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MEGASPORES OF THE TURMA ZONALES FROM THE CARBONIFEROUS OF POLAND. PART II — RECONSIDERATION OF THE GENUS TRIANGULATISPORITES

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Abstract. — The genus Triangulatisporites is emended. The descriptions of the four known species are supplemented and five new species are described. The structure of the spore wall was studied with the SEM and in transmitted light; the main wall layers are: mesospore, exospore and perispore. The perispore structure in Triangulatisporites is the basic taxonomic feature. The natural relationships of these megaspores are discussed.

INTRODUCTION

In the Carboniferous microfloras, spores of the herbaceous lycopods are of great importance; among these the megaspores of the genus Triangulatisporites occur in great numbers in the Upper Carboniferous deposits and especially in the Westphalian. The observations of these megaspores in reflected light commonly used hitherto, do not permit to learn more closely about their organization. The satisfactory results may be obtained only when the spores are studied in reflected and transmitted light and with the SEM. All these methods have been employed in the present study. This

paper is based upon the material from the Upper Silesian Coal Basin, Lublin Coal Basin and Jan Zerndt's collection which comprises specimens from various mines from the Upper Silesian Coal Basin.

1. The samples from the Upper Silesian Coal Basin representing the whole sections were taken from the following mines: Janina (18 samples) — Westphalian D; Ziemowit (17 samples) — Westphalian C; Wesoła (16 samples) — Westphalian A, B; Brzeszcze (24 samples) — Namurian C-Westphalian B/C; Silesia (25 samples) — Namurian C-Westphalian C; Chwałowice (13 samples) — Namurian C-Westphalian A; 8 samples were taken from the coal seam no 510 (Namurian B) from Sosnowiec and Milowice mines; 3 samples from mine Wieczorek (Westphalian A) and some samples were taken from the Spytkowice 103 borehole (Westphalian C/D).

2. The material from the Lublin Coal Basin were taken from Chełm I-IG borehole (one sample) — Westphalian A and Wygnanów IG-1 borehole (35 samples) — Westphalian A/B.

3. The megaspores from the Zerndt's collection come from the Namurian B to the Westphalian D deposits from the following mines: Wujek, Wolfgang (Walenty), Saturn (Czerwona Gwardia), Kazimierz, Paryż (Generał Zawadzki), Waleska, Kleofas, Wieczorek, Radzionków, Koszelew, Libiąż and Piast.

The megaspore material comprises more than two thousand well preserved specimens stored dry; I have also prepared one hundred seventeen slides for observations in transmitted light. These were prepared in a similar way as the Coronate megaspores (Karczewska, 1975). Each specimen was mounted in separate slide, the particular spore fragments were detached and prepared mechanically and verified under the microscope.

My present investigations allowed to establish that there is a considerable differentiation of species within the genus *Triangulatisporites*. It appears, that in spite of the uniform organization and similar size ranges of these spores, the species can be distinguished basing on the perispore structure and sculpture.

This paper was prepared in the Institute of Geology, the Warsaw University. The material signed Kr. Zonal, is in charge of the present author.

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TERMINOLOGY

In the present paper the terminology which has been used is that introduced by Grebe (1971), except the terms concerning the wall stratification. Since the electron microscopy was introduced in palynology a new discussion concerning the spore wall structure have been started. Numerous papers, former and most recent, did not result in establishing an univocal terminology concerning this problem. Due to this the descriptions of the megaspore wall are not always clear. For megaspores a specific division of the wall layers should be employed. In my opinion this should be a two-degree one. Firstly, the main wall layers should be distinguished namely the ones which can be observed with the light microscope, without considering the genesis of the layers and which may be easily detached. The second problem is the further division of these layers by using the electron microscope. Accordingly, I have distinguished in the megaspores *Triangulatisporites* three main wall layers. These are:

1. mesospore (= inner body, endexine, nexine 2 ect.) — the layer adjoining the intine, which is not preserved in fossil state. In megaspores the mesospore is a thin layer;

2. exospore (= ektexine, exoexine, exine 1, sexine ect.) — the layer outside the mesospore, which forms the central body and is more closely connected with the mesospore only in the region of the tetrad mark. In megaspores the exospore is the thickest, very heavy layer of granular structure;

3. perispore (perine) which cannot correspond to the exine outer layer. This layer envelops completely the central body, or, in some megaspores possibly forms some elements of ornamentation. The perispore of megaspores is a laminated layer, thinner or thicker but never as thick as the exospore and never as heavy.

Only when the general plan of the megaspore wall stratification is known, the right, detailed observations by the SEM may be accomplished. I can not agree with Kempf (1973) that the megaspore walls of the Palaeozoic and Mesozoic Lycophyta, such as *Setosisporites hirsutus* or *S. brevispinosus*, consist of extremely thin exine, while the perine shows an enormous thickness (Kempf, 1973, p. 794, pl. 102, figs 1—3). The layer called exine by Kempf represents the mesospore and that called perine corresponds with the exospore; the megaspores *Setosisporites* do not possess the perispore. When the order of the three main megaspore wall layers is known and when one considers that in all megaspores, the Palaeozoic and the Mesozoic ones, the innermost wall layer is the thin mesospore, one may avoid many mistakes. In fact, the exine is the middle layer of the threelayered sporoderm, but only when the perispore is present, and when it is assumed that the intine is in Recent megaspores the fourth layer, not preserved in fossil state. In this meaning the terms: mesospore, exospore and perispore are used in the present paper.

I have also used some conventional designations for the width of the zona and height of laesurae:

Zona narrow	< 80	μm
Zona of medium		
width	81 100	μm
Zona wide	> 100	μm
Laesurae low	< 60	μm
Laesurae of		
medium height	61 - 100	μm
Laesurae high	> 100	μm

STRUCTURE OF ZONATE MEGASPORES AND ITS TAXONOMIC VALUE

The megaspores belonging to various species of the genus *Triangulatis*porites are similar in size and have similar structure, what presented some difficulties in recognizing the particular species. Consequently some authors (Dijkstra, 1946; Winslow, 1959) assigned all these megaspores to one species, *Triangulatisporites triangulatus* (Zerndt). Dijkstra (l.c.) claimed that these spores differ one from another mainly in the structure of the distal reticulum. The differences in the reticulate pattern were considered by Dijkstra (l.c.) and Guennel (1954) to be a physical phenomenon, i.e. in loosely fitting perispore the lumina were supposed to be large and regular while in a closely appressed one the lumina would be small and perispore would be elongated into radial folds.

My present investigations are at variance with this suggestion. After the perispore had been detached from exospore it appeared that the particular species are characterized by different structure of the distal reticulum which does not depend on the perispore being loosely or closely connected with the central body.

Several authors distinguished a few species of *Triangulatisporites* basing on the structure of the distal reticulum. Zerndt recognized, in his earlier papers (1930, 1931) *T. triangulatus Type I*, *II*, and *III*. Later (1934, 1937) he assigned them to one type because they were difficult to distinguish one from another.

The most detailed study of the megaspores Triangulatisporites was that by Schopf (1938); this author pointed out that characteristic features of these megaspores should be considered for each type of spore as a who-

le because the single features are not correlated in any way. Schopf stressed also the necessity of using both the reflected and the transmitted light for taxonomic studies of megaspores of this kind. These were the first attempts to acquire a more detailed knowledge on the megaspores *Triangulatisporites*. However, Schopf could not accomplish the final classification of this "group called perfunctorily *T. triangulatus*" as the structure of the proximal surface of these spores was not sufficiently recognized and the European material, which was not in this author's possession, was not adequately described. Nevertheless, Schopf pointed out that the distal ornamentation and development of the laesurae and zona were different in various forms of *Triangulatisporites*.

Potonié and Kremp (1956) basing on observations in reflected light, recognized four species of *Triangulatisporites*: *T. triangulatus*, *T. regalis*, *T. tertius* and *T. zonatus*. The methods of investigation of *Triangulatisporites*, advised by Schopf, have not been observed later and several authors still recognize only one species, *T. triangulatus* (Zerndt) sensu Dijkstra, within this genus.

My present study, accomplished by the use of reflected and transmitted light and the SEM, shows that this group of megaspores is strongly diversified, but the diagnostic features of the particular species may be seen only when using modern methods of investigation. It appears that most important taxonomically features are: the structure of the perispore, height of laesurae, width and structure of zona and ornamentation of both distal and proximal surfaces. These features should be considered as a whole; separately they have but little taxonomic value.

The megaspores Triangulatisporites have walls consisting of mesospore, exospore and perispore. The mesospore in all species of Triangulatisporites (text-figs 1, 2) consists of two parts; proximal one, with trilete mark, between the rays of which there are numerous cushions, is much thicker than the distal one, which is thin, homogenous and translucent, closely appressed to the inner exospore surface, often folded in various ways. The folding seems to be a secondary feature depending on the state of preservation. The mesospore is most closely attached to the exospore in the region of the tetrad mark. Exospore, which forms the spore central body, is least variable. It is also the thickest of the wall layers. It is most often of circular or oval amb, granular and heavy. Perispore is the outermost wall layer which envelops completely the exospore; easy to be separated from the spore body. This membraneous layer is thinner than exospore and forms the spore ornamentation, laesurae and zona. In all species of Triangulatisporites the laesurae extend to the outer margin of the zona. The zona may be variably developed as the width and the structure are concerned. There is a correlation between the devolopment of the laesurae and the zona. Most often the spores which have wide zona possess also high and similarly sculptured laesurae. In spores with radially striated zona also laesurae are radially

striated; infrareticulate zona is correlated with laesurae of similar structure and so on. The suggestion of Schopf (1938) that the only correlated features of these spores are high and sinuous laesurae with well developed proximal ornamentation, has not been corroborated by my study. Many



Fig. 1. Genus Triangulatisporites: I reconstruction of megaspore; above — polar view, proximal surface, below — equatorial view, median section; M mesospore, EX exospore, P perispore, C cushions; II diagram illustrating structure of distal muri in following species: a-T. regalis, b-T. tertius, c-T. bellus, d-T. zerndtii, e-T. vermiculatus morphological type I, f-T. vermiculatus morphological type II.

authors (Zerndt, Schopf, Dijkstra : *l.c.*) assumed that the distal reticulum is build of perispore; Guennel (1954) suggested that perispore forms the distal reticulum, laesurae and zona, all outside the contact faces. The existence of perispore over the contact faces was not accepted by these authors. However, I was able to separate the central body from the perispore and thus to proove that the perispore envelops completely the exospore (pl. XXIII, fig. 1, text-fig. 1) the contact faces including, similarly as in spores of several fern species of Polypodiaceae *sensu lato*.

The distal reticulum is most differentiated in the spores belonging to *Triangulatisporites*. The lumina may be circular or polygonal, more or less regular, closely spaced or scattered over the whole surface, separated by various kinds of muri. In some reticulum muri are wide, low, ridge-like with rounded edge; in other cases these may be narrow, flat, straight or sinuous with rounded, flattened or sharp edge. The edges may differ from the muri bases being frill-like or more or less lobate; the sharp or gentle lobes may be of various depth (pl. XX, fig. 1, text-fig. 1). The large

lumina of the reticulum may occur occasionally within a very fine reticulum, the lumina of which can not be seen in reflected light.

The proximal ornamentation is most often less pronounced that the distal one. Most often the ornamentation of the contact faces consists of reticulum or tubercles, vermicula or pila; variably developed, more or less densely spaced radial elements run from the contact faces towards the



Fig. 2. Genus Triangulatisporites: I drawing of megaspore, in equatorial view, illustrating types of ornamentation on contact face (A), distal surface (B) and structure of zona (Z) and laesurae (L); II mesospore in proximal view; (C) cushions.

spore equator over the zona. This radial ornamentation does not occur in all species of *Triangulatisporites*; in some species the zona is reticulate, infrareticulate or smooth.

The pattern of the proximal ornamentation as well as the way of development of the distal reticulum, the laesurae and zona are important features for species identification in *Triangulatisporites*. The distinction of several species within *Triangulatisporites* is justified also by the fact that spores of various species of recent herbaceous lycopods differ only very little in morphology.

POSSIBLE NATURAL RELATIONSHIPS

The megaspores of the genus *Triangulatisporites* belong unquestionably to herbaceous Lycophyta. There is a belief that they have belonged to fossil Selaginellales represented by *Selaginellites*. The two Palaeophytic herbaceous lycopods: *Lycopodites* and *Selaginellites*, which resemble the Recent *Lycopodium* and *Selaginella*, are very similar one to another as the sterile organs are concerned, but posses different spores. By way of analogy with the Recent genera the homosporous species have been at-

tributed to Lycopodites while the heterosporous ones to Selaginellites (Darrah, 1939). Therefore the megaspores Bentzisporites and Triangulatisporites are believed to have belonged to Selaginellites in spite of the fact that Triangulatisporites are very different from the megaspores of Selaginella. The Recent Selaginella does not possess spores with strongly developed zona; these spores are characterized by apiculate ornamentation and therefore appear more close to *Bentzisporites*. The second feature common to the megaspores of Selaginellales and to Bentzisporites is the occurrence of singular cushions on the mesospore interradial regions. In Triangulatisporites there are numerous cushions on the mesospore. The organization of the mesospore in Triangulatisporites is more similar to that of the Coronate megaspores than to that of Bentzisporites. Therefore while the belief that Bentzisporites have belonged to Selaginellales is justified it seems that this relation between Selaginellales and Triangulatisporites is doubtfull The megaspores Triangulatisporites are morphologically very similar to the reticulate miospores of Lycopodiaceae; the particular species of these plants possess miospores the general organization of which is very similar and the only specific difference is the type of ornamentation. In these miospores the distal surface is ornamented by different kinds of reticulum and the proximal one bears various sorts of sculpture; the lumina of the reticulum may be of various shape and size, muri are often high and narrow as in the megaspores of Triangulatisporites. The miospores of the Tertiary Lycopodiaceae were described in detail and systematized by Krutzsch (1963). This author distinguished five morphological types of reticulate miospores of Lycopodiaceae each type being represented by several species. The type of reticulum in Triangulatisporites is very close to that of some of the morphological types described by Krutzsch, especially to the morphological type Lycopodium clavatum. Also the spore wall structure is in Triangulatisporites more similar to that of Lycopodium miospores than of the megaspores of Selaginella. In Lycopodium clavatum (Erdtman, 1957, pl. 3, upper figure) the spore wall seen in section consists of two layers: the inner, granular and very heavy and the outer one, distinctly laminated, easy to detach, as in Triangulatisporites. On the other hand, in Selaginella (op. cit., pl. 3, lower figure) the megaspore wall is thick and spongy-granular while in Triangulatisporites the spore wall outside the mesospore consists of two distinct, loosely connected layers.

The Recent Lycopodiales do not possess megaspores and therefore only the homosporous species have been included in the Palaeophytic genus Lycopodites. The heterosporous species earlier included in Lycopodites have been transferred to Selaginellites. This concerns especially the two species: Selaginellites suissei (Zeiller, 1906), formerly Lycopodites ciliatus Kidston, 1901 and Selaginellites (= Lycopodites) primaevus (Goldenberg, 1355) Halle, 1908; in the sporangia of these plants the megaspores Triangulatisporites were found. The only species the anatomical features of which indicate its belonging to Selaginellales is *Selaginellites crassicinctus* Hoskins & Abbot, 1956. This species however is known only from petrified fructification and assignement of the megaspores known only from thin sections to *Triangulatisporites* seems risky. The heterospory can not be the feature of taxonomic value because in various groups of fossil plants the heterosporous and homosporous forms occur even within one genus. This concerns mostly the Palaeophyticum which was a period of rapid evolution and differentiation of Pteridophyta. Thus, in my opinion it is possible that there existed also heterosporous Lycopodiales in the Palaeophyticum but the heterospory has not persisted as a constant feature of these plants.

There is also some similarity between the organization of the megaspores *Triangulatisporites* and the megaspores of the Recent Isoetales; *Isoetes* coromandelina L. described by Pant and Shrivastava (1961) seems to be especially similar to *Triangulatisporites laevigatus*. Krasilov and Zakharov (1975) described megaspores from cones of *Pleuromeia olenekensis* Krasilov, 1975, which possess reticulate distal surface; such an ornamentation was not known in megaspores of other species of *Pleuromeia*, which, according to these authors, was due to poor state of preservation. The relationship between *Pleuromeia* and Isoetales is at present considered as very possible.

In the present state of knowledge I suggest that the megaspores *Trian*gulatisporites are of an intermediate structure, combining the features of all the three groups of herbaceous Lycophyta. They might also have belonged to some other group of herbaceous Lycophyta, the macrofossils of which are not known enough, which could have been the ancestor to Selaginellales as well as to Lycopodiales and Isoetales.

KEY TO IDENTIFICATION OF SPECIES.

- A. Megaspores with distinct distal reticulum:
 - A1. Megaspores with proximal reticulum more or less distinctly developed:
 - A1-1. Proximal surface with distinct reticulum: Triangulatisporites triangulatus
 - A1-2. Proximal surface reticulate-vermiculate: Triangulatisporites regalis
 - A1-3. Proximal surface reticulate-tuberculate:
 - A1-3a Megaspores with narrow zona: Triangulatisporites tertius
 - A1-3b Megaspores with wide zona: Triangulatisporites bellus
 - A2. Megaspores without distinct proximal reticulum: A2-1. Proximal surface blistery-conate:

Triangulatisporites zerndtii

- A2-2. Proximal surface distinctly vermiculate: Triangulatisporites vermiculatus
- B. Megaspores without distinct distal reticulum:
 - B1. Distal surface microreticulate or microreticulate-vermiculate:
 - B1-1. Zona of medium width: Triangulatisporites zonatus
 - B1-2. Zona weakly developed:
 - $Triangulatisporites\ microreticulatus$
 - B2. Proximal and distal surfaces almost smooth: Triangulatisporites laevigatus

DESCRIPTIONS

The system of classification employed in the present paper is that introduced for the Carboniferous and Permian megaspores by P. Piérart during the Seventh International Congress of Carboniferous Stratigraphy and Geology, Krefeld 1971 (Piérart, 1975).

> Anteturma **Megasporites** Pant, 1962 Turma **Triletes** (Reinsch) Potonié & Kremp, 1954 Suprasubturma **Zonales** (Bennie & Kidston) Potonié, 1954 Subturma **Zonotriletes** Waltz, 1935 Suprainfraturma **Zonati** Potonié & Kremp, 1954 Infraturma **Hymenozonati** Piérart, 1975

Genus Triangulatisporites (Potonié & Kremp, 1954) emend. Type species: Triangulatisporites triangulatus (Zerndt, 1930) Potonié & Kremp, 1954

Emended diagnosis. — Trilete megaspores of medium or small size: amb circular, subtriangular or triangular. Spore wall distinctly layered. There are three principal layers: perispore, exospore and mesospore. Mesospore with trilete mark between the rays of which there are numerous cushions. Mesospore is attached to the exospore over its whole surface; there is no cavum between these two layers. Exospore forms central body of the spores; this is more or less circular, surface smooth or finely granular. Exosporium is completely enveloped by perisporium which also forms laesurae and zona. Perispore is more or less attached cover of the megaspore. Laesurae straight or sinuous in various degrees, extending to the outer margin of zona. Proximal surface reticulate, granulate, vermiculate, tuberculate, blistery-conate or almost smooth. Zona evenly wide along equator only, more or less wide at apices. Zona finely granular, infrareticulate, reticulate but most often radially striate and more or less folded. Perispore of distal body surface usually reticulate, but may be also microreticulate, vermiculate or almost smooth. Distal reticulum may be developed in different ways.

Remarks. — The genus Triangulatisporites (Potonié and Kremp) emend. has an isolated position among the megaspores of the Palaeophyticum. It is closest to the

genus Zerndtisporites Bharadwaj, 1955, from which it differs in structure of zona, different sculpture of both proximal and distal sides and in being smaller.

On the other hand there is a considerable similarity between Triangulatisporites and the Rhaetian-Liassic genus Minerisporites Potonié, 1956; the megaspores of this genus have similarly developed laesurae and they possess also membranous, equatorial zona, reticulate sculpture of proximal surface and generally reticulate pattern of the distal elements of ornamentation. The megaspores Minerisporites differ from those of Triangulatisporites in having the zona strongly widened at apices in a form of auriculi and in bearing more or less elongated projections at apices of the distal reticulum. The occurrence of megaspores of the Triangulatisporites structure in the Mesophyticum seems to be certain; the Triassic species Macrosporites makowskii Fuglewicz, 1973 (Fuglewicz, 1973, p. 439, pl. 29, figs 5a, b) possesses all the features of the genus Triangulatisporites and none of Macrosporites (= Zonalesporites). The name of this species should be Triangulatisporites makowskii (Fuglewicz, 1973) nov. comb.

Affinities — Heterosporous, herbaceous Lycophyta.

Occurrence. — Upper Devonian?, Lower Carboniferous — Lower Triassic.

Triangulatisporites triangulatus (Zerndt, 1930) Potonié & Kremp, 1954

(pl. VII, VIII)

1930. Triletes triangulatus I Zerndt: 51, pl. 7: 19-24.

1931. Typ 17 Zerndt: 173.

1932. Triletes triangulatus Zerndt; Zerndt: 12, pl. 1: 4.

1934. Triletes triangulatus Zerndt; Zerndt: 19, pl. 18: 1-16; 21-24.

1937. Triletes triangulatus Zerndt; Zerndt: 3, pl. 5: 3, 5.

1938. Triletes triangulatus Zerndt; Schopf: 32, pl. 4: 1, 3, 7, 8; pl. 7: 5, 6?

1940. Triletes triangulatus Zerndt; Zerndt: 136, pl. 10: 19-23.

1946. Triletes triangulatus Zerndt; Dijkstra: 52, pl. 4: only 33 ab, 34.

1950. Triletes triangulatus Zerndt; Arnold: 75, pl. 6: 1, 2, 4.

1951. Triletes triangulatus Zerndt; Kalibova: 44, pl. 3: 15.

1954. Triangulatisporites triangulatus (Zerndt); Potonié & Kremp: 163, pl. 14:62; pl. 20:103.

1955. Triletes triangulatus Zerndt; Dijkstra: 338, pl. 37:21; pl. 38: 32-34.

1955. Triangulatisporites triangulatus (Zerndt); Potonié & Kremp: pl. 9: 68-72.

1956. Triangulatisporites triangulatus (Zerndt); Potonié & Kremp: 130.

1956. Triletes triangulatus Zerndt; Bonet & Dijkstra; 260, pl. 54: 32-33, 34?

1958. Triangulatisporites triangulatus (Zerndt) Potonié & Kremp; Piérart: 58, pl. 3:6.

- 1959. Triletes triangulatus Zerndt (sensu Dijkstra); Winslow: 38, pl. 1, 2? 4, 5, 10.
- 1967. Triangulatisporites triangulatus (Zerndt) Potonié & Kremp; Karczewska: 318, pl. 7:8, 9.
- 1971. Triangulatisporites triangulatus (Zerndt) Pot. & Kr.; Loboziak: 67, pl. 8: 31a, b.

1975. Triangulatisporites triangulatus (Zerndt) Pot. & Kr.; Lachkar: 21, pl. 6: 2-4.

Material. — Over one thousand well preserved specimens. Dimensions (in microns): dry wet

	6	
Diameter of spore	462-545	616770
Diameter of spore body	407450	511 - 616
Height of laesurae		48- 66
Width of zone		71-79,2

Diameter of proximal	
mesospore side	440—500
Diameter of large lumina	
of distal reticulum	40 71
Diameter of small lumina of	
distal reticulum	9- 23
Diameter of lumina of	
proximal reticulum	14— 35

Description. — Megaspores examined in reflected light. Megaspores trilete; amb subcircular or triangular with convex sides and pointed apices. Laesurae distinct, extending to the outer margin of zona. Zona narrow, smooth or slightly wavy, up to one-fifth of spore radius. Proximal spore surface granulate — tuberculate, close to and within the zona radially striate. Distal surface reticulate; lumina more or less circular, seven to ten along body diameter.

Megaspores examined in transmitted light and with SEM. Exospore forms central spore body of circular amb, with trilete mark. Suturae simple, straight, half to three-fourth of spore radius. Exospore thick, of finely granular, compact structure. Thin, hyaline mesospore adheares to the inner exospore surface. It is thicker over proximal side, with triradiate mark. Between the trilete rays there are numerous cushions. Exospore is enclosed in perispore which also forms laesurae and zona. Laesurae low, slightly sinuous, more or less evenly high along their length the apex including, extending to the outer margin of the zona. Zona narrow, smooth or slightly wavy, ornamented with radially arranged muri which fork dichotomously several times near the outer zona margin. In well preserved specimens the outer zona margin is ornamented by spaced minute cones which represent terminations of some muri (pl. VIII, fig. 2). Structure of the zona is infrareticulate. Zona is widest at apices giving the spores distinctly triangular shape. Over proximal surface perispore is distinctly reticulate: lumina are irregularly polygonal and elongated. Close to the central body outer margin lumina are open towards the equator, thus, the reticulate pattern becomes the radially striate one, similar to that of the proximal surface of the zona. Perispore of the distal body surface is reticulate; lumina are of two kinds: small ones of irregular shape, the diameter of which is about half of that of the proximal ones, and large, circular lumina resulting probably from fusion of the smaller ones. These are distributed more or less regularly over the distal body surface, separated one from another by the finer reticulum, the lumina of which can be seen under high magnification only. In reflected light the fine reticulum appears as roughness or granulation of the surface. Close to the body equator the reticulate pattern changes into the radial one similar to that of the corresponding region of the proximal surface; the distal surface of the zona is also radially striate. Perispore is thin and delicate, distal muri are low.

Variability. — In the megaspores T. triangulatus variability concerns mostly the distal perispore. There are forms in which the distal reticulum consists of the small lumina exclusively. In some other ones there are only single large lumina (pl. VII, fig. 2) or these are regularly distributed over the body distal surface, separated by the fine network (pl. VIII, fig. 2). In spores of this species the thin and delicate perispore is often more or less destroyed; the most delicate and first to be damaged are the laesurae and the zona.

Remarks. — *T. triangulatus* is most similar to *T. regalis* but it differs from the latter by being smaller and having narrower zona, smaller and more widely spaced lumina of the distal reticulum; these are also of different shape and the muri are lower and narrower.

Occurrence. — Poland: Namurian A-Westphalian D. Czechoslovakia: Westphalian B-Stephanian B. Germany: Westphalian C. The Netherlands: Westphalian A-C. France: Westphalian A-Stephanian D. Spain: Westphalian A. Belgium: Westphalian C. Turkey: Namurian A-Westphalian D. USA.: Morrowan-Desmoinesian. USSR: Westphalian C.

Triangulatisporites regalis (Ibrahim, 1932) Potonié & Kremp, 1956 (pl. IX, X; text-fig. 1)

- 1932. Sporonites regalis Ibrahim in Potonié; Ibrahim & Loose: 449, pl. 16:24.
- 1933. Zonales-sporites triangulatus regalis (Zerndt); Ibrahim: 29, pl. 3:24.
- 1938. Triletes triangulatus Zerndt; Schopf: pl. 4:2.
- 1946. Triletes triangulatus Zerndt; Dijkstra: pl. 4: 25.
- 1956. Triangulatisporites regalis (Ibrahim) nov. comb.; Potonié & Kremp: 129, pl. 9: 63, 64.
- 1965. Triangulatisporites regalis (Ibrahim) Pot. & Kr.; Spinner: 98, pl. 14: 10-12; pl. 15:10.

Material. — Over one hundred well preserved specimens. Dimensions (in microns):

	dry	wet
Diameter of spore	540-790	440-974
Diameter of spore body	450-680	393—817
Height of laesurae		62 87
Width of zone		72— 97
Diameter of lumina		
of proximal reticulum		16— 30
Diameter of lumina of		
distal reticulum		60—110
Height of muri of		
distal reticulum		24— 44

Description. — *Megaspores examined in reflected light.* Megaspores trilete; amb triangular with convex sides. Laesurae slightly sinuous extending to the outer margin of zona. Zona of medium width up to 1/3 of spore radius, slightly wider at apices. Arcuate ridges marked by change of ornamentation on central body proximal surface. Proximal surface granulate-tuberculate, close to and over zona radially striate. Distal surface reticulate; lumina circular, polygonal or kidney-shaped, closely spaced; ten to twelve lumina may be counted along body diameter.

Megaspores examined in transmitted light and with SEM. Central body (exospore) circular or oval with trilete mark; trilete rays straight, up to half of body radius. Exospore thick (24—31 μ m). Thin, homogenous, transparent mesospore adheres to the inner exospore surface; its oval-triangular proximal side is distinctly marked. Perispore envelops completely the exospore forming also laesurae and zona. Laesurae of medium height, slightly sinuous, striate similarly as the zona, diminishing in height over the zona, extending to the outer spore margin. Zona of medium width, wavy and finely striate over proximal side, infrareticulate over distal one; outer margin ornamented by fine cones. Zona widest at apices. Over contact faces perispore is reticulate-vermiculate; lumina irregular, polygonal or elongated, muri wide. Reticulate pattern changes into radial striation over the zona. Over the distal side perispore forms reticulum with large, polygonal (most often hexagonal) lumina regularly distributed over whole distal body surface, which gives the reticulum a very characteristic appearance of a honey-comb. Muri high, narrow, considerably raised at cor-

ners where several muri join (text-fig. 1). In compressed spores the lumina become kidney shaped due to flattening of muri (pl. X, fig. 4).

Remarks. — The megaspores of T. regalis are not very variable. High muri of the pronounced distal reticulum may become destroyed to various extent thus, the spores may have different appearances due to the state of preservation. In megaspores T. regalis the distal zona surface is reticulate while in most other species of Triangulatisporites it is radially striate. T. regalis resembles most T. triangulatus (see p. 344). Megaspores of T. regalis are also somewhat similar to T. bellus sp.n. from which they differ in having narrower zona, less pronounced laesurae, more delicate ornamentation of the proximal surface and thinner exospore.

Occurrence — Poland: Westphalian A-D. Germany: Westphalian B. France: Westphalian B-C. USA.: Desmoinesian (Herrin No. 6). England: Westphalian D.

Triangulatisporites tertius Potonié & Kremp, 1956 (pl. XI–XIII; text-fig. 1)

- 1931. Triletes triangulatus III Zerndt; Stach & Zerndt; 1123, pl. 3: 32, 33.
- 1934. Zonalesporites regalis Ibrahim; Loose: pl. 7:34.

1956. Triangulatisporites tertius Potonié & Kremp: 130, pl. 9: 65-67.

1971. Triangulatisporites tertius Pot. & Kr.; Loboziak: 68, pl. 8: 34 a, b.

1975. Triangulatisporites tertius Pot. & Kr.; Lachkar: 22, pl. 6:1; pl. 14:5, 6.

Material. — Approximately one hundred well preserved specimens. Dimensions

(in microns):	dry	wet
Diameter of spore	400-612	500 - 732
Diameter of spore body	362 - 467	418-710
Height of laesurae		33 57
Width of zona		44— 77
Diameter of lumina		
of proximal reticulum		16 - 38
Diameter of lumina of		44—110
distal reticulum		m or < 10

Description. — Megaspores examined in reflected light. Megaspores trilete; amb distinctly triangular with convex sides. Laesurae low, almost straight, extending to the outer zona margin. Zona narrow, up to one-fifth spore radius, wider at apices which are thus distinctly pointed. Proximal surface finely granulate; over the zona granulation is indistinctly radially arranged. Distal surface of body reticulate; lumina circular or polygonal.

Megaspores examined in transmitted light and with SEM. Central body (exospore) circular or subcircular, with trilete mark; triradiate rays straight, half to two third of body radius. Exospore of medium thickness. Thin, homogenous mesospore adheres to the inner exospore surface. Proximal mesospore side is more or less triangular. Exospore is completely enveloped in perispore which forms also laesurae and zona. Laesurae evenly high along their length; their height is equal to the width of zona. They are densely striate and finely sinuous. Zona narrow, slightly wavy and finely radial y striate over proximal surface. In transmitted light its reticulate structure and fine cones at its margin may be seen. Perispore is reticulate-tuberculate over the contact faces. Lumina are irregular and indistinct; over the zona the reticulate pattern becomes partially a striate one with the striae and muri very densely set. Distal perispore forms reticulum; lumina more or less circular, crater-like, but not deep. Muri with very characteristic wavy and denticulate crests (pl. XIII, fig. 1b, text-fig. 1). Each lumen is encompassed by a separate murus; the neighbouring muri do not always touch each other (pl. XIII, fig. 1a). Close to the zona lumina are open towards the spore margin, thus the reticulate pattern becomes a radially striate one.

Variability. — In this species small spores differ in structure from the large ones. The large normally developed megaspores (probably the ripe specimens) possess distinctly reticulate distal surface and reticulate-tuberculate proximal one, while in small specimens observed in reflected light and under magnification 100 x both surfaces appear rough (granulate) and are ornamented by fine tubercles. Even in transmitted light the perispore structure is indistinct; in very strong light it appears as a very complicated infrareticulate one. The small specimens of T. tertius have a relatively thick exospore and perispore which makes observations in transmitted light difficult. The examination with the scanning electron microscope permitted to recognize their structure and to include them to T. tertius. The proximal surface of these spores, as seen using the SEM, appears to have the same ornamentation in both small and large spores. The distal surface is in small spores very finely reticulate; muri are high and lumina are deep and crater-like. The crests of muri are denticulate. Due to flattening of the reticulum the distal surface of the small spores appears squamose (pl. XI, fig. 4), the lumina of the reticulum may be seen only under high magnifications. In large (ripe) spores the particular lumina are fused forming large, circular ones delimited by wide areas filled with the fine reticulum.

Remarks. — T. tertius is most similar to T. triangulatus from which it differs in having less distinctly reticulate proximal surface, different structure of the distal reticulum and narrower zona. The small specimens are similar to spores of T. zonatus, but they have narrower zona, lack the proximal reticulum and have the distal reticulum of a different structure. The small specimens were probably included by various authors to T. zonatus or to T. triangulatus sensu Dijkstra.

Occurrence. — Poland: Westphalian B-D. Germany: Westphalian B-Stephanian A. France: Westphalian B-C (?).

Triangulatisporites bellus sp.n. (pl. XIV—XVI; text-fig. 1)

Holotypus: Kr. No. Zonal. II/AO-242; pl. XIV, fig. 3.

Stratum typicum: Namurian C.

Locus typicus: Mine Kleofas, Upper Silesian Coal Basin.

Derivatio nominis: Lat. bellus — beautiful.

Diagnosis. — Megaspores in which perispore forms distinct distal reticulum; proximal surface reticulate-tuberculate, tubercles large, densely spaced; zona wide, densely radially striate; laesurae high, strongly raised at apex.

Material. - More than eighty well preserved specimens. Dimensions (in microns):

	ary	wet
Diameter of spore	402-625	550-970
Diameter of spore body	303 - 25	400 - 770
Height of laesurae		102-110
Width of zona		103 - 120
Diameter of lumina		
of proximal reticulum		27- 38
Height of proximal		
tubercles		11 33
Diameter of lumina		
of distal reticulum		55 80
Number of lumina		
of distal reticulum		18- 80

Description. — Megaspores examined in reflected light. Megaspores trilete; amb distinctly triangular with pointed apices and slightly convex sides. Laesurae high, distinctly raised at apex, extending to the outer margin of zona. Zona wide, one-third to half of spore radius. Arcuate ridges distinct. Proximal surface ornamented with densely spaced, large tubercles, close to zona and over zona radially striate. Distal surface of body reticulate, zona radially striate, lumina usually circular, delimited by granulate areas. Five to eight lumina along body diameter.

Megaspores examined in transmitted light and with SEM. Central body (exospore) of oval or subtriangular amb, with trilete mark; triradiate rays straight, approximately half of body radius. Exospore thick. Mesospore adheres to inner exospore surface; its proximal side is of triangular amb, with trilete mark between the rays of which there are numerous, small cushions. Proximal mesospore part is thicker than the distal one; the latter is thin, homogenous and concentrically folded. Exospore is completely enveloped in perispore which also forms laesurae and zone. Laesurae very high, the highest at apex where they form a distinct elevation. They are closely connected with zona which they join at the distance of half spore radius from apex. They are strongly sinuous, with upper margin covered by numerous, fine cones. Zona wide and thick, supported by densely spaced radial muri which fork near the margin and anastomose at margin. Zona is stiff, slightly or not wavy, margin is almost smooth. Perispore of proximal side is reticulate-tuberculate; tubercles large, densely spaced cover the contact areas which are distinctly delimited by bases of laesurae and arcuate ridges. Outside arcuate ridges ornamentation is distinctly radial. Perispore of distal side forms reticulum consisting of large circular lumina, densely spaced, grouped mostly within central part of distal surface. Large lumina are of different size and have high muri with sinuous crests; they are separated by finely locular reticulum which also occupies the area close to body equator where reticulate ornamentation becomes a radial one. The radial muri are densely spaced; they pass over the distal side of the zona.

Remarks. — The variability of spores of this species is small; it concerns the number of the distal lumina. The megaspores T. bellus are most similar to those of T. triangulatus having similar ornamentation of distal surface. They differ in having wider zona, more pronounced laesurae and strongly tuberculate proximal surface. T. bellus is also similar to T. regalis (see p. 346).

Occurrence. - Poland: Namurian C-Westphalian B/C.

Triangulatisporites zerndtii sp.n. (pl. XVII, XVIII; text-fig. 1)

1937. Triletes triangulatus Zerndt: pl. 5: 1, 2, 4.

Holotypus: Kr. No. Zonal. II/AP-5; pl. XVII, fig. 5. Stratum typicum: Westphalian A.

Locus typicus: Mine Wesoła, Upper Silesian Coal Basin.

Derivatio nominis: in honour of Jan Zerndt, one of the first investigators of the Carboniferous megaspores.

Diagnosis. — Megaspores of very thick exospore and perispore. Distal surface ornamented by bowl-like structure. Muri high, finely sinuous. Zona very wide, strongly and deeply folded. Perispore of proximal side is blistery-conate.

Material. — About forty well preserved specimens. Dimensions (in microns):

	dry	wet
Diameter of spore	537655	590—770
Diameter of spore body	380 - 500	420-550
Height of laesurae		101-128
Width of zona		102 - 132
Diameter of lumina		
of distal reticulum		100-132

Description. — Megaspores examined in reflected light. Megaspores trilete; amb triangular or subtriangular. Laesurae high, extending to the outer margin of zona. Zona very wide, strongly folded, up to one-third of spore radius. Arcuate ridges usually weak. Proximal surface smooth or tuberculate. Distal surface distinctly reticulate; lumina large, closely spaced. Seven to twelve lumina may be counted along the body diameter.

Megaspores examined in transmitted light and with SEM. Central body (exospore) very thick, of oval or circular amb, with trilete mark. Mesospore with trilete mark, adheres to the inner exospore surface. Exospore is enclosed in perispore which also forms laesurae and zona. Laesurae very high, slightly raised at apex, evenly high along their length outside apex, extending to the outer zona margin. They are strongly sinuous, supported by dense parallel muri. Upper laesura margin finely denticulate (pl. XVII fig. 1). Zona very wide, folded with deep folds, which in transmitted light appear as thick and wide, widely spaced radial ribs (five to six within each interradial region). Zona is infrareticulate. Perispore of proximal side strongly wrinkled, blistery-conate (pl. XVII, fig. 4); this structure is easy to be destroyed and then the proximal surface is almost smooth. Perispore of distal surface reticulate; lumina large, circular or oval, densely spaced over whole body surface. Muri wide and quite high, often double forming distinct, separate bowl-like structures. Muri are regularly sinuous from base to crest. Perispore is relatively thick and closely appressed to exospore.

Remarks. — The position of *T. zerndtii* within the genus *Triangulatisporites* is quite exceptional; these spores possess the thickest perispore and exospore and the widest zona. This is so strongly folded as in no other species of Triangulatisporites. Also the ornamentation of the proximal surface is quite particular.

Occurrence. - Poland: Namurian B-Westphalian A.

Triangulatisporites vermiculatus sp.n. (pl. XIX—XX; text-fig. 1)

Holotypus: Kr. No. Zonal. II/AD-37; pl. XIX, fig. 3.

Stratum typicum: Namurian A.

Locus typicus: Mine Koszelew, Upper Silesian Coal Basin.

Derivatio nominis: because of the vermiculate ornamentation of the proximal surface.

Diagnosis. - Megaspores possessing distal reticulum with distinctly pentagonal lumina and high, narrow muri with sharp crests, which occupies the whole distal spore surface. Proximal side vermiculate.

Material. - More than sixty well preserved specimens.

Dimensions (in microns):

	dry	wet	
Diameter of spore	442-482	660-728	
Diameter of spore body	350412	550-616	
Height of laesurae		46— 51	
Width of zona		60 66	(80—90)
Diameter of lumina			
of distal reticulum		41- 80	
Height of distal muri		10 20	

Description. — Megaspores examined in reflected light. Megaspores trilete; amb rounded-triangular with hardly protruding apices and strongly convex sides. Laesurae low extending to outer margin of zona. Zona of medium width or narrow. Arcuate ridges slightly marked. Proximal surface finely granulate. Distal surface reticulate; lumina pentagonal, closely spaced, muri narrow. Five to nine lumina along the spore diameter.

Megaspores examined in transmitted light and with SEM. Central body (exospore) oval with trilete mark the rays of which are straight, two-third of body radius long. Exospore of medium thickness. Mesospore with trilete mark adheres to inner exospore surface. Its proximal side is thick, distal side thin, homogenous, translucent. Exospore is completely enveloped in perispore which also forms laesurae and zona. Laesurae low, narrow, slightly sinuous, almost evenly high along their length, slightly lower over the zona, extending to the zona outer margin. Zona of medium width or narrow, densely radially striate; outer margin smooth or covered with fine, densely spaced cones. Zona usually widest at apices. Perispore of proximal side microvermiculate, which may be observed only in transmitted light or using the scanning electron microscope. Perispore of distal surface forms reticulum of large, densely spaced lumina. These are pentagonal; muri high, raised at apices, with denticulate or frill-like crests.

Variability. — Two morphological types of megaspores of T. vermiculatus may be distinguished; these differ in shape of distal muri and in width of zona:

Morphological type I. Muri high, closely connected with the neighbouring ones raised at apices in a form of a spine. Slightly smaller "spine" occurs in the middle of each murus.

Morphological type II. Muri narrower and lower than in the morphological type I, with frill-like, slightly sinuous crest (pl. XX, fig. 1, text-fig. 1). Zona wider than in the type II.

Remarks. — Megaspores T. vermiculatus are somewhat similar to those of T. tertius, but they differ in the structure of the proximal perispore which is reticulatetuberculate in T. tertius and vermiculate in T. vermiculatus. Also the distal reticulum, when observed using the SEM is different in these two species.

Occurrence. — Poland: Namurian A-Westphalian A.

Triangulatisporites zonatus (Ibrahim, 1932) Potonié & Kremp 1956 (pl. XXII, XXIII)

- 1932. Sporonites zonatus Ibrahim in Potonié, Ibrahim & Loose: 448, pl. 16:23.
- 1933. Zonales-sporites triangulatus secundus Zerndt; Ibrahim: 30, pl. 3:23.
- 1934. Zonales-sporites zonatus Ibrahim; Loose: 150, pl. 7:31.
- 1938. Triletes triangulatus Zerndt; Schopf: pl. 4:4?
- 1946. Triletes triangulatus Zerndt; Dijkstra: pl. 4:29, 30.
- 1956. Triangulatisporites zonatus (Ibrahim) nov. comb.; Pot. & Kr.: 131, pl. 9: 73-75.

1971. Triangulatisporites zonatus (Ibrahim) Pot. & Kr.; Loboziak: 67, pl. 8:32a, b. 1975. Triangulatisporites zonatus (Ibrahim) Pot. & Kr.; Lachkar: 22, pl. 6: 6-8.

Material. — Approximately one hundred well preserved specimens.

Dimensions (in microns):	dry	wet
Diameter of spore	400-525	660-704
Diameter of spore body	380450	480-600
Height of laesurae		44— 60
Width of zone		55—77
Diameter of lumina		
of proximal reticulum		10— 24
Diameter of lumina		
of distal reticulum		4—12

Description. — Megaspores examined in reflected light. Megaspores trilete; amb triangular or subtriangular. Laesurae low, narrow, more or less sinuous, extending to the outer margin of zona. Zona narrow, smooth or slightly wavy, margin almost smooth. Proximal surface granulate, grana occasionally radially arranged over the zona. Distal surface granulate-tuberculate.



Fig. 3. Triangulatisporites zonatus: megaspore in transmitted light, showing laesurae slightly destroyed.

Megaspores examined in transmitted light and with SEM. Central body (exospore) of circular or subtriangular amb, with trilete mark; triradiate rays straight, half of spore radius. Exospore thick ($24 \mu m$). Thin, homogenous mesospore adheres to the inner exospore surface. Distal mesospore side translucent, proximal one thicker, closely appressed to exospore in the region of trilete mark. Between the triradiate rays the mesospore bears numerous cushions. Outside the triangular proximal part mesospore is thin and slightly wrinkled. Exospore is completely enveloped in perispore which forms also laesurae and zona. Laesurae low and narrow, slightly sinuous, more or less evenly high along their length, extending to the outer zona margin. They are often destroyed over the zona. Zona thin, narrow, smooth or slightly wavy. Margin flat, smooth or almost so. Structure of the zona is infrareticulate. Perispore is microreticulate over the proximal surface; lumina are very small, muri low, narrow and delicate, easy to be destroyed; then the reticulate pattern becomes obliterated. Because the muri are low the reticulum is to be seen only in transmitted light in very well preserved specimens. Perispore of the distal surface does not form a typical reticulum but rather a pseudo-reticulum or reticulate-vermiculate pattern; this is almost the same over the zona. Perispore is relatively thick and of compact structure over the distal body surface while its part forming laesurae and zona is thin and almost devoid of the radial muri (pl. XXII, fig. 1).

Variability. — In the megaspores T. zonatus, the variability concerns mostly the proximal perispore, which may be reticulate or not (with the reticulum obliterated). The zona and the laesurae are in these spores very delicate and can be easily destroyed (text-fig. 3); this is probably the reason why some authors (Potonié & Kremp, 1956) stated that the triradiate rays are in T. zonatus occasionally shorter than the spore body radius; the present study does not corroborate this suggestion.

Remarks. — The megaspores *T. zonatus* are most similar to those of *Triangulatis*porites microreticulatus sp.n., from which they differ in having wider zona without radial muri, less distinct proximal reticulum and thicker exospore and perispore.

Occurrence. — Poland: Westphalian A-C. Germany: Westphalian B. France: Westphalian B-C.

Triangulatisporites microreticulatus sp.n. (pl. XXIV—XXVI)

Holotypus: Kr. No. Zonal. II/AN-15; pl. XXIV, fig. 2.

Stratum typicum: Westphalian B.

Locus typicus: Mine Brzeszcze, Upper Silesian Coal Basin.

Derivatio nominis: because of the microreticulate structure of perispore.

Diagnosis. — Megaspores with microreticulate proximal perispore and microreticulate-vermiculate distal perispore. Laesurae very low, zona very narrow.

Material. - Approximately thirty well preserved specimens.

Dimensions (in microns):	dry	wet
Diameter of spore	475	500—650
Diameter of spore body	412-500	450—594
Height of laesurae		34-42
Width of zone		30— 52
Diameter of lumina		
of proximal reticulum		11— 31
Diameter of lumina		
of distal reticulum		4 11

Description. — Megaspores examined in reflected light. Trilete megaspores; amb triangular or subtriangular with pointed apices. Laesurae very low, extending to the outer margin of zona. Zona weakly developed. Proximal surface granulate, distal surface rough, finely granulate.

Megaspores examined in transmitted light and with SEM. Central body (exospore) circular, with trilete mark; triradiate rays straight, approximately half of body radius. Exospore thick (21 μ m). Mesospore adheres to the inner exospore surface. It is thicker over proximal side, with trilete mark, between the rays of which there

are numerous fine cushions. Distal mesospore side very thin, translucent, homogenous, strongly wrinkled (pl. XXVI fig. 1). Exospore is completely enveloped in perispore which also forms laesurae and zona. Laesurae weakly developed, almost equally high along their length, of reticulate-striate structure. Zona also weak, not typical of the genus, reticulate, hardly protruding from body equator. Proximal perispore reticulate; lumina polygonal and irregular, muri very narrow and low. Close to equator the sculpture is similar , only the lumina are slightly larger and elongated forming a "pseudozona". Distal perispore microreticulate. The microreticulum has several layers (the spongy, felt-like structure), which is best to be observed in slightly damaged specimens possessing irregular secondary foveolae where deeper perispore layers may be seen. Lumina of the distal reticulum are smaller than those of the proximal one.

Remarks. — The megaspores T. microreticulatus sp.n. are most similar to those of T. laevigatus sp.n. from which they differ in having reticulate perispore, which is easy to observe in transmitted light and using the SEM. They also do not possess typical membranous zona and well developed laesurae.

Occurrence. - Poland: Westphalian B-C.

Triangulatisporites laevigatus sp.n. (pl. XXVII, XXVIII)

Holotypus: Kr. No. Zonal. II/AO-215; pl. 28, fig. 3. Stratum typicum: Westphalian B.

Locus typicus: Mine Brzeszcze, Upper Silesian Coal Basin.

Derivatio nominis: because of the almost smooth perispore.

Diagnosis. — Megaspores with almost smooth perispore, very narrow zona and low laesurae.

Material. — About sixty well preserved specimens.

Dimensions (in microns):	drv	wet
Dimensions (in microns):	ary	
Diameter of spore	400—550	594—805
Diameter of spore body	350 - 495	550 - 742
Height of laesurae		30— 51
Width of zona		25 52
Longest diameter of		
abortive spores		100
Shortest diameter of		
abortive spores		86

Description. — Megaspores examined in reflected light. Megaspores trilete; amb circular or subtriangular. Laesurae very low, extending to the outer margin of zona. Zona narrow or very narrow, smooth or delicately radially striate. Distal and proximal surface smooth or granulate.

Megaspores examined in transmitted light and with SEM. Central body (exospore) circular, with trilete mark. Sutures straight, half to two-third of body radius. Mesospore adheres to the inner exospore surface; it is slightly thicker over proximal part, with trilete mark between the rays of which there are numerous cushions. Distal mesospore side thin, homogenous, translucent. Exospore is completely enveloped by perispore which also forms laesurae and zona. Laesurae very low and delicate, equaly wide along their length, slightly sinuous, extending to the outer margin of zona. Zona very narrow, smooth, infrareticulate which may be seen when strongly magnified, occasionally striate; striation often hardly discernible even under high magnification. Perispore of proximal and distal sides is also devoid of any distinct ornamentation. In well preserved specimens under high magnification some roughness of the surface may be seen.

Remarks. — The megaspores T. *laevigatus* sp.n. do not display high variability. The most variable is width of the zona but only within a small range (always very narrow). This width may be 1/10 to 1/8 of spore radius. In spores of this species the zona may be detached from the body as a whole. In connection with normally developed megaspores some minute abortive ones were found (pl. XXVIII, fig. 1b). The megaspores T. laevigatus sp.n. are similar to those of T. membranatus Butterworth and Spinner, 1967, but there is a considerable difference in the time of their occurrence as T. membranatus was described from the Lower Carboniferous and T. laevigatus occurs only in the Westphalian and is more common only in the Westphalian B. Occurrence. -- Poland: Westphalian A-B.

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JADWIGA KARCZEWSKA

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MEGASPORY Z GRUPY ZONALES Z KARBONU POLSKI. CZĘŚĆ II – REWIZJA RODZAJU *TRIANGULATISPORITES*

Streszczenie

W pracy niniejszej opisano 9 gatunków megaspor karbońskich z rodzaju Triangulatisporites, który emendowano. Poszerzono opisy czterech znanych gatunków i opisano pięć nowych. Autorka dysponowała ponad 2 tysiącami okazów bardzo dobrze zachowanych (w tym okazy z oryginalnej kolekcji Jana Zerndta) oraz 117 preparatami megaspor do badań w świetle przechodzącym. Okazy pochodzą z Górnośląskiego Zagłębia Węglowego i Lubelskiego Zagłębia Węglowego. Z kolekcji Zerndta zostały zbadane na nowo okazy opisane i ilustrowane przez tego autora.

Stosowane dotychczas powszechnie metody badań megaspor w świetle odbitym nie pozwalają na dokładne poznanie budowy, zwłaszcza tak małych form jakie występują w rodzaju Triangulatisporites. W pracy niniejszej zastosowano trzy metody badań: w świetle odbitym, przechodzącym i w skanningowym mikroskopie elektronowym. Autorka dowodzi, że mimo podobnego ogólnego planu budowy i podobnych rozmiarów megaspor rodzaj Triangulatisporites charakteryzuje się dużym zróżnicowaniem gatunkowym. Stwierdziła ona w ścianie wszystkich megaspor rodzaju Triangulatisporites występowanie trzech głównych warstw: mesosporium, eksosporium i perisporium. U wszystkich megaspor tego rodzaju występuje dobrze rozwiniete mesosporium z licznymi "cushions"; eksosporium tworzy ciało centralne spor, jest najgrubszą warstwą ściany sporowej i ma budowę ziarnistą; perisporium pokrywa całą powierzchnię ciała centralnego, tworzy również listewki znaku zrostowego i wypustkę równikową. Listewki znaku zrostowego u wszystkich gatunków tego rodzaju przechodzą do zewnętrznego brzegu wypustki równikowej a ich wysokość pozostaje w ścisłej zależności od szerokości wypustki równikowej (im szersza zona tym wyższe listewki znaku zrostowego). Gatunki rodzaju Triangulatisporites charakteryzuje głównie budowa perisporium tj. następujący zespół cech: wysokość i budowa listewek znaku zrostowego, szerokość i budowa wypustki równikowej, oraz ornamentacja cześci dystalnej i proksymalnej; cechy te pojedynczo nie mają znaczenia systematycznego.

Autorka przedstawia swoje poglądy na temat naturalnego pokrewieństwa megaspor z rodzaju *Triangulatisporites*. Stwierdziwszy, że megaspory tego rodzaju mają budowę pośrednią, łączącą cechy wszystkich trzech grup zielnych widłakowych: Selaginellales, Lycopodiales i Isoetales, autorka wnioskuje, że spory te mogły być produkowane przez odrębną grupę zielnych widłakowych, której części wegetatywnych nie znamy; stanowiłaby ona grupę wyjściową dla wszystkich trzech wymienionych rzędów roślin widłakowych.

ЯДВИГА КАРЧЕВСКА

МЕГАСПОРЫ ГРУППЫ ZONALES В КАРБОНЕ ПОЛЬШИ. ЧАСТЬ II— РЕВИЗИЯ РОДА *TRIANGULATISPORITES*

Резюме

В работе представлено описание 9 видов мегаспор карбона из рода Triangulatisporites, который был изменен. Дополнены описания четырех ранее известных видов и описаны пять новых видов. Автор располагал свыше 2 тысячами экземпляров в очень хорошей сохранности и 117 препаратами мегаспор для наблюдений в проходящем свете. Экземпляры были собраны в Верхнесилезском и Люблинском угольных бассейнах. Кроме того, вновь исследовались некоторые экземпляры из оригинальной коллекции Яна Церндта (Верхнесилезский угольный бассейн), описанные и проиллюстрированные этим автором.

Распространенный метод изучения мегаспор в отраженном свете не дает возможности детального исследования строения, особенно таких мелких форм, которые относятся к роду Triangulatisporites. В работе применялись три метода наблюдений — в отраженном свете, в проходящем свете и под электронным сканирующим микроскопом. Автор доказывает, что несмотря на общее сходство строения и размеров, мегаспоры рода Triangulatisporites характеризуются значительным видовым разнообразием. В строении стенки всех мегаспор рода Triangulatisporites участвуют три основных слоя: мезоспорий, экзоспорий и периспорий. Все мегаспоры этого рода отличаются хорошо развитым мезоспорием с многочисленными "cushions", экзоспорий слагает центральное тело спор, является самым толстым слоем стенки и характеризуется зернистым строением, периспорий покрывает всю поверхность центрального тела, образует также лучи щели разверзания и экваториальную оторочку. Лучи щели разверзания у всех видов этого рода переходят до внешнего края экваториальной оторочки и их высота зависит от ширины экваториальной оторочки (чем шире зона, тем выше лучи щели). Виды рода Triangulatisporites, отличаются, главным образом, строением периспория, т.е. следующими чертами: высотой и строением лучей щели разверзания, шириной и строением экваториальной оторочки и орнаментацией не только дистальной, но и проксимальной сторон. Отдельно взятые эти признаки не имеют систематического значения.

Автор излагает свои взгяды относительно естественного родства мегаспор рода *Triangulatisporites* и делает вывод, что мегаспоры этого рода характеризуются промежуточным строением, объединяющим признаки всех трех групп плауновидных: Selaginellales, Lycopodiales и Isoetales. Эти споры, вероятно, относятся к отдельной группе плауновидных, макроостатки которой еще детально не изучены. Она могла являться исходной группой по отношению к всем трем порядкам плауновидных.

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EXPLANATION OF PLATES

Plate VII

Triangulatisporites triangulatus (Zerndt, 1930) Potonié & Kremp, 1954

- Fig. 1. Distal part of perispore illustrating types of reticulum, from scanning electron microscope. Kr. No. Zonal. II/SEM-7/2/; \times 300. Mine Wesoła, Westphalian B.
- Fig. 2. right distal part of perispore showing single large lumina within fine reticulum; left — central body in focus showing mesospore with numerous folds; in transmitted light. Kr. No. Zonal. II/AM-2; ×120. Mine Wesoła, Westphalian B.
- Fig. 3. Distal surface, polar compression, in reflected light. Kr. No. Zonal. II/AN-37; \times 100. Mine Brzeszcze, Namurian C.
- Fig. 4. Distal part of perispore, in transmitted light. Kr. No. Zonal. II/AM-25; \times 175. Mine Brzeszcze, Westphalian B/C.
- Fig. 5. Megaspore in lateral view, in reflected light. Kr. No. Zonal. II/AN-1; \times 100. Mine Brzeszcze, Westphalian B/C.
- Fig. 6. Proximal surface, polar compression, in reflected light. Kr. No. Zonal. II/AN-34; $\times 100$. Mine Brzeszcze, Westphalian B.

Plate VIII

Triangulatisporites triangulatus (Zerndt, 1930) Potonié & Kremp, 1954

- Fig. 1. Distal surface, polar compression from scanning electron microscope. Kr. No. Zonal. II/SEM -7/2/; \times 150. Mine Wesoła, Westphalian B.
- Fig. 2. left part of perispore showing two kinds of distal reticulum; right part of perispore with proximal reticulum and striated zona well visible, in transmitted light. Kr. No. Zonal. JI/AM-23; ×175. Mine Ziemowit, Westphalian C.

Plate IX

Triangulatisporites regalis (Ibrahim, 1932) Potonié & Kremp, 1956

- Fig. 1. Proximal surface, polar compression, in reflected light. Kr. No. Zonal. II/AN-42; \times 100. Mine Chwałowice, Westphalian A.
- Fig. 2. Part of specimen illustrating types of ornamentation on proximal perispore. in transmitted light. Kr. No. Zonal. II/AM-20; \times 175. Mine Chwałowice, Westphalian B.
- Fig. 3. Part of specimen illustrating ornamentation on proximal surface, from scanning electron microscope. Kr. No. Zonal. II/SEM-7(10); × 200. Mine Janina, Westphalian D.
- Fig. 4. Megaspore in median focal plane in transmitted light. Kr. No. Zonal. II/AM-20; \times 50. Mine Chwałowice, Westphalian B.
- Fig. 5. Abortive megaspore in transmitted light. Kr. No. Zonal. II/AM-10; \times 120. Mine Janina, Westphalian D.

Plate X

Triangulatisporites regalis (Ibrahim, 1932) Potonié & Kremp, 1956

Fig. 1. Distal part of perispore with reticulum well visible, in transmitted light... Kr. No. Zonal. II/AM-5; \times 120. Mine Chwałowice, Westphalian A.

- Fig. 2. Distal surface, polar compression, in reflected light. Kr. No. Zonal. II/AN-42; \times 100. Mine Chwałowice, Westphalian A.
- Fig. 3. Part of distal reticulum in transmitted light. Kr. No. Zonal II/AM-11; × 120. Mine Wesoła, Westphalian B.
- Fig. 4. Part of distal perispore with reticulum well visible, from scanning electron microscope. Kr. No. Zonal. II/SEM-7(7); \times 300. Mine Janina, Westphalian D.

Plate XI

Triangulatisporites tertius Potonié & Kremp, 1956

- Fig. 1. a proximal surface; b distal surface, polar compression, in reflected light. Kr. No. Zonal. II/AO-233; × 100. Mine Libiąż, Westphalian D.
- Fig. 2. Part of megaspore with zona well visible, in transmitted light. Kr. No. Zonal. II/AM-8; \times 120. Piast, Westphalian C.
- Fig. 3. a proximal surface; b distal surface, polar compression, in reflected light. Kr. No. Zonal. II/AP-162; \times 100. Piast, Westphalian C.
- Fig. 4. a distal surface, \times 360; b part of distal reticulum; \times 600; from scanning electron microscope. Kr. No. Zonal. II/SEM-1(6). Piast, Westphalian C.

Plate XII

Triangulatisporites tertius Potonié & Kremp, 1956

- Fig. 1. Part of zona in median focal plane, in transmitted light. Kr. No. Zonal.. II/AM-34; × 175. Mine Silesia, Westphalian C.
- Fig. 2. Megaspore with distal surface in focus, in transmitted light. Kr. No. Zonal. II/AM-42; × 120. Libiaż, Westphalian D.
- Fig. 3. a proximal surface, × 100; b part of specimen with laesurae and zona well visible; × 260; c part of specimen illustrating detail of zona, × 480. Kr. No. Zonal. II/SEM-1(3). Libiąż, Westphalian D.

Plate XIII

Triangulatisporites tertius Potonié & Kremp, 1956

Fig. 1. a distal surface, \times 200; b part of distal reticulum, \times 500; from scanning electron microscope. Kr. No. Zonal. II/SEM-1(2). Libiąż, Westphalian D.

Plate XIV

Triangulatisporites bellus sp.n.

- Fig. 1. Proximal part of specimen with zona well visible, in transmitted light. Kr. No. Zonal. II/AM-21; ×175. Mine Wesoła, Westphalian B.
- Fig. 2. a proximal surface, \times 110; b part of specimen illustrating types of ornament on contact face and zona, \times 300; from scanning electron microscope. Kr. No. Zonal. II/SEM-2(4). Mine Ziemowit, Westphalian C.
- Fig. 3. a proximal surface; b distal surface, polar compression, in reflected light. Holotype. Kr. No. Zonal. II/AO-242; \times 100. Mine Kleofas, Namurian C.

Plate XV

Triangulatisporites bellus sp.n.

Namurian C, Mine Kleofas

- Fig. 1. Megaspore with proximal surface in focus, showing tubercles on contact faces and mesospore, in transmitted light. Kr. No. Zonal. II/AM-7; \times 120.
- Fig. 2. a proximal surface, \times 160; b part of specimen showing laesurae and zona, \times 300; from scanning electron microscope. Kr. No. Zonal. II/SEM-1(10).
- Fig. 3. Proximal surface in reflected light. Kr. No. Zonal. II/AO-244; \times 100.

Plate XVI

Triangulatisporites bellus sp.n.

- Fig. 1. a part of specimen showing distal reticulum and zona, \times 300; b distal surface, \times 170; from scanning electron microscope. Kr. No. Zonal. II/SEM-1(11). Mine Kleofas, Namurian C.
- Fig. 2. Distal part of perispore with reticulum well visible, in transmitted light. Kr. No. Zonal. II/AM-22; \times 175. Mine Wesoła, Westphalian B.
- Fig. 3. Mesospore with numerous cushions in median focal plane, in transmitted light. Kr. No. Zonal. II/AM-9; × 120. Mine Brzeszcze, Westphalian B.
- Fig. 4. Distal surface, polar compression, in reflected light. Kr. No. Zonal. II/AO-244; \times 100. Mine Kleofas, Namurian C.

Plate XVII

Triangulatisporites zerndtii sp.n.

- Fig. 1. a proximal surface; b distal surface, polar compression, in reflected light. Holotype. Kr. No. Zonal. II/AP-5; \times 100. Mine Wesoła, Westphalian A.
- Fig. 2. Part of specimen illustrating types of ornament on distal surface, in transmitted light. Kr. No. Zonal. II/AM-24; × 175. Mine Paryż, Namurian B.
- Fig. 3. Megaspore in lateral view, in reflected light. Kr. No. Zonal. II/AP-4; \times 100. Mine Wesoła, Westphalian A.
- Fig. 4. Part of specimen illustrating ornamentation on contact face, in SEM. Kr. No. Zonal. II/SEM-7(6); \times 200. Mine Paryż, Namurian B.
- Fig. 5. Proximal part of perispore with laesurae well visible, from scanning electron microscope. Kr. No. Zonal. II/SEM-7(3); × 300. Mine Paryż, Namurian B.

Plate XVIII

Triangulatisporites zerndtii sp.n.

Namurian B, Mine Paryż

- Fig. 1. Distal part of megaspore illustrating types of reticulum. Kr. No. Zonal. II/SEM-7(9); \times 400.
- Fig. 2. Proximal surface. Kr. No. Zonal. II/SEM-7(5); \times 400.

All figures in SEM

Plate XIX

Triangulatisporites vermiculatus sp.n.

Morphological type I

- Fig. 1. a proximal surface, polar compression, \times 120; b part of specimen illustrating ornamentation on contact face and laesurae, \times 240, in scanning electron microscope. Kr. No. Zonal. II/SEM-1(8). Mine Koszelew, Namurian A.
- Fig. 2. Part of specimen with proximal surface in focus, in transmitted light. Kr. No. Zonal. II/AM-19; × 120. Mine Brzeszcze, Westphalian A.
- Fig. 3. a proximal surface; b distal surface, polar compression, in reflected light. Holotype. Kr. No. Zonal. II/AD-37; \times 100. Mine Koszelew, Namurian A.

Plate XX

Triangulatisporites vermiculatus sp.n.

- Fig. 1. Fragment of distal reticulum with muri well visible, in scanning electron microscope. Morphological type II. Kr. No. Zonal. II/SEM-1(9); \times 720. Mine Koszelew, Namurian A.
- Fig. 2. Part of specimen with distal surface in focus, in transmitted light. Kr. No. Zonal. II/AM-17; \times 120. Mine Brzeszcze, Westphalian A.
- Fig. 3. a distal surface, polar compression, \times 120; b part of distal reticulum, \times 300, in scanning electron microscope. Kr. No. Zonal. II/SEM-1(7). Mine Koszelew, Namurian A.

Figs 2, 3 — morphological type I

Plate XXI

Triangulatisporites vermiculatus sp.n.

Namurian A, Mine Koszelew; morphological type II

Fig. 1. a megaspore in lateral view, \times 200; b part of specimen illustrating distal ornamentation, \times 360, in scanning electron microscope. Kr. No. Zonal. II/SEM-1(9).

Plate XXII

Triangulatisporites zonatus (Ibrahim, 1932) Potonié & Kremp, 1956

- Fig. 1. Part of specimen illustrating distal ornamentation, in scanning electron miccroscope. Kr. No. Zonal. II/SEM-7(13); \times 300. Mine Ziemowit, Westphalian C.
- Fig. 2. Part of perispore showing distal ornamentation, in transmitted light. Kr. No. Zonal. II/AM-15; × 120. Mine Silesia, Westphalian B.
- Fig. 3. a proximal surface; b distal surface, polar compression, in reflected light. Kr. No. Zonal. II/AN-3; × 100. Mine Brzeszcze, Westphalian B/C.

Plate XXIII

Triangulatisporites zonatus (Ibrahim, 1932) Potonié & Kremp, 1956 Fig. 1. a perispore without exospore inside; b exospore in proximal focus, in transmitted light. Kr. No. Zonal. II/AM-1; × 175. Mine Ziemowit, Westphalian C. Fig. 2. a proximal surface, polar compression; \times 95; b part of specimen showing proximal ornamentation of zona, \times 360; in scanning electron microscope. Kr. No. Zonal. II/SEM-2(9), Mine Wesoła, Westphalian A.

Plate XXIV

Triangulatisporites microreticulatus sp.n.

- Fig. 1. Proximal surface, polar compression, in scanning electron microscope. Kr. No. Zonal. II/SEM-5(5); × 210. Mine Wesoła, Westphalian B.
- Fig. 2. a proximal surface; b distal surface, polar compression, in reflected light. Holotype. Kr. No. Zonal. II/AN-15; × 100. Mine Brzeszcze, Westphalian B.

Plate XXV

Triangulatisporites microreticulatus sp.n.

- Fig. 1. Megaspore with proximal reticulum well visible, in transmitted light. Kr. No. Zonal. II/AM-27; \times 175. Mine Ziemowit, Westphalian C.
- Fig. 2. Proximal surface of mature specimen with adhering abortive megaspore, in reflected light. Kr. No. Zonal. II/AD-38; ×100. Mine Ziemowit, Westphalian C.
- Fig. 3. a part of perispore illustrating proximal reticulum and laesurae; b abortive megaspore, in transmitted light. Kr. No. Zonal. II/AM-6; \times 120. Mine Ziemowit, Westphalian C.
- Fig. 4. Distal part of perispore, in transmitted light. Kr. No. Zonal. II/AM-26; \times 175. Mine Ziemowit, Westphalian C.
- Fig. 5. Fragment of the distal part of perispore, in scanning electron microscope. Kr. No. Zonal. II/SEM-5(6); \times 210. Mine Wesoła, Westphalian B.
- Fig. 6. Part of specimen illustrating reticulum on proximal surface, in scanning electron microscope. Kr. No. Zonal. II/SEM-5(5); × 500. Mine Wesoła, Westphalian B.

Plate XXVI

Triangulatisporites microreticulatus sp.n. Mine Ziemowit, Westphalian C.

- Fig. 1. Distal part of mesospore, in transmitted light. Kr. No. Zonal. II/AM-6; imes120.
- Fig. 2. Distal surface, polar compression, in reflected light. Kr. No. Zonal. II/AP-6; \times 100.
- Fig. 3. Megaspore in lateral view, in scanning electron microscope. Kr. No. Zonal. II/SEM-01; \times 300.

Plate XXVII

Triangulatisporites laevigatus sp.n.

- Fig. 1. Proximal surface, polar compression, in scanning electron microscope. Kr. No. Zonal. II/SEM-5(3); × 210. Mine Silesia, Westphalian B.
- Fig. 2. Fragment of distal part of megaspore, in scanning electron microscope. Kr. No. Zonal. II/SEM-5(2); \times 500. Mine Silesia, Westphalian A.

- Fig. 3. Proximal surface, polar compression, in reflected light. Kr. No. Zonal. II/AN-21; × 100. Mine Brzeszcze, Westphalian B.
- Fig. 4. Part of specimen with laesurae well visible, in scanning electron microscope. Kr. No. Zonal. II/SEM-1(13); \times 360. Mine Silesia, Westphalian A.

Plate XXVIII

Triangulatisporites laevigatus sp.n.

- Fig. 1. a fertile megaspore; b abortive megaspore, in transmitted light. Kr. No. Zonal. II/AM-16; × 120. Mine Brzeszcze, Westphalian B.
- Fig. 2. a part of megaspore in median focal plane showing mesospore and zona, \times 120; b fragment of zona, \times 175, in transmitted light. Kr. No. Zonal. II/AM-3. Mine Silesia, Westphalian B.
- Fig. 3. a proximal surface; b distal surface, polar compression, in reflected light. Holotype. Kr. No. Zonal. II/AO-215, \times 100. Mine Brzeszcze, Westphalian B.

















































