

A Reappearance of an Archaic Structure in the Latest Permian Seeds

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Abstract—A new seed-genus *Lazarospermum* Krassilov gen. nov. is described from the uppermost Permian of eastern Kazakhstan. It is characterized by an archaic integument structure, distally open, with long spine-like lobes, as in the Devonian and a few Carboniferous seeds. Such seed structures were not hitherto reported from the Permian. A reappearance of the archaic seed structure might have been related to a new function acquired by the integument as an exozoochorous adaptation arising in the stressed environments of the latest Permian.

INTRODUCTION

A collection of fossil plants from the Upper Permian locality of Karaungir in eastern Kazakhstan (Novozhilov, 1970) contains seed remains that are of particular interest in the phylogeny of Paleozoic gymnosperms. The seed shows structural features characteristic of preovules produced by the most primitive gymnosperms that appeared at the dawn of seed-plant history in the middle Devonian.

Recent studies of primitive ovules and preovulate structures have shown that seed-coats were formed of syntelomic branch systems surrounding megasporangia of ancestral free-sporing plants. The ultimate branchlets became fused in their proximal parts remaining free distally. Micropyles are lacking in such primitive preovulate structures. Instead, the pollen-receptive structures developed from the nucellar apex variously modified for this function. The integumental appendages apparently played a role in capturing pollen grains or in aerodynamically directing them to the pollen chamber.

In the Late Devonian–Early Carboniferous, micropyles developed in different gymnosperm lineages, while the pollen-capture function was transferred from the nucellar apex to the integument. This process was virtually completed by the end of the Early Carboniferous, with open integuments retained in a few archaic groups alone. The latter include pteridosperms with many-seeded cupules, such as *Gnetopsis* or *Calathospermum*. Dispersed seeds of *Calathospermum* are assigned to the seed-genus *Salpingostoma*. Both *Gnetopsis* and *Salpingostoma* developed long, densely pubescent integumental appendages that supposedly functioned as elements of their pollination mechanism. These peculiar plants apparently became extinct before the end of the Carboniferous. The more puzzling is a find of a dispersed seed with preovulate integumental structure in the uppermost Permian Akkolkanskaya Formation of eastern Kazakhstan correlated with the

Upper Tatarian Substage of the stratotype area in the Volga Basin.

Whether this find represents a relict gymnosperm that had survived from the Early Carboniferous or an archaic morphology of primitive preovules that had reappeared because of a character reversal remains an open question. The resurrection hypothesis seems plausible with respect to evolutionary events associated with the major biospheric crisis at the end of the Permian. Character reversals might occur in morphological structures no longer phenotypically apparent but retained as a genetic potential.

In recent years the problem of survival after near extinctions attracts attention from conservation biology and biodiversity studies. The “resurrected” forms are called Lazarus species, alluding to Lazarus of the Bible. Resurrection seems applicable not only to taxa, but also to the temporarily unexpressed morphological features. The seeds with an open lobed integument found in the upper horizons of the Permian can certainly be considered as a Lazarus morphotype. The reappearance of such Lazarus morphotypes at a time of geological crises is a noteworthy phenomenon awaiting further analysis.

SYSTEMATIC PALEONTOLOGY

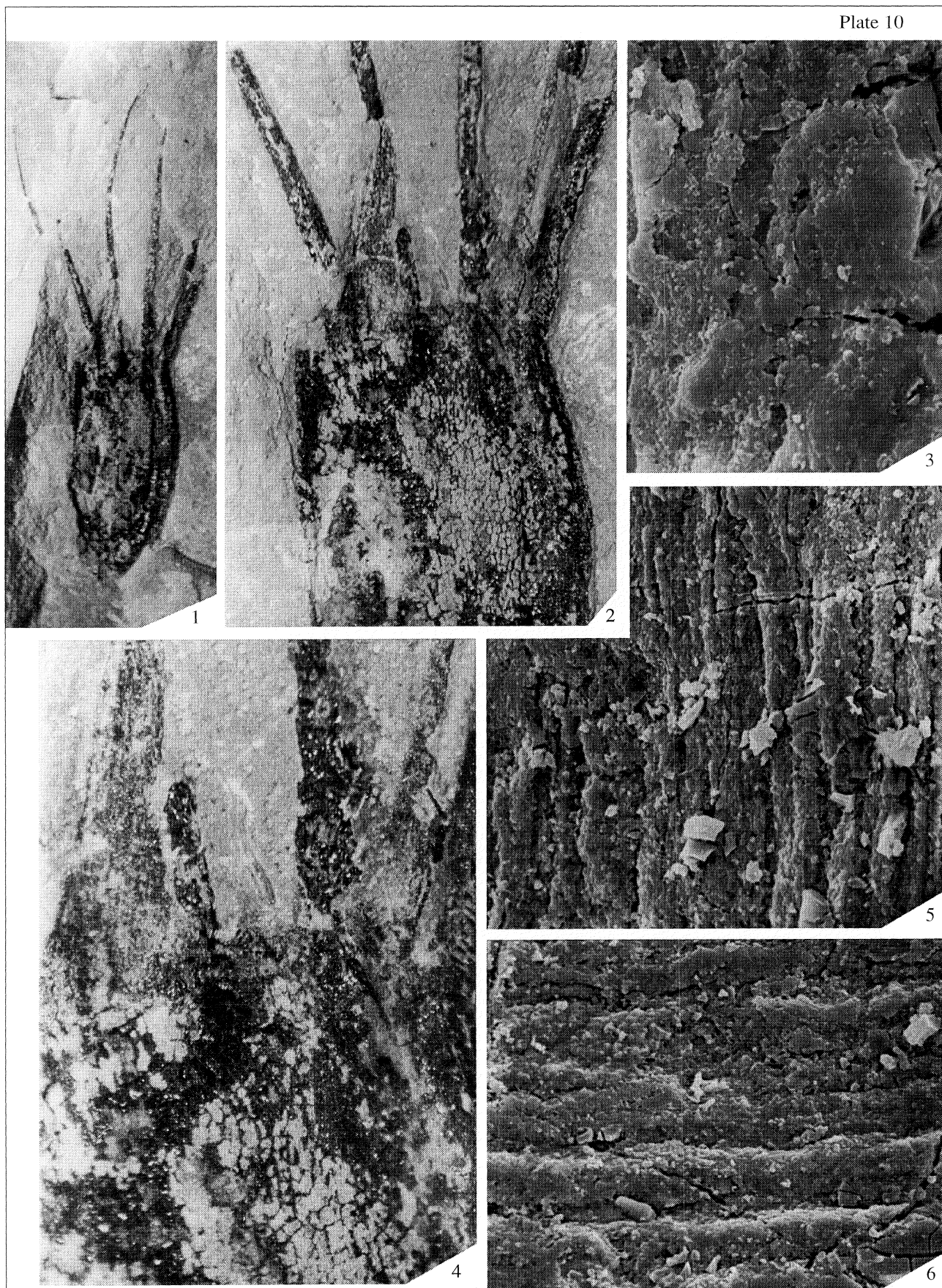
Genus *Lazarospermum* Krassilov, gen. nov.

Etymology. After Lazarus of the Bible and Greek *spermum* (seed).

Type species. *Lazarospermum permicum* Krassilov, sp. nov.; Upper Permian, Tatarian Stage; Eastern Kazakhstan.

Diagnosis. Seed with integument distally divided into eight linear stiff spine-like lobes longer than seed body. The latter elongate-obovate, ribbed, gradually tapering to base. Nucellus free from integument, with apex slightly protruding between integumental lobes.

Plate 10



Comparison. Among the primitive seeds or pre-ovules with an open distally lobed integument at least two genera are similar to the Kazakhstani form both in general morphology and the ratio of body length to the length of the apical appendages. These genera are *Gnetopsis* and *Salpingostoma*, differing from each other mainly in the mode of attachment: the preovules are sessile in the former genus, stalked in the latter. In both genera the apical integumental appendages are much longer than the seed body. The seeds of *Gnetopsis* are represented in the Late Carboniferous by a few finds of *G. elliptica* Renault et Zeiller (Doubinger *et al.*, 1995). They are much larger than the Permian form and typically have only three apical appendages that are dichotomously divided. Among the Carboniferous species of *Salpingostoma* the most similar is *S. prinsii* Van Amerom from the Westphalian of The Netherlands (Van Amerom, 1990). In the latter species the seed body is considerably shorter than in the Kazakhstani form, whereas the apical integumental appendages are of nearly the same length. There are six apical appendages and a respective number of surface ribs showing scattered pits at the hair bases. In *Tantalosperma* and *Dolichosperma* the integumental lobes are relatively short, not exceeding the length of the body.

The new genus differs from other genera of the same morphological group in the relatively short apical integumental assemblages, the length of which only slightly exceeds the body length, a greater number of appendages and, respectively, the surface ribs of the body, as well as in the reduced pollen-receptive structures of the nucellar apex.

Species composition. Type species alone.

Lazarospermum permicum Krassilov, sp. nov.

Plate 10, figs. 1–6

Name. From the Permian.

Holotype. PIN, no. 4744-1; Eastern Kazakhstan, northern slope of the Saur Range, right bank of the Karaungir River, the shore cliff 400–500 m downstream of the Maychat Creek; Upper Permian, Tatarian Stage, Vyatkian Substage, Bykovskian Horizon, Akkolkanskaya Formation, 3–5 m above the boundary with the Maychatskaya Formation (Plate 10, figs. 1–6).

Diagnosis. As for the genus.

Description. A single specimen of the seed is elongate in outline, gradually tapering to the base. The length of the body without apical appendages is 6 mm, with appendages –13 mm, maximal width in the distal part 3 mm. The seed apex with eight spine-like appendages slightly longer than the body. The body surface shows broad slightly protruding ribs each of which

ends in a spiny appendage. The nucellar apex protrudes as a low knob between the bases of integumental lobes (Pl. 10, fig. 4). The lobes are directed forward, spread at an acute angle and slightly curved forming an apical cluster. Six appendages are fully preserved in the bedding plane, the seventh is broken at the base and the eighth is seen in the distal part of the tuft. The appendages are about 0.3–0.4 mm thick, expanded to 0.8 mm at the base. The expanded basal part shows longitudinal striations. The rest of the appendages is smooth, lacking any traces of trichomes.

The outer integumental cuticle consists of elongate thick-walled cells, rounded at the ends, about 20–25 μm wide, arranged in slightly arched longitudinal files (Pl. 10, fig. 6). In SEM the body surface shows pits conceivably corresponding to the hair bases (Pl. 10, fig. 3). The surface layer is separated from the nucellar cuticle by a coaly layer about 0.5 mm thick perhaps representing the stone tissue. The nucellar cuticle is traced to the base of the seed body, thick, with ribbed longitudinal cell walls (Pl. 10, fig. 5). The nucellar cells are narrow, elongate, with wedge-shaped or truncate ends, about 10–12 μm wide, arranged in regular longitudinal files.

Material. The holotype.

DISCUSSION

The morphological diversity of Paleozoic plants is assessed by the remains of both their vegetative and reproductive organs, in particular, the dispersed seeds or ovules. Structural characters of the latter are evidence of dispersal modes in Paleozoic plants. A considerable part of Paleozoic seeds lack any special dispersal structures, although their relatively large size and thick seed-coats might suggest a zoochorous adaptation. At the same time, there were various winged samaroid seeds the most widespread among which were forms with a bilateral wing interrupted at the micropyle. Such forms constitute a considerable part of seed assemblages in both Euramerian and Angarian realms. Less widespread were forms with a one-sided wing, as in *Sylvella* occurring in the fossil plant localities of the Angarian and Subangarian realms. The one-sided wing provides for the spin of the seed that screws it into the ground. Such adaptations are typical for plants that shed their seeds in winter or early spring falling on snow or moist ground. Their appearance in Paleozoic plants of the Angarian realm has, therefore, a certain paleoclimatological meaning.

The new find shows that the morphological diversity of the seed types in Permian plants might have been

Explanation of Plate 10

Figs. 1–6. *Lazarospermum permicum* sp. nov., holotype PIN, no. 4744-1, Upper Permian, Tatarian Stage, Karaungir locality, Eastern Kazakhstan: (1) seed outline, $\times 7$; (2) seed apex with appendages, $\times 15$; (3) pits of hair bases on the seed-body surface, SEM $\times 1100$; (4) nucellar apex protruding between the bases of appendages, $\times 30$; (5) nucellar cells, SEM, $\times 600$; (6) integumental cells, SEM, $\times 600$.

greater than expected. Other forms with various appendages have recently been discovered in the Permian fossil plant localities (Dilcher *et al.*, 1997). Although the new form is morphologically similar to the Carboniferous preovules with long lobes of open integument, the functional significance of the apical appendages could be entirely different. In the Carboniferous forms the appendages were densely pubescent and pappus-like, probably serving for wind-dispersal. In the larger seeds of *Gnetopsis* that were too heavy for wind dispersal the appendages might function as a pollen-capture device. In the Permian form the appendages are glabrous, spine-like, perhaps functioning as glochidia by sticking to the hair of animal dispersal agents. Since derived forms of therapsid reptiles appearing in the latest Permian might have been covered with hair or hair-like scales, the archaic seed structure retained in some gymnosperm lineages might have acquired a new functional meaning with respect to exozoochorous dispersal.

Thus, the long survival of the archaic seed morphology with an open integument apically divided into long linear lobes seems related to the change of function with the developing exozoochorous mode of dispersal. A morphological similarity with *Salpingostoma prinsii* may evidence phylogenetic links between the Permian

Lazarospermum and the Westphalian forms in which the ovules developed in the polyspermic cupules. Such cupules are not yet discovered in the Permian plants. Moreover, no forms with open integument were found in the long stratigraphic interval separating the Westphalian and Late Permian species. Thus the archaic structure, typical of early gymnosperms, was probably retained as a genetical potential through the Late Carboniferous and Permian to reappear in the terminal representatives of Paleozoic lineages at the time of radical restructuring of the vegetation.

REFERENCES

- Dilcher, D., Mei, M., and Du, M., A New Winged Seed from the Permian of China, *Rev. Palaeobot. Palynol.*, 1997, vol. 98, no. 3/4, pp. 247–256.
- Doubinger, J., Vetter, P., Langiaux, J., Galtier, J., and Brouin, J., *La flore fossile du bassin houiller de Saint-Étienne*, *Mém. Mus. Nat. d'Histoire Natur.*, 1995, vol. 164, pp. 1–355.
- Novozhilov, N.I., *Vymershie limnadioidei* (The Extinct Kimnadioideans), Moscow: Nauka, 1970.
- Van Amerom, H.W.J., *Salpingostoma prinsii* nov. sp. and *Gnetopsis robusta* nov. sp., Two New Seeds from the Westphalian A/B of Southern Limburg, *Meded. Rijks Geol.*, 1990, vol. 44-2, pp. 2–11.