

# Ovuliferous Organs of *Trisquamales* Gordenko et Broushkin ordo. nov. (Gymnospermae) from the Middle Jurassic of the Kursk Region, European Russia

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**Abstract**—The ovuliferous organs *Trisquama valentini* Gordenko et Broushkin, gen. et sp. nov. from the Bathonian deposits of the Mikhailovskii Rudnik locality (Kursk Region) are described. The ovuliferous organs consist of three scales fused at the base. The long scale, together with the stalk of ovuliferous organ compose a sterile structure, which is vascularized by C-shaped in section collateral vascular bundle, and bears a lobed fertile structure of ovuliferous organ on its anatomically abaxial side. The latter consists of two short scales and an outgrowth between them, and is vascularized by concentric amphicribal vascular bundle, which is divided in its distal part into three separate collateral plates. These plates are associated with the lobes of fertile structure and three small orthotropous seeds situated from xylem side of these vascular bundles. Seeds are ellipsoidal, with not protruding micropyle; the integument is sclerified, megaspore membrane is thick. The ovuliferous organs under description possess unique features, which preclude their assignment to any large group of gymnosperms; authors place them in a separate order, *Trisquamales* ordo. nov., systematic position of which within *Gymnospermae* is uncertain.

**Keywords:** Gymnosperms, morphology, anatomy, systematics, Middle Jurassic

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## INTRODUCTION

The diversity of Mesozoic gymnosperms strike the imagination of researchers perhaps not less than diversity of extant flowering plants. Despite intense investigations in this field, the state of knowledge of Mesozoic gymnosperms is still very incomplete, many of key questions of phylogeny, systematics, and taxonomy remain unresolved. Along with groups, relationships of which with ancestral and descendent forms can be traced, there are significant number of taxa of high taxonomic rank, such as *Czekanowskiales* (Lep-tostrobales; Krassilov, 1968; Meyen, 1987), *Petriel-lales* (Taylor et al., 1994; Bomfleur et al., 2014), *Pent-oxylales* (Sahni, 1948, Taylor et al., 2009), *Schmeiss-neriales* (Kirchner and Van Konijnenburg-Van Cittert, 1994; Wang et al., 2007; etc.), “*Iraniales*” (Schweitzer, 1977; for discussion of nomenclature see Shipunov and Sokoloff, 2003), *Dordrechtiales* (Anderson and Anderson, 2003; Bergene et al., 2013), phylogenetic affinities of which, due to insufficient understanding and/or unusual structure, remain unclear. The new finding is another contribution to the treasury of enigmatic Mesozoic gymnosperms. The ovuliferous organs *Trisquama valentini* gen. et sp. nov. display a unique combination of taxonomically important structural features, it is impossible to relate them with any presently known large group of gymnosperms.

The new plant is placed by the authors in a separate order, *Trisquamales* ordo nov., the position of which within *Gymnospermae* is uncertain.

## MATERIAL AND METHODS

The material described in this paper comes from deposits of the Arkinsk Formation (Middle Jurassic, Bathonian; *Unifitsirovannaya* ..., 1993) of the Mikhailovskii (Mikhailovskii Rudnik) open mine near the town of Zheleznogorsk, Kursk Region. In this locality, the section of the Arkinsk Formation represent a ter-rigenous sequence of alluvial genesis, more than 10 m thick, underlain by the Devonian strata or rocks of the Proterozoic basement. Plant remains were collected from a clayey lens about 1.5 m thick at the base of the section, exposed in the northern wall of the northern open mine. This part of the section supposedly represents sediments of floodplain complex, in places, with signs of pedogenesis; upward in the section, these deposits are overlain by a thick layer of cross-bedded channel sands. Besides of remains of *Trisquama val-entini* gen. et sp. nov., here were found abundant plant remains: *Matonia* sp., *Osmunda* sp., *Mirovia eximia* (Gordenko) Nosova, *Vladimaria octopartita* Gordenko, *Pachypteris rutenica* Gordenko, *Pachypteris* sp., *Lepto-toma* sp., *Ginkgo huttoni* Harris, *Benneticarpus* sp., *Pti-*

*lophyllum riparium* Gordenko, *Sympterothymum sympinnatum* Gordenko et Broushkin, *Otozamites* sp., *Zamites* sp., numerous fragments of bennettitalean bracts, *Schizolepidopsis* sp., *Elatocladus* sp., *Pityocladus* sp., and wood *Phyllocladoxylon* (Gordenko, 2007a, 2007b, 2010; Gordenko and Broushkin, 2010). The plants are represented by coalified (lignified) remains, usually with preserved cellular structure.

The ovuliferous organs studied were extracted from enclosing rock and cleaned from matrix; some exemplars were placed in hydrofluoric acid; then, the material was photographed, using a Leica M165C stereomicroscope and Leica DFC 420C digital camera. The anatomical structure of ovuliferous organs and seeds was studied on orientated splits under a Tescan SEM (in the low and high vacuum); the course of vascular bundles was traced on series of successive tomograms obtained with the aid of SkyScan 1172 Micro Computer Tomography System. Cuticular films were obtained using the standard maceration method in nitric acid with subsequent placement in KOH solution; cuticle preparations of the ovuliferous organ and seed coats were studied using an Axioplan-2 light microscope (with Leica DFC 420 digital camera), and SEM. The material is housed in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN), collection no. 5137.

## SYSTEMATIC PALEOBOTANY

### DIVISION GYMNOSPERMAE

Order Trisquamales Gordenko et Broushkin, ordo nov.

E t y m o l o g y. From the type family.

D i a g n o s i s. Ovuliferous organs consist of one sterile and one fertile (seed-bearing) structures. Sterile structure, comprising stalk of ovuliferous organ and undissected distal part, vascularized by C-shaped in section collateral vascular bundle, and bears fertile structure on its anatomically abaxial side. Fertile structure lobed, vascularized by concentric amphicribal vascular bundle, which departs from phloem side of sterile structure vascular bundle. Concentric bundle in its distal part divided into separate collateral segments, associated with lobes of fertile structure. Cavity with seeds closes through joining of distal part of sterile structure and lobes of fertile structure. Seeds orthotropous, with not protruding somewhat shifted micropyle, vascularized from xylem side of fertile structure vascular bundle segments. Integument single, sclerified, without sarcotesta; nucellus free from integument more than one half, megaspore membrane thick.

T y p e f a m i l y. Trisquamaceae fam. nov.

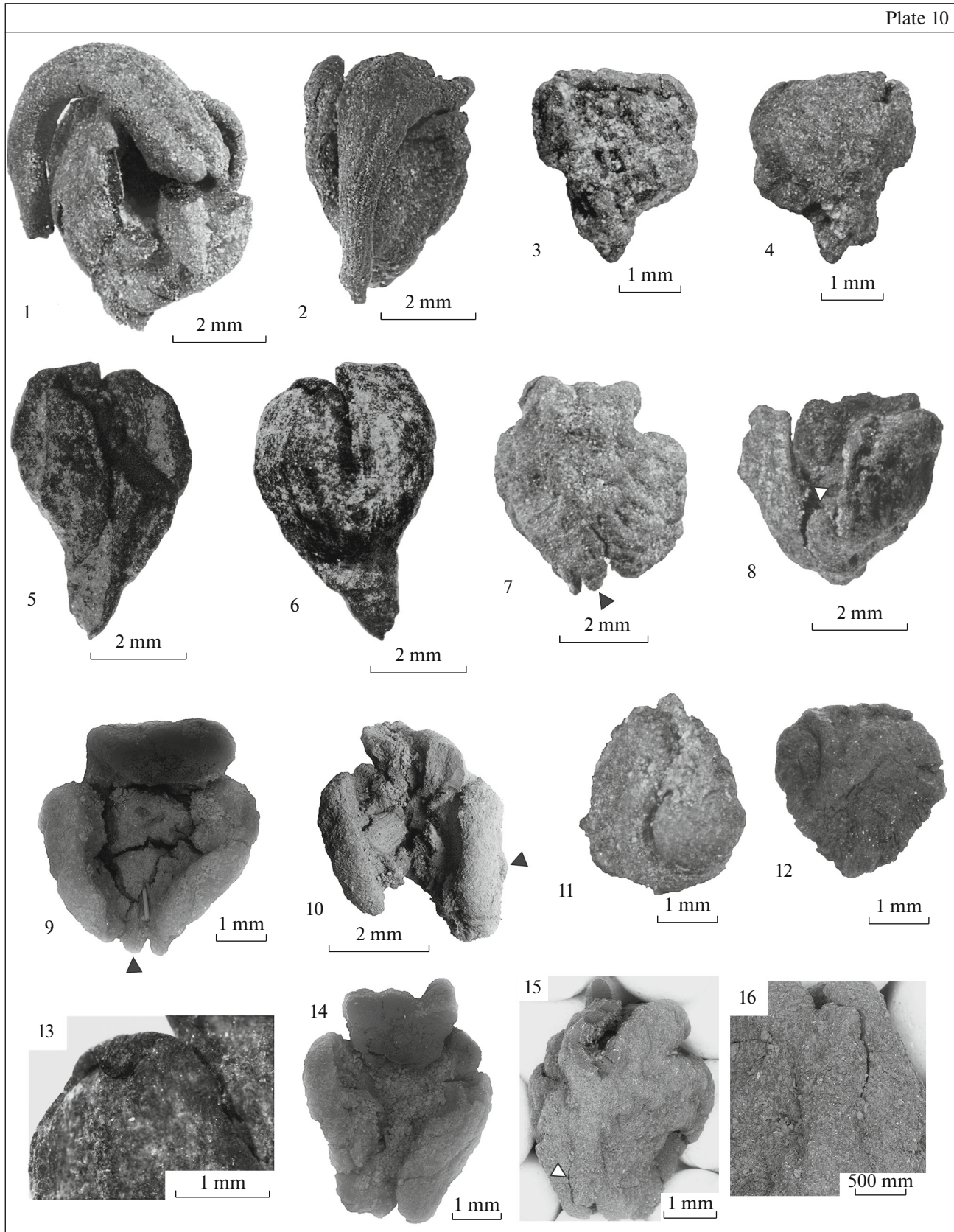
C o m p o s i t i o n. Monotypic order.

C o m p a r i s o n. The combination of the basic structural features, characteristic for Trisquamales ordo nov., is not known in representatives of any large systematic group of gymnospermous plants. The position of seeds from the xylem side of seed-bearing

structure vascular bundles relatively rarely occurs in gymnosperms; it is characteristic for the Paleozoic and Mesozoic orders Glossopteridales, Petriellales, and Dordrechtiales, and is supposed for Caytoniales; also, it is characteristic for angiosperms (Taylor and Taylor, 1992; Taylor et al., 1994; Doyle, 2006; Taylor et al., 2009; Bergene et al., 2013; etc.).

The most important difference of the new plant order from all listed groups is the presence in ovuliferous organs of Trisquamales ordo nov. of the unique sterile structure, which comprises the stalk of ovuliferous organ and undissected distal part, vascularized by C-shaped in transverse section collateral vascular bundle, and bears the fertile structure on the anatomically abaxial side (i.e., on the side, to which the convex surface of the collateral C-shaped vascular bundle with phloem is directed; hence also probable orientation of the ovuliferous organs *Trisquama* gen. nov. with the long scale towards the apex of axis that bore them). In *Dordrechtites* H.M. Anderson, a structure, similar to the sterile structure of *Trisquama* gen. nov., bears a cupule not on the abaxial, but on adaxial side (Anderson and Anderson, 2003; Bergene et al., 2013).

Substantial differences are present also in morphology and vascularization of seed-bearing structures and in structure of seeds. The fertile structures of Trisquamales ordo nov. are lobed, vascularized by concentric amphicribal vascular bundle, which splits in its distal part into separate collateral segments, associated with the lobes of the fertile structure; closing of cavity with seeds occurs through covering by the sterile structure distal part of the contact area between the lobes of fertile structure. The seed-bearing structures of the groups compared are essentially different in their organization. The Glossopteridales are characterized by the arrangement of fertile structures (usually interpreted as megasporophylls or axillary complexes bearing megasporophylls) on the adaxial side or in the axil of underlying leaf. These structures vary greatly in their morphology, in particular, there are lobed forms bearing (sub)terminal seeds or uniovulate cupules (Taylor et al., 2009; McLoughlin, 2011; Srivastava and Srivastava, 2016; etc.). The anatomical structure was described for one of the lobed forms compared with *Arberia* White and *Rigbya* Lacey, van Dijk et Gordon-Gray; at the base, the fertile structure was vascularized by C-shaped vascular bundle, divided above into vascular bundles of lobes, bearing terminal cupules (Taylor et al., 2007, 2009). The seed-bearing structures of Petriellales and Caytoniales represent branching systems, possessing in the latter supposedly pinnate organization; they bore terminal multiovulate cupules, formed by transverse folding of undissected lamina (megasporophyll). In Petriellales, the cupule was vascularized by several vascular bundles, departing from a common bundle in the stalk; the pattern of cupule vascularization in Caytoniales is unclear (Reymanóvna, 1973; Taylor et al., 1994). In Dordrechtiales, seed-bearing structures are arranged in strobili, in which they form fascicles of 3–4 (?); these struc-



tures bear cupules with seeds on their adaxial side, and are vascularized by C-shaped collateral vascular bundle, with which vascularization of seeds is related (Anderson and Anderson, 2003; Bergene et al., 2013).

Trisquamales ordo nov. significantly differ from Glossopteridales, Petriellales, and Caytoniales in the stratification of the seed coat (Reymanówna, 1973; Taylor et al., 1994; Ryberg and Taylor, 2013; etc.); seeds of Dordrechtiales possess a protruding micropyle, which forms a long pollen tube (Bergene et al., 2013). In the seeds of Glossopteridales, bilateral symmetry is usually well pronounced, characteristic thickenings of integument in the micropylar area are present (Taylor and Taylor, 1992; Ryberg and Taylor, 2013; etc.). Although seeds of flowering plants are situated from the xylem side of carpel vascular bundles, the presence in this group of two integuments, outer of which should be homologized with cupules of plants with single integument (Doyle, 2006; and references therein), excludes possibility of close affinity between Trisquamales ordo nov. and angiosperms (also see Discussion).

#### Family Trisquamaceae fam. nov.

**E t y m o l o g y.** From the type genus *Trisquama* gen. nov.

**T y p e g e n u s.** *Trisquama* gen. nov.

**D i a g n o s i s.** As for order.

**C o m p o s i t i o n.** Type genus.

#### Genus *Trisquama* Gordenko et Broushkin, gen. nov.

**E t y m o l o g y.** From the Latin *tres* (genitive *trium*, three) and *squama* (scale).

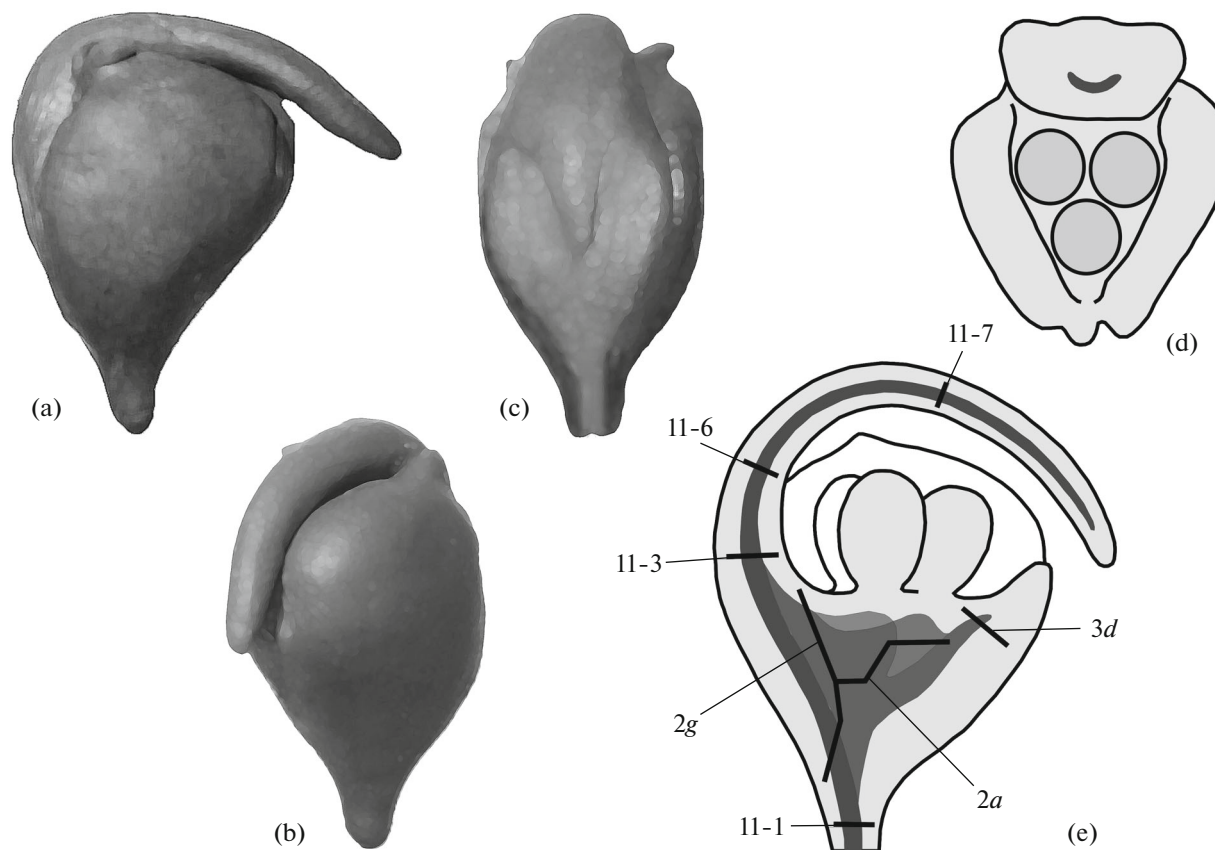
**T y p e s p e c i e s.** *Trisquama valentinii* Gordenko et Broushkin, gen. et sp. nov.

**D i a g n o s i s.** Small ovuliferous organs consist of three thick scales, cup-like fused at base. Free parts of scales encircle inner space of ovuliferous organ, with triangular floor, in central part of which three small orthotropous seeds attached. At base, ovuliferous organ gradually tapers into stalk, crescent-shaped in transverse section. Long scale located from side of stalk, and morphologically represents its extension,

forming together with stalk sterile structure of ovuliferous organ. Long scale wide, trapezoid in section at its base, then gradually tapers into long subulate apex, which bends toward pair of short scales, covering area of their contact in immature ovuliferous organs, and closing cavity with seeds. Short scales significantly shorter than long one, wider, flattened in transverse section, semicircular in form, terminated by triangular tooth, which bent outwards. At place of junction of short scales, small outgrowth presented; together with short scales it forms fertile (seed-bearing) structure of ovuliferous organ. Through outgrowth and opposed to it long scale, plane of general bilateral symmetry of ovuliferous organ passes; symmetry broken by unequal width of short scales and differences in course of associated with them vascular bundles. In stalk of ovuliferous organ presented single collateral vascular bundle, which possesses in section form of shallow "C" with xylem on concave side, oriented outward of ovuliferous organ. This bundle vascularizes sterile structure of ovuliferous organ, passing immediately into long scale and terminating in its apical part. In lower part of ovuliferous organ, from phloem side of sterile structure vascular bundle, at wide angle amphicribal concentric vascular bundle departs, vascularizing fertile structure of ovuliferous organ. This bundle at its base possesses form of very tall narrow ellipse in transverse section; narrow zone in its central part, corresponded to gap in vascular bundle of sterile structure, consists of fibers and transfusion cells. Distally, elliptical vascular bundle splits at its upper extremity, becoming U-shaped; towards floor of ovuliferous organ, distal bent upward part of this bundle divides into two unequal collateral plates. Shorter plate (right one when ovuliferous organ oriented by floor facing observer and long scale upward; associated with wider of short scales) bent outwards; longer left plate, hook-shaped in transverse section, divides again. Finally resulting three plates in their position correspond to two short scales and outgrowth between them, and also to three seeds, situated from xylem side of these vascular bundles. Beneath floor of ovuliferous organ these bundles wedge out, replaced by mass of transfusion tissue. Free parts of short scales not vascularized. Cortex of ovuliferous organ consists of two zones, outer of which sclerified; secretory canals and cavities

#### Explanation of Plate 10

**Figs. 1–16.** Ovuliferous organs *Trisquama valentinii* gen. et sp. nov.: (1, 2) holotype PIN, no. 5137/60: (1) view from side of the long scale; (2) view from side of pair of the short scales; (3, 4) paratype PIN, no. 5137/65, abortive ovuliferous organ with preserved ovules, photographs from different sides of the short scales; (5, 6) paratype PIN, no. 5137/64: (5) view from side of the long scale (apex removed); (6) view from side of pair of the short scales; (7–9) paratype PIN, no. 5137/61 (arrows point to the outgrowth between short scales): (7) view from side of the stalk of ovuliferous organ; (8) view from side of pair of the short scales; (9) view from above, apex of the long scale is removed, the floor of ovuliferous organ is visible, SEM; (10) paratype PIN, no. 5137/62, ovuliferous organ, from which seeds were extracted, view from above, apex of the long scale is removed, SEM (arrow points to the apical tooth of short scale); (11, 12) paratype PIN, no. 5137/63, abortive ovuliferous organ: (11) view from side of the long scale (apex not preserved); (12) view from side of the base of ovuliferous organ; (13) detail of Fig. 6, apical part of the short scale with a triangular tooth; (14–16) holotype PIN, no. 5137/60, SEM: (14) view from above, apex of the long scale is removed, the floor of ovuliferous organ is seen; (15) view from side of the base (arrow points to the outgrowth between short scales); (16) outgrowth between short scales.

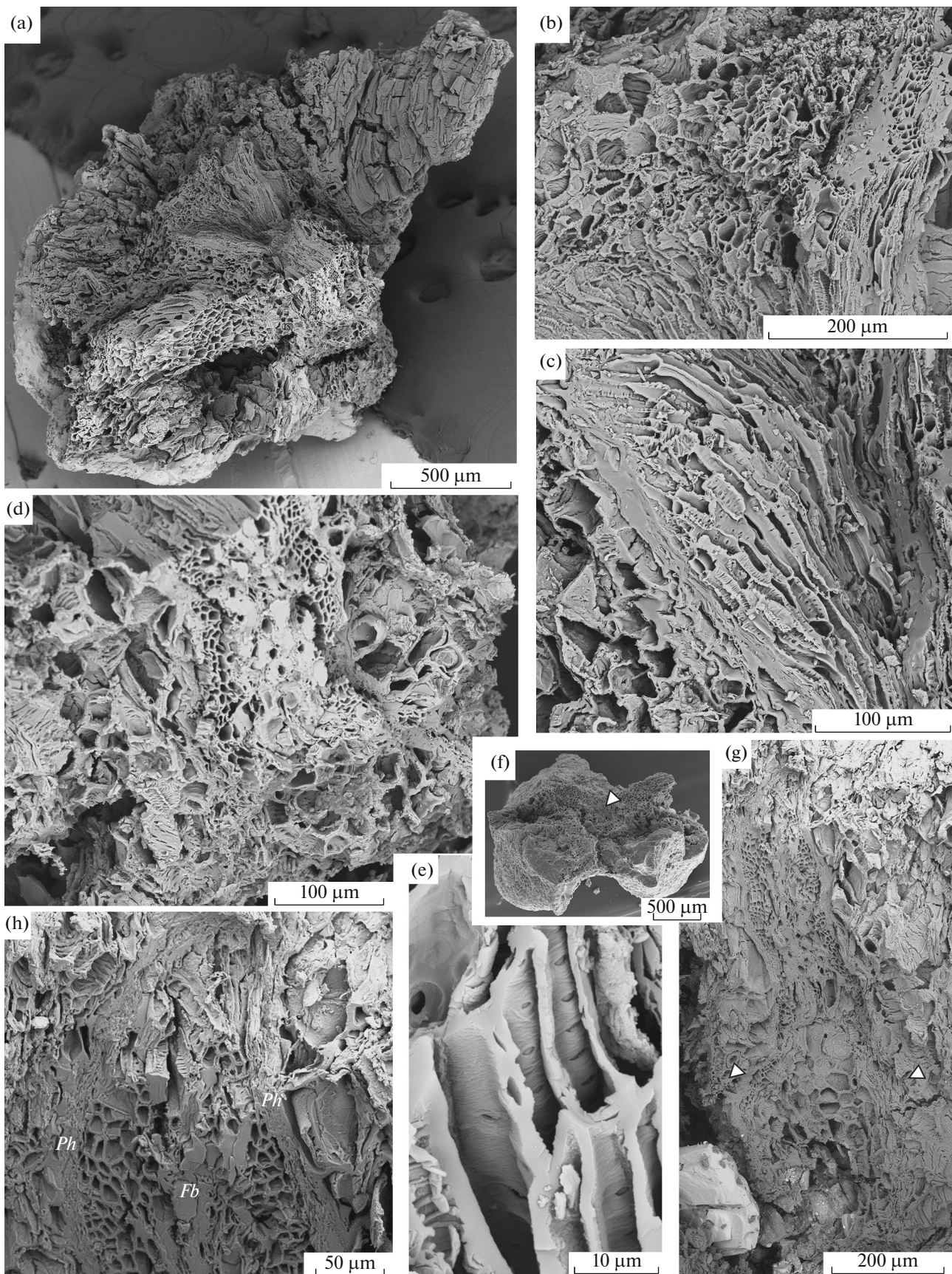


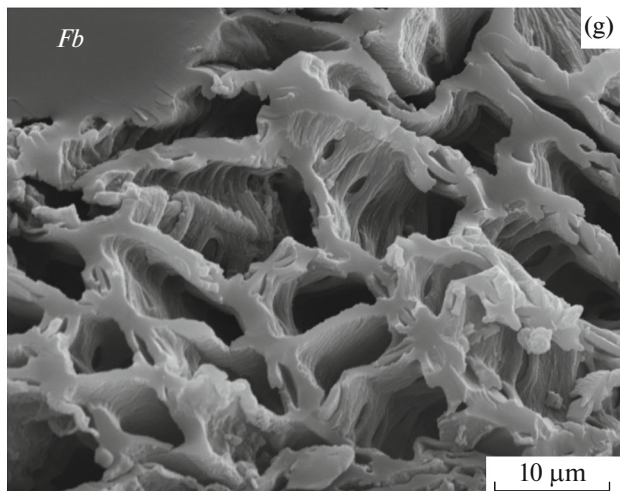
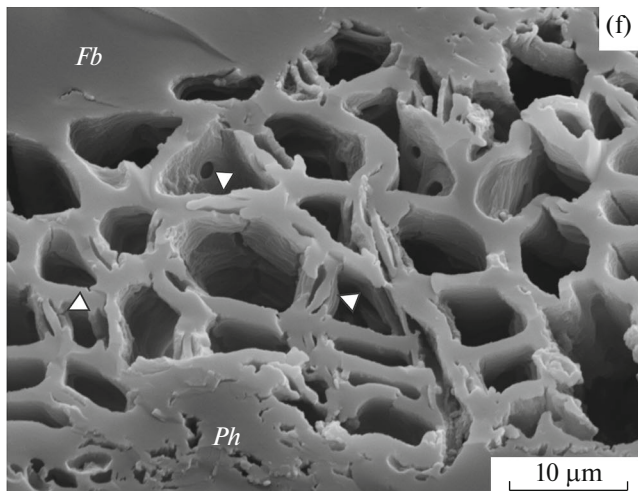
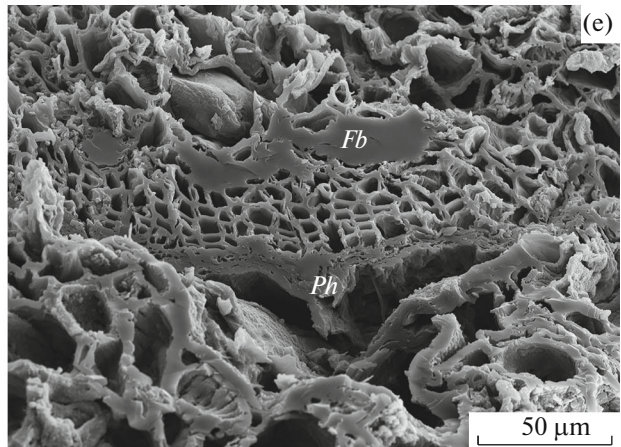
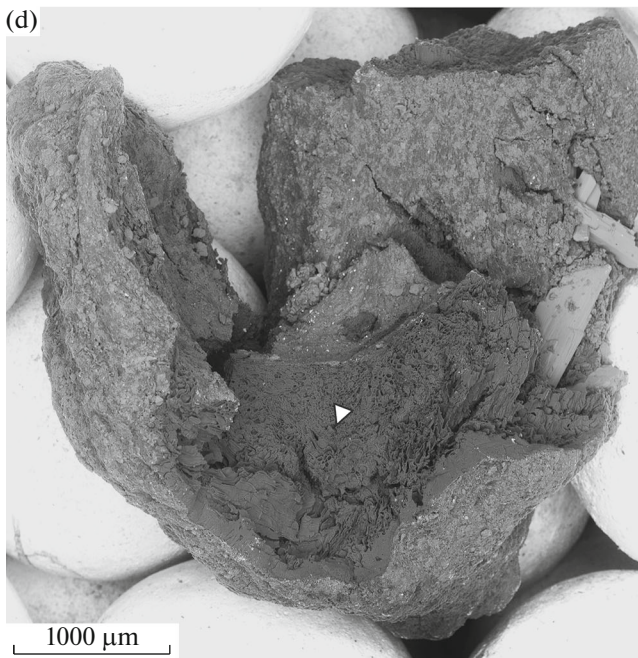
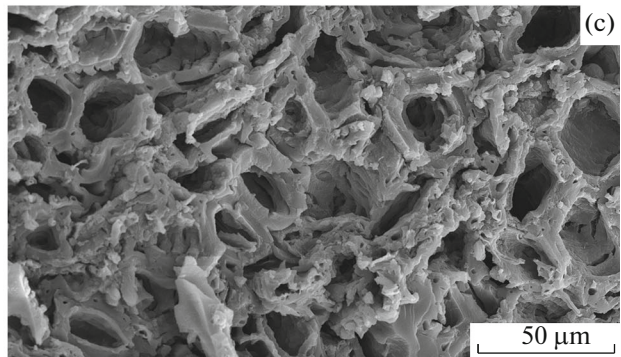
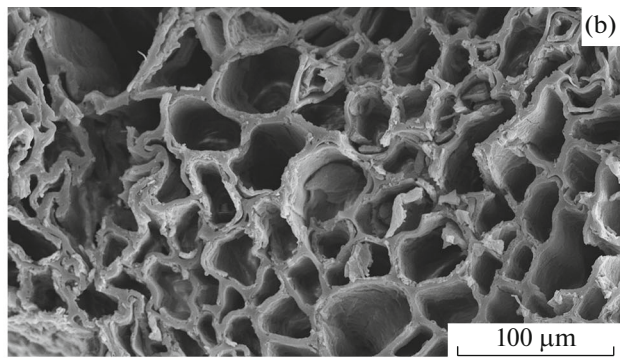
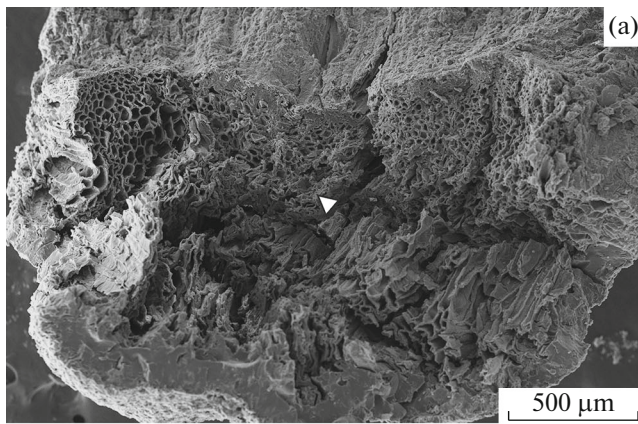
**Fig. 1.** Ovuliferous organs *Trisquama valentinii* gen. et sp. nov.: (a–c) reconstruction of the external appearance of ovuliferous organ: (a) side view, long scale bent apart; (b) view from side of pair of the short scales, ovuliferous organ in a closed state; (c) view from side of the long scale; (d, e) scheme of seed arrangement, top and side views, outlines of vascular bundles are shown in gray (dark gray is vascular bundle of the sterile structure, lighter gray is vascular bundle of the fertile structure); in (e) directions of the main splits studied under SEM are indicated; designations of the splits correspond to their images in the paper.

absent. Cuticular covering of ovuliferous organ thin, epidermis of outer surface with numerous monocyclic stomata, epidermis of inner surface of scales without stomata, in short scales with thinly cutinized papillae. Seeds ellipsoidal, with not protruding micropyle,

somewhat shifted relative to longitudinal axis of seed. Integument three-layered, consists of exotesta (epidermis), sclerified mesotesta, and multilayered papery endotesta. Nucellus free from integument more than one half, megaspore membrane thick.

**Fig. 2.** Ovuliferous organs *Trisquama valentinii* gen. et sp. nov., paratype PIN, no. 5137/61, SEM: (a) stepped split through the lower part of ovuliferous organ, illustrating course of vascular bundles under its floor (direction of the split is shown in Fig. 1e, removed long scale was at lower right, the outgrowth between short scales was at upper left); two plates of vascular bundle of the ovuliferous organ fertile structure (longer plate is on the right, shorter plate is on the left) are visible, as well as connection of the plates with branches of the sterile structure vascular bundle on longitudinal part of the split, in the lower part of figure; (b) detail of (a), split of the distal upward bent part of longer plate, and transfusion tissue, that fills the inner space between diverging plates; from right to left: vitrified phloem, xylem tracheids, group of fibers, small-celled and large-celled transfusion tissue; (c) detail of (a), from right to left: lower level of the split-narrow zone between the plates (closely spaced at this level) of the fertile structure vascular bundle, the zone consists of more or less longitudinally oriented fibers and transfusion cells; upward bent part of shorter plate with weakly developed xylem, gradual transition from tracheids to small-celled transfusion tissue elements, and collapsed phloem are visible; large-celled transfusion tissue, located external to the vascular bundle; (d) detail of (a), longitudinal split, base of the elliptical vascular bundle of fertile structure, corresponds to the lower part of (g) (reverse side of the split); two plates of the fertile structure vascular bundle and their connection with the branches of the sterile structure vascular bundle at the bottom are visible; zone between the plates consists of fibers and transfusion cells, the plates are outlined externally by large-celled transfusion tissue; (e) detail of (b), xylem tracheids with bordered pits; (f) base of the long scale, split off from the fragment depicted in (a), view from side of the ovuliferous organ stalk; arrow marks position of the split shown in (g); (g) longitudinal split, base of the elliptical vascular bundle of fertile structure; two plates of this bundle, fusing at the top, as well as connection of the plates with the branches of disrupted vascular bundle of sterile structure (marked by arrows), are visible; (h) detail of (g), fusion of the plates of the fertile structure vascular bundle near the floor of ovuliferous organ, fibers (*Fb*) and collapsed phloem (*Ph*) can be seen.





## Composition. Type species.

*Trisquama valentinii* Gordenko et Broushkin, sp. nov.

Plate 10, figs. 1–16; Plate 11, figs. 1–8

**E t y m o l o g y.** In honor of Valentin Abramovich Krassilov.

**H o l o t y p e.** PIN, no. 5137/60, ovuliferous organ, Mikhailovskii open mine, vicinity of the town of Zheleznogorsk, Kursk Region, European Russia; Arkinsk Formation, Upper Bathonian, Middle Jurassic (Pl. 10, figs. 1, 2, 14–16); designated here.

**D i a g n o s i s.** As for genus. Ovuliferous organs up to 6 mm high, up to 4.5 mm in diameter. Long scale about 2 mm wide near base, up to 6.5 mm long; short scales 2–2.8 mm long, up to 4 mm wide; apical tooth up to 0.5 mm long. Outgrowth between short scales 1 mm long, 0.7 mm wide. Vascular bundle of sterile structure in stalk of ovuliferous organ about 400  $\mu$ m wide, at base of long scale 600  $\mu$ m wide. Elliptical vascular bundle of ovuliferous organ fertile structure at base more than 800  $\mu$ m high, 200  $\mu$ m wide. Plates after its division in transverse section have length 750  $\mu$ m (short), 1000  $\mu$ m (long), 220  $\mu$ m (separated incurved part of long plate). Xylem consists of tracheids 5–15  $\mu$ m in diameter, with circular bordered pits, mainly uniseriate, separate; apertures of pits circular and elliptical to slit-like, 1–3  $\mu$ m long. Xylem up to 8 cells thick. Fibers on inner side of xylem up to 20  $\mu$ m in diameter. Xylem accompanied by small-celled transfusion tissue with diameter of elements up to 20  $\mu$ m; large-celled transfusion tissue, which surrounds vascular bundles externally, consists mainly of elements with reticulate secondary wall thickenings, 30–50  $\mu$ m in diameter. Cells of inner zone of cortex prosenchymatous, thin-walled, up to 300  $\mu$ m long, up to 80  $\mu$ m in diameter; cells of outer sclerified zone up to 100  $\mu$ m long, up to 50  $\mu$ m in diameter, with filled cell lumens. Cells of fibrose tissue on inner side of scales with thickened walls, 5–10  $\mu$ m in diameter. Cuticle about 1.5  $\mu$ m thick. Stomata longitudinally or obliquely orientated, with 5–6 subsidiary cells. Subsidiary cells of stomata with small proximal papillae, guard cells sunken, bean-shaped, up to 50  $\mu$ m long; width of stomata about 50  $\mu$ m, length of aperture up to 15  $\mu$ m. Papillae on inner surface of short scales with rounded bases up to 10  $\mu$ m in diameter, height of papillae up to 20  $\mu$ m. Seeds 2.6–2.8 mm long, up to 1.6 mm in diam-

eter. Exotesta consists of rectangular epidermal cells up to 40  $\mu$ m wide, about 60  $\mu$ m long. Mesotesta up to 10 cells thick, consists of isodiametric sclereids 10–40  $\mu$ m in diameter. Endotesta consists of several layers of rectangular and polygonal cells, up to 50  $\mu$ m long, up to 5  $\mu$ m wide, with thin straight anticlinal walls. Nucellus thinly cutinized; cells of nucellus from rectangular to pentagonal, 20–40  $\mu$ m wide, up to 100  $\mu$ m long. Megaspore membrane up to 5  $\mu$ m thick.

**D e s c r i p t i o n** (Figs. 1–7). The collection contains five exemplars of ovuliferous organs (Pl. 10, figs. 1, 2, 5–12, 14, 15), in one of which comparatively ripe seeds are preserved (Figs. 7d–7i), and one abortive ovuliferous organ with attached ovules (Pl. 10, figs. 3, 4; Figs. 7a–7c). Ovuliferous organs are small, up to 6 mm high and up to 4.5 mm in diameter, consist of three thick scales fused at the base to form a cup-like structure (Pl. 10, figs. 1–12, 14, 15; Figs. 1a–1e; 3d). Free parts of scales border the inner space of ovuliferous organ, with a triangular floor, in the central part of which three small orthotropous seeds were attached (Pl. 10, figs. 9, 10, 14; Fig. 1d, 1e; 3d; 7a–7c). The ovuliferous organ gradually tapers toward the base to form a small stalk up to 2 mm long (preserved part), about 1 mm wide, crescent-shaped in cross section (Pl. 10, figs. 3–8, 12, 15; Fig. 4a). The long scale (Pl. 10, figs. 1, 2) is up to 6.5 mm long, about 2 mm wide near its base, located from side of the stalk of the ovuliferous organ, and represents morphologically its extension, forming together with the stalk the sterile structure of ovuliferous organ. At the base, the long scale is wide, trapezoid in section (Pl. 10, figs. 9, 14; Pl. 11, fig. 3); further, it gradually tapers into a long subulate apex, which bends toward pair of short scales, covering the area of their contact in immature ovuliferous organs, and in this manner closing the cavity with seeds (Pl. 10, figs. 1, 2; Figs. 1a–1c). Free parts of short scales are 2–2.8 mm long, up to 4 mm wide, more or less semicircular, flattened in cross section (Pl. 10, figs. 1–10, 14; Fig. 3a); short scales are terminated by a triangular tooth, which bends outwards, up to 0.5 mm long, displaced somewhat toward the long scale (Pl. 10, figs. 6, 10, 13). Between two short scales, a small outgrowth, 1 mm long, up to 0.7 mm wide, is located. The outgrowth together with the short scales forms the fertile (seed-bearing proper) structure of ovuliferous organ. Toward tip of the outgrowth, as well as toward the teeth of short scales, longitudinal rows of

**Fig. 3.** Ovuliferous organs *Trisquama valentinii* gen. et sp. nov., paratype PIN, no. 5137/61, SEM: (a) split at the base of the short scale, outer sclerified (at the bottom) and inner prosenchymatous tissues of cortex, as well as fibrose tissue on the inner side of scale (at the top center) are visible; arrow marks position of cells similar to those of transfusion tissue; (b) detail of (a), cells of inner prosenchymatous tissue of cortex; (c) detail of (a), cells similar to those of transfusion tissue; (d) split of the lower part of ovuliferous organ, view from the side of pair of short scales (one of them is removed); arrow marks position of the fertile structure vascular bundle plate, associated with the outgrowth between the short scales; (e) plate, marked by arrow in (d) (reverse side of the split), on the right, replacement of xylem tracheids by the elements of small-celled transfusion tissue can be observed; (f) detail of (e), the central part of vascular bundle, tracheids with circular bordered pits and presumable tori (indicated by arrows); (g) detail of (e), edge of vascular bundle, replacement of xylem tracheids by the elements of small-celled transfusion tissue. Legend: (Ph) phloem, (Fb) fibers from xylem side of vascular bundle.



epidermal cells converge (Pl. 10, figs. 7–9, 14–16). The plane of general bilateral symmetry of the ovuliferous organ passes through this outgrowth and long scale opposing it. Symmetry is partly broken by unequal width of short scales: the short scale, situated to the right when the ovuliferous organ is oriented by the floor facing an observer and long scale upward, is wider than the left one (Pl. 10, figs. 9, 10, 14); with the left short scale, the outgrowth is partly fused (Pl. 10, figs. 14–16). Morphological asymmetry is corroborated also by differences in the course of vascular bundles, associated with short scales. The attachment of seeds (ovules) was observed only in one abortive ovuliferous organ, in which the ovules in their arrangement can be correlated with two short scales and outgrowth between them (Figs. 1d, 1e, 7a, 7b).

In the stalk of ovuliferous organ, single collateral vascular bundle is presented, which possesses in section form of very shallow “C”, about 400  $\mu\text{m}$  wide (Pl. 11, figs. 1, 2). Conducting tissues in this part of the ovuliferous organ are poorly preserved in all available exemplars; the position of xylem along the concave side of this vascular bundle, which is oriented outward of ovuliferous organ, is inferred from its position at higher levels of vascular system. On tomograms of the stalk, outlines of the C-shaped inner zone are visible (Figs. 4a, 5a), corresponded to vascular bundle and transfusion tissue, which encircles the bundle (on sections of the base of ovuliferous organ it is difficult to delimit them from each other). This C-shaped vascular bundle vascularizes the sterile structure of ovuliferous organ, passing immediately into the long scale; changes in its course and configuration (Figs. 4b–4g, 5b–5h, 6a–6c) in the lower part of ovuliferous organ are related with emission of the fertile structure vascular bundle; in the free part of the long scale, the initial configuration of this bundle is restored (Pl. 11, figs. 3, 4; Fig. 5i). At the base of the long scale, this bundle is about 600  $\mu\text{m}$  wide; further, it flattens and terminates in the apical part of the long scale (Pl. 11, figs. 6–8; Fig. 1e).

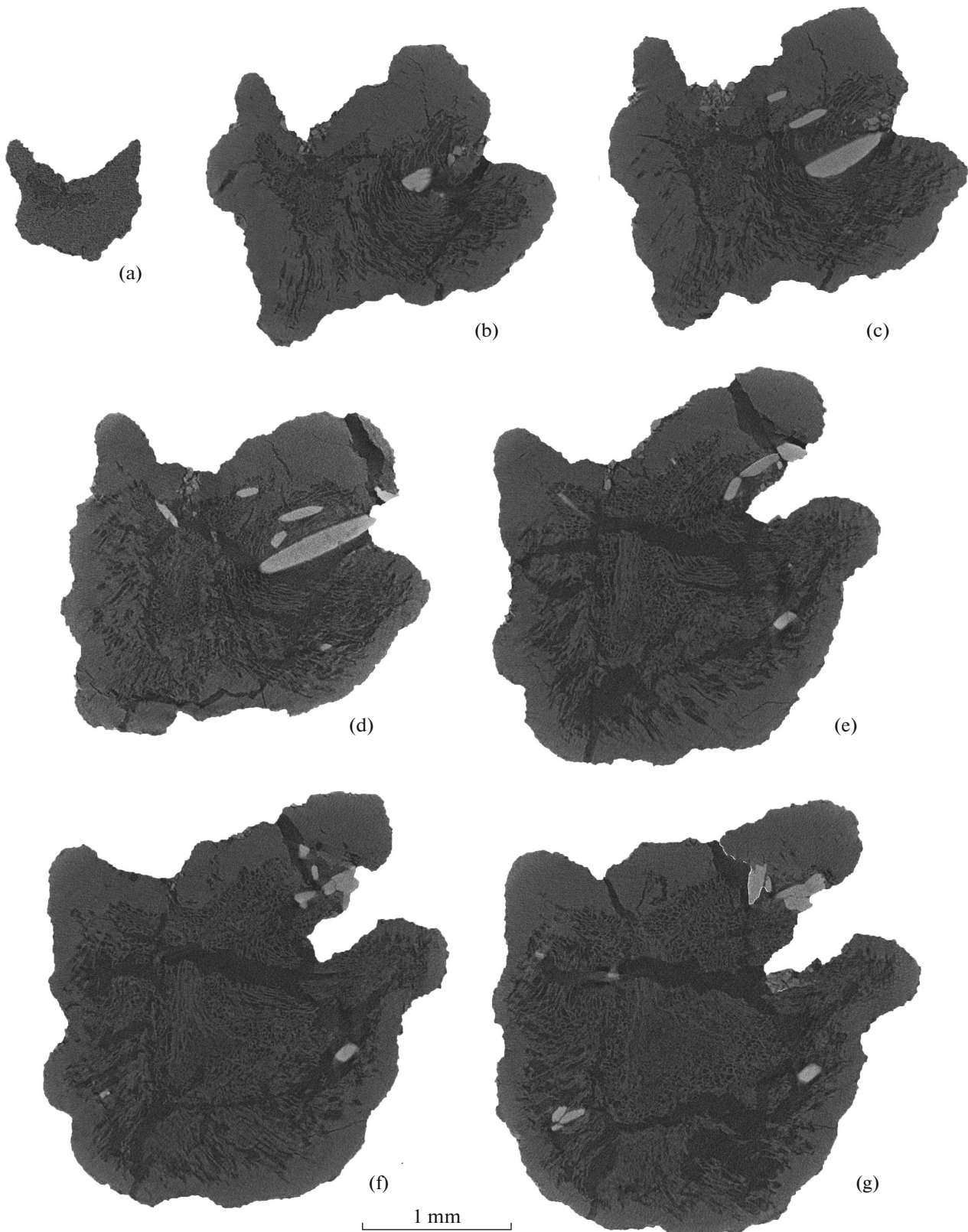
The vascular bundle, vascularizing the fertile structure of ovuliferous organ, departs at wide angle from the phloem side of the vascular bundle of sterile structure; the general course of its emission can be traced on the series of transverse tomograms (Figs. 4b–4g, 5b–5h, 6a). Initially, outlines of the inner zone (vascular bundle with associated transfusion tissue)

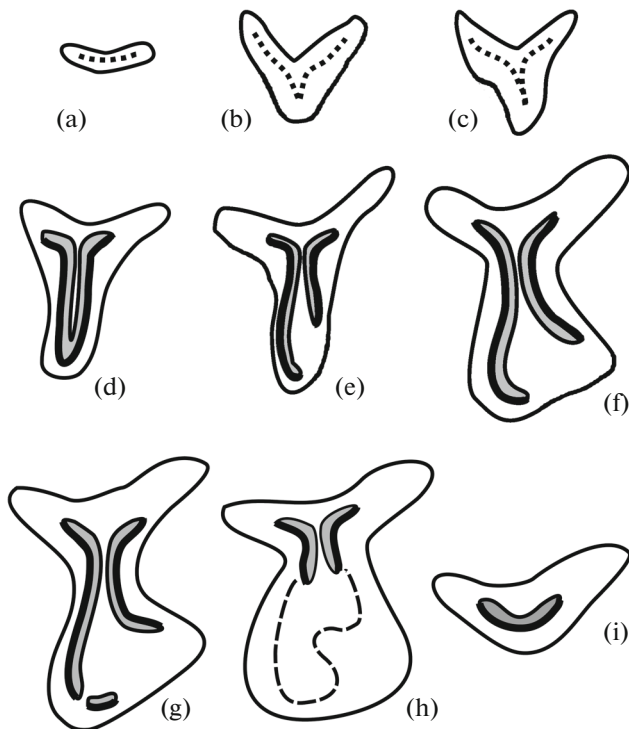
become V-shaped, branches of “V” lengthen, in the center a short third ray appears, the inner zone acquires Y-shaped configuration (Fig. 4b, 4c, 5b, 5c). Upwards, the third ray becomes longer and somewhat thicker, vascular tissues in its proximal part (near the long scale) become more distinct in tomograms; in the axial part of the third ray, a histologically distinguished zone appears (Figs. 4d, 5d). On the split under SEM (Figs. 2a, 2d; directions of splits illustrated in the paper are shown in Fig. 1e) one can see that the fertile structure vascular bundle in the proximal part of the third ray is represented at this level by two closely spaced parallel thin collateral plates, with the phloem on the exterior; orientation of vascular tissues cells here is more or less longitudinal (parallel to the floor of the ovuliferous organ; Figs. 2a, 2d). Each of these plates is connected to one of two branches of disrupted vascular bundle of the sterile structure of ovuliferous organ (these branches are seen in the lower part of longitudinal split in Figs. 2a, 2d, 2g; compare also transverse tomograms in Figs. 4d–4g, 5d–5g). A narrow zone between the plates of fertile structure vascular bundle is composed of fibers and transfusion cells (Figs. 2a, 2c, 2d, 2g).

On the longitudinal split of the lower part of ovuliferous organ at the base of long scale, one can observe (Figs. 2g, 2h) that the plates of fertile structure vascular bundle upward continue to run parallel to each other, fusing near the floor of ovuliferous organ. Thus, the vascular bundle of ovuliferous organ fertile structure at its base in transverse section possesses form of very tall narrow ellipse, with phloem along the periphery; the narrow “medullar” zone in the center of elliptical bundle corresponds to a gap in vascular bundle of the sterile structure of ovuliferous organ. Distally, the elliptical vascular bundle soon splits at its upper extremity, becoming U-shaped (Figs. 1e, 5h, 6a).

The course of vascular bundle of the fertile structure in its distal bent upward part can be traced on transverse tomograms. In its basal part, this vascular bundle is entire (Figs. 4d, 5d); upwards, the two plates of this bundle asymmetrically disjoin (Figs. 4e, 5e). The shorter plate is 750  $\mu\text{m}$  long, associated with the right (for orientation of ovuliferous organ, see above), wider of short scales, bends outward at wide angle (Figs. 4f, 4g, 5f, 5g); on the split under SEM one can see that in the upper part of this plate, bent toward the floor of the ovuliferous organ, xylem is poorly devel-

**Fig. 4.** Ovuliferous organs *Trisquama valentinii* gen. et sp. nov., paratype PIN, no. 5137/61, series of successive transverse (some-what oblique) tomograms of the lower part of ovuliferous organ, in direction from the stalk toward the floor: (a) section of the stalk of ovuliferous organ, C-shaped inner zone, corresponded to the sterile structure vascular bundle with the surrounding transfusion tissue, is visible; (b) base of ovuliferous organ, beginning of emission of the fertile structure vascular bundle: outlines of the inner zone become V-shaped; inner prosenchymatous and outer sclerified tissues of cortex are clearly discernible; (c) outlines of the inner zone become Y-shaped (the third ray appears); (d) the third ray becomes longer; in its proximal part, two plates of the fertile structure vascular bundle, separated by a narrow histologically distinguished zone, are discernible; (e) asymmetric disjoining of the plates of the fertile structure vascular bundle in distal part; (f, g) divergence of the plates in distal part, shorter right plate bends outward; inner space between the plates is filled here by small-celled transfusion tissue, as well as by large-celled transfusion tissue, invading through gap between the plates from the periphery.





**Fig. 5.** Ovuliferous organs *Trisquama valentinii* gen. et sp. nov., scheme of changes in the vascular bundles configuration on transverse sections of the lower part of ovuliferous organ, on the basis of tomograms and splits studied under SEM; xylem is shown in gray, phloem in black, transfusion tissue left white: (a) C-shaped inner zone in the stalk of ovuliferous organ; configuration of the sterile structure vascular bundle is shown in dotted line; (b, c) beginning of emission of the fertile structure vascular bundle: outlines of the inner zone (corresponded to vascular bundles with surrounding transfusion tissue) become V- and Y-shaped, the third ray appears; the presumed configuration of vascular bundle is shown in dotted line; (d) the third ray becomes longer, its vascular bundle (vascular bundle of the ovuliferous organ fertile structure) represents two plates, joined in distal part; each of these plates is connected with one of two branches of disrupted vascular bundle of sterile structure; (e) asymmetric disjoining of the plates of the fertile structure vascular bundle in distal part; (f) divergence of the plates in distal part, the shorter right plate bends outward; (g) separation of the incurved part of the longer left plate; (h) section near the floor of ovuliferous organ, slightly below the place of fusion of the plates of the fertile structure elliptical vascular bundle; in the distal part, the plates are completely wedged out, replaced by mass of transfusion tissue; outlines of the zone composed of small-celled transfusion tissue are shown in dashed line; (i) the sterile structure vascular bundle, restored its initial configuration in the base of the long scale free part.

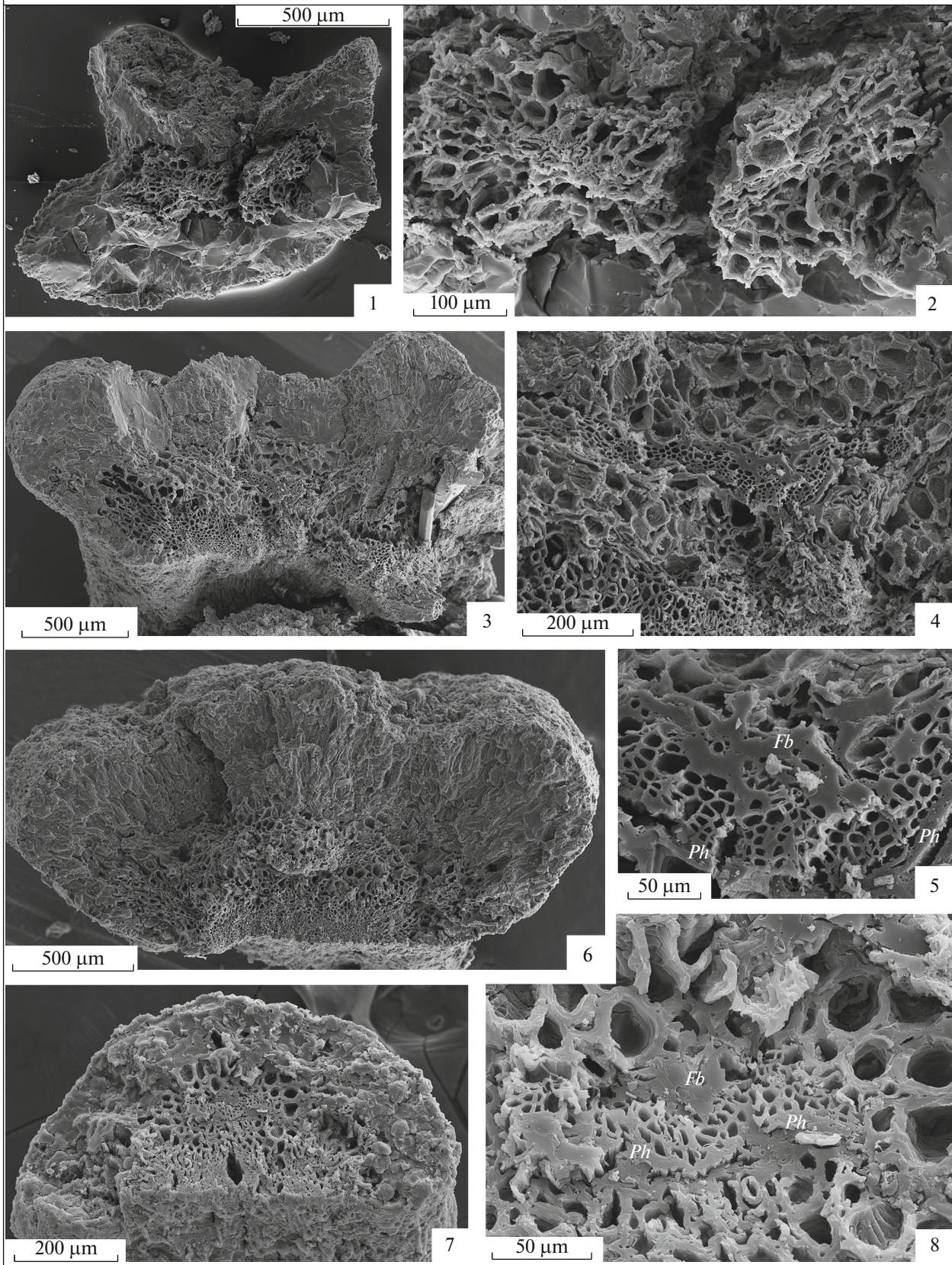
oped (Figs. 2a, 2c). The longer left plate, about 1000  $\mu\text{m}$  long, with a hook-like bent distal end, only slightly changes its direction; the incurved part of this plate, 220  $\mu\text{m}$  long, above detaches, directing toward the outgrowth between short scales (Figs. 3d, 3e, 5g). Thus, finally resulting three plates of the fertile structure vascular bundle in their position correspond to two short scales and outgrowth between them, and also to three seeds, situated from the xylem side of these vascular bundles (Fig. 1e). The inner space between the plates is filled here mostly by small-celled transfusion tissue, as well as by large-celled transfusion tissue, invading through gaps between the plates from periphery (Figs. 2a–2c, 3d, 3e, 4g). Beneath the floor of ovuliferous organ, the plates wedge out, replaced by a mass of transfusion tissue, with which vascularization of seeds is related (Figs. 5h, 6a–6c). Free parts of short scales and outgrowth between them are not vascularized; within the central area of the short scales bases, cells similar to those of transfusion tissue were observed (Fig. 3a, 3c).

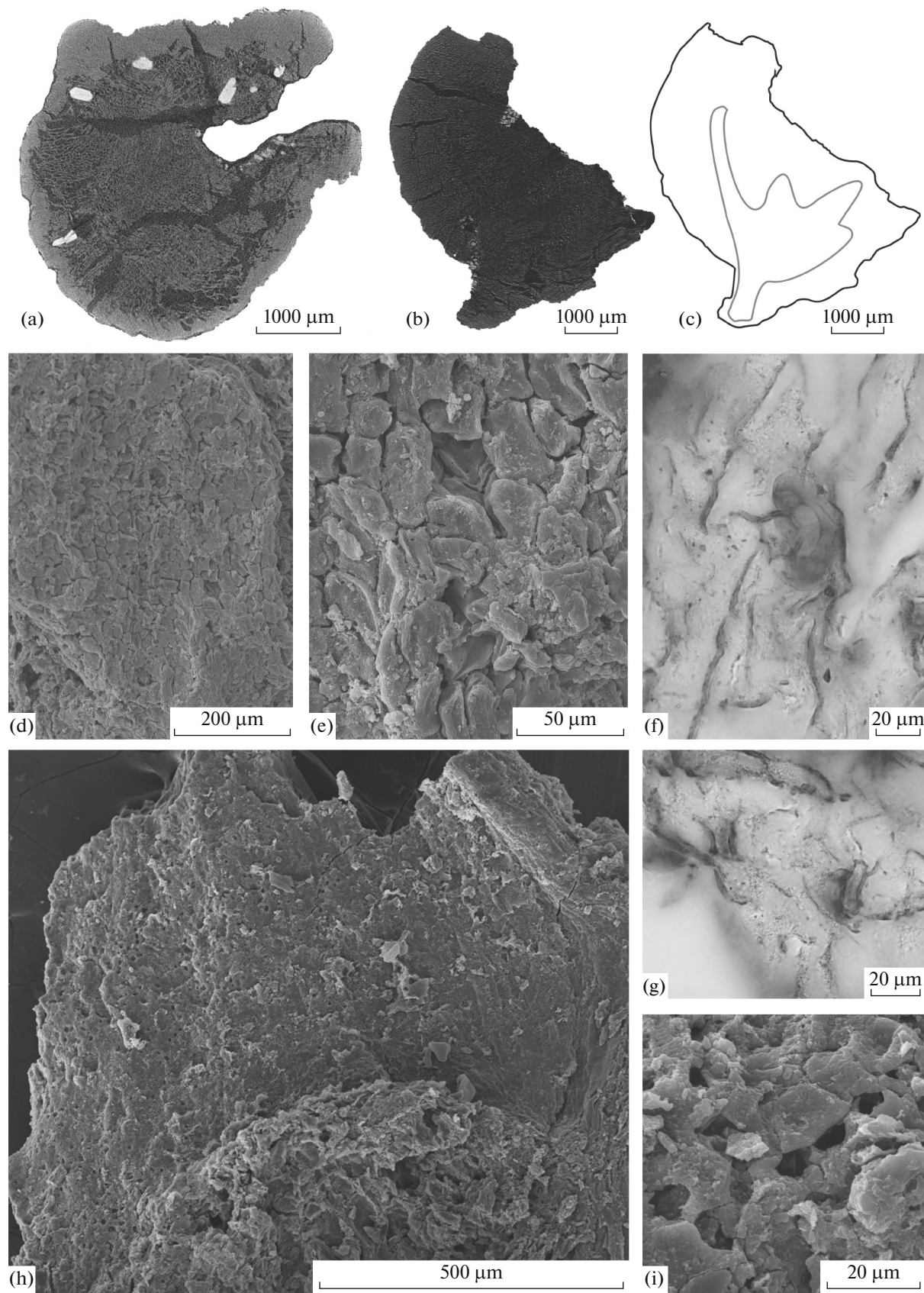
Xylem consists of tracheids with circular bordered pits 5–15  $\mu\text{m}$  in diameter (Figs. 2b, 2c, 2e, 3e, 3f). Pits are predominantly separate, confined to tracheid end parts, arranged in one, rarely two rows; the pit apertures are circular and elliptical to slit-like, 1–3  $\mu\text{m}$  long (Figs. 2c, 2e, 3f), possibly tori are present (pointed out by arrows in Fig. 3f). Early metaxylem elements are usually poorly preserved, protoxylem is unable to localize with confidence. The degree of xylem development varies in different parts of vascular bundles. In a more complete variant (Pl. 11, figs. 4, 5; Figs. 2b, 2d, 2g, 2h, 3e), tracheids of inner parts of vascular bundles are replaced externally by rectangular in cross section tracheids, arranged in radial rows; here, xylem attains a thickness of six–eight cells. In the case of weak development, xylem is only two–three cells thick, tracheids are rapidly replaced by transfusion elements (Fig. 2c). Phloem of vascular bundles is poorly preserved, usually collapsed phloem cells form a vitrified band up to 25  $\mu\text{m}$  thick (Pl. 11, figs. 5, 8; Figs. 2b–2d, 2h, 3e, 3f). On the inner side of xylem, there are fibers up to 20  $\mu\text{m}$  in diameter, with filled cell lumens, usually arranged in groups (Pl. 11, figs. 4, 5, 8; Fig. 2b, 2d, 2h, 3e–3g).

Vascular bundles are accompanied by small-celled transfusion tissue, concentrated predominantly later-

#### Explanation of Plate 11

**Figs. 1–8.** Ovuliferous organs *Trisquama valentinii* gen. et sp. nov.: (1–6) paratype PIN, no. 5137/61, SEM: (1) transverse split through base of ovuliferous organ near the stalk; (2) detail of Fig. 1, poorly preserved C-shaped vascular bundle of the ovuliferous organ sterile structure and transfusion tissue, which encircles the bundle, are visible; (3) transverse split near the base of long scale, vascular bundle of the ovuliferous organ sterile structure, restored its initial configuration after emission of the fertile structure vascular bundle, is visible; (4) detail of Fig. 3, vascular bundle, surrounded by large-celled transfusion tissue; in the lower part of the image, cells of fibrose tissue of the inner side of scale are seen; (5) detail of Fig. 4, collapsed phloem (*Ph*) and fibers from side of xylem (*Fb*) are visible; (6) transverse split of the long scale in its lower third, from the bottom up: fibrose tissue of the inner side of scale, C-shaped vascular bundle surrounded by large-celled transfusion tissue, and well-developed sclerified tissue of the outer zone of cortex, cells of which have here an almost palisade orientation; (7, 8) paratype PIN, no. 5137/62, SEM: (7) transverse split of the long scale in its upper part; (8) detail of Fig. 7, vascular bundle with collapsed phloem (*Ph*) and fibers from the side of xylem (*Fb*).





ally and inside to xylem, and also replacing xylem where the bundles wedge out (Figs. 2b, 2c, 3e, 3g). Transition from xylem to transfusion cells is gradual: tracheids become shorter and wider, the secondary wall thickenings become discrete, splitting into separate bands (Figs. 2c, 3g). Subsequently, wall thickenings become reticulate, well-developed bordered pits disappear, orientation of cells becomes irregular (Fig. 2b, 2c). The elements of small-celled transfusion tissue are up to 20  $\mu\text{m}$  in diameter; on tomograms, they are frequently indistinguishable from xylem; this tissue is most developed between the plates of the fertile structure vascular bundle and beneath the floor of ovuliferous organ (Figs. 2a–2c, 3d, 3e, 4f, 4g, 6a–6c). Large-celled transfusion tissue is composed of short wide cells, 30–50  $\mu\text{m}$  in diameter, often irregularly disposed (Pl. 11, figs. 2, 4, 8; Figs. 2b–2d, 2h, 3e, 7q). These cells are characterized by a wide variety of wall thickenings, most common are the elements with reticulate wall thickenings; occasionally circular bordered pits occur (Fig. 7q). Large-celled transfusion tissue is clearly discernible on tomograms, and surrounds externally vascular bundles, accompanied by the small-celled transfusion tissue (Pl. 11, figs. 1–4, 6–8; Figs. 2a, 2c, 2d, 2h, 2g, 3d, 3e, 4a–4g, 5a–5i). Together with the latter, the large-celled transfusion tissue composes the mass of transfusion tissue beneath the floor of ovuliferous organ (Figs. 5h, 6a, 6b).

The cortical region of ovuliferous organ consists of two zones, outer of which is sclerified; secretory canals and cavities are absent. The inner zone of cortex consists of large thin-walled prosenchymatous cells up to 300  $\mu\text{m}$  long, up to 80  $\mu\text{m}$  in diameter, arranged in more or less longitudinal rows. This tissue is predominantly developed in the lower part of ovuliferous organ (before divergence of scales) and in free parts of short scales, almost completely absent in the long scale. The zone is up to 500  $\mu\text{m}$  thick (Figs. 2a, 3a, 3b, 4b–4g, 6a, 6b). The outer zone of cortex consists of columnar to isodiametric cells, up to 100  $\mu\text{m}$  long and up to 50  $\mu\text{m}$  in diameter, with filled cell lumens; orientation of cells of the zone in different parts of ovuliferous organ varies from longitudinal to palisade (Pl. 11, figs. 1, 3, 6, 7; Figs. 3a, 3d, 4a–4g, 6a, 6b). This tissue is developed throughout the outer surface of ovuliferous organ, the maximum thickness (more than 500  $\mu\text{m}$ ) reaches on the outer surface of the long scale (Pl. 11, figs. 3, 6). On the inner side of free parts of scales, the

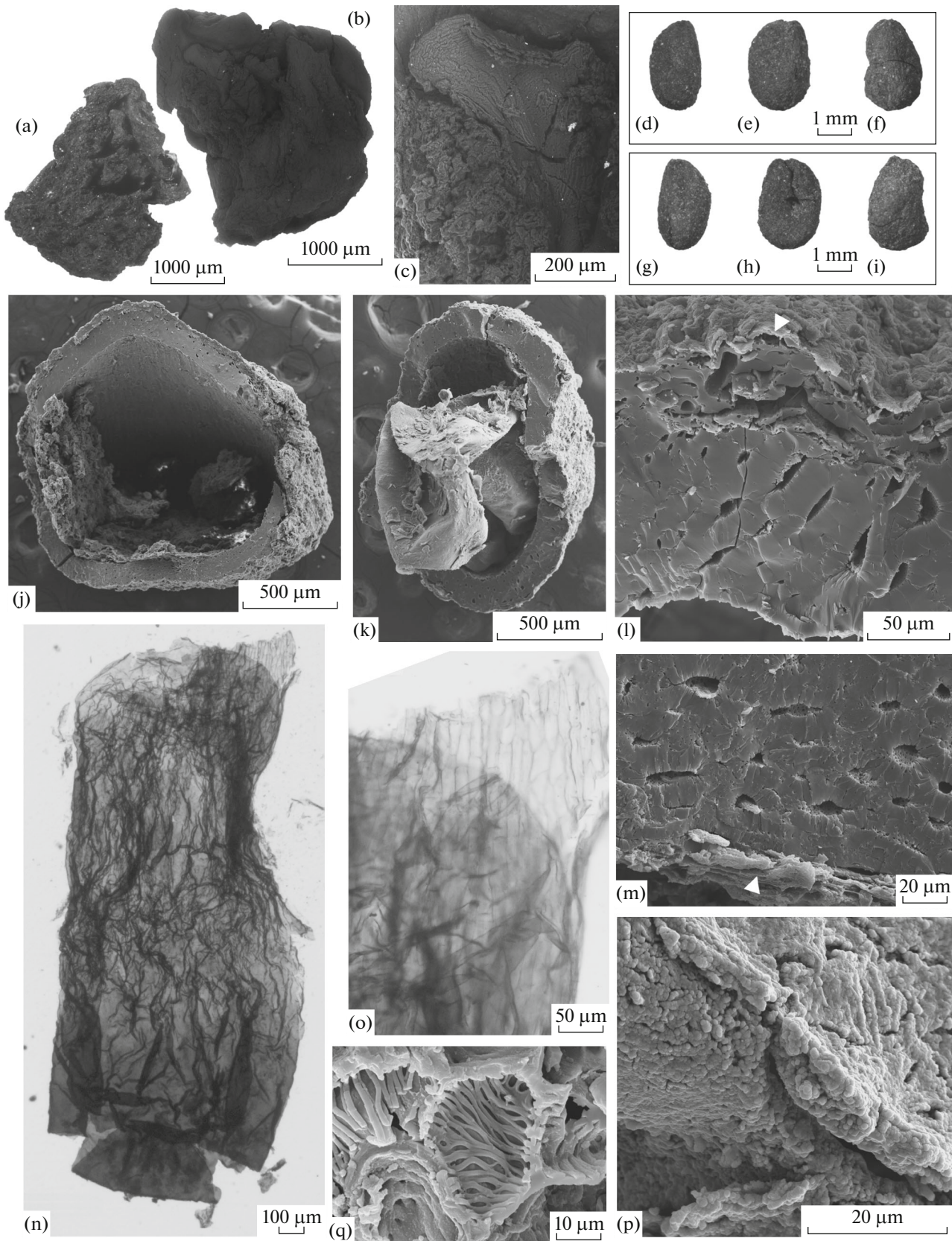
fibrose tissue is developed, which composed of prosenchymatous cells with thickened walls, 5–10  $\mu\text{m}$  in diameter, arranged in longitudinal rows; this tissue is up to 250  $\mu\text{m}$  thick; similar tissue covers the floor of ovuliferous organ (Pl. 11, figs. 3, 4, 6, 7; Figs. 3a, 3d).

The epidermal covering of ovuliferous organ is single-layered, cuticle is very thin, about 1.5  $\mu\text{m}$  thick. The epidermis of the outer surface of scales with numerous monocyclic stomata, orientated obliquely or longitudinally, with five–six subsidiary cells (Figs. 6d–6g). Subsidiary cells of stomata with small proximal papillae, guard cells are sunken, bean-shaped, up to 50  $\mu\text{m}$  long; the stomata are about 50  $\mu\text{m}$  wide; the aperture is up to 15  $\mu\text{m}$  long. The epidermis of the inner surface of scales lacks stomata, in short scales with numerous thinly cutinized papillae; the diameter of papillae bases is up to 10  $\mu\text{m}$ , height of papillae is up to 20  $\mu\text{m}$  (Figs. 6h, 6i).

The ovuliferous organ comprises three seeds (Figs. 1d, 1e, 7a–7i). The seeds are small, 2.6–2.8 mm long, about 1.6 mm in diameter, ellipsoidal, with not protruding micropyle, somewhat shifted relative to the longitudinal axis of seed (Figs. 7d–7i). The testa is up to 250  $\mu\text{m}$  thick, consists of exotesta, mesotesta, and endotesta (Figs. 7j–7m). The exotesta is poorly preserved, single-layered, composed of rectangular epidermal cells up to 40  $\mu\text{m}$  wide and about 60  $\mu\text{m}$  long (Fig. 7l). The mesotesta is up to 10 cells thick, composed of isodiametric sclereids 10–40  $\mu\text{m}$  in diameter (Figs. 7j–7l). The endotesta is preserved as a papery layer sloughing from the mesotesta (Fig. 7l); it consists of rectangular and penta-hexagonal cells up to 50  $\mu\text{m}$  long, about 5  $\mu\text{m}$  wide, with thin straight anticlinal walls. The nucellus is thinly cutinized, free from integument for more than one half (Figs. 7n, 7o). Cells of the nucellus are from rectangular to pentagonal in shape, 20–40  $\mu\text{m}$  wide, up to 100  $\mu\text{m}$  long. In seeds investigated, the apical part of the nucellus is not preserved. The megaspore membrane is thick, up to 5  $\mu\text{m}$  of thickness, consists of short branching rods and granules (Figs. 7n–7p).

**Remarks.** Since the ovuliferous organs studied were found only isolated, and cannot be directly correlated with any known taxa, it remains unclear, whether they represent entire reproductive structures or parts of a more complex structure (for example, a loose strobilus). Nothing can be said about the habit of plant, which bore these ovuliferous organs, since there

**Fig. 6.** Ovuliferous organs *Trisquama valentinii* gen. et sp. nov.: (a) paratype PIN, no. 5137/61, transverse tomogram near the floor of ovuliferous organ, slightly below the place of fusion of the plates of the fertile structure elliptical vascular bundle; in distal part, the plates are completely wedged out, the center is occupied by mass of transfusion tissue, outlines of the zone composed of small-celled transfusion tissue are discernible; (b, c) holotype PIN, no. 5137/60, longitudinal tomogram near the plane of symmetry of ovuliferous organ; on the left, bending outward vascular bundle of sterile structure, passing from the stalk of ovuliferous organ into the base of long scale; from this bundle, the fertile structure vascular bundle departs, dividing into separate segments distally; outlines of vascular bundles, accompanied by small-celled transfusion tissue (shown in drawing (c)), and the mass of transfusion tissue beneath the floor of ovuliferous organ, are visible; (d–i) paratype PIN, no. 5137/65: (d) epidermis of the scale outer surface with stomata, SEM; (e) stomata, detail of the preceding image, SEM; (f, g) stomata with small proximal papillae on subsidiary cells, LM; (h) inner surface of the short scale, SEM; (i) papillae and their bases, detail of the preceding image, SEM.



are no reliable correlates that allow them to be related with vegetative organs found in association.

**Material.** Six exemplars represented by three-dimensionally preserved coalified remains of ovuliferous organs.

## DISCUSSION

When considering the ovuliferous organs *Trisquama* gen. nov., first of all attention is drawn to the contradiction between their morphology and vascularization. Morphologically, these ovuliferous organs resemble reduced cones of some conifers like *Juniperus* L., with three scales fused into a cupule-like structure, and orthotopous seeds located in its center. On the contrary, vascularization reveals that the long scale, similar in many aspects to the short scales, in actuality comprises an organic whole with the stalk of the ovuliferous organ, and the short scales represent the lobes of the seed-bearing structure. This discrepancy once again confirms the exceptional importance of the data on vascularization of plant reproductive organs for understanding their structure, and the necessity to be cautious in interpreting a material, for which the anatomical structure is unknown. With regard to *Trisquamales* ordo nov., this contradiction between morphology and vascularization may indicate that reproductive organs of this phylogenetic line, specializing in the direction of development of the cupule-like structure *Trisquama* gen. nov., have deviated far enough away from their prototype; it is likely that in ancestral forms of the order in question, homologues of the sterile structure distal part represented something fundamentally different from the long scale of *Trisquama* gen. nov. Along with other unusual structural features of these ovuliferous organs, lack of information about other parts of the plant, and absence of reliable correlates that could point directly to their relationship with a particular line of gymnosperms, this significantly complicates a search for possible ancestral forms of *Trisquamales* ordo nov., among other, not allowing to ascertain, exactly on what basis and in what way such reproductive structures could evolve.

Outside the context of a certain phylogenetic line of gymnosperms, interpretation of the ovuliferous organs under consideration encounters considerable difficulties; there are many hypothetical variants of morpho-

logical transformations, of which rare can be excluded completely. The sterile structure of *Trisquama* gen. nov., comprising of the stalk of ovuliferous organ and undissisted distal part (the long scale), vascularized by collateral vascular bundle, and bearing the fertile structure on its anatomically abaxial side, resembles most of all some transformed leaf-like organ, to which the fertile structure has fused from below. Such a leaf-like organ could be a modified leaf, sterilized megasporophyll, or overlying bract (compare fusion with overlying bracts of sporangiophores of the calamitalean *Pendulostachys* Good, 1975). It can not be excluded also that the sterile structure of *Trisquama* gen. nov. represents a vestige of an axis, which originally bore several fertile structures: during the reduction of this axis, only one of them has remained; the axis itself has been strongly simplified and has lost its radial organization; such a hypothesis is consistent with the position of the fertile structure from the phloem side of the sterile structure vascular bundle, and also with absence in the ovuliferous organ stalk of independent vascular bundle of fertile structure. In its organization, the sterile structure of *Trisquama* gen. nov. resembles the “bearing elements” of a variety of reproductive organs, such as arms of *Dordrechtites*, stalk+sterile extension of sporophyll of *Doylea* Rothwell et Stockey, etc. (Bergene et al., 2013; Rothwell and Stockey, 2016). The suggestion, that the ovuliferous organs *Trisquama* gen. nov. could evolve on the basis of such elements,—via the appearance of the fertile structure as a novel organ,—is at variance with the well-developed vascular system of the fertile structure, and also with the presence of the outgrowth and apical teeth of short scales, suggesting probable directional growth (compare, for example, outgrowths of the collar in representatives of *Ginkgo* sensu lato: Gordenko and Broushkin, 2015). On the contrary, reproductive organs of such basic construction, with abaxial seeds, can be derived from ovuliferous organs of *Trisquama* gen. nov. through reduction of the fertile structure: at loss by the fertile structure of its own vascular system, seeds formally move from it to the sterile structure, appearing from the phloem side of the vascular bundle of the latter (indications of the onset of such reduction in *Trisquama* gen. nov. may be the absence of vascular bundles in the free parts of the short scales, in the presence of cells, similar to those of transfusion tissue, in the area where vascular bundles could previously be

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**Fig. 7.** Ovuliferous organs *Trisquama valentinii* gen. et sp. nov.: (a–c) paratype PIN, no. 5137/65: (a) abortive ovuliferous organ, view from above, three ovules in the central part of triangular floor, enclosed by pair of short scales (at the top of the image) and partly preserved base of the long scale (at the bottom), are visible; (b) the same, one of the short scales is completely removed, SEM; (c) detail of (b), attachment of ovule to the floor of ovuliferous organ; (d–p) paratype PIN, no. 5137/62: (d–f) three seeds, extracted from the ovuliferous organ, lateral view; (g–i) the same, view from the opposite side; (j) transverse split of the seed figured in (f, i), SEM; (k) transverse split of the seed figured in (e, h), nucellus with megaspore membrane is visible, SEM; (l) detail of (j), transverse split of testa: mesotesta, represented by sclerotesta, and epidermis (exotesta, marked by arrow) are visible, SEM; (m) detail of (j), transverse split of testa: mesotesta, represented by sclerotesta, and endotesta (marked by arrow), SEM; (n) nucellus with megaspore membrane, LM; (o) detail of (n), outlines of cells of nucellus are visible, LM; (p) external surface of megaspore membrane, SEM; (q) paratype PIN, no. 5137/61, large-celled transfusion tissue elements with various thickenings of cell wall; in one of the elements, circular bordered pits are visible, SEM.



localized: Figs. 3a, 3c). The presently known reproductive organs of the corresponding basic construction (characteristic for Umkomasiales, with which we also ally *Doylea*, and the forms close to them), at the same time significantly differ in the structure of seeds, and arose on a fundamentally different basis (Meyen, 1984, 1987; Klavins et al., 2002; Rothwell and Stockey, 2016; Shi et al., 2016).

The fertile structure of the ovuliferous organs *Trisquama* gen. nov. may be interpreted as a leaf-like organ (megasporophyll in a broad sense) with the same orientation (adaxial/abaxial sides) as the sterile structure,—longitudinally folded and partly fused, bearing seeds on its anatomically adaxial surface. Asymmetry in the arrangement of lobes of the fertile structure, emphasized by the arrangement of segments (plates) of its vascular bundle, could argue in favor of pinnate organization of such hypothetical sporophyll, but available evidence is very unreliable. Also, the fertile structure of *Trisquama* gen. nov. may represent a simplified compound organ like a strongly reduced cone or cone scale of conifers; vascularization of the fertile structure by the concentric amphicribal vascular bundle may suggest its initial axial nature.

Some structural characters of seeds (micropyle shifted relative to longitudinal axis of seed, presence of single three-layered integument without sarcotesta, relatively thinly cutinized nucellus), as well as characteristic xylem tracheids with uniseriate circular bordered pits and presumable tori, absence of normal tracheids with scalariform bordered pits, etc., ally *Trisquama* gen. nov. with conifers. The reduction of seed scale in conifers results in forms like *Thuja occidentalis* L., in which orthotropous seeds are borne in the axil of bract, vascularized only by abaxial vascular bundles (Zhang et al., 2004); possible also is the shifting of seeds to the adaxial surface of such bract, with their vascularization from the xylem side of its vascular bundles (such kind of shifting to the underlying leaf adaxial surface of the axillary complex, with reduction of the latter, occurs in Glossopteridales and aberrant forms of *Ginkgo* L.: Bierhorst, 1971; Doyle, 2006; etc.). The assumption that ovuliferous organs of *Trisquamales* ordo nov. could evolve on the basis of such reproductive organs of representatives of Coniferopsida, is in contradiction, first of all, with the absence in the latter of analogues of the sterile structure of *Trisquama* gen. nov.; all forms with dissected bracts, known among archaic conifers (such as *Otovicia* Kerp, Poort, Swinkels et Verwer, *Rissikia* Townrow, etc.: Townrow, 1967; Kerp et al., 1990; Taylor et al., 2009), possess also well-developed seed scales.

Although structure of the ovuliferous organs *Trisquama* gen. nov. is known in detail, it is impossible to relate them with any presently known large group of gymnosperms; for this reason, the authors place *Trisquama* gen. nov. in a separate order within Gymnospermales. *Trisquamales* ordo nov. enters in the sub-

stantial list of gymnosperm groups, which demonstrate unique combination of characters of high taxonomic rank, and which position in the system of Gymnospermales is uncertain. Presence of large number of groups that do not fit into the overall system, as well as: insufficient understanding of many key taxa used in phylogenetic reconstructions (such as *Caytonia* Thomas, *Peltaspermum* Harris, *Leptostrobus* Heer, etc.); essential controversies in the estimation of general ways of diversification of gymnosperm lineages; ambiguities with the origin of many important groups, in particular, Angiospermales,—reflect extremely uneven and insufficient state of knowledge of Mesozoic gymnosperms at the present time. Along with comparatively well-understood lineages, in which ancestral relationships of groups can be traced, there are vast areas, where so far one can only assume individual taxa interrelations.

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