

# New Interpretation of Seeds *Grenana* Samylina (Gymnospermae) from the Middle Jurassic of Angren, Uzbekistan

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**Abstract**—The seeds described by Samylina (1990) from the Middle Jurassic of Angren (Uzbekistan) as *Grenana angrenica* are revised. Samylina also described under this name the ovuliferous organs and leaves found in the same locality in association with these seeds, selected a leaf specimen as a holotype, and interpreted *G. angrenica* as a peculiar seed fern. The revision shows that the seeds exhibit structure characteristic of the Ginkgoales. The seeds, leaves, and ovuliferous organs were not found in organic connection with one another. Therefore, they cannot be described under the same name, despite the considerable similarity in epidermal-cuticular features. The dispersed seeds of ginkgoalean affinity are usually attributed to the genus *Allicospermum* Harris. On the basis of reexamination of the Angren material, a new species, *Allicospermum budantsevii* sp. nov., is described.

**Keywords:** Middle Jurassic, *Allicospermum* Harris, gymnosperms, Ginkgoales

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## INTRODUCTION

The genus *Grenana* was established by V.A. Samylina (1990) based on studying fragments of narrow cuneate dichotomously dissected leaves, ovuliferous organs, and seeds found in association in the same sample of cuticular coals, coming from the Middle Jurassic locality Angren, Uzbekistan. Based on the considerable similarity in the epidermal structure of leaves, ovuliferous organs, and seeds, Samylina described them under the same generic and species name and designated a leaf fragment as a holotype. She also proposed a reconstruction of the plant in which the terminal segments of leaves bore terminal single-seeded cupules. Based on this reconstruction, Samylina placed *Grenana* in the pteridosperms. The subsequent authors repeatedly pointed out affinity of *Grenana* to the Ginkgoales (Zhou, 1997, 2009; Kvaček et al., 2005; Naugolnykh, 2007), since the ovuliferous organs from Angren have collars characteristic of the Ginkgoales. However, this material has not been revised.

Earlier the author of the present paper described seed organs of the pteridosperm *Vladimaria octopartita* Gordenko from the Middle Jurassic Mikhailovskii Rudnik locality that outwardly resemble seed organs of *Ginkgo* L. but fundamentally differ from them in structure (Gordenko, 2010). In *V. octopartita* the stalk expands into a collar and is virtually undistinguishable from the collar of *Ginkgo* in morphology. Since the presence of a collar was established in a representative of another order of gymnosperms and, thus, it ceased

to be a unique feature of the genus *Ginkgo*; hence the necessity to revise the material from Angren.

Previously Nosova and Gordenko (2012) carried out a preliminary study that corroborates the attribution of the leaves, ovuliferous organs, and seeds to ginkgoaleans. Nosova (2013) revised the leaves together with the associated ovuliferous organs.

In a separate publication Zavialova et al. (2013) presented preliminary data on morphology and ultrastructure of pollen grains found in the pollen chamber of *Allicospermum budantsevii* sp. nov. This paper revises the seeds that were found in association with the leaves and ovuliferous organs and were attributed by Samylina to *Grenana angrenica*.

## MATERIAL

The material studied comes from a sample of cuticular coal that was taken by L.Yu. Budantsev in 1976 from a dump of a coal seam in the Middle Jurassic (Aalenian–Bajocian) deposits of the Angren Formation (Angren coalfield, Uzbekistan) and passed by him to Samylina for studying. Samylina extracted from the sample seeds together with numerous fragments of leaves and ovuliferous organs. Based on this association Samylina (1990) established a new genus and species *Grenana angrenica*. Some of the material on seeds presented in this paper has been published; however, no detailed study has been carried out. Samylina (1990) only studied the outer cuticle of seed integument and pointed out the presence of a stony layer in

the seeds. Recently Nosova extracted additional material from the same sample, and some of this is studied in the paper.

The seeds under study were first cleaned in concentrated hydrofluoric acid, subsequently examined using an electron scanning microscope Tescan without gold coating in low vacuum mode and a BSE detector. Some of them were then macerated using a standard technique: they were first treated with Schulze's solution for 3 hours and then washed with distilled water and treated with KOH solution.

In most of the seeds only the outer cuticle of integument has been preserved. Only one seed has yielded a cuticle of integument, cuticle of the upper third of nucellus, and a fragment of the megaspore membrane; in the pollen chamber monosulcate pollen grains have been revealed. The light microscope photographs of the general view of seeds, fragments of nucellus, and resin canals were taken under a stereomicroscope Leica M165C with a digital camera DFC 420C, the photographs of the pollen chamber and outer cuticle of integument were taken under a microscope Axioplan-2 with a digital camera DFC 420.

Some preparations of the outer cuticle of integument, resin canals, and nucellus cuticle were mounted on stubs, sputter-coated with gold, and examined with scanning electron microscopes Camscan and Tescan in high-vacuum mode using a BSE detector; in the same mode the ultrastructure of megaspore membrane was examined with a microscope Tescan.

The ultrastructure of megaspore membrane is described in terminology adopted by Zhou (1993) and Yang et al. (2008).

Collection no. 813 is repositied in B.L. Komarov Botanical Institute of the Russian Academy of Sciences (BIN).

## SYSTEMATIC PALEOBOTANY

### GYMNOSPERMAE

#### *Genus Allicospermum* Harris, 1935

*Allicospermum budantsevii* Gordenko, sp. nov.

*Grenana angrenica* Samylina: Samylina, 1990, p. 848, pl. II, figs. 4–6; pl. III, figs. 13–16.

**E t y m o l o g y.** In honor of the paleobotanist Lev Yustinianovich Budantsev.

**H o l o t y p e.** BIN, no. 813/1 N 48, seed; Uzbekistan, Angren coalfield; Angren Formation, Middle Jurassic; Figs. 1a, 1b; 2a–2c, 2f (Samylina, 1990, p. 848, pl. III, figs. 13, 14); designated here.

**D i a g n o s i s.** Seeds bilateral, ellipsoidal, rounded or pointed in their apical part, rarely abruptly narrowed near chalaza, 5–10.7 mm long, 3.9–9.8 mm wide. Micropyle protruding, mucronate.

Integument consists of sarcotesta, containing numerous resin bodies, and sclerotesta. The outer integument cuticle thick, with numerous scattered, randomly orientated stomata. Stomata monocyclic or

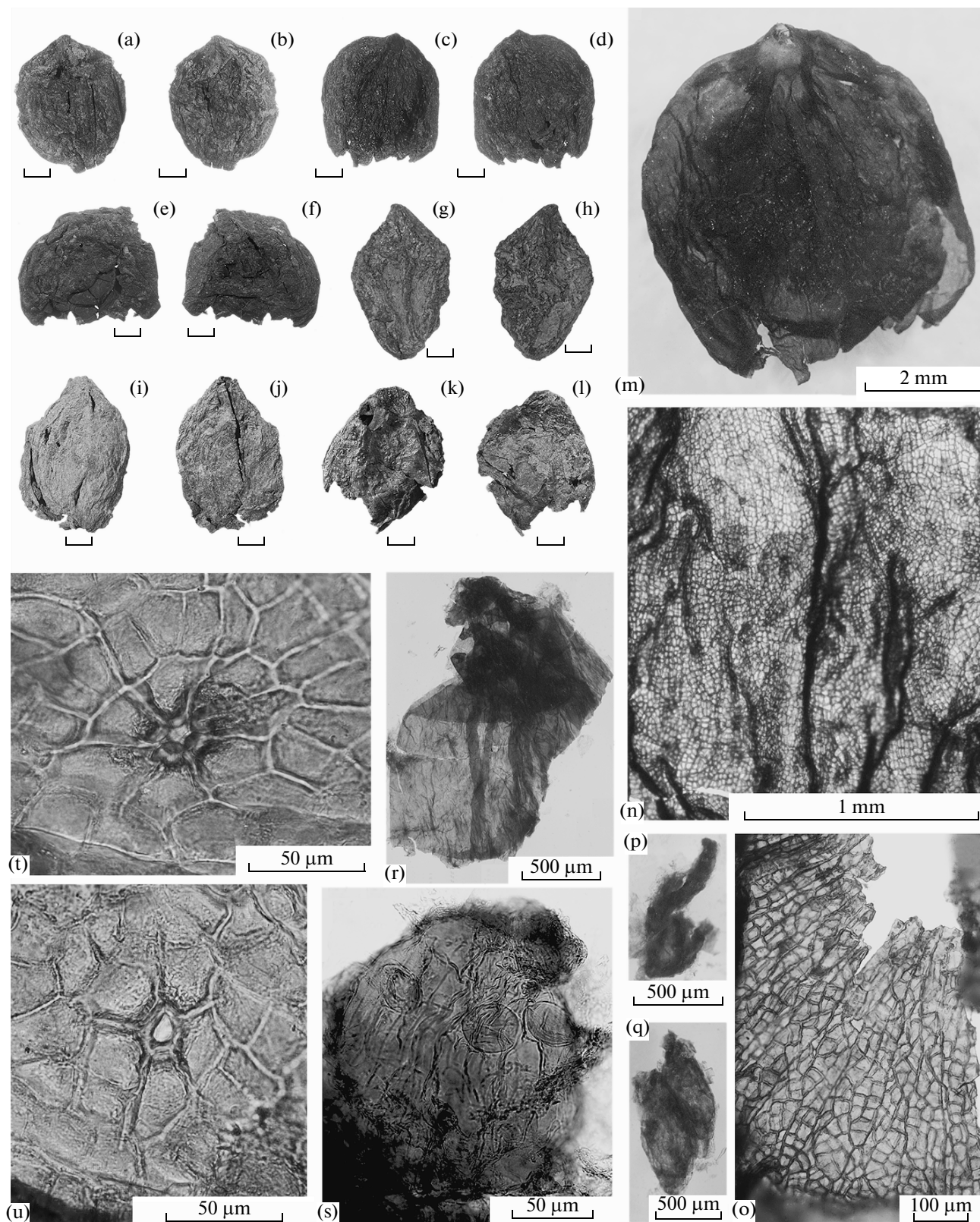
very rarely incompletely amphicyclic, with 5–8 (usually 7–8) subsidiary cells. In the middle part of seed, subsidiary cells often bear variously developed proximal papillae, near seed base and micropyle predominantly without papillae. Subsidiary cells of the same size as ordinary epidermal cells. At base and in apical part of seed, ordinary epidermal cells form longitudinal chains, prominent in outer surface relief; in the middle part of seed, ordinary cells form cell packets. Anticlinal cell walls straight or slightly curved, cell corners rounded. Periclinal cell walls dome-shaped, thickened.

Nucellus free from integument on at least one third, with well distinguished pollen chamber, containing monosulcate pollen grains. Nucellus cuticle thin, consists of longitudinally elongated tetragonal, less common pentagonal cells. Cell corners slightly rounded. Periclinal cell walls flat.

Megaspore membrane up to 3 µm thick, consists of alveolar and foot layers. Foot layer finely granular, 0.3 µm thick. Alveolar layer consists of irregularly branched and coalescent bacula, 0.3–1.5 µm long, about 0.2–0.3 µm thick, orientated obliquely relative to foot layer.

**Description** (Figs. 1a–1u; 2a–2h; 3a–3k, 4a–4g; 5). The collection contains detached presumably almost mature seeds (Figs. 1a–1l) and their fragments. The seeds are bilateral, variously compressed, strongly flattened, and usually incompletely preserved. The cell base and micropyle are often broken. The most completely preserved specimens are ellipsoidal or widely fusiform in outline; they narrow near the chalaza and have a projection resembling a stalk (Figs. 1a, 1b, 1k, 1l), near the micropylar pole they are rounded or slightly pointed, with a short tapered micropylar end and protruded micropyle (Figs. 2e, 2f). The seeds are 5.00–10.70 mm long and 3.90–9.80 mm wide. The protruded part of the micropylar end is 0.10–0.15 mm long. The relief of seed surface is randomly folded (Fig. 2a), which is caused by changes during the fossilization. The integument consists of sarcotesta and sclerotesta (Fig. 2d). Both sarcotesta and sclerotesta are 0.2–0.5 mm thick. In all specimens the stone is strongly deformed, with average dimensions of 4.5 × 3.5 mm. Maceration of the seeds reveals a thick outer cuticle of integument (Fig. 1m), slender cuticle of nucellus, and megaspore membrane (Fig. 1r). On the surface of some seeds there are sporadic circular structures 200–600 µm in diameter, outlets of secretory canals (Fig. 2h).

The outer cuticle of integument is relatively thick, 3–6 µm, becoming thinner to the seed base and in the micropyle region. The ordinary epidermal cells are tetragonal or pentagonal (occasionally triangular or hexagonal), frequently form short longitudinal chains (Figs. 2c; 3b). The anticlinal walls of ordinary epidermal cells are straight or slightly curved and well cutinized, the cell corners are usually rounded. Closer to the micropyle the ordinary cells are slightly longitudi-



nally elongated and form more or less distinct rows (Fig. 1o). In the relief of the outer cuticular surface of the seed apex the chains of ordinary cells correspond to the longitudinal ridges of the same length (Figs. 2e, 2f). In the middle part of the seed the ordinary cells are predominantly more or less isodiametric, with convex thickened periclinal walls (Figs. 1n; 2c; 3a, 3b). In addition, they are assembled in fairly well-defined accumulations, cell packets in T. Harris's terminology (Harris, 1935); the number of cells in such accumulations varies from four to forty (Fig. 1n). The cell packets that can be seen in the upper third of the seed are longitudinally elongated, two or three cells in width (Fig. 1o). Closer to the seed base the cells are again arranged in long chains; they correspond to the longitudinal ridges in the relief of the outer surface (Fig. 2b). The ordinary epidermal cells are 10–40  $\mu\text{m}$  long and 10–36  $\mu\text{m}$  wide.

The outer cuticle of integument reveals more or less uniformly scattered and randomly oriented stomata (Figs. 1n, 2c; 3a). The density of stomatal apparatuses varies greatly and can attain 29 per 1  $\text{mm}^2$ . The stomata are often abortive (Fig. 3h). The stomatal apparatus are monocyclic, very infrequently incompletely amphicyclic, actinocytic (Figs. 1t, 1u; 3g–3k), there occur adjacent stomatal apparatuses with common subsidiary cells (Fig. 3h). There are five to eight subsidiary cells, usually seven or eight. They have the same measurements as the ordinary cells. Occasionally subsidiary cells are cutinized stronger than ordinary cells (Fig. 3j). In the middle part of the seed they frequently bear small proximal papillae about 5  $\mu\text{m}$  long, overhanging the aperture (Figs. 1t; 3b–3d), there also occur stomatal apparatuses devoid of papillae (Figs. 1u; 3e). Closer to the seed apex and base, the subsidiary cells usually have no papillae or papillae are restricted to some cells of the stomatal apparatus (Fig. 3f). The subsidiary cells with central papillae are of extremely rare occurrence (Figs. 3d). The stomatal aperture is 7–20  $\mu\text{m}$  long. The guard cells are sunken, in addition usually only their apertural walls are strongly cutinized (Figs. 3g–3i, 3k). In case the cutinization of the outer periclinal walls of guard cells retains, it is of wing-shaped outlines (Fig. 3j). Depending on the degree of cutinization of the outer periclinal walls, the cutinized parts of guard cells vary in length from 20 to 44  $\mu\text{m}$  and the stomata vary in width from 20 to 38  $\mu\text{m}$ . The cutinization of the polar

extensions is not always preserved. The polar extensions are up to 21  $\mu\text{m}$  long.

The sarcotesta contains numerous resin bodies of ellipsoidal or, more rarely, circular outlines with imprints of cells of secretory canals on their surface (Figs. 1p, 1q; 2g); the resin bodies can reach 1000  $\mu\text{m}$  in size, 100–500  $\mu\text{m}$  on average.

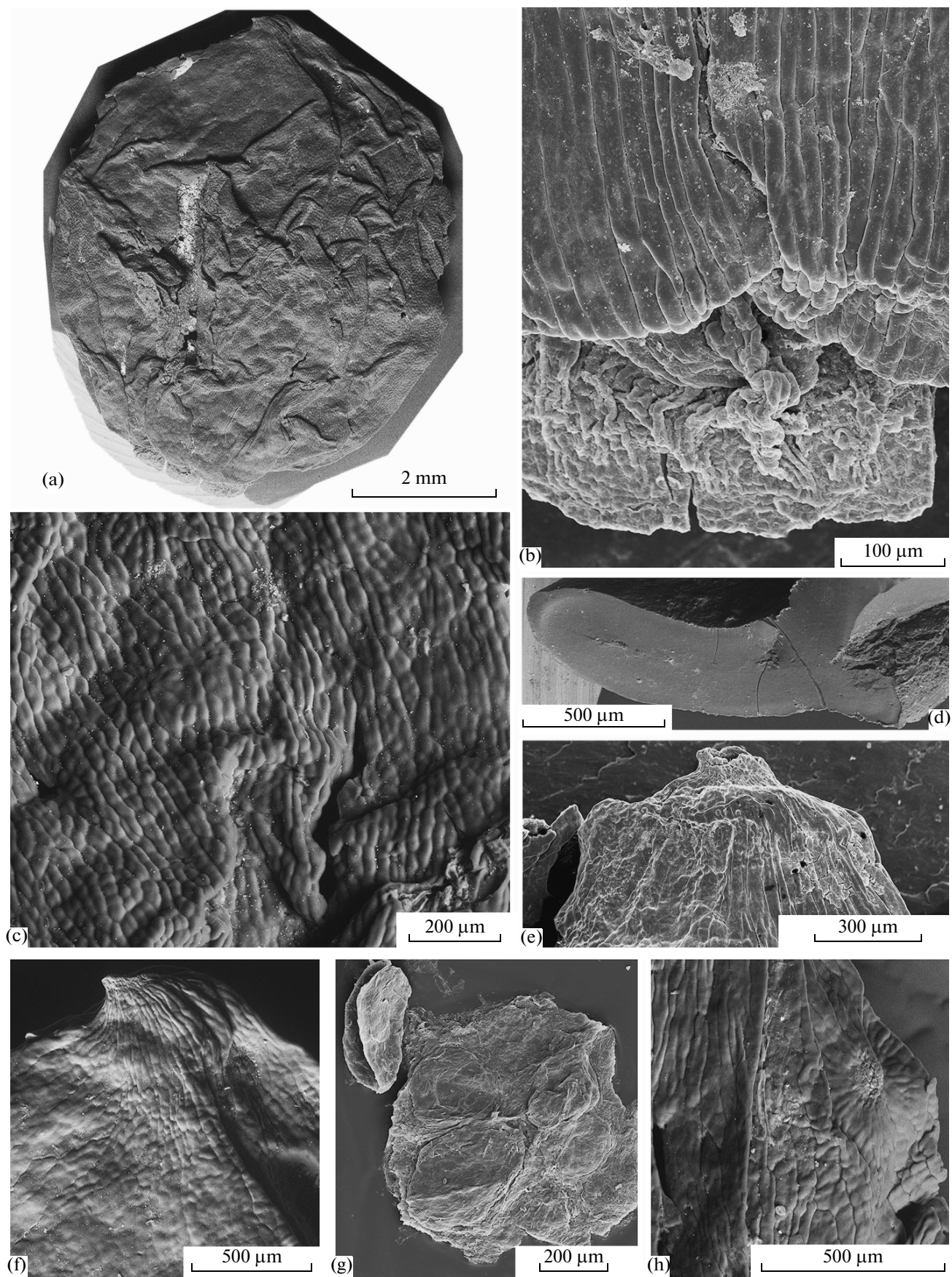
More than one-third of the nucellus is free from the integument, and there is a well-defined pollen chamber (Figs. 1r, 1s). The pollen chamber contains monosulcate pollen grains (Fig. 1s).

The nucellus cuticle is relatively thin, about 1.5  $\mu\text{m}$  thick. The cells are predominantly tetragonal or, more rarely, pentagonal, longitudinally elongated, 15.0–35.0  $\mu\text{m}$  wide, up to 30.0–80.0  $\mu\text{m}$  long (Figs. 4f, 4g). The anticlinal cell walls are thinly cutinized, more or less straight, the cell corners are slightly rounded. The periclinal cell walls are flat.

The megaspore membrane is approximately 2.0  $\text{mm}$  wide, more than 2.5  $\text{mm}$  long, and up to 3  $\mu\text{m}$  thick. The outer surface of the membrane bears imprints of nucellus cells (Fig. 4a). There are a well-defined finely granulated foot layer, which is up to 0.3  $\mu\text{m}$  thick, and an alveolar layer, which is up to 2.7  $\mu\text{m}$  thick (Figs. 4b–4e). The alveolar layer is formed by irregularly branched and coalescent bacula, 0.3–1.5  $\mu\text{m}$  long, on average 0.2–0.3  $\mu\text{m}$  thick. The alveoli are on average 0.7–1.5  $\mu\text{m}$  wide, but in some cases they are 3.0  $\mu\text{m}$  wide. The zonality of the alveolar layer is not clearly defined. The bacula at the base of the alveolar layer are oriented obliquely in respect to the foot layer (Fig. 4d).

**Comparison and remarks.** The examination of the seeds reveals structure that in general is characteristic of the Ginkgoales (Fig. 5). They are bilateral and possess an integument consisting of the sarcotesta with mucilage cavities and sclerotesta, thick outer cuticle of the integument, and thinly cutinized nucellus more than one-third of which is coalescent with the integument. The pollen chamber contains monosulcate pollen grains. These seeds are regarded in the framework of the genus *Allicospermum*, since they were not found in organic connection with ovuliferous organs. *Allicospermum* is a collective genus, comprising seeds of various groups of plants, including also fossil Ginkgoales. Here we will only discuss *Allicospermum* species, which are supposed to belong to the ginkgoales.

**Fig. 1.** *Allicospermum budantsevii* sp. nov.: (a, b) holotype BIN, no. 813/1N 48: (a) seed, lateral view; (b) another lateral view; (c, d, m–s) paratype BIN, no. 813/88: (c) seed, lateral view; (d) another lateral view; (m) outer integumental cuticle; (n) topography of the outer integumental cuticle in the middle part of the seed showing cell packets, LM; (o) topography of the outer integumental cuticle near the seed apex showing cell packets, LM; (p) casts of mucilage canals; (q) resin bodies; (r) fragment of a nucellus with a megaspore membrane; (s) monosulcate pollen grains inside the pollen chamber, a fragment of (r), LM; (e, f) paratype BIN, no. 813/89: (e) seed, lateral view; (f) another lateral view; (g, h, t, u) paratype BIN, no. 813/63: (g) seed, lateral view; (h) another lateral view; (t) stomatal apparatus with proximal papillae on subsidiary cells, LM; (u) stomatal apparatus without papillae, LM; (i, j) paratype BIN, no. 813/1N 49: (i) seed, lateral view; (j) another lateral view; (k, l) paratype BIN, no. 813/90: (k) paratype BIN, no. 813/91, fragment of a seed, lateral view; (l) another lateral view. Scale bar (a–l) 1 mm.





The seeds under consideration most closely resemble the seeds of *Allicospermum xistum* Harris from the Lower Jurassic sediments of Greenland (Harris, 1935). In this species the seeds are similar in size (up to 11 mm long), epithelial cells of the integument form cell packets, and the stomata are also fairly numerous. The new species differs from *A. xistum* in the larger number of subsidiary cells (four to six in *A. xistum* instead of five to eight in *A. budantsevii* sp. nov.) and in the presence of papillae on the subsidiary cells of stomatal apparatus. Harris (1935) noted that in *A. xistum* the micropyle is not protruding; however, there is a possibility that in the specimens studied by him the micropylar ends were partly destroyed. The ultrastructure of megaspore membrane in *A. xistum* has not been studied, thus preventing a more complete comparison of these two species.

There is a certain similarity between the seeds of the new species and the seeds extracted from the same sample and determined as *Allicospermum* sp. Under this name Nosova (2013) figured two specimens of incomplete preservation, in which only the cuticle of integument was preserved. She also presented several photographs of the outer cuticle of the integument of these seeds. The structure of the stomatal apparatus and relief of the outer surface of the integument of *Allicospermum* sp. is similar to that of *A. budantsevii* sp. nov. Probably, these seeds may be attributed to *A. budantsevii* sp. nov.; however, the presented photographs are not enough to draw a definite conclusion on the species affinity of these seeds. In particular, no images of the cell packets, cuticle of nucellus, and megaspore membrane of *Allicospermum* sp. have been presented.

The seed of *A. adnicanicum* Krassilov from the Lower Cretaceous beds of Primorye (Krassilov, 1972) has dimensions similar to the seeds of *A. budantsevii* sp. nov. In contrast to *A. budantsevii* sp. nov., however, its micropyle is not protruding, stomata on the outer surface of its integument are very rare, and the subsidiary cells of its stomatal apparatuses have no papillae. In addition, the ordinary epidermal cells of this species are longitudinally elongated, with slender, in places slightly sinuous, anticlinal walls. The cuticle of nucellus also differs from that of *A. budantsevii* sp. nov. in the presence of elongated cells with pointed ends. The megaspore membrane has not been found.

In *A. burejense* Krassilov from the Lower Cretaceous beds of Primorye (Krassilov, 1972) the seeds are considerably larger than in *A. budantsevii* sp. nov., the micropyle is not protruding, the stomata are rare, and the ordinary cells of the outer surface of integument

are papillose. The ultrastructure of the megaspore membrane has not been studied.

*A. baierianum* Tralau from the Middle Jurassic of Sweden (Tralau, 1966) is close in morphology and size to *A. budantsevii* sp. nov. In this species the micropyle is protruding, and the ordinary cells on the outer surface of integument form small cell packets (Tralau, 1966, pl. 23, fig. 8d). However, in *A. baierianum* the stomatal apparatuses are very rare on the outer surface of integument. In addition, in *A. baierianum* only the outer cuticle of integument has been preserved, which prevents a correct comparison.

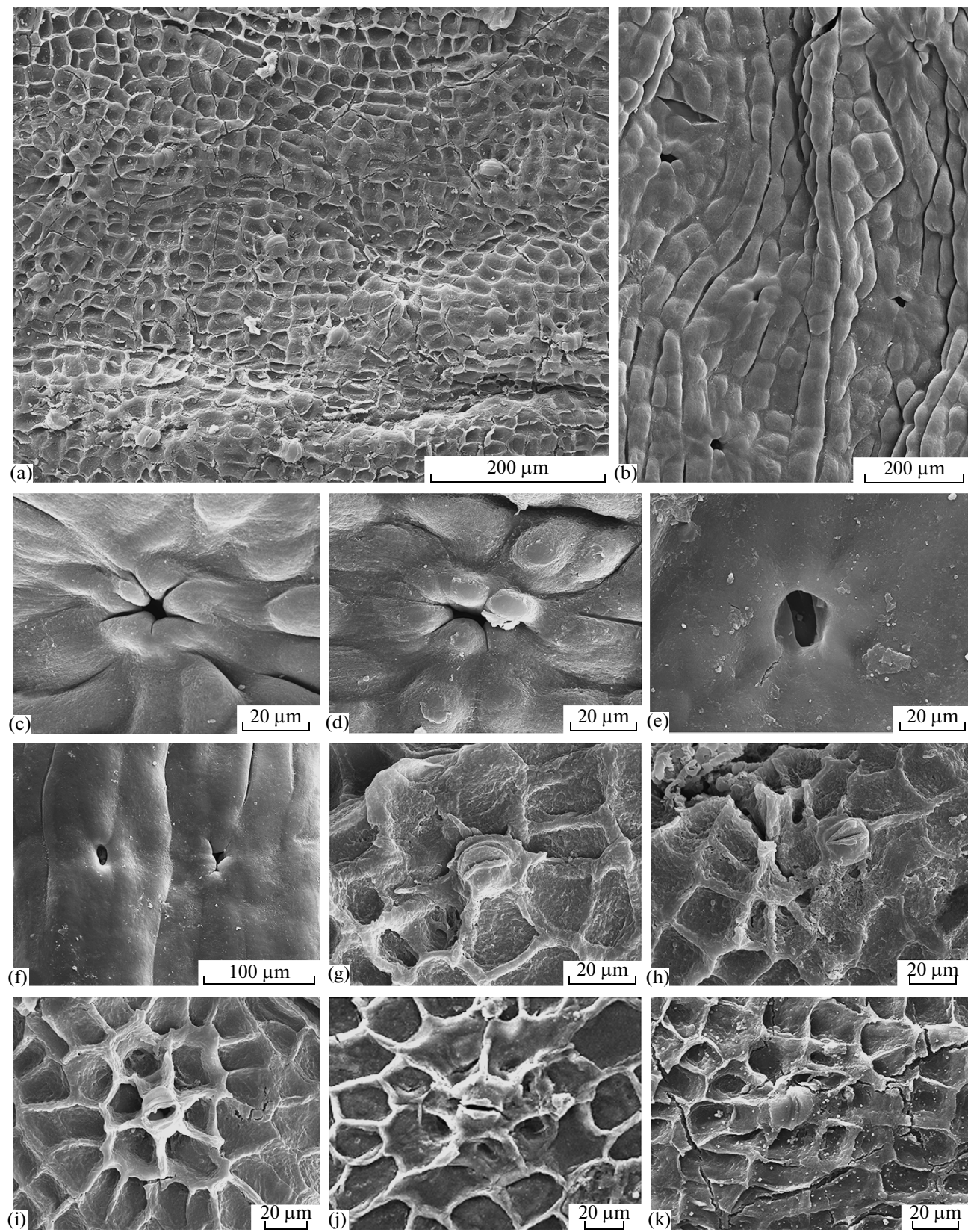
In the alveolar layer of the megaspore membrane of the seeds of *Allicospermum angrenicum* N. Nosova (2013), coming from the same sample as *A. budantsevii* sp. nov., there are bacula similar in size to the bacula of *A. budantsevii* sp. nov. However, the bacula of the first species are predominantly oriented vertically, whereas in the second species the bacula are oriented obliquely. In addition, the megaspore membrane in the new species is substantially thinner than that of the seeds of *A. angrenicum*. Besides the seeds of *A. angrenicum* are smaller and ellipsoidal in outline. In these seeds the outer cuticle of integument is thinner than in *A. budantsevii* sp. nov. and bears only few abortive stomata (in some specimens they are completely lacking). The inner cuticle of integument, which Nosova (2013) interpreted as the cuticle of nucellus, is relatively thick in *A. angrenicum*, whereas in the seeds under consideration this cuticle is so thin that it is destroyed by maceration. One more distinguishing feature of these seeds is a very thin cutinization of the nucellus and its distinctive preservation: some cells of the nucellus have not been dissolved after maceration and are visible on some preparations (Nosova, 2013: pl. X, figs. 11, 17, 20, 21). The latter character is the most important difference between *Allicospermum angrenicum* and *A. budantsevii* sp. nov.

From the other representatives of the genus *Allicospermum* that are attributed to ginkgoales, the specimens under study differ more substantially, in particular in the presence of stomata on the outer surface of integument.

Comparison of the epidermal characters of the seeds discovered in organic connection with ovuliferous organs and assigned to different species of the genus *Ginkgo* shows a high degree of their similarity to each other. In addition, all of them are extremely similar to the seeds of the present-day species *G. biloba* L. The seeds under study also show a considerable similarity to the seeds of fossil species of *Ginkgo*.

In size and outline the seeds of *A. budantsevii* sp. nov. are closest to the seeds of the Mesozoic represen-

Fig. 2. *Allicospermum budantsevii* sp. nov., SEM: (a–c, f) holotype BIN, no. 813/1N 48: (a) seed, lateral view; (b) seed base showing longitudinal ridges; (c) surface of the middle part of seed; (f) seed apex; BIN, no. 813/90, sclerotesta on the transverse split; (e, h) BIN no. 813/89: (e) seed apex with the micropyle; (h) more apical seed surface showing cell packets and outlet of a secretory canal; (g) paratype BIN, no. 813/63, fragment of a sarcotesta with resin bodies.



tatives of the genus *Ginkgo*: *G. yimaensis* Zhou et Zhang from the Middle Jurassic of China (Zhou and Zhang, 1989), *G. ginkgoidea* (Tralau) Yang, Friis et Zhou from the Middle Jurassic of Sweden (Yang et al., 2008), *G. huttoni* (Sternberg) Heer from the Middle Jurassic deposits of England (Harris et al., 1974), *Ginkgo gomolitzkyana* N. Nosova from the Middle Jurassic of Angren (Nosova, 2012), and *G. apodes* Zheng et Zhou from the Lower Cretaceous of China (Zheng and Zhou, 2004). At the same time, they differ from the seeds (with preserved cuticle of integument) that were established to belong to the genus *Ginkgo*, in the presence of distinct cell packets in the outer epidermis of integument. The presence of cell packets in *G. yimaensis* was noted, but unfortunately they are not visible in the available images. In addition, *A. budantsevii* sp. nov. differs from the seeds of *G. ginkgoidea* from the Middle Jurassic of Sweden in the presence of papillae on the subsidiary cells of the stomatal apparatuses and in the convex periclinal walls. In *G. ginkgoidea* and *G. yimaensis* the ultrastructure of megaspore membrane was studied (Zhou, 1993; Yang et al., 2008). In these taxa it hardly differs from that of the present-day *G. biloba*. The megaspore membrane of *Allicospermum budantsevii* sp. nov. differs from the megaspore membrane of the aforementioned representatives of the genus *Ginkgo* in the measurements of bacula and alveoli, while retaining the general type of structure. In *Allicospermum budantsevii* sp. nov. the bacula are three times shorter.

From the seeds of *Ginkgo gomolitzkyana* the seeds under study differ also in the thicker outer cuticle of the integument and in the considerably larger number of stomata. In *G. gomolitzkyana* the density of stomatal apparatuses does not exceed 12 per mm<sup>2</sup>, whereas in *Allicospermum budantsevii* sp. nov. it attains 29 per mm<sup>2</sup>. In contrast to *A. budantsevii* sp. nov., the cells of nucellus in *Ginkgo gomolitzkyana* have strongly rounded corners. In addition, the bacula in the alveolar layer of megaspore membrane in *G. gomolitzkyana* are twice as long as the bacula of *A. budantsevii* sp. nov.

In the seeds of *G. huttoni* and *G. apodes*, the epidermal structure remains unknown, which does not allow a more detailed comparison between them and the new species.

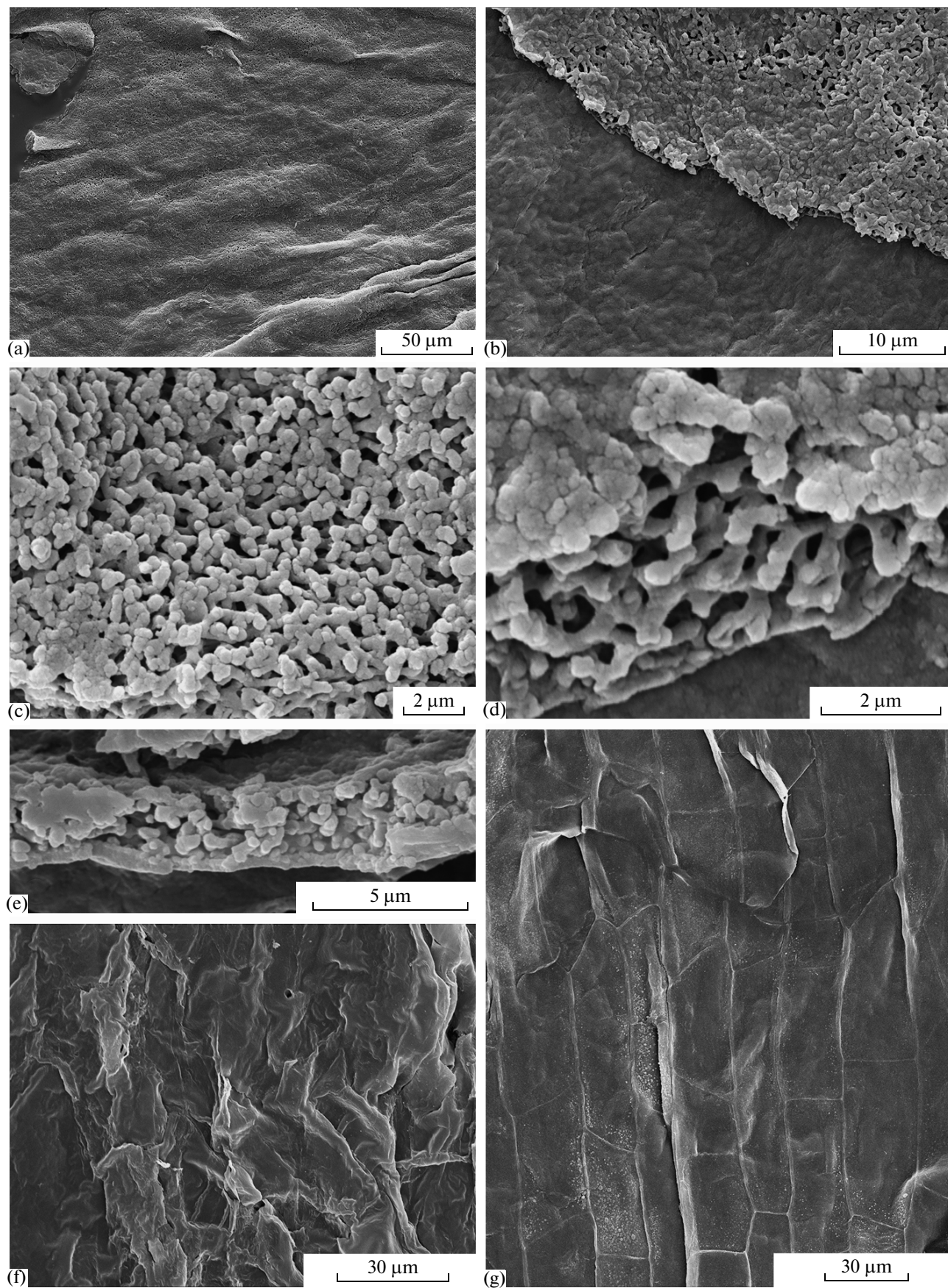
Although the seeds of the Cenozoic representatives of the genus *G. cranei* Zhou from the Paleogene of the United States (Zhou et al., 2012) and the present-day *G. biloba* are similar in morphology to the seeds of *Allicospermum budantsevii* sp. nov., they differ from them in the considerably larger size. In addition, *Ginkgo*

*cranei* has a very thick (up to 12 µm) outer cuticle of integument, predominantly incompletely amphicyclic stomata, and subsidiary cells devoid of papillae. The structure of nucellus and megaspore membrane in this species remains unknown. In *G. biloba* the stomata on the outer surface of integument are more numerous and their subsidiary cells have central dome-shaped papillae, whereas in *Allicospermum budantsevii* sp. nov. the papillae are predominantly proximal (central papillae occur extremely infrequently).

Seeds similar to the seeds of *A. budantsevii* sp. nov. are present in the species of the genus *Yimaia* Zhou et Zhang from the Middle Jurassic of China (Zhou and Zhang, 1992; Zhou et al., 2007). The ornamentation of the outer surface of the outer cuticle of the integument of *A. budantsevii* sp. nov. is similar to that of *Y. capituliformis* Zhou, Zheng et Zhang (Zhou et al., 2007). *Y. capituliformis* differs from *A. budantsevii* sp. nov. in the substantially higher density of stomata, larger papillae on the subsidiary cells of the stomatal apparatus, absence of cell packets, and in the presence of beaded thickenings on the anticlinal walls of the ordinary cells. *Y. recurva* Zhou et Zhang (Zhou and Zhang, 1992) is also similar in morphology and size to the seeds under study; however, it differs from them in the flat periclinal walls of the ordinary cells on the outer surface of integument, uneven thickness of anticlinal walls (there are beaded thickenings), lower density of stomata, fewer subsidiary cells of the stomatal apparatus, and in the presence of trichomes on the surface of nucellus. In addition, the structure of the megaspore membrane of *Allicospermum budantsevii* sp. nov. shows a closer similarity to that of the representatives of the genus *Ginkgo* rather than *Yimaia*. Thus, in *Yimaya recurva* and *Y. capituliformis* the bacula are large, frequently arranged radially, and only occasionally connected by perpendicular anastomoses (Zhou, 1993). *Y. qinghaiensis* Wu, Yang et Zhou is of special interest, since these reproductive structures were discovered in association with the leaves of *Baiera* cf. *furcata* (Lindley et Hutton) Braun (Wu et al., 2006), which are similar in morphology to the leaves described by Samylina as *Grenana angrenica*. *Yimaya qinghaiensis* is similar to *Allicospermum budantsevii* sp. nov. in size and outline, as well as in the similar number of subsidiary cells of the stomatal apparatuses. There is also a similarity in the degree of manifestation of papillae. At the same time, the periclinal walls of the ordinary epidermal cells of the outer surface of the integument in *A. budantsevii* sp. nov. are convex and thickened, whereas in *Yimaya qinghaiensis* they are almost flat.

Fig. 3. *Allicospermum budantsevii* sp. nov., SEM: (a, e, f, k) paratype BIN, no. 813/88: (a) inner surface of the outer integumental cuticle, topography; (e) stomatal apparatus without papillae, exterior view; (f) stomatal apparatus in the lower third of the seed, exterior view; (k) incompletely amphicyclic stomatal apparatus, interior view; (b–d), (g–j) paratype BIN, no. 813/63: (b) outer surface of the seed in the middle part showing stomatal apparatus with variably developed papillae; (c) stomatal apparatus with proximal papillae; (d) stomatal apparatus with proximal and central papillae; (g) stomatal apparatus, interior view; (h) adjacent stomatal apparatuses with common subsidiary cells (one of them abortive); (i) stomatal apparatus with strong cutinization of subsidiary cells, interior view; (j) stomatal apparatus with wing-shaped cutinization of guard cells.





← **Fig. 4.** *Alliospermum budantsevii* sp. nov., paratype BIN, no. 813/88, SEM: (a) outer surface of the megaspore membrane showing imprints of nucellar cells; (b) inner and outer surfaces of the megaspore membrane; (c) outer surface of the megaspore membrane showing irregularly branched bacula; (d) megaspore membrane on an oblique split showing the foot and alveolar layers; (e) megaspore membrane on a transverse split showing the foot and alveolar layers; (f) outer surface of the nucellar cuticle; (g) inner surface of the nucellar cuticle.

*Y. qinghaiensis* contains no cell packets. In addition, the nucellus of *Y. qinghaiensis* is free from the integument almost to the base. The megaspore membrane in this species is strongly deformed and thus gives only an incomplete picture of its structure; however, in general it differs from the megaspore membranes of *Y. recurva* and *Y. capituliformis* in the more frequent branching of bacula. It is difficult to judge about the degree of its similarity to the megaspore membrane of *A. budantsevii* sp. nov., but it is possible that it could be significant.

The seeds of another genus undoubtedly belonging to the family Ginkgoales, *Nehvizdyella* Kvaček, Falkon-Lang et Dašková from the Upper Cretaceous beds of the Czech Republic (Kvaček et al., 2005), exhibit similarity in morphology to the new species, but they are insufficiently preserved for a satisfactory comparison. In particular, in seeds of *Nehvizdyella* the cuticle of nucellus and megaspore membrane have not been preserved. The outer cuticle of the integument bears stomata with six or seven subsidiary cells, but the stomata relatively more numerous than those in *Alliospermum budantsevii* sp. nov. In addition, the ordinary cells of epidermis in *Nehvizdyella* form no cell packets. In our opinion, the inner cuticle of sarcotesta and outer cuticle of sclerotesta discovered in seeds of *Nehvizdyella* (Kvaček et al., 2005) are an artefact of preservation.

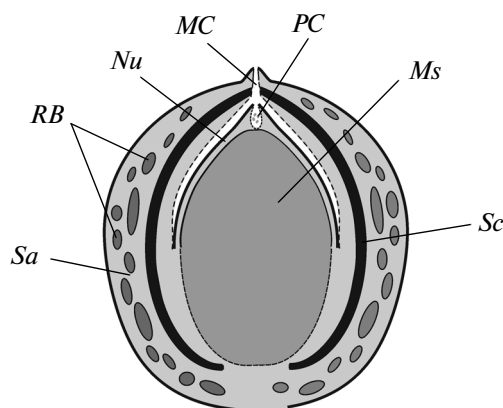
The dispersed seeds described from the Rhaetian–Liasic deposits of Franconia (Germany) (Kirchner, 1992) in association with the leaves of *Baiera muensteriana* (Presl in Shternberg) Heer and attributed to this species have the same measurements and show a significant similarity in morphology to the seeds of *Alliospermum budantsevii* sp. nov. In addition, in these seeds the periclinal walls of the ordinary cells on the outer surface of integument are convex, as in *Alliospermum budantsevii* sp. nov., and the stomatal apparatus have a similar number of subsidiary cells. At the same time, the dispersed seeds described as *Baiera muensteriana* have no cell packets on the outer surface of integument, extremely low density of stomata (1.5 per mm<sup>2</sup>), and the anticlinal cell walls of the nucellus are serrate or, occasionally, sinuous. It is unclear whether they had papillae on the subsidiary cells of the stomatal apparatus. The structure of the megaspore membrane of these seeds remains unexamined, which hinders a more detailed comparison. In addition to the dispersed seeds, some seeds attached to ovuliferous organs from the same locality were described and attributed to *Baiera muensteriana*. These ovuliferous organs are insufficiently preserved

for their confident identification. In addition, they differ from each other in morphology. In one immature seed in organic connection with an ovuliferous organ, which because of its poorly preserved morphology may be assigned both to *Ginkgo* and to *Yimaya*, only the outer cuticle of the integument has been preserved. The epidermal structure of this immature seed differs from that of the dispersed seeds from the same locality. It is similar to *Alliospermum budantsevii* sp. nov. in the number of subsidiary cells but differs from the latter in the more numerous stomata.

The strong deformation of the seeds of *A. budantsevii* sp. nov. hinders the reconstruction of their original morphology; however, in general it can be argued that initially they were almost spherical. The projection preserved at the seed base in some seeds, including the holotype designated here, was mistaken by Samylina for a stalk (Samylina, 1990). The presence of such a projection at the base of a seed is apparently due to the drying of sarcotesta. Drying unevenly, the spherical seeds of *Ginkgo* become ellipsoidal and are often shaped like the most completely preserved seeds under study. During their lifetime the latter seeds were apparently almost spherical, like those of *G. biloba*, but were substantially smaller in size.

Specimen 813/1 N 55, figured in Samylina's paper (1990, pl. III, fig. 19), is a collar rather than a seed with its stalk, which was established during the revision.

Specimen 813/1 N 54, figured in Samylina's paper (1990, pl. III, fig. 18), is a seed that cannot be identi-



**Fig. 5.** Schematic reconstruction of the seed of *Alliospermum budantsevii* sp. nov. in longitudinal section. Designations: (Sa) sarcotesta; (RB) resin bodies; (Sc) sclerotesta; (Nu) nucellus; (MC) micropylar canal; (PC) pollen chamber; (Ms) megaspore. The dotted lines show lost details of the structure.

fied with certainty because of the absence of the sarco-testa.

**Material.** Seven specimens represented by seeds and their fragments preserved in the form of phytoleims.

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