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SEEDS OF *ALLICOSPERMUM SZAFERI* SP. NOV. CONTAINING BISACCATE POLLEN GRAINS FROM THE POLISH LIAS

Nasiona *Allicospermum szaferi* sp. nov. zawierające dwuworkowe ziarna pyłku z polskiego liasu

ABSTRACT. Seeds of *Allicospermum szaferi* sp. nov. from the Lias of Northern Poland preserved as compressions showed after maceration inner cutinized membranes, such as the megaspore membrane, the cuticle of the nucellus and fragments of the integument. Bisaccate pollen grains were present on inner cuticles and in maceration fluid and in two seeds there is evidence of a pollen chamber. The apex of the nucellus is unusual, forming a flat funnel. The reconstruction of the seed is given and its affinities discussed. Most probably it is the seed of a pteridosperm.

INTRODUCTION

It is well known that Palaeozoic and Mesozoic seeds may show details of structure such as layers of the seed and even its tissues. Particularly well preserved are petrified Carboniferous seeds from coal balls. As had been shown by several authors, but particularly in many papers by the late Professor T.M. Harris, in Mesozoic strata most seeds are preserved as compressions which on maceration show only the cutinized membranes of their internal layers and pollen grains which penetrated inside during pollination, occasionally also other elements. Usually such data are not sufficient to establish the affinity of detached seeds. Therefore they are assigned to form-genera which are „not assignable to a family, although they may be referable to a taxon of higher rank" (Greuter 1988, p. 4).

Nevertheless, also the study of macerated seed compressions allowed to establish some interesting facts. E.g. the finding of pollen grains in the micropyle and pollen chamber of Jurassic *Caytonia* seeds, believed at first to belong to an angiosperm, were evidence of the gymnospermous way of pollination and gymnospermous affinity of this plant (Harris 1933). Similarly, *Eucommiidites* pollen grains believed at first to come from an angiosperm were found in the micropyle and pollen chamber of Cretaceous and Jurassic seeds. This gymnospermous mode of pollination is regarded as evidence of

the gymnospermous affinity of their mother plant (e.g. Hughes 1961, Reymanówna 1968). In both cases the observations were confirmed on more than one species of the seed from different localities.

In 1985 we received from the State Geological Institute in Warsaw seeds from the borehole Borzynowo in Northern Poland. Although our investigations added nothing to the determination of their age by the geologists (Lias – ? Pliensbachian), we found during maceration of the seeds some interesting structures. We are aware that structures observed in one or two specimens may be accidental and not represent the normal structures of the species, therefore we abstain from far reaching comparisons. Nevertheless, we publish our results and comments as they appear interesting. This paper had been presented during the Conference „L'Evolution des Gymnospermes", Montpellier 1986 (Wcisło-Luraniec & Ichas 1986).

The work concerning seeds had been carried out by one author (E.W.-L.), that concerning pollen grains by the other author (J. I.-Z.).

MATERIAL AND METHODS

The material received from the State Geological Institute in Warsaw consists of seeds washed out of the sediment from the borehole Borzynowo IG-1 near Elbląg in Northern Poland from the depth 953,40 m and 953,9 m. They are of Liassic (?Pliensbachian) age and are preserved as compressions. Of eleven seeds nine were macerated in nitric acid followed by ammonia, only five of them gave useful cuticle fragments. Certain products of maceration such as stone cells were fixed with ammonia acetate and calcium chloride (Reymanówna 1973). One seed was coated with gold and studied in the SEM.

During maceration of 6 seeds were found 22 pollen grains, four of them inside one seed, one inside another seed, the remaining ones loose on cuticle fragments or in the maceration fluid. Only 20 pollen grains were considered in further investigations, as one was excluded because of its much larger size, and another because of bad preservation.

SYSTEMATIC DESCRIPTIONS

Class ?*Pteridospermophyta*

Form-genus *Allicospermum* Harris 1935

Allicospermum szaferi sp. nov.

Pl. I, figs 1-3; Pl. II, figs 1-6; Pl. III, figs 1-2; Figs 1-3

Diagnosis. Unmacerated seeds orthotropous, ovate, micropyle not projecting, surface granulate, size of seed 1-2 x 0.8-1.5 mm. Integument showing two layers (surface layer usually incomplete). Macerated seeds with thickly cutinized, dark brown, almost circular megaspore membrane about 1.1 x 1.3 mm in diameter with granular structure. Outside megaspore membrane in upper part of seed present nucellar cuticle consisting of elongated cells about 35 x 10 μm; nucellar apex widening into a flat funnel with recurved margin, it widest diameter

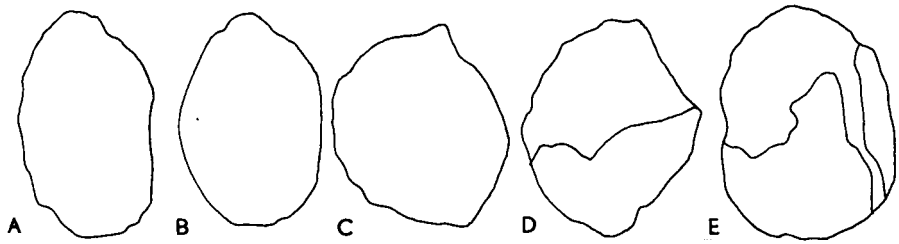

Fig. 1. *Allicospermum szaferi* sp. nov. Some seeds before maceration. x 20. A - no slides; B - slides IB PAN PM S934, IB PAN PM S940; C - slides IB PAN PM S932, IB PAN PM S935; D,E - no slides

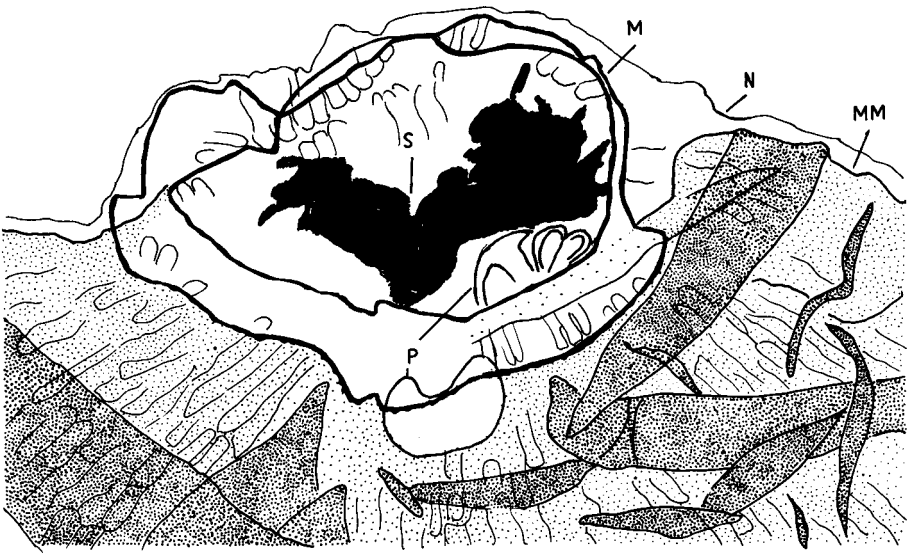

Fig. 2. *Allicospermum szaferi* sp. nov. Seed after maceration showing nucellar apex with recurved margin. Holotype, slide IB PAN PM S924, x about 2000. N - cuticle of nucellus; M - recurved margin of nucellar apex; S - dark substance sealing off nucellus; MM - megaspore membrane /stippled/; P - pollen grains in pollen chamber

0.6 mm. At seed apex below nucellar cuticle and above megaspore membrane present bisaccate pollen grains (which is interpreted as presence of pollen chamber). Outside nucellus visible fragments of cuticle of inner epidermis of integument, stone cells and a second cuticle.

Holotype. Microscopic slides No IB PAN PM S924, IB PAN PM S925 (PL. II, figs 1,5-6; Pl. III, fig. 1; Fig. 2).

Isotype. Specimen No IB PAN PM S926 (Pl. I, figs 1-2). Place of preservation of holotype and isotype: Władysław Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Lubicz 46.

Locus typicus. Borzynowo near Elbląg.

Age. Liassic (?Pliensbachian).

Derivatio nominis. In honour of the late Professor Władysław Szafer who wished that the palaeobotanical investigations of Jurassic plants in Poland be continued.

Discussion. Structure and reconstruction of the seed. Only two macerated seeds gave a more or less complete megaspore membrane and nucellar cuticle and only one of them showed a complete nucellar apex. The cuticles belonging to the integument appeared only in fragments, accompanied by fragments of the layer of stone cells. Using this information the reconstruction of the seed was drawn, taking as model the seed of *Ginkgo biloba*. Beginning from the inside, there are present the following structures:

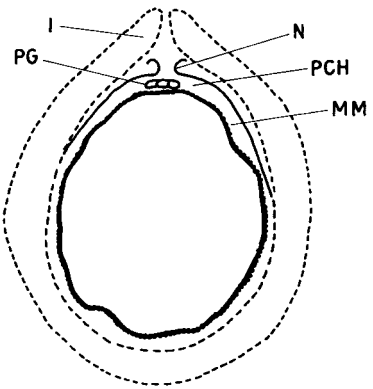

Fig. 3. *Allicospermum szaferi* sp. nov. Reconstruction of the seed in longitudinal section. MM - megaspore membrane: N - nucellus; PCH - pollen chamber; PG - pollen grain; I - integument

1. Megaspore membrane. It is thickly cutinized, distinct, with many folds and shows no cell outlines.

2. Nucellus. In the upper half of the seed the megaspore membrane is surrounded by a distinct cuticle of the nucellus which shows outlines of elongated cells. The nucellar apex in the form of a flat funnel with a recurved margin is unusual. The funnel shows inside a dark substance, possibly sealing it off after pollination.

3. Pollen chamber. In two seeds bisaccate pollen grains were found below the nucellar apex and above the megaspore membrane. By changing the focus it could be observed that pollen grains were below the nucellar cuticle (Pl. II, figs 1, 5-6; Pl. III, fig. 1 and Fig. 2). This is taken as evidence that a pollen chamber was present.

4. Pollen grains. In addition there were found pollen grains of the same type on cuticle fragments and in the maceration fluid of the same two seeds and of three other seeds.

5. Integument. In unmacerated seeds the integument appears to consist of two layers, the outer one tending to be partly broken. In maceration it disintegrates into groups of stone cells and fragments of at least two cuticles showing cell outlines which are interpreted as cuticles of the inner and outer epidermis of the integument. In the reconstruction the integument is tentatively represented as a single layer.

Attribution to the genus *Allicospermum*. In 1935 Harris instituted four form – genera for isolated seeds showing cuticular structure. Among them the genus *Allicospermum* is meant for orthotropous seeds which possess a strongly cutinized integument, a weakly cutinized nucellus and a megaspore membrane. The presence of the megaspore membrane and nucellus allows to attribute the described seeds to the form — genus *Allicospermum*. *A. szaferi* differs from other species by the funnel-shaped apex of the nucellus.

Anteturma *Variegerminantes*
Turma *Saccites*
Subturma *Disaccites abstriates*
Genus *Alisporites* (Daugherty 1941) Jansonius 1971
Alisporites sp. 1
Pl. I, fig. 3; Pl. II, figs 5-6; Pl. III, figs 1-5; Pl. IV, figs 1-6

Description. Pollen grains (found during maceration of seed) bisaccate, corpus circular to broadly elliptical with fusiform sulcus, length of sacci about equals that of corpus. Exine of corpus granulate to papillate, 1.6-2.8 μm thick, sacci reticulate, lumina of reticulum polygonal (3-8 sides), 1.0-4.8 μm in diameter, muri about 0.4 μm thick.

Dimensions of 6 specimens in lateral transverse view: corpus length 41.6-49.0 μm, saccus length 43.8-52.5 μm. Widest part of saccus 17.6-24.5 μm in diameter. Dimensions of one specimen in polar view: corpus length 47.2 μm, saccus length 48.0 μm, corpus breadth 47.6 μm, saccus breadth about 28 μm, overall breadth 74.8 μm.

Attribution to genus and species. Among Mesozoic pollen grains, those obtained from *Allicospermum szaferi* recall among others the species *Podocarpidites marwickii* Couper 1953 described by Archangelsky and Romero (1974). In general, however, the pollen grains are most similar to those of the genus *Alisporites* (Potonié 1956, 1958, 1960, 1966, 1970). I include them into this genus, because they are similar to the generotype of *Alisportes opii* Daugherty (Daugherty 1941 in Potonié 1958, the diagnosis quoted in Jansonius 1971). Jansonius in his emended generic diagnosis of *Alisporites* and his illustrations of the holotype of *Alisportes opii* shows a fine reticulation of the sacci. To my mind, this is different from the original diagnosis of the genus and from the original illustration of the generotype by Daugherty which shows a distinct reticulum of the sacci. In this character the pollen grains from Borzynowo seem closer to the understanding of *Alisporites* by Daugherty.

Daugherty as well as Jansonius mentions in the diagnosis of *Alisportes* the occurrence of a sulcus on the corpus. The sulcus is, however, distinct only in an advantageous view and in well preserved pollen grains. In the material from Borzynowo the pollen grains tend to be

in the lateral transverse view (cfr. Pl. III, figs 2-5; Pl. IV, figs 1, 5-6) or in a more or less oblique view (Pl. II, figs 5-6; Pl. III, fig. 1; Pl. IV, fig. 2). On grains in lateral transverse view the sulcus is visible on the corpus, but it is difficult to establish with certainty its structure and shape. Only one grain is in polar view (Pl. IV, figs 3-4) but here the exine of the corpus is torn which does not allow to determine the shape of the sulcus.

The 20 pollen grains found during maceration of *Allicospermum szaferi* seeds are similar in size and morphology and give the impression that they belong to one species. It is different from all species of *Alisporites* known to me therefore I describe it as *Alisporites* sp. 1.

Affinities. Bisaccate pollen grains are produced by conifers (Erdtman 1972) and pteridosperms (Townrow 1962b). In general *Alisporites* is regarded as pollen of pteridosperms. Pollen grains of the *Alisporites* type were extracted e.g. from the fructification *Pteruchus (Corystospermales)*. *Alisporites* pollen grains tend to have a different type of reticulum from conifer pollen grains and the occurrence of the reticulum appears inconsistent (Taylor et al. 1984). Nevertheless, Townrow (1962a, b) describes and illustrates pollen grains extracted from the fructifications *Pteruchus dubius* and *P. simmondsi* which show a distinct reticulation. In *Pteruchus* the cappula shows a groove of distinct outline which is sharply delimited from the surrounding exine. He understands that this is the germination area.

Some authors e.g. Townrow (1962b) are of the opinion that a sulcus is characteristic of the pollen grains of certain pteridosperms, while pollen of conifers show only a thinning of the exine (leptoma). Other authors, however, e.g. Konijnenburg - Cittert van (1971) do not agree.

According to Townrow (1962a, b) pollen grains of *Pteruchus* have no clear analogy in living conifers to compare them with. Having studied pollen preparations of about 60 species of recent *Pinaceae* and *Podocarpaceae* I think that the pollen grains from the fossil seeds recall in some respects those of *Picea abies* and *P. engelmannii,* but they have a different sculpture on the corpus. In addition, the lumina of the reticulum near the saccus attachment are more or less isodiametrical in Picea, while they are elongated in the fossil pollen. Elongated lumina occur e.g. in *Pinus contorta* and in some *Podocarpaceae* e.g. *Podocarpus amarus*. In general, it was not possible to find a recent type of pollen grain corresponding with the fossil form.

GENERAL DISCUSSION. AFFINITIES OF *ALLICOSPERMUM SZAFERI*

On the one complete preparation of the nucellar apex (Fig. 2) are visible certain interesting characters such as bisaccate pollen grains present inside the nucellus, the nucellar apex in the form of a flat funnel and the dark substance inside this funnel. The first one suggests the presence of a pollen chamber. The funnel like apex of the nucellus recalls similar structures in seeds of Carboniferous pteridosperms in which the integument did not form a micropyle (Rodkiewicz 1984). The dark substance inside the funnel of the nucellar apex reminds of the central column which seals off the nucellus after pollination. The central column occurs in seeds of Carboniferous pteridosperms and also e.g. of the recent *Ginkgo biloba* (Rodkiewicz 1984).

The presence of such characters seems to suggest the affinity of *A. szaferi* with pteridosperms, nevertheless it is not safe to draw conclusions based only on one or two specimens. There are a few more indications suggesting the affinity with pteridosperms. According to

Harris (1935) „The form – genus *Allicospermum* would include among recent plants, the seeds of *Ginkgo*, Cycads and some Conifers and among fossils, the seeds of *Nilssonia*, *Lepidopteris* and *Stachyotaxus*". As there are present bisaccate pollen grains, only pteridosperms and conifers can be taken into consideration. It is, however, generally accepted that the presence of a distinct pollen chamber in conifers is doubtful (Rodkiewicz 1984). Finally, the pollen grains found during maceration of seeds can be attributed to the genus *Alisporites* which is usually regarded as pollen of pteridosperms.

It may be interesting to quote here the opinion of Emberger (1968) on the affinities of pteridosperms and certain other plant groups which is based on the structure of their seeds. According to Emberger, as seeds of those plants do not show embryos, they are not true seeds, only ovules which contain a prothallus. They differ from true seeds also in certain other characters, among them in possessing a well developed pollen chamber. Emberger created for plants with this type of seed (*Pteridospermales, Cordaitales, Nilssoniales, Cycadales* and *Ginkgoales*) the new group *Prephanerogamae,* so that in the *Gymnospermae* remain only the *Bennettitales* and *Coniferales*.

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REFERENCES

Archangelsky S. & Romero E. J. 1974. Polen de Gymnospermae (Coniferas) del Cretacico superior y Paleoceno de Patagonia. Ameghiniana, 11(3): 217-236.

Emberger L. 1968. Les plantes fossiles. Masson et C^{ie}, Editeurs. Paris.

Erdtman G. 1972. Pollen and spore morphology Plant taxonomy. Hafner Publ. Comp., New York.

Greuter W. (ed.) 1988. International Code of Botanical Nomenclature. Regnum vegetabile vol. 118, Koeltz Scientific Books., Königstein.

Harris T.M. 1933. A new member of the Caytoniales. New Phytol., 32: 97-114.

– 1935. The fossil flora of Scoresby Sound, East Greenland, 4. Medd. Gronland, 112(1): 1-176.

Hughes N.F. 1961. Further interpretation of *Eucommiidites* Erdtman 1948. Palaeontol., 4: 292-299.

Jansonius J. 1971. Emended diagnosis of *Alisporites* Daugherty 1941. Pollen et Spores, 13(2): 349-357.

Konijnenburg-Cittert J.H.A. van 1971. In situ gymnosperm pollen from the Middle Jurassic of Yorkshire. Acta Bot. Neerl., 20(1): 1-97.

Potonié R. 1956, 1958, 1960, 1966, 1970. Synopsis der Gattungen der Sporae dispersae. Teil I-V, Beih. Geol., Jb., 23, 31, 39, 72, 87.

Reymanówna M. 1968. On seeds containing *Eucommiidites troedssonii* pollen from the Jurassic of Grojec, Poland. J. Linn. Soc. London Bot., 61(384): 147-152.

— 1973. The Jurassic flora from Grojec near Kraków in Poland. Part II. *Caytoniales* and anatomy of *Caytonia.* Acta Palaeobot., 14(2): 45-87.

Rodkiewicz B. 1984. Embriologia roślin nagozalążkowych. PWN, Warszawa.

Taylor T.N., Cichan M.A. & Baldoni A.M. 1984. The ultrastructure of Mesozoic pollen: *Pteruchus dubius* (Thomas) Townrow. Rev. Palaeobot. Palynol., 41(3-4): 319-327.

Townrow J.A. 1962a. On *Pteruchus*, a microsporophyll of the *Corystospermaceae*. Bull. Br. Mus. (Nat. Hist.) Geol., 6(2): 289-320.

— 1962b. On bissaccate pollen grains of Permian to Middle Jurassic age. Grana Palynol., 3(2): 13-44.

Wcisło-Luraniec E. & Ichas J. 1986. Resumes des Communications. Colloque: L'Evolution des Gymnospermes. Montpellier p. 56-57.

STRESZCZENIE

Liasowe (dolna jura) nasiona *Allicospermum szaferi* sp. nov. z Polski północnej nazwano na cześć Profesora Władysława Szafera, który życzył sobie, aby badania w dziedzinie paleobotaniki mezozoiku Polski były kontynuowane.

W paleobotanice starszej szczególnie ważna jest znajomość obowiązującej terminologii. Praca ta dotyczy kopalnych nasion. Obecnie jednak termin zalążek i nasienie jest używany przez paleobotaników zamiennie. W przypadku okazów kopalnych najczęściej nie potrafimy stwierdzić, czy posiadały one zarodki, czy nie. Wynika to ze sposobu zachowania tych nasion i trudności w interpretacji. Gdy nasiona są dobrze zachowane, wtedy często brak w nich zarodków.

Francuski paleobotanik Emberger (1968) dzieli rośliny zaliczane obecnie do nagozalążkowych na dwie grupy. Pierwsza grupa obejmuje rośliny wytwarzające zalążki z prothallium, a więc jego zdaniem, nie prawdziwe nasiona. Nazwał tę grupę *Prephanerogamae.* W jej skład wchodzą *Pteridospermales, Cordaitales, Nilssoniales, Cycadales* i *Ginkgoales.* Druga grupa to *Bennettitales* i *Coniferales*. Rośliny te tworzą już prawdziwe nasiona, tzn. z zarodkiem. Te dwie grupy różnią się też innymi cechami, jak np. występowaniem rozwiniętej komory pyłkowej u *Prephanerogamae.*

Opisane przez nas nasiona *Allicospermum* ukazały po zmacerowaniu szereg struktur, takich jak błona megaspory, kutikula nucellusa z charakterystycznym szczytem w kształcie

lejka oraz fragmenty kutikuli epidermy integumentu z komórkami kamiennymi. W 5 z 9 macerowanych nasion obserwowano także dwuworkowe ziarna pyłku. Te ziarna pyłku w liczbie 20 wydają się należeć do jednego gatunku, który nazwano *Alisporites* sp. 1. Uważa się na ogół, że ziarna pyłku z rodzaju *Alisporites* są wytwarzane przez *Pteridospermales*.

W dwóch nasionach ziarna pyłku występowały w komorze pyłkowej. Obecność komory pyłkowej pozwoliła zaliczyć nasiona *Allicospermum szaferi* do *Pteridospermales*. Wykluczyłoby to opisane nasiona z *Gymnospermae* w ujęciu Embergera, a należałoby je zaliczyć do *Prephanerogamae*.

Na powyższy temat wygłosiłyśmy referat na Międzynarodowej Konferencji „L' Evolution des Gymnospermes" w Montpellier w 1986 roku.

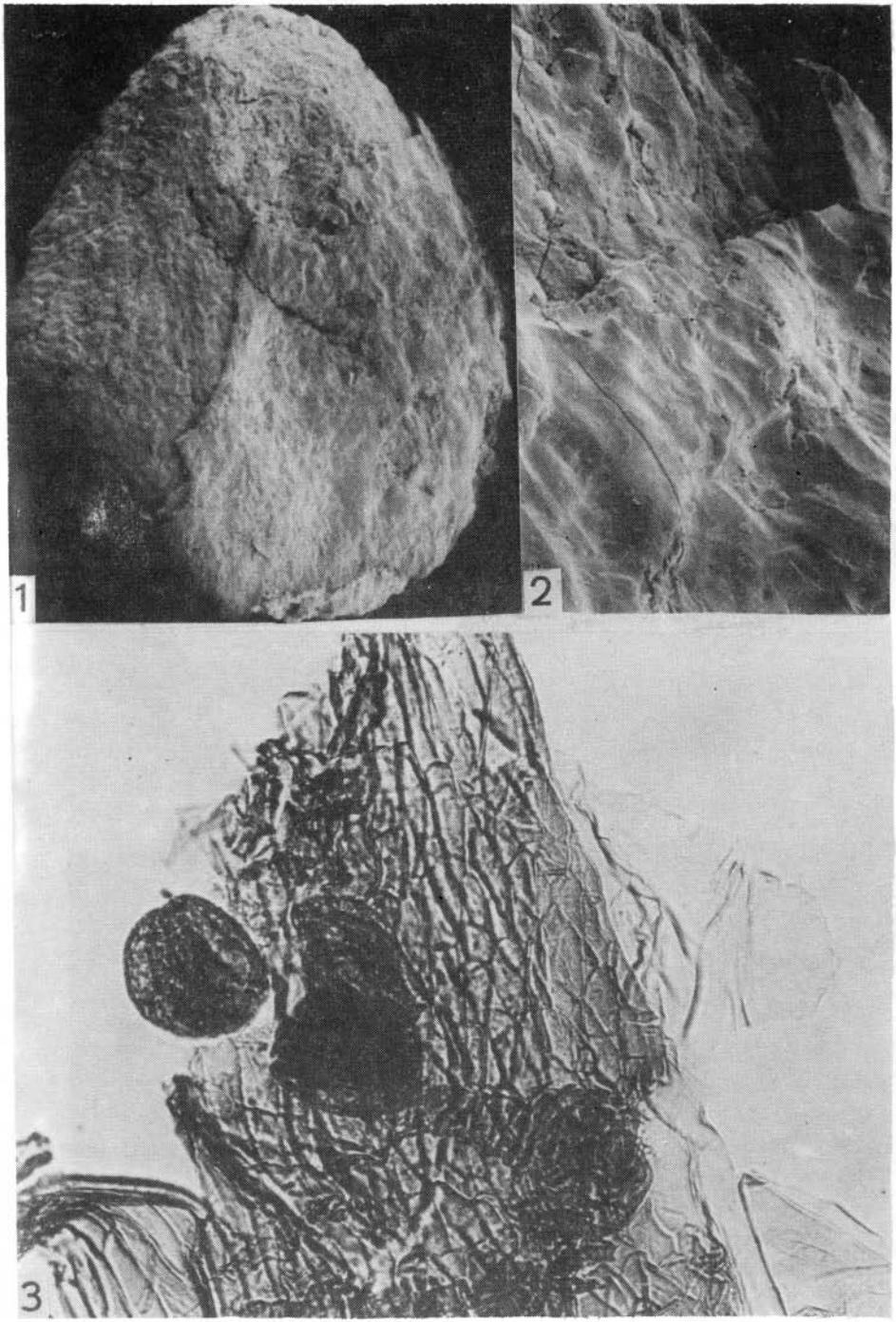
PLATES

PLATE I

Allicospermum szaferi sp. nov.

1. Seed with incomplete outer layer. Isotype. IB PAN PM S926, SEM x 45.
2. Surface detail of the same seed, showing margin of outer layer, SEM x 300
3. Bisaccate pollen grains and fragments of cuticle of nucellus and integument, IB PAN PM S930, x 430

Plate I



E. Wcisło-Luraniec and J. Ichas-Ziaja
Acta Palaeobotanica 30/1,2

PLATE II

Allicospermum szaferi sp. nov.

1. Apex of macerated seed (explanations with Fig. 2). Holotype, slide IB PAN PM S924, x 250
2. Stone cell of integument, IB PAN PM S929, x 1200
3. Megaspore membrane, IB PAN PM S928, x 250
4. Megaspore membrane, IB PAN PM S927, x 1200
5. Pollen grain of *Alisporites* sp. 1 below cuticle of nucellus and above megaspore membrane of the holotype, IB PAN PM S924, x 940
6. The same grain at higher focus

Plate II

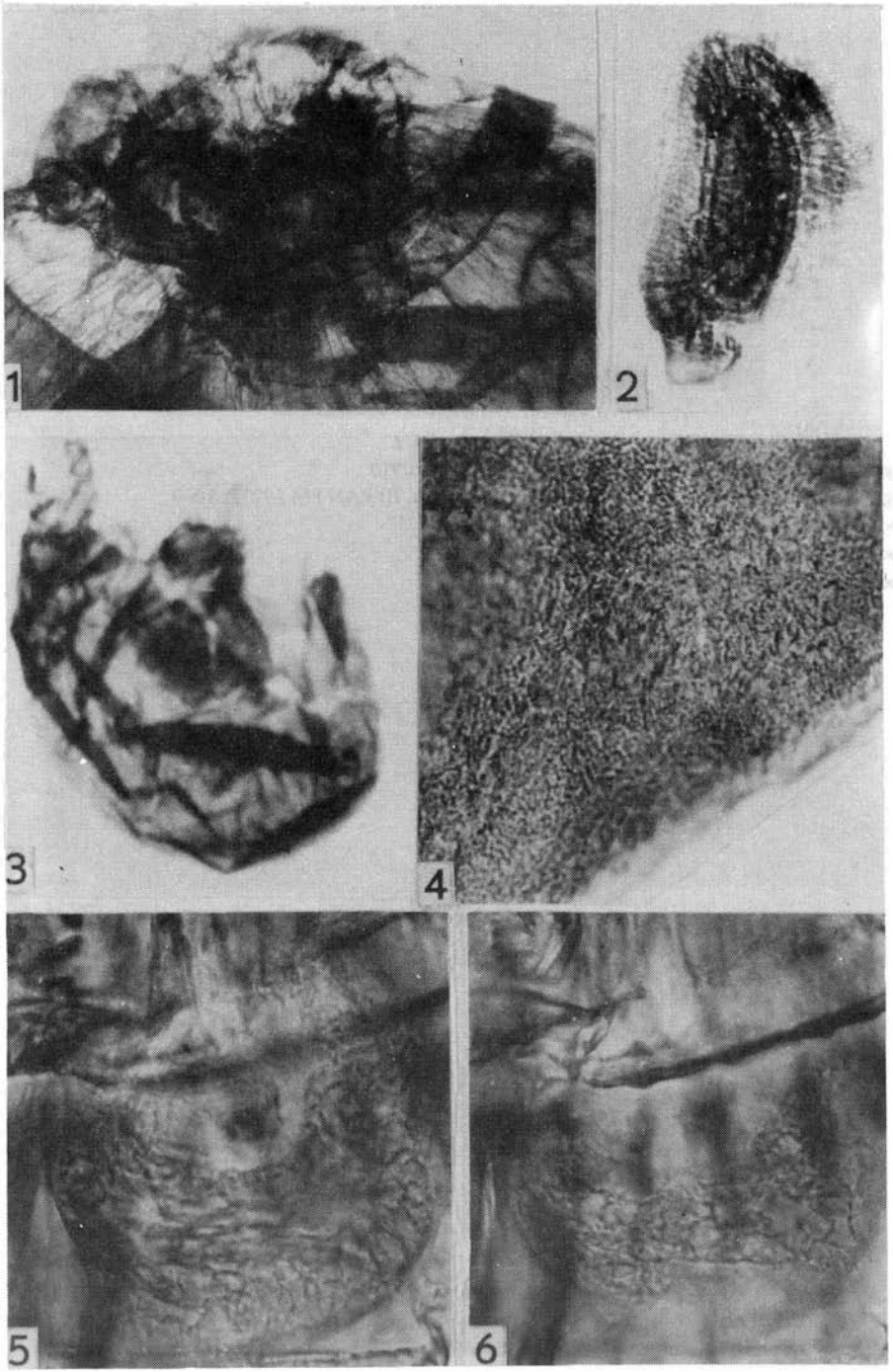


PLATE III

Alisporites sp. 1

1. Pollen grain inside seed of the holotype, IB PAN PM S924, x 910
2. Pollen grain in lateral transverse view with cuticle fragments, IB PAN PM S927, x 1060
3. Same pollen grain at lower focus
4. Same pollen grain at still lower focus
5. Same pollen grain at lowest focus

Plate III

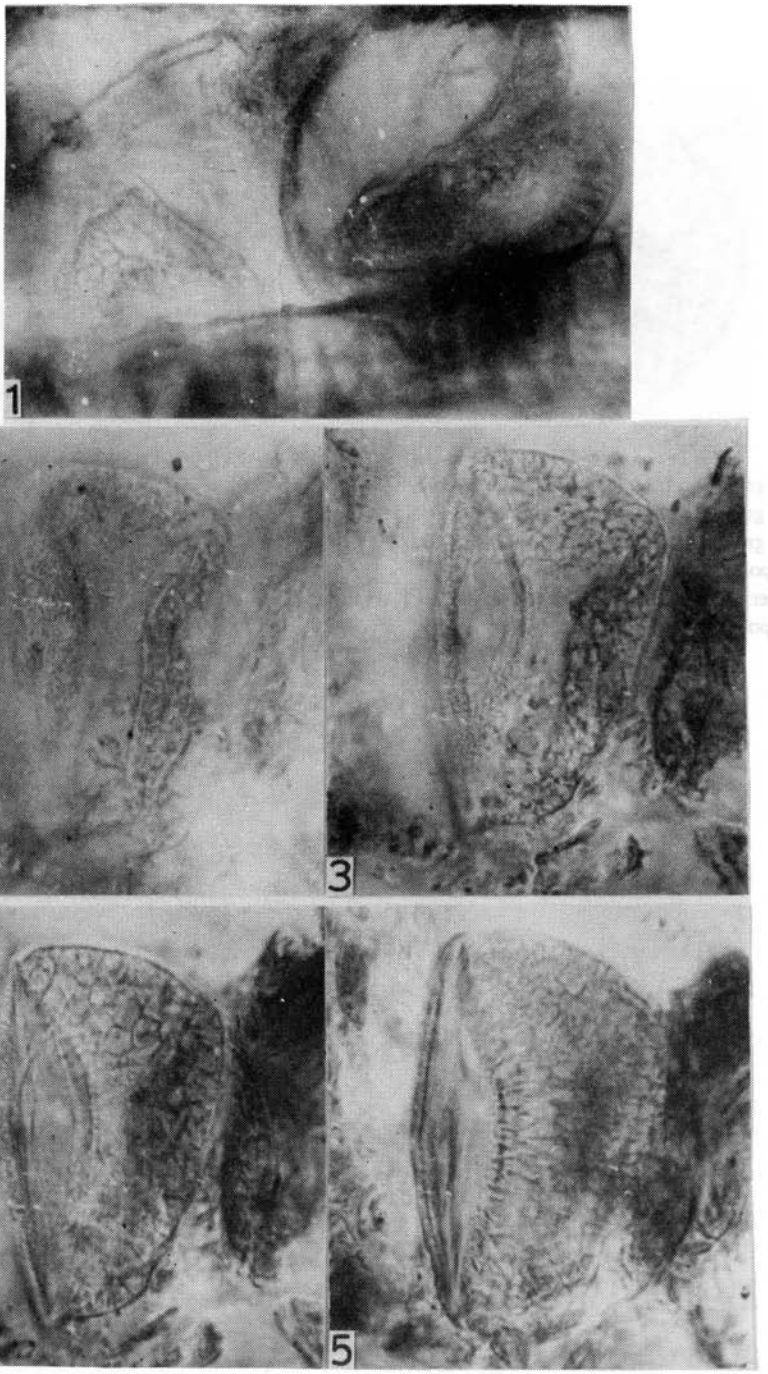
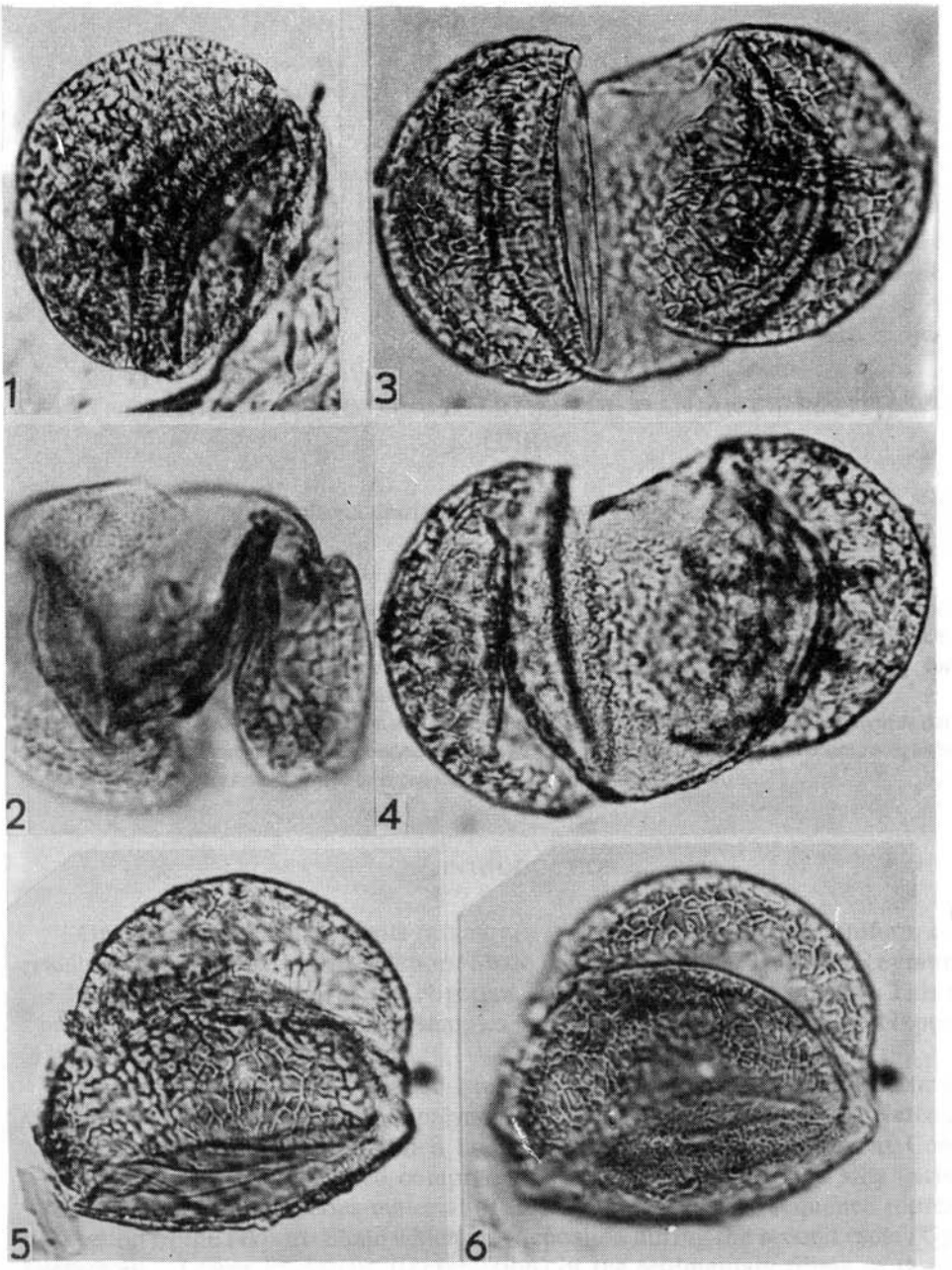


PLATE IV

Alisporites sp. 1 (found in maceration fluid of seeds)

1. Pollen grain and fragment of nucellar cuticle, IB PAN PM S930, x 1000
2. Pollen grain in approximately lateral longitudinal view, IB PAN PM S937, about x 1000
3. Pollen grain in polar view, IB PAN PM S932, x 1000
4. Same pollen grain at lower focus
5. Another pollen grain from the same seed, IB PAN PM S932, x 1000
6. Same pollen grain at different focus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