

Vladimariales ordo nov. (Gymnospermae) from the Middle Jurassic Deposits of the Mikhailovskii Rudnik Locality (Kursk Region, European Russia)

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Abstract—Composite seed-bearing capsules (formed by fusion of eight radially arranged elementary capsules), assigned to a new monotypic order Vladimariales ordo nov., were found in the Upper Bathonian deposits of the Mikhailovskii rudnik locality (Zheleznogorsk town, Kursk Region). In its morphology, the new order demonstrates valuable, phylogenetically conditioned similarity to Peltaspermales and Umkomasiales, but it is evolutionarily more advanced than these latter. A base of the composite capsule is supported by a collar on a stalk, which in external appearance is not different from collar of Ginkgo L., but has stalk, vascularized in a different way (its conducting tissue consisted of eight radially arranged collateral vascular bundles; each vascular bundle correspond to one of eight fused elementary capsules, each of which contain a solitary seed). Capsules and seeds are inverted relative to the collar; as a result, collar protects micropilar tips of seeds. The presence of collar and whole aspect of the new plant composite capsules give them the significant superficial similarity with seed-bearing organs of modern Ginkgo. Mature composite capsule in Vladimariales ordo nov. dehisced along the lines of fusion of elementary capsules, forming the composite capsule, and scattered seeds; opened composite capsule detached from axis. The significance of the new order for gymnosperm phylogeny is discussed.

Key words: Middle Jurassic, Bathonian, gymnosperms, Ginkgoopsida, morphology, anatomy, systematics.

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INTRODUCTION

It is believed that only Caytoniales and Umkomasiales survived in the Jurassic of all bygone diversity of seed ferns. These two orders appeared in the Triassic, the latter was represented by relatively high diversity of forms. The representatives of the first order in the Jurassic are known both by their leaf remains (*Sagenopteris* Presl) and by reproductive structures (seed-bearing capsules *Caytonia* Thomas and *Reymanownaea* Barbacka et Bóka (Barbacka and Bóka, 2000), pollen organs *Caytonanthus* Harris (Harris, 1964)). The second order is represented by leaves of *Pachypteris* Brongn. and, supposedly, *Cycadopteris* Zigno, seed-bearing (*Umkomasia* Thomas) and pollen organs (*Pteruchus* Townrow and *Pteroma* Harris) (Kirchner and Müller, 1992; Taylor et al., 2006; Taylor and Taylor, 2009; Taylor et al., 2009). It should be noted, that another point of view exists, according to which leaves *Pachypteris* were assigned to protocycadales (Krassilov and Doludenko, 2004). Meyen (1984, 1987) believed that the Caytoniales are united by close affinity with Peltaspermales, Ginkgoales, and

Czekanowskiales. He regarded the corystosperms (umkomasians) as a family within the order Peltaspermales. In recent years, they are often regarded as a separate order—Umkomasiales (Anderson and Anderson, 2003; Taylor et al., 2006; Taylor and Taylor, 2009). I also believe that umkomasians are an independent order. Meyen included all listed orders to comprehensive classis Ginkgoopsida, erected for plants with bilaterally symmetrical seeds without secondary integument (Meyen, 1984, 1987). He derived the Caytoniales, Ginkgoales, and Czekanowskiales directly from Peltaspermales with their umbrella-shaped seed-bearing organs, through the family Angaropeltidaceae (a new name of Cardiolepidaceae, established by Meyen, 1977). The Peltaspermales (I exclude of them umkomasians), evidently, appeared already in the Carboniferous (Kerp et al., 2001; Naugolnykh, 2007), still demonstrated diversity in the Triassic, but completely disappeared to the beginning of Jurassic. According to Meyen, the Ginkgoales and Czekanowskiales are united by close affinity to Peltaspermales. The vast majority of foreign scientists at present

day rank Umkomasiales and Caytoniales with seed ferns, and Czekanowskiales and Ginkgoales regard as detached groups, and they often bring Ginkgoales together with Coniferales and Cordaitales (Doyle et al., 1994; Doyle, 2006; Hilton and Bateman, 2006; Taylor et al., 2006; Zou, 2009; etc.). But so was Meyen really wrong, when supposed the affinity of Ginkgoales and Czekanowskiales with Peltaspermales?

Besides above-mentioned genera of the Mesozoic seed ferns, it is worth noting one find that is important for us. Samylina (1990) described seed-bearing organs in association with leaves of new genus *Grenana* Samylina from the Jurassic of Angren (Uzbekistan). According to her interpretation, seeds with collars, like those in Ginkgo, were attached to the tips of lobes of palmate-dichotomously dissected leaves of *Baierella-Leptotoma* type; in each terminal lobe of leaves entered a single vein. The collar was interpreted as reduced cupule. Samylina believed that *Grenana* is nothing but a new Mesozoic seed fern, of yet unknown affinity. The leaves, collars and seeds were not found in the organic connection. Other researchers did not agree with this sufficiently unusual reconstruction and placed *Grenana* directly to the family Ginkgoaceae (Zhou, 1997, 2009; Naugolnykh, 2002). In the light of obtained data, may be that Samylina really was not too far from the truth.

This paper describes seed-bearing organs, assigned to a new order Vladimariales ordo nov. This order is of interest by the fact that it quite may be assigned to “the Mesozoic seed ferns” (*sensu* Taylor et al., 2006 etc.). It allows looking several morphological features of Ginkgoales and Czekanowskiales from a different angle and proposing some new approaches to the problem of their systematic and phylogeny.

MATERIAL AND METHODS

The collection, which served the material for present paper, was collected during several field seasons in 2004–2009. Plant remains were found in sandy siltstones of plant-bearing lens about 1.5 m thick in the northern wall of the Northern Quarry of Mikhailovskii Rudnik (near Zheleznogorsk town, Kursk Region) from continental deposits of the hypostratotype of Arkinsk Formation, Middle Jurassic, Upper Bathonian (*Unified...*, 1993). Apart from the new ovuliferous organs, in the plant-bearing lens, were found numerous predominant leaf remains of other plants: *Cladophlebis* sp., *Pachypteris rutenica* Gordenko, *Pachypteris* sp., *Ptilophyllum caucasicum* Doludenko, *Otozamites* sp., *Bennetticarpus* sp., bennettitalean leaves *Sympterothyllum* Gordenko et Broushkin, numerous bennettitalean “floral” bracts, *Leptotoma prynadii* Travina, *L. lenaensis* Samylina, *Ginkgo hutoni* Harris, *Mirovia eximia* (Gordenko) Nosova,

brachyblasts and Auxiblasts of *Pityocladus* sp., shoot fragments of *Elatocladus* sp., cones of *Schizolepis* Braun–type, dispersed seeds of ginkgoaleans and conifers. Here also abundant fragments of branches and trunks of *Podocarpoxydon* sp. and *Cupressinoxylon* sp. with well-distinguishable growth rings were found (Gordenko, 2008).

To describe the new ovuliferous organs, we use the term “composite capsule”. The term means the aggregation, which was formed by fusion of several elementary capsules.

The studied material is represented mainly by phytoliteims of dehiscent composite ovuliferous capsules and dispersed collars; two undeiscent composite capsules were found in the organic connection with their collars. The material preservation allowed investigation of not only epidermal structure, but of many significant details of anatomical structure of the new ovuliferous organs.

To obtain cuticle preparations, phytoliteims initially were placed in concentrated hydrofluoric acid to remove matrix, and subsequently macerated by standard method in concentrated nitric acid. Obtained cuticle preparations were studied using light microscopy (LM) and scanning electron microscopy (SEM). Individual fragments prepared for study under SEM without maceration process.

The collection no. 5137 is kept in the Borissiak Paleontological Institute of Russian Academy of Sciences.

SYSTEMATICS

DIVISION GYMNOSPERMAE

CLASSIS GINKGOOPSIDA

Order Vladimariales ordo nov.

Etymology. From the type family Vladimariaceae fam. nov.

Diagnosis. Plants with peltate, radially symmetrical seed-bearing organs—composite capsules, formed by fusion of several closed elementary capsules, which arranged in whorl on thin axis and inverted relative to it and base of composite capsule.

Composite capsule dehiscent on several lobes along line of fusion of elementary capsules. Each capsule contained solitary seed. Seeds, sitting on short stalks, inverted relative to composite capsule axis. Seeds fusiform, slightly curved, with chalaza slightly asymmetrical and weakly concave in place of stalk attachment; micropile very long, with apex fused to margins of small opening in distal margin of capsule. Nucellus fused with integument more than on two thirds, megaspore membrane absent. Axis base of composite capsule sustained by collar on thick stalk, protecting micropilar tips of seeds. Stalk with several radially arranged collateral vascular bundles. Their quantity

corresponds to quantity of elementary capsules, forming composite capsule. Metaxylem tracheids in vascular bundles with scalariform bordered pits. Extensive resin canals and cavities presented in cortex of stalk, collar, and composite capsule. Outer epidermis of composite capsule strongly cutinized, bearing numerous perigenous mono- or polycyclic stomatal apparatuses, without sutures, despite of area sustained by collar, where radially arranged sutures distinctly expressed on cuticle. Sutures mark lines of fusion of capsules. Stalk, bearing collar, upper surface of collar near its axial part, composite capsule axis, and all area of composite capsule sustained by collar, papillose; other surface of composite capsule without papillae.

Composition. Monotypic order.

Comparison and remarks. Composite radially symmetrical capsules, sustained by a collar, protecting micropilar openings, were not found earlier in the Ginkgoopsida. The new order exhibits the most similarity with Peltaspermales, Umkomasiales, Caytoniales, Petrielleales, Czekanowskiales, and Ginkgoales. Capsules are known in the all enumerated orders, excluding Ginkgoales. Capsules are constant character of Caytoniales, Petrielleales, and Czekanowskiales. Among Peltaspermales, Angaropeltidaceae possessed simple capsule (unlike composite capsules of the new order), and seeds with long micropilar tubes, extending to the slit between the stalk and capsule margin. *Umkomasia uniramia* Axsmith, E.L. Taylor, T.N. Taylor et Cúneo from the Triassic of Antarctica (Axsmith et al., 2000), in which capsules form a whorl on the apex of strobilus axis, may be an example of capsule possessor in Umkomasiales.

By its peltate organization and seed orientation, the new order is similar to Peltaspermales, but in the latter capsules are simple and formed by bending down of peltoid margins (Meyen, 1984), not by fusion of closed capsules, arranged in a whorl. Moreover, in the Peltaspermales, unlike Vladimariales ordo nov., seeds have free and well-cutinized nucellus and thin cuticle of outer integument.

The similarity of the new order with Umkomasiales is in the presence of dehiscing capsules, which were noted in several Umkomasiales (in particular, in whorled arrangement of capsules in *Umkomasia uniramia*), and position of seed within a capsule. The resin canals and cavities are characteristics of Umkomasiales (Meyen, 1984; Klavins et al., 2002; Taylor et al., 2006). However, the composite capsules are unknown in Umkomasiales, and their seeds are similar to seeds of Peltaspermales both by their morphology and by anatomy.

The new order has pollination mechanism, convergently similar to that of Caytoniales. A seed in the Vladimariales ordo nov. has long micropilar canal, extending towards narrow opening in an elementary

capsule. The micropilar canal lumen is very narrow (15–20 μm , which must prevent the penetration of larger pollen grains of other plants). Pollen grains might penetrate into micropile with pollination drop. In the Caytoniales, long canals continued from capsule mouth and reached short micropiles of seeds, enclosed in the capsule. The pollen could be transported with pollination drop inside the capsule to seeds through the canals. For the Caytoniales, various interpretations of the canals exist, but more often they are regarded as canals, adjacent to a seed micropile, rather than micropilar canals (Reymanówna, 1973; Krassilov, 1977, Taylor et al., 2006). This not changes the implication of the pollination mechanism, which is qualified to restrict the penetration of alien pollen into the capsule (Reymanówna, 1973; Krassilov, 1977). The valuable distinction of Vladimariales ordo nov. from Caytoniales consists in that the capsule of the latter encloses several seeds and formed by transverse, rather than longitudinal, folding of megasporophyll. In the Vladimariales ordo nov., the elementary capsule might be formed by longitudinal folding of megasporophyll, or by fusion of two lobes of a cupulate structure (for example, cupule of Umkomasiales), containing a solitary seed. Seeds in the both orders are also essentially different. Therefore, the peltate composite capsule of Vladimariales ordo nov. significantly differs from bilaterally symmetrical capsule of the Caytoniales. The dissimilarity in epidermal structure between representatives of these two orders is also should be noted.

The new order differs from Petriellales by presence of composite capsule and other structure of seeds. The capsule of Petriellales differs from composite capsules of Vladimariales ordo nov. more sufficiently, than capsule of Caytoniales. It was formed like in Caytoniales, but its seeds are adaxial and have another configuration (they are distinctly triangular) and lack long micropilar canals (Taylor et al., 1994, 2006).

The similarity of radially symmetrical composite capsule of Vladimariales ordo nov. to capsules of Leptostroboles is conditioned mainly by the presence of dehiscing mechanism. Representatives of the both orders dispersed their seeds. Unfortunately, the scanty data have been obtained on the inner structure of capsules in the Leptostroboles, including that fact that it is nothing known about their seeds. Strongly cutinized megaspore membranes, extracted from capsules of Leptostroboles (Krassilov, 1972), probably may be resin bodies. Probably, the seeds of the Leptostroboles were similar to seeds of Vladimariales ordo nov. and were separated each from other by partition-walls (in this case, capsules of Leptostroboles might be composite), but this hypothesis is in need of verification.

The Vladimariales ordo nov. possess a collar, which is believed to be the distinctive feature of some Gink-

goales (in particular, of *Ginkgo* L.). Exteriorly, it is not distinguishable from collar in *Ginkgo*. The outer appearance of the seed-bearing organs and their arrangement are very similar to that in Ginkgoales. The outer cuticle of composite capsule is covered with stomata, as well as outer integument in seeds of *Ginkgo*, resin canals are developed within cortex of the capsule, like in outer integument of *Ginkgo*. But stalk in the plants of new order was vascularized by another way, than in ginkgoes, which have in their stalk two vascular bundles, forming on the level of collar an anomalous ring of metaxylem (Shaw, 1908). Moreover, the collar sustains several seeds, inverted relative to it, rather than single (as a rule, orthotropous) like in the Ginkgoaceae.

Family Vladimariaceae Gordenko, fam. nov.

Etymology. From the type genus.

Type Genus. *Vladimaria* Gordenko, gen. nov.

Diagnosis. As for order.

Composition. Monotypic family.

Genus *Vladimaria* Gordenko, gen. nov.

Etymology. In honor of parents of the author, from names Vladislav and Maria.

Type species. *Vladimaria octopartita* gen. et sp. nov.

Diagnosis. As for family.

Composition. Monotypic genus.

Remarks. Dehiscent composite capsules *Vladimaria* gen. nov. may be easily mistaken with reproductive organs of Bennettitales, particularly with *Weltrichia* Carruthers and *Williamsoniella* Thomas. Resin canals and their imprints may be mistaken as synangia or nectaries. In fact, Harris (1969, 1973) pointed on the presence in the bases of bracts *Weltrichia* of peculiar bodies, indissoluble during maceration process, which he interpreted as nectaries. According to the author opinion, which he proved experimentally, the sugary matter under coalification process may turn resin-like and indissoluble in water and acids. Undehiscent composite capsules in the representatives of the new genus also may be easily mistaken as Ginkgoaceae

based on the presence of collar. Probably, one should assign to *Vladimaria* gen. nov. the imprints, described as *Weltrichia regalis* Anderson et Anderson (Anderson and Anderson, 2003) from the Upper Triassic of South Africa, *Weltrichia* sp. from Upper Triassic of Ukraine (Stanislawsky, 1971), remains, identified as *Williamsoniella karataviensis* Turutanova-Ketova (Doludenko and Orlovskaya, 1976), and seed-bearing organs, described in association with leaves *Grenana* Samylinina from the Middle Jurassic of Angren, Uzbekistan (Samylinina, 1990). The most similarity in its morphology the new genus demonstrates with seed-bearing organs in association with leaves *Grenana*. Is my suggestions are correct, the representatives of the new genus may be found in the Mesozoic of Northern, as well as Southern hemisphere, beginning from the Upper Triassic.

Composition. Type species.

***Vladimaria octopartita* Gordenko, sp. nov.**

Pl. 8, figs. 1–16; Pl. 9, figs. 1–7; Pl. 10, figs. 1–6; Pl. 11, figs. 1–9; Pl. 12, figs. 1–9; Pl. 13, figs. 1–4; Pl. 14, figs. 1–8; Pl. 15, figs. 1–7; Pl. 16, figs. 1–4; Pl. 17, figs. 1–6; Pl. 18, figs. 1–6; Pl. 19, fig. 1–6; Pl. 20, figs. 1–6; Pl. 21, figs. 1–6.

Etymology. From the Latin *octo* (eight) and *partitus* (divided).

Holotype. PIN, no 5137/39; undehiscent composite seed capsule with a collar, preserved as phytolite; Russia, Kursk Region, Zhelesnogorsk town vicinity, Michailovskii open-mine; Middle Jurassic, Upper Bathonian, Arkinsk Formation (Pl. 10, fig. 1; Pl. 12, figs. 1, 2).

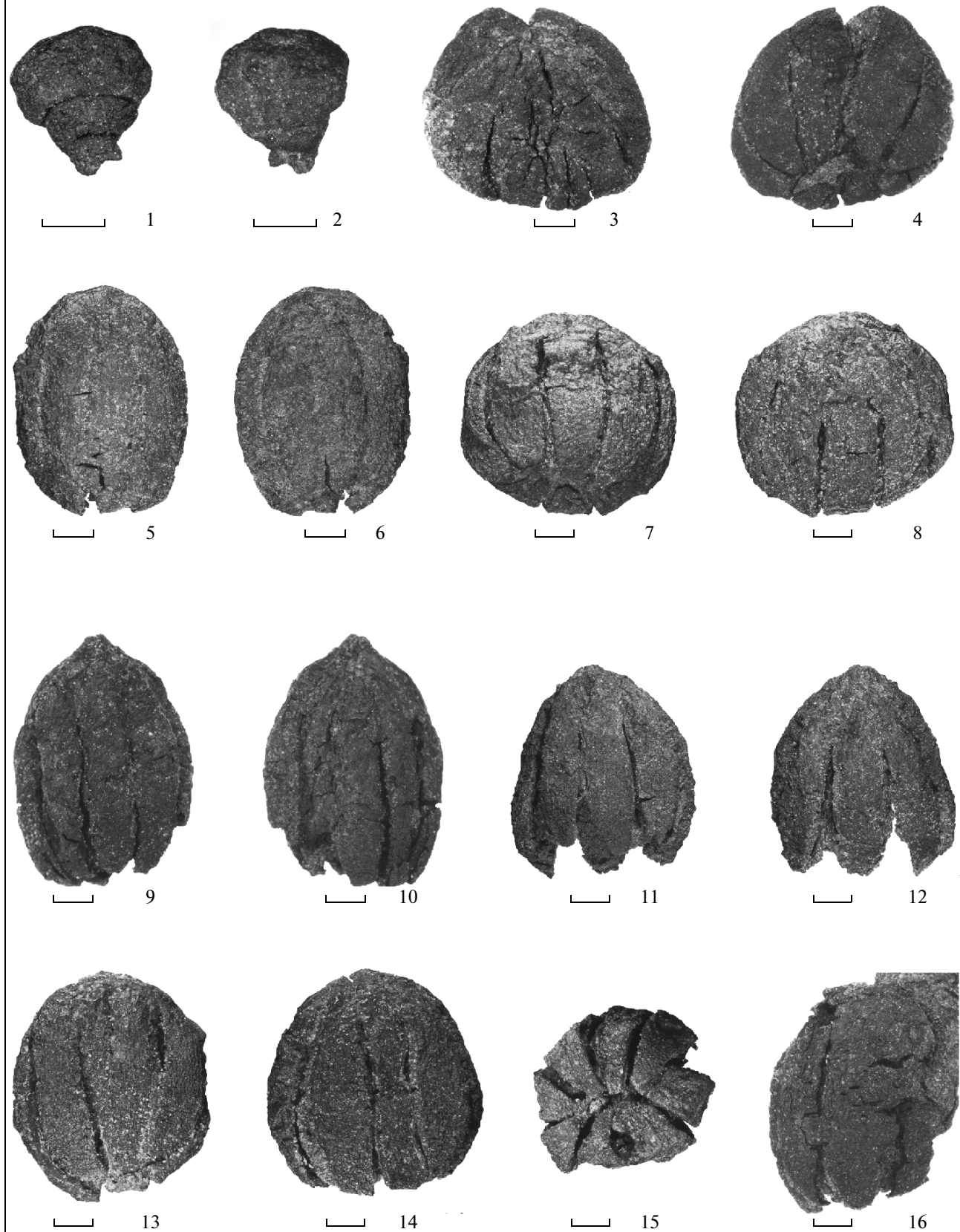
Diagnosis. As for genus. Premature composite capsules nearly spherical, slightly oblate, 2.7–3 mm high, 4–4.5 mm in diameter; mature composite capsules from nearly spherical to ellipsoidal, slightly oblong, 10–13 mm high, 8.6–10 mm in diameter. Composite capsule always consists of eight elementary capsules. Eight seeds corresponding to number of capsules. Seeds (without micropilar part) up to 5360 µm long, 300–840 µm in diameter. Micropile long, gradually tapers towards tip; micropilar canal more than 1000 µm long, 15–20 µm wide. Segments (correspond to outer walls of elementary capsules, which constitute composite capsule), formed after composite capsule

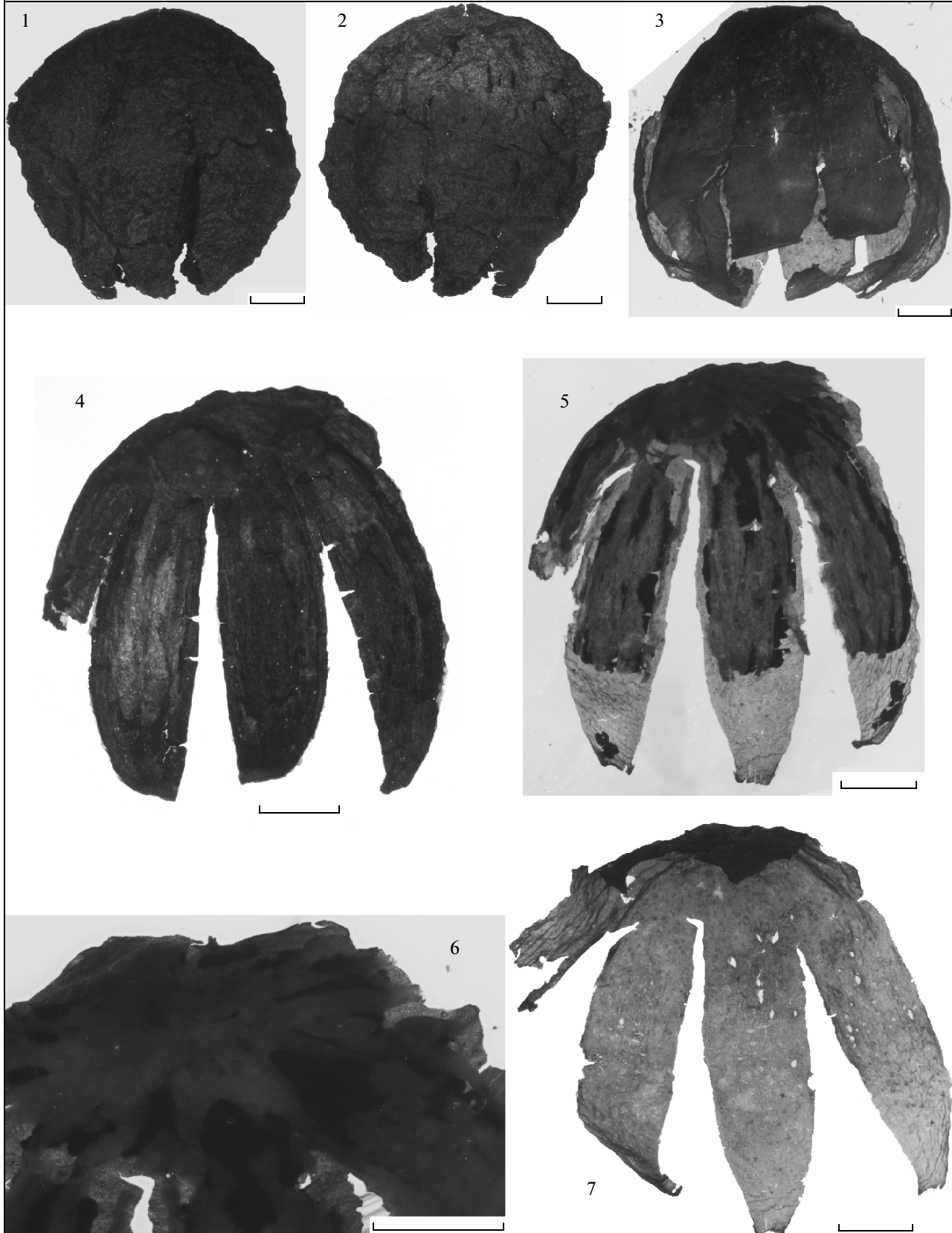
Explanation of Plate 8

Figs. 1–16. *Vladimaria octopartita* gen. et sp. nov.: (1, 2) no. 5137/28, LM: (1) abortive composite capsule with preserved collar, the lateral view; (2) the same, view from the back side; (3, 4) no. 5137/29: (3) dehiscent and crushed composite capsule, detached from a collar, the distal view; (4) the same in the proximal view; (5, 6) no. 5137/30: (5) incompletely dehiscent composite capsule, detached from a collar, the lateral view; (6) the same, view from the back side; (7, 8) no. 5137/31: (7) completely dehiscent composite capsule, detached from a collar, the lateral view; (8) the same, view from the back side; (9, 10) no. 5137/32: (9) completely dehiscent composite capsule with slightly tapered apex, the lateral view; (10) the same, view from the back side; (11, 12) no. 5137/33: (11) completely dehiscent composite capsule; (12) the same, view from the back side; (13, 14) no. 5137/34: (13) completely dehiscent composite capsule, the lateral view; (14) the same, view from the back side; (15) no. 5137/35, dehiscent composite capsule, detached from a collar, proximal view; (16) no. 5137/36, incompletely dehiscent composite capsule, detached from a collar, the lateral view.

Figs. 1–16. Scale bar 2 mm.

Plate 8





dehiscence, take up to 3/4 of its length, 2.3–2.6 mm width in middle area, taper to 0.5 mm towards capsule apices. Diameter of composite capsule axis base 0.4–0.7 mm, axis tapers to nearly 0.2 mm towards its apical part. Stele in base of composite capsule axis about 230 μm in diameter, composed of 8 collateral vascular bundles, 75 μm in diameter. Tracheids 6–10 μm in diameter. Diameter of composite capsule stalk 0.6–2 mm, length up to 2 mm. Collar 1.8–5 mm in diameter.

Ordinary epidermal cells of composite capsule in more or less distinct longitudinal rows. They mainly quadrangular-pentagonal, nearly isodiametric, more rarely transversally or longitudinally elongated, 15–60 μm long, 10–40 μm wide. Anticlinal walls straight or slightly curved. Stomatal apparatuses with 4–8 subsidiary cells forming Florin ring, and 1–2 rings of neighboring cells (amphicyclic). Guard cells of outer cuticle of composite capsule sunken, wing-shaped, 50–60 μm long, 40–50 μm wide; guard cells of axis semi-circular in form, 20–36 μm long, 24–28 μm wide. Polar subsidiary cells rare. Stomatal density 14 per mm^2 .

Papillae on ordinary cells in base of composite capsule, on ordinary cells of composite capsule axis, and upper surface of collar central, dome-shaped or calyptriform.

Description (Figs. 1–3). The collection contains premature and mature radially symmetrical peltate ovuliferous organs representing composite capsules, sustained by a collar on stalk (Figs. 1a, 1b). Only two exemplars were found in organic connection with collars; they represent premature abortive composite capsules (Pl. 8, figs. 1, 2; Pl. 10, fig. 1; Pl. 12, figs. 1, 2; Fig. 2). Dehiscence composite capsules (Pl. 8, figs. 3–15; Pl. 9, Figs. 1, 2, 4; Fig. 3), detached from collar and without seeds, prevail. Dispersed seeds on short stalks are found more rarely (Pl. 10, figs. 3, 5; Pl. 11, figs. 5–9; Pl. 13, fig. 1). One specimen (Pl. 11, figs. 8, 9) shows two collars, which were attached to a forked axis, judging by imprint. One incompletely dehiscence composite capsule (Pl. 8, fig. 16) contained seeds.

Radially symmetrical composite capsules were formed by lateral fusion of eight elementary capsules, arranged in whorl on the apex of thin axis and inverted relative to it and composite capsule base. The diameter of composite capsule axis base is 0.4–

0.7 mm; towards the apex, the axis is thinning approximately to 0.2 mm. The stele in the composite capsule axis base is about 230 μm in diameter, consisting of eight collateral bundles, which are about 75 μm in diameter (Pl. 13, figs. 1–3). The metaxylem tracheids of vascular bundles with scalariform bordered pits (Pl. 13, figs. 4). Diameter of tracheids is 6–10 μm . Premature composite capsules are nearly spherical, slightly dorsoventrally flattened, 2.7–3 mm high, 4–4.5 mm in diameter; the mature ones are from nearly spherical to ellipsoidal, and slightly elongated dorsoventrally, 10–13 mm high and 8.6–10 mm in diameter. The composite capsule always consists of eight elementary capsules. The composite capsule opened by dehiscence on eight lobes along fusion lines of elementary capsules (Fig. 3). The lobes (corresponds to outer walls of elementary capsules, forming composite capsule) formed when composite capsule dehiscence; their length is up to 3/4 from the whole composite capsule length, width in the middle part is 2.3–2.6 mm. They are tapering to 0.5 mm towards the apices of elementary capsules (Pl. 2, figs. 2–5, 7). Each elementary capsule in composite capsule contains a solitary seed, sitting in the weakly cutinized locule (Pl. 12, figs. 6–9; Fig. 1 b). The seeds, attached to short stalks, are inverted relative to the composite capsule axis (Pl. 14, fig. 8, 10; Pl. 15, fig. 1). The seeds are fusiform, indistinctly bilaterally symmetrical, slightly curved, with somewhat asymmetrical, rounded or slightly concave chalazal part (Pl. 16, figs. 1, 2). Nucellus fused with integument more than on two thirds; megaspore membrane is absent, micropile is very long (more than 500 μm) and thin (diameter of apex is about 30 μm), with apex, coalescent with margins of a small opening in the distal part of elementary capsule (Pl. 12, fig. 9; Pl. 15, fig. 7). The diameter of micropilar canal is 15–20 μm . The nucellus cuticle is very thick, composed of large cells, which are from nearly isodiametric to polygonal in the chalazal part, and to rectangular and fusiform in the middle part (Pl. 16, figs. 1–4). The cells with flat or strongly prominent outer periclinal walls, or with indistinct large central papillae (Pl. 15, fig. 5, Pl. 16, fig. 3). Nearer to the micropile, the ornamentation in form of irregular cord-shaped ribs is observed (Pl. 16, fig. 4).

Explanation of Plate 9

Figs. 1–7. *Vladimaria octopartita* gen. et sp. nov.: (1–3) no. 5137/37, LM: (1) incompletely dehiscence composite capsule, detached from a collar, lateral view; (2) the same, view from the back side; (3) macerated cuticle of composite capsule, eight lobes, corresponding to eight capsules, are visible; (4–7) no. 5137/38: (4) composite capsule fragment (inner view), free of seeds (lighter areas correspond to resin canals); the same after maceration, partly removed coaly matter (resin canals are visible); (5) initial phase of maceration, resin canals are distinctly visible; (6) detail of fig. 5, resin canals in the apical part of composite capsule, radially departing into the lobes, are visible; (7) final phase of maceration, cuticular covering of three lobes of complex capsule is visible. Figs. 1–7 Scale bar 2 mm.

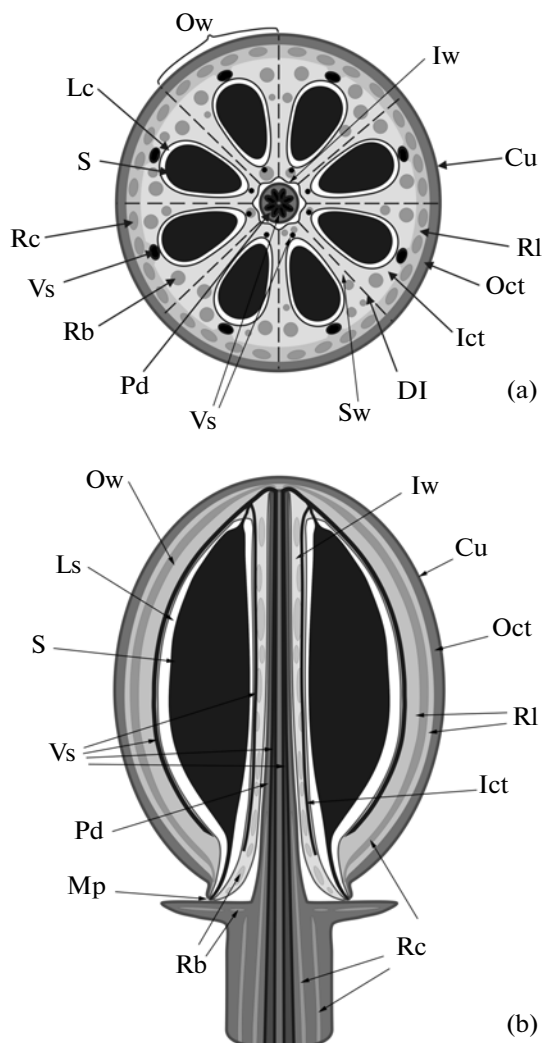


Fig. 1. The structure of composite capsule *Vladimaria octopartita* gen. et sp. nov.: (a) in the transverse section through the middle part; (b) in the radial section. Legend: (Ow) the outer wall of an elementary capsule, comprising in the composite capsule (corresponds to a lobe of dehiscent composite capsule); (DI) composite capsule dehiscence lines; (Iw) inner wall of the elementary capsule; (Sw) common wall of adjacent capsules; (Cu) cuticle; (Oct) outer cortex; (RI) layer of cortex, containing resin canals; (Rc) resin canals; (Vs) vascular bundles coated with transfusion tissue; (Rb) resin bodies; (Ict) inner cortex; (Pd) composite capsule axis; (S) seed; (Mp) the micropylar opening of seed; (St) stalk; (Ls) seed locule.

The anticlinal walls of cells are thick, projecting in form of slanting ribs in the chalazal part.

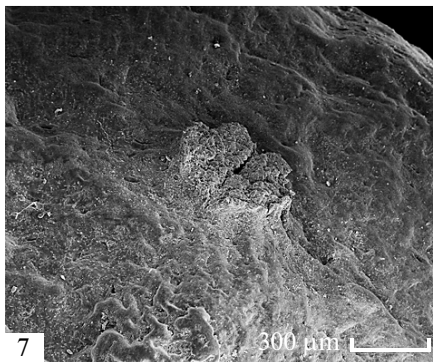
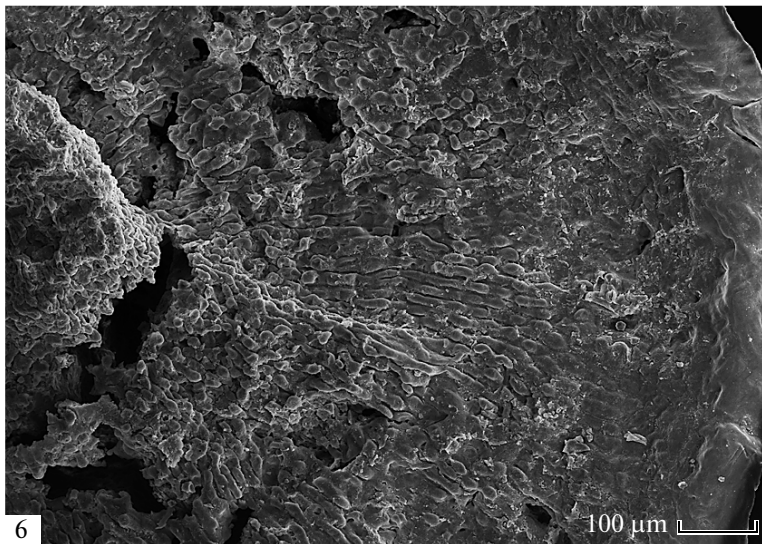
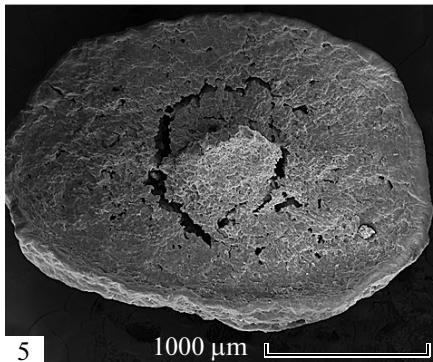
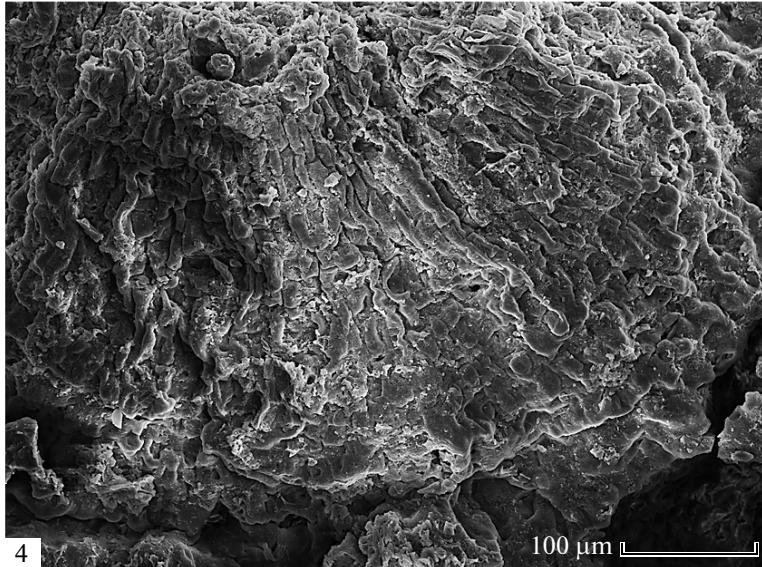
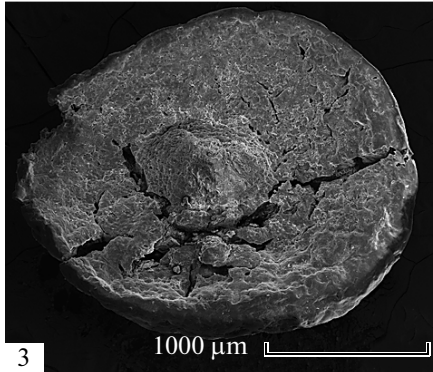
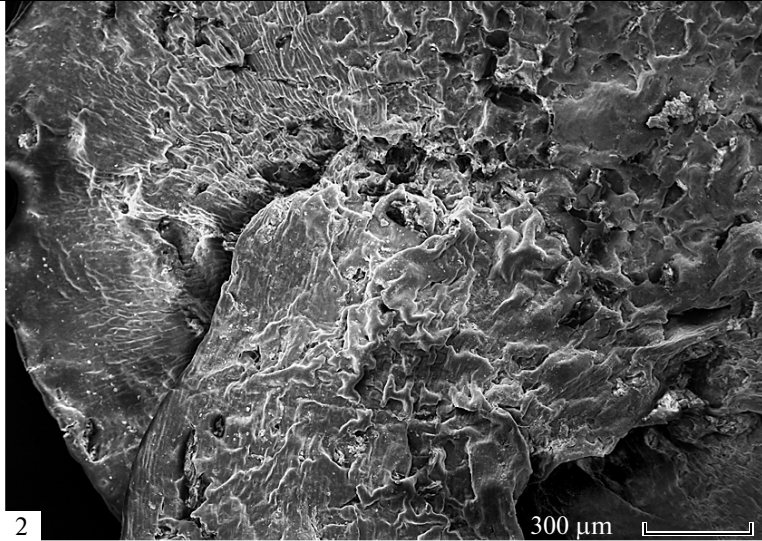
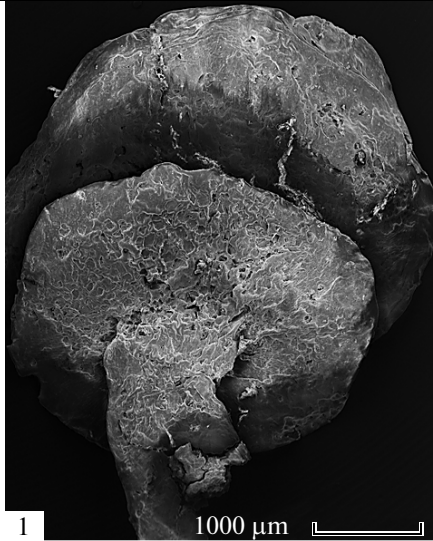
From the composite capsule axis into the base of each elementary capsule, one vascular bundle enters and follows into a lobe (it may be traced by the presence of transfusion tissue in the lobe axial part, Pl. 21,

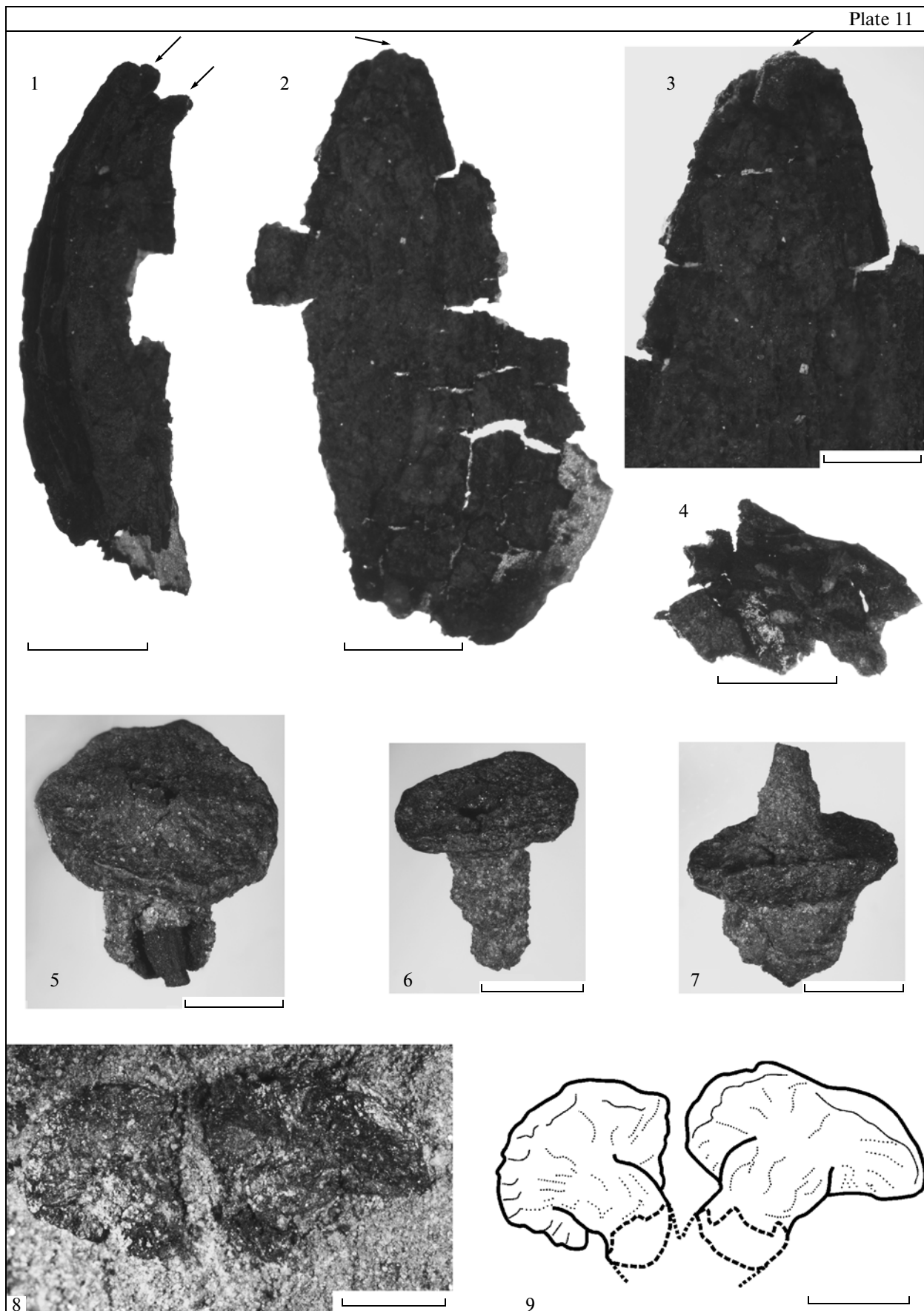
fig. 1; Figs. 1a, 1b). Short branch departs from the bundle to the chalazal part of seed. Except for the short branch, there is another, following in parallel to the long axis of seed, within the capsule inner wall, adjacent to the composite capsule axial part. This is thin vascular bundle, only a few tracheids thick (Pl. 15,

Explanation of Plate 10

Figs. 1–7. *Vladimaria octopartita* gen. et sp. nov., SEM: (1, 2) holotype, no. 5137/39: (1) premature composite capsule, attached to a collar; (2) detail of stalk and lower side of collar surfaces; (3, 4) no. 5137/40: (3) collar in the upper view; prominence in the central part corresponds to the base of composite capsule axis; (4) surface details of the composite capsule axis base; (5, 6) no. 5137/41: (5) collar in the upper view; prominence in the central part corresponds to the base of composite capsule axis; (6) detail of collar upper surface; (7) no. 5137/42, chipped apex of composite capsule; radially arranged coalescent bases of inverted capsules are visible.

Plate 10





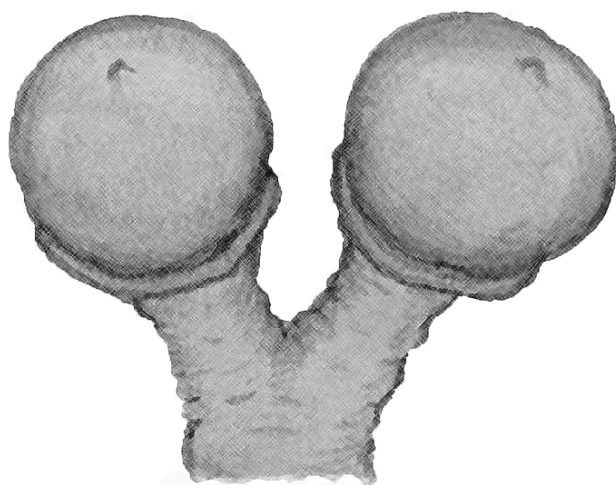


Fig. 2. Reconstructed premature composite capsules of *Vladimaria octopartita* gen. et sp. nov.

fig. 8), possessing lining of transfusion cells of the same type as in the composite capsule lobes (Pl. 21, fig. 3). The tracheids are scalariform, approximately 10 μ m in diameter.

The diameter of composite capsule stalk at collar base is 0.6–2 mm, width is up to 2 mm. The collar is slightly asymmetrical, fleshy, 1.8–5 mm in diameter.

The base of composite capsule axis is sustained by collar on thick stalk, protecting micropilar openings of seeds. The collar in its morphology is indistinguishable from collar of *Ginkgo*, but vascularized in other way. Eight radially arranged vascular bundles follow through the stalk; their quantity corresponds with the quantity of elementary capsules, comprising the composite capsule. The collar is disciform or calyptriform, often somewhat asymmetrical, 1.8–5 mm in diameter. The stalk diameter at the base of composite capsule collar is 0.6–2 mm, the width is up to 2 mm. The extensive resin canals and ellipsoidal resin cavities, containing maceration resistant matter, are developed on the cortex of stalk and collar (Pl. 9, figs. 4–6; Pl. 12, figs. 3–6; Pl. 14, figs. 4, 5, 9; Pl. 20, figs. 5, 6; Fig. 1). The diameter of the resin canals is 70–500 μ m; resin cavities are 600–1010 μ m long and 200–300 μ m wide.

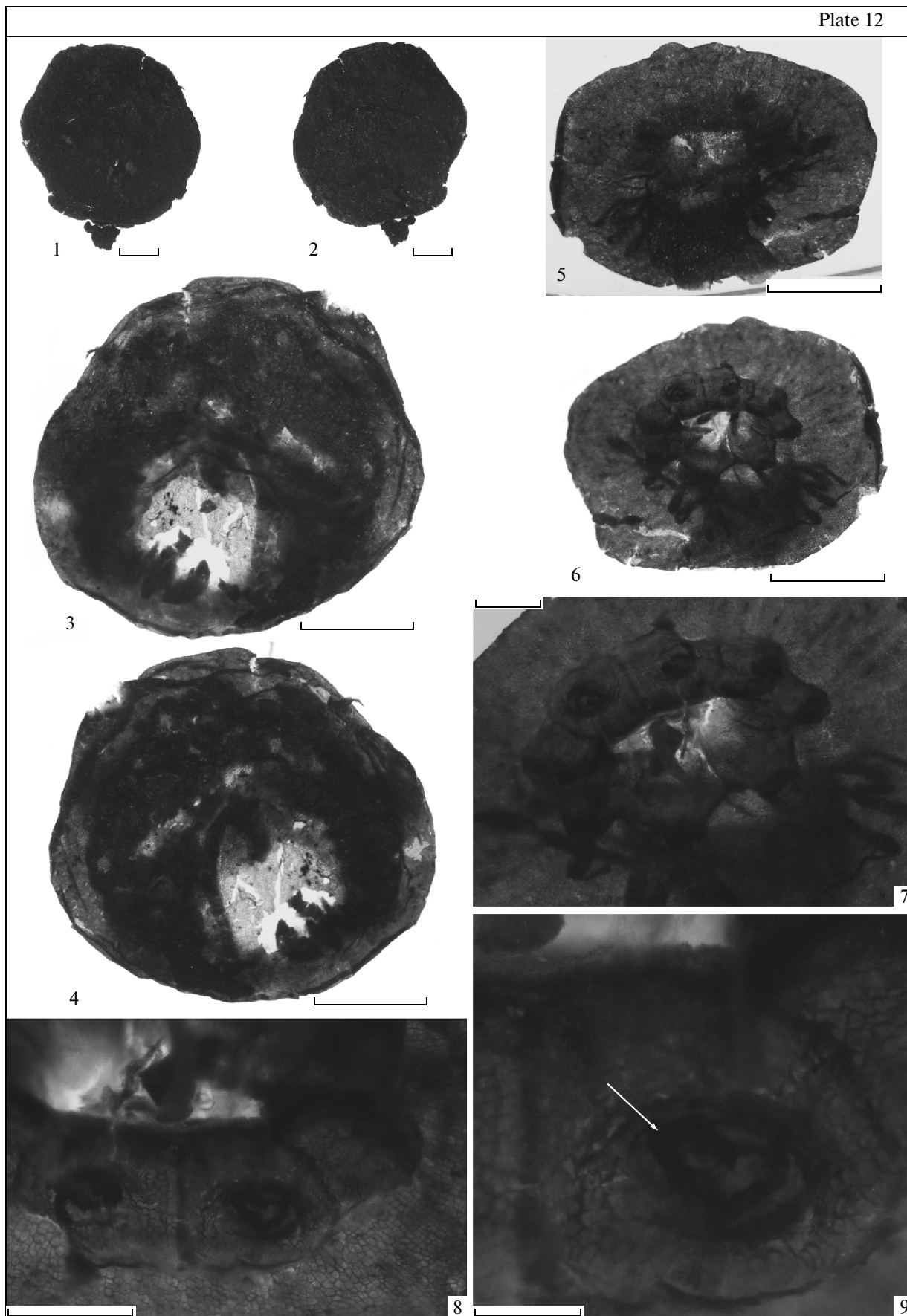
The outer epidermis cuticle of the composite capsule, stalk, collar lower surface and margins is thick, 7–10 μ m. The cuticle in the collar upper surface closer to the axial part and in the composite capsule axis is relatively thin, 1.5–2 μ m. The composite capsule cuticle is without sutures, excluding the area, protected by a collar, where the cuticle demonstrates distinct radially arranged sutures, marking fusion lines of capsules (Pl. 12, figs. 6–9).

The epidermal pavement cells of the composite capsule and its axis are congregated in more or less distinct longitudinal rows (Pl. 16, figs. 1, 2; Pl. 20, fig. 1; Pl. 21, fig. 4); in the collar, the cells form rows, radially departing from a stalk (Pl. 12, fig. 7). They are mainly rectangular–pentagonal, nearly isodiametric, more rarely transversally or longitudinally elongated, 15–60 μ m long and 10–40 μ m wide. The anticlinal walls are straight or slightly curved. The pavement cells on the collar upper surface, closer to its axial part, on the composite capsule axis, and in the area of composite capsule base, protected by collar, are predominantly papillose. The papillae are central or marginal, dome-shaped or calyptriform, often asymmetrical, with base diameter 15–30 μ m and up to 20 μ m high. Here the cells with central ribs or with prominent periclinal walls are present,

Explanation of Plate 11

Figs. 1–9. *Vladimaria octopartita* gen. et sp. nov.: (1–4), specimen no. 5137/36, LM: (1) fragment of composite capsule (inner surface), two fused capsules are visible (they are partially destroyed, with base orientated upward), micropilar openings are noted by arrows; (2) fragment of composite capsule with preserved base of one of elementary capsules (with the base orientated upward), micropilar opening is indicated by an arrow; (3) detail of fig. 2, micropilar opening is noted by arrow, lighter areas corresponds to resin bodies; (4) a fragment of composite capsule apical part (inner view) with resin bodies; (5) no. 5137/43, a collar, vascular bundle is visible on the chip of stalk; (6) no. 5137/44, a collar; (7) no. 5137/45, collar with preserved base of composite capsule axis; (8, 9) no. 5137/46: (8) two collars; (9) redraw of fig. 8.

Figs. 1–9. Scale bar 1 mm.



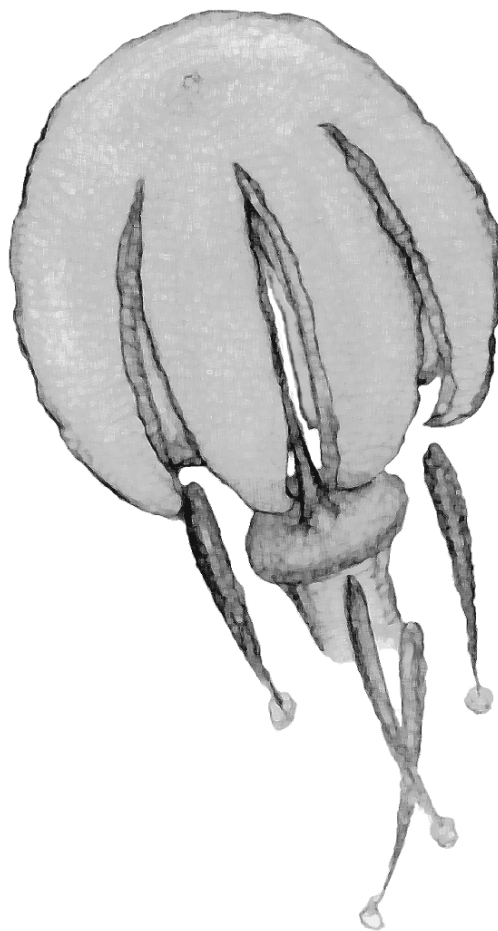


Fig. 3. Reconstructed composite capsule of *Vladimaria octopartita* gen. et sp. nov. at the moment of dehiscing and seed dispersal.

besides the papillose cells. The outer surface of the stalk cuticle is longitudinally ribbed. The ribs are radial on the collar lower surface. The pavement cells of other surface of a seed bearing organ are without papilla, with flat, or more rarely, slightly prominent periclinal wall.

Stomata are present on the outer epidermis of the composite capsule (excluding the papillose apices of the elementary capsules) on the cuticle of composite capsule axis, on collar (excluding margins), and on

stalk. As a rule, only stomata of the composite capsule outer epidermis are well developed. When the stomata are present, they are spaced more or less evenly and sometimes form short rows of a few stomata. The stomatal apparatuses are orientated randomly. The stomatal apparatuses are perigenous (Pl. 18, fig. 5), with four–eight subsidiary cells, forming the Florin ring, and with one–two circles of neighboring cells (amphicyclic type). The anticlinal walls in subsidiary and neighboring cells, as a rule,

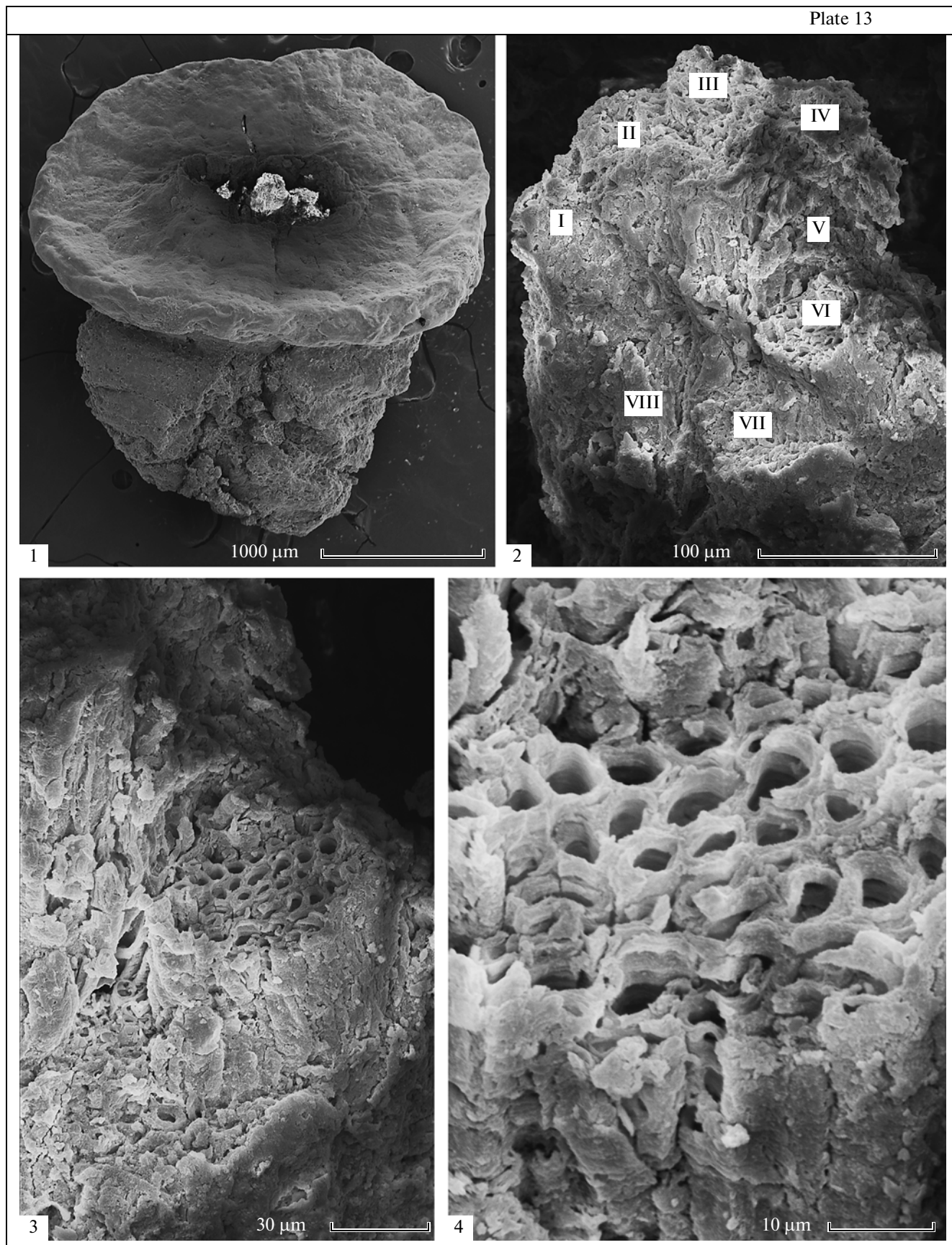
Explanation of Plate 12

Figs. 1–9. *Vladimaria octopartita* gen. et sp. nov., holotype, no. 5137/39, LM: (1) premature composite capsule in the organic connection with a collar; (2) the same, the view from the side of collar base; (3) premature composite capsule after maceration (view from the side of base), dark inclusions are resin canals and bodies; (4) the same, the view from the side of composite capsule apex; resin canals, radially departing from apex to the base, are visible; (5) cuticular covering of collar, view from the side of stalk, dark inclusions are radially departing resin canals; (6) the same, view from the side of composite capsule base; eight apices of fused capsules with concentric signs of seed micropilar tips attachment are visible; (7) detail of fig. 6, concentric signs of seed micropilar tips attachment are well-marked visible; (8) detail of fig. 7; (9) detail of fig. 8, a scar of micropile is noted by arrow.

Figs. 1–6. Scale bar 1 mm.

Figs. 7, 8. Scale bar 0.5 mm.

Fig. 9. Scale bar 0.2 mm.



are less cutinized than anticlinal walls in the pavement cells. The guard cells on the composite capsule outer cuticle are sunken, wing-shaped, 50–60 μm long, 40–50 μm wide, with well-developed polar extensions (Pl. 16, fig. 3; Pl. 20, figs. 2–4); guard cells of axis and upper surface of collar are in form of half-circle, radially striated, 20–36 μm long, 24–28 μm wide, or nearly reduced, the polar extensions are not developed (Pl. 18, figs. 4, 6; Pl. 20, figs. 5, 6). The polar subsidiary cells are rarely present. The stomatal density is 14 stomata per mm^2 .

R e m a r k s. The presence of two vascular bundles may point to the origin of elementary capsule by fusion of two lobes, each of which had its own vascular bundle (it testifies on the similarity with *Umkomasiales*). Probably, the vascularization of individual capsules had been more complex, than it may be deduced on the available material.

The stomata on the axis of composite capsule and upper surface of collar are nearly twice smaller than normally developed stomata of the composite capsule outer surface. They might carry out secretory function, moistening the area around micropilar openings.

M a t e r i a l. More than 50 exemplars, presented by phytoteleims.

DISCUSSION

The new plant, due to its specialized ovuliferous organs, nearly completely enclosing seeds, enlarges the comprehensive group of Proangiosperms. Among the representatives of Meyen's *Ginkgoopsida* line, Krassilov (1989) placed the *Leptostrobales* and *Caytoniales* within Proangiosperms. It is difficult to judge on the pollination mechanism in the new plant, but special mechanisms for pollination of seeds, situated within nearly closed capsules, evidently were present. These are papillose stigmalike structures around micropilar aperture. The pollen, most probably, got in the relatively narrow space between a collar and composite capsule base, where was caught with pollination drop, secreted by micropile. With this pollination method, ovuliferous organs in *Vladimaria* gen. nov. must not be drooping as in *Ginkgo*, but standing, as it was reconstructed for the ginkgoalean *Nechvizdiella* Kvaček, Falcon-Lang et Dašková (Kvaček et al., 2005). Most probably, the “seeds” of enigmatic pteridosperms, described together with ginkgoalean-like leaves as *Grenana* (Samylina, 1990)

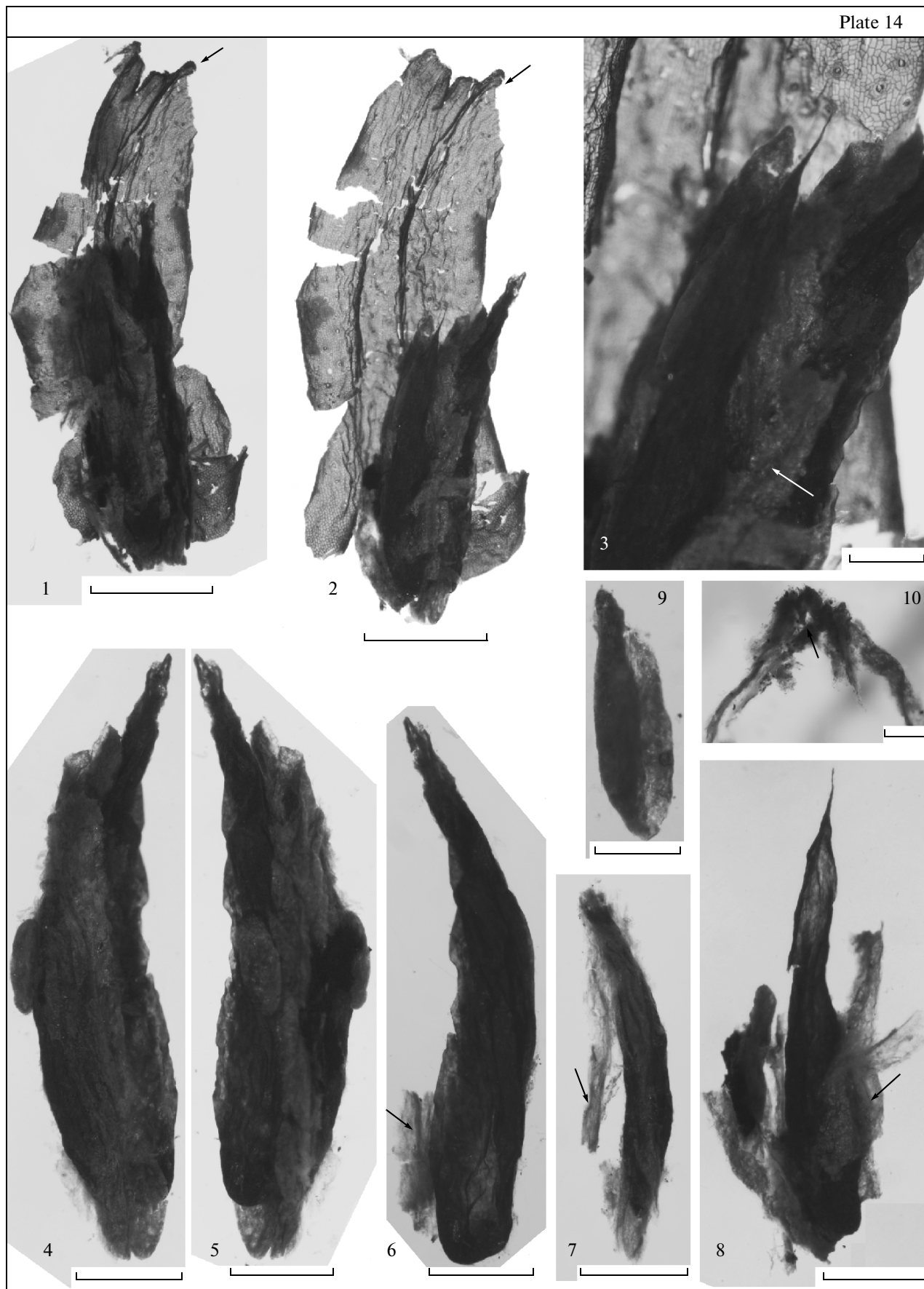
and, at present day, assigned by many researchers to the family *Ginkgoaceae*, in fact may be capsules, similar to *Vladimaria* gen. nov., but this question needs an additional investigation. “Seeds” were not been found in the organic connection with leaves *Grenana*, but they demonstrate similarities in the epidermal structure with the latter. Anyway, the generic name *Grenana* must be assigned to vegetative, but not reproductive structures, found in association with the leaves. The interesting feature of leaves *Grenana* is the mononerve terminal lobes in a leaf blade (Samylina, 1990). In the association with *Vladimaria* gen. nov., leaves of various morphotypes have been found. The vast majority of the leaves must not be related to the genus (part of the leaves is assigned to ferns, conifers, and bennettites). Of interest, is the presence in the locality of leaves *Leptotoma*, possessing mononervous lobes like *Grenana*, and leaves *Pachypteris*, which are known in association with ovuliferous organs of *Umkomasia* (Kirchner and Müller, 1992). However, I suppose that, both leaves probably were not related to the new seed-bearing organs, since the leaves lack resin canals. Moreover, no one of morphotypes, found in the Mikhailovskii rudnik, do not demonstrate sufficient similarity with the new genus in the epidermal structure. Unfortunately, the question is still open.

Undehisced composite capsules of the new plant demonstrate surprising similarity to the ovuliferous organs of *Ginkgo*; the dehisced ones may be easily mistaken as bennettitalean strobili (*Weltrichia*, *Williamsonia* etc.), as it was said earlier. The latter circumstance may be regarded as no more than the casual *lusus naturae*, but the first requests more intent attention.

On the examination of the cuticular covering of undehisced composite capsule in *Vladimaria* gen. nov., it is impossible to leave without attention its amazing similarity to the cuticular covering of seeds in *Ginkgo*. The anatomical details of the composite capsule wall are very similar to these of the fleshy part of integument in *Ginkgo*. I suppose that the abundance of stomata in the epidermis of the integument definitely indicates its “foliar” nature. Therefore, the homologue of seed-bearing peltoid in *Ginkgo* is not the collar, as supposed Meyen, but the outer fleshy part of integument (and probably, part of sclerotesta). The outer part of integument may be relatively easily derived of two lobes of umkomasian cupule. The vascular bundles in seeds of *Ginkgo* may prove to be deriv-

Explanation of Plate 13

Figs. 1–4. *Vladimaria octopartita* gen. et sp. nov., no. 5137/47, SEM: (1) a collar; (2) detail of fig. 1 in the area of base of composite capsule axis, vascular bundles of the axis are noted by roman numerals, their number corresponds to the number of composite capsule segments; (3) detail of fig. 2, collateral vascular bundle; (4) detail of fig. 3, the metaxylem tracheids of vascular bundle with scalariform bordered pits.



atives of two fused lobes of capsule, rather than vascularized primary integument. Anyway, we see in *Vladimaria* gen. nov. that in the presence of collar the homologues of foliar organs are elementary capsules of the composite capsule. Therewith, we observe two vascular bundles in each elementary capsule. Any evidence of the presence of vascular bundles in the integument of *Vladimaria* gen. et sp. nov. is absent. In connection with the assumption on the “capsule” origin of sclerotesta in *Ginkgo*, it is necessary to notice the presence of inner stone layer in capsules of *Doylea* Stockey et Rothwell, assigned by the authors to corysperms (Stockey and Rothwell, 2009).

We have no direct arguments that collar in *Vladimaria* gen. nov. is a homologue of collar in *Ginkgo*, but both of them have one main function—the sustention of sufficiently large ovuliferous organ. Since the collar can not be a reduced peltoid (or cupule), it may be a usual enlargement of stalk (Naugolnykh, 2002) or derivate of foliar appendages in the strobilus base (like a pair of small leaflets, which are presented in *Umkomasia uniramia*). Krassilov (1972) based on morphological features of ovuliferous organs of ginkgoalean *Umlatolepis* Krassilov, proposes similar interpretation of collar in *Ginkgo*. He believes that the ginkgoalean collar is not a new formation and has leaf nature, and Ginkgoales in their development might pass a stage of seed scale (therefore, they did not originate directly by oligomerization of pinnate ovuliferous organs of Trichopitiaceae). As far as we know, that a collar may be formed independently from the fertile structure, sustained by the collar, we can not agree with hypothesis of Naugolnykh (2005, 2007, 2008) on the origin of ginkgoalean collar as the result of recapitulation of features of “pre-karkenian” ancestors, possessing foliar ovuliferous organs (like in *Hamshawvia* Anderson et Anderson, *Stiphorus* S. Meyen, *Biarmopteris* Zalessky, and *Cheirocladus* Naugolnykh). J.M. Anderson and H.M. Anderson also placed *Hamshawvia* in the order Ginkgoales (Anderson and Anderson, 2003). All enumerated genera, on my opinion, can not be

placed directly in the order Ginkgoales. The suggestion that the collar in *Ginkgo* is not a cupule, is affirmed by the data on its ontogenesis (Douglas et al., 2007).

The whorled arrangement of fused elementary capsules in *Vladimaria* gen. nov. gives the latter similarity with *Umkomasia uniramia* from the Upper Triassic of Antarctica (Axsmith et al., 2000) and testifies on close interrelations between the new order and umkomasians. The similarity is emphasized by the presence of dehiscing mechanism. Unfortunately, it is known nothing on the details of inner structure in *U. uniramia* because of its poor preservation. Dehiscing capsules are also present in other Umkomasiales. For example, the capsule in *Kannascopia* Anderson et Anderson (the authors placed the genus in the order Ginkgoales) from the Upper Triassic of South Africa contained a solitary seed and opened by dehiscing on three or four lobes (Anderson and Anderson, 2003); the capsules of *Doylea* opened by dehiscing on three lobes (Stockey and Rothwell, 2009).

The Vladimariales ordo nov., due to its peculiarity, is not a link between the Ginkgoales and Umkomasiales, however, the order demonstrates some features, characterizing these two orders. Therefore, we see in the Ginkgoales the extreme specialization degree, rather than primitive elementary structure. The latter assumption seems more possible, since the other representatives of the lineage possess capsules with complex structure. In this case, any representatives with naked seeds without capsule protection have not remained within the Ginkgoopsida lineage already in the Middle Mesozoic. If the assumption is correct, the Ginkgoales are typical and strongly specialized representatives of the proangiosperms.

The above mentioned gives evidence that supposition on the origin of Ginkgoales from Umkomasiales, stated by Krassilov (1989), was correct. I believe that the Leptostrobales also will be proved the descendants of Umkomasiales in case of more detailed investigation.

Explanation of Plate 14

Figs. 1–10. *Vladimaria octopartita* gen. et sp. nov., no.5137/36, LM: (1) partly macerated fragment of composite capsule, figured on Pl. 4, fig. 1., the base is orientated upward, shows the cuticle of lobes, as well as seeds, enclosed into partly destroyed thin cuticular films, corresponding to a lining of locule, which contained a seed; micropilar openings are noted by arrows; (2) the next maceration stage of composite capsule fragment, the orientation of seeds is visible; micropilar tips are noted by arrows and orientated towards of composite capsule base; (3) detail of fig. 2, the micropile of one of seeds is visible; common wall between two neighboring capsules is noted by arrow; (4) two seeds, separated by common wall of neighboring capsules; the wall contains numerous resin bodies; (5) the same, view from the back side; (6) a seed with destroyed micropilar part and remains of locule cuticle; the position of a vascular bundle within inner wall of capsule is noted by arrow; (7) incomplete seed with remains of locule cuticle, the position of a vascular bundle within inner wall of capsule is noted by arrow; (8) seed, enveloped by remains of locule cuticle, with large resin bodies, adhered to it; the position of a vascular bundle within inner wall of capsule is noted by arrow; (9) a resin body from the wall between two neighboring capsules; (10) cuticle fragment of the locule, enclosing a seed (the place of seed stalk attachment is noted by arrow).

Figs. 1–2. Scale bar 2 mm.

Figs. 3, 9, 10. Scale bar 0.5 mm.

Figs. 4–8. Scale bar 1 mm.

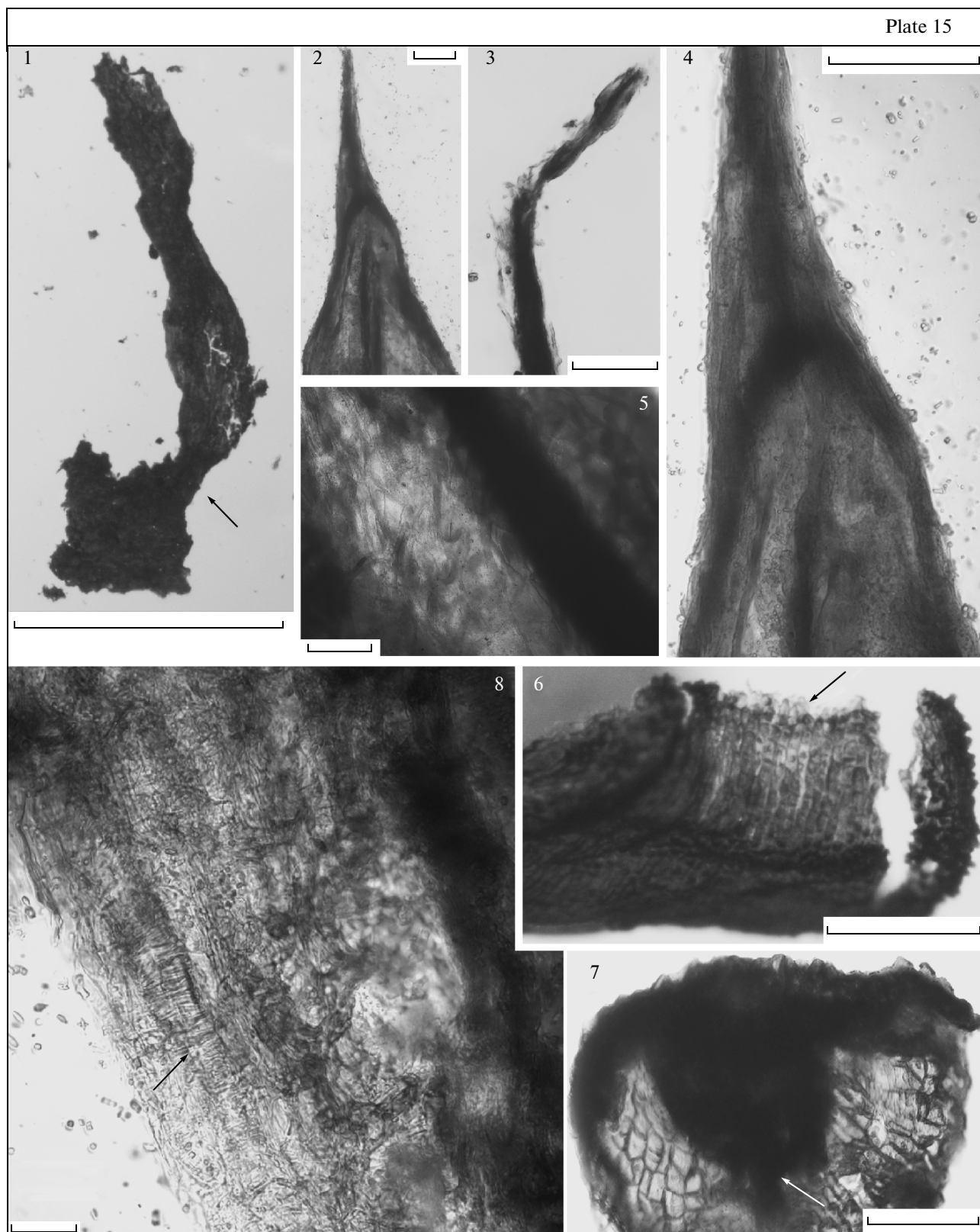
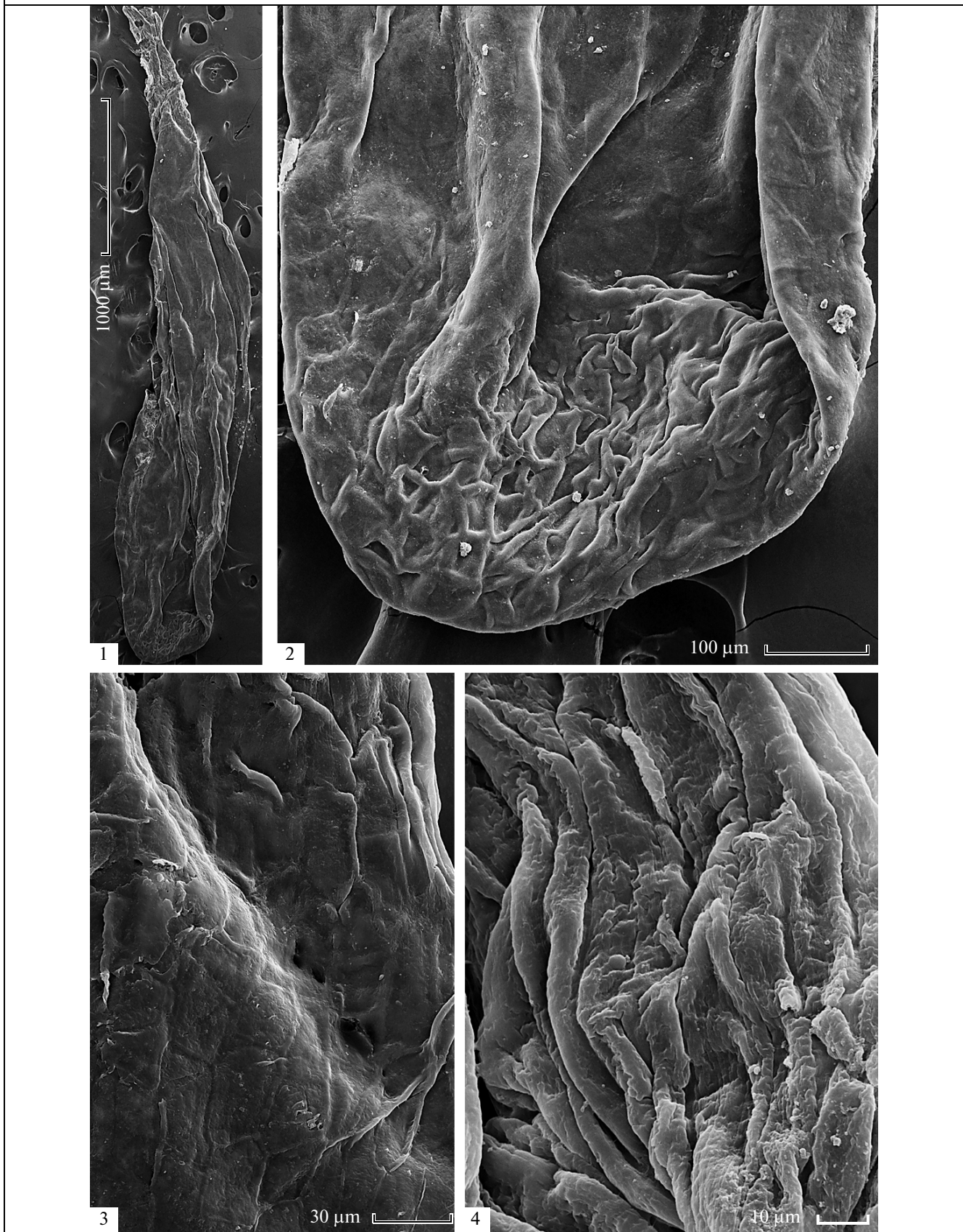


Plate 16



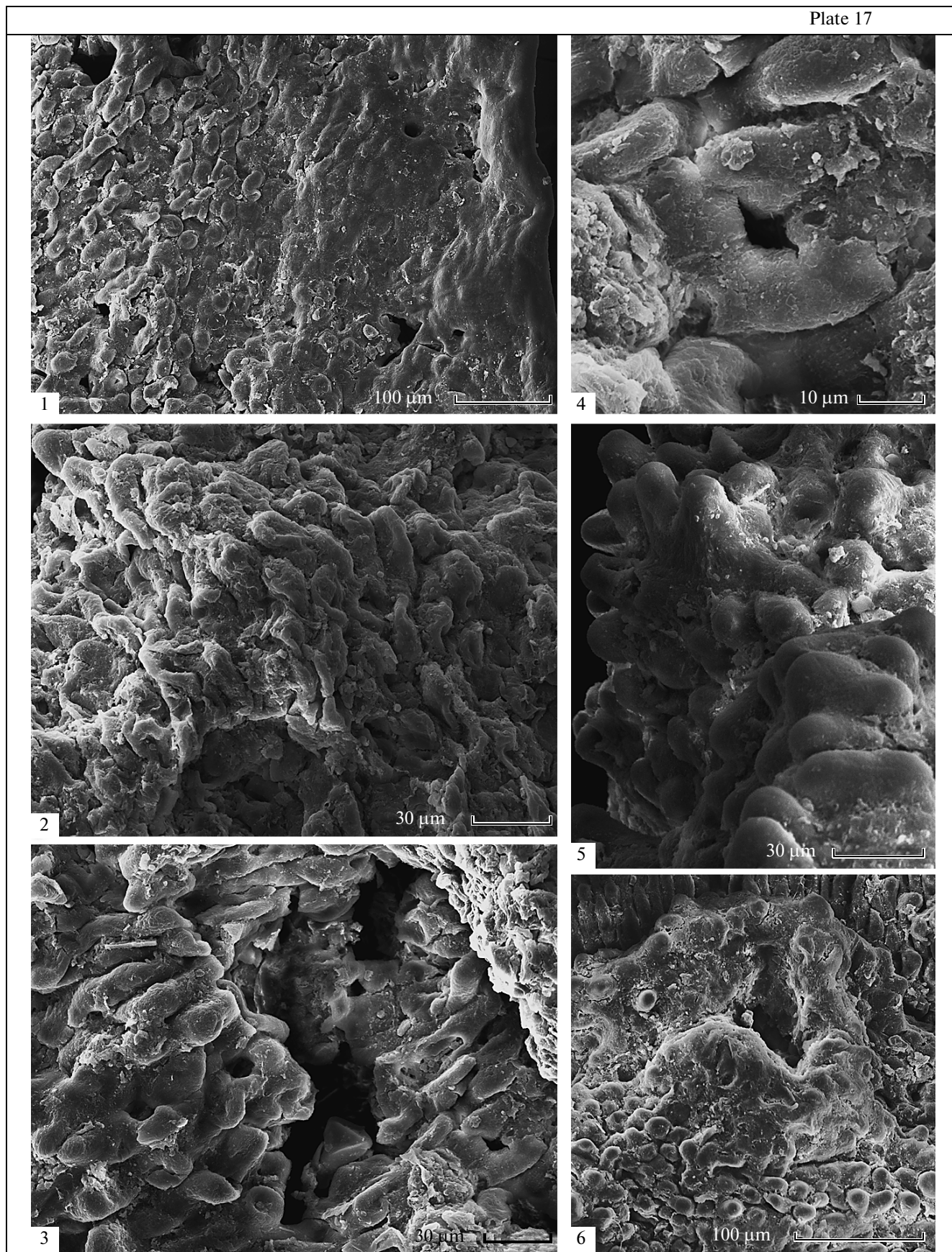
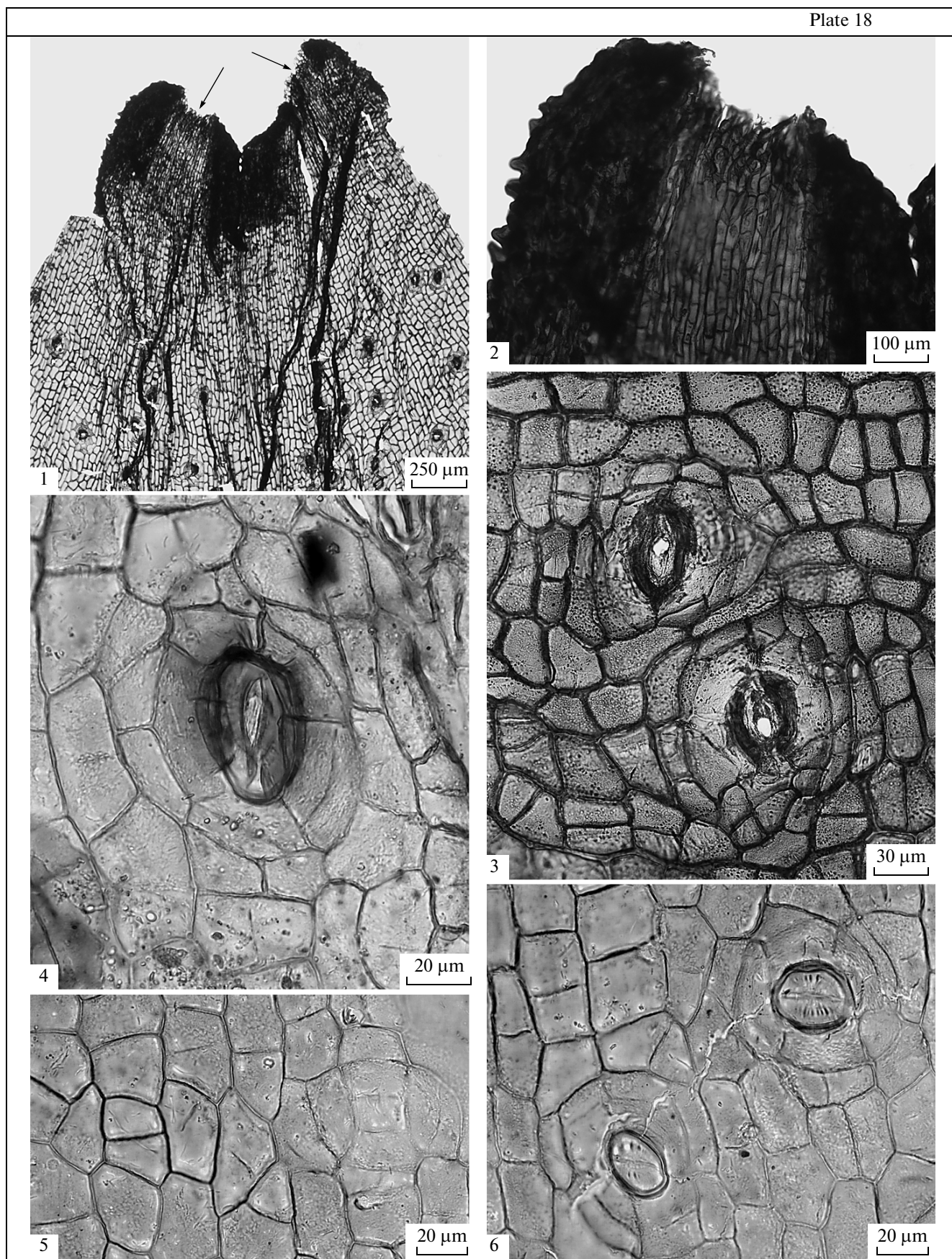


Plate 18



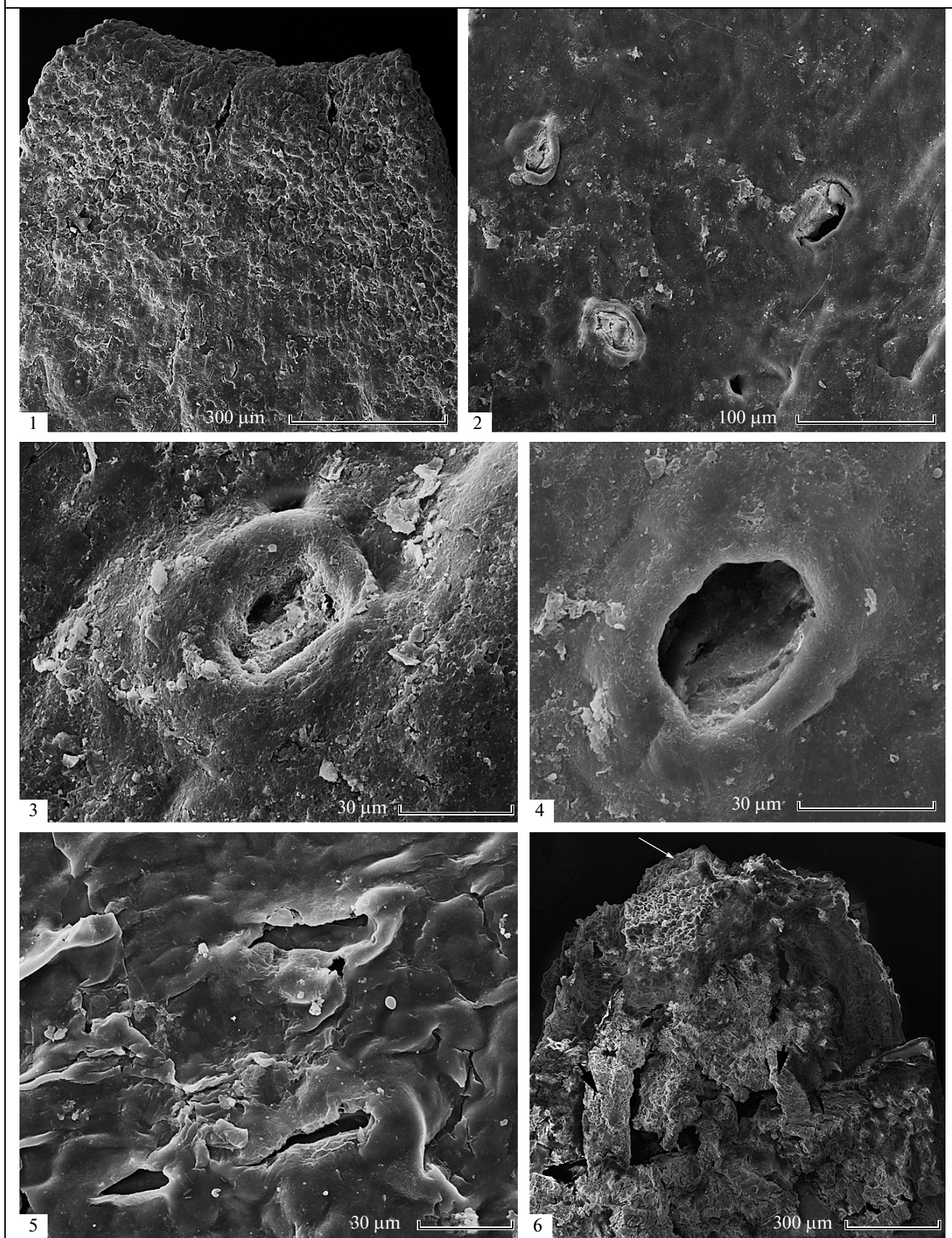
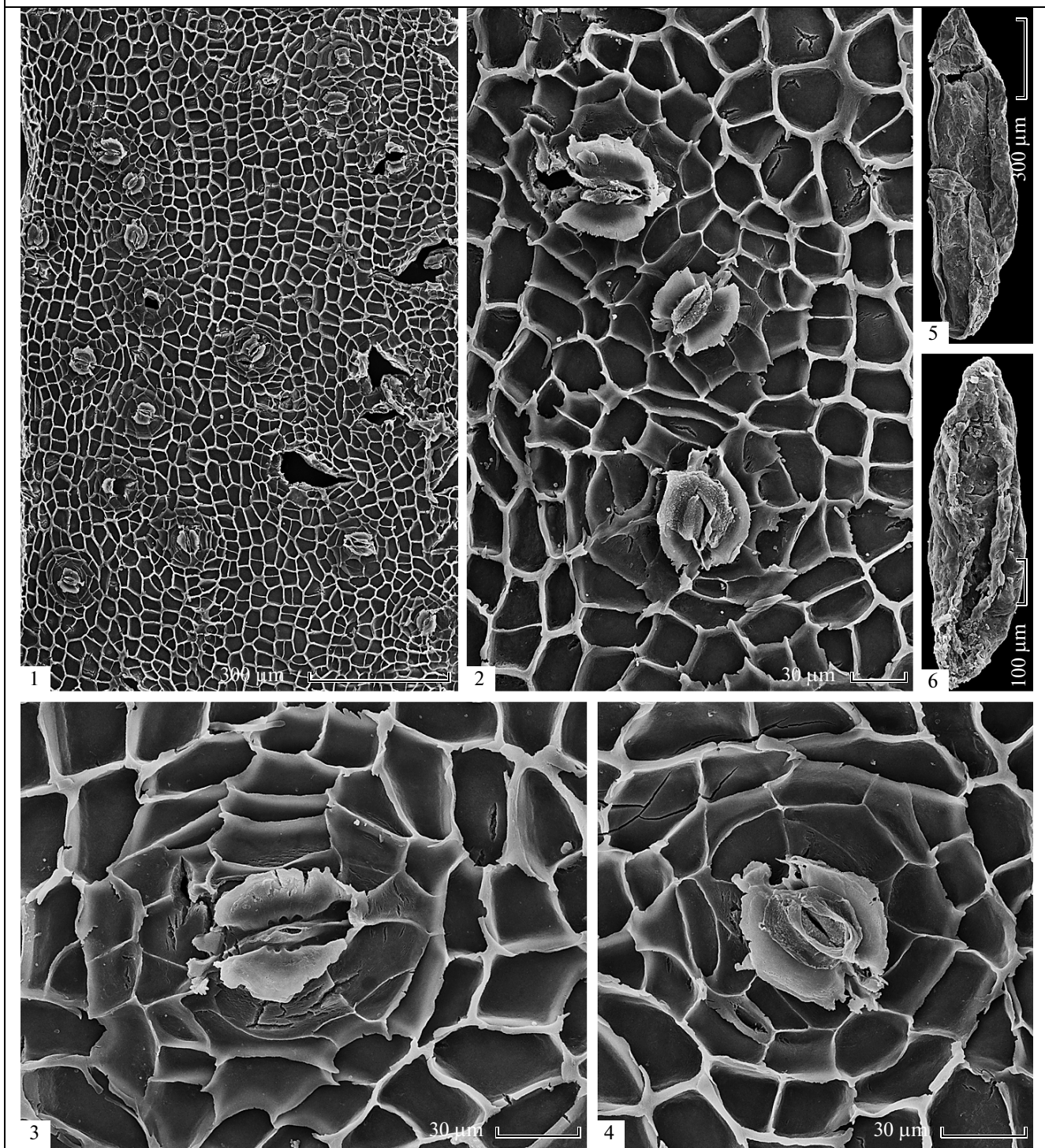
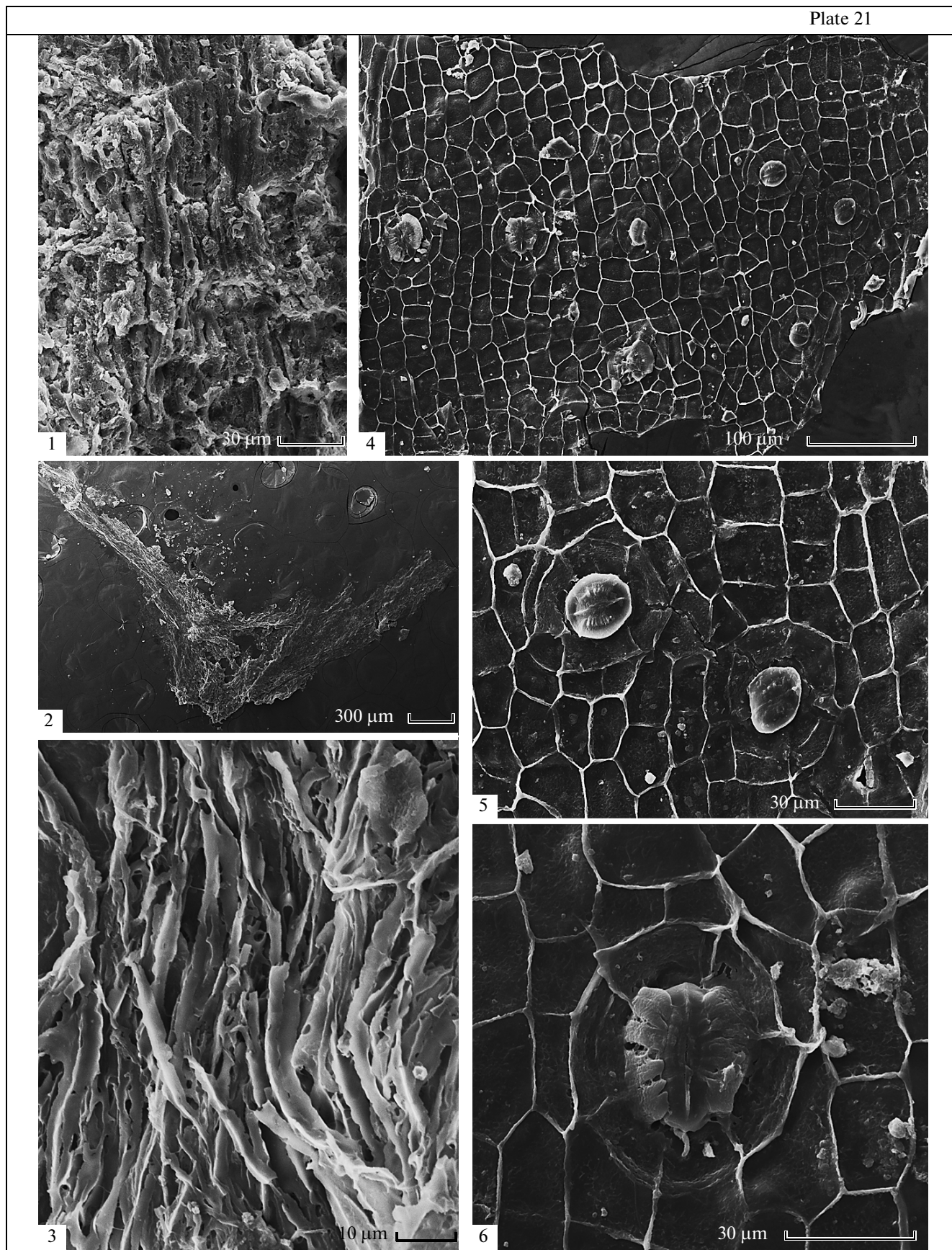


Plate 20



Explanation of Plate 20

Figs. 1–6. *Vladimaria octopartita* gen. et sp. nov., no. 5137/36, SEM: (1) inner side of cuticle of the outer surface in the middle part of composite capsule; (2) detail of fig. 1, incompletely amphicyclic stomatal apparatuses; (3) detail of fig. 1, an amphicyclic stomatal apparatus with wing-shapely cutinized periclinal walls of the guard cells; (4) an amphicyclic stomatal apparatus with partly preserved cutinization of the inner periclinal walls of guard cells; (5) two ellipsoidal resin bodies from the common wall of two neighboring capsules; (6) an ellipsoidal resin body from the common wall of two neighboring capsules.



Explanation of Plate 15

Figs. 1–8. *Vladimaria octopartita* gen. et sp. nov., LM: (1) no. 5137/48, a base of abortive ovule, its stalk is noted by arrow; (2–5, 7, 8) no. 5137/36: (2) detail of the seed, figured on Pl. 7, fig. 8, a long micropile is visible; (3) detail of micropile of the seed, figured on Pl. 7, fig. 8; (4) detail of fig. 2, outer and inner cuticles of integument and nucellus apex are visible; (5) detail of outer cuticle of the seed integument near chalaza, indistinct outlines of cells with prominent periclinal walls are visible; (7) macerated fragments of the apical part of capsule (inner view) with attached to it apex of seed micropile (noted by arrow); (8) vascular bundle within the inner wall of capsule, a tracheid with scalariform thickenings is noted by arrow; (6) no. 5137/38, the apex of one of lobes in dehiscent composite capsule, the line of dehiscing, along that the apical part of capsule dehiscent to disengage a seed, is noted by arrow.

Fig. 1. Scale bar 1 mm.

Figs. 2–5. Scale bar 100 μ m.

Fig. 6. Scale bar 200 μ m.

Fig. 7. Scale bar 50 μ m.

Fig. 8. Scale bar 10 μ m.

Explanation of Plate 16

Figs. 1–4. *Vladimaria octopartita* gen. et sp. nov., no. 5137/36, SEM: (1) seed with destroyed micropilar tip; (2) halazal part of the seed, detail of fig. 1; (3) cuticle of the seed integument in the middle part; (4) outer cuticle of the integument closer to micropile, detail of fig. 1.

Explanation of Plate 17

Figs. 1–6. *Vladimaria octopartita* gen. et sp. nov., SEM: (1) no. 5137/40, detail of the upper surface of a collar; (2–4) no. 5137/41: (2) papillae on the cuticle of composite capsule base; (3) papillae and stomatal pits on the upper surface of a collar, near composite capsule axis base; (4) detail of fig. 3, subsidiary cells form a Florin ring around the stomatal pit; (5, 6) no. 5137/36: (5) papillae in the apical part of a composite capsule lobe; (6) the micropilar opening.

Explanation of Plate 18

Figs. 1–6. *Vladimaria octopartita* gen. et sp. nov., no. 5137/36, LM: (1) outer cuticle of two fused capsules, the composite capsule base is orientated upward, the position of micropilar opening is noted by arrows; (2) detail of fig. 1, papillae around the micropilar opening are visible; (3) the outer cuticle of a composite capsule middle part, amphicyclic stomata are visible; (4) the cuticle of composite capsule axis shows a stomatal apparatus with weakly developed cutinization of guard cells; (5) abortive stomata point on the perigenous development of stomatal apparatuses; (6) stomatal apparatuses with rudimentary cutinization of guard cells on the cuticle of composite capsule axis.

Explanation of Plate 19

Figs. 1–6. *Vladimaria octopartita* gen. et sp. nov., no. 5137/36, SEM: (1) outer surface a composite capsule lobe, papillae in apical part of lobe are visible; (2) outer surface of cuticle in the middle part of composite capsule, three stomatal pits, surrounded by Florin rings, are visible; (3, 4) Florin rings on stomatal pits; (5) the outer surface of composite capsule axis cuticle, three stomatal pits and pavement cells with prominent periclinal walls are visible; (6) partly destroyed capsule with the apex is orientated upward, micropilar opening is noted by white arrow, resin canals are noted by black arrows.

Explanation of Plate 21

Fig. 1–6. *Vladimaria octopartita* gen. et sp. nov., no. 5137/36, SEM: (1) the fragment of inner surface of the lobe axial part in dehiscent composite seed capsule, long transfusion cells are visible; (2) thin cuticular film, covered a seed locule; from the side of the lobe axial part, thin vascular bundle, coated with transfusion cells, flanks to the film (noted by arrow); (3) transfusion cells, detail of fig. 2; (4) the inner side of the composite capsule axis cuticle, stomatal apparatuses with variously cutinized guard cells are visible; (5) detail of fig. 4, incompletely amphicyclic stomatal apparatuses with partly cutinized outer periclinal walls of guard cells; (6) detail of fig. 4, a monocyclic stomatal apparatus with weakly cutinized outer periclinal walls of guard cells.

Florin (1949) supposed earlier that the Ginkgoales derived directly from Trichopitiaceae by oligomerization. In that case, the Trichopitiaceae and Ginkgoales are allied with stachyospermids (Cordaitanthales and Coniferales). Recently, this point of view is supported by the vast majority of researchers (Crane, 1985; Zhou and Zhang 1988, 1989; Zou, 1991, 2009; Doyle et al., 1994; Zheng and Zhou, 2004; Hilton and Bateman, 2006; Taylor et al., 2009 etc.). In the case of presence of secondary integument in the Ginkgoales, their evolutionary line followed most likely through Umkomasiales; this excludes the “direct” origin way of Ginkgoales from Trichopitiaceae, whatever the interpreta-

tion of their seed-bearing organs is (shoots, according to Florin, or foliar structures, according to Meyen).

Insects, finding the leaves and ovules of Ginkgoopsida an available nutritive resource, might play significant role in the origin of various capsules within the Ginkgoopsida lineage. The evidence, that insects were eating actively both the vegetative, and reproductive parts of the Peltaspermales (Krassilov and Rasnitsyn, 1997, 1999 etc.), was found as early as in the Permian. Again in the Permian, the forms with seeds, protected by capsule (Angaropeltidaceae), make their appearance; the phenomenon has widespread in the Triassic. Numerous large and small damages, healed with resin

matter, were found in the composite capsule cuticle of the new genus *Vladimaria* gen. nov. This testifies that the plant was a subject of active blast attacks. The composite capsule substantially complicated the access to ovules, even micropiles of which were covered up.

CONCLUSIONS

Summing up all stated above, it is possible to make several main conclusions:

The collar of *Ginkgo* is not an unique feature of the genus. Though we can not say that collars in *Ginkgo* and *Vladimaria* gen. nov. are homologous and formed by the same way, yet it is obvious, that the collar might appear in various, probably phylogenetically related plant groups, and had a quite simple function—the mechanical support of relatively large reproductive structure. The collar could be formed as an enlargement of stalk, or be the derivative of leaves at base of strobilus. In this relation, seed-bearing organs of *Umaltolepis* are of the particular interest.

The collar is not a reduced cupule (its cupulate function, for example in the case of *Hechvizdiella* (Kvaček et al., 2005), is secondary) and not homologous to seed-bearing peltoid of Peltaspermales. Therefore, ovuliferous organs of Ginkgoaceae might not be formed by everting of peltoid, as Meyen (1984, 1987) supposed.

In the Jurassic, more advanced descendants of the Triassic umkomasians and peltasperms acquired capsules. Among them, it seems, there were no more plants with naked seeds.

The Umkomasiales are the most probable progenitors of Ginkgoales and Vladimariales ordo nov. The Ginkgoales might not originate directly from trichopityans. They are later, very specialized product of evolutionary transformations in the Umkomasiales and correspond to the proangiosperm development level. The assignment of genus *Trichopitys* Saporta to Ginkgoales is devoid of substantial reasons.

Capsules of Leptostrobales most probably will prove to be composite, like those of Vladimariales ordo nov. This assumption needs to be tested on undehiscent capsules of the former. The inverted position of seeds in the composite capsule of the Vladimariales ordo nov. to some extent helps with understanding of inverted seed position in Leptostrobales. Ginkgoales by set of features more logically ally with umkomasians, Leptostrobales and Vladimariales ordo nov., rather than with conifers. Classis Ginkgoopsida, proposed by Meyen and did not accepted by many researches, is well substantiated, though one can agree or disagree with its composition, especially as regards some oldest representatives of seed plants, included in this classis by Meyen.

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