jest nowy gatunek *Codonotheca silesiaca* sp. nov. (langset Sosnowca) o słabo wyrażonej symetrii promienistej i niewielkim zrośnięciu zarodni, którego istnienie postulowano w drzewach rodowych rzędu Medullosales (Taylor *et al.* 2009), jest to równocześnie pierwsze notowanie rodzaju *Codonotheca* (Sellards, 1903) Pacyna & Zdebska, emend. nov. z karbonu Europy, znanego dotychczas tylko z Ameryki Północnej.

Bardziej zaawansowane ewolucyjnie są opisane gatunki *Aulacotheca campbellii* (White, 1900) Halle, 1933 (duckmant Wałbrzycha) o synangium pałeczkowato-cylindrycznym, *Boulayatheca fertilis* (Kidston, 1914) Taylor & Kurmann, 1985 Pacyna & Zdebska, emend. nov. (duckmant Wałbrzycha) o gruszkowatym synangium oraz nowy gatunek *Boulayatheca ciliata* sp. nov. (langset Sosnowca) o synangium bardzo podobnym do poprzedniego gatunku, ale owłosionym. Cecha ta nie była wcześniej znana u tego rodzaju. Gatunek *Aulacotheca campbellii* (White, 1900) Halle, 1933, dotyczczas znany był tylko z Ameryki Północnej, został po raz pierwszy stwierdzony z Europy.

Po raz pierwszy z Polski został opisany rodzaj *Boulayatheca* Taylor & Kurmann, 1985 i gatunek *Boulayatheca fertilis* (Kidston, 1914) Taylor & Kurmann, 1985 Pacyna & Zdebska, emend. nov., Dla gatunku *Boulayatheca fertilis* (Kidston, 1914) Taylor & Kurmann, 1985 Pacyna & Zdebska, emend. nov. zaproponowano nową, poprawioną diagnozę. Z duckmantu Wałbrzycha pochodzi nowy gatunek *Boulayatheca saganii* sp. nov. o silnie wydłużonym synangium. Nową poprawioną diagnozę zaproponowano dla gatunku *Boulaya hallei* Gothan 1941 i nową kombinację z poprawną nazwą rodzajową – *Boulayatheca hallei* (Gothan, 1941) Pacyna & Zdebska, emend. et comb. nov.

Z Dolnego Śląska (Wałbrzych) zostały opisane nowe gatunki rodzaju *Whittleseya* Newberry, 1853a emend. Halle, 1933. Te nowe materiały wskazują na heterogeniczność rodzaju *Whittleseya*, który uważano za zbudowany z pierścienia licznych, silnie wydłużonych zarodni (tak zbudowany jest gatunek typowy *W. elegans* Newberry, 1853a stwierdzony też w langsecie Wałbrzycha). Nowe okazy, będące podstawą opisania tu dwóch nowych gatunków tego rodzaju wskazują, że niektóre wśród nich mogły tworzyć złożone synangia, w których mikrosynangia (złożone z kilku zarodni każde), były ze sobą ściśle zrośnięte tworząc zwarty organ. Część okazów zaliczanych wcześniej do gatunku typowego *Whittleseya elegans* Newberry, 1853a wydzielono w tej pracy jako nowy gatunek *Whittleseya silesiaca* sp. nov. reprezentowany przez liczne, dobrze zachowane okazy. Różni się on od gatunku typowego kształtem synangium i skupianiem się mikrosporangiów w grupy. Nowy gatunek *Whittleseya campanulata* sp. nov. ma stosunkowo duże synangium i zarodnie również skupione w grupy.

Po raz pierwszy również w stanie uwęglonym rozpoznano połączone synangia Medullosales zbudowane z kilku mikrosynangiów (każde mikrosynangium złożone z kilkunastu zarodni) zebranych razem, ale nie zrośniętych. Były one dotychczas znane jedynie z buł węglowych – rodzaj *Parasporotheca*. Na podstawie okazów z kopalni Piast (Oświęcim) opisano ich nowy rodzaj i gatunek – *Kotasotheca annaeadamii* gen. et sp. nov.

Dzwonkowate, złożone synangium zbudowane z kilkuset ściśle zrośnietych zarodni umieszczonych w tkance podstwowej zidentyfikowano jako nowy gatunek *Dolerotheca migierii* sp. nov. (langset Sosnowca). Rodzaj *Dolerotheca* Halle, 1933 został po raz pierwszy rozpoznany w karbonie Polski.

Nowo opisanymi taksonami potwierdzono model ewolucji organów pyłkowych paproci nasiennych z rzędu Medullosales zaproponowany przez T.N. Taylora (Taylor 1988; Taylor & Taylor 1993; Taylor *et al.* 2009). Umieszczono w jego obrębie opisane nowe rodzaje i gatunki (Fig. 2).

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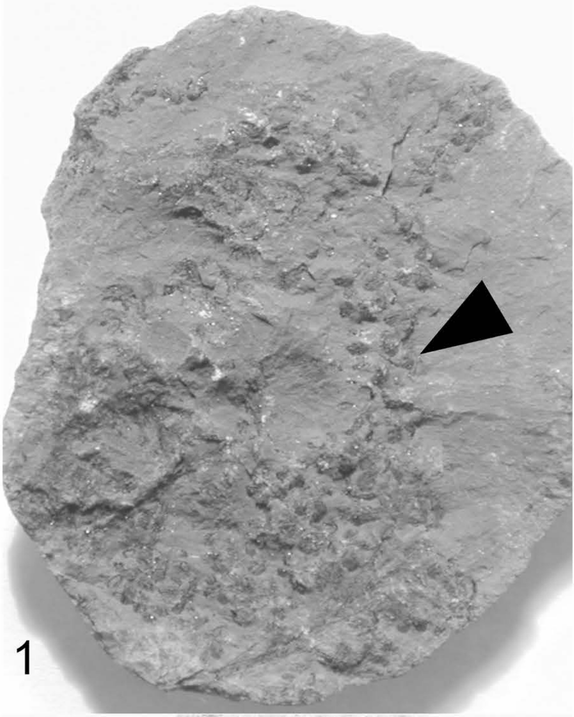
PLATES

PLATE 1

Silesiatheca formosa Pacyna & Zdebska, gen. et sp. nov.
Sosnowiec, Langsettian

1. Holotype (mould) synangia visible (arrow), S/100/P5a, x 2.
2. Laminar pinnae at the base of branching system (arrow), S/100/P5b, x 3.
3. Holotype (cast) monopodially branching system (arrow) of axis bearing terminal synangial whorls, S/100/P5b, x 2.
4. A few whorls of synangia enlarged from Figure 3, note ovate synangium with elongate sporangia (arrow), S/100/P5b. Scale bar = 1.5 mm.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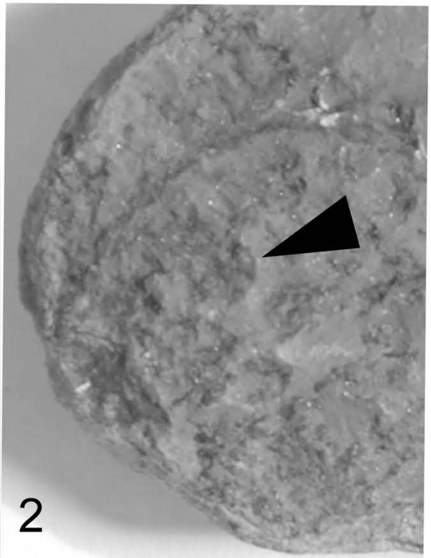
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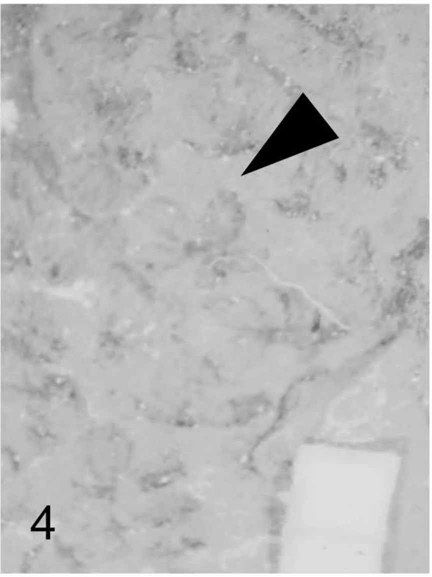
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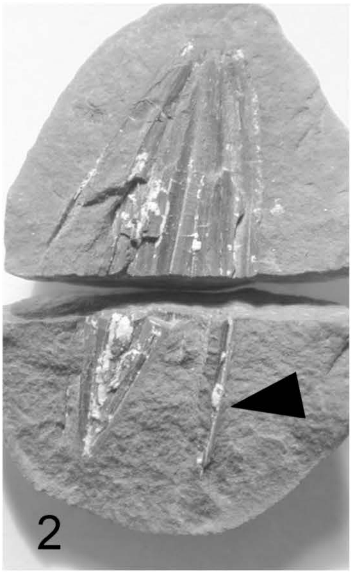
PLATE 2

Codonotheca silesiaca Pacyna & Zdebska, sp. nov.
Sosnowiec, Langsettian

1. Holotype (mould) note proximal fusion of sporangia (arrow), S/100/867a.
2. Holotype (cast) note single sporangium showing prominent probably sclerenchymatous band arising from the basal portion and entering the distal sporangium tip (arrow), S/100/867b.
3. Specimen S/100/868a (mould) note well visible sporangia showing prominent probably sclerenchymatous bands.
4. Cast of the specimen from Figure 3, S/100/868b.
5. Specimen S/100/869a (mould) note proximal fusion of sporangia at organ base.
6. Cast of the specimen from Fig. 5, S/100/869b. Scale bar = 10 mm.


1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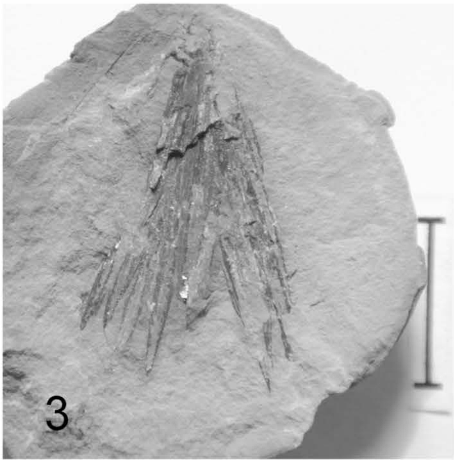
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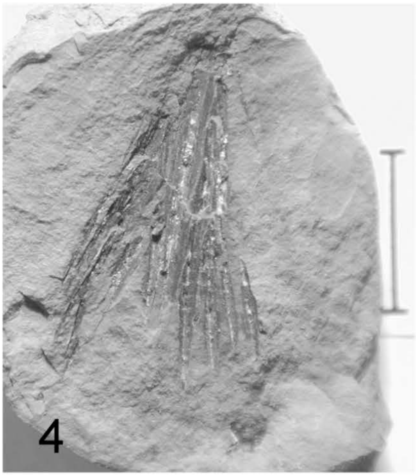
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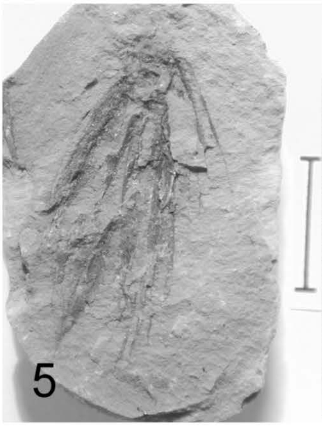
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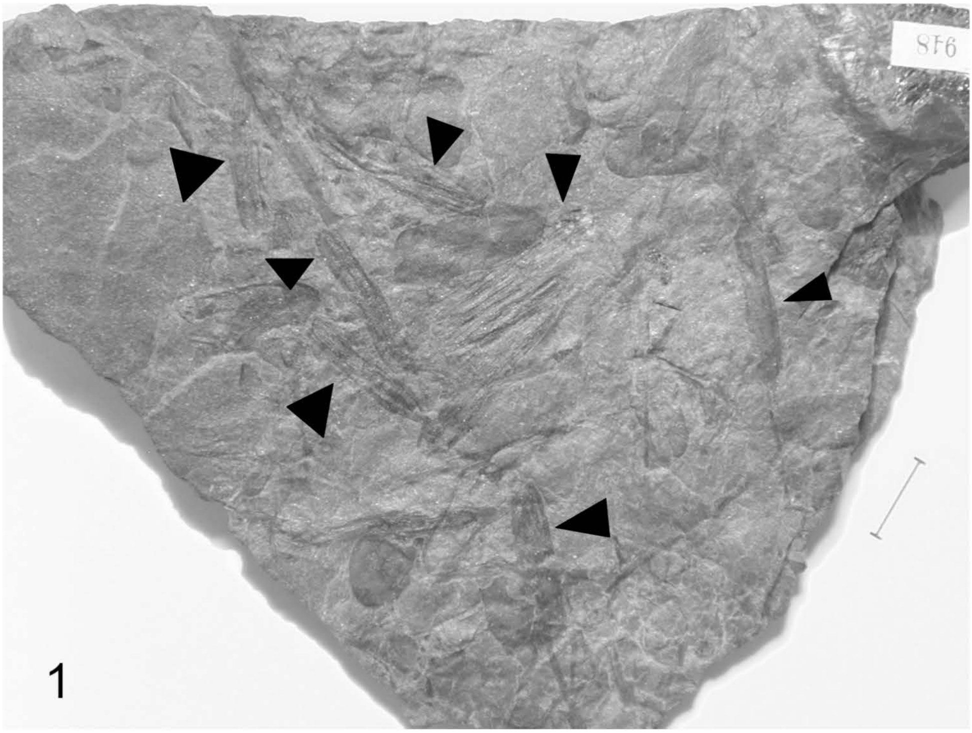
6

PLATE 3

Aulacotheca campbellii (White, 1900) Halle, 1933
Wałbrzych, Chrobry mine, Duckmantian

1. Ten well preserved specimens on shale slab, the well-preserved specimens arrowed, MW 948. Scale bar = 10 mm.
2. Three best preserved synangia enlarged from figure 1, arrows: A – longitudinal ridge corresponding to the sporangium, B – contracted synangium apex, C – synangial apex which is truncated, rounded, indistinctly toothed, x 3.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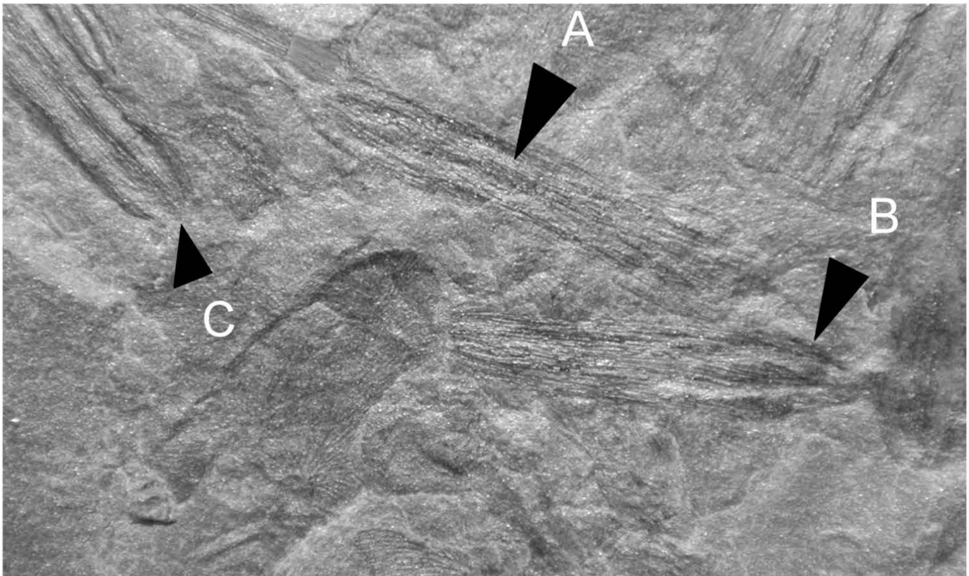

A
B
C
2

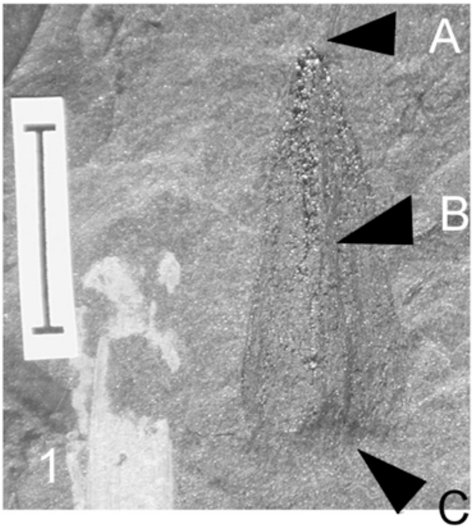
PLATE 4

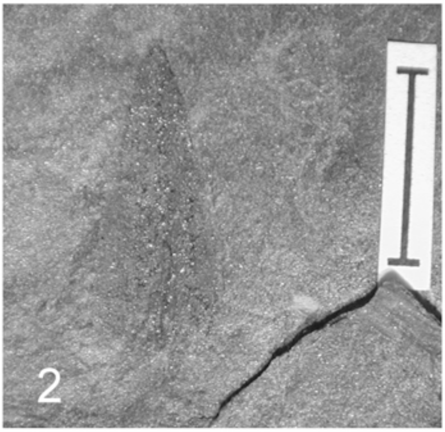
Boulayatheca fertilis (Kidston, 1914) Taylor & Kurmann, 1985 Pacyna & Zdebska, emend. nov.
Wałbrzych, Duckmantian

1. Very well preserved synangium, note synangium surface covered with longitudinal striation, arrows: A – synangium base, B – central convexity (the rest of central hollow cavity filled with sediment), C – poorly visible sporangial distal tips, MW 946.
2. Specimen a little bit less well preserved, note elongated, pyriform shape of synangium, MW 947.

Boulayatheca ciliata Pacyna & Zdebska, sp. nov.
Sosnowiec, Langsettian

3. Holotype (mould) note longitudinal striation of synangium (arrow), S/100/P2a.
4. Holotype (cast), note lobate, free distal tips of sporangia (arrow), S/100/P2b.
5. Specimen S/100/P4a (mould) note well visible elongated, pyriform shape of synangium.
6. Cast of the specimen from Fig. 5, note well visible central concavity (the rest of central hollow cavity preserved after compression of the specimen) (arrow), S/100/P4b. Scale bar = 10 mm.


A
B
C
1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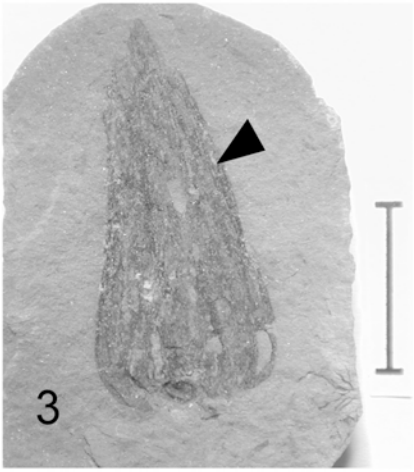
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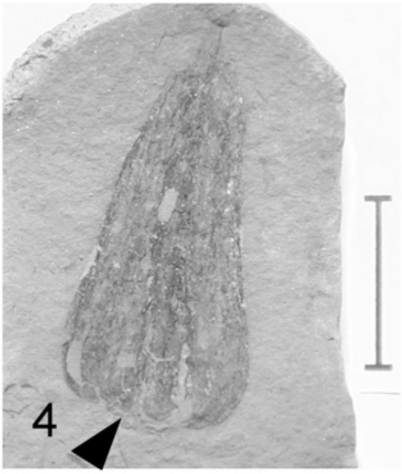
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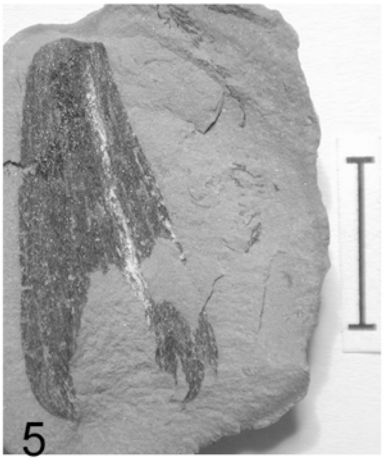
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6

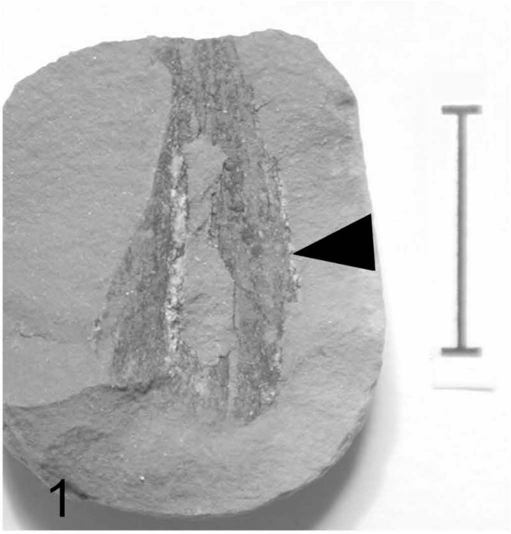
PLATE 5

Boulayatheca ciliata Pacyna & Zdebska, sp. nov.
Sosnowiec, Langsettian

1. Specimen less well preserved, arrow indicate area enlarged in Figures 3-5, S/100/P7b (cast). Scale bar = 10 mm.
2. Mould of the specimen from Figure 1, mineral deposit which filled up the empty hollow cavity inside synangium during fossilization is visible (arrow). Scale bar = 10 mm.
3. Enlargement of synangium surface, note thin, needle-shaped, expanded to base hairs (arrow), S/100/P7b, x 7.5.
4. Enlargement of synangium surface, note thin, needle-shaped, expanded to base hairs (arrow), S/100/P7b, x 12.
5. Enlargement of synangium surface, note hair bases visible as dark spots (A) and filled empty hollow cavity inside synangium (B), S/100/P7, x 15.

Boulayatheca saganii Pacyna & Zdebska, sp. nov**.**
MW 944, Wałbrzych, Westphalian

6. Type specimens visible also on Plate 6, A – base of holotype specimen synangium, B – apex of holotype specimen synangium, C – central concavity on paratype specimen, x 2.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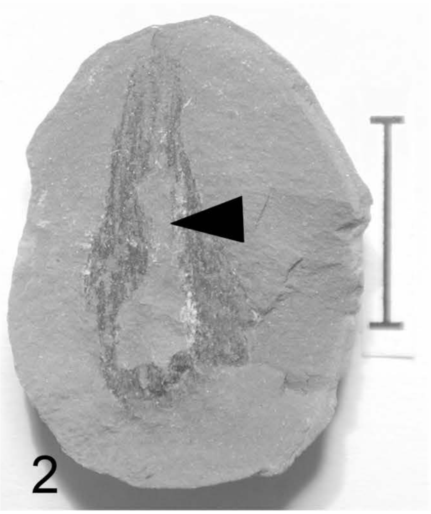
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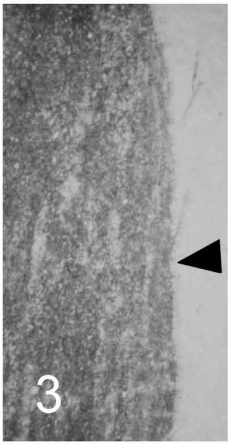
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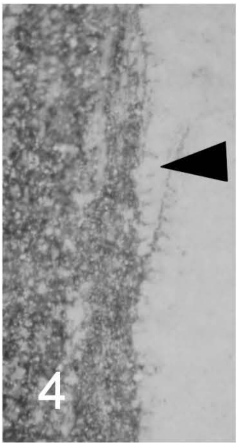
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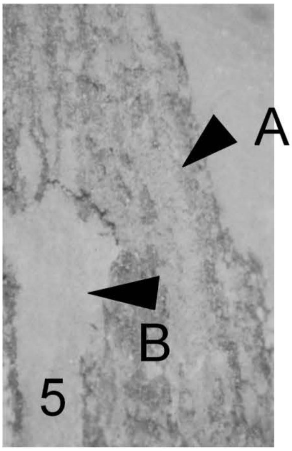

A
B
5

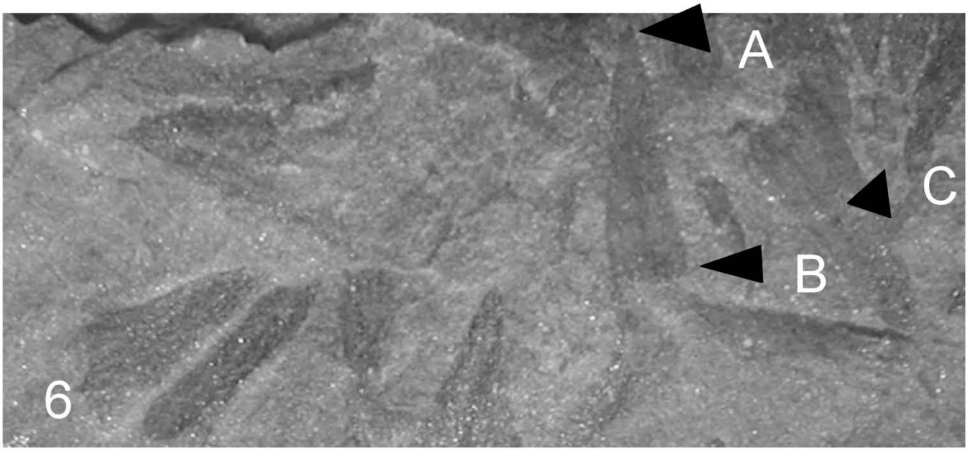

A
C
B
6

PLATE 6

Boulayatheca saganii Pacyna & Zdebska, sp. nov**.**
MW 944, Wałbrzych, Westphalian

1. Type specimens – holotype and paratypes, tens of specimens on one shale slab.
2. Enlargement of specimen from Fig. 1, note several best preserved synangia, holotype specimen arrowed. Scale bar = 10 mm.


1

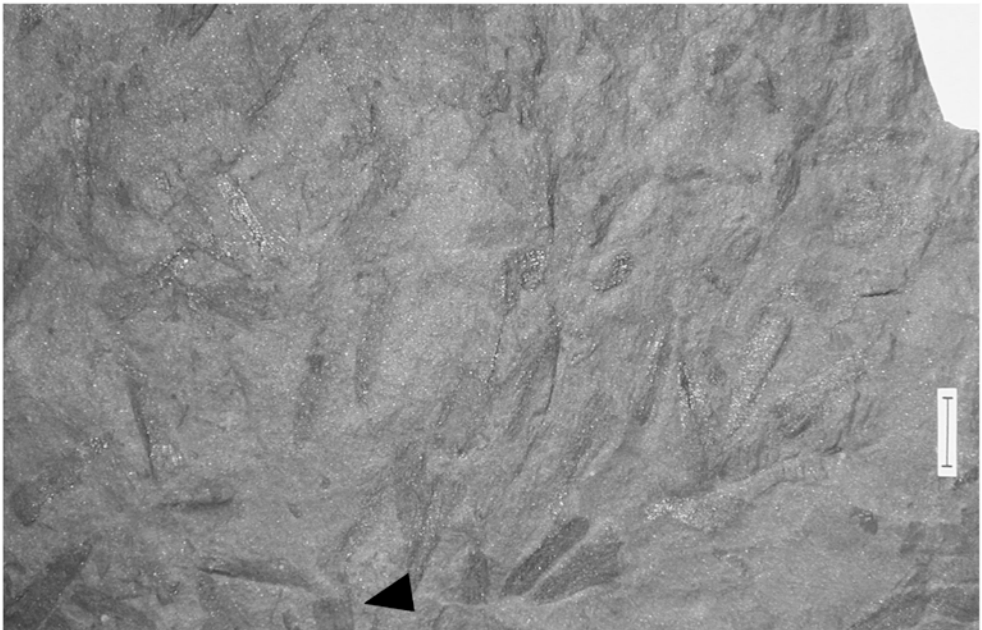

2

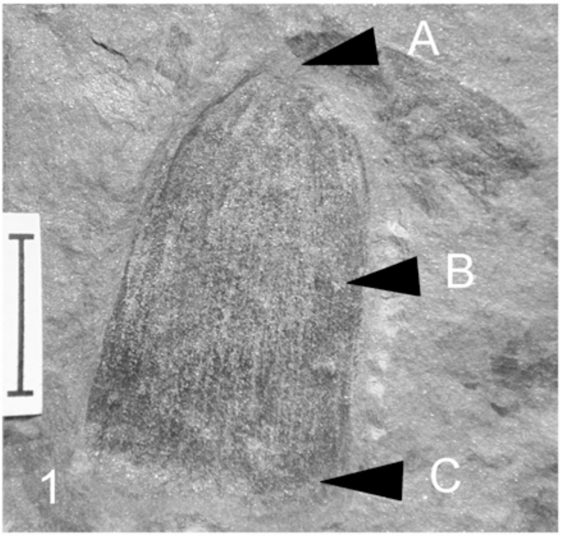
PLATE 7

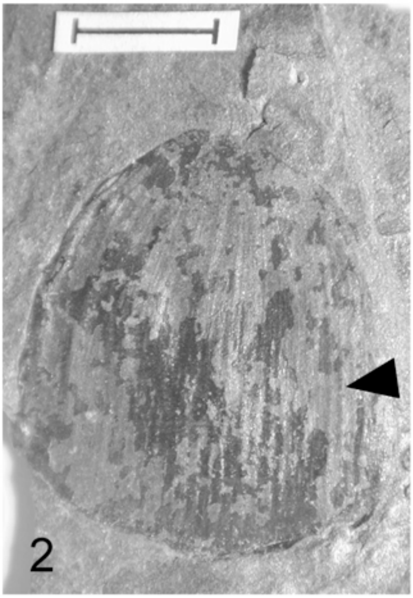
Whittleseya elegans Newberry, 1853a emend. Halle, 1933
Wałbrzych, Upper Carboniferous

1. Synangium, arrows: A – contracted, widely rounded organ base, B – narrow, parallel sporangia, C – broadly truncated synangium apex, acute sporangial distal tips (teeth) poorly visible .

Whittleseya silesiaca Pacyna & Zdebska, sp. nov.

2. Specimen MW 952, note well visible sporangia (arrow), Gorce, Langsettian.
3. Holotype, note narrow, parallel to oneself, strongly marked sporangia (arrow), the line indicates the breadth of the cluster of eight sporangia, MP IB UJ 101/1/1, Wałbrzych, Upper Carboniferous.
4. Paratype, note contracted organ base (arrow), MP IB UJ 101/1/2, Wałbrzych, Upper Carboniferous.
5. Specimen MW 950, note rounded, truncate sporangial distal tips (teeth) (arrow), Gorce, Langsettian. Scale bar= 10 mm.


A
B
C
1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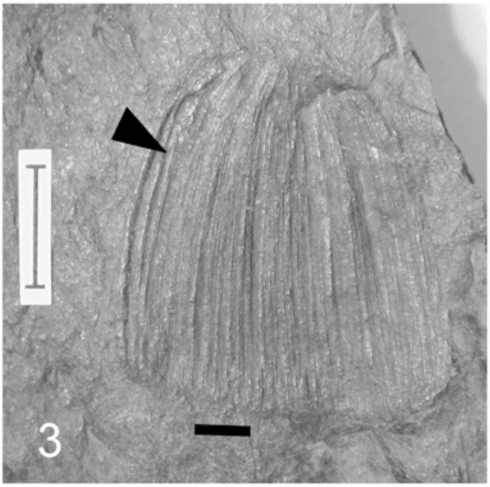

3


4

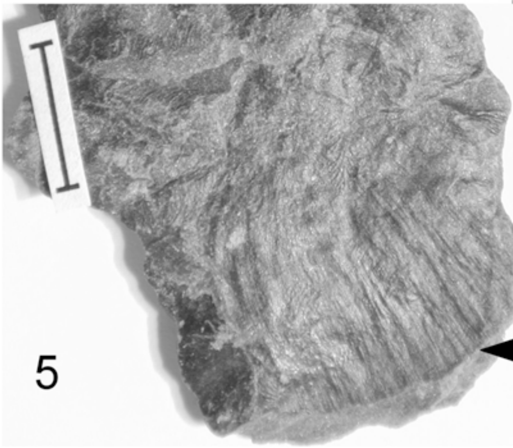
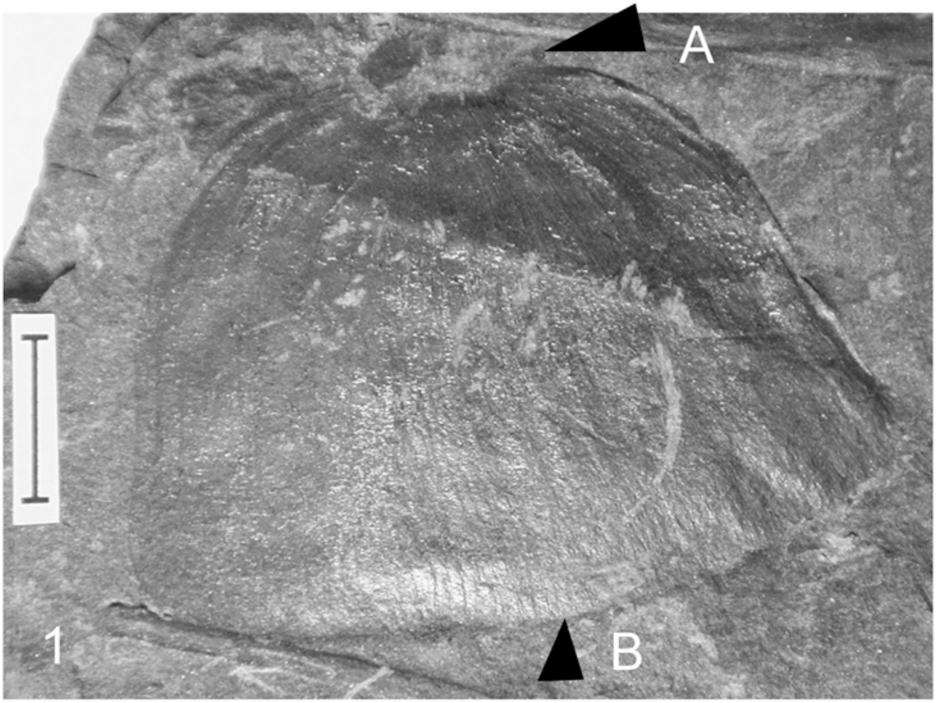

5

PLATE 8

Whittleseya campanulata Pacyna & Zdebska, sp. nov.
MW 2, Gorce, Westphalian A-C

1. Holotype (mould), note track of the broken off stalk (A) and rounded sporangial distal tips (teeth) (B).
2. Holotype (cast), black rectangles indicate the breadth of the clusters of sporangia. Scale bar = 10 mm.

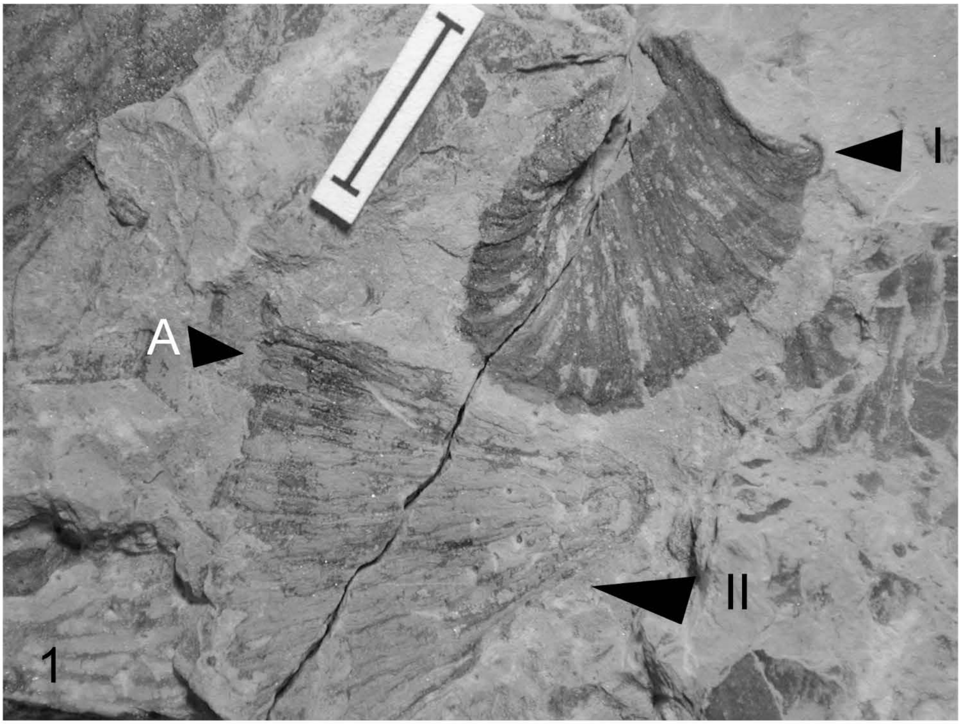

A
B
1


2

PLATE 9

Kotasotheca annaeadamii Pacyna & Zdebska, gen. et sp. nov.
Oświęcim, Duckmantian

1. Synangia preserved in mudstone, arrows: I – holotype – MP IB UJ 101/2/1 – the specimen preserved scoop-like shape, II – paratype – MP IB UJ 101/2/2 – the specimen flattened, A – slightly protruberant, rounded off sporangial distal tips.
2. Paratype − MP IB UJ 101/2/2 – distal part of synangium, note apex lightly turned up outside, A – ground tissue between sporangia, B – sporangium visible on cast of this specimen. Scale bar = 10 mm.


I
A
II
1

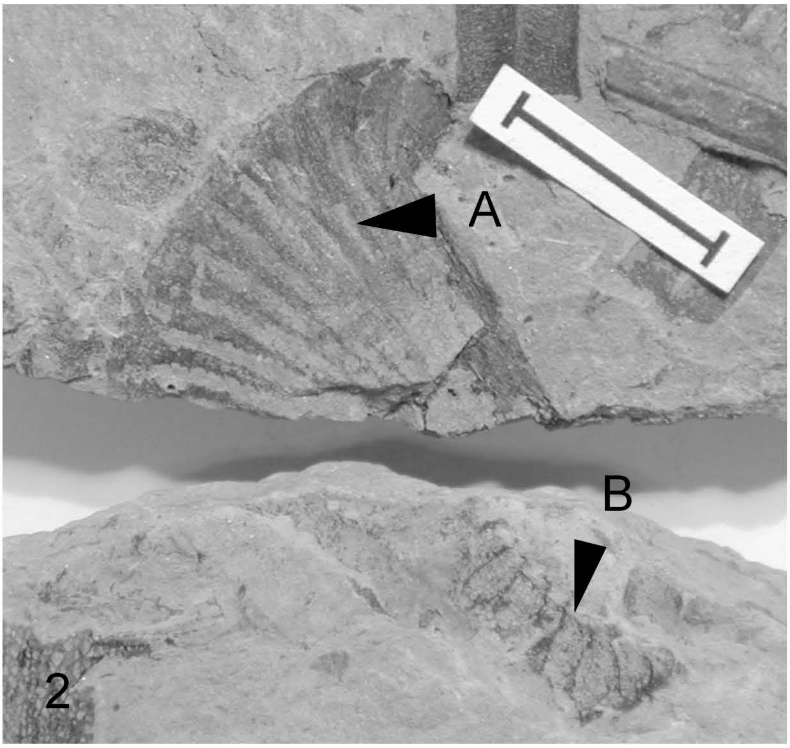
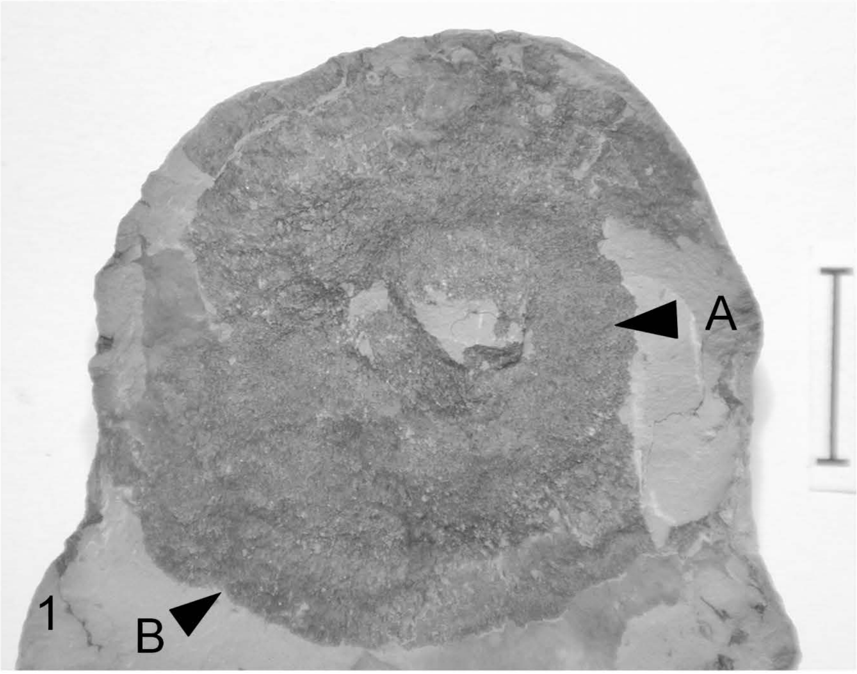

A
B
2

PLATE 10

Dolerotheca migierii Pacyna & Zdebska, sp. nov.
Sosnowiec, Langsettian

1. Holotype (mould), synangium visible from above, arrows: A – sporangia packed very densely, B – synangium margin, S/100/P12a.
2. Holotype (cast), A – centrally placed synangium stalk, B – strips of coalified tissue between sporangia, S/100/P12b. Scale bar = 10 mm.

1



2