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Formal System of Dispersed Leaf Cuticles of Pteridosperms (Peltaspermaceae) from the Permian and Triassic of the Russian Platform

E. V. Karasev

Borissiak Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya, 123, Moscow, 117997 Russia
e-mail: karasev@paleo.ru

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Abstract—A formal system of dispersed leaf cuticles of peltaspermaceous pteridosperms is proposed. It is based on the epidermal groups established on the basis of correlation between epidermal features and leaf morphology of peltasperms.

Keywords: dispersed cuticles, gymnosperms, Permian, Triassic, Russian Platform
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INTRODUCTION

Plant mesofossils, in particular, dispersed leaf cuticles supplement information about the taxonomic composition of paleofloras and taxonomic diversity of extinct plant communities. In some cases, plant mesofossils are almost the only source of paleobotanic information. In the presence of macroremains, dispersed cuticles of plants can be additionally used for determination of features of paleoenvironments (Kurschner, 1996; McElwain and Chaloner, 1996; Retallack, 2001). Systematically ordered dispersed cuticles can bear diagnostic function in the case of finding leaves similar in epidermal structure. In addition, they can be used for comparison with similar dispersed cuticles from other localities. In the long run, dispersed leaf cuticles can be used for comparison of paleofloristic assemblages from various localities.

The data on dispersed leaf cuticles are presented in many works (Meyen, 1965; Krassilov, 1968; Roselt and Schneider, 1969; Oldham, 1976; Kovach and Dilcher, 1984; Kerp and Barthel, 1993; Upchurch, 1995; Gomankov, 1997; Tewari and Agarwal, 2001; Pole, 2007, etc.).

To date, several formal classifications have been proposed for dispersed cuticles. The best known are the system by Meyen (1965) for dispersed cuticles of the gymnosperms and the system by Roselt and Schneider (1969) mostly for dispersed cuticles of angiosperms. The latter was improved by Kovach and Dilcher (1984). The Meyen`s system is based on a limited number of epidermal characters and comprises a certain number of formal taxa. The system of Rozelt and Schneider includes high-rank taxa, such as turmas and subturmas. It is based on the division by the type and arrangement of stomata. The division into formal taxa of generic and species ranks is based on congregational principle.

The formal classification developed in the present study differs from differs from Meyen's classification (1965) in the absence of restrictions on the number of genera and, in contrast to the classification of Rozelt and Schneider (1969) it takes into account specific stomatal types characteristic of fossil gymnosperms. This reduces the loss of important information for assignment to higher taxa.

Meyen (1987, 2009) indicated the main distinction between natural and formal taxa. Natural taxa can be distinguished by any characteristic of the whole organism. The choice of characteristics depends on the researcher and available technical equipment. When establishing parataxa, only characters preserved in dispersed parts are used. Thus, the diagnoses of formal taxa should not contain characteristics that are difficult or impossible to diagnose in mesofossils. Suitable characteristics include features of the epidermal structure in marginal and midvein zones, petioles, etc.

In the present study, I propose a formal system for dispersed cuticles of peltaspermaceous pteridosperms based on extensive material from the Permian–Triassic deposits of the Nedubrovo and Vyazniki localities. The system reflects stable epidermal types in this gymnosperm group; it inherits the principle of division into turmas (depending on a stomatal arrangement on the leaf cuticle) from the formal system of Rozelt and Schneider (1969).

The following requirements are imposed on the system of dispersed cuticles of peltaspermaceous leaves: (1) the system should be suitable for comparison of dispersed cuticles from different localities; (2) whenever possible, the system should be tightly

connected with leaf morphology, promoting reconstruction of the morphology of initial objects (leaves) and specification of taxonomic diversity.

MATERIALS AND METHODS

The collection of dispersed cuticles consists of leaf phytoleim fragments of peltasperms and conifers from the Vyazniki, Vyazovka (Late Permian), and Nedubrovo (Permian–Triassic) localities (Lozovskii et al., 2001; Krassilov and Karasev, 2009; Benton et al., 2010). The material was collected by researchers of the Laboratory of Paleobotany and the Laboratory of Arthropods of the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN).

Plant fragments were macerated by a standard technique, using Schultz solution without potassium chloride addition and, then, washed in sequence by KOH and distilled water. The cuticle fragments obtained were studied with an AXIOPLAN-2 light microscope and a CAMSCAN (SAM) electron scanning microscope. The material is stored in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow; collection nos. 4180 and no. 5160.

Epidermal features of dispersed cuticles were analyzed with the Delta Key Program (Dallwitz, 1980); biometric studies were made using the Image J Program (Sheffield, 2007).

TERMINOLOGY

In the present paper, dispersed leaf cuticles mean fragments of leaf phytoleims retaining epidermal features, but without distinct morphological characteristics suitable for the determination of known taxa or description of a new one.

The epidermal structure of dispersed cuticles is described using the standard terminology (Stace, 1965; Krassilov, 1968; Dilcher, 1974; Anderson and Anderson, 1989). The peltaspermaceous stomata are described using special terms proposed by Gomankov and Meyen (1986). The structure located around the stomatal aperture on the outer side is termed the Florin ring, which is defined by Anderson and Anderson (1989) as a raised ring-shaped structure formed by papillate periclinal walls of subsidiary cells.

Some terms demand additional explanation. The stomatal outline formed by tangential (distal) walls of subsidiary cells is considered regular if none of subsidiary cells protrudes for more than half length relative to the other subsidiary cells. The stomatal outline is considered irregular if at least one subsidiary cell protrudes for more than half length from the contour formed by other subsidiary cells. The orientation of stomatal apertures is described relative to costal and intercostal zones or to the leaf margin, if differentiation into zones is absent.

FOUNDATION AND PRINCIPLES OF FORMAL CLASSIFICATION

Upchurch (1989) suggested to subdivide all dispersed cuticles into three types: (1) cuticle fragments of abaxial epidermis characterized by a large number of diagnostic features important for classification; (2) cuticle fragments of adaxial epidermis usually showing fewer systematically important features (stomata are few or absent); and (3) cuticle fragments of stems, petioles, and rachises. Rows of longitudinally elongated ordinary cells are characteristic of such fragments (stomata are few or absent).

The division of cuticles into these categories and priority use of dispersed cuticles of the first type resolve two problems which are inevitably raised in the course of classification: (1) If cuticles of the upper and lower leaf sides are found separately, these cuticles can be classified to different formal groups, especially of hypostomatal leaves (or leaves with different structure of adaxial and abaxial parts); (2) the problem of different structure of epidermis, depending on leaf parts.

Cuticles of the second and third types can be used for identification of characteristic epidermal features and diagnostics of morphotaxa. They also can be assigned to formal taxa, comparing with cuticles of the first type.

The newly established turma Peltarimatae unites all dispersed leaf cuticles of peltaspermaceous pteridosperms. The identification of dispersed cuticles of peltasperms requires a set of characters that distinguishes them from other plant groups. The diagnosis of Peltaspermaceae provided by Gomankov and Meyen (1986) lacks epidermal characteristics. It is evident that, among the entire set of cuticular epidermal features, it is impossible to recognize a unique marker character that would provide reliable attribution of dispersed leaf fragments to peltaspermaceous pteridosperms. However, this also concerns morphological leaf features. Note that the epidermis of peltasperms is rather distinctive, but largely uniform.

The family Peltaspermaceae includes about 30 genera based on leaves and shoots. Almost two-thirds of them are not characterized by epidermal characters; these taxa were mostly established from leaf imprints (Thomas, 1933; Townrow, 1960; Gomankov and Meyen, 1986; Taylor et al. 2006; *Mesozoic Seed Ferns* ..., 2009). The characteristics of ten genera contain epidermal features. Epidermal features which are useful for generic identification of dispersed cuticles of peltasperms are shown in Table 1.

If the necessary epidermal features on dispersed cuticles are available, it is possible to determine with sufficient confidence three genera of peltaspermaceous leaves: *Tatarina* Meyen, *Vjaznikopteris* Naugolnykh, and *Autunia* Krasser.

The genus *Tatarina* is distinguishable, if a large cuticle fragment with a zone of longitudinally elongated ordinary cells above the midvein is present. The

Table 1. Epidermal characters used in diagnoses and descriptions of genera of the family Peltaspermaceae

Genus	Leaf type	Stomatal distribution	Orientation of stomatal apertures	Stomatal type	Number of subsidiary cells	Guard cells
	amphistomatal (A), amphihypostomatal (AH), hypostomatal (H)	irregular (I), in rows (R), in bands (B), in groups (G)	random (R)	monocyclic, dicyclic	maximum–minimum (mode)	sunken (S), not sunken
Callipteris (subgenus *Feonia*)	A	I	I	M, D	4–7(6)	S
Permophyllocladus	A	I	I	M, D	4–7(6)	S
Lepidopteris	A	I, R	I	M, D	4–7(5, 6)	S
Scytophyllum	A, AH	I	I	M, D	4–7(5, 6)	S
Tatarina	A	I, R, B	I	M, D	3–7(4, 5)	S
Vjaznikopteris	A	I, **H**	I	M, D	4–6	S
Kirjamkenia	A	I	I	M, D	4–7	S
Compsopteris	A	I, B	I	M, D	–	S
Autunia	AH, **H**	?	I	M, D	–	**N**

* In relation with costal and intercostal zones.

genus *Vjaznikopteris* is distinguished by large guard cells with a butterfly-like type of cutinization and by a characteristic group accumulation of stomata. The genus *Autunia* is distinguishable if it is possible to determine the submergence of guard cells and if both lower and upper cuticles are preserved.

In other cases, epidermal features of dispersed cuticles in diagnoses and descriptions of genera are unsuitable for the identification of peltasperm genera.

The analysis of available data has revealed characteristic features allowing confident determination of dispersed cuticles of peltasperms, which are used for the diagnosis of the new turma Peltarimatae. Leaves of other families (Angaropeltaceae, Umkomasiaceae, Trichopityaceae) of Peltaspermales have a different stomatal structure, distinguishing their dispersed cuticles from peltasperms.

There are several debatable genera established based on leaves, which are included in Peltaspermales without indication of the family. For example, the genus *Glenopteris* Sellards is attributed to Peltaspermales based on leaf morphology. Its epidermal structure was described in detail by Krings et al. (2005). The structure of stomata and outline of ordinary cells of *Glenopteris* considerably differs from a typical epidermal structure of peltasperms.

Some representatives of Ginkgoales sensu lato are similar in epidermal structure to peltasperms (Meyen, 1983; Naugolnykh, 2007). In particular, the family Matatiellaceae was transferred from Ginkgoales to Peltaspermales based among other things on the epidermal structure (Bomfleur et al., 2011). The main target of the present work is to examination of the epidermal structure of peltasperms. In the future, it is necessary to compare the epidermal leaf structure of representatives of Ginkgoales and Peltaspermales. At the moment, possible belonging of particular dispersed cuticles to Ginkgoales is offered to indicate in remarks accompanying the description.

The turma Peltarimatae is divided into subturmas based on correlation of the epidermal structure and leaf morphology. Key features for this division are the stomatal arrangement and differentiation of ordinary cells into cells of stomatal and nonstomatal zones.

As a result, the following three subturmas are established: Dispeltarae with irregularly arranged stomata, Verspeltarae with the stomata arranged in rows, and Taenpeltarae with the stomata arranged in bands.

Formal lower-rank taxa are recognized based on the epidermal structure and unification of natural taxa of peltasperms on the generic and species level indistinguishable without the use of morphological features. Table 2 shows the equivalence of natural taxa to the formal taxa established here.

The epidermal characteristics of peltaspermaceous species considered in the literature are listed in Fig. 1. Comparisons of taxa with a large number of features by means of the IntKey Program allowed the recognition of the epidermal types indistinguishable in dispersed cuticles. As the taxonomic significance of epidermal features of leaves with known morphology was revealed, they were ranked. As a result, features of generic and species levels were recognized and used in the formal system.

Examples of features on the generic level are the orientation of stomatal apertures, outline and orientation of ordinary cells, prevalence of stomata with regular or irregular outlines, stomatal recurrence, and cutinization and extent of submergence of guard cells.

Examples of features on species level are the extent of sinuosity of anticlinal walls, prevailing number of subsidiary cells, cutinization of periclinal subsidiary cells in relation to that of ordinary cells, raising of the Florin ring, and the size and intensity of papillae on the periclinal walls of subsidiary cells.

As a new formal taxon is described, the epidermal types rather than isolated dispersed cuticles should be considered to prevent taxonomic inflation. In addition, it is necessary to estimate carefully the taxonomic value of distinctive characters of new formal taxa. The recognition of the epidermal types based on samples of identical dispersed cuticles provides correct identification of stomatal arrangement. If the size of dispersed cuticles is small, so that it is impossible to reveal the stomatal arrangement, they should be assigned to the turma with irregularly arranged stomata. The stomatal arrangement on one side of the leaf is frequently regular, while on the other, it is irregular. In this case, dispersed cuticles are suggested to be attributed to the subturma with the regularly arranged stomata.

SYSTEMATIC PALEOBOTANY

TURMA *PELTARIMATAE* KARASEV, TURMA NOV.

Diagnosis. Stomata actinocytic, monocyclic, incompletely dicyclic or tricyclic, with four to seven polygonal or trapezoidal subsidiary cells. Subsidiary cells not sunken. Periclinal walls of subsidiary cells with proximal, distal, or medial papillae or smooth. Cutinization of anticlinal walls of subsidiary cells proximal, starlike, distal, rotate, or similar to that of epidermal cells. Contour formed by tangential walls of subsidiary cells varying from irregular to rounded and convex. Guard cells narrow beanlike or butterfly-like, sunken, with polar appendages or without them.

SUBTURMA *DISPELTARAE* KARASEV, SUBTURMA NOV.

Etymology. From the Latin *disperse* (scattered) and the family Peltaspermaceae.

Diagnosis. Stomata scattered.

Generic composition. *Aequapeltacutis* gen. nov., *Enormipeltacutis* gen. nov., *Tatarinopsis* Gomankov, 1997.

Comparison and remarks. The irregular arrangement of stomata occurs in the majority of peltaspermaceous genera (Table 2). For example, for the leaves of *Lepidopteris* Shimper and *Scytophyllum* Bornemann, only scattered stomata have been described. Specimens with scattered stomata are known in each species of *Tatarina* and *Kirjamkenia* Prynada. Stomata of *T. lobata* Meyen and *T. rinatata* Karasev are scattered on both lower and upper leaf sides. Other species of the genus *Tatarina* usually have irregularly arranged stomata on the side with a conspicuous axial zone. *Compsopteris* Zalessky and *Callipteris* (subgenus *Feonia*) Meyen et Megdissova have scattered stomata in stomatal bands only. The subturma Dispeltarae is subdivided into three formal genera (*Aequapeltacutis* gen. nov., *Enormipeltacutis* gen. nov., and *Tatarinopsis* Gomankov, 1997) based on the outlines of ordinary cells and stomata and extent of development of the costal zones. The genus *Tatarinopsis* was described based on dispersed cuticles from the Kazanian deposits of the Shikhovo-Chirki locality. The genus included two species, *T. superior* Gomankov and *T. inferior* Gomankov. Gomankov (1997) attributed the genus *Tatarinopsis* to the subturma Disanomorae (turma Anomorimatae) of the classification of Rozelt and Schneider (1969). This genus is transferred to the subturma Dispeltarae of the turma Peltarimatae because the epidermal structure of *Tatarinopsis* is undoubtedly similar to that of peltasperms, which was noted even in the original description of the genus (Gomankov, 1997). *Tatarinopsis* is distinguished from *Enormipeltacutis* gen. nov. and *Aequapeltacutis* gen. nov. by the slitlike front cavities.

Genus *Aequapeltacutis* Karasev, gen. nov.

Etymology. From the Latin *aequus*, the family Peltaspermaceae, and the Latin *cutis* (cuticle).

Type species. *Aequapeltacutis rectus* sp. nov.

Diagnosis. Differentiation of epidermal cells of stomatal and nonstomatal zones absent. Epidermal cells isogonal and isodiametrical. Anticlinal walls straight.

Species composition. Type species.

Comparison and remarks. The epidermal structure similar to that of *Aequapeltacutis* gen. nov. usually occurs in small leaves with indistinct venation and, rarely, in large linguiform leaves (Table 2). *Aequapeltacutis* gen. nov. differs from the most similar genus *Enormipeltacutis* gen. nov. in the isogonal and

Table 2. Distribution of diagnostic characters and natural taxa in the formal system proposed for dispersed cuticles

Turma	Peltarimatae					
Subturma	Dispeltarae			Verspeltarae		Taenpeltarae
Genus	*Aequapeltacutis*	*Enormipeltacutis*		*Interpeltacutis*	*Ordopeltacutis*	*Segmenpeltacutis*
Species	*A. rectus*	*E. communis*	*E. nervus*	*I. conformis*	*O. vulgaris*	
Stomatal distribution	irregular			in rows		in bands
Costal and intercostal zones	indistinct	indistinct	distinct	indistinct	distinct	distinct
Outlines of ordinary cells	isogonal	polygonal	polygonal	isogonal	polygonal	polygonal
Anticlinal walls	straight	curved	curved	straight	curved	curved
Stomatal contour	regular	irregular	irregular	regular	irregular	irregular
Orientation of aperture	random	one direction prevail			random	
Natural taxa	Lepidopteris	Lepidopteris	Lepidopteris	Tatarina	Tatarina	Tatarina
	L. martinsii	*L. heterolateralis*	*L. microcellularis*	*T. conspicua*	*T. sadovnikovii*	*T. olferievii*
	L. archaica	Scytophyllum	*L. africana*		*T. conspicua*	*Tatarina meyenii* [D]
	L. haizeri	*S. bashkiricum*	Scytophyllum		*T. olferievii*	*Tatarina conspicua*
	L. evidens	*S. nerviconfluens*	*S. neuburgianum*		*T. mira*	Kirjamkenia
	L. callipteroides	*S. karevae*	*S. vulgare*			*K. lobata*
	L. remota	*S. papillosum*		*Callipteris?* (Feonia)	Kirjamkenia	Ustyugia
	Permophyllocladus	Kirjamkenia	Kirjamkenia	*Callipteris?* (Feonia) sp1	*K. orenburgense*	*U. pinnata*
	P. polymorphus	*K. chalyshevii*	*K. chalyshevii*			Callipteris (Feonia)
	Scytophyllum	*K. prynadae*	*K. prynadae*		Ustyugia	*C.* (F.) *lepidopteroides*
	S. apoldense	*K. lobata*	*K. lobata*		*U. pinnata*	*C.* (F.) *aequbilis*
	Kirjamkenia	Tatarina	Tatarina			*C.* (F.) *sadovnikovii*
	K. synensis	*T. lobata*	*T. mira* [U]			Compsopteris
		T. olferievii	*T. rinatata*			*C. adzvensis*
		T. conspicua				
		Rhaphidopteris	*Callipteris?* (Feonia)			
		R. antiqua	*C?* (F.) *aequbilis*			
		R. kiuntzeliae				

Note: Key in square brackets after specific name: (U) upper and (D) lower cuticles.

Data chart of epidermal characters of leaves of peltaspermaceous pteridosperms

Taxon\Epidermal character	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	Reference
Callipteris? (Feonia) aequbilis	1	1		2	1/2	1/2	3	2			2	1/2	1	2	4	1	1/2	2	2	2	3	2		1		1	Meyen and Migdisova, 1969
Callipteris? (Feonia) lepidopteroides	1	2	1	1	2	3/4		2	1	2	2	1/2	1	2	5	1	1/2/3	2	2	2	3	1	1	1			Meyen and Migdisova, 1969
Callipteris? (Feonia) sadovnikovii	1	2		2	2	1/4		2	1	2	2	1/2	1	2	4	1	1/2	1/4	2	3	3	2		1			Meyen and Migdisova, 1969
Compsopteris adzvensis	1			1	2	3/4	3	2	1	2		1/2	1	2		1	1	2/4	1/2	1							Zalessky, 1934; Meyen and Migdisova, 1969
Kirjamkenia (Maria) chalyshevii	1	2	2	1	1			2	1	1/3	2	1/3	1	2	5	1	1	1	1	1			2	2			Dobruskina, 1980; Sadovnikov, 1983
Kirjamkenia (Maria) prynadae	1	2	2	1	1			2	1	2	2	2/3	1	2	5	1	1	2	1	2	3	2	1	1			Dobruskina, 1980; Sadovnikov, 1983
Kirjamkenia (Maria) synensis	1		2	1	1			1	1	1/2	1/2	1/2	1			1	1	2	1/2	2	3		1	1			Dobruskina, 1980; Sadovnikov, 1983
Kirjamkenia lobata	1	1			2	1/3	3	2	1	2	2	1/2	1	2	5	1	1	2	1								Sadovnikov, 1983
Lepidopteris africana	1	2	2	2	1			2	1	2	1/2	1/2/3	1	2	4	1	1	1/2	1/3	2	3	3	2				Anderson and Anderson, 1989
Lepidopteris callipteroides	1		1		1			2			2								2	2							Retallack, 2002
Lepidopteris evidense	1	1		1	1		3	1	2	1	2	1	1			1	1	2	1	2	3			1			Kirichkova and Khramova, 1980
Lepidopteris haizeri	2	1	2	1	1		3	1	1	1	2	1	1			1	1	1/2	1	2	3	1/2	1	1			Dobruskina, 1980
Lepidopteris heterolateralis	2	2	2	1	1		3	1	1	1/2	2	1/2/3	1			1	1	1/2	1	2	3	3	1	1			Dobruskina, 1980
Lepidopteris martinsii	1	1	2	1	1		3	1	2	1	1/2	1	1			1	1	2	2	2	3	1/2	1	1	1	2	Townrow, 1960; Poort and Kerp, 1990
Lepidopteris microcellularis	1	2	2	1	1			2	1	1	2	1/2	1	2	4	1	1	2	1	2	3		1	1			Dobruskina, 1980
Lepidopteris ottonis	1	1	1	1	1			1	1	1	1/2/5	1/2/3	1			1	1	2	1/3	2	3	1	1	1	1		Kirichkova, 2006
Lepidopteris remota	1	2	2	2	1			1	1	2	1	1	1			1	1	1/2/4	1	2	3			1			Dobruskina, 1980
Lepidopteris stormbergensis	2	2	2	2	1			2	1	2	2/5	2/3	1	2	4/5	1	1	1	1	2/3	3	1	2	1			Anderson and Anderson, 1989
Permophyllocladus polymorphus	1	1	2	1	1		3	1	2	1	2	1	1			1/2	1	1/2	1	2	3	1/2	1	1	1	2	Karasev and Krassilov, 2007
Rhaphidopteris antiqua	1	1	1	1	1			1	1	2	1/2/4	2	1			1	1	3	1/2								Gomankov and Meyen, 1986
Rhaphidopteris kiuntzeliae	1	1	1	2	1			1	1	2	1/2	1/2	2			1/3	1	3	1/2	3	3	2	2				Gomankov and Meyen, 1986
Scytophyllum abramovii	3			1	1			1	1	4	2	1	1			1	1	2	3	2	3	1	2	1			Dobruskina, 1969
Scytophyllum apoldense	1	1	2	2	1			1	1	2	1	1	1			1	1/2	2/4	3	1				1/2			Dobruskina, 1969
Scytophyllum bashkiricum	1		2	1	1			2			2	3							1/3	2							Dobruskina, 1969
Scytophyllum nerviconfluens	1	1	1	2	1			1	1	2	2	1/2	1			1	1/2	2/4	1	2				1			Dobruskina, 1969
Scytophyllum neuburgianum	1	1	2		1			2	1		1	1/3	1			1	1/2	2	1	2	3	2	1	1			Dobruskina, 1969
Scytophyllum papillosum	1		2		1		3	1	1	2	2	1/3	1			1	1	2/4	1/3	2	3	1		1			Dobruskina, 1969
Scytophyllum vulgare	3	2		2	1		3	2	1	2	1/2	2	1	2		1	1	1	1	2	3	2		1			Kirichkova and Khramova, 1980; Krassilov, 1995
Tatarina conspicua	1	2	2	1	1/2	1/2		2	1	1/2	2/5	1/2	1	2	3	1	1	2	1/2	2/3	3		2	1	2	1	Gomankov and Meyen, 1979, 1986
Tatarina lobata	1	2	1	1	1		3	1/2	1	2	2	1/2/3	1		1	1	1/2	3	2	2	3	3	2	1	2		Gomankov and Meyen, 1986
Tatarina meyenii	1	2	2	1	2	2		2	1	2	2	1/2	1	2/3	5	1	1/3	2	2	2	3	2		1			Naugolnykh, 2006
Tatarina mira	1	2	1	1	2	3		2	1	1/2	2	1/2	1	2	4	1	1	2		2	3		2	1	2	1	Gomankov and Meyen, 1986
Tatarina olferievii	1	2	2	1	1/2	1/4		2	1	2	1/2	1/2	1	2	4	1	1/3	2/3/4	1/2	2	1	2	2	1	2	1	Gomankov and Meyen, 1986
Tatarina rinatata	1	2	2	1	1			1/2	1	3	2/3/6	1/2	1	2	1	1	1	2		2/3	3	3	1	1	2	1	Karasev, 2007
Tatarina sadovnikovii	1	2		2	1/2	1		2	1	3	2	1/2/3	1	2			1/2	1		2	3						Meyen and Gomankov, 1980
Ustyugia pinnata	1	2	1	1	1/2	3		2	1	2	2	1/2	1	1/2	4	1	1	2	1/2	2	3		2	1	2	1	Gomankov, 2008
Vjaznikopteris rigida	1	1	2	1	1		3	1	1	1/2	1/2	1/2	1			1	3	1	1/3	1/2	3	2	2	1	3	2	Naugolnykh, 2006

isometric ordinary cells with straight anticlinal walls and in the regular outline of stomata. It differs from the genus *Tatarinopsis* in the isometric or irregular outline of the front cavity.

***Aequapeltacutis rectus* Karasev, sp. nov.**

Plate 13, figs. 1–5

Etymology. From the Latin *rectus* (straight).

Holotype. PIN, no. 4820/792, dispersed leaf cuticle; Vologda Region, left bank of the Kichmenga River, near the town of Nedubrovo, Nedubrovo locality; Upper Permian–Lower Triassic, Vetlugian Group, Vokhmian Horizon, Nedubrovo Member (Pl. 13, figs. 1–5).

Diagnosis. Subsidiary cells are cutinized proximally or star-shaped. Periclinal walls with proximal papilla. Periclinal walls of subsidiary cells equally or less cutinized than those of ordinary epidermal cells.

Description. The stomata are arranged irregularly (Pl. 13, fig. 1). Ordinary cells are not differentiated into costal and intercostal cells. The aperture of stomata are irregularly oriented. Ordinary cells are penta- to octagonal (Pl. 13, fig. 2). Anticlinal walls are thick, straight or slightly curved. Each periclinal wall has a large median papilla (Pl. 13, fig. 3). Stomata are monocyclic or actinocytic (Pl. 13, fig. 4). There are four to seven subsidiary cells. Cutinization of periclinal walls is similar to that of ordinary cells (Pl. 13, fig. 5). The star-shaped type of cutinization sometimes occurs. Periclinal papillae of subsidiary cells are smaller in diameter, but higher than in ordinary cells (Pl. 13, fig. 3). The contour of distal walls of subsidiary cells is regular, rounded or polygonal.

Material. Four cuticle fragments of shoots from the type locality.

Genus *Enormipeltacutis* Karasev, gen. nov.

Etymology. From the Latin *enormis*, Peltaspermaceae family and the Latin *cutis* (cuticle).

Type species. *Enormipeltacutis communis* sp. nov.

Diagnosis. Ordinary epidermal cells polygonal, irregularly orientated. Anticlinal walls curved or sinuous.

Species composition. *E. communis* sp. nov. and *E. nervus* sp. nov.

Comparison and remarks. Dispersed cuticles of a large number of taxa with an irregular arrangement of stomata and irregular polygonal cells (Table 2) can be attributed to this genus. It differs from *Aequapeltacutis* gen. nov. in the polygonal ordinary cells, the curved or sinuous anticlinal walls of ordinary cells, and the irregular outlines of stomata. The new genus differs from *Tatarinopsis* in the isometric or irregular outline of the front cavity.

***Enormipeltacutis communis* Karasev, sp. nov.**

Plate 13, figs. 6–9

Etymology. From the Latin *communis* (ordinary).

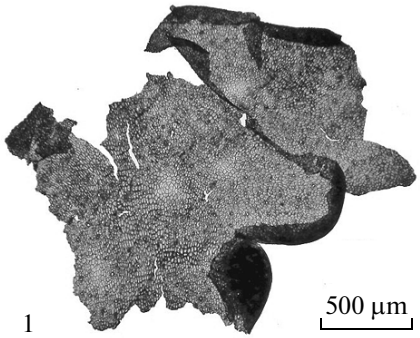
Holotype. PIN, no. 5160/160, dispersed leaf cuticle; Vladimir Region, Vyaznikovskii District, right bank of the Klyaz`ma River, gully between the town of Vyazniki and Bykovskii quarry, Sokovka locality, Upper Permian, Tatarian, Vyatkian Stage (Pl. 13, figs. 6–8).

Diagnosis. Differentiation of ordinary cells of costal and intercostal zones absent. Anticlinal walls curved. Apertures irregularly oriented. Stomata outline regular or irregular.

Description. The stomata are irregularly arranged (Pl. 13, fig. 6). Stomatal apertures are oriented in two or one prevailing direction. Differentiation of ordinary cells in the costal and intercostal zones is absent. Ordinary cells are polygonal, variously

Fig. 1. Letters (columns) and figures (lines) designate (a) type of leaves: (1) amphistomatal, (2) almost hypostomatal, (3) hypostomatal; (b) topography of epidermis of the upper and lower leaf sides: (1) similar, (2) different; (c) density of stomata on the leaf: (1) similar, (2) different; (d) cutinization of leaf sides: (1) equal, (2) different; (e) stomatal arrangement: (1) irregular, (2) regular; (f) regular stomata are distributed (1) in straight rows, (2) irregular bands, (3) irregular rows, (4) in straight bands; (g) aperture orientation: (1) longitudinal, (2) transversally random, (3) random, (4) transverse, (5) longitudinally random; (h) differentiation of ordinary cells in costal and intercostal zones: (1) absent, (2) present; (i) outline of ordinary cells of intercostal zones (unspecialized): (1) polygonal, (2) isogonal, (3) amorphous; (j) orientation of ordinary cells: (1) isodiametrical, (2) random, (3) transversely extended, (4) longitudinally extended; (k) periclinal walls of ordinary cells: (1)smooth, (2) papillate, (3) swollen, (4) wavy, (5) with trichomes, (6) with hairs; (l) anticlinal walls: (1) sinuous, (2) straight, (3) curved; (m) cuticular spikes at the nodes of cell walls: (1) absent, (2) present; (n) ordinary cells of costal zones: (1) similar to cells of intercostal zones, (2) longitudinally extended, (3) transversely extended; (o) width of costal zones: (1) without rows, (2) 1–2 cell rows, (3) more than 4 cell rows, (4) 2–3 cell rows, (5) 3–4 cell rows; (p) stomata: (1) actinocytic, (2) encyclocytic, (3) brachyparacytic; (q) number of cycles of subsidiary cells: (1) monocyclic, (2) almost dicyclic, (3) amphicyclic); (r) cutinization of subsidiary cells: (1) similar to ordinary cells, (2) starlike, (3) distal, (4) labelloid, (5) rotate; (s) cutinization of periclinal walls: (1) similar to ordinary cells, (2) stronger than in ordinary cells, (3) weaker than in ordinary cells); (t) periclinal walls: (1) smooth, (2) with proximal papillae, (3) with median papillae, (4) with distal papillae; (u) periclinal papillae positioned (1) on a half of subsidiary cells, (2) on each subsidiary cell, (3) on some subsidiary cells; (v) size of periclinal papillae in comparison with ordinary papillae: (1) smaller, (2) larger, (3) similar; (w) Florin ring: (1) raised, (2) nonraised; (x) guard cell type: (1) sunken, (2) not sunken; (y) cutinization type of guard cells: (1) narrow, (2) bean-shaped, (3) butterfly-shaped, (4) hourglass-like; (z) guard cell polar appendages: (1) present, (2) absent.

Plate 13



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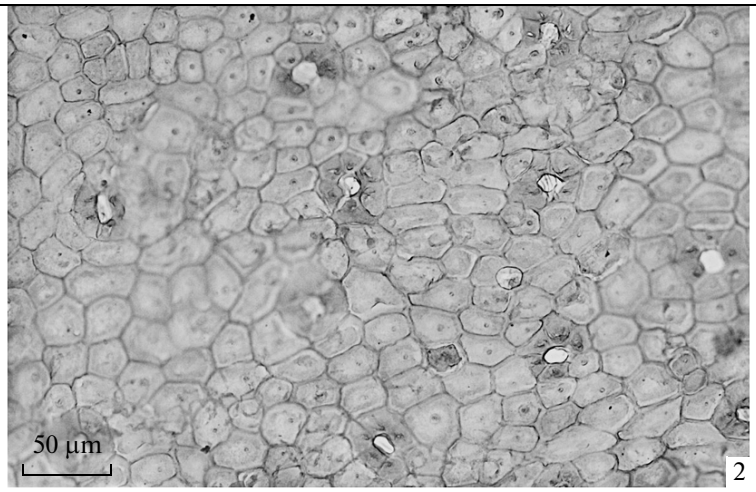

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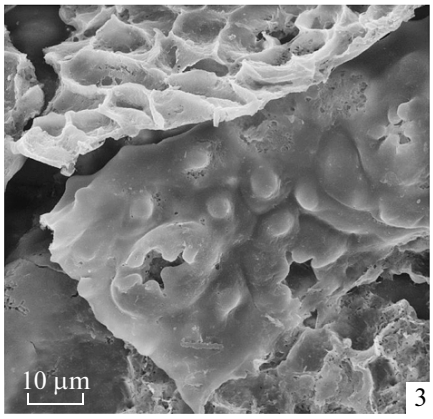

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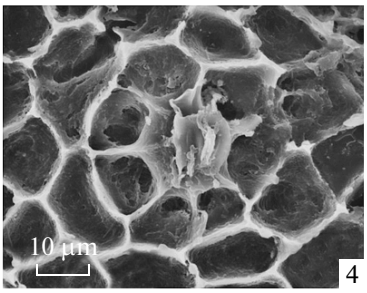

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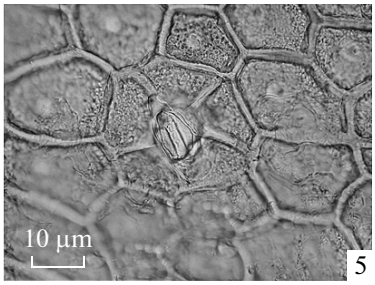

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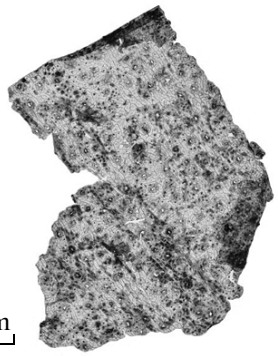

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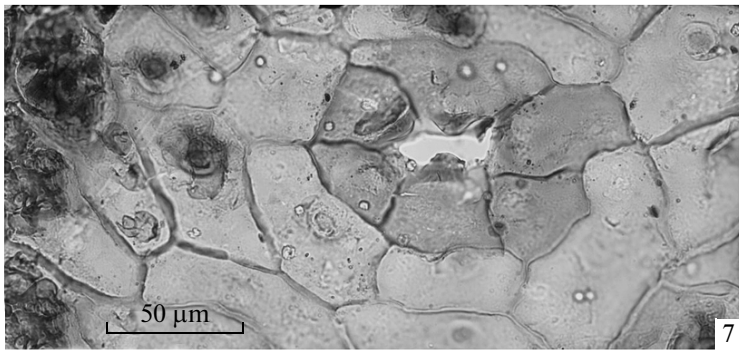

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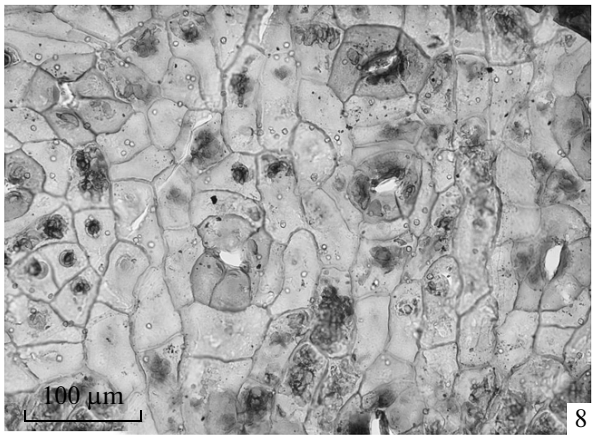

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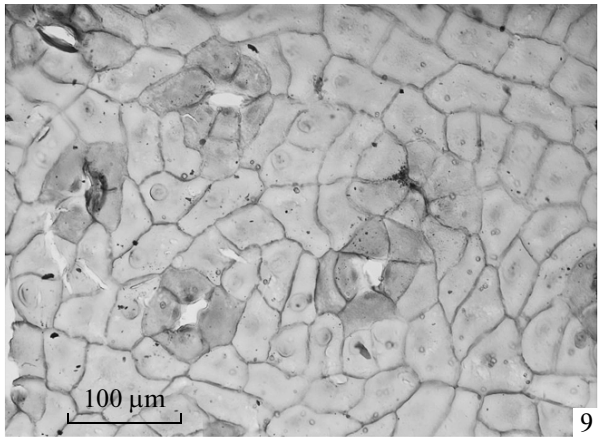


9

oriented (Pl. 13, figs. 8, 9). Periclinal walls of ordinary cells have papillae; the anticlinal walls are straight, curved or sinuous. The stomata are actinocytic, monocyclic or almost dicyclic. Periclinal walls of subsidiary cells have proximal papillae (Pl. 13, fig. 7). Cutinization of periclinal walls of subsidiary cells is stronger than that of ordinary cells. Guard cells are sunken.

Comparison. The new species differs from *E. nervus* sp. nov. in the absence of differentiation of ordinary cells in the costal and intercostal zones.

Material. Six dispersed leaf cuticles.

***Enormipeltacutis nervus* Karasev, sp. nov.**

Plate 14, figs. 1–4

Etymology. From the Latin *nervus* (vein).

Holotype. PIN, no. 5160/143, dispersed leaf cuticle; Vladimir Region, Vyaznikovskii District, vicinity of the town of Vyazniki, Balymotikha locality; Tatarian, Vyatkian Stage (Pl. 14, figs. 1–4).

Diagnosis. Differentiation of ordinary cells in costal and intercostal zones present. Ordinary cells of costal zones longitudinally elongated. Anticlinal walls curved. Aperture orientation with predominance of one or two directions. Outline of stomata irregular.

Description. The stomata are irregularly arranged (Pl. 14, fig. 1). Ordinary cells of the costal and intercostal zones are distinctly differentiated. Cells of the intercostal zones are polygonal. The costal zones are present, but poorly pronounced, represented by two rows of extended rectangular polygonal ordinary cells (Pl. 14, fig. 2). Periclinal walls of ordinary cells have median papillae. Anticlinal walls are straight or slightly curved. Papillae on the periclinal walls in costal zones are absent, or less developed than on ordinary cells of intercostal zones (Pl. 14, fig. 3). The stomata are monocyclic or incompletely dicyclic. Subsidiary cells are trapezoid. The number of subsidiary cells varies from four to seven. The contour formed by distal walls of subsidiary cells is polygonal or irregular, about 60 μm in diameter. Cutinization of periclinal walls is slightly stronger than that of ordinary cells (Pl. 14, fig. 4). Subsidiary cells have median or proximal papillae. Anticlinal walls of subsidiary cells are straight, proximally thickened. The Florin ring is nonraised. Guard cells are bean-shaped or large wing-shaped.

Material. Six dispersed leaf cuticles.

SUBTURMA VERSPELTARAE KARASEV, SUBTURMA NOV.

Etymology. From the Latin *versus* (row, line) and the family Peltaspermaceae.

Diagnosis. Stomata in distinct rows.

Generic composition. *Interpeltacutis* gen. nov. and *Ordopeltacutis* gen. nov.

Remarks. The stomata arranged in rows occur in four genera and eight species of leaves of the Peltaspermaceae (Table 2). The dispersed cuticles can be attributed to *Interpeltacutis* gen. nov. and *Ordopeltacutis* gen. nov. (subturma Verspeltarae) based on the extent of differentiation of ordinary cells in the costal and intercostal.

Genus *Interpeltacutis* Karasev, gen. nov.

Etymology. From the Latin *inter* (between), the family Peltaspermaceae, and the Latin *cutis* (cuticle).

Type species. *Interpeltacutis conformis* sp. nov.

Diagnosis. Stomatal apertures irregularly orientated. Epidermal cells of costal and intercostal zones differentiated to greater or lesser extent. Ordinary epidermal cells polygonal, irregularly orientated; in costal zones, longitudinally elongated. Anticlinal walls straight or curved. Stomata actinocytic and monocyclic; outlines irregular.

Comparison and remarks. Dispersed leaf cuticles of *Tatarina, Kirjamkenia*, and *Ustyugia* (Table 2) can be attributed to this genus. The new genus differs from the similar genus *Ordopeltacutis* gen. nov. in the distinct stomatal and nonstomatal zones and longitudinally elongated ordinary cells in the costal zones.

***Interpeltacutis conformis* Karasev, sp. nov.**

Plate 14, figs. 5–7

Etymology. From the Latin *conformis* (equal).

Holotype. PIN, no.4820/775, dispersed leaf cuticle; Vologda Region, left bank of the Kichmenga River, near the town of Nedubrovo, Nedubrovo locality; Upper Permian–Lower Triassic, Vetlugian Group, Vokhmian Horizon, Nedubrovo Member (Pl. 14, figs. 5–7).

Explanation of Plate 13

Figs. 1–5. Dispersed leaf cuticle of *Aequapeltacutis rectus* gen. et sp. nov., holotype PIN, no. 4820/792: (1) general view; (2) arrangement of stomata and outlines of ordinary cells; (3) external cuticular surface with distinct periclinal papillae and Florin ring; (4, 5) stomatal structure. Nedubrovo locality, Vologda Region, left bank of the Kichmenga River, near the town of Nedubrovo; Upper Permian–Lower Triassic, Vetlugian Group, Vokhmian Horizon, Nedubrovo Member;
Figs. 6–9. Dispersed leaf cuticle of *Enormipeltacutis communis* gen. et sp. nov.: (6–8) holotype PIN, no. 5160/160: (6) general view; (7) stomatal structure, cutinization of subsidiary cells is visible; (8) arrangement of stomata; (9) PIN, no. 5160/164, outlines of ordinary cells. Balymotikha locality, Vladimir Region, Vyaznikovskii District, near the town of Vyazniki; Tatarian, Vyatkian Stage.
(1–2, 5–9) LM, (3, 4) SEM.

Diagnosis. Cutinization of periclinal walls of subsidiary cells stronger than that of ordinary cells.

Description. The stomata are arranged in rows (Pl. 14, fig. 5). Ordinary cells of the costal and intercostal zones are not differentiated. Ordinary cells are polygonal, almost square or rectangular (Pl. 14, fig. 6). Periclinal walls of the majority of ordinary cells have median papillae. Anticlinal walls are straight or slightly curved. The stomata are monocyclic or incompletely dicyclic. Subsidiary cells are trapezoid. There are four or five subsidiary cells. The contour formed by distal walls of subsidiary cells is polygonal or irregular, about 50 μm in diameter. Cutinization of periclinal walls of subsidiary cells is greater than that of ordinary cells (Pl. 14, fig. 7). Subsidiary cells have proximal papillae. Anticlinal walls of subsidiary cells are straight, proximally thickened. The Florin ring is nonraised.

Material. Five dispersed leaf cuticles.

Genus *Ordopeltacutis* Karasev, gen. nov.

Etymology. From the Latin *ordo* (row), the family Peltaspermaceae, and the Latin *cutis* (cuticle).

Type species. *Ordopeltacutis vulgaris* sp. nov.

Diagnosis. Stomata in distinct rows. Stomatal apertures irregularly orientated, with one or two prevailing directions. Epidermal cells of costal and intercostal zones differentiated. Ordinary epidermal cells polygonal, irregularly orientated. Anticlinal walls straight, curved, or sinuous. Epidermal cells in costal zones longitudinally elongated. Stomata actinocytic and monocyclic, or almost dicyclic.

Species composition. Type species.

Remarks. Dispersed cuticles of the adaxial side of leaves of *Tatarina conspicua* and *T.* (*Pursongia*) *meyenii* apparently belong to this genus.

Ordopeltacutis vulgaris Karasev, sp. nov.

Etymology. From the Latin *vulgaris* (common).

Holotype. PIN, no.4820/758, dispersed leaf cuticle; Vologda Region, left bank of the Kichmenga River, near the town of Nedubrovo, Nedubrovo locality; Upper Permian–Lower Triassic, Vetlugian Group, Vokhmian Horizon, Nedubrovo Member (Figs. 2a–2e).

Diagnosis. Width of costal zones ranging from two to four rows of cells.

Description (Figs. 2a–2e). The stomata are arranged in distinct rows (Fig. 2a). Stomatal apertures are irregularly orientated. Ordinary cells are differentiated into costal and intercostal zones (Fig. 2b). The costal zones consist of two or three rows of longitudinally elongated ordinary cells. Periclinal walls of ordinary cells have well-pronounced papillae. Ordinary cells of the intercostal zones are polygonal (often triangular or rectangular). Anticlinal walls are straight, slightly curved, or sinuous. The stomata are actinocytic, monocyclic or incompletely dicyclic. Subsidiary cells are trapezoid, five, rarely, four or six in number. Cutinization of periclinal walls of subsidiary cells is frequently stronger than that of ordinary cells. The periclinal walls have thin radial undulation (Fig. 2c). Proximal papillae are poorly developed, 3–5 μm in diameter at the base and about 3 μm high (Fig. 2d). Cutinization of anticlinal walls is star-shaped. The contour formed by the distal walls of subsidiary cells is rounded, quadrangular, or irregular. The florin rings are nonraised. Guard cells are sunken, narrow bean-shaped, with polar appendages (Fig. 2e).

Material. Nine dispersed leaf cuticles.

SUBTURMA TAENPELTARAE KARASEV, SUBTURMA NOV.

Etymology. From the Latin *taenia* (ribbon) and the family Peltaspermaceae.

Diagnosis. Stomata in distinct bands.

Generic composition. *Segmenpeltacutis* gen. nov.

Remarks. The stomata arranged in bands are characteristic of large leaves of peltaspermaceous pteridosperms. Such leaves are attributed to the following genera: *Callipteris* (subgenus *Feonia*), *Compsopteris*, *Tatarina*, *Ustyugia* Gomankov, and *Kirjamkenia*. The bands vary in distinctness. The most distinct stomatal bands usually occur on the lower leaf side (with a distinct axial zone). Within the bands, the stomata are arranged irregularly or in more or less distinct rows. The majority of species show irregular arrangement of stomata in bands. More or less distinct stomatal rows are known in *Callipteris* (*Feonia*) sp. 1 (Meyen and Migdisova, 1969). Short stomatal chains occur in *Tatarina olferievii*, *Ustyugia pinnata* (Meyen et Gomankov) Gomankov, and *Kirjamkenia lobata*. The formal genus *Segmenpeltacutis* gen. nov. established here comprises dispersed cuticles with irregular

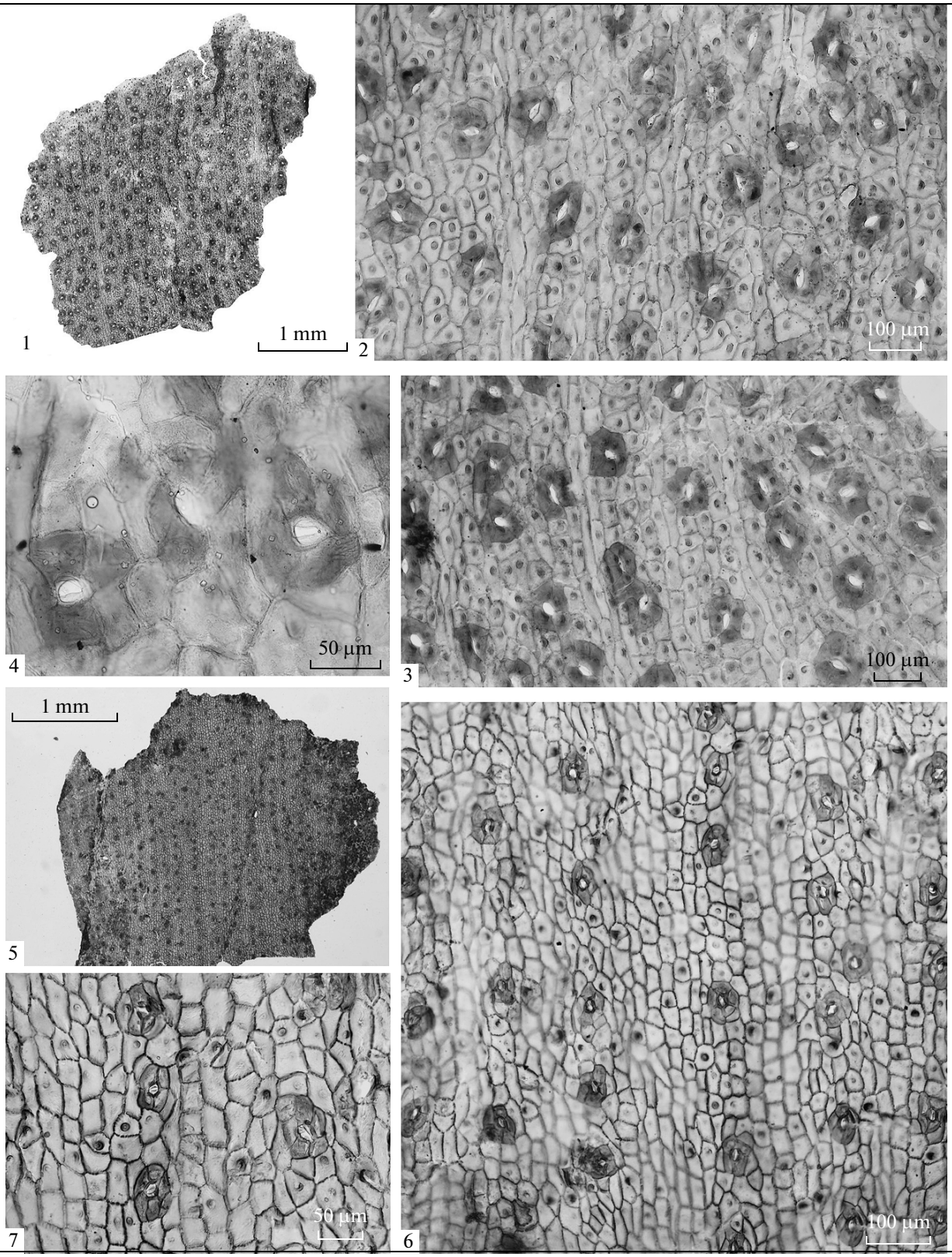
Explanation of Plate 14

Figs. 1–4. Dispersed leaf cuticle of *Enormipeltacutis nervus* gen. et sp. nov., holotype PIN, no. 5160/143: (1) general view; (2, 3) arrangement of stomata and outlines of ordinary cells; papillae are absent on the periclinal walls of ordinary cells in costal zones; (4) stomatal structure; cutinization of subsidiary cells is visible. Balymotikha locality, Vladimir Region, Vyaznikovskii District, near the town of Vyazniki; Tatarian, Vyatkian Stage.

Figs. 5–7. Dispersed leaf cuticle of *Interpeltacutis conformis* gen. et sp. nov., holotype PIN, no. 4820/775; (5) general view; (6) arrangement of stomata; (7) stomatal structure. Nedubrovo locality, Vologda Region, left bank of the Kichmenga River, near the town of Nedubrovo; Upper Permian–Lower Triassic, Vetlugian Group, Vokhmian Horizon, Nedubrovo Member.

(1–7) LM.

Plate 14



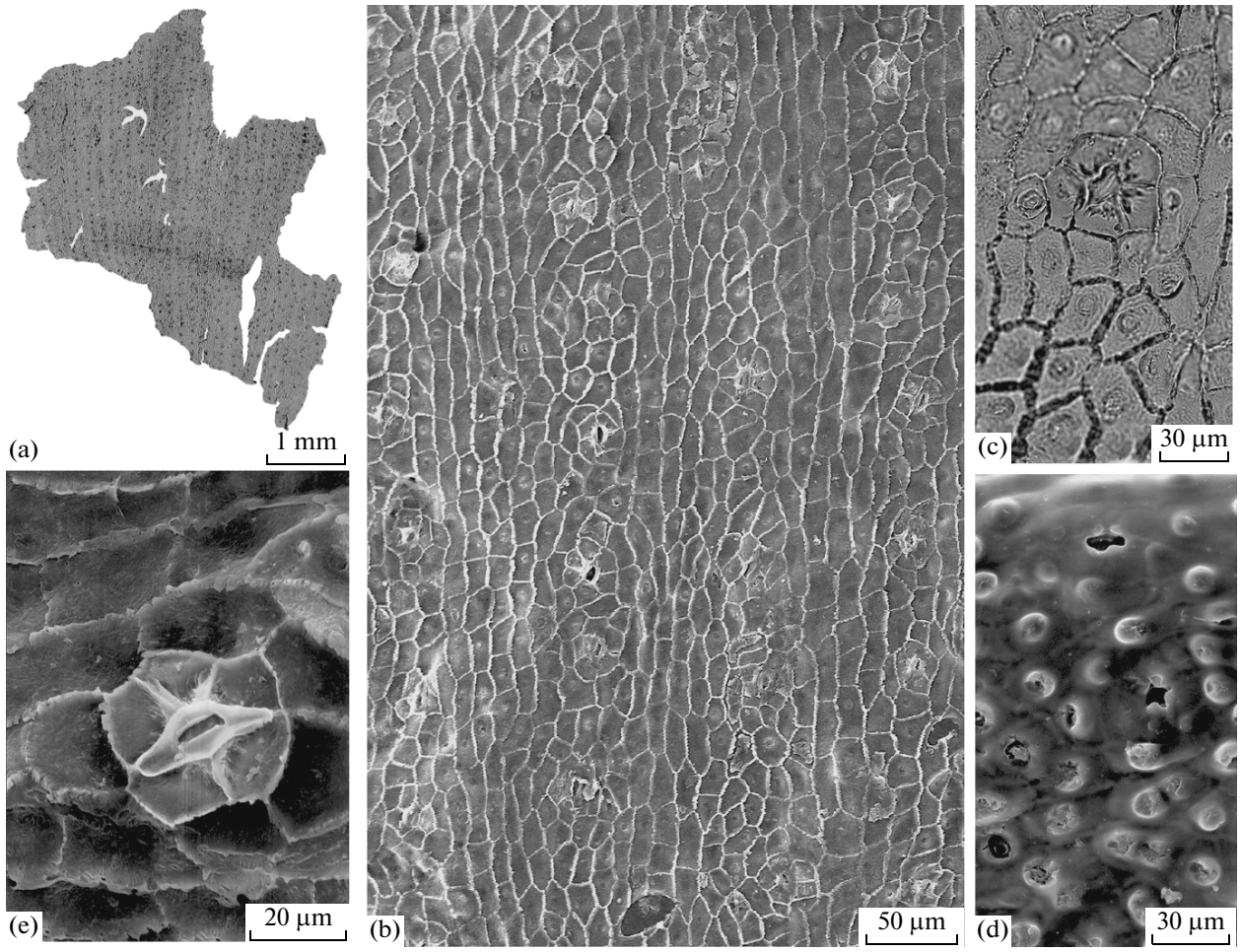


Fig. 2. *Ordopeltacutis vulgaris* gen. et sp. nov., dispersed leaf cuticle, holotype PIN, no. 4820/758; Vologda Region, left bank of the Kichmenga River, near the town of Nedubrovo, Nedubrovo locality; Upper Permian–Lower Triassic, Vetlugian Group, Vokhmian Horizon, Nedubrovo Member: (a) general view of leaf cuticle,; (b) stomatal arrangement; (c) stoma, starlike cutinization of subsidiary cells is visible; (d) external surface of cuticle, distinct periclinal papillae are visible; (e) stoma, cutinization of guard cells is visible.(a, c) LM, (b, d, e) SEM

arrangement of stomata in bands. Perhaps, in the future, it is expedient to establish a new formal genus for dispersed cuticles with the stomata arranged in rows within the bands.

Genus *Segmenpeltacutis* Karasev, gen. nov.

Etymology. From the Latin *segmentum* (band), the family Peltaspermaceae, and the Latin *cutis* (cuticle).

Type species. *Segmenpeltacutis pitispapilla* sp. nov.

Diagnosis. Stomata arranged irregularly within bands. Stomatal apertures obliquely or longitudinally orientated. Epidermal cells of costal and intercostal zones differentiated. Ordinary epidermal cells polygonal, varying in orientation. Anticlinal walls straight or curved. Epidermal cells in costal zones longitudinally elongated.

Species composition. Type species.

Comparison and remarks. Dispersed cuticles attributed to the formal genus *Segmenpeltacutis*, possibly belong to several species of peltaspermaceous pteridosperms established based on complete leaves (Table 2). It is proposed to use the width of costal zones, extent and character of cutinization of subsidiary cells for division of dispersed cuticles into formal species in the genus *Segmenpeltacutis*. Among the species established based on complete leaves, the width of costal zones ranges from four or five (about 100 μm) to ten and more rows (about 200 μm) of ordinary cells. Periclinal walls of subsidiary cells are usually cutinized stronger than, or to the same extent as, in ordinary cells. For example, this occurs in *Kirjamkenia lobata*. In the future, it is expedient to establish a formal species for dispersed cuticles with narrow costal zones and more strongly cutinized periclinal walls of subsidiary cells in comparison with walls of ordinary cells.

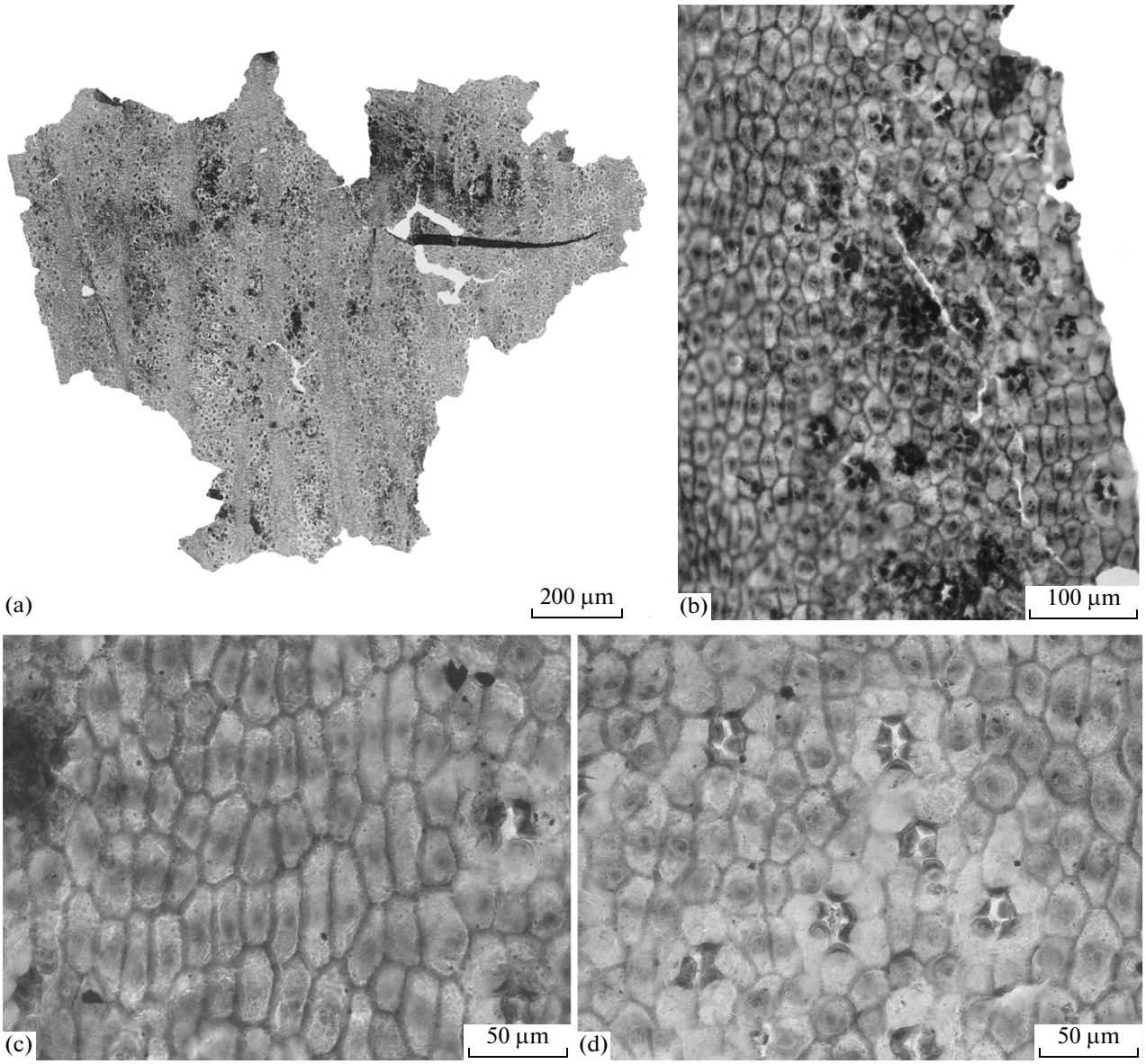


Fig. 3. *Segmenpeltacutis pitispapilla* gen. et sp. nov., dispersed leaf cuticle, holotype PIN, no. 5160/141, LM; Vladimir Region, Vyaznikovskii District, near the town of Vyazniki, Balymotikha locality; Tatarian Series, Vyatkian Stage: (a) general view of leaf cuticle, (b) stomatal band, (c) ordinary cells of nonstomatal band, (d) monocyclic stomata with large clavate papillae on subsidiary cells.

***Segmenpeltacutis pitispapilla* Karasev, sp. nov.**

Etymology. From the Latin *pitis* (head) and *papilla* (protuberance, papilla).

Holotype. PIN, no. 5160/141, large fragment of leaf cuticle; Vladimir Region, Vyaznikovskii District, vicinity of the town of Vyazniki, Balymotikha locality; Tatarian, Vyatkian Stage (Figs. 3a–3d).

Diagnosis (Figs. 3a–3e). Width of costal zones more than ten cell rows. Cutinization of periclinal walls of subsidiary cells weaker than that of ordinary cells. Subsidiary cells with large proximal papillae on periclinal walls.

Description. Dispersed cuticles of one leaf side macerated in natural conditions. The stomata are arranged in distinct bands; within the bands, the stomata are arranged disorderly at a distance of 50–100 μm from each other (Figs. 3a, 3b). The stomatal bands are about 300 μm wide. Ordinary cells of stomatal zones are polygonal (hexa- to octagonal), isogonal (Fig. 3c). Anticlinal walls are straight, rarely slightly curved. Each periclinal wall of an ordinary cell has a clavate or small spherical papilla. Ordinary cells within the stomatal zones are 27–40 μm in size. Stomatal bands are separated by distinct rows of costal cells, which differ from intercostal cells in the more extended shape and better pronounced papillae on the

periclinal walls (Fig. 3d). The width of nonstomatal bands includes is more than ten rows of ordinary cells (180–200 μm). The stomata are monocyclic. Subsidiary cells are trapezoid, five or six in number. The contour of stomata formed by the distal anticlinal walls is irregular. Cutinization of periclinal walls of subsidiary cells is weaker than that of ordinary cells. Periclinal walls of subsidiary cells have large clavate proximal papillae. Proximal papillae are hanging over the front cavity (Fig. 3e). The front cavity is rounded to elliptic.

R e m a r k s. The dispersed cuticle designated as the holotype of *S. pitispapilla* apparently belongs to the middle part of a rather large leaf. The morphology of the costal zones suggests that it has a radial venation, with dichotomously branching veins. Possibly, the leaf belonged to a representative of ginkgophyts, the stomata of which are similar to that of peltasperms.

M a t e r i a l. Two dispersed naturally macerated leaf cuticles.

ACKNOWLEDGMENTS

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REFERENCES

Anderson, J.M. and Anderson, H.M., *Palaeoflora of Southern Africa, II*, Rotterdam: A.A. Balkema, 1989.

Benton, M.J., Sennikov, A.G., and Newell, A.J., Murchison's First Sighting of the Permian, at Vyazniki in 1841, *Proc. Geol. Ass.*, 2010, vol. 121, no. 3, pp. 313–318.

Bomfleur, B., Taylor, E.L., Taylor, T.N., et al., Systematics and Paleoecology of a New Peltaspermalean Seed Fern from the Triassic Polar Vegetation of Gondwana, *Int. J. Plant Sci.,* 2011, vol. 172, no. 6, pp. 807–835.

Dallwitz, M.J., General System for Coding Taxonomic Descriptions, *Taxon*, 1980, vol. 29, no. 1, pp. 41–46.

Dilcher, D., Approaches to the Identification of Angiosperm Leaf Remains, *Bot. Rev.*, 1974, vol. 40, no. 1, pp. 1–157.

Dobruskina, I.A., Genus *Scytophyllum*: Morphology, Epidermal Structure, and Taxonomic Position, in *Pteridospermy verkhnego paleozoya i mezozoya* (Pteridosperms from the Upper Paleozoic and Mesozoic), Moscow: Nauka, 1969, pp. 35–58.

Dobruskina, I.A., Stratigraphical Position of the Plant-bearing Triassic Strata of Eurasia, *Tr. Geol. Inst. Akad. Nauk SSSR*, 1980, vol. 346, pp. 1–164.

Gomankov, A.V., Dispersed Cuticles from the Shikhovo-Chirki Locality (Kazanian Stage of the Vyatka River), *Paleontol. Zh.*, 1997, no. 2, pp. 33–39.

Gomankov, A.V., Tatarian Peltaspermaceae of the Russian Platform: Morphology, Ecology, Evolution, in *Voprosy paleofloristiki i sistematiki iskopaemykh rastenii: Chteniya pamyati A.N. Krishtofovicha* (Questions of Paleofloristics and Taxonomy of Fossil Plants: Memories A.N. Krishtofovich), St. Petersburg: Botan. Inst. Ross. Akad. Nauk, 2008, vol. 6, pp. 42–60.

Gomankov, A.V. and Meyen, S.V., On Members of the Family Peltaspermaceae from the Permian Beds of the Russian Platform, *Paleontol. Zh.*, 1979, no. 2, pp. 124–138.

Gomankov, A.V. and Meyen, S.V., Tatarian Flora: Composition and Distribution in the Late Permian of Eurasia, *Tr. Geol. Inst. Akad. Nauk SSSR*, 1986, vol. 401, pp. 1–174.

Karasev, E.V., A New Species of *Tatarina* S. Meyen and the Problem of Differentiation between Some Late Permian Peltasperms on the Basis of Epidermal Characters, *Paleontol. J.*, 2007, vol. 41, no. 11, pp. 1103–1107.

Karasev, E.V. and Krassilov, V.A., Late Permian Phylloclades of the New Genus *Permophyllocladus* and Problems of the Evolutionary Morphology of Peltasperms, *Paleontol. Zh.*, 2007, no. 2, pp. 80–86.

Kerp, J.H.F. and Barthel, M., Problems of Cuticular Analysis of Pteridosperms, *Rev. Palaeobot. Palynol.*, 1993, vol. 78, nos. 1–2, pp. 1–18.

Kirichkova, A.I., On the Typification of Species of *Lepidopteris ottonis* (Goppert) Schimper, 1869 (Pteridospermae, Cycadofilicales), in *Neftegazovaya geologiya. Teoriya i praktika* (Oil-and-Gas Geology: Theory and Practice), 2006, vol. 1, pp. 1–15.

Kirichkova, A.I. and Khramova, S.N., On Certain Pteridosperms from the Triassic Beds of the Eastern Ural Mountains, in *Novoe v stratigrafii triasa Paleourala* (New Data on the Triassic Stratigraphy of the Paleourals), Sverdlovsk: Ural. Nauchn. Tsentr Akad. Nauk SSSR, 1980, pp. 3–18.

Kovach, W.L. and Dilcher, D.L., Dispersed Cuticles from the Eocene of North America, *Bot. J. Linn. Soc.*, 1984, vol. 88, nos. 1–2, pp. 63–104.

Krassilov, V.A., On Classification of Stomatal Apparatus, *Paleontol. Zh.*, 1968, no. 1, pp. 102–109.

Krassilov, V.A., *Scytophyllum* and the Origin of Angiosperm Leaf Characters, *Paleontol. J.*, 1995, vol. 29, no. 1A, pp. 63–74.

Krassilov, V. and Karasev, E., Paleofloristic Evidence of Climate Change Near and beyond the Permian–Triassic Boundary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 2009, vol. 284, nos. 3–4, pp. 326–336.

Krings, M., Klavins, S.D., DiMichele, W.A., et al., Epidermal Anatomy of *Glenopteris splendens* Sellards nov. emend., an Enigmatic Seed Plant from the Lower Permian of Kansas (USA), *Rev. Palaeobot. Palynol.*, 2005, vol. 136, nos. 3–4, pp. 159–180.

Kurschner, W.M., Leaf Stomata As Biosensors of Palaeoatmospheric CO2 Levels, in *LPP Contrib. Ser. 5. LPP Foundation Utrecht,* 1996, p. 153.

Lozovsky, V.R., Krassilov, V.A., Afonin, S.A., et al., On the Recognition of a New Member in the Structure of the Vokhminskian Formation of the Lower Triassic of the Moscow Syneclise, *Byull. Region. Mezhved. Stratigr. Kom. Tsentr. Yug. Russ. Platf.*, 2001, no. 3, pp. 151–163.

McElwain, J.C. and Chaloner, W.G., The Fossil Cuticle As a Skeletal Record of Environmental Change, *Palaios*, 1996, vol. 11, no. 4, pp. 376–388.

Meyen, S.V., On Classification of Dispersed Cuticles, *Paleontol. Zh.*, 1965, no. 4, pp. 75–87.

Meyen, S.V., Systematics of Peltasperms Their Position in Phylogeny of Gymnosperms, *Byull. Mosk. Ob-va Ispyt. Prir. Otd. Biol.,* 1983, vol. 88, no. 3, pp. 3–14.

Meyen, S.V., *Fundamentals of Paleobotany*, London–New York: Chapman and Hall, 1987.

Meyen, S.V., *Teoreticheskie osnovy paleobotanicheskikh issledovanii (neizdannye glavy k "Osnovam paleobotaniki")* (Theoretical Foundations of Paleobotanic Studies: Unpublished Chapters to "Fundamentals of Paleobotany"), Moscow: GEOS, 2009.

Meyen, S.V. and Gomankov, A.V., Peltasperm Pteridosperms of the Genus *Tatarina*, *Paleontol. Zh.*, 1980, no. 2, pp. 116–132.

Meyen, S.V. and Migdisova, A.V., Epidermal Study of Angaraland *Callipteris* and *Compsopteris*, in *Pteridospermy verkhnego paleozoya i mezozoya* (Pteridosperms of the Upper Paleozoic and Mesozoic), Moscow: Nauka, 1969, pp. 59–84.

Naugolnykh, S.V., The Vyazniki Flora and Nature of Permian–Triassic Extinction, *Tr. Geol. Inst. Ross. Akad. Nauk*, 2006, vol. 580 (Cause–Effect Relations and Factors of Global Biosphere Reorganizations in the Phanerozoic), pp. 83–89.

Naugolnykh, S.V., Foliar Seed-bearing Organs of Paleozoic Ginkgophytes and the Early Evolution of the Ginkgoales, *Paleontol. J.*, 2007, vol. 41, no. 8, pp. 815–859.

Oldham, T.C.B., Flora of the Wealden Plant Debris Beds of England, *Palaeontology*, 1976, vol. 19, pp. 437–502.

Pole, M., Early Eocene Dispersed Cuticles and Mangrove to Rainforest Vegetation at Strahan-Regatta Point, Tasmania, *Palaeontol. Electr.*, 2007, vol. 10, no. 3, p. 66.

Poort, R.J. and Kerp, J.H.F., Aspects of Permian Palaeobotany and Palynology: XI. On the Recognition of True Peltasperms in the Upper Permian of Western and Central Europe and a Reclassification of Species Formerly Included in *Peltaspermum* Harris, *Rev. Palaeobot. Palynol.*, 1990, vol. 63, nos. 3–4, pp. 197–225.

Retallack, G.J., A 300-Million-Year Record of Atmospheric Carbon Dioxide from Fossil Plant Cuticles, *Nature*, 2001, vol. 411, no. 6835, pp. 287–290.

Retallack, G.J., *Lepidopteris callipteroides*, the Earliest Triassic Seed Fern in the Sydney Basin, Southeastern Australia, *Alcheringa*, 2002, vol. 26, pp. 475–599.

Roselt, G. and Schneider, W., Cuticulae dispersae, ihre Merkmale, Nomenklatur und Klassifikation, *Paläontol. Abh.*, 1969, vol. 1, pp. 1–128.

Sadovnikov, G.N., New Data on the Morphology and Anatomy of the Genus *Kirjamkenia*, *Paleontol. Zh.*, 1983, no. 4, pp. 76–81.

Sheffield, J.B., ImageJ, a Useful Tool for Biological Image Processing and Analysis, *Microsc. Microanal.*, 2007, vol. 13, pp. 200–201.

Stace, C.A., Cuticular Studies As an Aid to Plant Taxonomy, *Bull. Brit. Mus. (Natur. Hist.) Bot.*, 1965, vol. 4, no. 1, pp. 1–78.

Taylor, E.L., Taylor, T.N., Kerp, H., and Hermsen, E.J., Mesozoic Seed Ferns: Old Paradigms, New Discoveries, *J. Torrey Bot. Soc.*, 2006, vol. 133, no. 1, pp. 62–82.

Taylor, T.N., Taylor, E.L., and Krings, M., Mesozoic Seed Ferns, in *The Biology and Evolution of Fossil Plants*, Amsterdam: Academic, 2009, pp. 621–650.

Tewari, R. and Agarwal, A., Distinctive Stomatal Structure from Dispersed Leaf Cuticle of Sindhudurg Formation, Ratnagiri District, Maharashtra, India, *Curr. Sci.*, 2001, vol. 81, no. 12, pp. 1638–1641.

Thomas, H.H., On Some Pteridospermous Plants from the Mesozoic Rocks of South Africa, *Phil. Trans. Roy. Soc. B: Biol. Sci.*, 1933, vol. 222, pp. 193–265.

Townrow, J.A., The Peltaspermaceae, a Pteridosperm Family of Permian and Triassic Age, *Palaeontology*, 1960, vol. 3, pp. 333–361.

Upchurch, G.R., Dispersed Angiosperm Cuticles, in *Phytodebris: Notes for a Workshop on the Study of Fragmentary Plant Remains*, Tiffney, B.H., Ed., Toronto: Paleobot. Sec. Botan. Soc. Am., 1989, pp. 65–92.

Upchurch, G.R., Dispersed Angiosperm Cuticles: Their History, Preparation, and Application to the Rise of Angiosperms in Cretaceous and Paleocene Coals, Southern Western Interior of North America, *Int. J. Coal Geol.*, 1995, vol. 28, nos. 2–4, pp. 161–227.

Zalessky, M.D., Observations sur les végétaux permiens du bassin de la Petchora: I, *Bull. Acad. Sci. URSS*, 1934, nos. 2–3, pp. 241–290.

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