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A New Genus *Navipelta* (Peltaspermales, Pteridospermae) from the Permian/Triassic Boundary Deposits of the Moscow Syneclise

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Abstract—A new genus of peltaspermalean ovuliferous organs *Navipelta* gen. nov. is described from the terrestrial deposits of the Nedubrovo locality (village of Nedubrovo, Vologda Region, Russia), belonging to the base of Vetlugian Group (Upper Permian–Lower Triassic). Data on the anatomy of the peltate bilateral ovuliferous organs are obtained for the first time. Vascular strands in the peltoid depart from that of a stalk and branch up to three times distally. Transfusion tissue around the vascular strands is well developed. The new genus had a system of radially arranged resin canals, broaden into large secretory cavities.

Key words: Peltaspermaceae, ovuliferous organs, *Peltaspermum*, *Autunia*, Permian/Triassic boundary, Vetlugian Group, systematics.

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INTRODUCTION

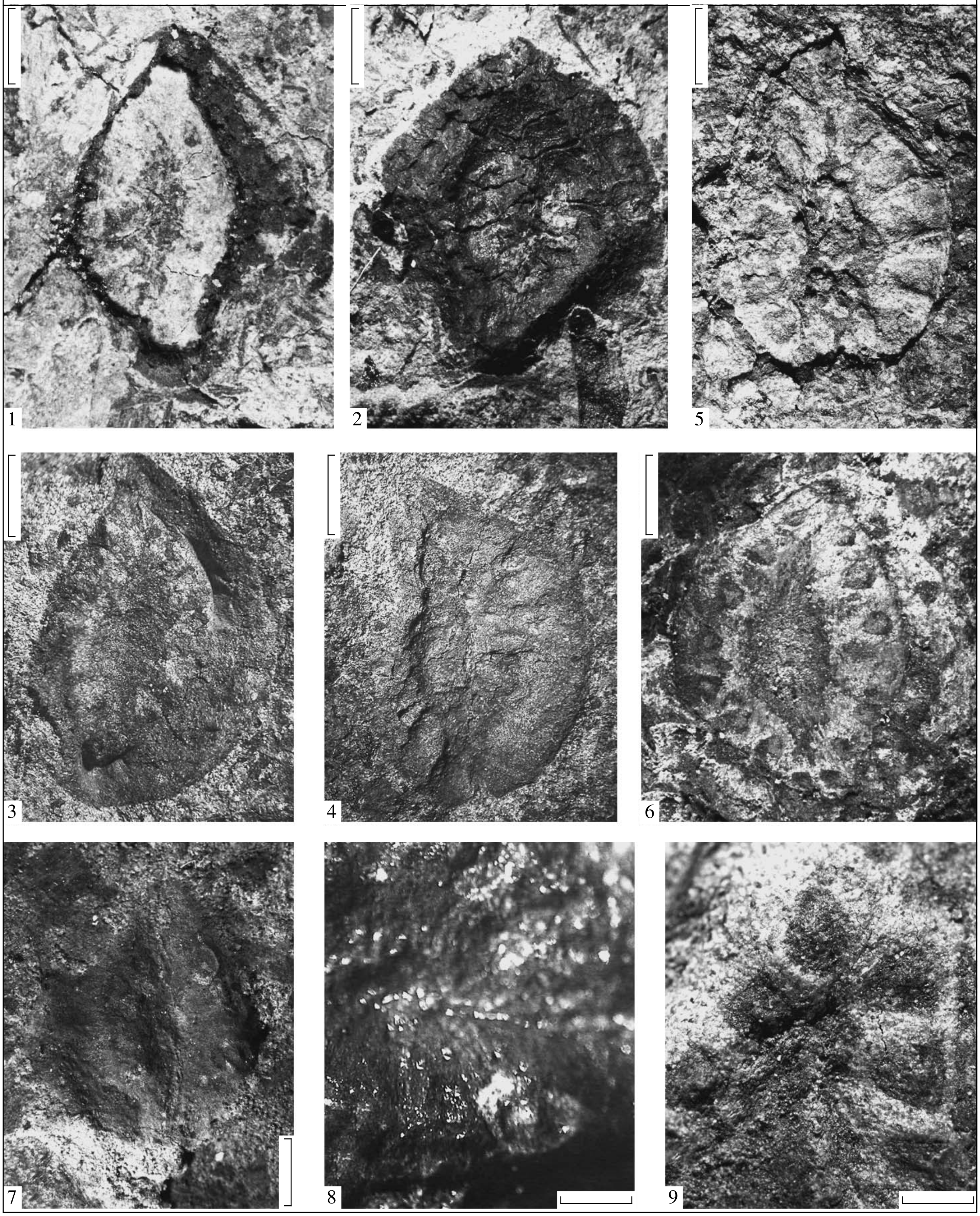
The family Peltaspermaceae attracts attention of many researchers, because its members were the main component of the Late Permian Angaraland floras. They escaped the global crisis on the Permian/Triassic boundary and transited in the Mesozoic, where dominated during the Middle and Late Triassic of the Northern as well as Southern hemispheres. The family currently includes more than 25 genera based on vegetative organs; 11 genera were established on the basis of reproductive organs. Female generative organs of the Peltaspermaceae are represented by four confidently distinguishable genera: peltate radially symmetrical in *Peltaspermum* Harris and nonpeltate bilaterally symmetrical in *Autunia* Krasser emend. Kerp, *Stiphorus* Meyen, and *Sporophyllites* Chalyshev ex Fefilova emend. Meyen (Harris, 1937; Meyen, 1982; Meyen, 1983; Kerp and Haubold, 1988). Other genera are very similar in their morphology and were established for seed-bearing organs of different preservations (*Lopadiangium* Zhao ex Gomankov et Meyen and *Autuniopsis* Poort et Kerp) or on the basis of their association with different foliage (*Peltaspermopsis buevichiae* Gomankov et. Meyen and *Meyenopteris*, Poort et Kerp) (Gomankov and Meyen, 1986; Poort and Kerp, 1990).

The morphology and epidermal structure of seed-bearing organs in the Peltaspermaceae were studied relatively well (Townrow, 1960; Gomankov and Meyen, 1979; Kerp, 1982; Dobruskina, 1982; Meyen, 1983; Gomankov and Meyen, 1986; Naugolnykh and Kerp, 1996), whereas data on their anatomical structure are virtually absent. A few papers were devoted to anatomically preserved leaves and stems–genera *Kirjamkenia* Pryn. emend. Sadovnikov (Sadovnikov, 1983) and *Rhachiphyllum* Kerp (Sadovnikov, 1983; Naugolnykh, 2001). Data on anatomical structure of the seed-bearing organs of the genera *Peltaspermum*, *Peltaspermopsis*, *Stiphorus,* and *Autunia* are absent. In papers published, there are only hypothetical schemes, illustrating topography of vascular strands in *Peltaspermum* and *Autunia*

Explanation of Plate 17

Figs. 1–9. *Navipelta resinifera* gen. et sp. nov., morphology of peltoids: (1, 2) holotype PIN, no. 4820/141: (1) impression of the adaxial side with partially preserved phytoleim of a bordering; (2) a phytoleim from the adaxial side shows circular concavity and bordering; (3) PIN, no. 4820/702, a transversal split, the adaxial side is partly degaged; (4) the same, the abaxial side is partly degaged; (5) PIN, no. 4820/712, an impression of the adaxial side; sub-triangular seed scars and ribs, corresponding to grooves on the peltoid, are visible; (6) PIN, no. 4820/139, impression, rounded seed scars are visible; (7) PIN, no. 4820/23, impression of the adaxial side; (8) the same, vascular bundle coming to a seed scar; (9) PIN, no. 4820/38, impression, sub-triangular seed scars are visible. The Vologda Region, left bank of the Kichmenga River, near the village of Nedubrovo, locality Nedubrovo; Upper Permian–Lower Triassic, Vetlugian Group, Vokhma Horizon, Nedubrovo Formation. Scale bar: (1–7) 2 mm; (8, 9) 1 mm.

Plate 17



(Townrow, 1960; Retallack and Dilcher, 1988; Naugolnykh, 2001a). Resin bodies were found in the mesophyll of cladosperms in *Stiphorus* (Gomankov and Meyen, 1986).

As a rule, remains of seed-bearing organs in the Late Permian and Triassic deposits are represented by imprints, cuticular coverings with coalified contents, or, more rarely, by casts and cavities. Well-preserved ovuliferous organs of a new peltaspermaceous genus were found in the continental Permian–Triassic deposits of the Nedubrovo locality (village of Nedubrovo, Vologda Region, Russia). The find allowed obtaining the first data on the anatomical structure of seed-bearing organs of the group.

MATERIAL AND METHODS

The material was collected in 1999–2007 years by V.A. Krassilov, S.A. Afonin, N.V. Gordenko, and N.E. Zavialova (A.A.Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia, PIN) and V.R. Losovskii (Russian State University for the Humanities, Moscow, Russia) and the author from the Permian–Triassic deposits of the Nedubrovo locality (village of Nedubrovo, Vologda Region). The material is represented by permineralizations, impressions with phytoleims of the adaxial and abaxial sides, splits through the inner part of the peltoid, and casts. The general morphology of the remains was studied with MBS-10 and Leica MZ-16 stereomicroscopes using method of degagements with steel needles. The micromorphology and details of cellular structure in mineralized samples were observed using a Camscan scanning electron microscope. Transfer preparations on lacquer film were prepared of some samples by placing them in concentrated HF. Resin bodies were examined in transmitted light using an Axioplan-2 light microscope and under SEM. Phytoleim fragments were macerated by standard methods using nitric acid and then alkali (KOH). The samples were photographed using Nikon CoolPix 4500 and Leica DFC 420 digital cameras.

In description of seed-bearing organs, the author use terminology proposed by Meyen (1987).

The material is housed at PIN, collection no. 4820.

SYSTEMATIC PALAEOBOTANY

Order Peltaspermales

Genus *Navipelta* Karasev, gen. nov.

E t y m o l o g y. From the Latin *navis* (boat), and Latin-Greek *pelta* (shield).

T y p e s p e c i e s. *Navipelta resinifera* sp. nov.

D i a g n o s i s. Ovuliferous organs peltate, bilaterally symmetrical, elliptical to rounded-rhomboidal in plane. Abaxial surface of peltoids slightly convex or flat, and adaxially surface concave. Peltoids 5–8 mm in length and 4–6 mm in width, central part up to 2 mm thick. Around scar of stalk, peltoids have ring-shaped concavity, which is divided into indistinct sectors by radial grooves. Scar of stalk elliptical, up to one third of peltoid length. Adaxial surface of peltoid bears 11 or, more rarely, 6–14 scars, corresponding to places of seed attachment. Seed scars rounded-triangular to rounded and widely oval, about 0.7 mm in diameter. Margins of peltoids smooth or slightly wavy. Vascular strands come from peltoid stalk and branch up to three times. They alternate with fusiform or beaded secretory cavities. Vascular strands consist of primary xylem tracheids. Transfusion tissue well developed and concentrated around vascular strands.

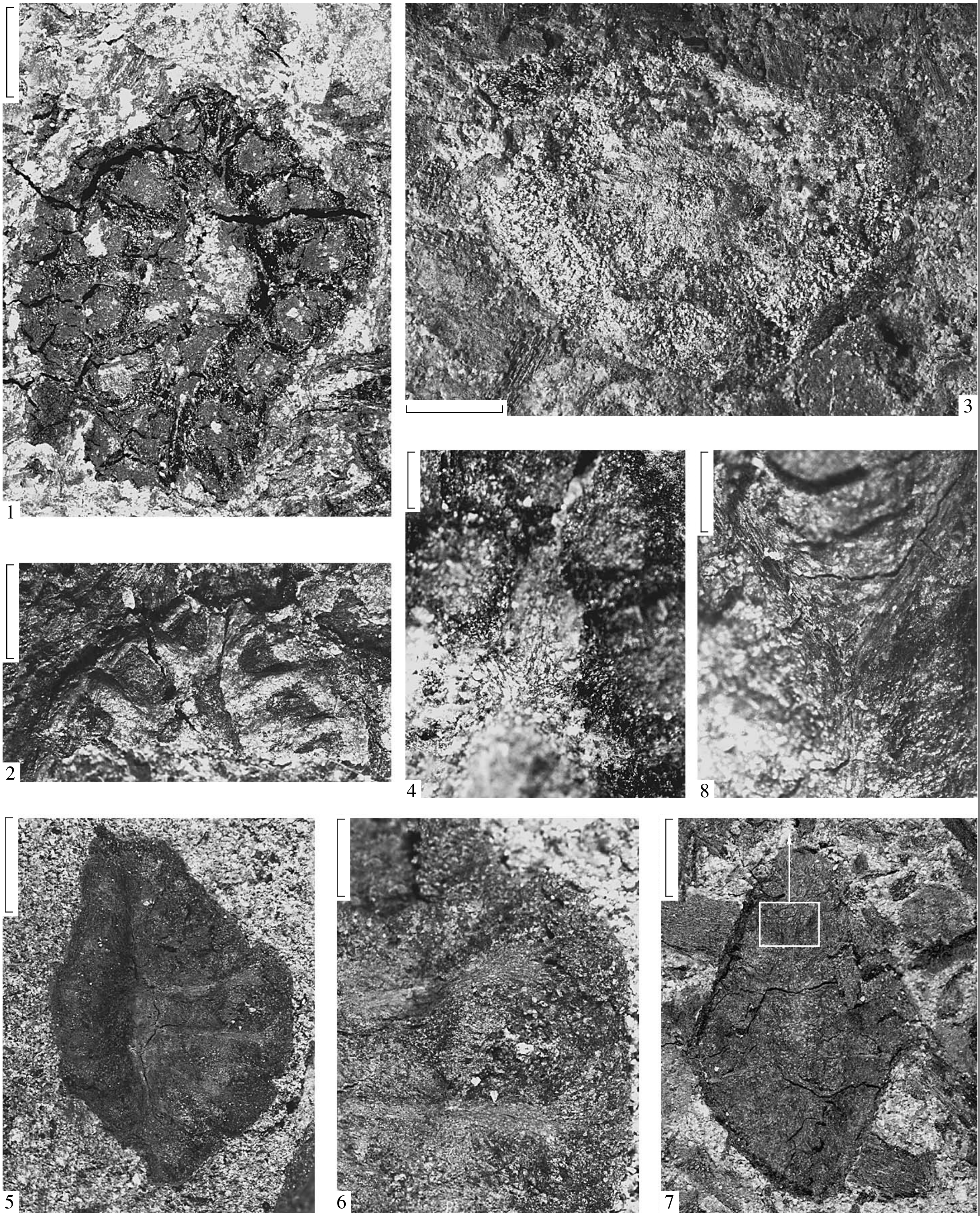
C o m p a r i s o n. In their peltate organization, ovuliferous organs of the new genus exhibit the greatest similarity to ovuliferous organs of *Peltaspermum* and *Peltaspermopsis*. There are no crucial differences between *Peltaspermum* and *Peltaspermopsis* in the morphology of their peltoids, therefore, the comparison between *Navipelta resinifera* gen. et sp. nov. and these genera will be provided jointly. Ovuliferous organs of the three genera are peltate, with a centrally attached stalk; seed scars are disposed around the peltoid axis in the same manner. However, peltoids in *Navipelta resinifera* gen. et sp. nov., as opposed to peltoids of the two other genera, are bilaterally symmetrical, with rhomboidal outlines, straight margins, and of great thickness, tissues of the peltoids contain abundant secretory canals and cavities. Moreover, vascular strands in the new genus are ramified, which was not observed in *Peltaspermum* and *Peltaspermopsis*. The type species of *Peltaspermum* bears characteristic blisters on the surface of peltoid and its stalk, which were not observed in the peltoids from the Nedubrovo.

Peltoids of the new genus in their several essential characters, such as a bilateral symmetry, the presence of numerous secretory cavities, and pinnate branching (ramification) of vascular bundles, are comparable with bilaterally symmetrical non-peltate seed-bearing organs of *Autunia*, *Stiphorus*, and *Sporophyllites*. A distinction between the new genus and all these genera consists in the attachment of a stalk to the central part of the peltoid. The new genus also differs from *Stipho-*

E x p l a n a t i o n o f P l a t e 18

Figs. 1–9. *Navipelta resinifera* gen. et sp. nov., morphology of the adaxial side, vascular strands of peltoids are visible: (1) paratype PIN, no. 4820/711, phytoleim with preserved cuticle; (2) the same, impression; (3) PIN, no. 4820/15, phytoleim of peltoid of three-dimensional preservation with preserved cuticle; (4) PIN, no. 4820/714, petrified fragment, seed scars and preserved cells of vascular elements are visible; (5) PIN, no. 4820/719, vascular strands reaching the peltoid margin; (6) the same, split through the lower part of peltoid; (7) PIN, no. 4820/716, vascular system; (8) the same, branching of vascular strands. The Vologda Region, left bank of the Kichmenga River, near the village of Nedubrovo, locality Nedubrovo; Upper Permian–Lower Triassic, Vetlugian Group, Vokhma Horizon, Nedubrovo Formation. Scale bar: (1–3, 5, 7) 2 mm; (4, 8) 0.5 mm; (6) 1 mm.

Plate 18



Explanation of Plate 19

Figs. 1–9. *Navipelta resinifera* gen. et sp. nov., vascular elements of peltoids, SEM: (1) PIN, no. 4820/703, fragment of peltoid in the bordering area, transversal split; (2–7) PIN, no. 4820/14: (2) peltoid in the area of attachment to a stalk, tangential split; (3) elongated tracheids in the axial part of peltoid; (4) short tracheids in the area of ring-shaped concavity; (5) casts of transfusion cells with circular pits; (6) cast of tracheid lumen with impressions of inner tertiary thickenings and pit cavities; (7) alternating rounded bordered pits on the outer walls of tracheids; (8) PIN, no. 4820/703, casts of thin tracheids of vascular bundle showing uniseriate pitting; (9) PIN, no. 4820/716, tracheids of vascular strand with tertiary thickenings and uniseriate bordered pits. The Vologda Region, left bank of the Kichmenga River, near the village of Nedubrovo, locality Nedubrovo; Upper Permian–Lower Triassic, Vetlugian Group, Vokhma Horizon, Nedubrovo Formation. Scale bar: (1, 2) 1 mm; (3, 4, 8, 9) 30 μm; (5, 6) 5 mm; (7) 10 μm.

rus and *Sporophyllites* by having roundly-rhomboidal outlines of peltoids, and from *Autunia* by having numerous (10–12) seeds and entire peltoid margin. I also consider *Autunia thomasii* (Harris) Kerp (former *Peltaspermum thomasii* Harris) within the frameworks of the genus *Autunia*.

Navipelta resinifera **Karasev, sp. nov.**

Plate 17, figs. 1–9; Plate 18, figs. 1–8; Plate 19, figs. 1–9; Plate 20, figs. 1–9

Etymology. From Latin *resinifer* (resiniferous).

Holotype. PIN, no. 4820/141; phytoleim and imprint of the abaxial side of peltoid; Vologda Region, left bank of the Kichmenga River, near the village of Nedubrovo, locality Nedubrovo; Upper Permian–Lower Triassic, Vetlugian Group, Vokhma Horizon, Nedubrovo Formation (Pl. 17, figs. 1, 2).

Diagnosis. As for the genus.

Description (Figs. 1, 2). Isolated oviliferous organs are bilaterally symmetrical. They consist of a peltoid, attached to a stalk, with seed scars arranged astride of it. The peltoids are from rounded rhomboidal to nearly elliptical, or ovoid in plane; they are pointed on one extremity and obtuse on the other (Pl. 17, figs. 1–7). The length of peltoids is from 5 to 8 mm, width–from 4 to 6 mm, in the middle part they attain a thickness 2 mm. The abaxial (upper) surface of peltoids is flat, with a small concavity in its central part (Pl. 17, fig. 4). The stalk was attached to the central part of the adaxial (lower) side of peltoid. The stalk scar is elliptical, massive, constitutes up to one third of peltoid diameter (Pl. 17, fig. 2). A ring-shaped concavity encircles the stalk scar; it is divided into indistinct sectors by radial grooves (Fig. 1a). Seed scars are situated between the grooves, one scar per sector of the concavity. As a rule, the number of seed scars is 12, but it can vary from 6 to 14; often, the number may differ on the two sides of the peltoid. The scars are from rounded-triangular to rounded and broadly-oval (Pl. 17, figs. 5–9, Pl. 18, figs. 1, 2). The seed scars are 0.5–0.7 mm in diameter, their size varies depending on their number on the peltoid. The thickness of peltoids of the new genus is no less than 1.5 mm (Pl. 18, fig. 3). From the peripheral part of the ring-shaped concavity towards the margins, the peltoid thickness abruptly decreases to form a bordering (Fig. 1a). The peltoid margins are smooth or slightly wavy.

Longitudinal, transverse (Pl. 18, figs. 4–8; Pl. 19, fig. 1), and tangential (Pl. 19, fig. 2) sections (splits) of the peltoids demonstrate vascular tissue elements of stalk and numerous secretory cavities. Vascular bundles depart from the stalk to seed scars, and then reach peltoid margins (Pl. 18, figs. 5, 6). Vascular bundles, departing to the extremities of peltoid, are branched alternately one or two times (Pl. 18, figs. 7, 8; Fig. 2). Conductive elements of a stalk are presented by tracheids and transfusion cells. The tracheids of metaxylem with rounded bordered pits and inner spiral thickenings of walls form the major part of the stalk vascular bundle; in transversal sections, they are polygonal or rounded, 20–40 μm in diameter. In central part of the stalk, the tracheids are more than 250 μm long (Pl. 19, fig. 3). The outlines of pit borderings are rounded, 3 μm in diameter, pit apertures are about 1 μm in diameter (Pl. 19, figs. 6, 7). In peripheral zones of the stalk, the tracheids became more shorter (about 90 μm long), with rapidly attenuated ends (Pl. 19, fig. 4), and are replaced by elongated transfusion cells with numerous circular pits (Pl. 19, fig. 5). Pitting of tracheid walls is alternate, bi- or triseriate. Pitting on both radial and tangential tracheid walls is the same. Tracheids in vascular bundles of the peltoid have tertiary thickenings and mainly uniseriate or, more rarely, biseriate bordered pits. They are much longer and thinner than tracheids of the stalk (Pl. 19, figs. 8, 9). Laterally, the tracheids are replaced by transfusion cells.

The secretory system of peltoids is well developed and consists of fusiform or beaded secretory canals, which occasionally widen to form secretory cavities (Pl. 20, figs. 1–6). The secretory canals are radially situated around the stalk, in grooves between seed scars (Pl. 20, fig. 1). The canals pass into peltoid margins, alternating with vascular bundles (Fig. 2). The length of secretory canals is 1–1.5 mm, and the width is about 0.4 mm. Several spherical secretory cavities are disposed mainly in the central or upper part of the peltoid (Pl. 20, figs. 2, 3), and also they often occur in its marginal zones. The epithelium of secretory cavities is formed of large (50–100 μm) polygonal cells (Pl. 20, fig. 5) and small (about 20 μm) drop-shaped cells (Pl. 20, fig. 6). Occasionally, cavities are filled with resinous content. Size of the secretory cavities varies from 0.2 to 1 mm.

The cortex is thin and parenchymatous. In the inner part of the peltoid, cells are oblong, ovate or reniform, 40 × 100 μm (Pl. 20, fig. 7); nearer to the peltoid surface, the cells are nearly isometric, smaller, 30–50 μm, and of irregular form (Pl. 20, fig. 8).

Plate 19

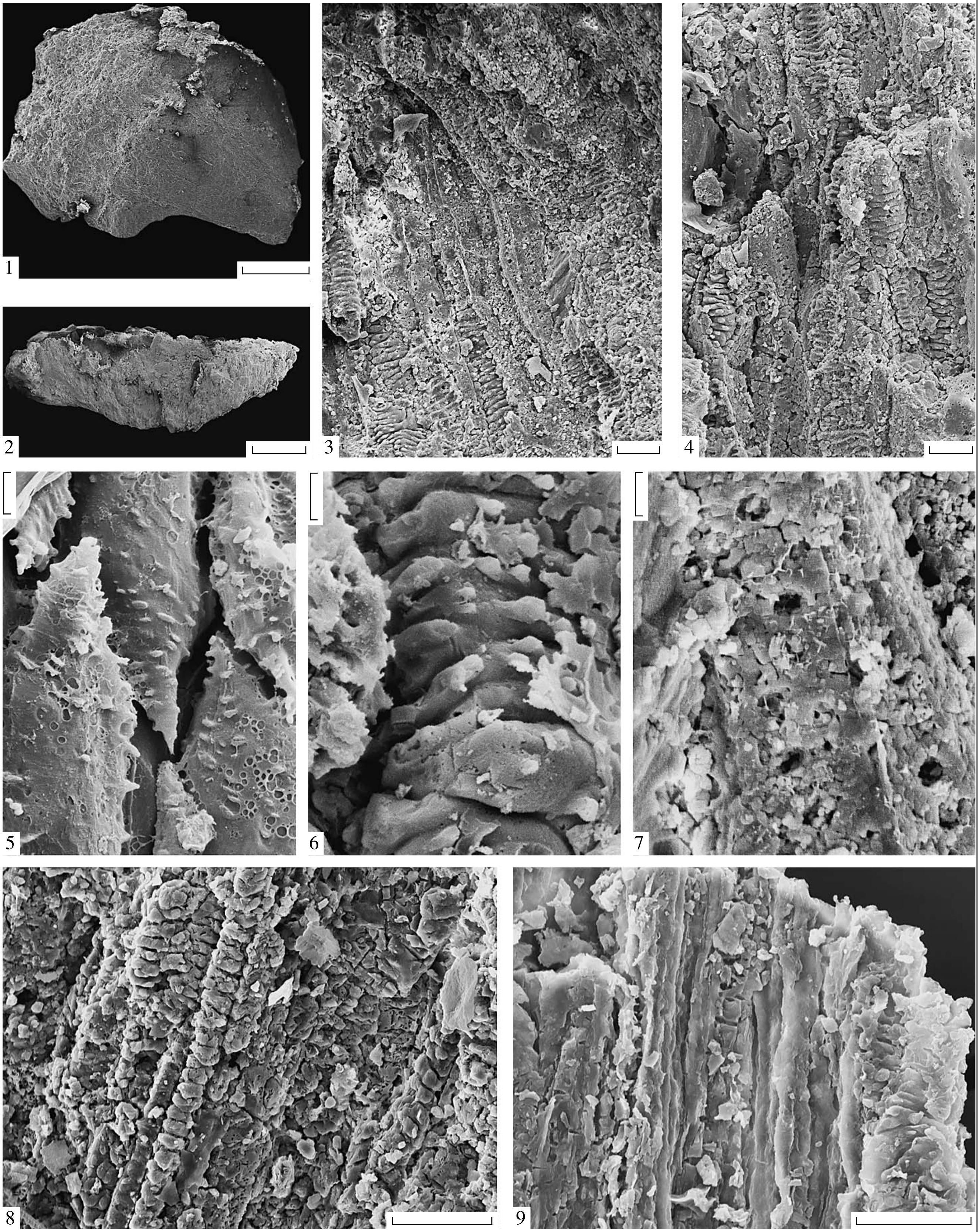
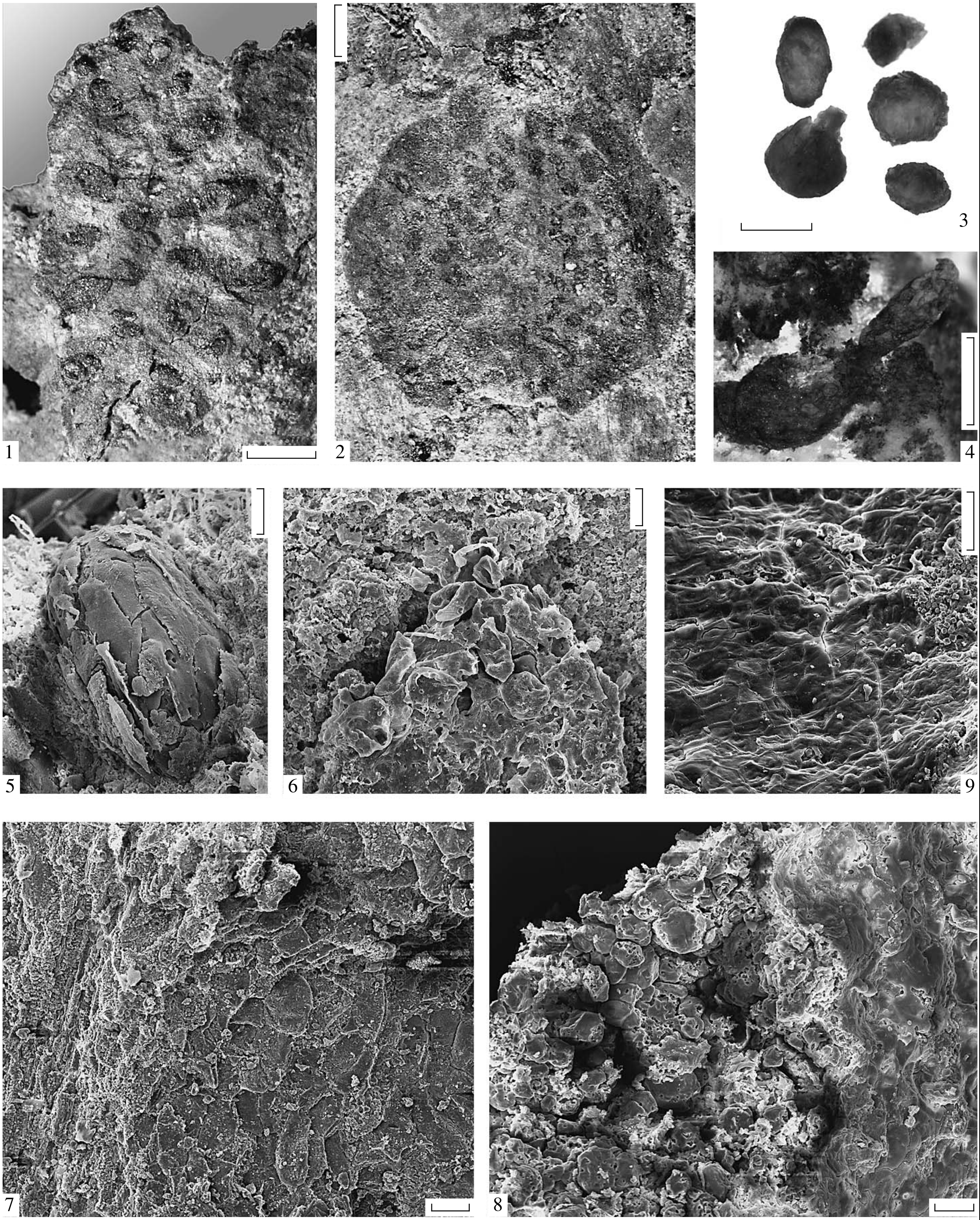


Plate 20



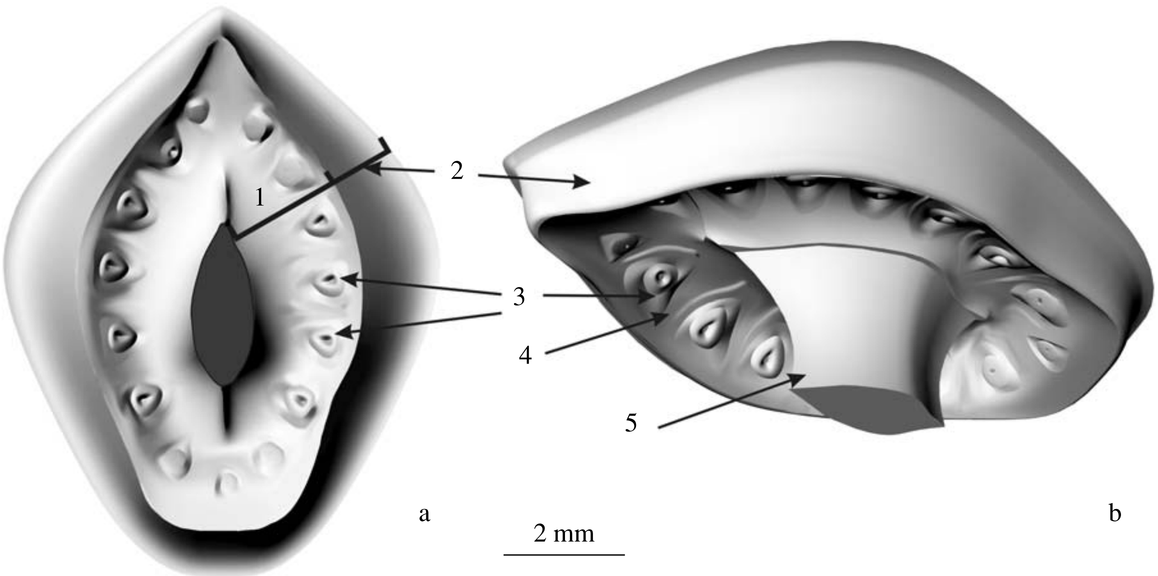


Fig. 1. *Navipelta resinifera* gen. et sp. nov., reconstruction of ovuliferous organs: (a) adaxial side of peltoid; (b) half-turned peltoid; (1) ring-shaped concavity; (2) bordering of peltoid; (3) seed scars; (4) grooves between the seed scars; (5) stalk of peltoid.

The peltoids are weakly cutinized. The lower cuticle is 1 μm thick. Ordinary epidermal cells are rectangular, measure 20 × 30 μm. The periclinal walls are flat. The anticlinal walls are straight or slightly curved. Stomata on the cuticle of the lower side are lacking (Pl. 20, fig. 9).

R e m a r k s. Probably, the variability of peltoids outlines in plane and seed scars is related to the course of the split through various parts of the peltoid. Depending of the split position and preservation, the outlines of peltoids may by nearly circular (split through the middle part), rhomboidal (split through the lower part), or ellipsoidal (split through the upper part of the peltoid). The scar outlines vary from circular to triangular. The true surface of seed scars was rounded-triangular with a small scar of a vascular strand in the central part (Pl. 17, fig. 8; Pl. 18, fig. 1). Ovuliferous organs of the new genus exhibit some similarity to the reconstructed peltoid of *Peltaspermum qualeni* Naug. from the Upper Permian of the southern Cis-Ural (Naugolnykh, 2002). I studied a single specimen of the latter species, its holotype. The holotype of *P. qualenii* is a three-dimensional impression of an axis bearing spirally arranged incompletely preserved peltoids. It is impossible to understand the morphology of the peltoids and, because of their insufficient preservation, compare them to peltoids of the new genus. The interpretation of the peltoid sides on the reconstruction gives rise to doubt. On the upper side of ovuliferous organs, oval objects were figured and interpreted by Naugolnykh as marks of scars of the lower side, impressed on the upper side because of the small thickness of the peltoids. It seems that the side interpreted as the upper side is in fact the adaxial side. The thickness of peltoids in the new genus was no less than 1.5 mm (Pl. 18, fig. 3; Pl. 19, fig. 2). Therefore, in spite of some similarity to this reconstruction, we prefer do not place our material within the genus *Peltaspermum*.

The bulk of information on details of the anatomical structure of the ovuliferous organs was obtained by means of the study of longitudinal splits through the lower part of peltoids. It is visible on splits that tracheids are preserved as casts of their lumens, sometimes with molds of pits cavities (Pl. 19, fig. 5). It is obvious from the studied material that vascular strands reached

E x p l a n a t i o n o f P l a t e 20

Figs. 1–9. *Navipelta resinifera* gen. et sp. nov.: (1) PIN, no. 4820/33, system of secretory canals and cavities of a peltoid, transversal split; (2) PIN, no. 4820/533, transversal split, passed nearer to the upper part of peltoid, numerous secretory cavities are visible; (3) PIN, no. 4820/14, secretory cavities of varied sizes, partially filled with resin content; (4) PIN, no. 4820/138, a beaded secretory canal, widening into secretory cavities; (5) the same, epithelial cells of a secretory canal; (6) PIN, no. 4820/14, a secretory cavity, large polygonal epithelial cells are visible; (7) PIN, no. 4820/703, large cells of inner tissues of peltoid (these cells, most probably, were adjacent to secretory cavity); (8) PIN, no. 4820/15, parenchymatous tissue of cortex in the area of peltoid bordering, preserved cuticle is on the right; (9) PIN, no. 4820/711, outer surface of the lower cuticle of peltoid in the area of ring-shaped concavity, polygonal form of epidermal cells is visible; (1–4) LM; (5–9) SEM. The Vologda Region, left bank of the Kichmenga River, near the village of Nedubrovo, locality Nedubrovo; Upper Permian–Lower Triassic, Vetlugian Group, Vokhma Horizon, Nedubrovo Formation. Scale bar: (1, 2) 1 mm; (3–4) 0.5 mm; (5–9) 50 μm.

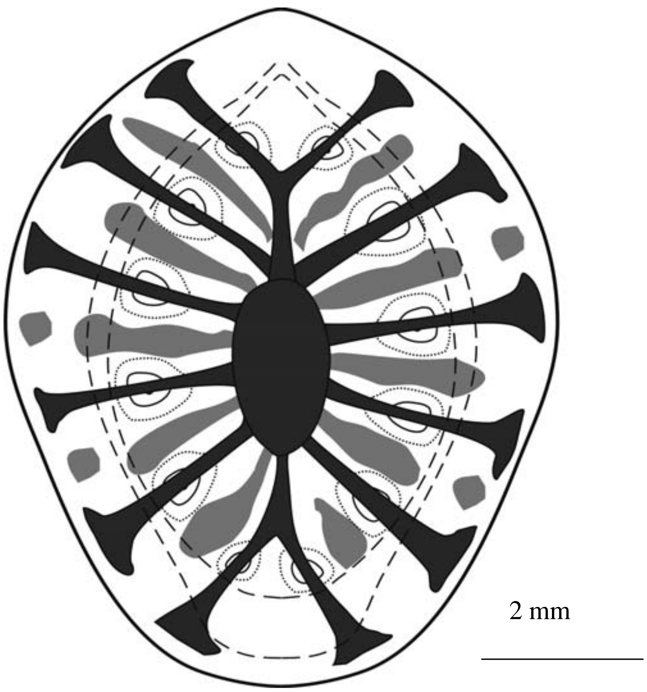


Fig. 2. *Navipelta resinifera* gen. et sp. nov., scheme of vascular bundles branching and disposition of secretory cavities. Vascular bundles are in dark; secretory cavities are light grey; seed scars are dotted; circular concavity is indicated by a broken line.

the margins of peltoid. Therefore, in the area of seed scars, a short vascular bundle departed from the vascular strand to a seed. Unfortunately, the vascular strand emission was impossible to observe directly. The considerable variability in peltoid dimensions and the number of seed scars is notable. The collection includes very small peltoids, 4 mm in diameter, as well as large peltoids, up to 10 mm in diameter; this points on the considerable variability of these characters in the new genus.

M a t e r i a l. Fifty-one specimens.

DISCUSSION

Morphologically, ovuliferous organs of the new genus occupy an intermediate position between more primitive bilateral *Autunia* and *Stiphorus* and peltate radially symmetrical *Peltaspermum* and *Peltaspermopsis*. This corroborates completely a theory of Meyen (1990, 1992), who compared transformations of ovuliferous organs in the Peltaspermaceae with transformations of symmetry in leaves of modern families of angiosperms and ferns. Meyen believed that cladosperms of *Stiphorus* are homologous to umbellate ovuliferous peltoids of *Peltaspermum* type. Meyen included *Stiphorus* in the Peltaspermaceae, because cladosperms of this genus were found in association with leaves of *Kirjamkenia* and *Tatarina* and have epidermal structure similar to that of these two genera (Sadovnikov, 1983; Gomankov and Meyen, 1986).

Earlier, it was supposed that *Autunia* is the oldest and most primitive genus, since it occurs in older Upper Carboniferous deposits and precedes the appearance of *Peltaspermum* in Permian and Mesozoic deposits. The first find of the oldest radially symmetrical ovuliferous organs was described as *P. retensorium* Naug. from the Lower Permian (Kungurian) deposits of the Cis-Ural. Ovuliferous organs of *P. retensorium* are associated with leaves *Rhachiphyllum*, which are similar to callipteroid leaves. Bilaterally symmetrical ovuliferous organs of *Autunia* type are also associated with callipteroid foliage. Naugolnykh and Kerp (1996) assumed that *P. retensorium* Naug. may represent a transitional form between ovuliferous organs of *Autunia* and *Peltaspermum* types. Recently, older peltoids of *Peltaspermum* type were found in the Upper Carboniferous and Lower Permian deposits of China, Cis-Ural, Germany, and Morocco (Liu and Yao, 2000; Kerp et al., 2001; Naugolnykh, 2001b). Evidently, typical peltoids of *Peltaspermum* type were rather widespread in the Northern hemisphere as early as the Early Permian. Naugolnykh believes that peltoids of *Peltaspermum* and bilaterally symmetrical organs were two independent lineages, which evolved independently. In this relation, he proposes to exclude taxa with bilaterally symmetrical ovuliferous organs from the Peltaspermaceae (Naugolnykh, 2005, 2007). Such a proposition agrees with a find in the South Africa of bilaterally symmetrical cladosperms of *Hamshawvia*, which are very similar to *Stiphorus*; they were found in organic connection with leaves of *Sphenobaiera* type and are included in the Ginkgoopsida (Anderson and Anderson, 2003). However, bilateral peltoids of the new genus with their branched vascular strands might have been a link between non-peltate bilaterally symmetrical organs and peltate radially symmetrical organs of the Peltaspermaceae.

Only detached ovuliferous organs of *Navipelta resinifera* gen. et sp. nov. were found. A smooth area is present in the place of stalk attachment in nearly all peltoids, which may point on the presence of an abscission layer. Retallack and Dilcher (1988) supposed that ovuliferous organs of *Autunia* (P.) *thomasii* might have an abscission layer and spread by water flows. Following the authors, I believe that ovuliferous organs of a new genus might spread in similar matter. Probably, boat-shaped form of the peltoids is adopted to the dispersal. Rhomboidal and elliptical outlines of peltoids, which are obtuse on one end and pointed on the other, supposedly also might be related to their close spacing on the strobilus axis.

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