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EARLIEST TRIASSIC (INDUAN) MEGASPORES FROM MOSCOW SYNECLISE, RUSSIA: TAXONOMY AND STRATIGRAPHY

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Abstract: This study describes the megaspore assemblages from the Ryabinsk Member of the Vokhma Formation of the Moscow Syneclise. The genus *Otynisporites* is emended, three new species, *Maexisporites meditectatus*, *M. rugulaeferus* and *Otynisporites maculosus*, are erected, and one new combination, *Maexisporites grosstriletus*, is proposed. Megaspore descriptions relate the gross morphology and fine structure of the exine surface of thirteen taxa. From the appearance of the exine surface and ornamentation processes, it appears that some forms currently included in certain genera according to their morphological features do not belong to them. The assemblage from Sholga is evidently of low diversity at the generic level, possibly reflecting the end-Permian biotic crisis. The composition of the megaspore assemblages indicates their Induan age.

Key words: megaspores, taxonomy, palynostratigraphy, Triassic, Induan, Russia.

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INTRODUCTION

Megaspores described in this paper have been recovered from the lowermost Triassic sediments of the Moscow Syneclise in Russia, specifically at the Sholga locality on the Yug River (Fig. 1). The stratigraphic position of these sediments is regarded by Lozovsky (1998) and Yaroshenko and Lozovsky (2004) as lower Induan. The first information on megaspores of the Permian–Triassic transition deposits of that region was obtained from the Nedubrovo Member of the Vokhma Formation at the Nedubrovo locality, whence *Otynisporites eotriassicus* Fuglewicz was identified (Krassilov *et al.*, 1999b).

Triassic megaspores attracted interest for almost a century and the literature on this subject is extensive, however, that concerning Induan assemblages from the northern hemisphere is still limited. The stratigraphic importance of megaspores of the Permian–Triassic boundary interval is well recognized because the index species of the Otynisporites eotriassicus Zone – *O. eotriassicus* – has a very wide geographical distribution; it has been recorded from northwestern China, through Europe. The first appearance of that species is dated by direct conodont data (Kozur, 1998).

In spite of the high correlation potential of the *O. eotriassicus* Biozone, detailed information on the composition of its megaspore assemblages is almost lacking, being limited to the data from Poland (Fuglewicz, 1977, 1980a, b; Marcinkiewicz, 1992a; Marcinkiewicz *et al.*, 2014). In this context, the present authors provide details on the assemblage of that biozone from the Moscow Syneclise in the hope that the data provided will be useful for the correlation of continental deposits of the lowermost Triassic. These data are also important for an understanding of the taxonomic diversity of spore-bearing plants during the recovery of vegetation after the end-Permian crisis.

The identification of genera and species of most fossil megaspores depends largely on gross morphological features because the taxonomy dates from the time when observations of fine megaspore features at high power were not obtainable. As noted by Batten (2012), data on exine ultrastructure are useful in showing that in some cases, species similar to each other in gross morphology have differing walls and should not be included in the same morphological genus. The authors consider that the precise data on the ultrastructure of exine surface and the appearance of ornamentation processes provided herein may also be useful, and, in the future, may help in construction of a more meaningful taxonomic system.

Fig. 1. Map of study area showing locations of the section studied and those mentioned in the text (asterisks).

REGIONAL SETTING

The continental Lower Triassic deposits of the Moscow Syneclise occur in its axial zone and on its northwestern slope. It has long been considered that the Permian–Triassic boundary was unconformable over most of the basin (Strok *et al.*, 1984). The hiatus was supposed to encompass the entire Changsingian Stage (Lozovsky and Essaulova, 1998). However, in the Vologda Region, a relatively complete transitional Permian–Triassic (Vyatkian–Vetlugian) sequence was discovered (Krassilov *et al.*, 1999b). The lithostratigraphic division of these deposits is that of Strok *et al.* (1984). They are included in the Vokhma Formation that comprises (in ascending order) the Nedubrovo, Astashinsk, and Ryabinsk members. On the basis of biostratigraphic and magnetostratigraphic criteria, the two lower members are considered to belong to the Permian, while the Ryabinsk Member represents the conchostracan Falsisca verchojanica Zone of the Germanic Basin that corresponds, by indirect correlation, to the conodont Hindeodus parvus Zone in marine sections of South China (Kozur and Weems, 2011; Lozovsky, 1998, 2013). The stratigraphic position of the latter strata of the Sholga locality is regarded by Yaroshenko as lower Induan based on the Densoisporites complicatus-Ephedripites sp. palynological assemblage (Yaroshenko and Lozovsky, 2004).

MATERIAL AND METHODS

Palynological samples were collected from a natural exposure on the left bank of the Yug River, 200 m upstream from the ferry pier of the village of Sholga (Kirov Region, Podosinovskii District; Fig. 1; GPS coordinates: N60°25' 54.65", E47°00'47.48"). The samples were kindly provided by M. A. Aref'ev. The exposed strata, less than 2 m thick, are marly limestone containing various microfossils. Algal remains identified as *Reduviasporonites chalastus* (= *Tympanicysta stoschiana* Balme) and the supposed zygnematalean zygospore *Maculatasporites* Tiwari were recognized among the palynomorphs (Krassilov *et al.*, 1999a; Afonin *et al.*, 2001; Foster *et al.*, 2002). Miospores were also studied (Yaroshenko and Lozovsky, 2004, see the following Section). In 2011, an expedition from the Arthropod Laboratory of the Paleontological Institute to the Sholga locality found some plant debris, conchostracans and insects. The insect association from Sholga corresponds to the Vokhma Insect Assemblage, and also includes elements of the entomofauna from the Entala and Nedubrovo localities (Vologda Region; Aristov *et al.*, 2013).

Megaspores were isolated from the rock by disintegration in water, followed by treatment with HCL, and finally by HF for the silica component. Megaspores were picked from a Petrie dish by needle and mounted on stubs for scanning electron microscopy, Tescan or CamScan. The megaspore collection is deposited in the Paleontological Institute, Russian Academy of Sciences, no PIN 5529.

PALYNOSTRATIGRAPHY

The megaspore assemblage from Sholga lacks representatives of *Dijkstraisporites* and *Narkisporites* recorded from the Middle Triassic of Europe (Rainhardt, 1963: Kozur, 1971; Kozur and Movshovich, 1976; Marcinkiewicz, 1992a; Marcinkiewicz *et al.*, 2014). Also absent are megaspores *Hughesisporites variabilis* Dettman described from the Upper Triassic of Tasmania and Australia (Dettman, 1961). This species first appears in the basal strata of the assemblage biozone Pusulosporites populosus Zone of Fuglewicz (1980b) and the assemblage biozone Trileites polonicus Zone of Marcinkiewicz (1992a) that are considered to belong to the Olenekian (Marcinkiewicz *et al.*, 2014). This species (determined as *H.* cf. *variabilis*) is also known from the Lower Triassic of Romania (Antonescu and Tougardeau-Lantz, 1973). Our assemblages lack also the representatives of the distinctive genus *Pusulosporites* (or *Talchirella*). In Poland, the first appearance of *P. populosus* Fuglewicz and *P. inflatus* Fuglewicz is the same as that of *H. variabilis* (Fuglewicz, 1980b, Marcinkiewicz *et al.*, 2014). In the late Olenekian assemblages, representatives of *Pusulosporites* occur in abundance (Fuglewicz, 1980b; Marcinkiewicz *et al.*, 2014). *Pusulosporites* is a common Lower Triassic genus recorded also from Romania (Antonescu and Taugourdeau-Lantz, 1973, Russia (Kozur and Movshovich, 1976), and India (Maheshvari and Banerji, 1975; Pal *et al.*, 1997) where it occurs in abundance (Pal *et al.*, 1997). It follows that the Sholga assemblage is older than the Olenekian.

On the basis of its taxonomic composition, our assemblage is assignable to the Otynisporites eotriassicus Zone distinguished by Fuglewicz (1980b), and Marcinkiewicz (1992a) in the subsurface deposits of the lower Buntsandstein (the Baltic Formation) in Poland. Our assignment is primarily based on the presence of *Otynisporites tuberculatus* Fuglewicz that is one of the characteristic species of the biozone. The presence of *O.* cf. *eotriassicus* confirms this assignment. Less significant is the presence of *Trileites* because the taxon is indistinctive. But at least some specimens of *Trileites* sp. Group I may represent *T. vulgaris* Fuglewicz (the first appearance in that biozone). *Hughesisporites* sp. 1 is similar to *H. simplex* Fuglewicz 1973, the species also occurring in that biozone. The succession of megaspore assemblages within the O. eotriassicus Zone is known only from the completely cored Otyń IG-1 borehole. In that borehole, the lower assemblage, recovered from the Sub-oolitic Beds, includes *O. eotriassicus* and *O. tuberculatus* (Fuglewicz, 1977, 1980a, b). The Sub-oolitic Beds of the Gorzów Wielkopolski IG-1 borehole yielded *Triangulatisporites reticulatus* Fuglewicz. The assemblages from the overlying Lower Oolitic Beds are more diversified; they include, in addition to the two *Otynisporites* species, *Echitriletes fragilispinus* Fuglewicz, *Hughesisporites simplex* Fuglewicz, *Maexisporites ooliticus* Fuglewicz, *Pusulosporites permotriassicus* Fuglewicz, and *Trileites vulgaris* Fuglewicz. Of these taxa, only single specimens of *H. simplex* and *E. fragilispinus* were found; more common are the other three taxa mentioned. It is worth noting that the highest assemblages from the Lower Oolitic Beds of the Otyń IG-1 borehole include only three species, i.e., *O. tuberculatus*, *M. ooliticus* and *T. vulgaris*. It is conceivable that these assemblages are similar in stratigraphic position to those from the Sholga locality.

The lower and the upper boundaries of the Otynisporites eotriassicus Zone in Poland, as defined by Fuglewicz (1980b), are not known because there is a barren interval below the zone in all sections, and a barren interval more than 200 m thick above its upper limit. Marcinkiewicz (1992a) and Marcinkiewicz *et al.* (2014) redefined that biozone, placing its lower boundary at the first appearance of *O. eotriassicus*. The latter distinctive species has been recognized in uppermost Permian and Induan strata of various areas of the northern hemisphere. In Jameson Land, East Greenland, it occurs in the Oksedal Member of the Schuchert Dal Formation (Looy *et al.*, 2005). That formation belongs to the Permian as the first appearance of *Hindeodus parvus* has been recorded from the overlying Wordie Creek Formation (Twitchett *et al.*, 2001). *O. eotriassicus* has been also recorded from the latest Permian Tesero Oolite of the southern Alps (Kozur, 1998), and the latest Permian Nedubrovo Member of the Moscow Basin (Krassilov *et al.*, 1999b; Lozovsky *et al.*, 2001; Krassilov and Karasev, 2008, 2009; Kozur and Weems, 2011). *O. eotriassicus* has been also recorded from the Changhsingian of the Junggar Basin, northwestern China (Ouyang and Norris, 1999; Metcalfe *et al.*, 2009; Kozur and Weems, 2011). It should be noted that the records of the distinctive, easily recognizable species *O. eotriassicus* are not provided with a description of the accompanying assemblage, the only exception being in Poland (Fuglewicz, 1977, 1978, 1980a, b; Marcinkiewicz, 1992a; Marcinkiewicz *et al.*, 2014).

Fuglewicz (1980b) placed the lower Buntsandstein (the Baltic Formation) and the O. eotriassicus Zone in the uppermost Permian, in agreement with Visscher (1971) on the basis of palynological studies. The debate on the stratigraphic position of the lower Buntsandstein in Poland has a long history (see Marcinkiewicz *et al.*, 2014). Magnetostratigraphic data (Nawrocki, 1997, 2004) indicated that the base of the Baltic Formation occurs close to the base of the Griesbachian (basal Induan). In several boreholes, the megaspore assemblages of the biozone under discussion are associated with miospores indicative of the Lundbladispora obsoleta–Protohaploxypinus pantii Zone (Orłowska-Zwolińska, 1984). Thus, the O. eotriassicus Zone in Poland is considered to be of Induan age (Marcinkiewicz *et al.*, 2014).

The megaspore assemblages of Sholga that are similar in composition to those from a higher part of the *O. eotriassicus* Zone in Poland are of the Induan age. This conclusion is consistent with the earlier miospore data from Sholga and other Lower Triassic localities of the Moscow Syneclise where Yaroshenko (in Yaroshenko and Lozovsky, 2004) distinguished four palyno-complexes. The upper part of the Astashinsk Member and the Ryabinsk Member were included in the Densoisporites complicatus-Ephedripites sp. palyno-complex characterized by the mass occurrence of *Densoisporites complicatus* Balme and other species of that genus, and by an abundance of *Ephedripites* (among others *E. steevesi* (Jansonius) de Jersey et Hamilton) and *Protohaploxypinus* spp. The species *Kraeuselisporites septatus* Balme, *Lundbladispora wilmotti* Balme, *L. brevicaula* Balme, and *L. obsoleta* Balme appear in this complex for the first time. On the basis of the composition of the assemblages, the Densoisporites complicatus-Ephedripites sp. palyno-complex has been correlated by Yaroshenko and Lozovsky (2004) with the Lundbladispora obsoleta–Protohaploxypinus pantii Zone of Orłowska-Zwolińska (1984).

PALAEONTOLOGICAL DESCRIPTIONS

This section includes descriptions of almost all taxa and morpho-groups encountered, even those represented by a few specimens or only one specimen. This is because there is a paucity of data on the Induan megaspores and still insufficient data on fine features of megaspore surfaces. The authors have used the traditional, morphological genera, but also have indicated the existence of some close similarities between morphologically differing taxa that share some features of the exine surface and occasionally in cross-section, as viewed at high power under the SEM (see Remarks for *Bacutriletes*, *Hughesisporites* sp. 1, and *Verrutriletes*).

Genus *Bacutriletes* (van der Hammen) Potonié, 1956

Type species: *Bacutriletes* (*Selaginellites*) *greenlandicus* (Miner) Potonié, 1956.

Bacutriletes sp.
Fig. 2A–D

Material: One specimen.
Description: Specimen rounded-triangular in equatorial outline, 295 μm in diameter. Trilete mark faint, laesurae 0.6 of radius in length, in the form of ridges in the apical part, diminishing in

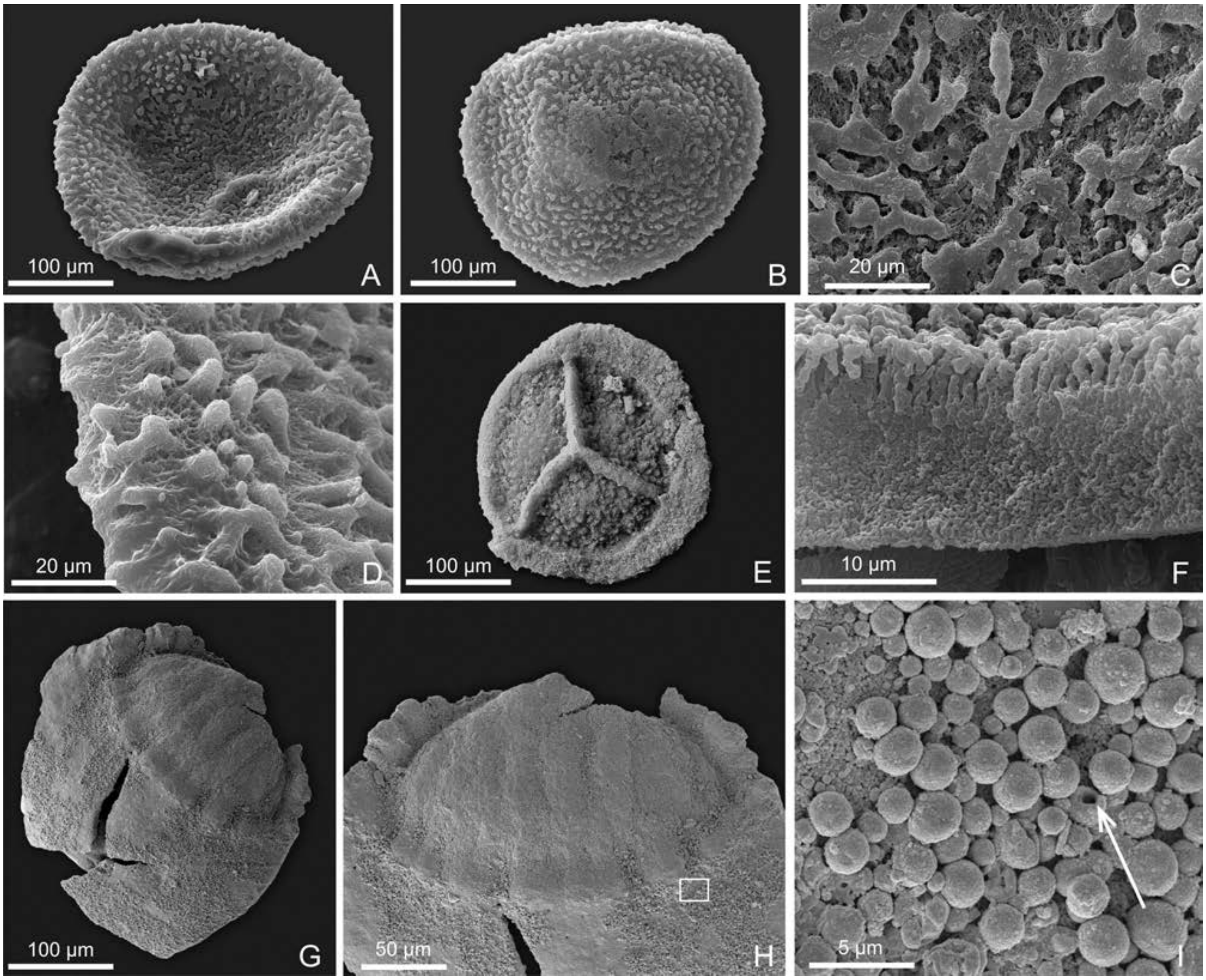

Fig. 2. Induan megaspores from Sholga locality. **A–D.** *Bacutriletes* sp., specimen PIN 5529/123: A, B – proximal and distal view, C – detail of proximal wall in apical area showing rugulate exine surface, D – detail of proximal wall showing baculate ornamentation. **E, F.** *Hughesisporites* sp. 1, specimen PIN 5529/14: E – proximal view, F – fragment of broken (distal or proximal) wall showing three-layered exoexine. **G–I.** *Hughesisporites* sp. 2, specimen PIN 5529/64: G – fragment of laterally flattened megaspore, H – radially folded or grooved contact face delimited by arcuate ridge, I – detail of wall covered by densely set, hollow (arrow) sphaerules.

height and width toward the equator where they become obscured by ornamentation (Fig. 2A). Contact area not delimited. In the apical area exine covered by rugules and granules 2–4 µm wide; exine surface between these elements, viewed at high power under SEM, is a fine mesh with muri about 0.25 µm wide (Fig. 2C). Remainder of exine is ornamented with bacula about 2.5 µm wide at the base and 7–9 µm long. The bacula consist of an apical head or knot of uneven surface, dense and pitted, and the basal part that is widest at the base, and is microreticulate with elements that have a slight alignment perpendicular to spore surface (Fig. 2D). The bacula are 2.5 to 4 µm apart, positioned on a micro-reticulate surface.
Remarks: We have included our specimen in *Bacutriletes* as the ornamentation processes are mostly bacula. But when viewed at high power under SEM, the bacula in our specimen differ from those in other *Bacutriletes* (when illustrated). The bacula of the Cretaceous species *Bacutriletes* sp. A. (in Taylor and Taylor, 1988, pl. 5, fig. 6), *B. nanus* (Dijkstra) Potonié (in Batten, 1988, pl. 6, figs 7, 8), *B. ferulus* Koppelhus and Batten (Koppelhus and Batten, 1989, p. 102, pl. 4, fig. 9), and *B. majorinus* Koppelhus and Batten (Koppelhus and Batten, 1989, 102, 104, pl. 5, fig. 2) do not consist of two distinct parts and their surface is an open reticulate meshwork. On the other hand, our specimen has some resemblance to megaspores included in *Maexisporites* – the bacula of the specimen of Sholga resemble those of *Maexisporites hammaephorus* Schulz et Knoll (in Koppelhus and Batten, 1989, pl. 2, fig. 7), and in *M. grosstriletes* (see Fig. 2F). With its faint tetrad mark and lack of curvaturae, this form differs from other Triassic representatives of *Bacutriletes*.

Genus *Hughesisporites* Potonié, 1956

Type species: *Hughesisporites* (*Triletes*) *galericulatus* (Dijkstra) Potonié.

Hughesisporites sp. 1
Fig. 2E, F

Material: One specimen.
Description: Trilete megaspore, rounded-triangular in equatorial outline, 225 µm in diameter. Laesurae straight, in the form of rounded ridges that are higher than wide, about 0.8 radius long. Contact area distinctly depressed, defined by differential orna-

mentation, bearing densely set, conate and verrucate elements about 10 µm in basal diameter. Beyond contact area, exine is corroded, appearing rough. When viewed at high power under SEM, exine surface is granular and pitted. Broken wall of the distal hemisphere shows that the exoexine is three layered (Fig. 2F). The outer layer represents a loose network of vertically arranged, about 4 µm long, perforated elements about 1 µm wide. The middle layer is about 5 µm in thickness, constructed of densely packed elements that are circular in cross-section, and 0.25 µm in diameter. The lower layer about 5.5 µm thick, is not distinctly delimited from the overlying one. It represents a network of rods that are less densely packed than the elements of the middle layer. The vertical elements of the outer exine layer form a surface covered by closely spaced, irregular elements of granular and pitted appearance (Fig. 2F, top).
Remarks: *Hughesisporites simplex* Fuglewicz (Fuglewicz, 1977, p. 423, pl. 40, fig. 4) from the Induan of Poland has the same type of sculpture on contact faces, but is finer. The exine ultrastructure of the broken wall of our specimen recalls that in *Maexisporites pyramidalis* Fuglewicz, 1973 (see Fig. 4L)

Hughesisporites sp. 2
Fig. 2G–I

Material: One specimen.
Description: Only one fragment of the obliquely flattened megaspore has been found. Its equatorial diameter may be estimated as 300 µm. The fragment represents part of the shallowly, radially folded contact face delimited by a distinct arcuate ridge; parts of 30 µm high triradiate ridges with crenulate crest are also present (Fig. 2H). Exine surface appears smooth; when observed at high power under SEM it is very compact and granular, with granules less than 0.25 µm in diameter. It is covered by patches of densely set sphaerules 2.5–4 µm in diameter, hollow inside (Fig. 2I, arrow).
Remarks: The specimen is too poorly preserved to enable specific determination. Similarly grooved contact faces occur in the Lower Triassic megaspores *Hughesisporites inflatus* Fuglewicz (Fuglewicz, 1973, p. 441–442, pl. 30, figs 1, 2) and *H. tumulosus* Marcinkiewicz (Marcinkiewicz, 1976, p. 197, pl. 29, fig. 7). The exine surface in the specimen 5529/64 is quite different from that in the specimen 5529/14.

The sphaerules on the exine surface resemble, in size and shape, the ornament of *Cabochonicus carbunculus* (Dijkstra) Batten and Ferguson (1987) and *Pusulosporites peromtriassicus* Fuglewicz (1977). Marcinkiewicz (1979, 1980) considered the sphaerules occurring in *C. carbunculus* as manifestation of fungal attack. Cantrill and Drinnan (1994) discussed the nature of these structures in *Cabochonicus*, and showed, using TEM section, that the sphaerules were composed of sporopollenin and were continuous with the outermost sporoderm layer, so they were not fungal. However, the patchy occurrence of our sphaerules and their hollowness indicates that they do not represent processes of ornamentation. Streaks of similar sphaerules occur also in some other specimens in our material.

Genus *Maexisporites* Potonié, 1956

Type species: *Maexisporites* (*Triletes*) *soldanellus* (Dijkstra) Potonié, 1956.

Maexisporites grosstriletus (Liu, Zhu and Ouyang, 2011) comb. nov.
Fig. 3A–H

*2011 *Biharisporites grosstriletus* sp. nov. – Liu, Zhu and Ouyang, p. 144, pl. IV, figs 1–9.

Material: Five specimens.
Description: Trilete megaspores, subcircular or subtriangular in equatorial outline, 175(274)363 µm in equatorial diameter (five specimens). Laesurae about 0.7 of spore radius long or almost reaching the equator, straight or slightly sinuous, in the form of apically rounded ridges about 15 µm wide near the apex, diminishing in height toward the equator. In their equatorial part, the ridges may be almost completely obscured by sculpture (Fig. 3B, D). Contact area not delimited or distinguished by a band of finer and more crowded sculpture surrounding it in the distal-equatorial region (Fig. 3D, arrow). Exine sculptured by densely set globular elements, discrete or fused into rows to form rugulae, averaging 5 µm in width but varying between 3–10 µm. These elements are discrete, but close to the apex (Fig. 3B) are crowded. The globules are uneven and pitted, elevated over the spore surface by the muri of surface micromesh. The muri are rods or wider, pitted elements (Fig. 3G, H).
Remarks: Our specimens conform to the general morphology and sculpture of *Biharisporites grosstriletus* from the Middle Permian of Chanxi, North China, but the fine, globular and rugulate (not spinose) sculpture suggests correct inclusion within *Maexisporites*. Liu *et al.* (2011) considered the sculpture of their species as not typical of *Biharisporites*.

Maexisporites mediornatus sp. nov.
Fig. 4A–F

Holotype: Specimen PIN 5529/88 (Fig. 4A, B).
Derivation of name: Medius (Lat.) = occurring in the middle; ornatus (Lat.) = ornamented.
Type locality: Sholga on the Yug River, Moscow Basin, Russia.
Type level: Vokhma Formation, Ryabinsk Member, Induan.
Deposition of type: A.A. Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Profsoyuznaya 123, Russia.
Material: Nine specimens.
Diagnosis: A species of *Maexisporites* with prominent laesurae almost reaching the equator, coarsely-sculptured over the central part of the proximal hemisphere, with finer sculpture outside that area. Polar axis longer than the equatorial diameter.
Description: Trilete megaspores usually preserved in polar or oblique compression, circular in equatorial outline. The equatorial diameter may not be precisely established because our specimens are often folded; it can be estimated as 175 (233) 294 µm (8 specimens); the polar axis is about 5–16% longer than the equatorial diameter. Proximal hemisphere low pyramidal, distal hemisphere rounded (Fig. 4C). Laesurae straight, in the shape of ridges that may become wider or narrower toward the equator, extending almost to equator. Contact area not delimited, may appear slightly swollen. Central part of the proximal hemisphere bears closely spaced elements of irregular shape about 5 µm in diameter (Fig. 4B). Viewed at high power under SEM, these elements have an uneven, perforated surface (Fig. 4F). The remainder of exine is rugulate, the rugulae are closely spaced and fine, about 1–2 µm wide.
Remarks: *Maexisporites* sp. cf. *M. pusillus* Li and Batten (in Lupia, 2011, p. 15–16, fig. 13/1–3), from the Santonian of USA, differs from our species in having a smooth distal hemisphere. The Cretaceous species *M. pusillus* Li and Batten (in Li *et al.*, 1987, p. 122, pl. 1, figs 2, 5), and Ladinian *M. meditectatus* (Reinhardt) Kozur (in Marcinkiewicz *et al.*, 2014, pl. 2, fig. 11) are much larger.

Maexisporites pyramidalis Fuglewicz, 1973
Fig. 4G–L

*1973 *Maexisporites pyramidalis* sp. nov. – Fuglewicz, p. 422–423, pl. XXI, 2, 3; pl. XXI, 6.

Material: Eighteen specimens.

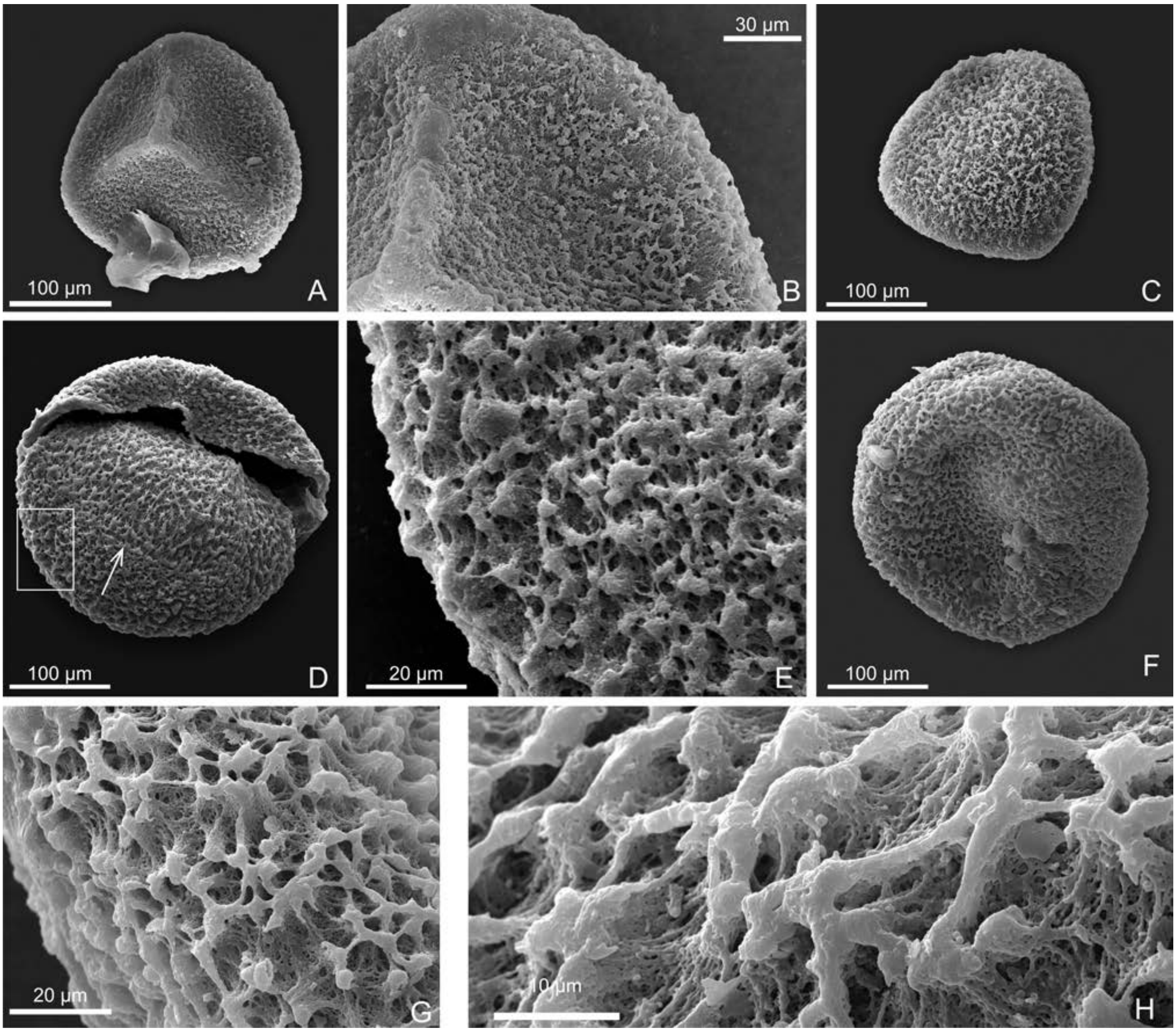

Fig. 3. Induan megaspores from Sholga locality. **A–H.** *Maexisporites grosstriletus* (Liu, Zhu and Ouyang) comb. nov.; A–C – specimen PIN 5529/17: A, C – proximal and distal view, B – detail of proximal hemisphere showing sculpture; D, E – specimen PIN 5529/18: D – equatorial view; note the denser sculpture at the equatorial area (arrow), and the tetrad mark almost completely obliterated by sculpture, E – detail of distal wall showing sculpture of globular elements; F–H – specimen PIN 5529/125: F – distal? view. G, H – details of wall showing sculpture.

Description: Trilete megaspores, subtriangular in equatorial outline, 136 (189) 210 µm (10 specimens) in equatorial diameter. Contact faces usually swollen in the central part and sunken at extremities. Laesurae straight or slightly sinuous, in the shape of rounded ridges about 20 µm wide, may become wider equatorially, extending almost to equator. At low magnification, exine appears granulate, and rugulate when viewed at high power under SEM. The rugulae are short, very densely set, 3–5 µm wide proximally, finer distally, appearing as clusters of fine granules less than 0.5 µm in diameter. The distal hemisphere may be folded into broad ridges and low, verruca-like protuberances (Fig. 4H, I). The gaping laesura of specimen PIN 5529/13 shows that the surface elements are vertical columns, perforated, 7 µm high, and the deeper part of exoexine is 9 µm thick; it comprises very dense network of elements, circular in cross-section, about 0.25 µm in diameter (Fig. 4L).
Remarks: Our specimens are slightly smaller than those described by Fuglewicz (1973, p. 422–423, pl. 21, figs. 2a, 2b; pl. 31, fig. 6).

Stratigraphical distribution: Olenekian, Poland (Fuglewicz, 1980b), Induan, Russia (present paper).

Maexisporites rugulaeferus sp. nov.
Fig. 5A–M

Holotype: PIN 5529/113 (Fig. 5A–D).
Derivation of name: Ruga (Lat.) = wrinkle; fero (Lat.) = bear.
Type locality: Sholga on the Yug River, Moscow Basin, Russia.
Type level: Vokhma Formation, Ryabinsk Member, Induan.
Deposition of type: A.A. Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Profsoyuznaya 123, Russia.
Material: twenty-five specimens.
Diagnosis: Megaspores ornamented by rugulate elements that are either discrete or interconnected to form an imperfect micro-reticulum. The sculpture is distinctly coarser over the proximal face.
Description: Trilete megaspores, subcircular in equatorial outline, 180 (256) 336 µm in diameter (10 specimens). Laesurae straight or

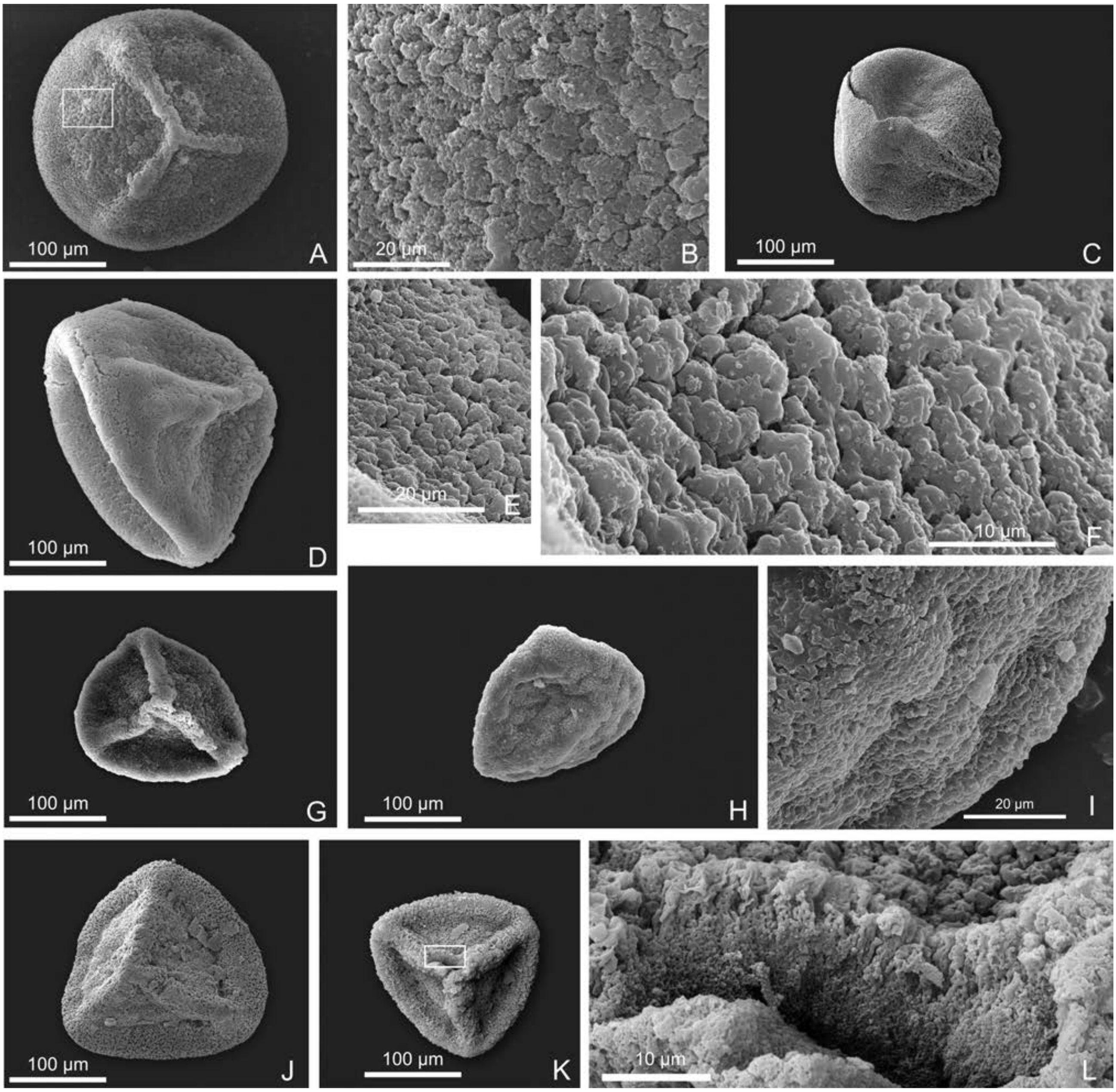

Fig. 4. Induan megaspores from Sholga locality. **A–F.** *Maexisporites mediornatus* sp. nov.; A, B – holotype, specimen PIN 5529/88: A – proximal view, B – sculpture of contact faces; C – specimen PIN 5529/57, laterally flattened megaspore; D – specimen PIN 5529/103, equatorial view; E, F – specimen PIN 5529/110, details of sculpture of contact faces. **G–L.** *Maexisporites pyramidalis* Fuglewicz 1973; G–I – specimen PIN 5529/15: G–H – proximal and distal view, I – distal hemisphere folded into broad ridges and low circular protuberances; J – specimen PIN 5529/81, proximal view; K, L – specimen PIN 5529/13: K – proximal view, L – fragment of open laesura showing ultra-structure of wall.

sinuous with low, narrow lips diminishing in width toward the equator, about 0.7 of spore radius or almost reaching the equator. Contact area delimited by differential ornamentation, may be slightly sunken. At low magnification exine appears rough or micro-reticulate, rugulate at high power under SEM (Fig. 5C, D) with occasional discrete granules on the proximal surface between the rugulae (Fig. 5G). The surface of these sculptural elements is granular. The rugulae are sinuous, discrete or interconnected to form an imperfect reticulum. The sculpture is distinctly coarser over the proximal face where the granules and rugulae are 2–8 µm wide; on the distal surface, the rugulae are up to 2 µm wide. Spaces between rugulae are mostly wider than the latter; but close to the apex, these elements may be closely set. Exine surface between rugulae is microreticulate, with lumina about 0.5–1 µm in diameter, and the muri are thinner (Fig. 5D, L).

Remarks: In this new species, the contact faces have coarser sculpture than the remaining spore surface; in that respect the species differs from *M.* sp. aff. *Biharisporites grosstriletus* Liu, Zhu and Ouyang from Sholga, *M. spongiosus* Fuglewicz (Fuglewicz, 1977, p. 409–410, pl. 28, fig. 8) from the Olenekian of Poland, and *M. magnuszewensis* Fuglewicz (Fuglewicz, 1977, p. 409, pl. 28, figs 6, 7) from the Middle Triassic of Poland.

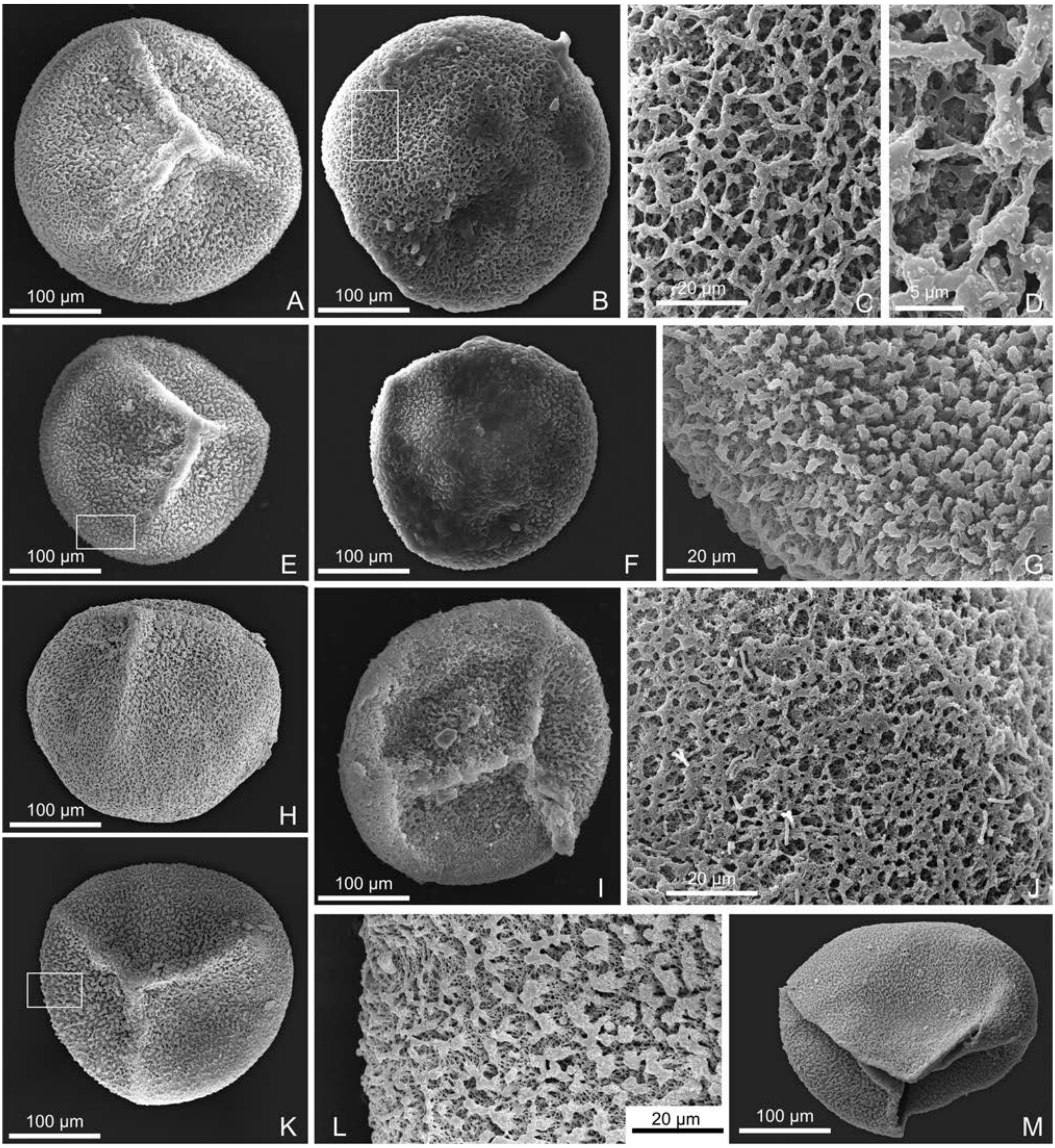

Fig. 5. Induan megaspores from Sholga locality. **A**–**M** – *Maexisporites rugulaeferus* sp. nov.; A–D – holotype, specimen PIN 5529/113: A–B – proximal and distal view, C, D – details of distal wall showing sculpture; E–G – specimen PIN 5529/105: E, F – proximal and distal view, G – detail of proximal wall showing sculpture; H – specimen PIN 5529/47, oblique compression, note finer sculpture over the distal hemisphere; I, J – specimen PIN 5529/100: I – proximal view, J – detail of proximal wall showing sculpture; K, L – specimen PIN 5529/43: K – proximal view. L – detail of proximal wall showing sculpture; M – specimen PIN 5529/46, oblique compression.

Genus *Otynisporites* Fuglewicz, 1977, emend.

Type species: *Otynisporites eotriassicus* Fuglewicz, 1977.

Emended diagnosis: A triradiate megaspore that bears agglomerations of long spines and bacula surmounting warts, tubercules or ribs, or occurring on essentially smooth exoexine.

Remarks: The diagnosis by Fuglewicz is emended to accommodate megaspores lacking tubercules, warts and ribs. Fuglewicz used the term "capilli" to describe the appendages surmounting various elevations, but we prefer bacula and spines (see Punt *et al.*, 1994) as better fitting the ornamentation features of all known species attributable to *Otynisporites*.

Otynisporites sp. cf. *O. eotriassicus* Fuglewicz, 1977
Fig. 6J–L

Material: One specimen.
Description: Megaspores apparently trilete, subcircular in equatorial outline, 330 µm in diameter. Exine ornamented with regularly, densely set circular, low verrucae covered by aggregated spines and bacula about 1 µm wide basally, up to 8 µm long (Fig. 6K, L). Exine surface between the verrucae is microreticulate, the lumina and the muri average 1 µm in diameter. Granules and short pila less than 1 µm wide surmount the muri.
Remarks: The ornamentation of this specimen is very similar to that of *O. eotriassicus* Fuglewicz (Fuglewicz, 1977, pl. 30, fig. 2) from the Induan of Poland, and of *Otynisporites* sp. from the Zechstein of Poland (Fuglewicz, 1980b, pl. 1, figs 1, 2), but confident specific assignment of the single specimen is not possible.

Otynisporites maculosus sp. nov.
Fig. 6A–E

Holotype: Specimen PIN 5529/19 (Fig. 6A–C).
Derivation of name: Maculosus (Lat.) = spotty, with ornamentation occurring in spots.
Type locality: Sholga on the Yug River, Moscow Basin, Russia.
Type level: Vokhma Formation, Ryabinsk Member, Induan.
Deposition of type: A.A. Borissiak Paleontologiczal Institute, Russian Academy of Sciences, Moscow, Profsoyuznaya 123, Russia.
Material: Ten specimens.
Diagnosis: A species of *Otynisporites* ornamented with subcircular, regularly distributed, discrete agglomerations of bacula and spines occurring on essentially smooth exoexine.
Description: Trilete megaspores, circular in equatorial outline, 283(336)411 µm (six specimens) in equatorial diameter. Laesurae straight to slightly sinuous or constricted along their length, in the form of ridges up to 30 µm high in the apical region, in some specimens diminishing in height toward the equator, about 0.9 of radius long. Contact area slightly sunken and defined by differential ornamentation; arcuate ridges lacking or very slight. Exine ornamented with bacula and spines that are often swollen near their termination. These appendages are usually 4–5 µm long and 1–2 µm wide, occasionally 7–8 µm long (Fig. 6B). They are arranged in discrete, regularly distributed, subcircular agglomerations, except for just beyond the contact area where they form a band of evenly distributed appendages (Fig. 6A). The ornament occurs on essentially smooth exoexine, but in some specimens (Fig. 6E), it occurs on very slight elevations. Exine surface between the agglomerations, when viewed at high power under SEM, is a fine mesh with oval lumina about 0.5–1 µm in diameter and muri about 0.5 µm wide, bearing granules 0.5–1 µm in diameter (Fig. 6B). The opening in the outer exospore of specimen PIN 5529/19 shows detached and folded intexine with a microreticulate sculpture (Fig. 6C).
Remarks: *Otynisporites maculosus* sp. nov. differs from *O. eotriassicus* and *O. tuberculatus* in having agglomerations of bacula and spines that occur directly on smooth exoexine and not on warts or tubercules. It differs from *O. tuberculatus* in lacking prominent arcuate ridges. The ornamentation of our species resembles *Biharisporites* cf. *foskettensis* Glasspool (Glasspool, 2003, p. 246, 249, pl. 2, figs 1-6) as described by Liu *et al.* (2011, p. 144, pl. V/10–12) from the Upper Permian (Wuchiapingian) of Shanxi, N. China, but the ornamentation elements of the latter are exclusively spines, and their size is given as 3(4)6 µm wide and 23(44)59 µm long (possibly erroneously because of disparity with the illustrations).

Otynisporites tuberculatus Fuglewicz, 1977
Fig. 6F–I

*1977 *Otynisporites tuberculatus* sp. nov. – Fuglewicz, p. 413, pl. 31, figs 1–3.
1980a *Otynisporites tuberculatus* Fuglewicz – Fuglewicz, pl. 2, fig. 5; pl. 3, fig. 7.
1980b *Otynisporites tuberculatus* Fuglewicz – Fuglewicz, pl. 2, fig. 3.
2009 *Otynisporites eotriassicus* Fuglewicz – Krassilov and Karasev, fig. 4.

Material: Five specimens.
Description: Trilete megaspores, subcircular in equatorial outline, 324(363)420 µm in equatorial diameter (five specimens). Laesurae extending almost to equator, straight, in the form of high, narrow bands, 30–50 µm high, of even height along the length or lowering near the terminations (Fig. 6F). Contact area delimited by distinct, narrow and low arcuate ridges (Fig. 6G). Exine ornamented with tuberculate and conate elements about 10–15 µm wide at the base, surmounted by one or more spines and bacula averaging 2.5–4 µm long (Fig. 6H). The tuberculate/conate elements are mostly connected with the neighbouring ones by fold-like elevations (Fig. 6I). The bands of the trilete rays are similarly ornamented. The ornamentation elements are finer adjacent to the arcuate ridges. Exine surface is microreticulate, lumina are 0.5–1.5 µm in diameter, and muri are narrower, bearing scattered single granules and short bacula.
Remarks: The description of *O. eotriassicus* and *O. tuberculatus*, and the statement of the differences are very generalized (Fuglewicz, 1977, pp 412–413). The typical form of the former taxon derived from the type material, i. e. the holotype (Fuglewicz, 1977, pl. 30, fig. 2) is ornamented by tubercules surmounted by brush-like agglomerations of baculate processes, low laesurae covered with elements of ornamentation, and curvaturae marked by rows of densely packed ornamentation elements. The specimen of that species in Fuglewicz (1977, pl. 30, fig. 1) has laesurae developed in the form of high ridges and bears distinct high arcuate ridges. That form is similar to *O. tuberculatus*, except for the ornamentation processes. The specimen of *O. eotriassicus* from the Nedubrovo locality in Russia (Krassilov *et al.*, 1999b, fig. 2/5–7; Lozovsky *et al.*, 2001, pl. 2/1, 2) is ornamented with discrete elevations like *O. eotriassicus*, but features prominent triradiate ridges that are more like those of *O. tuberculatus*. Some other specimens from the same locality (Krassilov and Karasev, 2009, fig. 4A–C) have discrete ornamentation processes, low triradiate and faint arcuate ridges. To sum up – both *O. eotriassicus* and *O. tuberculatus* are morphologically very variable, and it is often difficult to distinguish between them.
Occurrence: *O. tuberculatus* has been reported only from Poland; its range corresponds to that of. *O. eotriassicus*, i.e., Induan (Marcinkiewicz, 1992a, Marcinkiewicz *et al.*, 2014).

Genus *Trileites* (Erdtman) ex Potonié, 1956

Type species: *Trileites* (*Triletes*) *spurius* (Dijkstra) Potonié, 1956.
Remarks: The genera *Trileites* and *Banksisporites* Dettman emend. Glasspool are morphologically similar, and *Trileites* has priority. Megaspores included in *Trileites* lack distinct morphological characters on which to differentiate them. Because of this, and because we have only few specimens, we have neither assigned them to a known species, nor have we erected new taxa.

Trileites spp., Group I
Fig. 7A–C

Material: Ten specimens.
Description: Megaspores trilete, rounded-triangular to subcircular in equatorial outline, 244(267)330 µm in diameter (7 specimens). Trilete rays almost reaching the equator, in the form of bands about 20 µm high, diminishing in height equatorially,

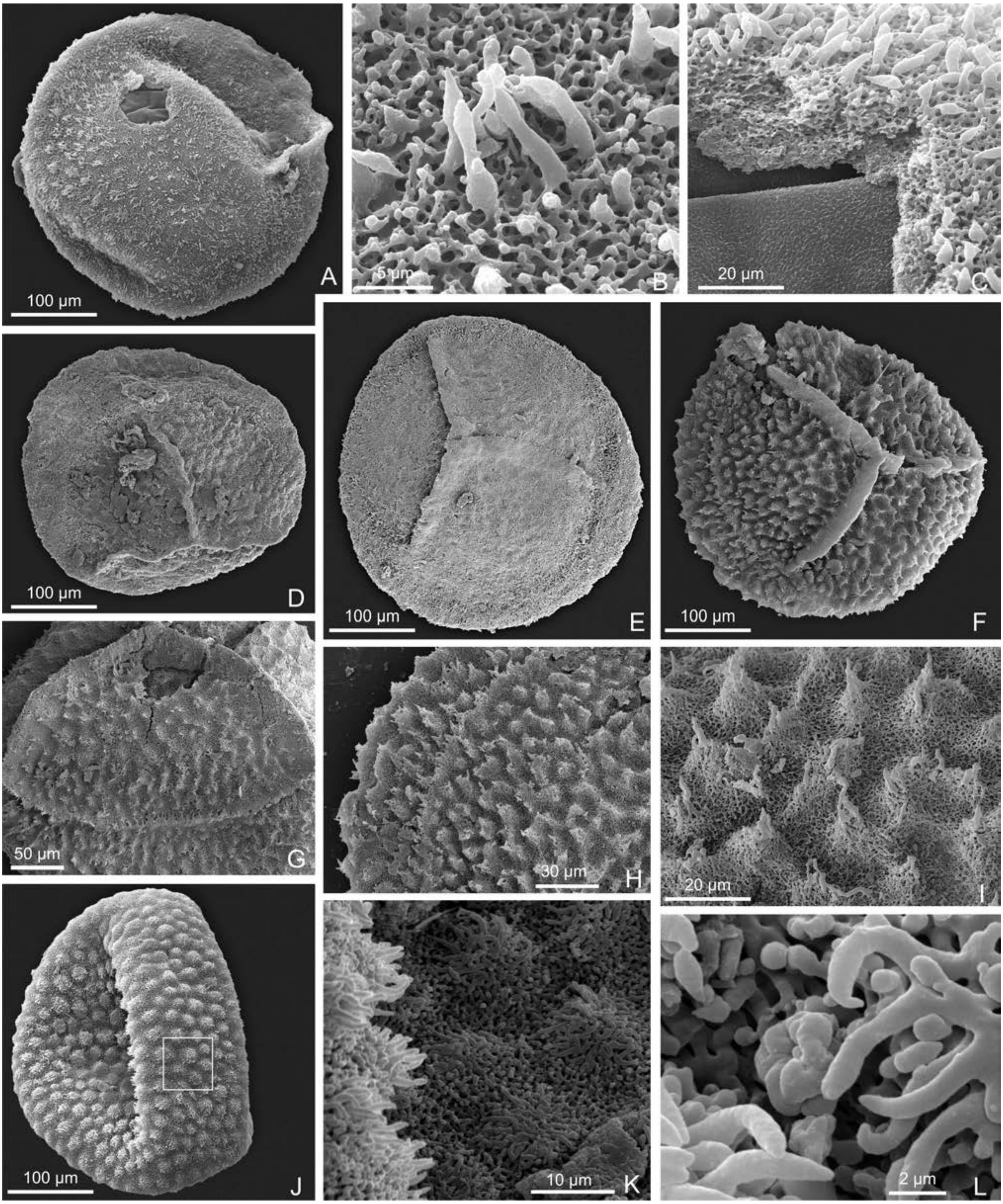

Fig. 6. Induan megaspores from Sholga locality. **A**–**E.** *Otynisporites maculosus* sp. nov.; A–C – holotype, specimen PIN 5529/19: A – laterally flattened megaspore, B – agglomeration of ornamentation appendages, C – opening in the outer exospore showing detached and folded intexine with a micro reticulate sculpture; D – specimen PIN 5529/73, oblique compression; E – specimen PIN 5529/71, proximal view. **F**–**I.** *Otynisporites tuberculatus* Fuglewicz 1977; F – specimen PIN 5529/3, proximal view; G – specimen PIN 5529/36, contact area; H, I – specimen PIN 5529/3, details of ornamentation of tuberculate/conate elements surmounted by bacula and spines. **J**–**L.** *Otynisporites* sp. cf. *O. eotriassicus* Fuglewicz 1977, specimen PIN 5529/6: J – obliquely flattened specimen, K, L – details of wall showing verrucae covered by agglomerations of spines and bacula.

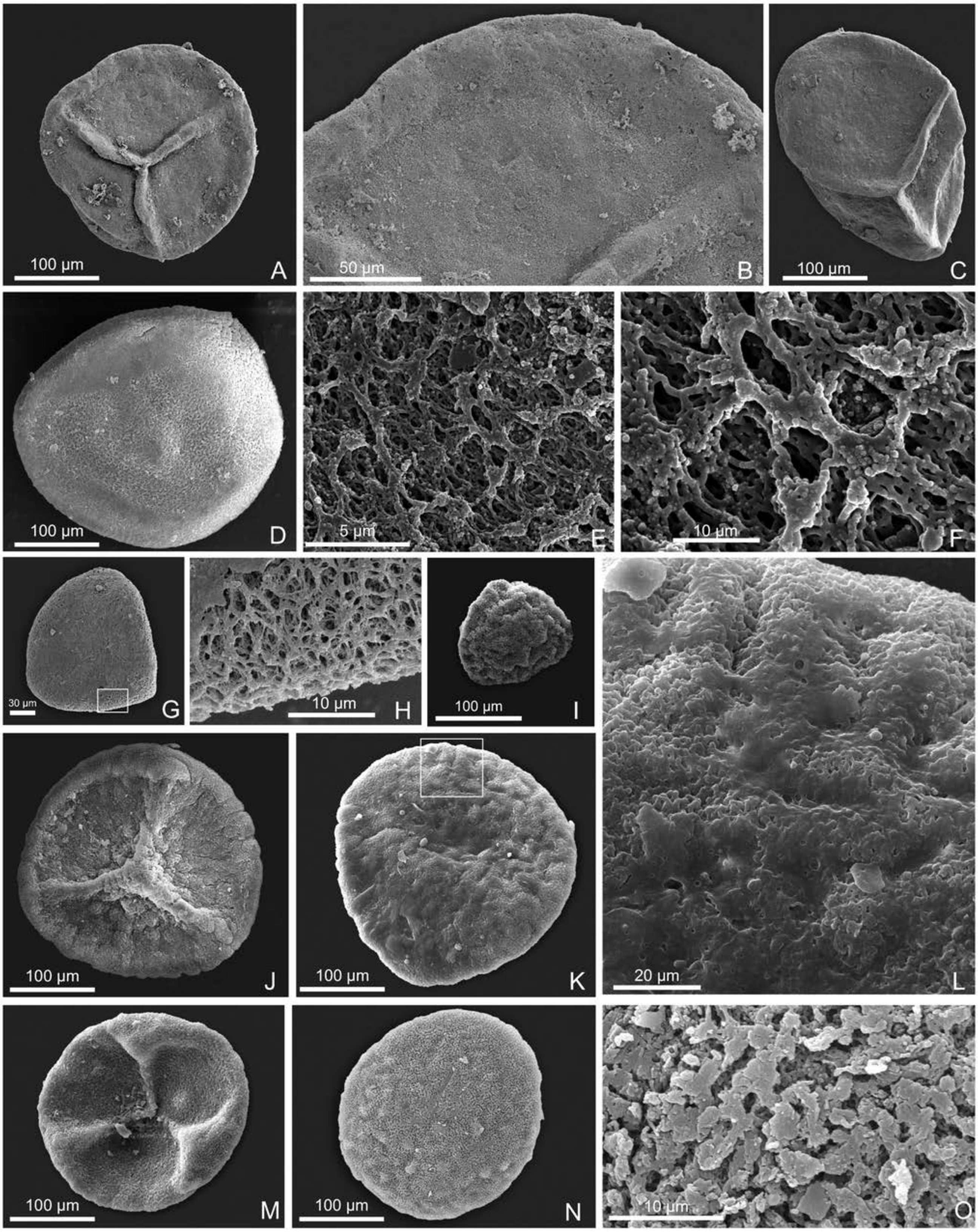

Fig. 7. Induan megaspores from Sholga locality. **A**–**C.** *Trileites* spp., Group I; A, B – specimen PIN 5529/77: A – proximal view, B – detail of proximal surface showing smooth exine; C – specimen PIN 5529/56, proximal view. **D**–**H.** *Trileites* spp., Group II; D–F – specimen PIN 5529/1: D – distal view, E, F – details of wall devoid of the outermost compact layer; G, H – specimen PIN 5529/82. **I**–**L.** *Verrutriletes*? sp. 1; I – specimen PIN 5529/33, distal view; J–L – specimen PIN 5529/98: J, K – proximal and distal view, L – detail of distal surface bearing low verrucae and elongate elements. **M**–**O** – *Verrutriletes* sp. 2, specimen PIN 5529/126: M, N – proximal and distal view, O – detail of distal wall covered by granular and rugulate elements.

straight or slightly sinuous. Contact faces not delimited or defined by very faint arcuate ridges (Fig. 7C). Exine surface in low magnification appears smooth; in high magnification, it is densely pitted, pits about 0.25 µm wide.
Remarks: *Trileites polonicus*, *T. sinuosus* and *T. vulgaris* are three Lower Triassic megaspore species described from Poland by Fuglewicz (1973). All are similar to the megaspores of Group I except that the diameters of the Sholga specimens are at the low end of the size range of the Polish species.

Trileites spp., Group II
Fig. 7D–H

Material: Two specimens.
Description: Megaspores apparently trilete, rounded-triangular in equatorial outline, 169 and 248 µm in diameter. Exine surface apparently smooth (Fig. 7D). At high power under SEM, the outer exine layer is dense and compact, and immediately beneath, exine comprises a three-dimensional network. In surface view, the lumina of the network are irregularly oval, 2.5–8 µm in longest diameter; the muri are 1–2 µm wide, consisting of rods and granules, and pitted (Fig. 7E, F, H). Several layers of this mesh may be seen through the openings.
Remarks: The ultrastructure of exine seen in the megaspores of Group II is very similar to that in *Trileites persimilis* (Harris) Dijkstra (in Koppelhus and Batten, 1989, pl. 1, figs 1, 2).

Genus *Verrutriletes* (Van der Hammen) Potonie 1956
emend. Binda et Shrivastava 1968

Type species: *Verrutriletes* (*Triletes*) *composipunctatus* (Dijkstra) Potonié 1956.

Verrutriletes? sp. 1
Fig. 7J–L

Material: One specimen.
Description: Trilete megaspore, circular in equatorial outline, 297 µm in diameter. Laesurae are prominent, apically rounded ridges, about 15 µm wide within their central part, slightly widening toward extremities, almost reaching equator. Contact faces distinctly delimited by curvaturae. The entire proximal surface covered by densely set, low verrucae 20–25 µm in basal width, up to 5 µm high at the equator. Distal surface bears an ornament of low verrucae and meandering elongate elements (Fig. 7L). Exine surface is granular, at high power under SEM, that of the proximal hemisphere presents a patchwork of closely set irregular elements 2.5– 3 µm wide, granular and pitted. Distal exine is similar, the elements are more granular, 1.5–2 µm wide.
Remarks: The exine surface of the specimen *Verrutriletes*? sp. 1 is granular and could be described as of *Maexisporites* type, unlike the microreticulate surface of at least some *Verrutriletes* e.g., *V. composipunctatus* (Dijkstra) Potonie in Batten (1988, pl. 4, figs 9, 10). The specimen described above is similar to *V. preutilis* Fuglewicz (Fuglewicz, 1977, p. 410, pl. 30, figs 3, 4, and Marcinkiewicz, 1992b, pl. 3, fig. 4) from the Ladinian of Poland, but the verrucae in the Sholga specimens are wider in proportion to the megaspore diameter.

Verrutriletes? sp. 2
Fig. 7 M–O

Material: One specimen.
Description: Trilete megaspore, circular in outline, 255 µm in diameter. Laesurae are distinct, in the form of ridges that widen toward the equator. Contact faces unornamented, distinctly delimited by sunken curvaturae of clover-leaf shape. Exine outside contact faces ornamented by verrucae 10 µm in basal diameter, up to 4 µm high, up to 8 µm apart. Exine surface granular, under high power SEM covered by closely set, rugulate elements having a granular and pitted appearance (Fig. 7O).
Remarks: The exine surface of the specimen is granular, and similar to that of *Maexisporites*.

THE POST-CRISIS MEGASPORE ASSEMBLAGE

The samples from the Ryabinsk Member from Sholga locality yielded 126 megaspore specimens. Of these, only 90 specimens were sufficiently well preserved to allow taxonomic assignment. The assemblage is dominated by representatives of *Maexisporites* which account for 63% of all recognizable specimens. The second commonest genus is *Otynisporites* (almost 18%), and the third is *Trileites* (13%). The authors have assigned some specimens to *Bacutriletes*, *Hughesisporites*, and *Verrutriletes*?, but as discussed in the systematic descriptive section, the exinal structure in these megaspores is of *Maexisporites* type and it differs thereby from some species of *Verrucosisporites* and *Bacutriletes* (see Remarks for *Bacutriletes*, *Hughesisporites* sp. 1, and *Verrutriletes*? sp. 1, sp. 2). Thus, the authors consider that the assemblage from Sholga is of low generic diversity. The assemblages of the O. eotriassicus Zone described by Fuglewicz (1977, 1980a, b) are similarly poor in taxa. These assemblages are best known from the Otyń IG-1 borehole where they were recovered from 14 core-samples. The commonest are representatives of *Trileites vulgaris* (10 samples) and *Otynisporites tuberculatus* (11 samples); less common are *O. eotriassicus* (6 samples) and *Maexisporites ooliticus* (4 samples). *Echitriletes fragilispinus* and *Pusulosporites permotriassicus* are rare (1 and 2 samples respectively). The low diversity of those earliest Triassic megaspore assemblages is evidently a manifestation of the end-Permian biotic crisis. It may be added that the miospore assemblages associated with the megaspores of the present authors (Yaroshenko and Lozovsky, 2004) contain numerous unseparated spore tetrads – a mutation characteristic of stressed environments (e.g., Visscher *et al.*, 2004).

The external morphology of the megaspores suggests that they were produced by lycopsids. The simple trilete spores with smooth exine surface assignable to *Trileites* (*Banksisporites*) have been widely reported from pleuromeiacean strobili (reviewed by Balme, 1995, see also Lugardon *et al.*, 2000, Grauvogel-Stamm and Lugardon, 2004), but also from selaginellalean fructifications (Balme, 1995). Sporoderm ultrastructure of *Otynisporites eotriassicus* has been studied by Looy *et al.* (2005), who considered this taxon to be of isoetalean (pleuromeiacean) affinity. The botanical relationship of the most common genus *Maexisporites* is not known. The exine surface in megaspores of this taxon is similar to that in some extant *Selaginella* megaspores, such as *S. denticulata* and *S. peruviana*, illustrated by Moore *et al.* (2006, figs 4B and 4D)

It has been already noted by Dettman (1961), who studied the Rhaeto–Liassic megaspore floras of Tasmania and

South Australia, that the Mesozoic megaspore floras were quite uniform over Pangea. This worldwide similarity is less pronounced in relation to the Early and Middle Triassic assemblages that differ considerably even between peninsular India and Australia (Scott and Playford, 1985). The assemblage of the present authors bears very little resemblance to the Gondwanan ones. Its dominant element – *Maexisporites*, and the widely distributed genus *Otynisporites* have not been found in the Gondwanan continents. The only exception is that representatives of *Maexisporites* are also known from Morocco (Lachkar, 1989, fide Kovach and Batten, 1989). The megaspore assemblages from Sholga share with those from the Gondwana only the representatives of *Trileites* and *Hughesisporites*.

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REFERENCES

Afonin, S. A., Barinova, S. S. & Krassilov, V. A., 2001. A bloom of *Tympanicysta* Balme (green algae of zygnematalean affinities) at the Permian-Triassic boundary. *Geodiversitas*, 23: 481–487.

Antonescu, E. & Taugourdeau Lantz, J., 1973. Considérations sur les mégaspores et microspores du Trias inférieur et moyen de Roumanie. *Palaeontographica*, *Abteilung B*, 144: 1–10.

Aristov, D. S., Bashkuev, A. S., Golubev, V. K., Gorochov, A. V., Karasev, E. V., Kopylov, D. S., Ponomarenko, A. G., Rasnitsyn, A. P., Rasnitsyn, D. A., Sinitshenkova, N. D., Sukatsheva, I. D. & Vassilenko, D. V., 2013. Fossil insects of the middle and upper Permian of European Russia. *Paleontological Journal*, 47: 641–832.

Balme, B. E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology*, 87: 81–323.

Batten, D. J., 1988. Revision of S.J. Dijkstra's Late Cretaceous megaspores and other plant microfossils from Limburg, the Netherlands. *Mededelingen Rijks Geologische Dienst, Nieuwe Serie*, 41: 1–55.

Batten, D. J., 2012. Taxonomic implications of exospore structure in selected Mesozoic lycopsid megaspores. *Palynology*, 36 (sup1.): 144–160.

Batten, D. J., Ferguson, D. J. P., 1987. *Cabochonicus*, a new genus for species of gemmate megaspores previously referred to *Verrutriletes*. *Journal of Micropalaeontology*, 6: 65–75.

Cantrill, D. J. & Drinnan, A. N., 1994. Late Triassic megaspores from the Amery Group, Prince Charles Mountains, East Antarctica. *Alcheringa*, 18: 71–78.

Dettmann, M. E., 1961. Lower Mesozoic megaspores from Tasmania and South Australia. *Micropaleontology*, 7: 71–86.

Foster, C. B., Stephenson, M. H., Marshall, C., Logan, G. A. & Greenwood, P. F., 2002. A revision of *Reduviasporonites* Wilson 1962: Description, illustration, comparison and biological affinities. *Palynology*, 26: 35–58.

Fuglewicz, R., 1973. Megaspores of Polish Buntersandstein and their stratigraphical significance. *Acta Palaeontologica Polonica*, 18: 401–453.

Fuglewicz, R., 1977. New species of megaspores from the Trias of Poland. *Acta Palaeontologica Polonica*, 22: 405–431.

Fuglewicz, R., 1978. Stratigraphy of the Bunter in the SW margin of the Fore-Sudetic monocline. *Acta Geologica Polonica*, 27: 471–479.

Fuglewicz, R., 1980a. Stratigraphy of Buntsandstein in the borehole Otyń IG-1 (Fore-Sudetic Monocline, Polad). *Rocznik Polskiego Towarzystwa Geologicznego*, 49: 277–287. [In Polish, with English summary.]

Fuglewicz, R., 1980b. Stratigraphy and palaeogeography of Lower Triassic in Poland on the basis of megaspores. *Acta Geologica Polonica*, 30: 417–470.

Glasspool, I. J., 2003. A review of Permian Gondwana megaspores, with particular emphasis on material collected from coals of the Witbank Basin of South Africa and the Sydney Basin of Australia. *Review of Palaeobotany and Palynology*, 124: 227–296.

Grauvogel-Stamm, L. & Lugardon, B., 2004. The spores of the Triassic lycopsid *Pleuromeia sternbergi* (Münster) Corda: morphology, ultrastructure, phylogenetic implications, and chronostratigraphic inferences. *International Journal of Plant Sciences*, 165: 631–650.

Koppelhus, E. B. & Batten, D. J., 1989. Late Cretaceous megaspores from Southern Sweden; morphology and paleoenvironmental significance. *Palynology*, 13: 91–120.

Kovach, W. L. & Batten, D., 1990. Catalog of Mesozoic and Tertiary Megaspores. *American Association of Stratigraphic Palynologists Foundation, Contribution Series* 24, 227 pp.

Kozur, H., 1971. Zur Verwertbarkeit von Conodonten, Ostracoden und ökologisch-fazielle Untersuchungen in der Trias. *Geologicky Zbornik, Geologia Carpatica*, 22: 105–130.

Kozur, H. W., 1998. Some aspects of the Permian-Triassic boundary (PTB) and of the possible causes for the biotic crisis around this boundary. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 143: 227–272.

Kozur, H. & Movshovich, E. V., 1976. Megaspores from the Triassic Gemmanella beds from the south-western part of the North Caspian Syneclise and their stratigraphic importance. *Izvestya Academii Nauk SSSR*, *Seria Geologicheskaya*, 3: 53–66. [In Russian.]

Kozur, H. W. & Weems, R. E., 2011. Detailed correlation and age of continental late Changhsingian and earliest Triassic beds: Implications for the role of the Siberian Trap in the Permian-Triassic biotic crisis. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 308: 22–40.

Krassilov, V. A., Afonin, S. A. & Barinova, S. S., 1999a. Tympanicysta and the terminal Permian events. *Permophiles*, 35: 16–17.

Krassilov, V. A., Afonin, S. A. & Lozovsky, V. R., 1999b. Floristic evidence of transitional Permian-Triassic deposits of the Volga - Dvina Region. *Permophiles*, 34: 12–14.

Krassilov, V. A. & Karasev. E., 2008. First evidence of plant – arthropod interaction at the Permian – Triassic boundary in the Volga Basin, European Russia. *Alavesia*, 2: 247–252.

Krassilov, V. A. & Karasev, E. V., 2009. Paleofloristic evidence of climate change near and beyond the Permian-Triassic boundary. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 284: 326–336.

Li, W., Batten, D. J., Zhang, D. & Zhang, L., 1987. Early Cretaceous megaspores from the Jalainor Group of northeast Inner Mongolia, P. R. China. *Palaeontographica*, *Abteilung B*, 206: 117–135.

Liu, F., Zhu, H. & Ouyang, S., 2011. Taxonomy and biostratigraphy of Pennsylvanian to Late Permian megaspores from Shanxi, North China. *Review of Palaeobotany and Palynology*, 165: 135–153.

Looy, C. V., Collinson, M. E., Van Konijnenburg-Van Cittert, J. H. A., Visscher, H. & Brain, A. P. R., 2005. The ultrastructure and botanical affinity of end-Permian spore tetrads. *International Journal of Plant Sciences*, 166: 875–887.

Lozovsky, V. R., 1998. The Permian-Triassic boundary in the continental series of Eurasia. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, 143: 273–283.

Lozovsky, V. R., 2013. Permo-Triassic crisis and its possible causes. *Bulletin of the Moscow Society of Naturalists*, *Geological series*, 88: 49–59. [In Russian.]

Lozovsky, V. R. & Esaulova, N. K., 1998. Permian-Triassic boundary in the continental series of East Europe. In: *International Symposium "Upper Permian Stratotypes of the Volga Region" GEOS*, Moscow, 246 pp. [In Russian.]

Lozovsky, V. R., Krassilov, V. A., Afonin, S. A., Burov, B. & Jaroshenko, O., 2001. Transitional Permian-Triassic deposits in European Russia, and non-marine correlations. In: Cassinis, G. (ed.), Permian continental deposits of Europe and other areas. *Regional reports and correlations: "Natura Bresciana", Annali del Museo Civico di Scienze Naturali di Brescia*, pp. 301–310.

Lugardon, B., Grauvogel-Stamm, L. & Dobrushkina, I., 2000. Comparative ultrastructure of the megaspores of the Triassic lycopsid *Pleuromeia rossica* Neuburg. *Comptes rendus de l'Académie Sciences*, *Sciences de la Terre et de planètes*, 330: 501–508.

Lupia, R., 2011. Late Santonian megaspore floras from the Gulf Coastal Plain (Georgia, USA). *Journal of Paleontology*, 85: 1–21.

Maheshwari, H. K. & Banerji, J., 1975. Lower Triassic palynomorphs from the Maitur Formation, west Bengal, India. *Palaeontographica*, *Abteilung B*, 152: 149–190.

Marcinkiewicz, T., 1976. Distribution of megaspore assemblages in Middle Bundsandstein of Poland. *Acta Palaeontologica Polonica*, 21: 191–200.

Marcinkiewicz, T., 1979. Fungi-like forms on Jurassic megaspores. *Acta Palaeobotanica Polonica*, 20: 123–128.

Marcinkiewicz, T., 1980. Jurassic megaspores from Grojec near Krakow. *Acta Palaeobotanica Polonica*, 21: 37–60. [In Polish.]

Marcinkiewicz, T., 1992a. Megaspore stratigraphical scheme of the Buntsandstein in Poland. *Biuletyn Państwowego Instytutu Geologicznego*, 368: 65–96. [In Polish, with English summary.]

Marcinkiewicz, T., 1992b. Remarks to the discussion on distribution of smooth spherules on Mesozoic megaspores with particular references to the species *Verrutriletes utilis* (Marcinkiewicz) Marcinkiewicz. *Geological Quarterly*, 36: 421–434.

Marcinkiewicz, T., Fiałkowska-Mader, A. & Pieńkowski, G., 2014. Megaspore zones of the epicontinental Triassic and Jurassic in Poland – overview. *Biuletyn Państwowego Instytutu Geologicznego*, 457: 15–42.

Metcalfe, I., Foster, C. B., Afonin, S. A., Nicoll, R. S., Mundil, R., Wang Xiaofeng & Lucas, S. G., 2009. Stratigraphy, biostratigraphy and C-isotopes of the Permian–Triassic non-marine sequence at Dalgonkou and Lucagou, Xinjiang Province, China. *Journal of Asian Earth Sciences*, 36: 503–520.

Moore, S. E. M., Hemsley, A. R. & Borsch, T., 2006. Micromorphology of outer coatings in *Selaginella* megaspores. *Grana*, 45: 9–21.

Nawrocki, J., 1997. Permian to Early Triassic magnetostratigraphy from the Central European Basin in Poland: implications on regional and worldwide correlations. *Earth and Planetary Science Letters*, 152: 37–58.

Nawrocki, J., 2004. The Permian–Triassic boundary in the Central European Basin magnetostratigraphic constraints. *Terra Nova*, 16: 139–145.

Orłowska-Zwolińska, T., 1984. Palynostratigraphy of the Buntsandstein in sections of western Poland. *Acta Palaeontologica Polonica*, 29: 161–194.

Ouyang, S. & Norris, G., 1999. Earliest Triassic (Induan) spores and pollen from the Junggar Basin, Xinjiang, northwestern China. *Review of Palaeobotany and Palynology*, 106: 1–56.

Pal, P. K., Ghosh, A. K. & Sannigrachi, A., 1997. Megaspores from the Panchet Formation of East Bokaro Coalfield, India. *Journal of the Palaeontological Society of India*, 42: 61–69.

Punt, W., Blackmore, S., Nilsson, S. & Le Thomas, A., 1994. Glossary of pollen and spore terminology. *LPP Contribution Series,* No. 1, 71 pp.

Reinhardt, P., 1963. Megasporen aus dem Keuper Thuringiens. *Freiberger Forschungshefte*, C164: 117–122.

Scott, A. C. & Playford, G., 1985. Early Triassic megaspores from the Rewan Group, Bowen Basin, Queensland. *Alheringa: An Australian Journal of Palaeontology*, 9: 297–323.

Strok, N. I., Gorbatkina, T. E. & Losovsky, V. R., 1984. *Upper Permian and Lower Triassic deposits of the Moscow Syneclise*. Nauka, Moscow, 139 pp. [In Russian.]

Taylor, W. A. & Taylor, T. N., 1988. Ultrastructural analysis of selected Cretaceous megaspores from Argentina. *Journal of Micropalaeontology*, 7: 73–87.

Twitchett, R. J., Looy, C. V., Morante, R., Visscher, H. & Wignall, P. B., 2001. Rapid and synchronous collapse of marine and terrestrial ecosystems during the end-Permian biotic crisis. *Geology*, 29: 351–354.

Visscher, H., 1971. The Permian and Triassic of the Kingscourt Outlier, Ireland. *Geological Survey Ireland Special Paper*, 1: 1–114.

Visscher, H., Looy, C. V., Collinson, M. E., Brinkhuis, H., van Konijnenburg-van Cittert, J. H. A. & Kürschner, W. M., 2004. Environmental mutagenesis during the end-Permian ecological crisis. *Proceedings of the National Academy of Sciences of the United States of America*, 101: 12952–12956.

Yaroshenko, O. P. & Lozovsky, V. R., 2004. Palynological assemblages of continental Lower Triassic in Eastern Europe and their interregional correlation. Paper 1: Palynological assemblages of the Induan stage. *Stratigraphy and Geological Correlation*, 12: 275–285. [In Russian.]