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THE GENUS *PTERIS* L. IN THE NEOGENE DEPOSITS OF WESTERN GEORGIA

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ABSTRACT. One of the most characteristic features of Neogene palynocomplexes of Western Georgia (Colchis) is the abundance of spores, among which the genus *Pteris* is particularly prominent. 16 forms of this taxon are described. Starting with the first appearance of *Pteris* in geological history we present data about its distribution in the deposits of Asia and Eastern Europe. The Neogene history of the whole pteridoflora of Western Georgia is outlined. In the process of its development those stages are identified, which have especial importance for the evolution of the whole vegetational cover of Colchis.

KEY WORDS: *Pteris*, spores, Neogene, Georgia

INTRODUCTION

Western Georgia is a stratotypical region where the Neogene and Quaternary are represented by a complete series of sediments. They contain the marine fauna which is the basis for the subdivision of the Late Cenozoic deposits into stages and horizons (Tab. 1).

The Miocene, Pliocene and Pleistocene deposits of Western Georgia are also rich in the remains of flora whose study allows us to reconstruct the history of the whole vegetational complex as well as the evolution of the separate taxa of the Tertiary flora.

In the Neogene floras of Western Georgia ferns formed one of the leading groups of plants. This is proved by their large systematic diversity and the abundance of spores in deposits. From the detailed morphological studies of fossil spores which have been carried out in recent years, about 70 forms have been established. Most of them have been determined up to genus or species level.

Having traced spore distribution through the separate layers we concluded that each period of the Neogene was characterized by a certain composition of ferns. This feature, along with other peculiarities of the palynocomplexes, can be used for the determination of the age of layers in which the remains of fauna are absent.

We began the study of Neogene ferns with the genus *Pteris*. This taxon is characterized by the peculiar morphology of its spores, a high percentage content in Neogene palynocomplexes and diverse specific composition. Both recent and fossil spores of *Pteris* have been studied under a light microscope. Some specimens were also examined under an electro-scanning microscope Jeol-35 by Prof. N. R. Meyer-Malikian to whom we express our thanks.

In the process of our work, in addition to the literature, we used herbarium material kept in the Institute of Palaeobiology of Georgian Academy of Sciences and the W. Szafer Institute of Botany, Polish Academy of Sciences. Comparison were made among the following species:

Pteris abrupta Reichenbach; *P. actinopteris* Christ, (from China); *P. actinopteroides* Christ, (China); *P. aculeata* Sw.; *P. affinis* Fougiers, (Guadaloupe); *P. allosora* Link; *P. altissima* Poir., (Costa Rica); *P. aspericaulis* Wall.; *P. argentea* Gmel.; *P. arguta* Ait.; *P. biaurita* L., (Nepal); *P. catoptera* Kze.; *P. caliaris* Eat. (Cuba) ; *P. crenata* Sw.; *P. cretica* L., (Cuba, Georgia); *P. dectylina* Hk., (China, Yunnan); *P. deccurens* Pr., (East Parana); *P. decussata* J. Sm.; *P. deflexa* L.; *P. deltodon* Bak.; *P. dentata* Forsk.; *P. distans* J. Sm., (Philippines); *P. endlicheriana* Ag., (New Zeland); *P. ensiformis*

Table 1. Scheme of stratigraphical subdivision of the Neogene and Quaternary deposits of Georgia

Section	Section	Stage / Horizon	
PLEISTOCENE	Upper	New Euxinian	
		Karangatian	
	Middle	Uzunlarian	
		Old Euxinian	
	Lower	Tschaudian	Tsvermagalian
			Natanebian
PLIOCENE	Upper	Gurian	Naderbasevian
			Khvarbetian
		Kuyalnikian (Egrissian)	Tsikhisperdian
			Etserian
			Skurdumian
	Middle	Kimmerian	
	Lower	Pontian	
MIOCENE	Upper	Meotian	
		Sarmatian	
	Middle	Konkian	
		Karthvelian	
		Karaganian	
		Tschokrakian	
		Tarkhanian	
	Lower	Majkopian	Kotsakhurian
			Sakaraulian
			Uplistsikhian

Burm., (Taiwan); *P. excelsa* Gaud., (Yunnan); *P. gigantea* Willd., (Venezuela); *P. goeldiana* Christ, (Paraguay); *P. grandifolia* L., (Cuba); *P. haenkeana* Pr., (Granada); *P. henryi* Christ, (China); *P. inaequalis* Bak., (Japan); *P. irregularis* Klf., (Hawaii); *P. kinschinensis* Hieron, (Japan); *P. kunzeana* Ag., (Bolivia); *P. lastii* C. Chr. (Madagascar); *P. leptophylla* Sw., (Brazil); *P. lineata* L.; *P. litoralis* Rechinger, (Samoa); *P. litobrochioides* Kl.; *P. longibrachiata* Ag.; *P. longifolia* L., (Zambezi); *P. longipinnula* Wall., (India); *P. macilenta* A. Rich., (New Zeland); *P. moluccana* Bl., (New Gwinea); *P. mutilata* L. (Cuba); *P. nana* Christ, (China); *P. paleacea* Roxb., (St. Helena); *P. pellucida* Pr., (Brazil); *P. podophylla* Sw. (Cuba); *P. pseudolonchitis* Bory; *P. pungens* Willd., (Panama); *P. quadriaurita* Retz. (Cuba); *P. remotifolia* Bak. (Madagaskar); *P. semipinnata* L., (Japan); *P. subundulata* Ros., (New Kaledonia); *P. tripartita* Sw., (Tahiti); *P. venusta* Kze.; *P. vieillardii* Mett., (New Kaledonia); *P. vittata* L., (Azerbaidjan); *P. wallichiana* Ag., (Japan); *P. yakushimensis* Tagawa, (Japan).

The contemporary genus *Pteris* L. contains about 200 species. All of them are dry land ferns, distributed in both hemispheres, mainly in zones with tropical or subtropical climates. *Pteris* grows in shady forest, often in open places or in drier rocky sites (Tryon & Lugardon 1990).

At the present time in the Caucasus only two species, *Pteris cretica* L. and *P. vittata* L., are known. *P. cretica* reaches its geographical limit of distribution in the Western Transcaucasus. Here it grows on damp rocks and in the forests of the lower mountain belt. Beyond the Caucasus the region of its natural distribution extends from the Mediterranean to Japan. It can also be found in Africa, Madagascar, Jamaica, Guatemala, the Bahamas and Florida (Gladkova 1978, Proctor 1985). The second species, *P. vittata* L., was found by Askerov (1983) not long ago on the Apsheronian peninsula. Later this fern was found in the Botanical Garden of Batumi between stones in the open soil. Although Askerov considers *P. vittata* to be an adventitious species, he includes it in the group of Caucasus ferns.

Pteris vittata L. is a Mediterranean species having a rather wide area of distribution. Crete and the southern regions of Turkey are the places closest to the Caucasus where this fern grows naturally (Askerov 1977).

Right up to the present time there is disagreements among researches about the systematic treatment of the Pteridaceae and the relationships among the groups of genera contained in this large family.

Christensen (1906) singled out the subfamily Pterideae which he included in the family Polypodiaceae.

Copeland (1947) considered the Pteridaceae to be one large family in which he placed 64 genera forming the following groups: dicksonioids, dennstaedtioids, pteridoids, gymnogrammoids and lindsaeoids.

Engler (1954) also included the pteridoid ferns in the family Polypodiaceae as a separate subfamily Pteridoideae, in which he combined 4 genera: *Pteris, Pteridium, Acrostichum* and *Stenochlaena*.

In 1975 Crabbe, with co-authors published a new clasification system for ferns. As the authors state, the family hardest to define is the Polypodiaceae, which is usually considered either as a single family or divided into as many as 33 families. In "A new generic sequence for the Pteridophyta Herbarium" (Crabbe et al. 1975) the pteridoid ferns are included in the family Adiantaceae, which consists of the three subfamilies, Adiantoideae, Vittarioideae and Pteridoideae, the last comprising the 5 genera *Pteris, Idiopteris, Copelandiopteris, Neurocallis* and *Acrostichum*. In an accompanying note it is stated "we believe – and there is an increasing opinion accepting – the adiantoid ferns to be a distinct group arising from schizaeaceous stock".

Gladkova (1978) also relates the pteridoids to the Adiantaceae and divides this family into 4 subfamilies: Adiantoideae, Vittarioideae, Pteridoideae and Ceratopteridoideae.

In 1986 Takhtadjan published a classification system for all taxa of vascular plants. The author considers Polypodiaceae, which is represented in modern floras by a large number of families, to be the most complicated. The classification of this taxon was radically revised by Takhtadjan. He established the order Pteridales in which the pteridoid ferns are considered as a separate family Pteridaceae.

In the opinion of Tryon and Lugardon (1990) 34 genera and six distinctive tribes are recognized in the family Pteridaceae. The tribes are the Taenitideae, Platyzomateae, ceratopteroideae, Pterideae, Cheilantheae and Adianteae.

The disagreements among taxonomists have arisen from the history of the development of the Pteridaceae. Nayar and Devi (1968) and Devi (1979) have discussed this problem on the basis of spore morphology. The authors accepted Copeland's point of view concerning the scape of the Pteridaceae and retraced the phylogeny of each group of ferns established by him.

Devi's morphological analysis was based on two main features, the nature of the germinal aperture and the ornamentation of the exine. Two apertural forms are met with in this family, the trilete which is considered as primitive and the monolete derived from it. The author believes the origin of the perine to be a unique phenomenon in the evolution of fern spores. Four morphotypes are distinguished in the process of evolution of these two features: trilete spores without a perine, trilete spores with a perine and monolete spores with or without a perine.

Guided both by the literature data and her own results, Devi (1979) came to the conclusion that parallel evolution had taken place within the family Pteridaceae. The pteridoid ferns, the gymnogrammoids and the lindsaeoids originated from the dicksonioid-dennstaedtioid complex and evolved along parallel lines. In relation to evolutionary advance, the pteridoids lead followed by the gymnogrammoids with trilete perinous (non-visible) and trilete perinous (visible) spores, with the lindsaeoids, represented by three morphotypes remaining the most primitive.

From the point of view of spore morphology, *Pteris* the type genus of the Pteridaceae, presents a high degree of uniformity. The spores are of the trilete-tetrahedral type with a thickset, rugulose-tuberculate type of ornamentation. The processes are crowded together and distinctly more prominent on the distal than on the proximal surface of the spore. It is uncommon for both the proximal and distal spore faces to be equally rugose (Tryon & Lugardon 1990).

The two surfaces are clearly separated from each other by a characteristic equatorial collar-like ridge encircling the spore. It can be narrow, wide, continuous, interrupted, straight or sinuous. The collar has no ornamentation (Nayar & Devi 1968).

The two faces of the *Pteris* spore have different forms, which are clearly seen in side view. The distal face can be convex, hemispherical or subconical; the proximal can be conical, convex, flat or concave.

As has been noted above, all spores of *Pteris* are trilete. There are cases when one of the laesura arms is longer than the others.

Many species of *Pteris* show abnormalities such as a four-armed laesura with a tetrangular amb and forked laesura arms (Devi 1979). Devi and Khare (1985) give an example of the presence of a round laesura among spores of *Pteris vittata* L., which, according to the authors, is due to irregularities during cytokinesis.

The exine of fern spores consists of several layers: the endexine (the inner exospore), the mesexine, ektexine and perine (perispore) which is formed as a result of tapetum cell activity (Meyer-Melikjian 1987). The equatorial collar present in the *Pteris* group is an enigmatic feature. As Devi (1980) notes, although extra exosporial in nature, it is doubtful whether the equatorial collar has played a distinct role in the evolution of the perispore. It is clearly a prolongation of the exospore in the equatorial plane and most often does not carry the exospore ornamentation on it. There are instances where the surface of the collar gets cracked along with the outermost layer of the exospore. As Devi supposes, this suggests the possible presence of an outermost continuous layer common to the exospore and the equatorial collar.

The spores of 70 species were examined by Tryon and Lugardon under the scanning electron microscope and transmission electron microscope. The following description of the *Pteris* spore structure was given: "The exospore consists of two layers, the outer forming numerous canals; the perispore is also formed of two layers conforming to the exospore contours, the inner thin and finely granular, the outer rougher, forming tiny rods in some species and sometimes enclosing globules" (Tryon & Lugardon 1990).

THE DISTRIBUTION OF FOSSIL REMAINS OF *PTERIS* IN THE MESOZOIC AND CENOZOIC DEPOSITS OF NORTHERN ASIA, EASTERN AND CENTRAL EUROPE AND THE CAUCASUS

ASIA AND EASTERN EUROPE

Mesozoic

In geological history *Pteris* is known from the Triassic (Tab. 2). Spores of this taxon were described from the deposits of South-Eastern Siberia (Vakhrameev 1963). Two forms of *Pteris* are given in the composition of the palynological complex of the Early Keuper and Rhaetian in Kazakhstan: *Pteris paleouncinata* Bolch. and *Pteris* sp. (Murakhovskaya 1968).

In the Lias microspore complex of the Tschulimo-Yeniseian and Kanskian basins, alongside a large quantity of Bennettitales and coniferous there are spores of some representatives of *Lycopodium, Selaginella, Osmunda* and *Pteris multiformis* Sach. (Sakhanova 1957).

Bolkhovitina (1956) determined the following forms of *Pteris* from the Early Jurassic deposits of the Villuian basin: *Pteris* sp., *P. paleouncinata* Bolch. and *P. multiformis* Sach.

Single spores of *Cyathidites, Anemiites* and *Pteris* are mentioned as occuring in the Bathonian deposits of Northern Siberia (Boitsova et al. 1960). In the Middle Jurassic layers of Narin (Northern Fergana), spores of *Pteris* aff. *paleouncinata* Bolch. were found (Nikitova & Vinogradova 1964).

In the Upper Jurassic deposits of the eastern slopes of the Urals, spores *of Lycopodium, Coniopteris, Pteris* and *Osmunda* are of major significance (Lyder 1957). In simultaneous layers in the Southern Kazakhstan *Pteris paleouncinata* Bolch. has been found, its spores occuring as single specimens (Sakulina 1968).

Pteris parvimamma (Naum.) Bolch. was described from the Lower Cretaceous and, as Bolkhovitina (1953) states, its spores had been initially described by Naumova from the Albian deposits of the Middle Ural under the name *Stenoronotriletes parvimamma* Naum. It is very likely that, in the Cretaceous, this fern was widely distributed, as its remains have been found in the deposits of Kazakhstan, the rivers Amba and Aiat, of the eastern slopes of

Table 2. The distribution of fossil remains of the genus *Pteris* in the Mesozoic and the Cenozoic deposits of Eurasia

The name of species	Triassic	Jurassic			Cretaceous		Palaeogene			Neogene	
		Lower	Middle	Upper	Lower	Upper	Palaeo-cene	Eocene	Oligoce-ne	Miocene	Pliocene
1	2	3	4	5	6	7	8	9	10	11	12
Asia											
Pteris sp.	+	+	+	+	+	+	+	+	+	+	+
P. palaeouncinata Bolch.	+	+	+	+							
P. multiformis Sach.	+	+									
P. parvimamma (Naum.) Bolch. (is compared with *P. longifolia*)					+						
P. cretacea Chlon. (is compared with *P. cretica* L. and *P. umbrosa* R. Br.)					+	+	+				
P. cf. *cretica* L.					+						
P. labyrinthea Botscharn. (is compared with *P. cretica* L.)								+			
Pterisisporites bellus Song, Li, Zhong								+			
P. ochiishiensis Takahashi						+	+	+			
P. trizonatus Song, Li, Zhong						+	+	+			
P. verrucatus Takahashi							+	+	+		
Pterisisporites ssp.						+	+	+	+		
Europe											
Polypodiaceoisporites saxonicus W. Kr. (is compared with *Pteris arguta* Alt.)										+	
P. lusaticus W. Kr. (is compared with *P. biaurita* L. var. arguta Moore)										+	
P. spiniverrucatus Trav. (is compared with *P. pellucida* Pr.)										+	
P. cf. *verruspeciosus* W. Kr. (is compared with *P. marginata* and *P. altissima*)										+	
P. boerzsoenyensis Nagy (is compared with *P. catoptera* Kze.)										+	
Cingulisporis corrutoratus (Nagy, 1985) Ważyńska comb. nov.										+	
Cingulisporis gracillimus (Nagy, 1963) Ważyńska comb. nov.										+	
Macroscopic remains											
Pteris oeningensis Ung.									+		
P. parschlugiana Ung.										+	
P. crenata Web.										+	
Pteris sp.										+	

the Middle Ural, in the Lower Cretaceous of the Moscow region, in the central regions of the Russian platform and in the Crimea. Bolkhovitina (1953) writes that the spores of *Pteris parvimamma* could be compared with thouse of modern *Pteris longifolia* L. From the Lower Cretaceous deposits also, two species of *Pteris* are known, *P. cretacea* Chlon. and *P.* cf. *cretica* L.

Pteris cretacea was first described by Khlonova (1960) from the Late Cretaceous deposits of the Tschulimo-Yeniseian basin. According to the author the spores of this species resemble those of the recent *P. cretica* L. and *P. umbrosa* R. Br., differing only in their sculpture. Later the spores of *Pteris cretacea* were found in the Senoman-Turonian layers of Western Siberia (Khlonova 1976).

Especially significant is the presence of spores of *Pteris* cf. *cretica* L. in the Lower Cretaceous deposits of the Turgaian depression. As is written in the description (Atlas of Lower Cretaceous spore and pollen complexes... 1964, p. 189), the fossil spores are provided with a thin perispore and the exine is covered with large compact tubercles.

Spores of *Pteris* sp. have also been found in the Lower Cretaceous deposits of the Pechora Basin (Griaseva 1968).

In the Lower Cretaceous (Aptian-Albian) deposits of Eurasia spores of the formal genus *Asbeckiasporites* Brelie are often present. It is included in the list of taxa, which were considered the most important (guide fossils) for the second half of the Early Cretaceous. Because of the remote resemblance with *Gleicheniidites angulatus* (Bolch.) Bolch. some authors consider this form to be related to the Gleicheniaceae (Bolkhovitina 1968, Voronova 1982). Thedorova-Shakhmundes (1976) compares the spores of *Asbeckiasporites* with those of two species *Pteris venusta* and *P. straminea* Mett. According to this author there is a resemblance in the outline of the spores, in the presence of a trilete leasura and also in the character of the equatorial collar. From the Aptian-Albian deposits of the Southern Baltic countries, the Dnieper-Don basin, Russian platform, Pricaspian region and the Mangishlak Peninsula, Thedorova-Shakhmundes (1976) describes three species: *Asbeskiasporites wirthi* v.d. Brelie, *A. hoennensis* v.d. Brelie and *A. borysthensis* (Voronova) Thedorova-Shakhmundes.

In the composition of the Upper Cretaceous complexes of different regions in the former USSR, *Pteris* sp. have been listed mainly on the basis of single spores found in the Turgaian depression, on Kamchatka, in the Lower Zaisanian depression and in the Crimea (Atlas of the Upper Cretaceous, Palaeocene...1960, Pokrovskaya 1966, Rotman 1979).

As a result of the palynological investigation of the Upper Cretaceous deposits of the Tschulimo-Yeniseian basin (Western Siberian Lowland) two complexes have been distinguished, the Tschulimian, which corresponds to the Senoman-Turon, and the Simsko-Danian (Klimko et al. 1956). The Polypodiaceae played an important role in the Tschulimian complex among which the spores of *Pteris cretacea* were the most frequent. In the complex of Simskian suite the rapid increase of representatives of the Polypodiaceae was observed, with other taxa rarely seen.

Lycopodium, Selaginella, Osmunda and Polypodiaceae along with *Pteris* spores have been found in the Upper Maastrichtian deposits of the Western, Central and Eastern steppe parts of the Crimea as well as in the stratotypical sections of boreholes in the Bakhchisarai region (Kuvaeva 1966, Rotman 1979).

In the spore-pollen complexes of the Campanian-Maastrichtian deposits of Eastern Kizil-Kum, fern spores formed up to 25% of the total with *Pteris* spp. included in this number.

Fern spores were practically absent in the deposits of Danian-Palaeocene age from Siberia and Middle Asia (Blyakhova 1966). Only in the Crimea there were spectra in which single spores of *Pteris* sp. were included (Rotman 1973).

Some species of the genus *Pterisisporites* Sung & Zheng have been described from the Upper Cretaceous and Palaeogene deposits of China and Japan (Song Zhichen et al. 1986, Takahashi 1991)

Palaeocene

The Lower Palaeocene complex of deposits located along the River Kuban and near Tscherkesk (Northern Caucasus) is characterized by a rich composition of ferns among which *Pteris* sp. have been distinguished (Panova 1968).

Up to 35% of the Upper Palaeocene palynospectra of South Kazakhstan consists of spores of *Pteris cretacea* Chlon. and *Pteris* sp. div. (Blyakhova 1976). The latter was also found in the Palaeogene complex of the southern part of the Western-Siberian lowland (Pokrovskaya 1966). Spores of *Pteris* have been recorded in the Palaeocene palynocomplexes of Armenia and the Crimea (Leye 1968, Rotman 1983). Further, single spores of *Pteris* sp. have been found in the spectra of the Upper Palaeocene-Lower Eocene deposits of Prialtaian region (Boitsova & Panova 1967).

Eocene

Ferns make up 50% of the composition of the Early Eocene palynological complex in the marine deposits of Kazakhstan. They consists mainly of Polypodiaceae and spores of *Pteris* sp. (Blyakhova et al. 1971).

The Lower Eocene marine deposits of Eastern Kizil-Kum contain spectra with a rich fern composition. Spores of *Pteris, Lycopodium* and *Selaginella* prevail. In the complex of the final layer of the Lower and the lowest layers of the Middle Eocene, *Pteris* and *Selaginella* predominate. In the succeding parts of the Middle Eocene deposits, spores of *Pteris.* are rarely found and are absent from the younger Palaeogene layers (Blyakhova 1971).

On the banks of the Kishi-Karoi lake and near Kinishi village the Ishim-Irtish confluence boreholes have been drilled in the Lower and Upper Eocene deposits which have been found to contain single spores of *Pteris* (Panova 1968).

Pteris have also been found in the Eocene palynospectra of Northern Tien Shan, the Tadjik depression, Azovian Sea, Crimea and Northern Caucasus (Baibulatova 1968, Panova 1968, Leye 1973, Mikhelis 1976, Pulatova 1983).

From the Eocene deposits of the Swerdlovsk region a new species, *Pteris labyrinthea* Botscharnikova was described. The author compares it with the contemporary *Pteris cretica* L. (Agranovskaya et al. 1960).

Oligocene

Spores of *Pteris* occur in the Oligocene deposits which developed in the region of the Tadjik depression, in the South of the Ukraine and on the Western-Siberian lowland (Boitsova & Panova 1967, Pulatova 1983).

Ashutassian suite (an outcrop near the Ashutas Mountain), correlated with the Upper Oligocene, is very rich from the palaeobotanical point of view. In addition to the pollen of coniferous, and broad-leaved trees there are also spores of *Osmunda, Pteris* and *Salvinia. Pteris oeningensis* Ung. has been described from extensive plant remains, (Vasilenko 1957).

Miocene

A small quantity of spores of *Pteris* is present in the deposits of the Maikopian series of the Volga-Don watershed (Pokrovskaya 1956). Krishtofovitch described extensive remains of *Pteris* from the Lower Miocene deposits of the Southern part of the Azovian Sea region (Sigova 1956).

The spore-pollen spectra of the Lower and Middle Miocene (Tarkhanian, Karganian, Konkian) deposits of the Southern Ukraine contain single spores of *Pteris* (Syabryay & Shchekina 1983).

Leaf prints of *Pteris parshlugiana* Ung. have been found in the composition of the the Upper Tortonian flora of the Southern Ukraine (Koval 1955), but according to Bajkowskaya (1955), these remains belong to the genus *Osmunda*.

In a village near Alexandrovka Krishtofovich discovered the remains of a *Pteris* sp., in Sarmatian deposits, similar to *Pteris oeningensis* Ung. (Krishtofovich 1931, Krishtofovich & Bajkovskaya 1965).

The Meotian complexes of the Kerch peninsula contained single spores of *Pteris* (Maslova 1960, Panova 1966). In the composition of the Late Miocene flora of the Transcarpathian, Bajkovskaya (1955) described the remains of *Pteris crenata* Web.

Pliocene

In the Pliocene palaeofloras of the northern part of Russia the genus *Pteris* is rarely found. Its remains can be seen in the deposits of the Kerch peninsula as a component of the Lower Kimmerian complex in which cryptogamous plants comprise up to 9.5% of the total (Shchekina 1977).

CENTRAL EUROPE

Neogene

In Central Europe fossil spores which possess similarities with those of *Pteris* appear in the Miocene. They have been determined mainly by artificial system of classification.

From the Miocene of Central Europe, Krutzsch (1967) described some forms under the name *Polypodiaceoisporites*. Two of them *P. saxonicus* W. Kr. and *P. lusaticus* W. Kr., are *Pteris arguta* Alt. and *P. biaurita* L. var *arguta* Moor. In Southern Poland spores *of Pteris* are known from Miocene spore-pollen complexes (Stuchlik & Shatilova 1987).

The following species were described from the Upper Miocene of Italy (Toskana): *Polypodiaceoisporites spiniverrucatus* Trevisan and *P. verruspecious* W. Kr. (Trevisan 1967). The former is similar to *Pteris pellucida* Pr. and the latter to *P. marginata* and *P. altissima*.

Nagy (1985) described some representatives of the formal genus *Polypodiaceoisporites* from Miocene deposits in Hungary. According to the author two of them possess spores similar to those of recent species of *Pteris*. *Polypodia-*

ceoisporites boerzsoenyensis Nagy resembles the modern *Pteris catoptera* Kze. and also *P.* aff. *quadriaurita* Retz. from the Pliocene deposits of Western Georgia (Shatilova & Mcheishvili 1980). The spores of *Polypodiaceoisporites spiniverrucatu* Trav. are comparable with *those of Pteris pellucida* Pr.

The spores of *Polypodiaceoisporites gracillimus* Nagy were at first considered by the author (Nagy, 1963) to be comparable with those the present-day family Schizaeaceae (*Lygodium*). In the opinion of Planderova (1990) this form belongs to the family Pteridaceae. Later Ważyńska described it as *Cingulisporis gracillimus* (Nagy). Ważyńska comb. nov. and without question it has spores of the *Pteris* type (Ziembińska et al. 1994).

The second species described by Nagy (1963) considered to be comparable whith the *Pteris* type was *Cingulisporis corrutoratus* (Nagy). Ważyńska comb. nov. At first this form was described as *Polypodiaceoisporites corrutoratus* Nagy (Nagy 1985).

CAUCASUS

In the Caucasus representatives of *Pteris* have been found in deposits dating from the Cretaceous period onwards. In the Northern Caucasus spores of *Pteris cretacea* Chlon. and *P. parvimamma* (Naum.) Bolch. were extracted from the Barremian and Aptian deposits (Yaroshenko 1965, Kuvaeva & Mikhailova 1965). These species have also been found in Azerbaijan in the Hauterivian and Barrenian layers (Kuvaeva et al. 1964; Aliev et al. 1976). From the Oligocene, Tschokrakian and Sarmatian deposits of this region, only one form of a *Pteris* sp. is known Dzhabarova & Kasumova 1961, Dzhabarowa 1967). A second species, *Pteris parschlugiana* Ung. was described from the extensive plant remains in the Sarmatian deposits of the Katar ridge (Fataliev 1960).

GEORGIA
(from the literature data)

The most ancient fossil findings of spores of *Pteris* in Georgia date from the Palaeogene age. In the Akhaltzikhian depression spores of *Pteris* have been extracted out from the Eocene and Oligocene deposits (Panova et al. 1984).

The Tarkhanian deposits in the vicinity of Bardnala village (basin of the River Tzkhenistzkhali) contain a spore and pollen complex of which up to 5% consists of *Pteris*. Ferns as a whole play a significant role in the complex. According to the authors Ananiashvili & Purtseladze (1976) ferns, along with evergreen thermophilous broad-leaved plants give the Tarkhanian flora of Western Georgia a subtropical character.

The Middle Miocene deposits of Georgia are very rich in plant remains. Both leaf prints and palynological complexes have been studied from the Karaganian and Konkian layers (Avakov 1979; Ramishvili 1982). According to the natural classification Ramishvili (1982) distinguished only one species – *Pteris* sp. Along with this must be noted the presence of spores, which were classified artificially but bore relation to the genus *Pteris*. As can be seen from Table 3 in the Middle Miocene the genus *Pteris* was taxonomically rather diverse and played a fairly significant role in the composition of plant communities.

Data on the Sarmatian flora are based mainly on the results of studies of macroscopic plant remains (Kolakovsky & Shakryl 1976, Uznadze & Tsagareli 1979, Chelidze 1987). Shortly after, the palynological study of the Sarmatian deposits of Western Georgia began (Shatilova et al. 1991).

In the Sarmatian deposits only macroremains of *Pteris* were found, but as the palynological investigations proved, the contribution made by this genus in the deposits was much greater.

After the Sarmatian the role of *Pteris* became more important. Spores of *Pteris longifolia* L. and *P. verus* (N. Mtched.) Pur. were found mainly in Meotian deposits (Purtseladze & Tsagareli 1974, Purtseladze 1977).

From Pontian deposits *Pteris venusta* Kze., P. aff. *grandifolia* L. and *Pteris* spp. were determined (Ramishvili 1969, Shatilova et al. 1988, Stuchlik & Shatilova 1987).

In the composition of the Kimmerian palynocomplexes the following forms were found: *Pteris venusta* Kze., *P.* aff. *togoensis* Hieron., *P.* aff. *grandifolia* L. and *Filicites verus* N. Mtched., (Mtchedlishvili 1963, Shatilova 1984, Stuchlik & Shatilova 1987).

Spores of *Pteris cretica* L., *P. venusta Kze.*, *P. vittata* L. and others (Tab. 3) were found in the Kuyalnikian and Gurian palynocomplexes (Shatilova 1967, 1984, Shatilova & Mchedlishvili 1980).

Table 3. The distribution of fossil remains of genus *Pteris* in the Mesozoic and Cenozoic deposits of the Transcaucasus (from the literature data)

Species of *Pteris*	Cretaceous	Eocene	Oligocene	Miocene				Pliocene				Pleistocene		
				Tarkhanian	Karaganian Kartvelian Konkian	Sarmatian	Meotian	Pontian	Kimmerian	Kuyalnikian (Egrissian)	Gurian	Tschaudian	Old Euxinian	Uzunlarian
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Polypodiaceoisporites triangulus W. Kr.					+									
P. gracillimus Nagy					+									
P. microverrucosus Sim.					+									
P. lusaticus W. Kr.					+									
P. helveticus Nagy					+									
Pteris sp.	+	+	+	+										
P. cretacea Chlon.	+													
P. parvimamma (Naum.) Bolch.	+													
P. cretica L.				+			+	+	+	+	+	+	+	+
P. longifolia L.							+							
P. verus (N. Mtched.) Pur. (*Filicites verus* N. Mtched.)							+		+	+	+			
P. aff *cretica* L.								+	+					
P. verusta Kze.								+	+	+	+			
P. vittata L.											+			
P. aff. *quadriaurita* Retz.										+	+			
P. aff. *togoensis* Hieron									+	+	+			
P. aff. *grandifolia* L.									+					
Macroscopic remains														
P. parschlugiana Ung. (*P. longifolia* L.)					+	+								
Pteris sp.						+								

DESCRIPTION OF SPORES OF *PTERIS* L.

At the present time there are many works in which descriptions and photographs of the fossil spores of *Pteris* in the Neogene deposits of Western Georgia are given (Mtchedlishvili 1963, Purtseladze & Tsagareli 1974, Shatilova 1987). All investigators have noted the presence of many forms of the genus *Pteris* in the flora but only some of them are determined under specific names. The others have been allocated under different numbers which have been used again during the description of spore-pollen complexes from various deposits of diverse age. This induced us to revise our knowledge of the spores of *Pteris* from Neogene deposits and classify systematically all the fossil material.

Our studies have allowed us to establish the existence of species unknown in the composition of the flora of Western Georgia untill now, to redetermine some spores and to unite morphologically similar spores from different deposits into one taxon.

For example, *Filicites verus* N. Mtchedlishvili from Kimmerian deposits (Mtchedlishvili 1963) and *Pteris verus* (Mtched.) Pur. from Meotian (Purseladze & Tsagareli 1974) are the same form as *Pteris* sp. from Gurian (Shatilova 1984). All these forms are similar to *Pteris crenata* Sw. and are described as *Pteridacidites verus*.

Comment is necessary about the spores which were determined as *Pteris cretica* L. or *P.* aff. *cretica* L. Study of the whole material showed that under these names different forms had been described. One of them is distinguished under the name *Pteridacidites pseudocreticus*.

We attributed *Pteris* aff. *cretica* from the Kimmerian deposits to *Pteridacidites longifoliiformis*. From the illustration in the work of Mtchedlishvili (1963), the similarity of the fossil form with the contemporary species *Pteris longifolia* L. is revealed in the looped sculpture of the distal spore face.

Pteris cretica L. has also been recorded from the Tarkhanian palynological complex (Ananiashvili & Purtseladze 1976). These data were published in an article without photographs so it is difficult to judge the morphology of spores which were determined under this name. But if we take into consideration the fact that forms typical for *Pteris cretica* only began to appear in deposits in the Kimmerian, it is difficult to imagine the possibility of the existence of such a recently evolved species in the lower part of the Middle Miocene.

Now, in Europe, fossil spores of *Pteris* are described under the name *Polypodiaceoisporites*. This genus has had a wide interpretation both from the geological and botanical points of view. The species of *Polypodiaceoisporites* are related by different authors to various recently evolved tropical and subtropical genera.

Chinese palynologists Sung and Zheng (in Song Zhichen et al. 1976) proposed a new name, *Pterisisporites*. Some species of this genus were subsequently described from the Upper Cretaceous and Palaeogene deposits of China and Japan (Song Zhichen et al. 1986, Takahashi 1991).

Unfortunatelly the diagnosis is given only in Chinese so the name is unvalid. By the courtesy of Prof. Dr. Cao Liu from the Nanking Institute of Geology and Palaeontology Chinese Academy of Sciences we got a letter with the English translation of this diagnosis, description and references. The documentation is as follows:

Pterisisporites Sung and Zheng (ms)[1], In: Sung[2], Lee and Li 1976. Mesozoic Fossils from Yunnan; fasc. I, p. 20 (Nanking Inst. Geol. Paleontol., Academia Sinica; Science Press, Peking).

Type species: *Pterisisporites undulatus* Sung and Zheng In: Sung, Lee and Li 1976, p. 21, Pl. 2 fig. 7

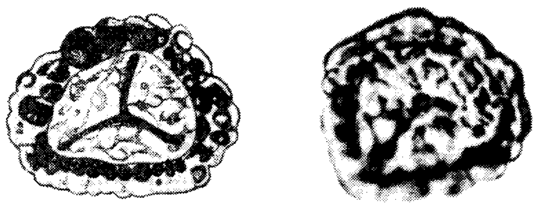

插图 1 *Pterisisporites undulatus* (from Sung, Lee & Li 1976, Pl. 2 fig. 7)

(same specimen as text-fig. 1, which is cited by authors as type of the genus).

Diagnosis: "polar outline is triangular to convex. The spore has annulated fringe, which is thick and dense and closely packed with warty laminations.

The fringe is usually narrow, with variable width ranging from 1/5–1/3 of the diameter of the spore. The trilete suture is generally visible but without labial structure or other accompaniments. It varies in length. Distal sculpture is verrucate, not reticulate; Proximal sculpture is redimentary or granular. The outline of the spore is wavy".

Cretaceous to Tertiary.

Description of type species: Spore diameter is 28–35 µm (including annulation). Spore outline is triangular or convex. The spore has annulated fringe, about 4.5 µm wide, which is thick and dense and closely packed with warty lamination. The trilete suture is slender and reaches inner annulation; the suture is simple, without labial structure. Sculpture is verrucate, distal one is more developed than the proximal one. The outline of the spore is wavy.

Moxie, Mengla County, Yunnan Province, China; upper part of Upper Cretaceous to lower part of Tertiary.

The name *Pterisisporites* suggests the botanical affinity to the genus *Pteris*, but after our opinion the genus *Pterisisporites* Sung & Zheng represents another genus or group of spores. It is probably an ancestor of the pteridoid group. Spores of *Pterisisporites* Sung & Zheng are much smaller (20–35 (40) µm) than recent spores of the genus *Pteris* (40 to over 100 µm, very rare a little lower than 40 µm).

Whereas spores of this group found in Neogene deposit of Georgia and Eastern Europe are of the same or similar size as recent spores of *Pteris*. Also the equatorial collar is in *Pterisisporites* Sung & Zheng more narrow and not so well developed as in recent *Pteris* spores and our fossil material.

After the rules of the International Code of Botanical Nomenclature (ICBN) the priority has the name *Pteridacidites* Sah created for fossil spores of the pteridoid group (Sah 1967). We also described spores from the Neogene deposits of Georgia under this name, bacouse of their undoupted affinity to this group.

[1] Information concerning northern part of Kiangsu Province was derived from Sung and Zheng (1965): Spore assemblage of the northern part of Kiangsu Province, Cretaceous to Tertiary (manuscript)

[2] Sung = Song

Our publication contains 18 plates of photographs of fossil specimens intended to show the variability of spores within the limits of one species, but this has not always been possible because of different degrees of material preservation.

Genus: *PTERIDACIDITES* Sah 1967

Type species: *Pteridacidites africanus* Sah 1967

Pteridacidites longifoliiformis Shatilova & Stuchlik **sp. nov.**
Pl. 1 figs 1–3, Pl. 2 figs 1–4, Pl. 3 figs 1–5

1963. *Pteris* aff. *cretica* L. Mtchedlishvili, p. 74, Pl. 2, Fig. 8.
1974. *Pteris longifolia* L. Purtseladze & Tsagareli, p. 131, Pl. 30, Figs. 10, 11.
1974. *Pteris* sp. I. Purtseladze & Tsagareli, p. 133, Pl. 31, Figs. 1, 2.
1977. *Pteris longifolia* L. Purtseladze, p. 93, Pl. 2, Fig. 3.

Type specimen. Pl. 1 fig. 1. Institute of Palaeobiology, slide No 12 (I), Pontian, Gogoreti village Ozurgetian region, Western Georgia.

Derivation of name. After the similarity with the recent species *Pteris longifolia* L.

Diagnosis. Spore 58–69 μm, with little variation in size. Amb (it should be noted that Nayar and Devi (1966), used the term "amb" in a rather restricted sense, to exclude the collar-like excrescence on the exine which occurs in this genus) rounded-triangular. Laesura arms 24–26 μm. Exine brown, tuberculate. On some specimens the area surrounding the laesura is smooth but separate tubercles are clearly visible at the margins of the spore. On the distal face the tubercles coalesce into sinuous, branched ridges. They form a reticulum with circular or elongate lumina. Some ridges have thin, sometimes double connecting strands (Pl. 3 figs 3–5). Separate tubercles can be seen in the centres of the lumina. Sometimes the reticulum is also on the proximal face. The ridges and tubercles are smooth with the equatorial collar interrupted or continuous, 7.5–8.0 μm wide.

Botanical affinity. Genus *Pteris* L., *P. longifolia* L.

Geofloristic element. Palaeotropical. Nowadays *Pteris longifolia* is known on the Antilles, in tropical America from Mexico to Brazil (Fig. 1). It grows on rocky coasts, and appears often as a pioneer beside newly constructed roads, at low to rather high elevations (Proctor 1985).

Occurrence. Meotian – Lower Kuyalnikian (Lower Skurdumian).

Remarks. The fossil spores are similar to, but somewhat larger than those of the recent *Pteris longifolia* L. (Pl. 4 figs 1–4). The similarity is apparent in the sculpture of the distal and proximal faces.

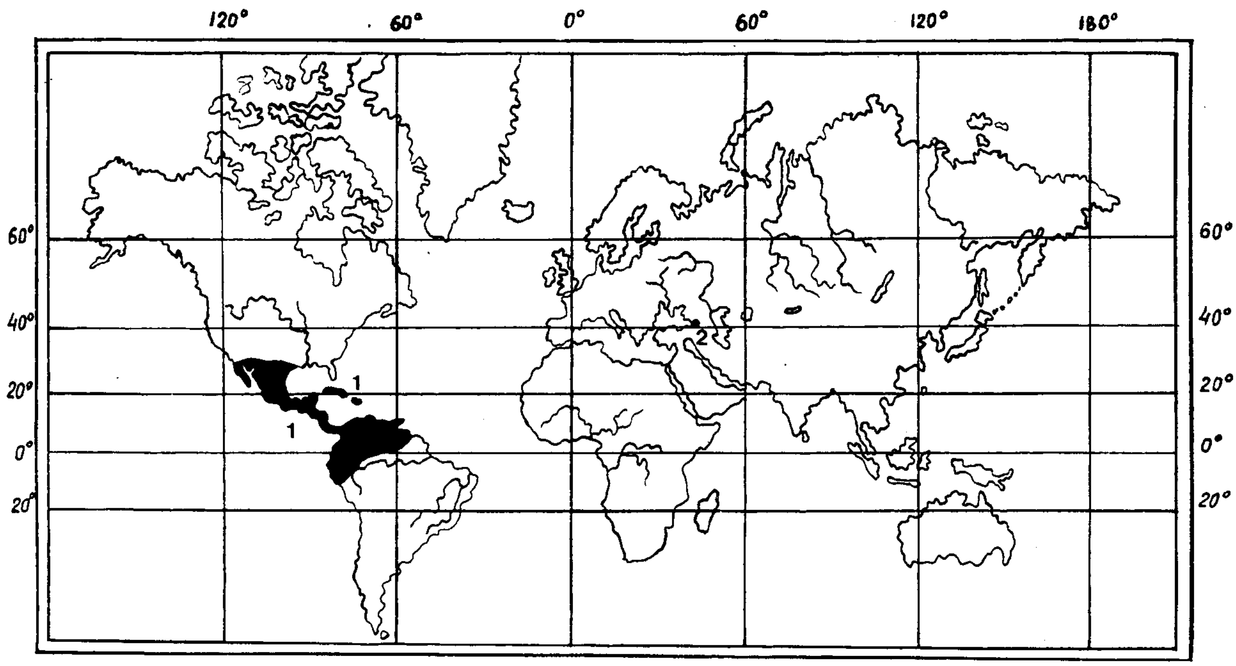

Fig. 1. Distribution of *Pteris longifolia* (1) and *Pteridacidites longifoliiformis* (2)

The spores differ from the morphologically similar spores of *Pteridacidites vittatioides* by greater size and brown colour of the exine which is very typical for fossil spores of *P. longifoliiformis*. Besides, the distal face of *P. vittatioides* is nearly always reticulate and the reticulum is more regular.

Pteridacidites vittatioides Stuchlik & Shatilova **sp. nov.**

Pl. 5 figs 1a-c, 2a, b

1988. *Pteris vittata* L. Shatilova, Ramishvili & Kuchukhidze, p. 334, Fig. 2 (9, 10).

Type specimen. Pl. 5 fig. 1a-c. Institute of Palaeobiology, slide No 1O, Gurian Horizon, Khvarbeti village, Ozurgetian region, Western Georgia.

Derivation of name. After the similarity with the recent species *Pteris vittata* L.

Diagnosis. Spores 38–44 μm, with little variation in size.

Amb rounded-triangular. Exine tuberculate. On the proximal face the tubercles are very variable in size and shape. In some cases they are arranged in ridges parallel to the arms of the leasura. On the distal face the tubercles are large (4.0–6.0 μm) varying in shape from elongate to circular. Coalescing, they form a reticulum of irregularly polygonal or elliptical lumina. There are isolated tubercles at the centres of some of the lumina. The equatorial collar is thin, equal in width to the height of the tubercles and sometimes of similar shape.

Botanical affinity. Genus *Pteris* L., *P. vittata* L.

Geofloristic element. Palaeotropical. *Pteris vittata* L. is a Mediterranean species (Fig. 2). In the Caucasus it is regarded as an adventive (Askerov 1977). Beyond the Caucasus it occurs in Crete, the southern regions of Turkey, in China and the Antilles. It grows on calcareous rocks at lower altitudes. In southern China it is found in pine forest (Kabanov 1971).

Occurrence. Kimmerian-Gurian.

Remarks. The fossil spores are similar to those of *Pteris vittata* L. (Pl. 4 figs 5–8). The similarity is in the sculpture of the proximal and distal faces, form of the equatorial collar and size of spores.

The sculpture of the distal face of spores of *Pteris vittata* L. is similar to that of the spores of *P. longifolia* L. which also have a reticulum. It is interesting to note that the spore of *P. longifolia* L. whose photograph appears in the work of Nayar and Devi (1966, p. 50I, Fig. 24) resembles the spore of *Pteris vittata* L.

Probably these two species have other features of similarity because in Index Filicum (Christensen 1906) *Pteris vittata* is not given as an independent species but as a variety of *P. longifolia* (*P. vittata* L. = *P. longifolia* var. *vittata* Christensen).

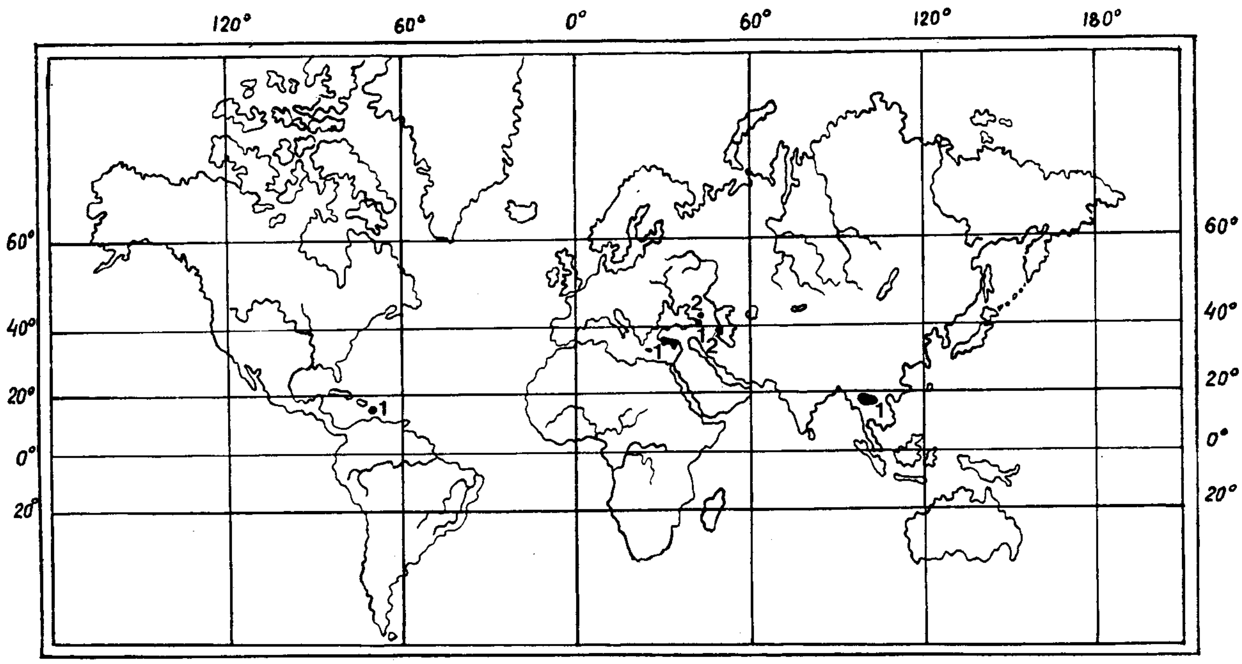

Fig. 2. Distribution of *Pteris vittata* (1) and *Pteridacidites vittatioides* (2)

Pteridacidites grandifoliiformis Stuchlik & Shatilova **sp. nov.**

Pl. 5 figs 3a, b, 4a, b; Pl. 7 figs 1a, b, 2; Pl. 8 figs 1–4

1963. *Pteris* sp. Mtchedlishvili, p. 75, Pl. 2, Fig. 9.
1980. *Pteris* sp. 5 Shatilova & Mchedlishvili, Pl. 4, Figs. 2, 2a.
1987. *Pteris* aff. *grandifolia* L. Stuchlik & Shatilova, Pl. 6, Figs. 15, 16.
1987. *Pteris* sp. Stuchlik & Shatilova, Pl. 7, Figs. 1–3.

Type specimen. Pl. 5 fig. 3a, b. Institute of Palaeobiology, slide No 2(I), Lower Skurdumian, Gogoreti village, Ozurgetian, region Western Georgia.

Geofloristic element. Palaeotropical. Nowadays *Pteris grandifolia* is a component of the flora of Florida, the Antilles and tropical regions of America (Fig. 3).

Occurrence. Sarmatian – Lower Kuyalnikian (Lower Skurdumian).

Remarks. The fossil spores are similar to those of the contemporary *Pteris grandifolia* L. (Pl. 7, Fig. 3a-c.).

The sculpture and outline of the equatorial collar show that the spores of *Pteris* sp. from the Kimmerian deposits (see in synonimics Mtchedlishvili, 1963) may be related to *Pteridacidites grandifoliiformis*.

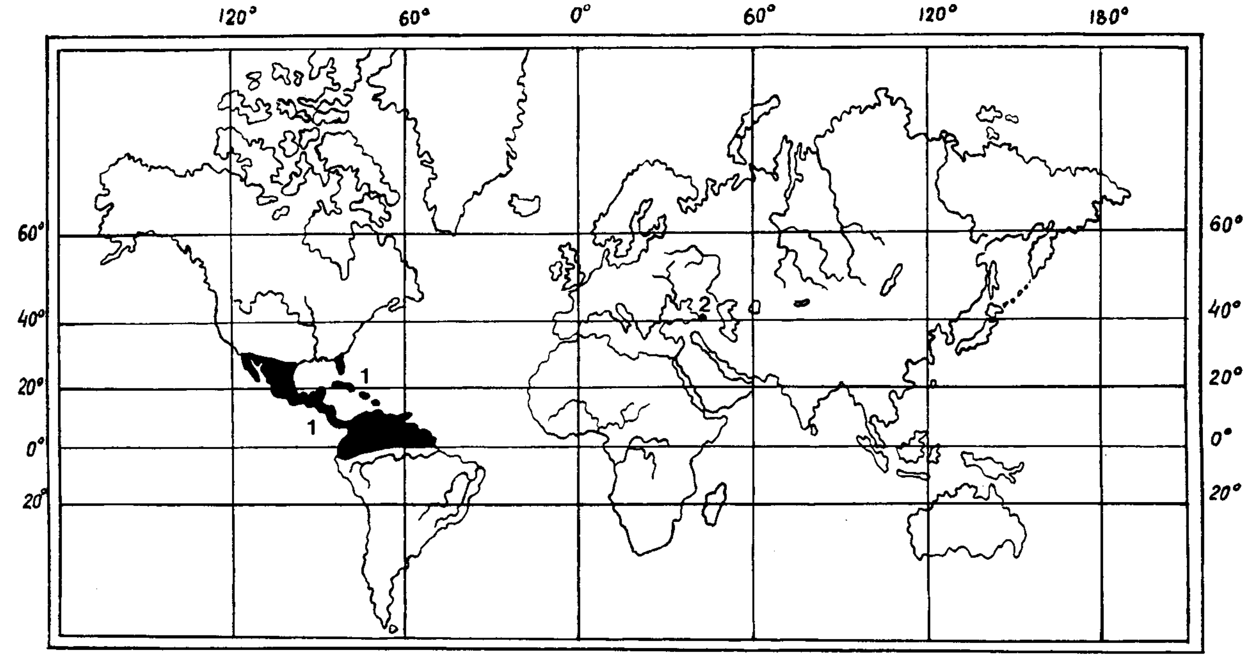

Fig. 3. Distribution of *Pteris grandifolia* (1) and *Pteridacidites grandifoliiformis* (2)

Derivation of name. After the similarity with the recent species *Pteris grandifolia* L.

Diagnosis. Spores 56–61 μm, with little variation in size. Amb rounded-triangular. Exine tuberculate. On the proximal face the tubercles are small (3.0–4.0 μm) and not always easily seen. Their shape varies from oblong and prominent to circular and scarcely raised. On the distal face the tubercles coalesce, forming a large-scale irregular pattern. The largest tubercles are at the angles of the spores. The tubercle surface is irregular (Pl. 8 figs 3, 4). The equatorial collar is wide, from 8.0 to 18 μm across narrowed or interrupted on the angles.

Botanical affinity. Genus *Pteris* L., *P. grandifolia* L.

Pteridacidites verus (N. Mtched.) Shatilova & Stuchlik. **comb. nov.**

Pl. 9 figs 1–6, Pl. 10 figs 2a, b; 3a, b.

1963. *Filicites verus* N. Mtched. Mtchedlishvili, p. 80, Pl. 5, Figs. 4–6.
1974. *Pteris verus* (N. Mtched.) Pur. Purtseladze & Tsagareli, p. 132, Pl. 31, Fig. 4.
1984. *Filicites verus* N. Mtched. Shatilova, Pl. 11, Figs. 8, 9
1984. *Pteris venusta* Kze. Shatilova, Pl. 9, Figs 1, 2.
1984. *Pteris* sp. 8 Shatilova, Pl. 11, Figs. 4, 5.

Type specimen. Pl. 9 fig. 1 a, b. Institute of Palaeobiology, slide No 2, Skurdumian, Tsikhisperdi village, Western Georgia.

Description. Spores 38.5–65 µm, with wide variation in size. Amb rounded-triangular. Both faces of the spore are covered in spinulose tubercles, with a wide base (2.3–5.0 µm). The tubercles are very similar in size but on the proximal face the sculpture elements are somewhat smaller and sparser than on the distal one.

The equatorial collar is sinuous, 6.0–10 µm wide, most often c. 7.7 µm.

Botanical affinity Genus *Pteris* L., *P.* aff. *crenata* Sw.

Geofloristic element. Palaeotropical. Nowadays *Pteris crenata* is found in tropical Australia, China, Polynesia, Ceylon and Japan (Fig. 4).

Pteridacidites variabilis Stuchlik & Shatilova sp. nov.

Pl. 10 fig. 4a-c, 5; Pl. 11 figs 1a-c, 2a-c

1980. *Pteris cretica* L. Shatilowa & Mchedlishvili, Pl. 4, Fig. 2 a, b.
1984. *Pteris cretica* L. Shatilova, Pl. 8, Figs. 1–3.
1987. *Pteris cretica* L. Stuchlik & Shatilova, Pl. 6, Figs. 3, 4.

Type specimen. Pl. 10 fig. 4a-c. Institute of Palaeobiology, slide No 4, Uzunlarian, Tskaltsminda village, Natanebian region, Western Georgia.

Derivation of name. After the great variability of the spores.

Diagnosis. Spores 35.5–55 µm, with wide variation in size. Amb rounded-triangular.

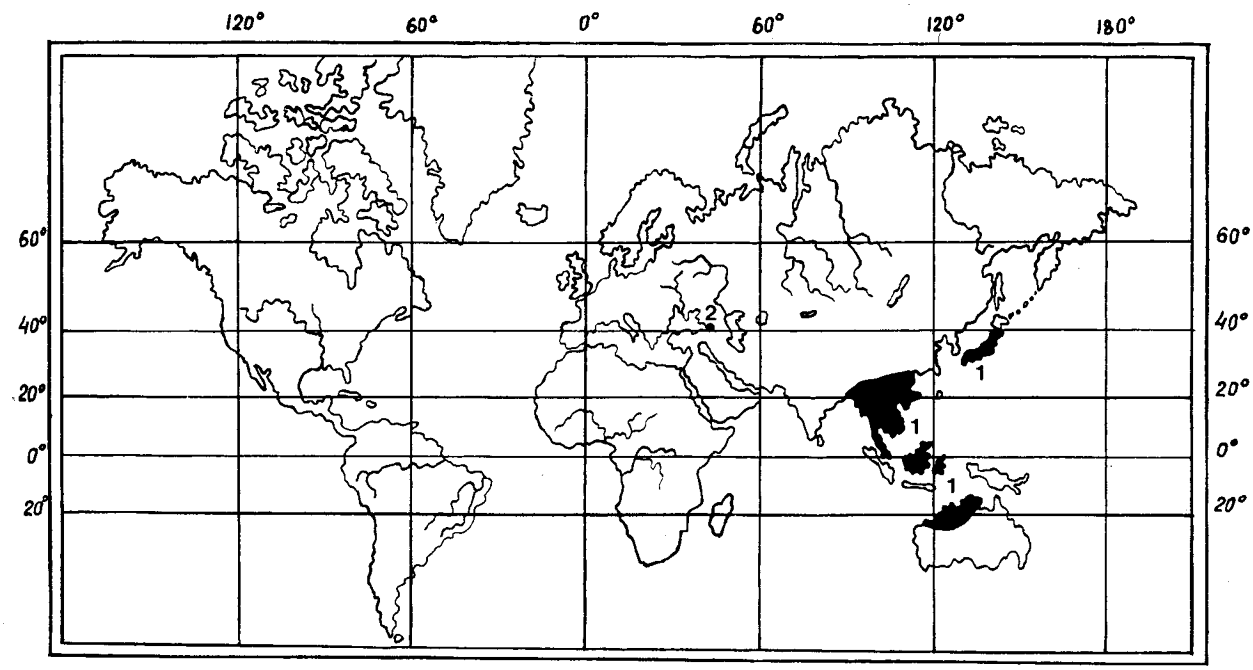

Fig. 4. Distribution of *Pteris crenata* (1) and *Pteridacidites verus* (2)

Remarks. The change of genus results from the determination of the botanical affinity of the fossil spores of *Filicites verus* to the recent species *Pteris crenata* Sw. (Pl. 10, Fig. 1a-c). There are similarities in the nature of the sculpture, in the form of the equatorial collar and in size. In slides both fossil and recent spores often take up a lateral position that is very seldom adopted by the spores of other species of *Pteris*.

Exine tuberculate. On the proximal face the tubercles are adjacent to the laesura, forming a scalloped border along it. On the distal face the tubercles are almost flat and the sculpture pattern is rugose. The equatorial collar is continuous or interrupted, on some specimens narrowed at the angles, 5.0–6.0 µm wide.

Botanical affinity. Genus *Pteris* L., *P.* aff. *cretica* L.

Geofloristic element. Palaeotropical. At the present time *Pteris cretica* is known from the Transcaucasus, Mediterranean, Africa, Madagascar, Florida, Cuba, the Bahamas,

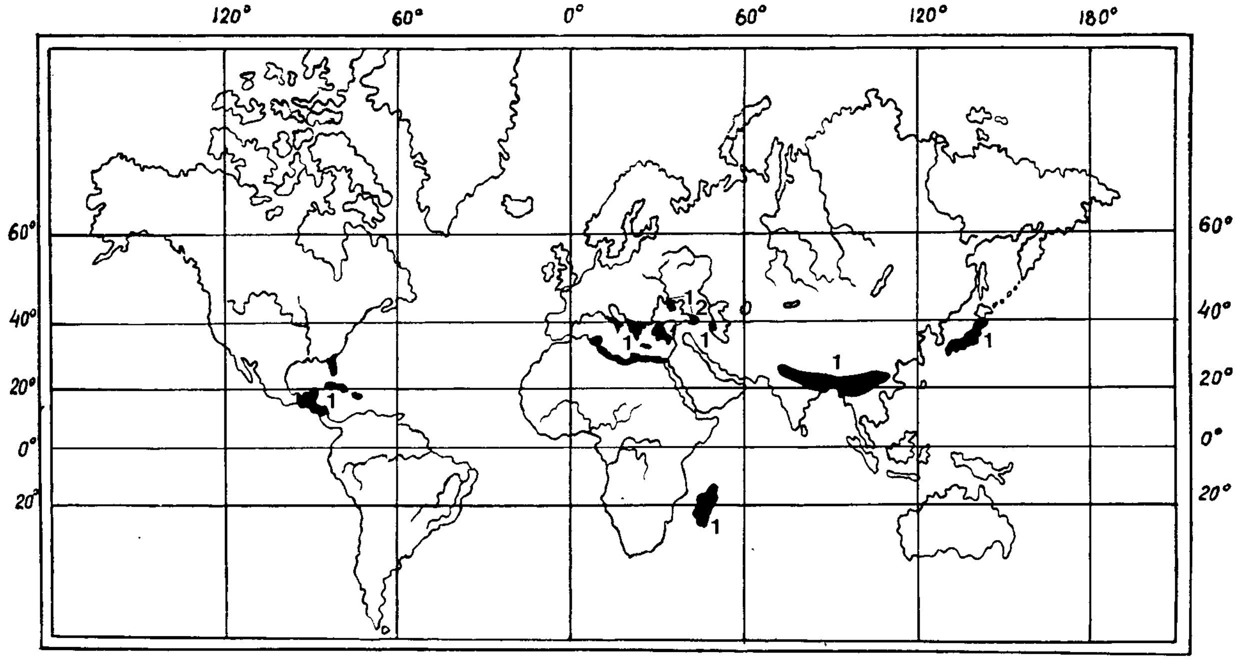

Fig. 5. Distribution of *Pteris cretica* (1) and *Pteridacidites variabilis* (2)

Jamaica, Guatemala and Argentina. It grows along streams and small rivers from 1070 to 1530 m a.s.l. (Proctor 1985). Kabanov (1981) mentioned *Pteris cretica* L. in the composition of the subtropical evergreen forest of China (Fig. 5).

Occurrence. Kimmerian – Upper Pleistocene.

Remarks. The spores of *Pteridacidites variabilis* are characterized by the great variability. In both the size of spores and the nature of the sculpture there is much variation. Most of the spores studied have flat, oblong tubercles, which coalesce forming a rugose pattern. At the same time there are spores which are more prominently sculptured.

A similar picture emerges in recent material. For example, in Plate 11, photographs of both forms are given. One is from Western Georgia (Pl. 11 fig. 5a, b)and the second from Cuba (Pl. 11 figs 3a, b, 4a, b).

The phenomenon of polymorphism in spores of *Pteris cretica* L. has been described by Sladkov (1957).

Pteridacidites dentatiformis
Shatilova & Stuchlik **sp. nov.**
Pl. 12 fig. 1a-c

Type specimen. Pl. 12 fig. 1a-c. Institute of Palaeobiology, slide No 3(2), Kimmerian, Bjuja river, Ozurgetian region, Western Georgia.

Derivation of name. After the similarity with the recent species *Pteris dentata* Forsk

Diagnosis. Spores 40–55 μm, often c. 45 μm. Amb round-triangular. Exine tuberculate. Tubercles small and on the proximal face sparsely distributed and not prominent. The equatorial collar is narrow, 6.0–8.0 μm, less wide on the angles.

Botanical affinity. Genus *Pteris* L., *P. dentata* Forsk.

Geofloristic element. Palaeotropical. Nowadays *Pteris dentata* is known from tropical Africa and Australia.

Occurrence. Kimmerian-Lower Kuyalnikian (Lower Skurdumian).

Remarks. The fossil spores are identical to those of *Pteris dentata* Forsk. (Pl. 12 fig. 2a, b, c). The similarity is evident in the sculpture of the proximal and distal faces of the spores and in the size and shape of the equatorial collar.

Pteridacidites venustaeformis
Stuchlik & Shatilova **sp. nov.**
Pl. 12 figs 3a-c, 4 a-e

1969. *Pteris* aff. *venusta* Kze. Ramishvili, p. 52, Pl. 3, Fig. 5
1984. *Pteris venusta* Kze. Shatilova, Pl. 11, Figs. 1–3.
1987. *Pteris venusta* Kze. Stuchlik & Shatilova, Pl. 6, Figs. 5–12.

Type specimen. Pl. 12 fig. 3a-c. Institute of Palaeobiology, slide No 4(2), Kuyalnikian, Tsikhisperdi village, Ozurgetian region, Western Georgia.

Derivation of name. After the similarity with the recent species *Pteris venusta* Kze.

Diagnosis. Spores 35–40 (-60)µm. Amb rounded-triangular. Exine tuberculate. On the proximal face the tubercles are low and rounded, but on the distal they are prominent, spinulose (4.0–6.0 µm). Both faces are fully covered by sculpture elements but on the proximal they are sparser than on the distal one. The equatorial collar is wide, 6.0–10 µm, narrowing at the angles, sometimes very sinuous.

Botanical affinity. Genus *Pteris* L., *P. venusta* Kze.

Geofloristic element. Palaeotropical. Presently *Pteris venusta* Kze. is known from tropical Africa, Java and the Philippines.

Occurrence. Sarmatian – Gurian horizon.

Remarks. The fossil spores are identical to those of the recent *Pteris venusta* Kze. The similarity is apparent in the sculpture on both faces of the spore and in the size and nature of the equatorial collar.

Pteridacidites remotifolioides Shatilova & Stuchlik **sp. nov.**

Pl. 13 figs 1a, b, 2a, b, 3a-c, 4

1974. *Pteris* sp. 2, 3. Purtseladze & Tsagareli, Pl. 31, Figs. 5, 7
1984. *Pteris* sp. 3. Shatilova, Pl. 10, Figs. 3, 4.

Type specimen. Pl. 13 fig. 1a, b. Institute of Palaeobiology, slide No 5 Kimmerian, River Bjuja, Ozurgetian region, Western Georgia

Derivation of name. After the similarity with the recent species *Pteris remotifolia* Bak.

Diagnosis. Spores 45–50 µm, with little variation in size. Amb triangular, the sides of some spores slightly concave. Exine tuberculate. On the proximal face the tubercles are small (2.0–5.0 µm.). Sometimes they coalesce and form a border along the laesura. On the distal face the tubercles are flat. Together they form a sinuous, marmoreal pattern. The equatorial collar is narrow, 3.0–5.0 µm wide, with straight sides, uninterrupted or interrupted at the angles.

Botanical affinity. Genus *Pteris* L., *P. remotifolia* Bak.

Geofloristic element. Palaeotropical. Currently known from Madagascar.

Occurrence. Meotian – Gurian horizon.

Remarks. The fossil spores are similar to those of the recent *Pteris remotifolia* Bak. (Pl. 13 fig. 5a-c). The similarity is apparent in the size of the spores and in the type of sculpture.

Pteridacidites spiniverrucatus (Trevisan, 1967) Stuchlik & Shatilova **comb. nov.**

Pl. 14 fig. 1a-c

1967. *Polypodiaceoisporites spiniverrucatus* Trevisan, Palaeotogr. Ital., 62, N. Ser., p. 10–11, Pl. 3, Figs. 1–2.
1985. *Polypodiaceoisporites spiniverrucatus* (Trevisan), Nagy, Geologica Hungarica, Fas. 47, p. 103, Pl. 34, Figs. 10–12.

Type specimen. Pl. 14 fig. 1a-c. Institute of Palaeobiology , slide No 117, Kimmerian, Bia village, Zugdidian region, Western Georgia.

Description. Spores 65–70 µm, with little variation in size. Amb rounded-triangular. Exine spinose on proximal face with each spine 1.0–4.5 µm in lenght. The sculpture elements are denser on the angles. The spore sides are almost smooth. On the distal face the tubercles are larger, particularly at the poles and gradually diminish in size towards the equator. The equatorial collar is uninterrupted, 8.0–9.0 µm wide.

Botanical affinity. Genus *Pteris* L., *P. pellucida* Pr.

Geofloristic element. Palaeotropical. Contemporaneously *P. pellucida* Pr. occurs in India, Java and the Philippines.

Occurrence. Kimmerian – Lower Kuyalnikian (Lower Skurdumian).

Remarks. The change of genus results from the determination of the botanical affinities of fossil spores to spores of the recent *Pteris pellucida* Pr. (Pl. 14 fig. 2). There is a small difference in size. Trevisan (1967) also compared this species with *Pteris pellucida* Pr.

Pteridacidites guriensis Shatilova & Stuchlik **sp. nov.**

Pl. 14 fig. 3a, b, Pl. 15 figs 1–4

1980. *Pteris* aff. *togoensis* Hieron. Shatilova & Mchedlishvili, Pl. 5, Fig. 1.
1984. *Pteris* aff. *togoensis* Hieron. Shatilova, Pl. 9, Figs. 5–8.

Type specimen. Pl. 14 fig. 3a, b Institute of Palaeobiology, slide No 5, Lower Skurdumian, Tsikhisperdi village, Ozurgetian region, Western Georgia.

Derivation of name. After the South-Western part of Georgia where the fossil material was obtained.

Diagnosis. Spore 45–48 (-50) µm. Amb rounded-triangular. Exine tuberculate. The proximal face is not always clearly visible. Sometimes it is possible to see a compact row along the laesura. The distal face is covered by large oblong tubercles with rounded apices, 4.0–6.0 µm in width and 4.0–5.0 µm in height. On some specimens the tubercles coalesce into long ridges. The equatorial collar is sinuous or straight, 5.0–7.0 µm wide.

Botanical affinity. Genus *Pteris* L., aff. *P. togoensis* Hieron.

Geofloristic element. Palaeotropical

Remarks. We compared the fossil spores with a photograph of a spore of the recent *Pteris togoensis* Hieron, which was described by Nayar and Devi (1966). Some similarity is evident in the sculpture of the proximal face.

Pteridacidites boerzsoenyensis
Stuchlik & Shatilova (Nagy) **comb. nov.**

Pl. 16 fig. 1a-c, Pl. 17 figs 1a, b; 2a, b

1974. *Pteris* sp. 5 Purtseladze & Tsagarelli, Pl. 31, Fig. 8.
1980. *Pteris* aff. *quadriaurita* Retz. Shatilova, Mchedlishvili, Pl. 6, Fig. 1.
1984. *Pteris* sp. 2 Shatilova, Pl. 10, Figs. 1, 2.
1985. *Polypodiaceoisporites boerzsoenyensis Nagy*, p. 96, Pl. 26, 29, Figs. 1–3.

Type specimen. Pl. 16 fig. 1a-c. Institute of Palaeobiology, slide No 14, Lower Skurdumian, Gogoreti village, Ozurgetian region, Western Georgia.

Description. Spores 50–60 µm, often ca. 55 µm. Amb rounded-triangular. Exine tuberculate. On the proximal face the tubercles vary in size and in shape from circular to oblong. The smaller tubercles surround the laesura and the larger ones are at the ends of the arms. Sometimes the tubercles form a dense row parallel to the collar. The tubercles on the distal face are larger and rather dense, from 2.0 to 10 µm in lenght. Some spores have long retrorse excrescences. The equatorial collar is wide, 5.0–10 µm across, straight or sinuous and narrowed on the angles.

Botanical affinity. Genus *Pteris* L.

Geofloristic element. Palaeotropical.

Occurrence. Sarmatian-Gurian horizon.

Remarks. The change of genus is the result of determining the botanical affinities of the fossil spores to the spores of *Pteris*. We compared our material with the recent *Pteris quadriaurita* Retz. The greatest similarity occurs in the sculpture of the proximal face of the spore, which is always better seen in slides.

As was noted by Nagy (1985) the spores, described from the Neogene deposits of Western Georgia as *Pteris* aff. *quadriaurit*a Hieron, resemble those of *Polypodiaceoisporites boerzsoenyensis* Nagy from the Neogene deposits of Hungary. Judging from the photographs the similarity is really quite striking. The author compares *P. boerzsoenyensis* with *Pteris catoptera*. From this species our form differs in the absence of ridges, which, on the proximal face, are situated along the edges of the spore. The recent spores of *Pteris catoptera* have been described by Tardieu-Blot (1963).

Pteridacidites rarotuberculatus
Shatilova & Stuchlik **sp. nov.**

Pl. 17 fig. 3a, b

1980. *Pteris* sp. 1. Shatilova & Mchedlishvili, Pl. 5, Fig. 3.
1984. *Pteris* sp. Shatilova, Pl. 9, Figs. 9, 10.

Type specimen. Pl. 17 fig. 3a, b. Institute of Paleobiology, slide No 1, Kimmerian, village Gogoreti, Western Georgia.

Derivation of name. After the nature of the sculpture.

Diagnosis. Spores 55–60 µm. Amb rounded-triangular. Exine tuberculate. On both faces tubercles are few. On the distal face they are large, long, with rounded apices or slightly flattened and oblong. Large excrescences alternate with smaller ones. The width of the tubercles at their base is 6.0–7.0 µm, and their height 4.0–8.0 µm. On the proximal face the pattern of sculpture is the same, but the tubercles are smaller.

Botanical affinity. Genus *Pteris* L.

Geobotanical element. Palaeotropical.

Occurrence. Kimmerian – Lower Kuyalnikian (Lower Skurdumian).

Remark. We have been unable to see any analogy with recent species of *Pteris*.

Pteridacidites pseudocreticus Stuchlik & Shatilova **sp. nov.**

Pl. 17 fig. 4a, b, Pl. 18 fig. 1a-c

1969. *Pteris cretica* L. Ramishvili, Pl. 18, Fig. 1a-c.
1974. *Pteris cretica* L. Shatilova, p. 73, Pl. 2, Fig. 3.
1974. *Pteris cretica* L. Purtseladze & Tsagareli, Pl. 31, Fig. 3
1980. *Pteris cretica* L. Shatilova & Mchedlishvili, Pl. 15, Fig. 2.
1984. *Pteris* sp. 6 Shatilova, Pl. 10, Figs. 5–10.
1988. *Pteris* aff. *cretica* L. Shatilova, Ramishvili & Kuchukhidze, p. 333, Fig. 1 (11–14).

Type specimen. Pl. 17 fig. 4a, b Institute of Palaeobiology, slide No 24, Kimmerian, Morokhvili village, Western Georgia.

Derivation of name. After the primary determination.

Diagnosis. Spore 45–60 μm, with little variation in size. Amb rounded-triangular. Exine tuberculate. On the proximal face the lenght of the separate tubercles ranges from 2.0 to 8.0 μm and their shape varies from circular to oblong. The tubercles are concentrated mainly at the poles. On the distal face the pattern is not clearly visible. Coalescing, the tubercles form a compact mass, in which it is impossible to see separate elements. They are located along the margins of the spore with the main mass concentrated at the poles. The equatorial collar is slightly sinuous, 6.7–7.0 μm wide.

Botanical affinity. Genus *Pteris* L.

Geofloristic element. Palaeotropical.

Occurrence. Meotian-Gurian horizon.

Remarks. As can be seen from the synonymy this type of spores was described mainly as *Pteris cretica* L. As would have been expected, most investigators gave details of the proximal face, which is more easily observed than the distal one. The sculpture of the latter is not clearly visible, is often flattened and concentrated at the poles but as a whole is different from that of the recent *Pteris cretica* L. The sculpture of the proximal face is different too, that of the spores of *Pteris cretica* L., being scalloped rather than tuberculate. The main difference is the shape of the equatorial collar which on most specimens of *P. pseudocreticus* is wide, uniform and not narrowed at the angles as it is in the majority spores of *Pteris cretica* L.

Pteridacidites kimmeriensis Shatilova & Stuchlik **sp. nov.**

Pl. 18 fig. 2a, b

1963. *Pteris* sp. 2 Mtchedlishvili, p. 75, Pl. 3, Fig. 1.

Type specimen. Pl. 18 fig. 2a, b. Institute of Palaeobiology, slide No 14 (2), Kuyalnikian, Gogoreti village, Western Georgia.

Derivation of name. After the deposits where the spores were first seen.

Diagnosis. Spores 55–60 μm, with little variation in size. Amb rounded-triangular. Exine tuberculate. Tubercles very large with rounded apices and wide bases, distant. Tubercles similar in size on both faces, 6.0 μm tall and 8.0 to 10 μm in wide. Equatorial collar slightly narrowed at the angles, 6.0–10 μm wide, sometimes sinuous.

Botanical affinity. Genus *Pteris* L.

Geofloristic element. Palaeotropical.

Occurrence. Pontian – Lower Kuyalnikian (Lower Skurdumian).

Remarks. We have been unable to see any analogy with recent species of *Pteris*.

Pteridacidites georgensis Stuchlik & Shatilova **sp. nov.**

Pl. 18 fig. 3

1974. *Pteris* sp. 4 Purtseladze, Tsagareli, Pl. 37, Fig. 6.

Type specimen. Pl. 18 fig. 3. Institute of Palaeobiology, slide No 2 (I), Meotian, Gogoreti village, Ozyrgetian region, Western Georgia.

Derivation of name. After the country where the fossil material was obtained.

Diagnosis. Spores 50–56 μm, with little variation in size. Amb rounded-triangular. Laesura open. Exine tuberculate. On the proximal face the tubercles are oblong and distributed along the laesura. Elsewhere on of the spore the sculpture is very small, although on the distal face the tubercles are somewhat larger (2.0 μm). Equatorial collar sinuous, 8.0 μm wide, narrowed at the angles.

Botanical affinity. Genus *Pteris* L.

Geofloristic element. Palaeotropical

Occurrence. Meotian.

Remarks. We have been unable to find any analogy with recent species of *Pteris*.

Pteridacidites helveticus (Nagy, 1969) Stuchlik & Shatilova **comb. nov.**

Pl. 18 fig. 4 c-e

1969. *Polypodiaceoisporites helveticus* Nagy, p. 346, Pl. 20, Figs. 14, 17.
1982. *Polypodiaceoisporites helveticus* Nagy, Ramishvili, Pl. 3, Fig. 5.
1985. *Polypodiaceoisporites helveticus* Nagy, p. 91, Pl. 30, Figs. 1–6.

Type specimen. Pl. 18 fig. 4 a-c. Institute of Palaeobiology, slide No 117, Sarmatian, Djgali village, Zugdidian region, Western Georgia.

Description. Spores 45–50 μm, amb rounded-triangular. Laesura open. Exine tuberculate. On the proximal face the tubercles are located along the laesura, forming a border. On the distal face the tubercles are tall (4.5–5.0 μm, with rounded or truncated apices. Equatorial collar about 8.0 μm wide, narrowed on the angles.

Botanical affinity. Genus *Pteris* L.

Geofloristic element. Palaeotropical.

Occurrence. Middle Miocene-Sarmatian.

Remarks. We have found it imposible to see analogy with any recent species of *Pteris*.

STAGES IN THE DEVELOPMENT OF THE PTERIDOFLORA OF WESTERN GEORGIA

The evolution of ferns was closely connected with the evolution of trees, under whose cover they grew and developed. The succession of dominants of the forest canopy was the main cause of change in the environment of the pteridoflora and resulted in the extinction of some ferns and the development of others.

The nature of the forest vegetation of Western Georgia changed from the subtropical and warm temperate forests of the Miocene and Pliocene periods, to the temperate forests of the Quaternary. The pteridoflora also changed during this period. After the Sarmatian, the extinct ferns were replaced by genera whose representatives continue to live today in different parts of the World. Among these were tropical and subtropical forms, which had already occupied the limited relict area in the Meotian period. Along with them were ferns able to live in both subtropical and warm temperate climates. Possessing a comparatively wide ecological tolerance, such forms thrived in the conditions of high mountain relief in the second half of the Neogene. Their prevalence continued throughout the Pliocene, by the end of which they had been completely replaced by ferns of temperate climates.

Table 4 showing the distribution of spores in the Neogene deposits is given below. The table contains our data as well as that of other investigators (Avakov 1979, Chelidze 1987, Kolakovsky & Shakryl 1976, Purtseladze & Tsagareli 1974, Ramishvili 1969, 1982, Uznadze & Tsagareli 1979).

Some recent fern taxa already existed on the territory of Georgia in the Mesozoic period (Karashvili 1973, 1977) but it was only in the Neogene that they flourished.

The complexes of the Middle Miocene period are characterized by the abundance and broad taxonomical diversity of the ferns. The pteridoflora of this time was represented mainly by extinct taxa, missing from the flora of Western Georgia after the Sarmatian. As Ramishvili (1982) first noted, forms similar to the Palaeogene and Early Miocene floras must be distinguished. Their presence gives an “ancient” appearance to the Middle Miocene flora of Georgia.

More often large spores are found, similar to those from the Oligocene and Early Miocene deposits of Europe, known under the name *Triletes multivalatus* W. Kr. Ramishvili described this form as *Lygodium multivalatum* (W. Kr.) comb. nov. Ram. Spores similar to the Late Palaeogene *Toroisporites lusaticus* W. Kr. can also be found in the deposits.

In the Middle Miocene flora the family Gleicheniaceae is represented by one recent genus *Gleichenia* and one extinct taxon *Clavifera* Bolch., which is characteristic for Cretaceous and Palaeogene deposits.

In the Karaganian and Konkian layers, spores of *Cyathea* are similarly often present. They differ from the Pliocene forms, and resemble *Leiotriletes wolfi* W. Kr., being typical for the Palaeogene complexes of Central Paratethys.

Spores of *Verrucatosporites histiopteroides* W. Kr., *V. allienus* (R. Pot.) Th. et Pf., *V. favus* (R. Pot.) Th. et Pf, as well as diverse species of the genus *Polypodiaceoisporites* are the constant components of Middle Miocene palynocomplexes.

From the Middle Miocene deposits, the leaf

Table 4. The distribution of remains of ferns (except *Pteris*) in Neogene and Pleistocene deposits of Western Georgia

Name of plants	Middle Miocene	Sarmatian	Meotian	Pontian	Kimmerian	Lower Kuyalnikian (L. Skurdumian)	Kuyalnikian (Middle – Upper)	Gurian	Tschaudian	Old Euxinian	Uzunlarian
1	2	3	4	5	6	7	8	9	10	11	12
Family Osmundaceae											
Osmunda cinnamomea L.							+	+	+		+
O. heeri Gaud.					+						
O. schlemnitziensis Pettko			+								
O. strozzi Gaud.			+								
O. aff. *clytoniana* L.					+	+	+	+			
O. regalis L.					+	+	+	+	+	+	+
Todea sp.				+	+						
Family Schizaeaceae											
Schizaeaceae gen. indet.					+						
Family Anemiaceae											
Anemia cf. *mexicana* Klat.	+										
Anemia sp.	+		+	+							
Mohria sp.	+		+								
Family Lygodiaceae											
Lygodium digitatum Presl.	+		+								
L. japonicum Sw.			+	+	+						
L. multivallatus W. Kr. comb. nov. Ram.	+										
Lygodium sp.	+	+									
Toroisporites lusaticus W. Kr. (*Lygodium* sp.)	+										
Family Pteridaceae											
Cryptogramma acrostichoides R. Br.				+			+	+	+		
C. crispa (L.) R. Br.									+		+
C. aff. *crispa* (L.) R. Br.			+	+	+	+	+	+			
Cryptogramma sp.			+	+	+	+	+	+			
Family Parkeriaceae											
Ceratopteris duabensis Kol.					+						
Family Adiantaceae											
Adiantum sp.		+	+								
Anogramma sp.	+		+	+	+	+	+	+			
Onychium sp.	+										
Pityrogramma sp.			+		+	+					
Family Gleicheniaceae											
Clavifera triplex Bolch.	+										
Gleichenia angulata Naum.	+		+	+							
Gleichenia sp.	+	+	+	+	+	+					
Family Atoniaceae											
Matonia sp.			+								
Family Polypodiaceae											
Polypodium aureum L.			+	+	+	+	+	+	+	+	

Table 4. Continued

1	2	3	4	5	6	7	8	9	10	11	12
P. australe Fee							+	+	+	+	+
P. palaeopectinatum Kol.				+							
P. palaeoserratum Kol.			+	+							
P. pliocenicum Ram.				+	+	+	+	+			+
P. tuberculatum N. Mtched.				+	+	+					
P. verrucatum Ram.	+	+									+
P. vulgare L.				+	+	+	+	+	+	+	+
Polypodiisporites potoniei Nagy	+										
Verrucatosporites alienus Th. et Pf. (*Polypodium* sp.)	+										
V. histiopteroides W. Kr. (*Polypodium* sp.)	+										
V. favus (R. Pot.) Th. et Pf. (*Polypodium* sp.)	+										
Pyrossis sp.						+	+				
Family Hymenophyllaceae											
Hymenophyllum rotundum N. Mtced	+			+	+						
Hymenophyllum sp.	+		+	+	+	+	+		+		
Vandenboschia cf. *radicus* (Swartz.) Copel		+									
V. fomini (Pal.) Kol		+									
Family Thyrsopteridaceae											
Cibotium glaucum (Sm.) Hu et Azn.				+							
C. guriensis Pur.	+		+								
Cibotium sp.		+									
Family Dicksoniaceae											
Dicksonia antarctica R. Br.	+	+	+	+	+	+					
D. luculenta Pur.			+		+	+					
D. reticulata Pur.	+	+	+	+	+	+	+	+			
D. unitotuberata Pur.	+	+	+	+	+	+	+	+			
D. spanditocincta Pur.			+								
D. aff. *fibrosa* Col.								+	+		
Dicksonia sp.	+	+	+	+	+	+	+				
Family Cyatheaceae											
Alsophyla sp.			+	+	+						
Cyathea sp.	+	+	+	+	+	+	+	+			
Divisisporites W. Kr. (*Cyathea* sp.)	+										
Leiotriletes miocaenicus Nagy (*Cyathea* sp.)	+										
L. wolfii W. Kr. (*Cyathea* sp.)	+										
Family Dennstaedtiaceae											
Pteridium oeningensis (Ung.) Kol.		+									
Pteridium sp.											+
Family Thelypteridaceae											
Thelypteris sp.							+	+	+	+	+
Family Aspleniaceae											
Asplenium wegmanni A. Br.	+		+								
Asplenium sp.		+	+			+	+	+			
Onoclea sp.										+	
Family Aspidiaceae,											
Athyrium felix-femina (L.) Roth										+	+

Table 4. Continued

1	2	3	4	5	6	7	8	9	10	11	12
Athyrium sp.									+		
Athyrium sp.									+		
Athyrium sp.									+		
Aspidium sp.			+					+			
Cyclophorus sp.					+						
C. (*Lastrea*) *fischeri* Heer	+	+									
C. stiriacus (Ung.) Ching et Takht		+									
Cystopteris fragilis (L.) Bernh.,											
Cystopteris sp.			+								
Dryopteris oreopteris (Ehrh.) Maton							+				
Dryopteris sp.					+	+	+	+	+	+	+
Gymnocarpium sp.					+	+	+	+	+	+	+
Lastrea sp.		+			+						
Polystichum lonchitis (L.) Both.			+								
Polystichum sp.							+	+			
Struthiopteris filicastrum All.					+						
Woodsia alpina (Both.) Gray					+	+	+	+			
W. aff. *polystichoides* Eaton									+		
Woodsia sp.		+									
Family Blechnaceae											
Woodwardia roessneriana (Ung.) Heer	+		+								
W. aff. *radicans* (L.) Smith			+								
Woodwardia sp.				+	+						
Family Salviniaceae											
Azolla sp.					+						
Salvinia palaeopilosa Shap.				+							
Salvinia sp.		+	+		+						

prints of *Pteris parchlugiana* Ung. were described. This form has been compared with *Pteris longifolia* L. (Avakov 1979).

On the whole, with the exception of some forms, the ferns of the Middle Miocene flora of Georgia were represented by extinct taxa, the typical for mainly ancient floras. The composition of the Middle Miocene ferns can be divided into three groups.

The first is the "ancient" group, typical for the Paleogene and Early Miocene floras of different regions of Paratethys. The majority of them have been determined by an artificial system of classification and it is not always possible to trace their botanical affinities. *Toroisporites lusaticus* W. Kr., *Clavifera triplex* Bolch., *Leiotriletes miocaenicus* Nagy, species of the genus *Polypodiaceoisporites* and others belong to this group.

The second group is composed of recent genera now growing mainly in relict areas, being restricted to tropical and subtropical zones of the Earth. These include *Anemia, Lygodium, Gleichenia, Dicksonia, Cyathea* and others.

The third group, not numerous in the Middle Miocene, has been preserved on the territory of Georgia untill the present time in single species of genera such as *Osmunda, Polypodium, Pteris, Hymenophyllum, Anogramma* and *Asplenium*.

The palynological data, as well as the results of studies of macroscopic plant remains, have proved the existence of certain vegetation belts in the Karaganian and Konkian. They were formed under the conditions of mountainous, but broken relief, which, however, were less prevalent in the Middle Miocene and the first half of the Sarmatian than in subsequent periods.

The coastal zone and lower and middle

mountain belts were occupied by humid subtropical forests of *Sterculia* with representatives of the families Araceae, Moraceae, Lauraceae, evergreen Fagaceae and other plants. It is probable that the majority of extinct ferns as well as *Cyathea, Dicksonia, Lygodium, Anemia* and *Hymenophyllum* inhabited these forests. There were also some representatives of *Pteris* and *Polypodium* typical for subtropical and tropical regions.

and the ferns *Dicksonia, Cibotium, Cyathea, Pteris* and *Polypodium* were growing. But the area of distribution of ferns of warm temperate and temperate climates, occupied the middle mountain belt. The communities peculiar to these climatic conditions were composed of *Carpinus, Castanea, Fagus, Tilia, Juglans, Cryptomeria, Cathaya, Keteleeria, Podocarpus* and other plants (Fig. 6).

Spores of *Polypodium verrucatum* Ram., known in the flora of Georgia from the Middle Miocene, were found in the Sarmatian deposits and the genus *Pteris* was represented by a number of species. It is interesting to note the presence of such species as *Pteridacidites boerzsoenyensis* and *P. venustaeformis* which flourished in Western Georgia during the Middle and Upper Pliocene. At the same time the spores of *Pteridacidites helveticus* were found, a form known to occur in the flora of Western Georgia after the Sarmatian.

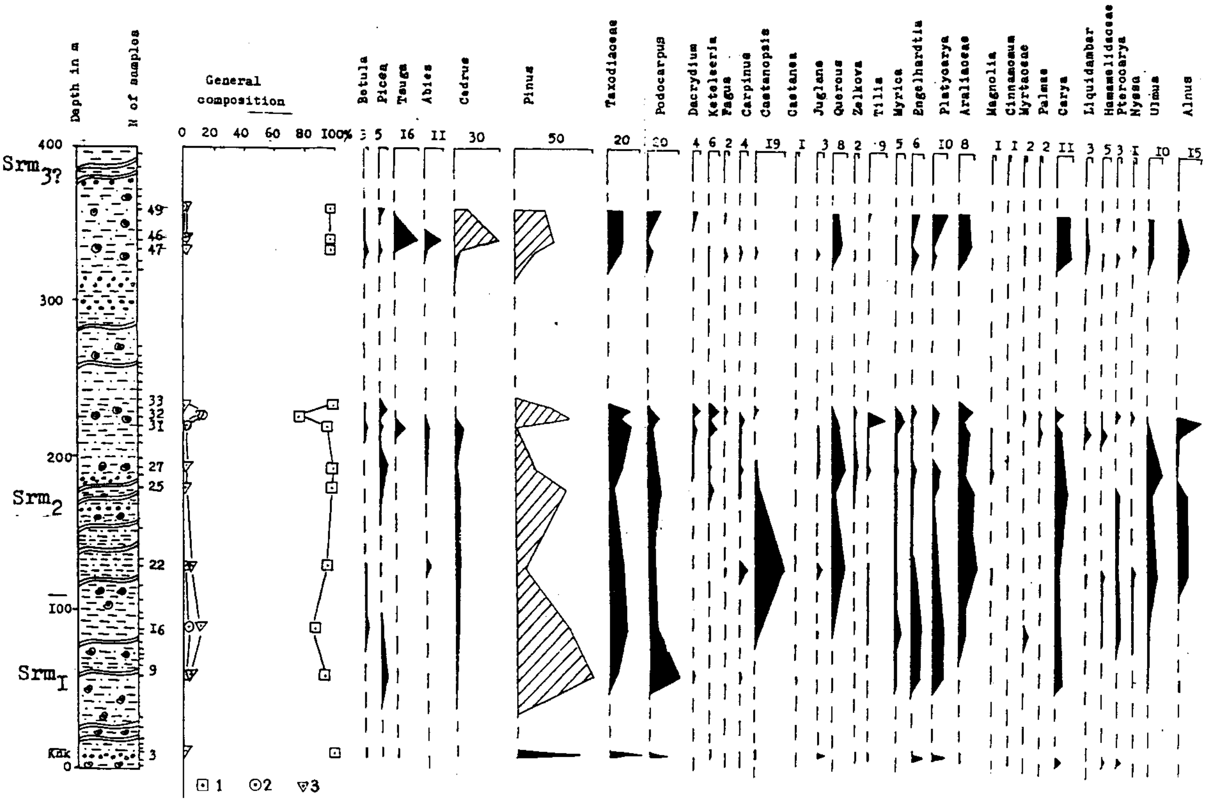

Fig. 6. Pollen diagram for the Sarmatian deposits on the Djgali river (Western Georgia) 1 – AP, 2 – NAP, 3 – spores

From palaeobotanical data (Kolakovsky & Shakryl 1976, Shatilova et al. 1991) we know about the existence in the Sarmatian time of a rich forest vegetation, which was distributed on the complex relief in accordance with different climatic conditions.

The maritime plains were occupied by marsh forests of *Taxodium, Alnus, Ulmus, Carya, Nyssa, Liquidambar*, representatives of the family Hamamelidaceae and other plants.

The vegetation of the lower mountain zone consisted of evergreen subtropical forests with a predominance of Lauraceae and Myrsinaceae (Kolakovsky & Shakryl 1976). Here also *Castanopsis*, some members of the *Araliaceae*, together with *Symplocos, Sycopsis, Fothergilla*

The end of the Middle Sarmatian was the turning-point in the Neogene history of the Caucasus; the great palaeogeographical changes, the forming of mountain relief, the division of the territory of Georgia into two regions – Western and Eastern and the isolation of Colchis were confined to this time (Figs 7, 8).

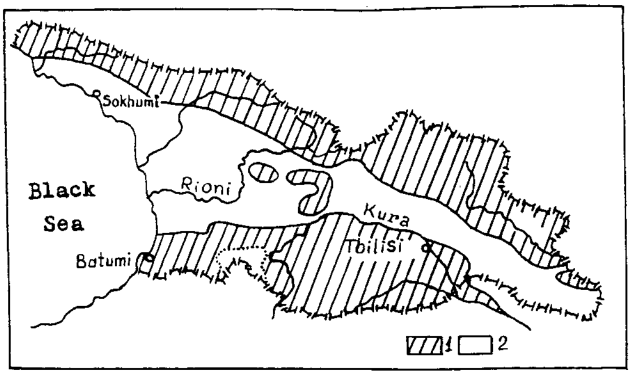

Fig. 7. The palaeogeography of Georgia in the Early Sarmatian (Uznadze 1965). 1 – dry land, 2 – sea

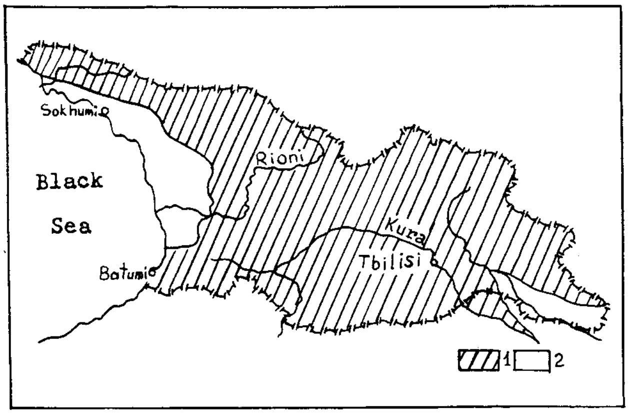

Fig. 8. The paleogeography of Georgia in the Late Sarmatian (Uznadze 1965). 1 – dry land, 2 – sea

After the Sarmatian a great many plants disappeared from the flora of Western Georgia, mainly evergreen trees and the most thermophilous coniferous and cryptogamic plants. Among the ferns, the extinct genera typical for the Early and Middle Miocene died out almost completely.

In the Meotian flora the most thermophilous group of ferns was represented by the genera *Anemia, Mohria, Gleichenia, Matonia, Cibotium* and *Dicksonia,* the last being notable for its specific diversity. At this time such forms as *Pteris* and *Polypodium* extended their areas of distribution. *Pteris* was characterized by prevalence of two species, *Pteridacidites longifoliiformis* and *P. grandifoliiformis*.

Maybe the extended distribution of the genera *Pteris* and *Polypodium* in the Meotian period was connected with changes in the vegetational cover, which had taken place in the Upper Sarmatian. To the end of this period the communities of warm temperate climates, which, in the Early and Middle Sarmatian had been restricted by the middle mountain zone, widened their area. They became distributed in the lower belt and partially occupied the territories of evergreen forests, whose area, after the Sarmatian, was reduced. Simultaneously the increase in taxonomic diversity of the genera *Pteris* and *Polypodium* and their extension of range occured. The subsequent history of these two genera was linked to the evolution of broad-leaved deciduous forests.

As a whole the ferns of the Meotian can be divided into two groups. The first and most numerous consisted of completely extinct species, and species preserved to the present day in tropical and subtropical regions of the World. To this group we can add related forms determined only up to genus level, which are either completely absent from the recent flora of Georgia or represented by one or two species whose morphology is well known. Such are: *Anemia* sp., *Mohria* sp., *Lygodium* sp., *Lygodium japonicum*, *Pteridacidites longifoliiformis, P. grandifoliiformis, P. verus, P. remotifolioides, P. boerzsoenyensis, P. pseudocreticus, P. georgensis, Gleichenia angulata, Pityrogramma* sp., *Matonia* sp., *Polypodium aureum, P. palaeoserratum, Polypodium* sp., (*Verrucatosporites histiopteroides*), *Cibotium guriensis, C. glaucum, Dicksonia antarctica, D. luculenta, D. unitotuberata, D. reticulata, D. spanditocincta, Alsophyla, Cyathea* sp., and others. The second small group consists of the ferns whose descendants have survived up to the present time in Western Georgia: *Cryptogramma crispa, Polypodium vulgare, Polystichum lonchitis* and others.

It has been conjectured that, in the Meotian period the dry land surrounding the sedimentary basin attained a height od some 2000 m (Purtseladze & Tsagareli 1974). The height and broken relief favoured diversity of vegetation. The plains and foothills were covered by subtropical communities (Kolakovsky & Shakryl 1970). Those peculiar to a warm temperate climate were located higher (Fig. 9) and it was probably here that the bulk of cryptogamous plants grew, forming the lower layers of subtropical and warm temperate forests. One of

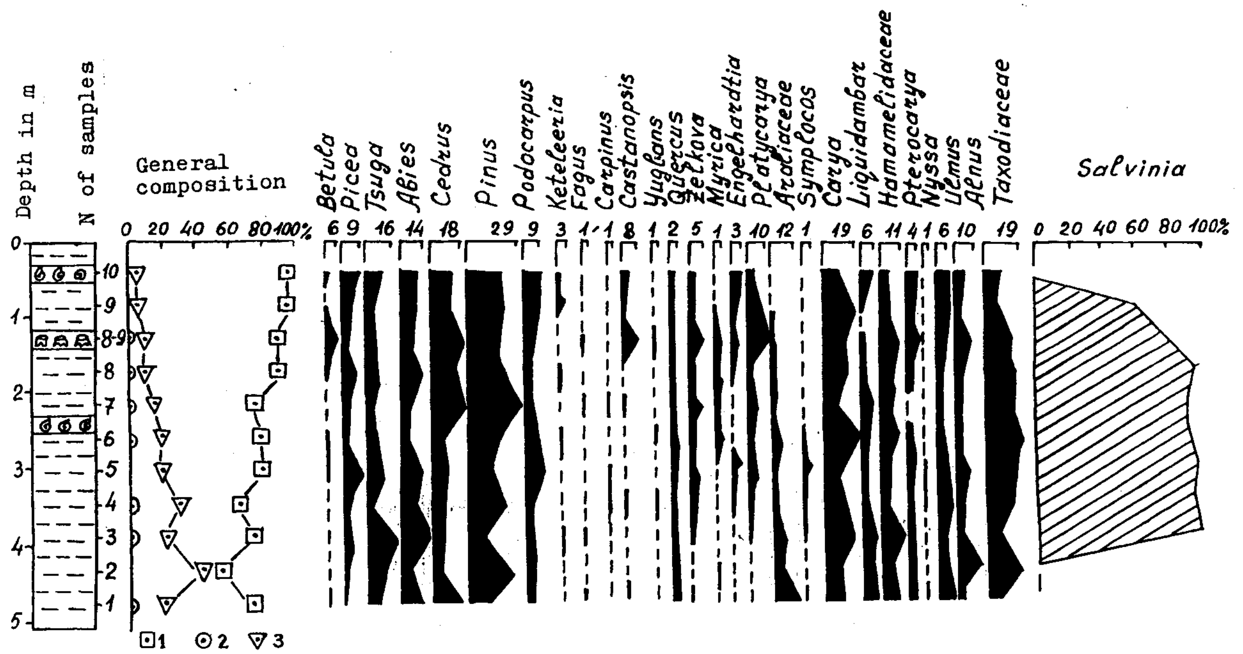

Fig. 9. Polen diagram of the Meotian deposits on the Gudou river (Western Georgia) 1 – AP, 2 – NAP, 3 – spores

the tree ferns identyfied in the Meotian flora, *Dicksonia antarctica,* now grows in temperate rain forests on the Eastern coast of Australia (Walter 1974) with *Eucalyptus, Nothofagus* and other plants.

Such ferns as *Matonia, Mohria* and *Cybotium guriensis* disappeared after the Meotian. But on the whole the composition of the group of thermophilous ferns remained rich. *Anemia, Gleichenia, Dicksonia* and *Cyathea* were still components of the palynocomplex of Pontian deposits but their percentage conten was much lower than that of *Polypodium* and *Pteris.* In the Pontian the latter was represented by the same species as in the Meotian, among which *Pteris longifolia* remained the most prevalent.

As far as the composition and character of the flora were concerned, there was not a big difference between Meotian and Pontian. The main features of the Early Pliocene flora had already been formed in the Late Sarmatian and were preserved untill the end of the Kimmerian.

Rich subtropical forests, which covered the coastal plain and foothills, continued to exist in Pontian time. With the heightening of relief they were displaced by dominant deciduous and coniferous formations. Most of ferns inhabited the lower and middle forest belts but it is not impossible that some of them reached higher altitudes.

After the Pontian the group of tropical and subtropical ferns underwent further impoverishment. In the Kimmerian deposits the spores of *Lygodium digitatum, Lygodium* sp., *Gleichenia angulata, Woodwardia roessneriana* and *W. radicans* are absent. At the same time the number of spores of *Polypodium* and *Pteris* continued to increase. The latter is represented by 14 forms (Tab. 5). In Kimmerian, *Pteridacidites longifoliiformis* and *P. grandifoliiformis* were not dominant species and the percentage of their spores in the composition of the complex is much lower than that of *P. venustaeformis, P. verus, P. remotifolioides, P. boerzsoenyensis, P. rarotuberculatus, P. pseudocreticus* and *P. kimmeriensis.*

The other characteristic feature of the Kimmerian pteridoflora was the increase of genera typical for temperate climates and which have survived on the territory of Georgia to the precent day, such as: *Cystopteris, Dryopteris, Gymnocarpium, Woodsia* and others.

Comparison of the composition of angiosperms from the Pontian and Kimmerian shows that about 125 forms disappeared between these two stages. The more thermophilous plants, typical for the forests of the plains and foothills, mainly died out. The Kimmerian marks the final stretch of the Pliocene when subtropical forests still existed in Western Georgia. It was a relict formation, whose area

Table 5. The distribution of spores of the genus *Pteridacidites* in Neogene and Pleistocene deposits of Western Georgia

Species of *Pteridacidites*	Miocene		Pliocene					Pleistocene	
	Sarmatian	Meotian	Pontian	Kimmerian	Lower Kuyalnikian (L. Skurdumian)	Kuyalnikian (Middle-Upper)	Gurian	Tschaudian	Old Euxinian – Uzunlarian)
Pteridacidites boerzsoenyensis	+	+	+	+	+	+	+		
P. dentatiformis		+	+	+	+				
P. georgensis		+							
P. grandifolliformis	+	+	+	+	+				
P. guriensis			+	+	+	+	+		
P. helveticus	+								
P. kimmeriensis			+	+	+				
P. longifoliiformis		+	+	+	+				
P. rarotuberculatus				+	+				
P. remotifolioides		+	+	+	+	+	+		
P. spiniverrucatus				+	+				
P. variabilis				+	+	+	+	+	+
P. venustaeformis	+	+	+	+	+	+	+		
P. verus		+	+	+	+	+	+		
P. vittatioides				+	+	+	+		

had already been significantly reduced. After the Kimmerian it disappeared completely. Only separate representatives of evergreen forests are preserved in the flora of the Late Pliocene and Pleistocene.

In Western Georgia a sharp fall in temperature occured in the Upper Kimmerian (Figs 10, 11). This fenomenon was one of the reasons why many angiosperms and cryptogams became extinct, including such ferns as *Anemia* and *Gleichenia*, representatives of the Schizaeaceae. From the whole group of thermophilous ferns, excluding *Pteris* and *Polypodium*, only *Anogramma, Pityrogramma, Cyathea* and *Dicksonia* have survived.

After the Kimmerian the vegetation of Western Georgia continued to develop under comparatively unstable climatic conditions. This was the main reason for the more or less sharp successional changes of vegetation during the Kuyalnikian (Egrissian) period (Fig. 12). Three stages, corresponding to the Skurdumian, Etserian and Tsikhisperdian horizons can be distinguished. In turn the Skurdumian can be divided into two parts, the lower with a rich flora and the upper with a spore-pollen complex in which coniferous pollen predominates.

In the Early Skurdumian the arboreal vegetation as a whole preserved features of similarity with that of the Kimmerian. The main communities at that time were dominant coniferous and deciduous forests, the prevailing components of which were *Cedrus, Abies, Pinus, Tsuga, Carya, Quercus, Pterocarya* and others. Among the subtropical plants *Podocarpus, Phyllocladus, Alangium* and *Aralia* were particularly important. The fern cover principally *Dicksonia, Cyathea, Polypodium* and *Pteris* was notable for its great diversity. The composition of the last in the Early Skurdumian was unchanged and all species typical for the Kimmerian were still present at this time. In order to emphasize this continuity, as well as the changes in the pteridoflora of Western Georgia during the Kuyalnikian, we have created a separate column in the Early Skurdumian (Table 5).

In the upper layers of the Skurdumian horizon the composition of the spore-pollen complex was changed. The amount of pollen of coniferous and broad-leaved plants was reduced, spores of thermophilous ferns disappeared and the prevailing component of the complex became the pine.

The changes in composition of the vegeta-

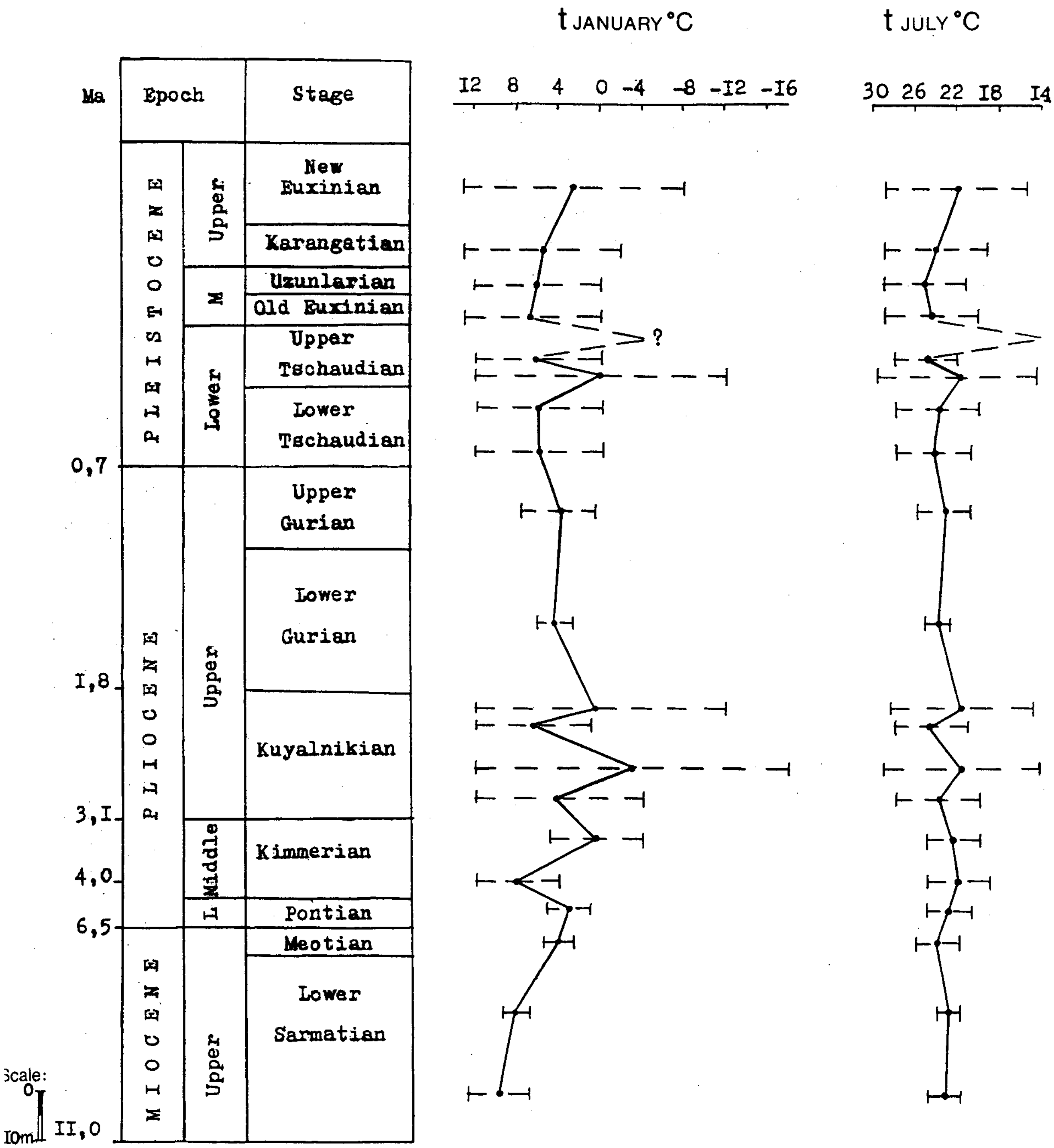

Fig. 10. Temperature fluctuation curve for Georgia during the Neogene and Pleistocene

tion, which took place in the second part of the Skurdumian were probably connected with the lowering of the Greater and Lesser Caucasus (Milanovski 1968, Tsagareli 1980). These changes in relief could explain the climatic fluctuations which occured. They also caused a reduction in the upper mountain belt, whose conditions were best suited for the development of coniferous forests. Under the influence of the climatic changes they were replaced by pine forests, which in the Upper Skurdumian occupied nearly all the mountain belts, except the narrow lower zone.

The Etserian horizon is characterized by rich and diverse spectra, mainly composed of *Pinus*, *Cedrus*, the coniferous, broad-leaved trees and ferns. The fern composition, compared with that of the Early Skurdumian and Kimmerian was somewhat poorer. The spores of *Pityrogramma* sp., *Dicksonia antarctica*, *D. luculenta*, *Pteridacidites longifoliiformis*, and *P. grandifoliiformis* all disappeared and *P. verus*, *P. ve-*

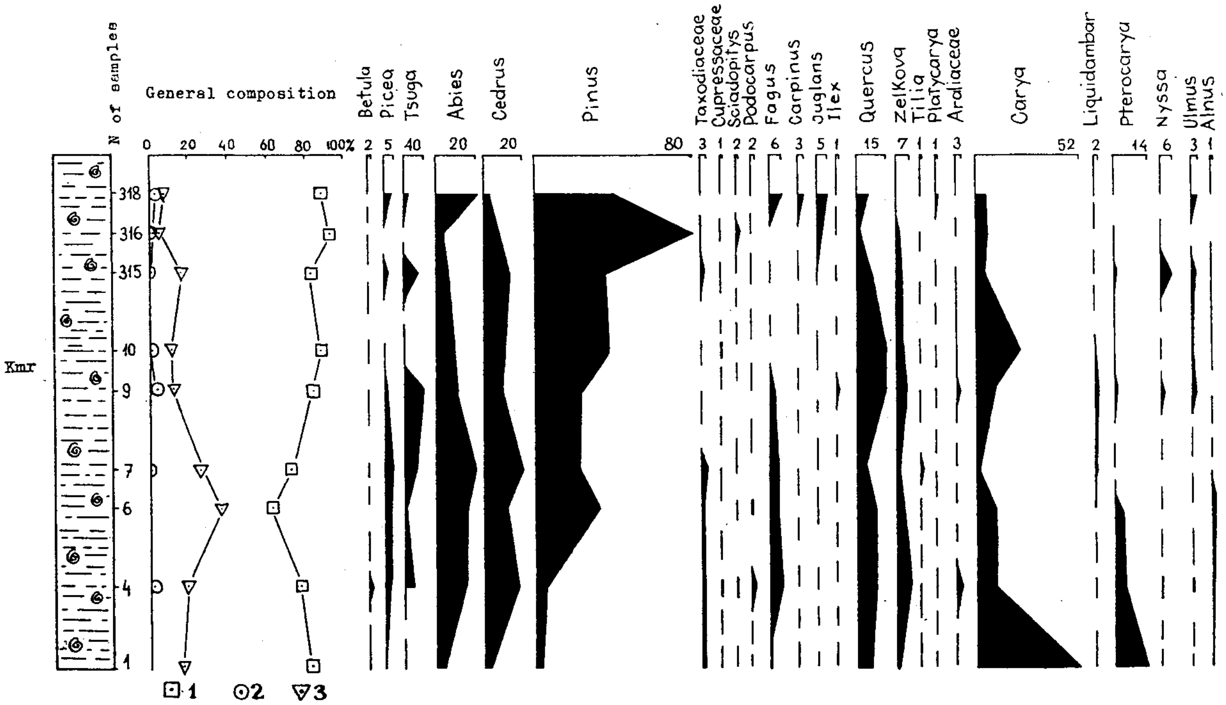

Fig. 11. Pollen diagram of the Kimmerian deposits on the Duabi river (Western Georgia) 1 – AP, 2 – NAP, 3 – spores

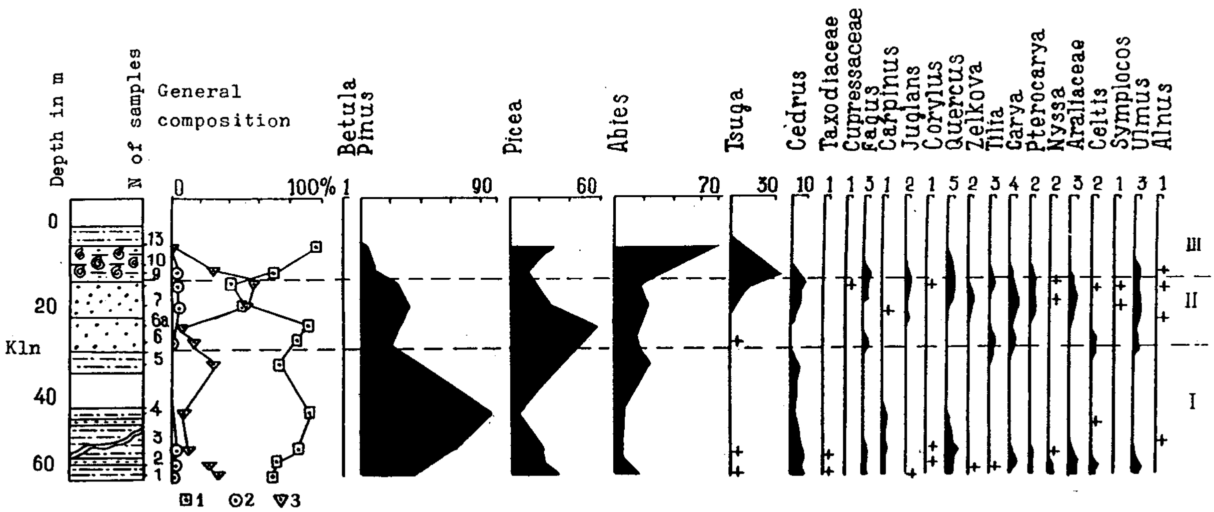

Fig. 12. Pollen diagram of the Kuyalnikian deposits near Tsikhisperdi village 1 – AP, 2 – NAP, 3 – spores

nustaeformis, P. remotifoliodes, P. boerzsoenyensis and various species of *Polypodium* became the prevailing components. Along with this, in the Kuyalnikian and especially in the Gurian the content of spores of ferns typical for the recent flora of Georgia continued to increase.

In the Kuyalnikian and Gurian, evergreen forests did not exist in Colchis. The lower and middle mountain zones were covered by species rich deciduous formations (Figs 12, 13). Probably most of the thermophilous ferns grew here as well. It is possible that forms less tied to a temperate regime were distributed higher, in the zone of the coniferous forests.

The end of the Pliocene was accompanied by great orogenic movements, giving the Greater and Lesser Caucasus this recent appearance (Antonov et al. 1977, Kogoshvili 1977, Tsagareli 1980). This involved changes in the character of the whole vegetational cover of Western Georgia. In the middle and upper

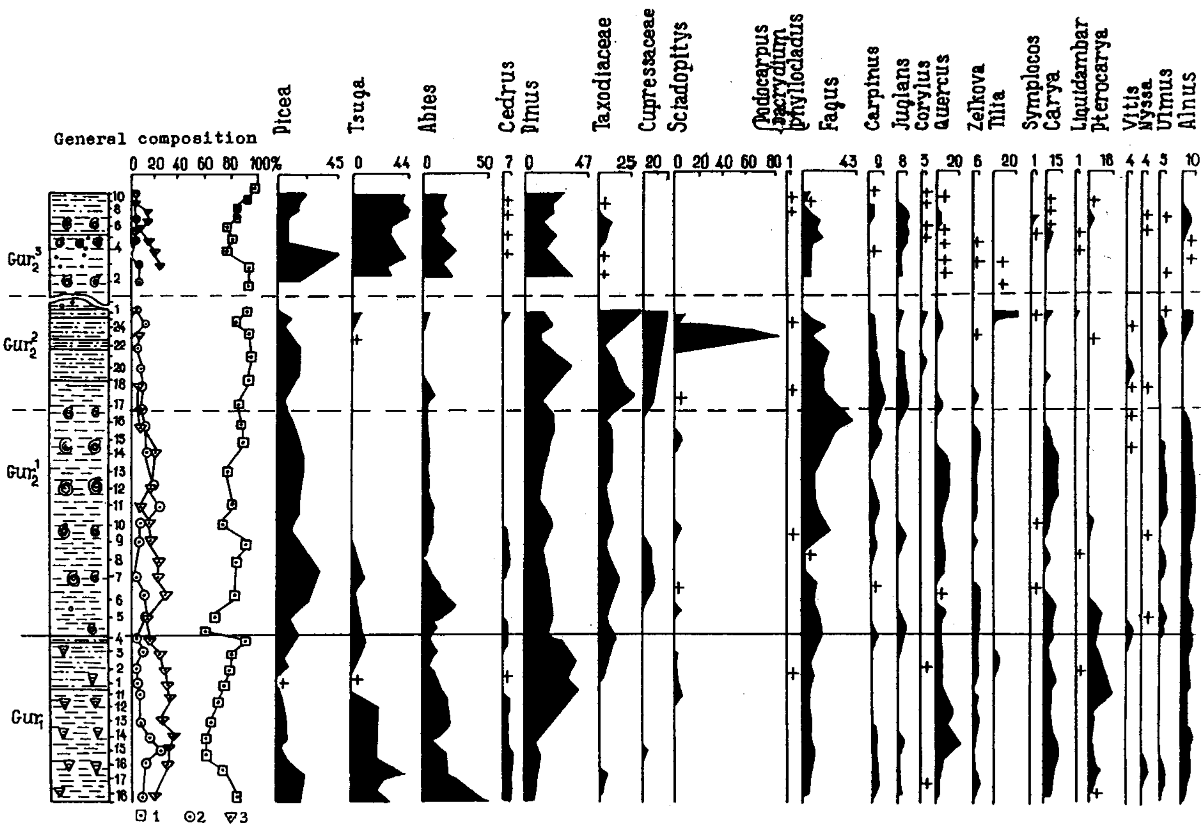

Fig. 13. Pollen diagram for the Gurian deposits near Khvarbeti village (Western Georgia) 1 – AP, 2 – NAP, 3 – spores

mountain zones communities dominated by one species became established and wide spread, whose characteristic feature was a poorness of fern cover.

To the end of the Pliocene and in the Early Pleistocene – Tschaudian, fir, spruce and beech forests became the prevailing type of vegetation (Fig. 14). The area of mixed communities was reduced and restricted mainly to the lower mountain zone. These changes involved the extinction of many thermophilous trees and ferns. *Dicksonia, Cyathea* and most *Polypodium* and *Pteris* spp. disappeared from the composition of the flora (Shatilova 1982).

Thus the evolution of ferns was closely connected with that of the arboreal vegetation of Western Georgia and proceeded under the influence of many biotic and abiotic factors. Among them the climate and general palaeogeographical changes which took place in the Caucasus during the Neogene were of the greatest importance.

In the history of the development of ferns in Western Georgia during the Neogene five stages can be traced.

The first corresponds to the Early and Middle Miocene. It was characterized by a predominance of extinct forms and genera surviving now in tropical and subtropical regions of the World. The genera typical for the recent flora of Georgia were represented by single forms.

The second stage comprised the Sarmatian, Meotian and Pontian. At this time the role of extinct taxa in the pteridiflora was reduced. The subtropical and tropical ferns formed a systematically diverse group, although they were already relict elements of the flora, especially in the Meotian and Pontian. The genera *Pteris* and *Polypodium* were represented by many species, whose area of distribution after the Sarmatian was significantly increased.

During the third stage which corresponds to the Kimmerian and Early Skurdumian the genera *Pteris* and *Polypodium* reached the peak of their development. The area more thermophilous ferns continued to reduce. Along with this, the role of ferns of temperate climates increased.

The fourth stage embraced the Middle Kuyalnikian and Gurian. It was a time of the gradual extinction of the Pliocene ferns and

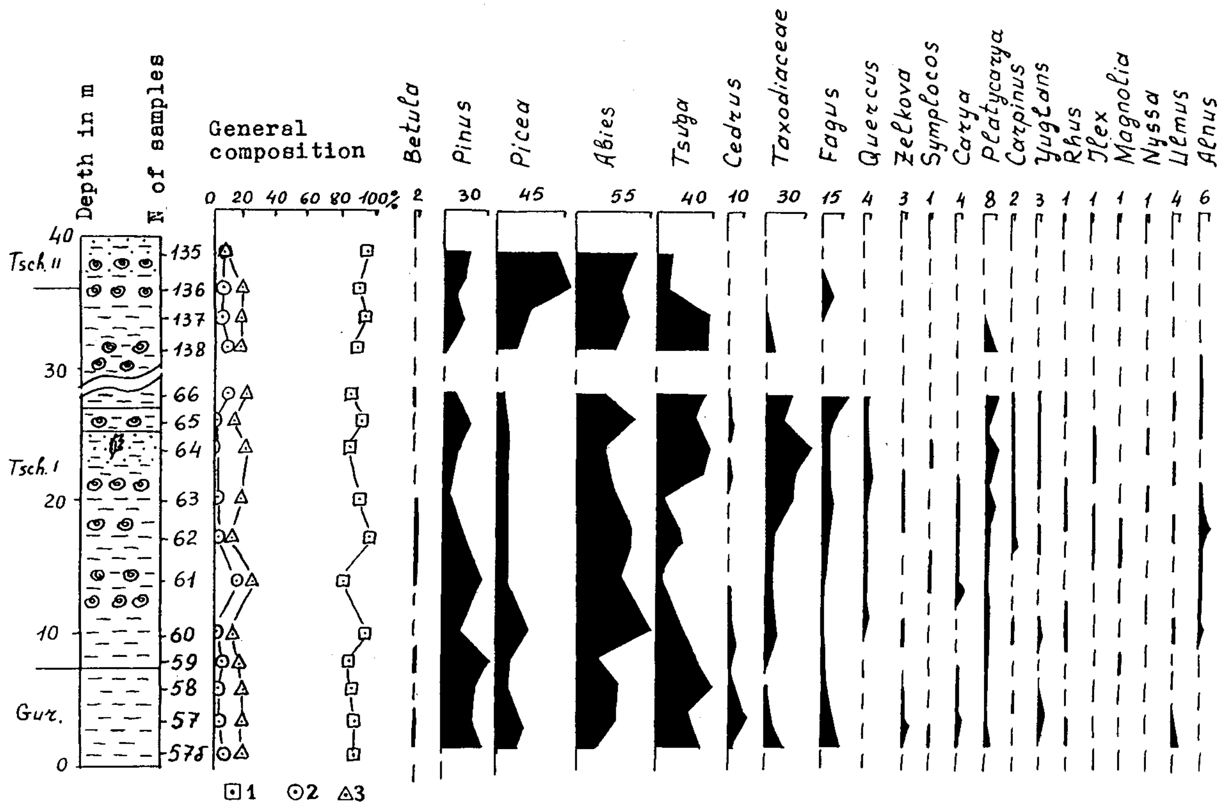

Fig. 14. Pollen diagram for the Tschaudian deposids on the Chakhvata river (Western Georgia) 1 – AP, 2 – NAP, 3 – spores

the distribution of genera typical for the Pliocene.

The fifth stage corresponded to the whole Quaternary. The pteridoflora of this time was almost without Pliocene elements, except for some forms which, disappeared after the Uzunlarian.

CONCLUSION

In Georgia the earliest discoveries of true ferns were made in deposits dated to the Mesozoic. The spores of *Hymenophyllum, Lygodium, Gleichenia, Cibotium* and *Dicksonia* were seen in Jura.

Ferns played a minor part in the composition of the Palaeogene flora. These plants began to flourish during the second half of the Miocene, when the predominant communities were subtropical forests, which covered nearly all levels of comparatively low relief. In the pteridoflora of the Middle Miocene mainly extinct taxa prevailed. The role of recent genera was insignificant.

In the second part of the Sarmatian in the Caucasus great orogenic and palaeogeographical changes occured. They involved the spread of coniferous and broad-leaved deciduous forests which in the first half of the Pliocene partially, and in the Upper Pliocene, completely, replaced the evergreen communities. These phenomena were the main reasons for the disappearance of most of the “ancient” and widely distributed *Polypodium* and *Pteris*. These taxa prevailed during the whole of the Pliocene until, in the lower and middle mountain zones species of rich forests bacame dominant and continued to flourish.

At the end of the Pliocene new orogenic movements began, as a result of which the vertical zonation of the landscape became more distinct. In the upper and middle mountain belts species of poor spruce-fir and beech forests occured. Under their canopy there was no opportunity for a dense cover of grasses and ferns to develop. This led to a reduction in the area occupied by many Pliocene ferns, the bulk of which had become extinct by the end of the Pliocene. Only a few representatives survived into the Quaternary flora, having disappeared from Western Georgia after the Middle Pleistocene. Simultaneously the role of genera typical for the Quaternary and recent flora of

Western Georgia gradually increased during the Kuyalnikian and Gurian.

The Neogene pteridoflora of Western Georgia developed in a complex way. The process was accompanied by the evolution of coniferous and flowering plants against by the background of great palaeogeogrphical changes and numerous biotic factors inside the phytocoenosis.

The typical representative of the Neogene pteridoflora of Western Georgia was the genus *Pteris*. The earliest fossil findings of this taxon in Georgia date from the Palaeogene. In the Eocene and Oligocene deposits of the Akhalzikhian depression the spores of *Pteris* spp. were found, but on whole the role of this genus in the palynocomplex was not great.

Beyond the Caucasus *Pteris* is known from the Mesozoic. Some species had already existed in the Triassic in Western Siberia. In this region *Pteris* flourishing during the Cretaceous, after which te systematic composition as well as the number of fossils in the deposits began to reduce.

In Eastern Europe *Pteris* is known from the Miocene. At this time it was represented by seven species. After the Sarmatian, whose second half was accompanied by large palaeogeographical changes and the reduction of the marine basins of Central Paratethys, the role of *Pteris* decreased, in common with that of ferns as a whole.

In Eurasia, one of the regions where *Pteris* prevailed during the whole of the Pliocene, and was characterized by a rich systematic composition, was Western Georgia.

In the Middle Miocene of this region, some species of *Polypodiaceoisporites* were determined, but only one was comparable with modern *Pteris* (see Tab. 3).

The role of taxa similar to the recent genus *Pteris* increased after the Sarmatian. From late Miocene and Pliocene deposits, sixteen species of *Pteridacidites* have been described: *Pteridacidites boerzsoenyensis, P. dentatiformis, P. georgensis, P. grandifoliiformis, P. guriensis, P. helveticus, P. kimmeriensis, P. longifoliiformis, P. pseudocreticus, P. rarotuberculatus, P. remotifolioides, P. spiniverrucatus, P. variabilis, P. venustaeformis* and *P. vittatioides*.

In the stratigraphical distribution of the separate species a dinstinct regularity is clear (see Tab. 5).

From four species of *Pteridacidites* whose spores were found in the Sarmatian deposits only one, *P. helveticus,* was a taxon typical for the Miocene flora of Paratethys. After the Sarmatian this species disappeared from the flora of Western Georgia. The other three taxa belonged to species widely distributed in Colchis during the Meotian and Pliocene.

For the Meotian and Pontian two species were typical, *Pteridacidites longifoliiformis* and *P. grandifoliiformis*, but *P. verus, P. remotifolioides* and *P. venustaeformis* were also of some importance. In total, the Meotian deposits contained eight species, and the Pontian nine.

In the Kimmerian and Early Skurdumian fourteen species of *Pteridacidites* were present. Among them the predominant species were: *Pteridacidites verus, P. venustaeformis, P. remotifolioides* and *P. boerzsoenyensis*.

In Western Georgia the *Pteridacidites* flourished principally in Kimmerian and Early Skurdumian, after which the gradual impoverishment of its systematic composition began. By the end of the Neogene most part of Pliocene species disappeared. In Tschaudian deposits only spores of *Pterdacidites variabilis* were found. This form was probably the closest ancestor of the contemporary *Pteris cretica*, which remains a component of the flora of Colchis to the present day.

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PLATES

Plate 1

× 1000

Pteridacidites longifoliiformis Shatilova & Stuchlik **sp. nov.**

1–3. Western Georgia, Gogoreti village, Pontian
1. a – distal face, b – proximal face
2. a – distal face, b – proximal face
3. a – distal face, b – proximal face

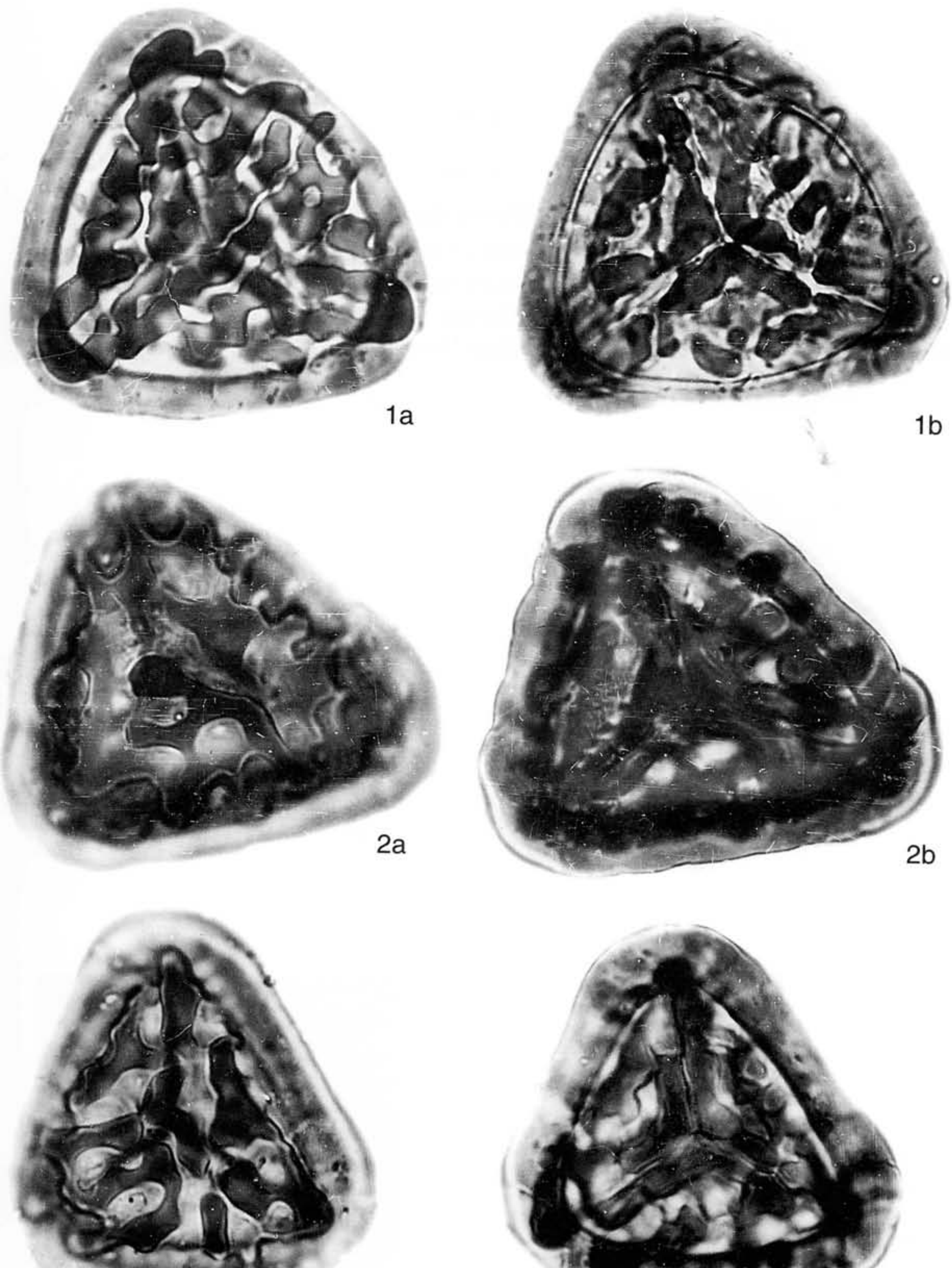

1a
1b
2a
2b
3a
3b

Plate 2

× 1000

Pteridacidites longifoliiformis Shatilova & Stuchlik **sp. nov.**

1. a – distal face, b – proximal face; Western Georgia, Tsikhisperdi village, Lower Skurdumian
2. a – distal face, b – proximal face; Western Georgia, Gogoreti village, Meotian
3. distal face; Western Georgia, Gogoreti village, Pontian
4. distal face, SEM; Western Georgia, Gogoreti village, Pontian

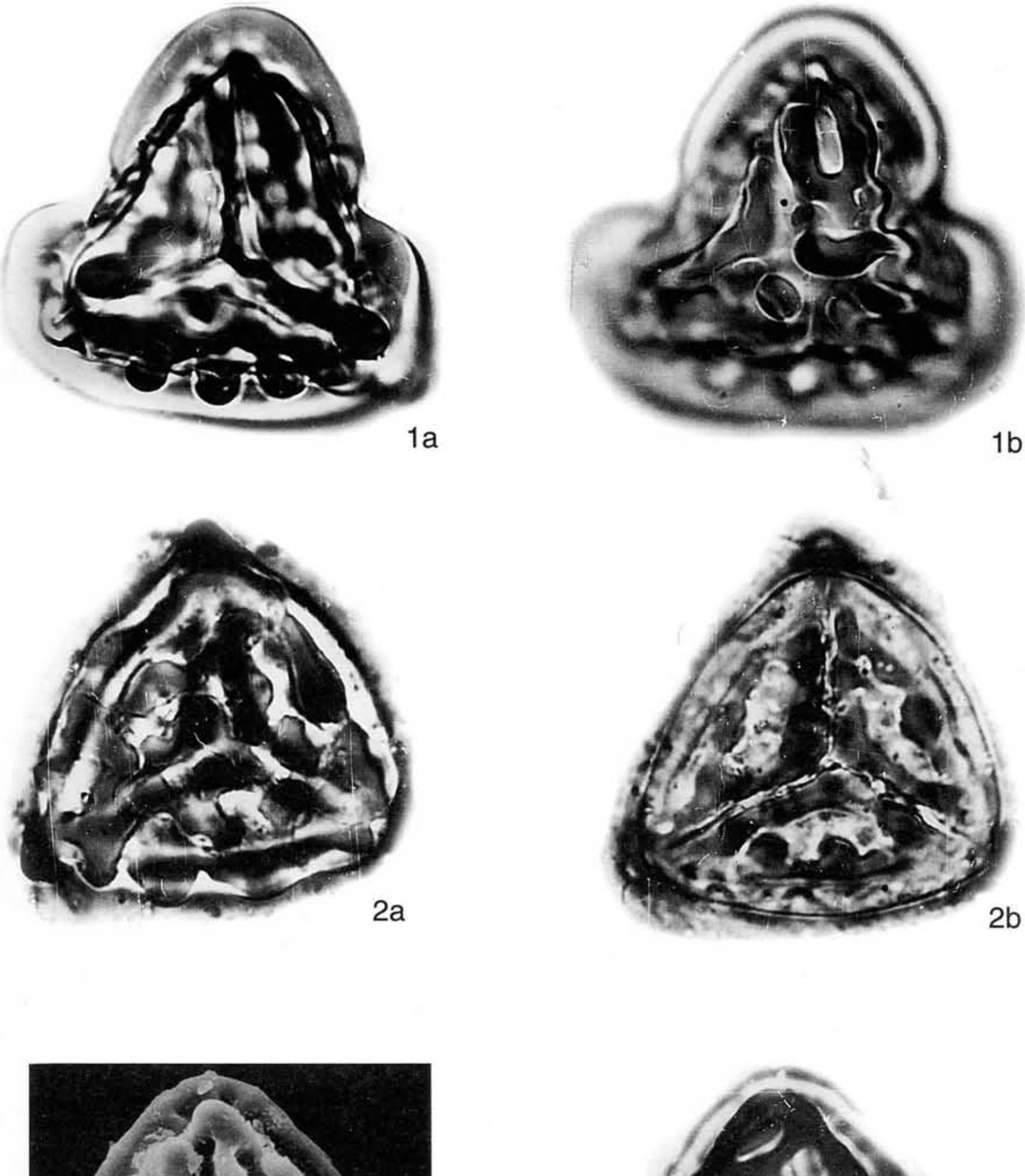

1a
1b
2a
2b
4
3

Plate 3

× 1000

Pteridacidites longifoliiformis Shatilova & Stuchlik **sp. nov.**

1–5. Western Georgia, Gogoreti village, Pontian
1, 2. distal face, SEM × 1000
3. fragment of sculpture, SEM × 5000
4. – × 7000
5. – × 10000

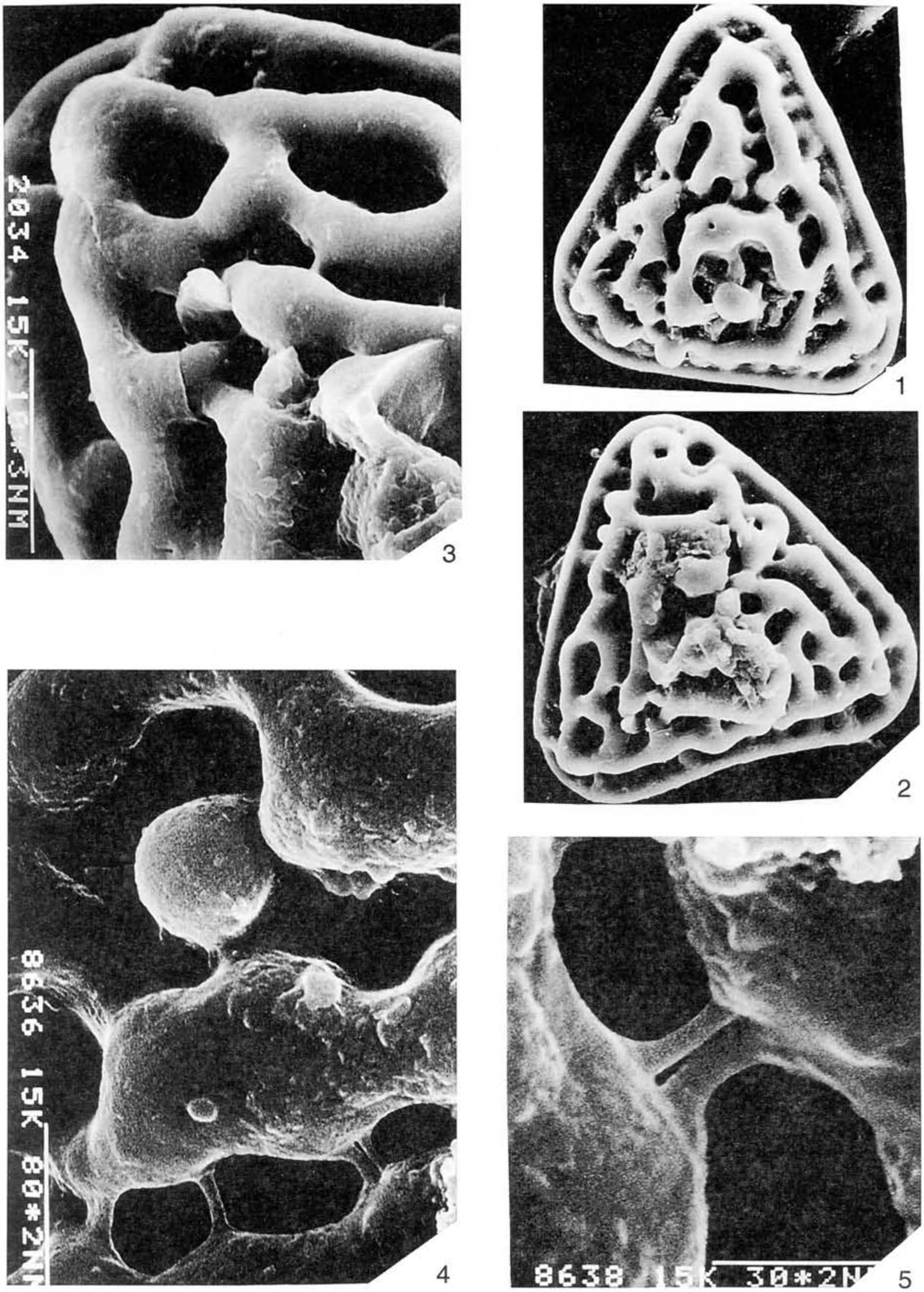

2034 15K
1
2
3
8636 15K
4
8638 15K
5

Plate 4

× 1000

Pteris longifolia L.

1–4. Recent spore, Cuba
 1, 2. two optical sections of proximal face,
 3, 4. two optical sections of distal face *Pteris vittata* L.

5–8. Recent spores, Florida
 5, 7. two optical sections of distal face,
 6, 8. two optical sections of proximal face

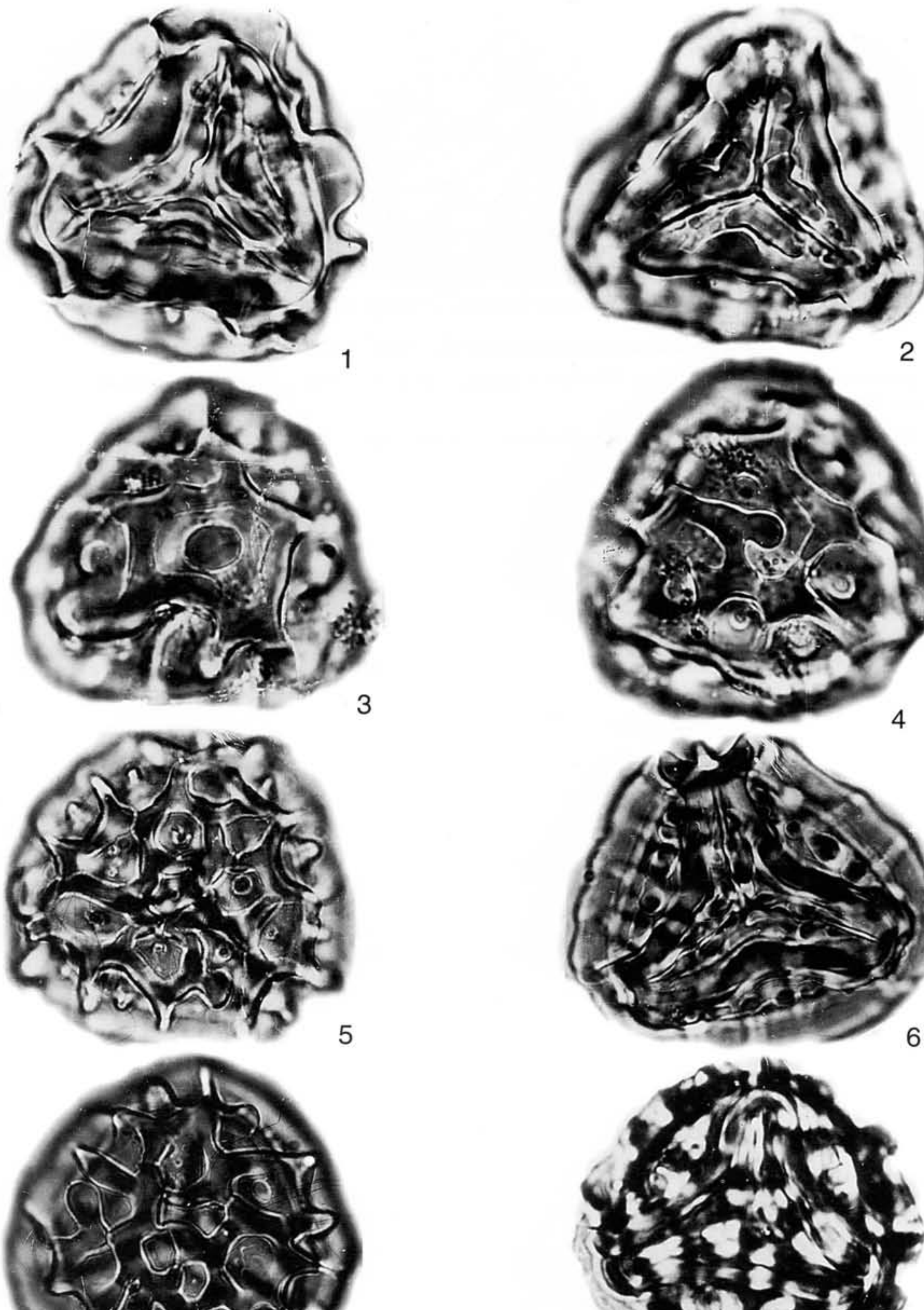

1
2
3
4
5
6
7
8

Plate 5

× 1000

Pteridacidites vittatioides Stuchlik & Shatilova **sp. nov.**

1. a, b, c – three optical sections of distal face, Western Georgia, Khvazbeti village, Gurain
2. a – distal face, b – proximal face, Western Georgia, Gogoreti village, Gurian

Pteridacidites grandifoliiformis Stuchlik & Shatilova **sp. nov.**

3. a – proximal face, b – distal face, Western Georgia, Gogoreti village, Lower Kuyalnikian (Lower Skurdumian)
4. a – two optical sections of distal face, Western Georgia, Djgali village, Sarmatian

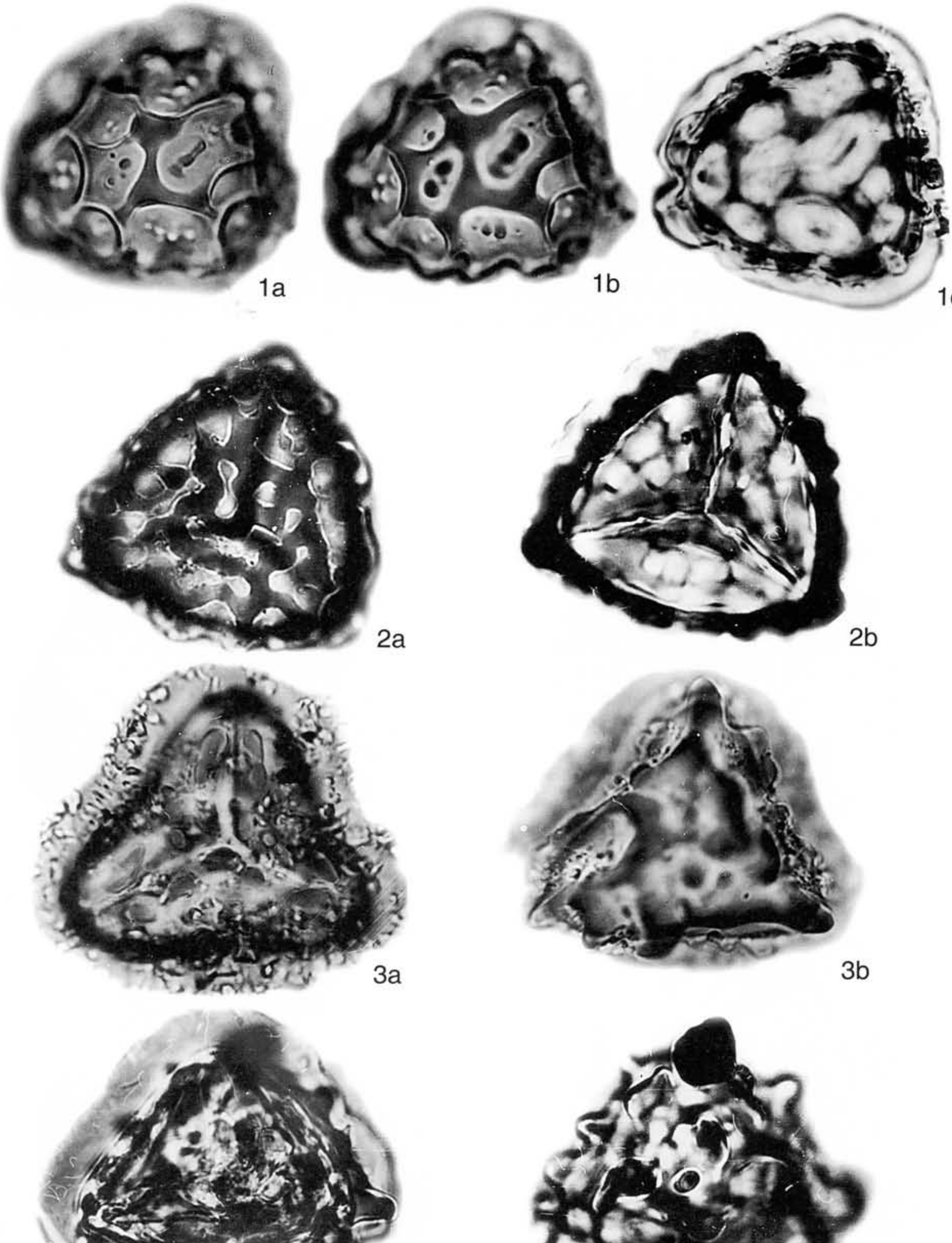

1a
1b
1c
2a
2b
3a
3b
4a
4b

Plate 6

× 1000

Pteridacidites grandifoliiformis Stuchlik & Shatilova **sp. nov.**

1. a – proximal face, b – distal face, Western Georgia, Bia village, Pontian
2. a – proximal face, b, c – two optical sections of distal face, Western Georgia, Czurgeti town, Kimmerian
3. distal face, Western Georgia, Duabi river, Kimmerian

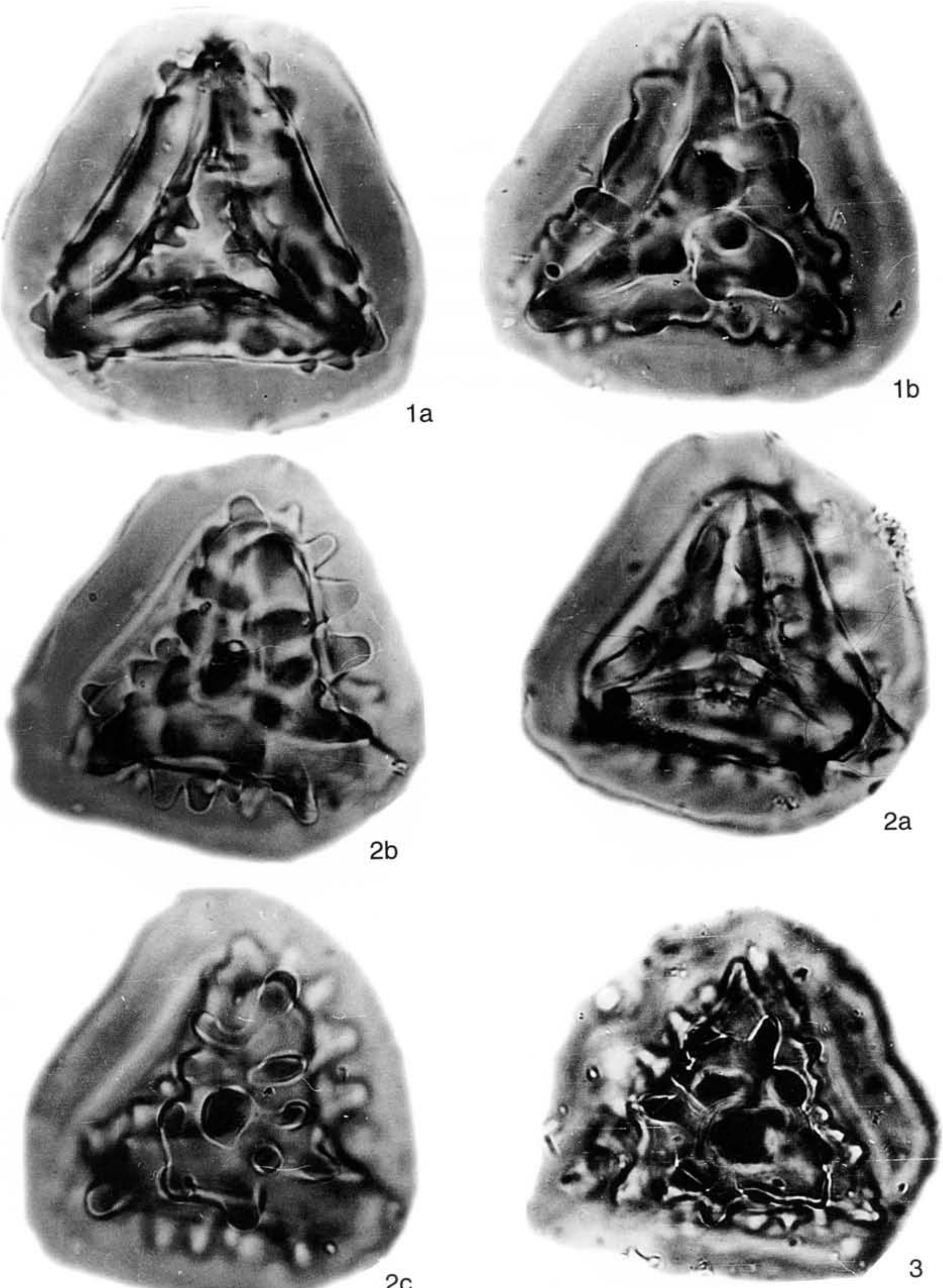

1a
1b
2b
2a
2c
3

Plate 7

× 1000

Pteridacidites grandifoliiformis Stuchlik & Shatilova **sp. nov.**

1. a – proximal face, b – distal face, Western Georgia, Bjuja river, Pontian
2. proximal face, Western Georgia, Gogoreti river, Pontian

Pteris grandifolia L.

3. a – proximal face, b – surface, c – distal face, recent spore, Cuba

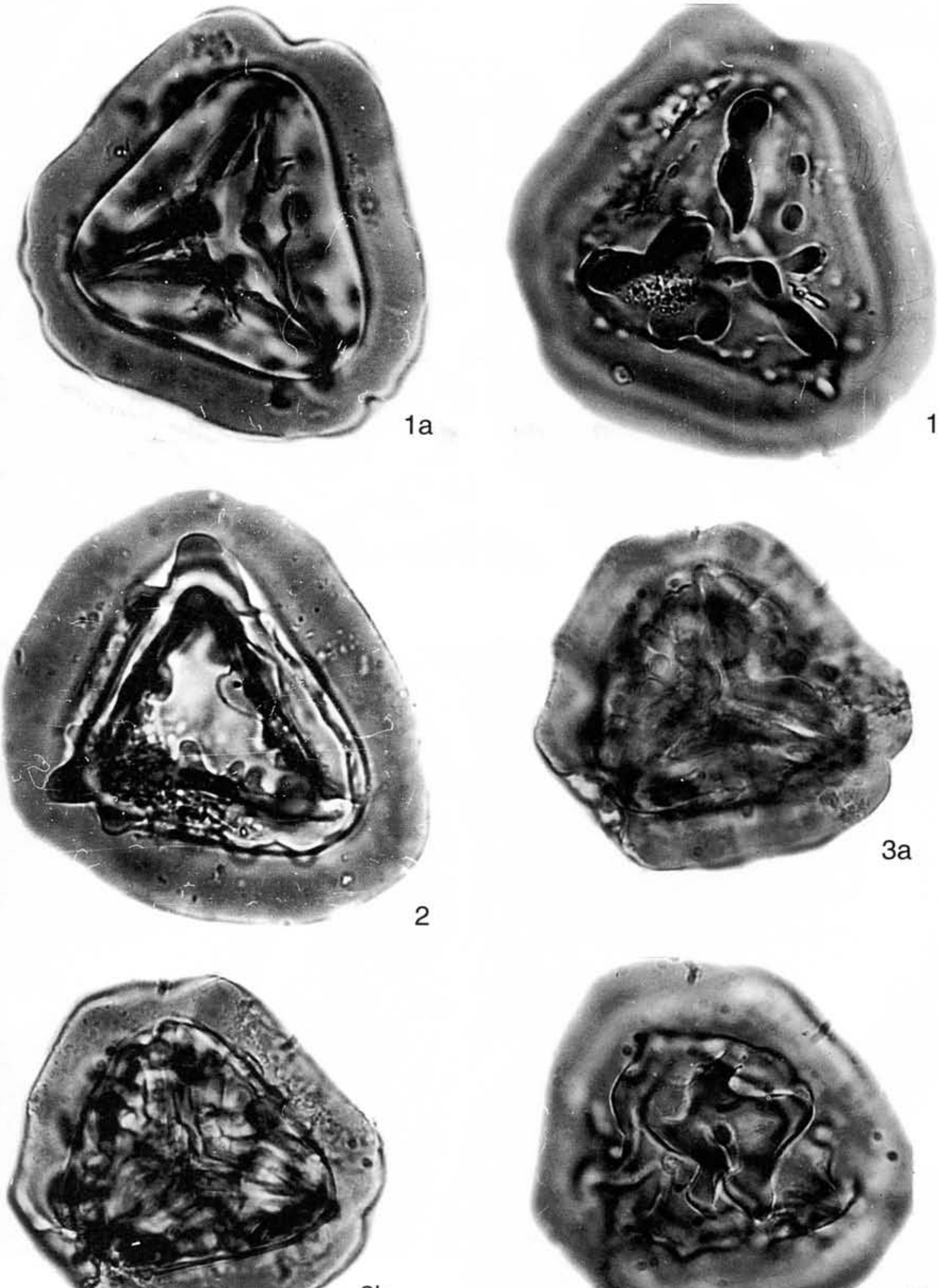
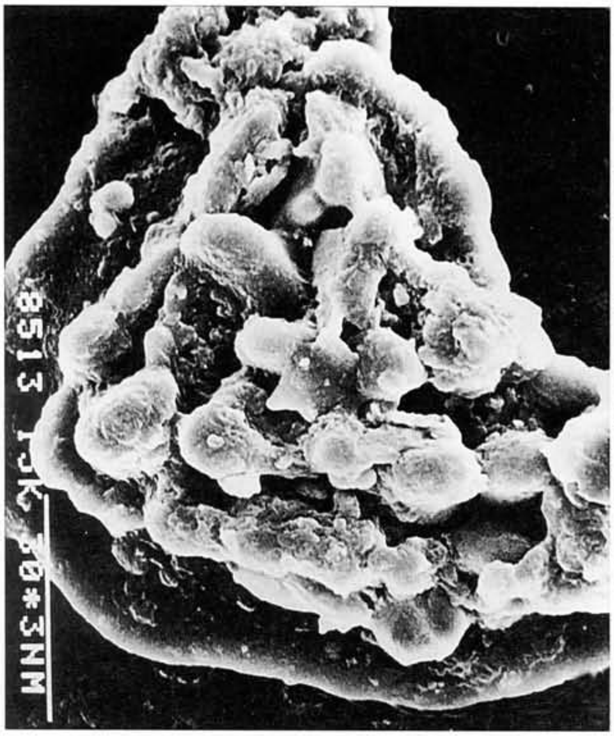

1a
1b
2
3a
3b
3c

Plate 8

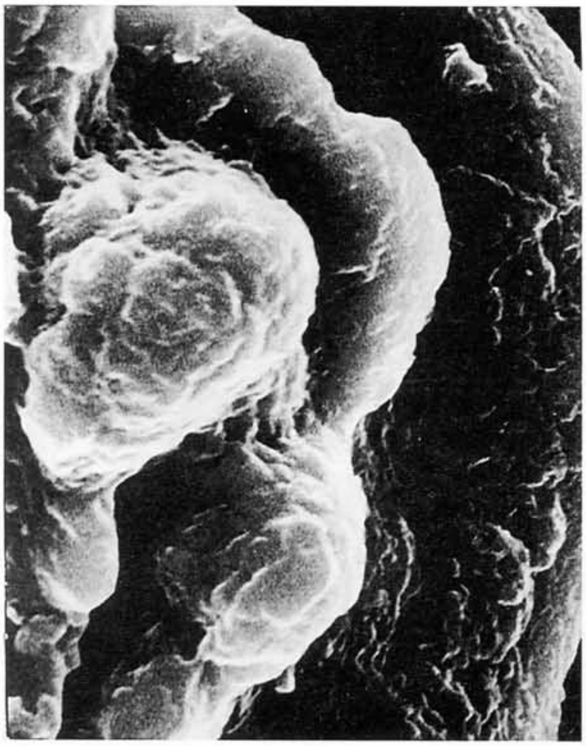
Pteridacidites grandifoliiformis Stuchlik & Shatilova **sp. nov.**

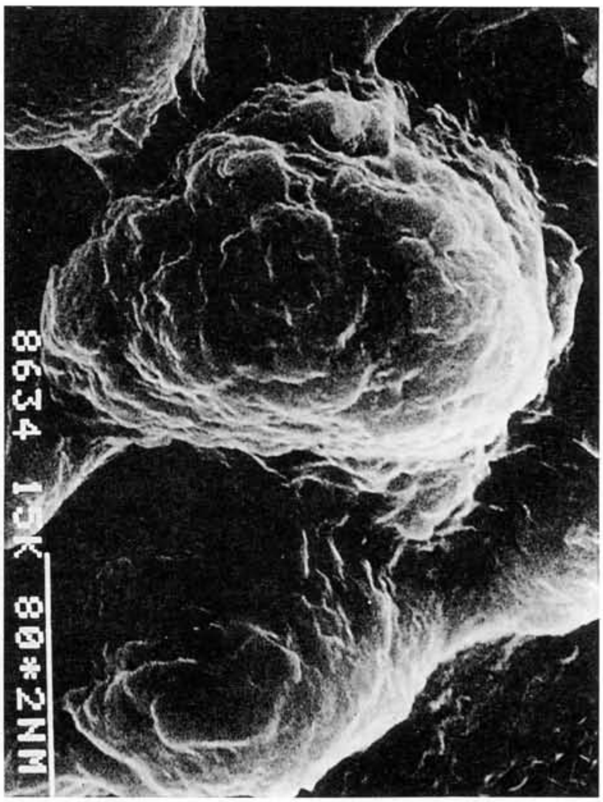
1–4. SEM, Western Georgia, Gogoreti river, Pontian
- 1. – × 1600
- 2. – fragment of sculpture × 5000
- 3. – × 7000
- 4. – × 10000



1


2


3



4

Plate 9

× 1000

Pteridacidites verus (N. Mchedlishvili) Shatilova & Stuchlik **comb. nov.**

1, 2. Western Georgia, Tsikhisperdi village, Lower Kuyalnikian (Skurdumian)
1. a – surface, b – distal face
2. Proximal face

3–6. Western Georgia, Shava river, Gurian
3. a – proximal face, b – distal face
4. a – surface, b – distal face
5. a – surface, b – distal face
6. a – surface, b – distal face

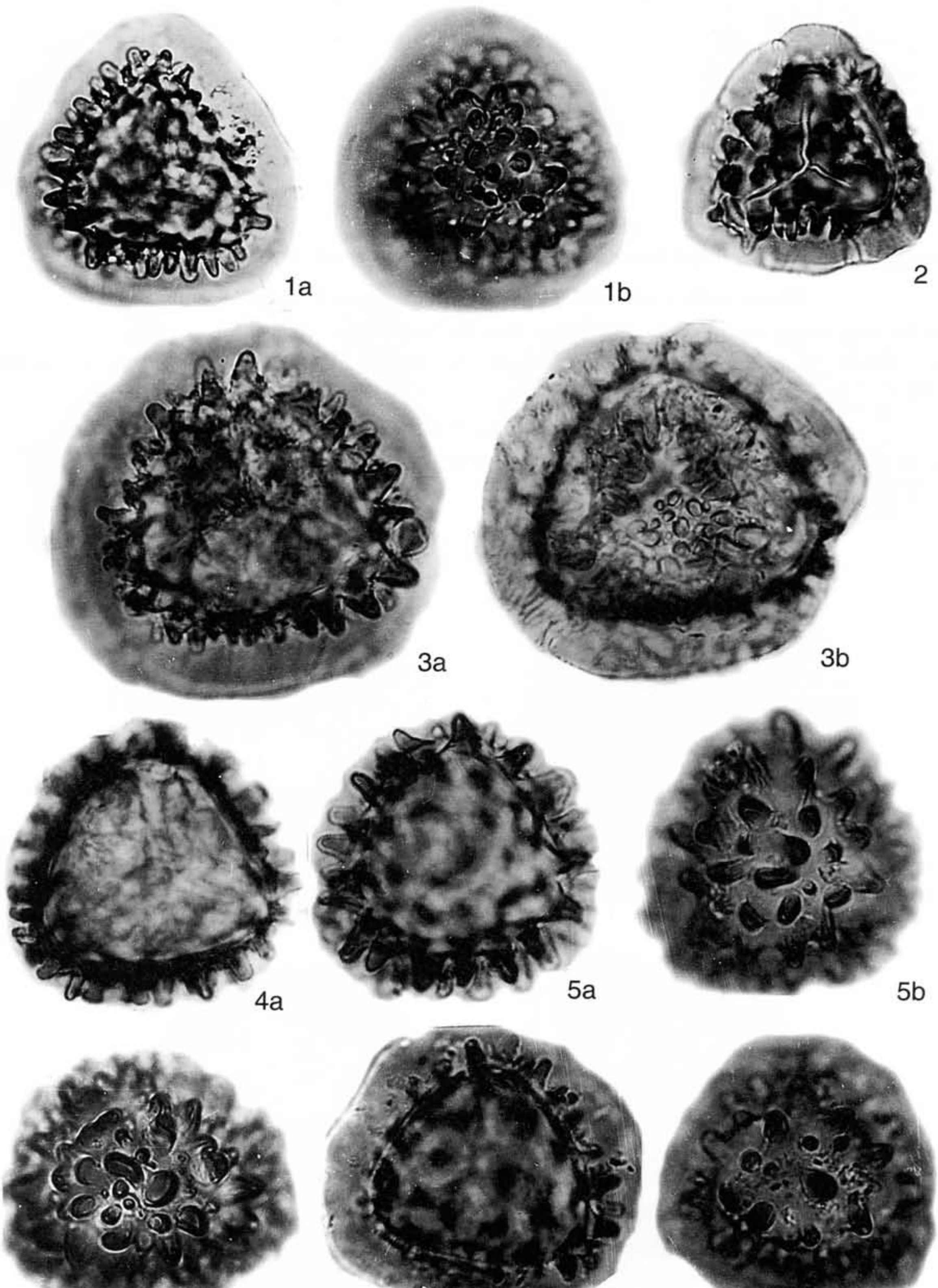

1a
1b
2
3a
3b
4a
5a
5b
4b
6a
6b

Plate 10

× 1000

Pteris crenata Sw.

1. a – proximal face, b – distal face, c – lateral position, recent spore, Japan

Pteridacidites verus (N. Mchedlishvili) Shatilova & Stuchlik **comb. nov.**

2. a, b – two optical lateral positions, Western Georgia, Tsikhisperdi village, Kuyalnikian
3. a – surface, b – proximal face, Western Georgia, Tsikhisperdi village, Lower Kuyalnikian (Lower Skurdumian)

Pteridacidites variabilis Stuchlik & Shatilova **sp. nov.**

4, 5. Western Georgia, Tskaltsminda village, Uzunlarian
  4. a – distal face, b – surface, c – proximal face
  5. proximal face

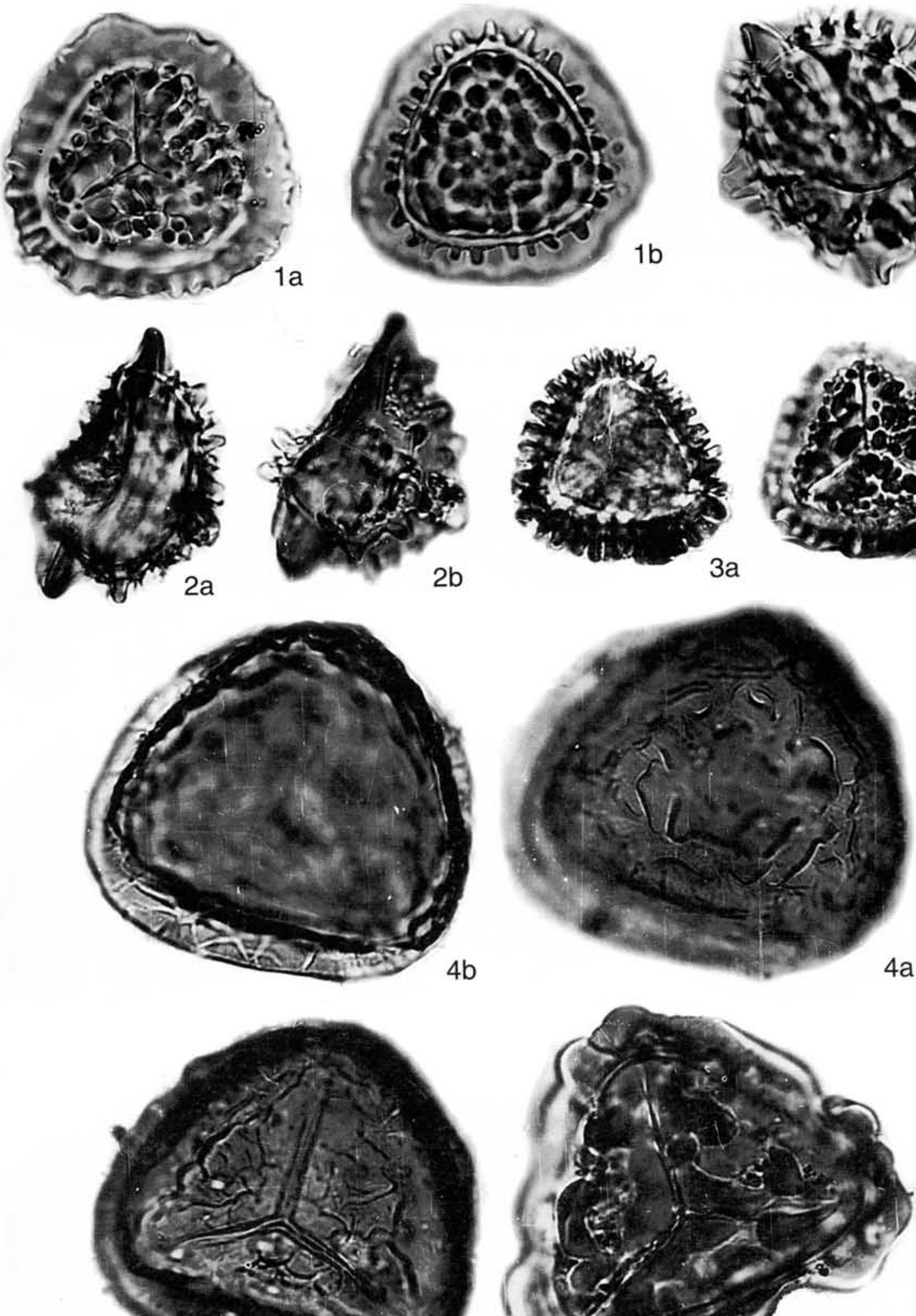

1a
1b
1c
2a
2b
3a
3b
4b
4a
4c
5

Plate 11

× 1000

Pteridacidites variabilis Stuchlik & Shatilova **sp. nov.**

1. two optical sections of proximal face, c – distal face; Western Georgia, Tskaltsminda village, Gurian
2. a – distal face, b – surface, c – proximal face, Western Georgia, Archeuli village, Gurian

Pteris certica L.

3, 4. Recent spore, Cuba
3. a – proximal face, b – surface
4. a, b – two optical sections of distal face
5. a – proximal face, b – distal face, recent spore, Western Georgia

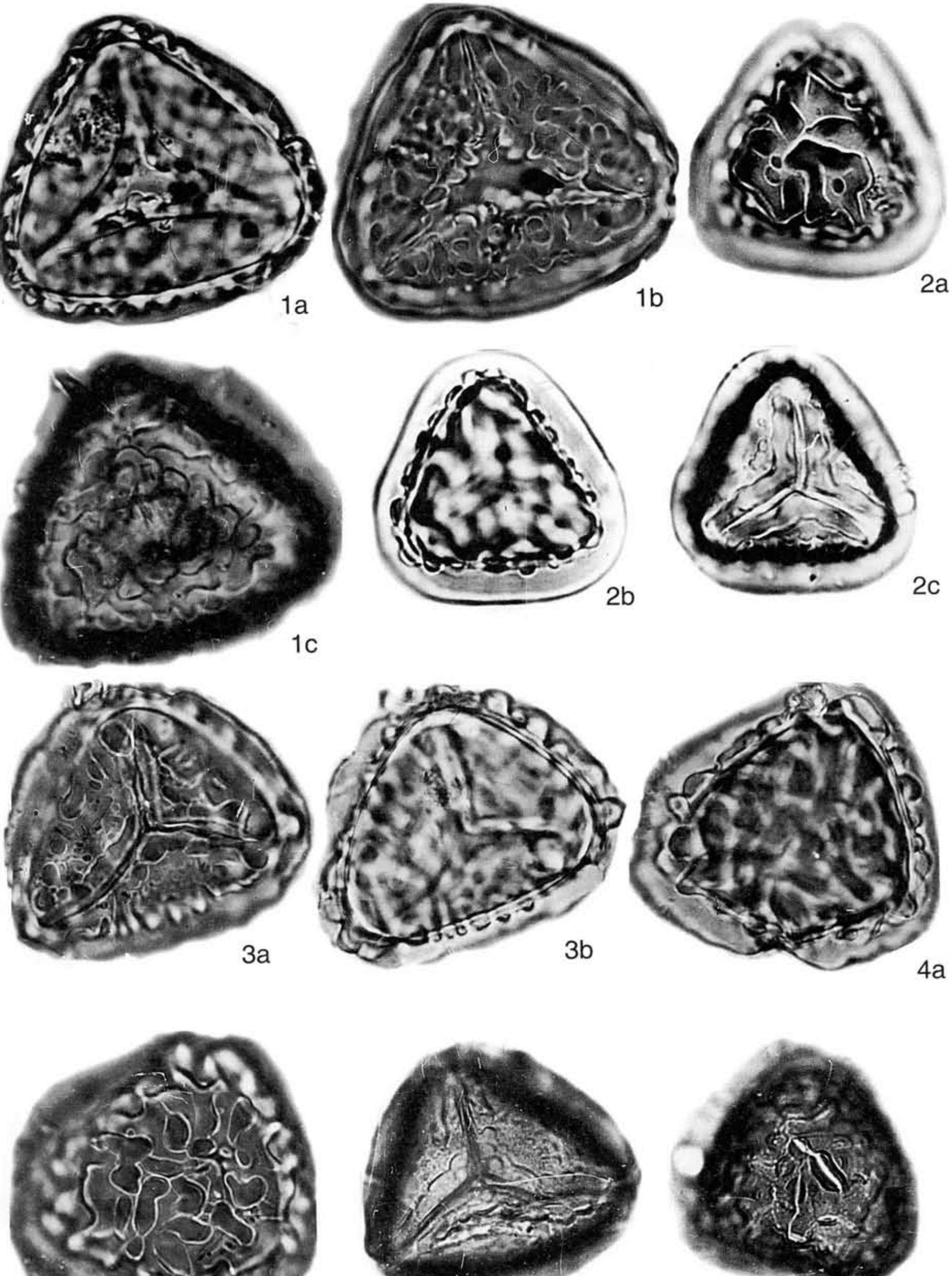

1a
1b
2a
1c
2b
2c
3a
3b
4a
4b
5a
5b

Plate 12

× 1000

Pteridacidites dentatiformis Shatilova & Stuchlik **sp. nov.**

1. a, b – two optical sections of proximal face, c – distal face, Western Georgia, Bjuja river, Kimmerian
2. a, b – two optical sections of proximal face, c – distal face, recent spore, Cuba

Pteridicidites venustaeformis Stuchlik & Shatilova **sp. nov.**

3, 4. Western Georgia, Tsikhisperdi village, Kuyalnikian
   3. a – proximal face, b – distal face, c – surface
   4. a, b – two optical sections of proximal face, c – distal face

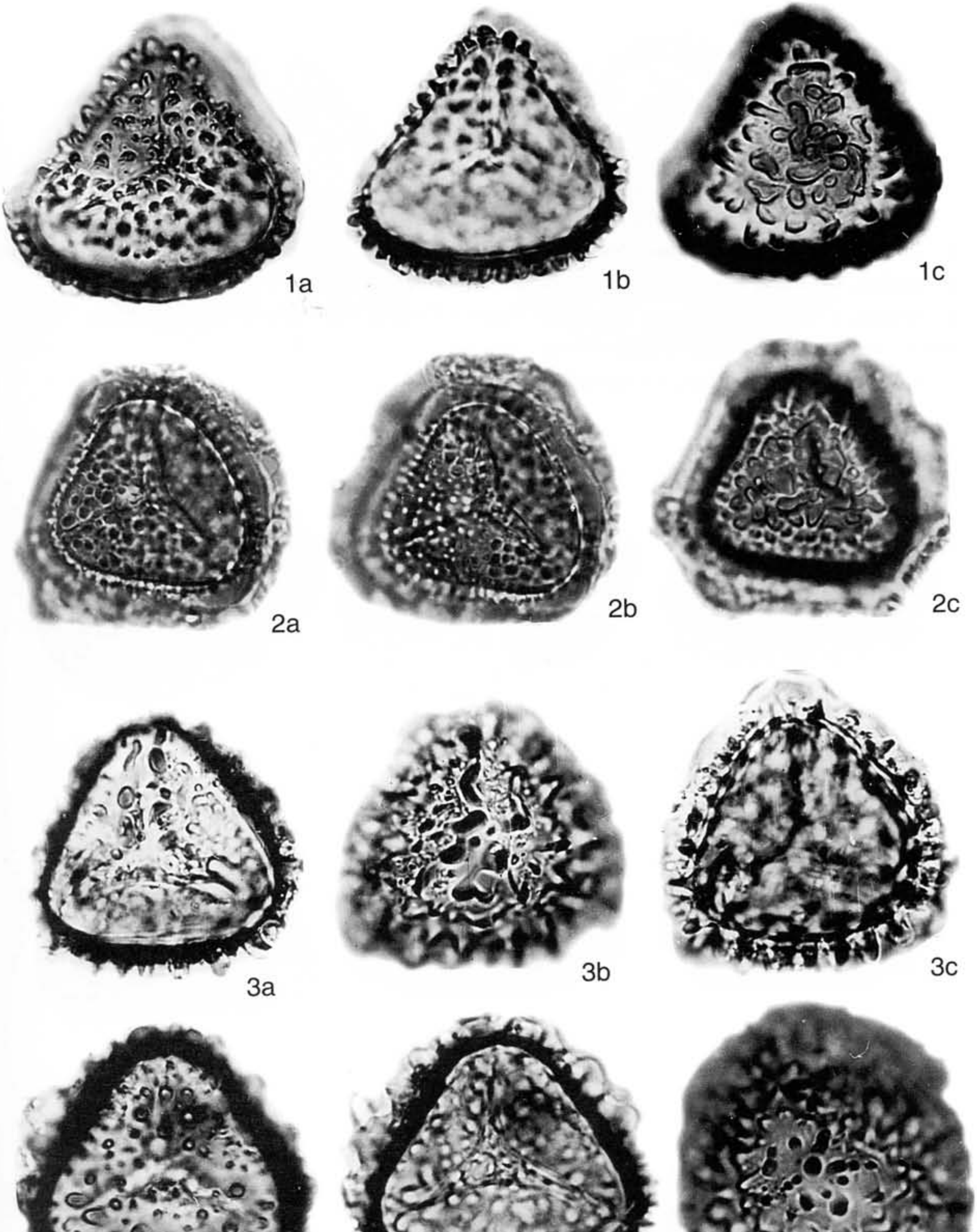

1a
1b
1c
2a
2b
2c
3a
3b
3c
4a
4b
4c

Plate 13

× 1000

Pteridacidites remotifolioides Shatilova & Stuchlik **sp. nov.**

1. a – proximal face, b – distal face, Western Georgia, Bjuja river, Kimmerian
2. a – surface, b – distal face, Western Georgia, Gogoreti village, Pontian
3. a – surface, b – proximal face, c – distal face, Western Georgia, Tsikhisperdi village, Meotian
4. distal face, Western Georgia, Gogoreti village, Meotian
5. a – surface, b – proximal face, c – distal face, recent spore, Madagascar

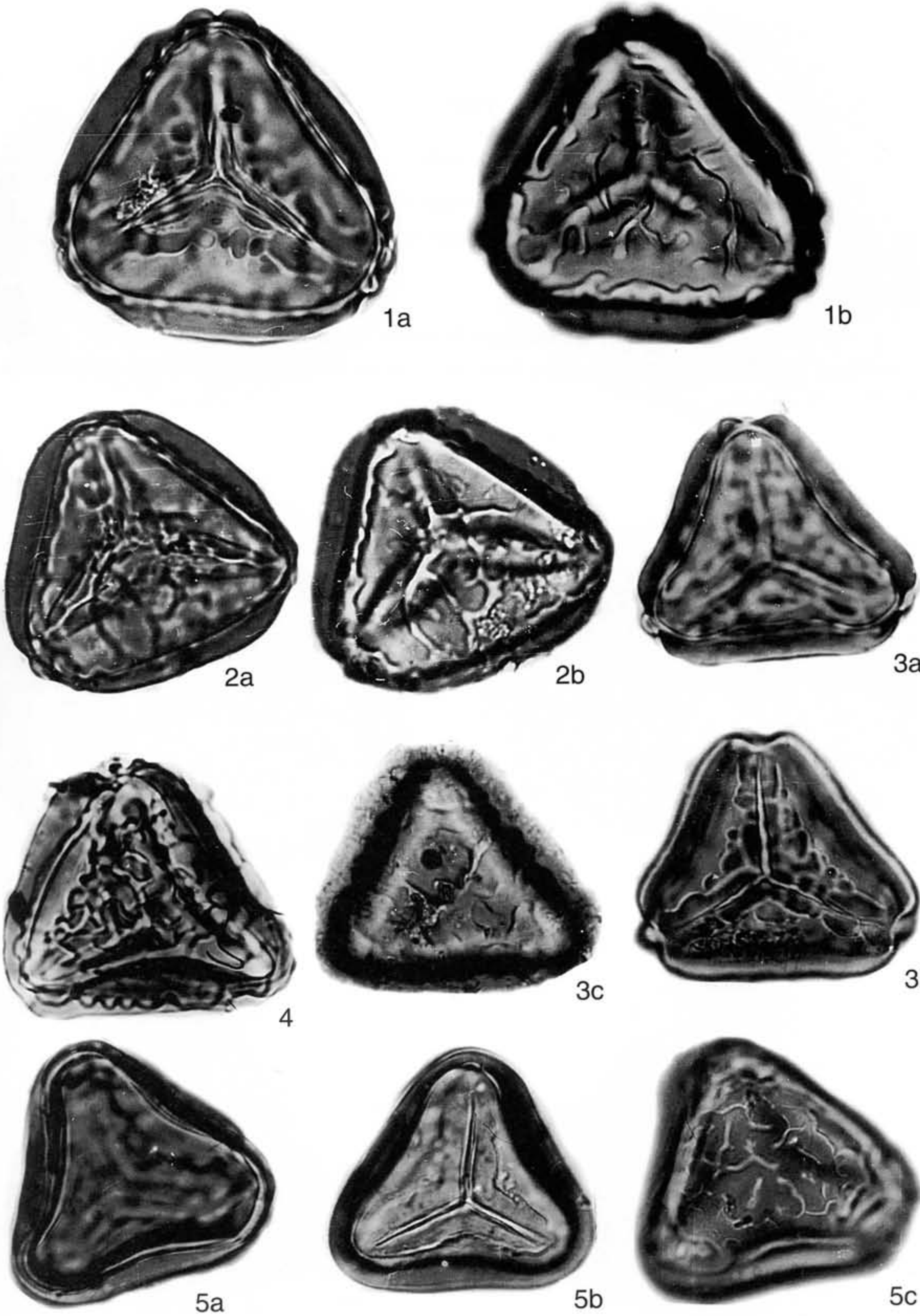

1a
1b
2a
2b
3a
4
3c
3b
5a
5b
5c

Plate 14

× 1000

Pterdacidites spiniverrucatus (Trevisan) Stuchlik & Shatilova **comb. nov.**

1. a, b – two optical sections of proximal face, c – distal face, Western Georgia, Bia river, Kimmerian *Pteris pellucida* Pr.
2. distal face, recent spore, India

Pteridacidites guriensis Shatilova & Stuchlik **sp. nov.**

3. a – proximal face, b – distal face, Western Georgia, Tikhisperdi village, Lower Kuyalnikian (Lower Skurdumian)

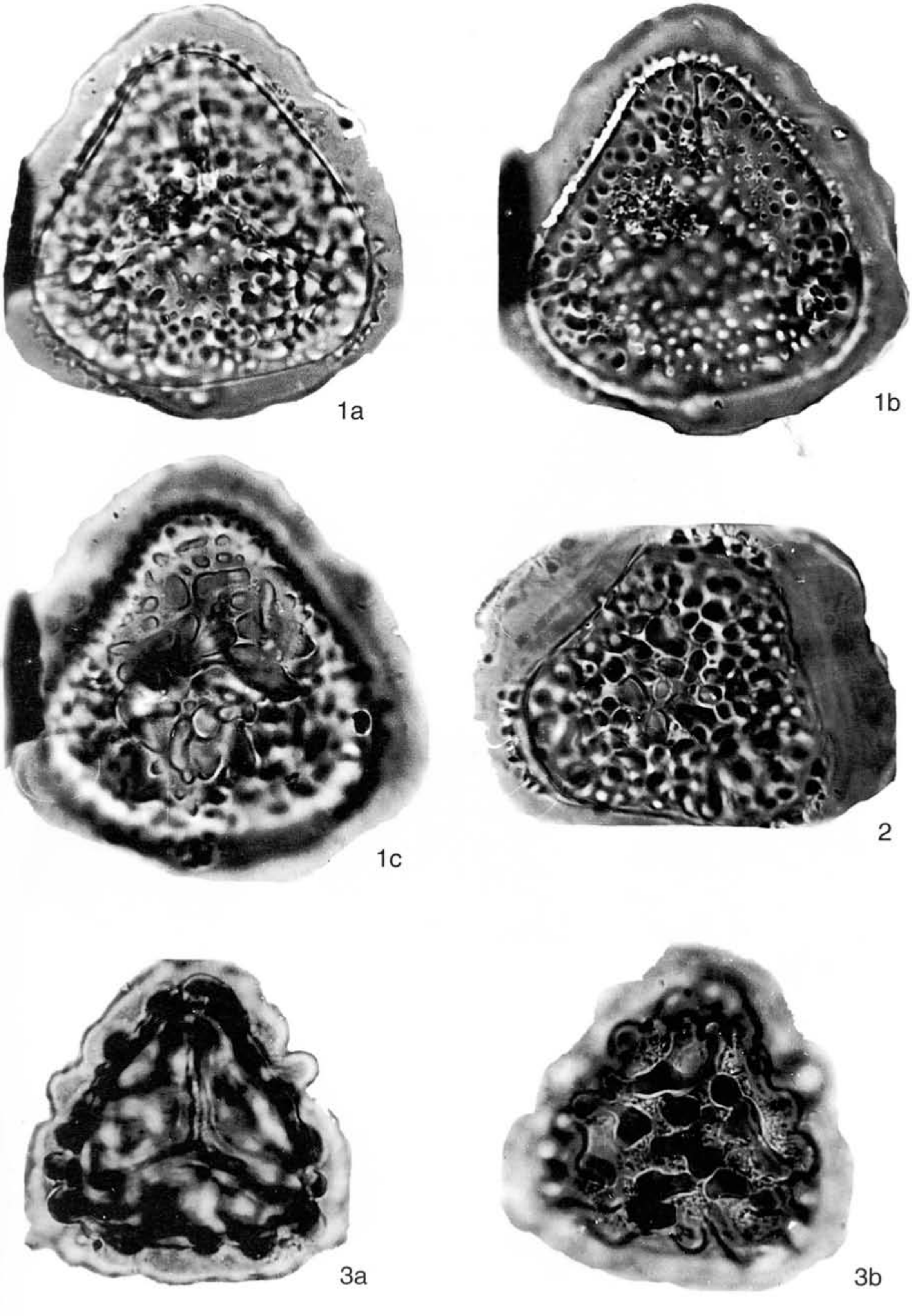

1a
1b
1c
2
3a
3b

Plate 15

× 1000

Pteridacidites guriensis Shatilova & Stuchlik **sp. nov.**

1, 2. Western Georgia, Gogoreti village, Kuyalnikian
1. a – proximal face, b, c – two optical sections of distal face
2. a – surface, b – distal face
3. a – surface, b – distal face, Western Georgia, Tikhisperdi village, Kuyalnikian
4. a – distal face, b – surface, Western Georgia, Morokhvili village, Kimmerian

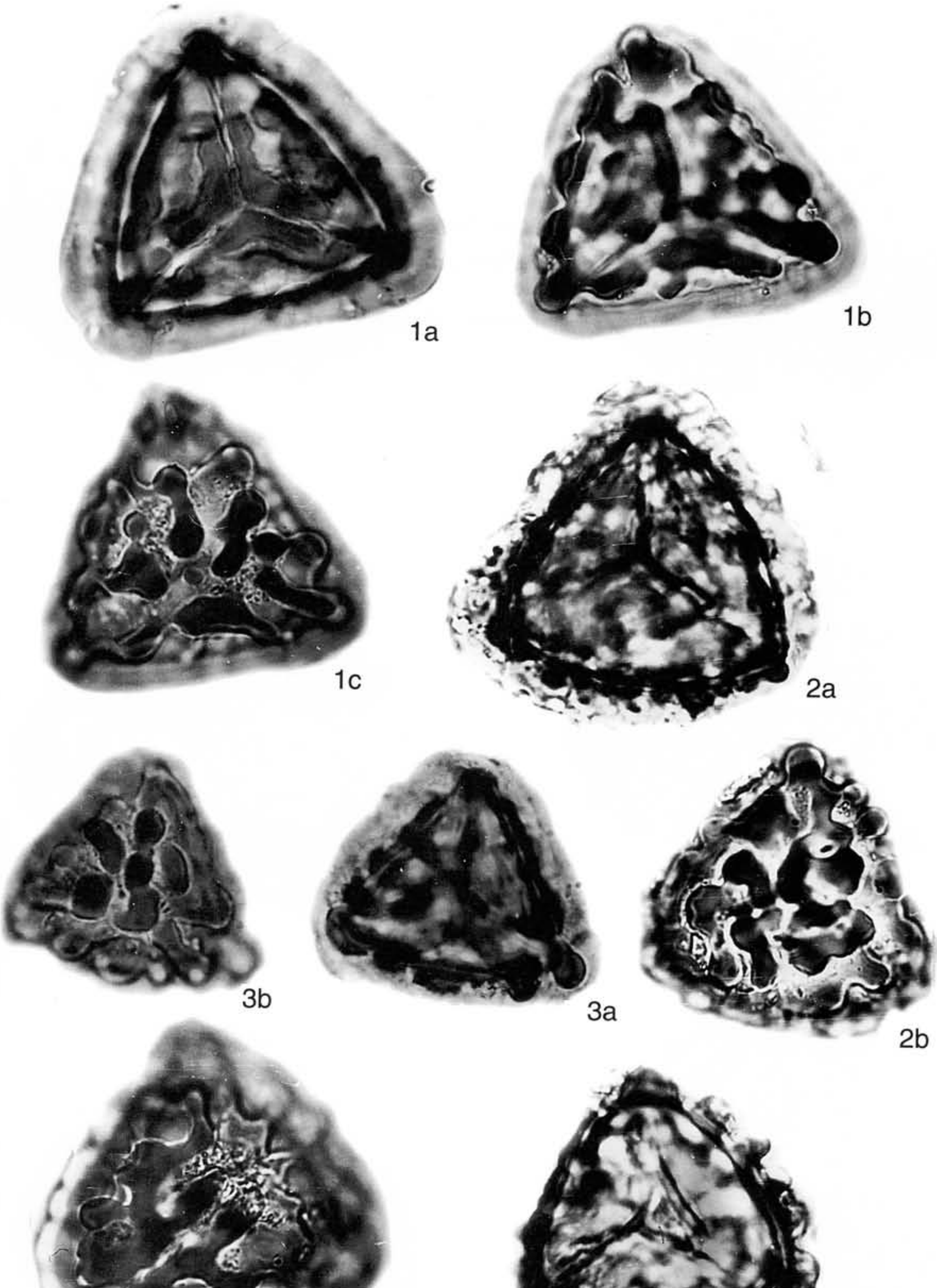

1a
1b
1c
2a
3b
3a
2b
4a
4b

Plate 16

× 1000

Pterisisporites boerzsoenyensis (Nagy) Stuchlik & Shatilova **comb. nov.**

1. a – proximal face, b, c – distal face, Western Georgia, Gogoreti village, Lower Kuyalnikian (Lower Skurdumian)
2. a, b – two sections of proximal face, c – distal face, Western Georgia, Bjuja river, Kimmerian

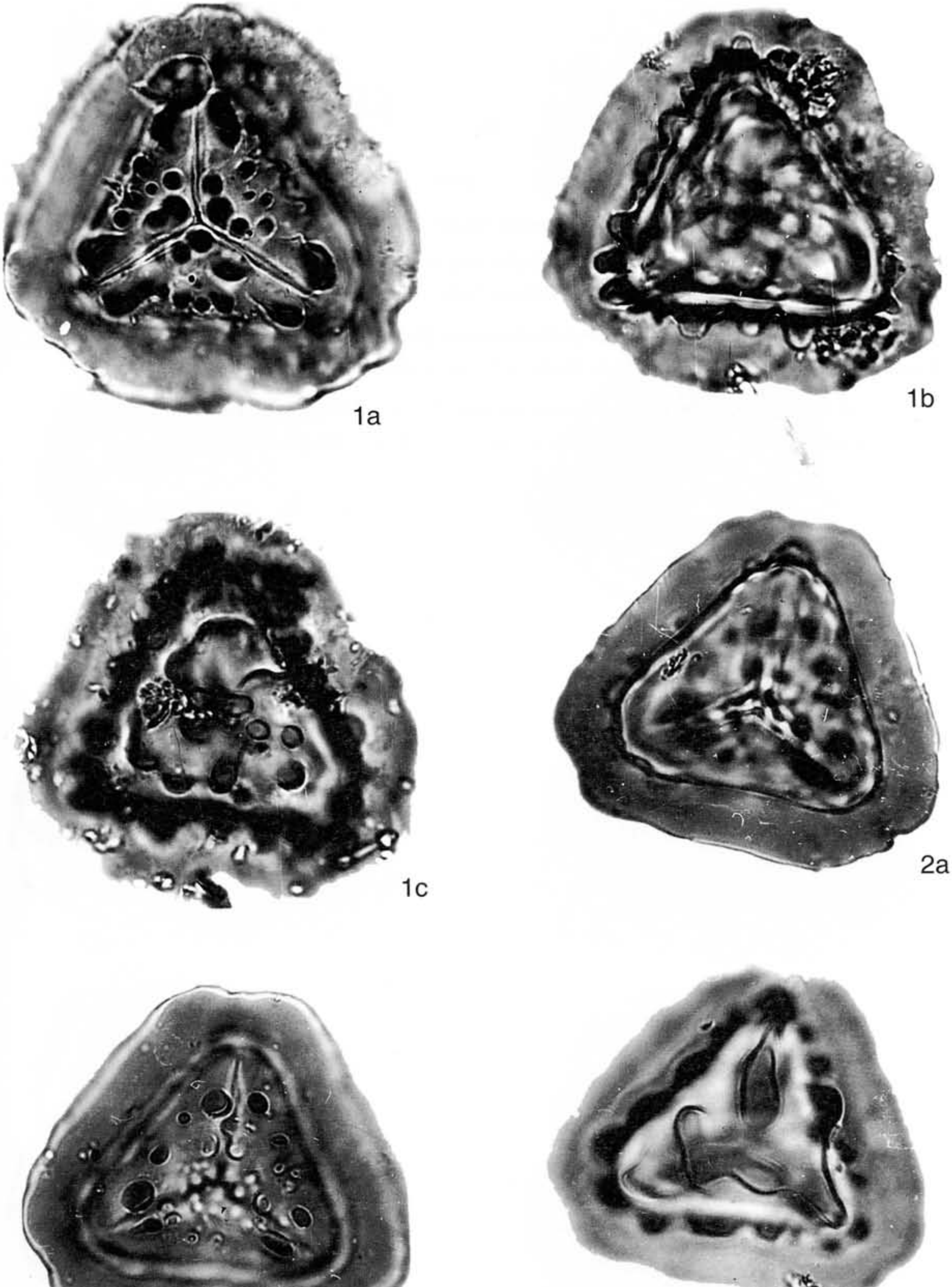

1a
1b
1c
2a
2b
2c

Plate 17

× 1000

Pteridacidites boerzsoenyensis (Nagy) Stuchlik & Shatilova **comb. nov.**

1. a – surface, b – proximal face, Western Georgia, Gogoreti village, Lower Kuyalnikian (Lower Skurdumian)
2. a – surface, b – proximal face, Western Georgia, Vake village, Sarmatian

Pteridacidites rarotuberculatus Shatilova & Stuchlik **sp. nov.**

3. b – two optical sections of distal face, Western Georgia, Gogoreti village, Kuyalnikin

Pteridacidites pseudocreticus Stuchlik & Shatilova **sp. nov.**

4. a – proximal face, b – distal face, Western Georgia, Morokhvili village, Kimmerian

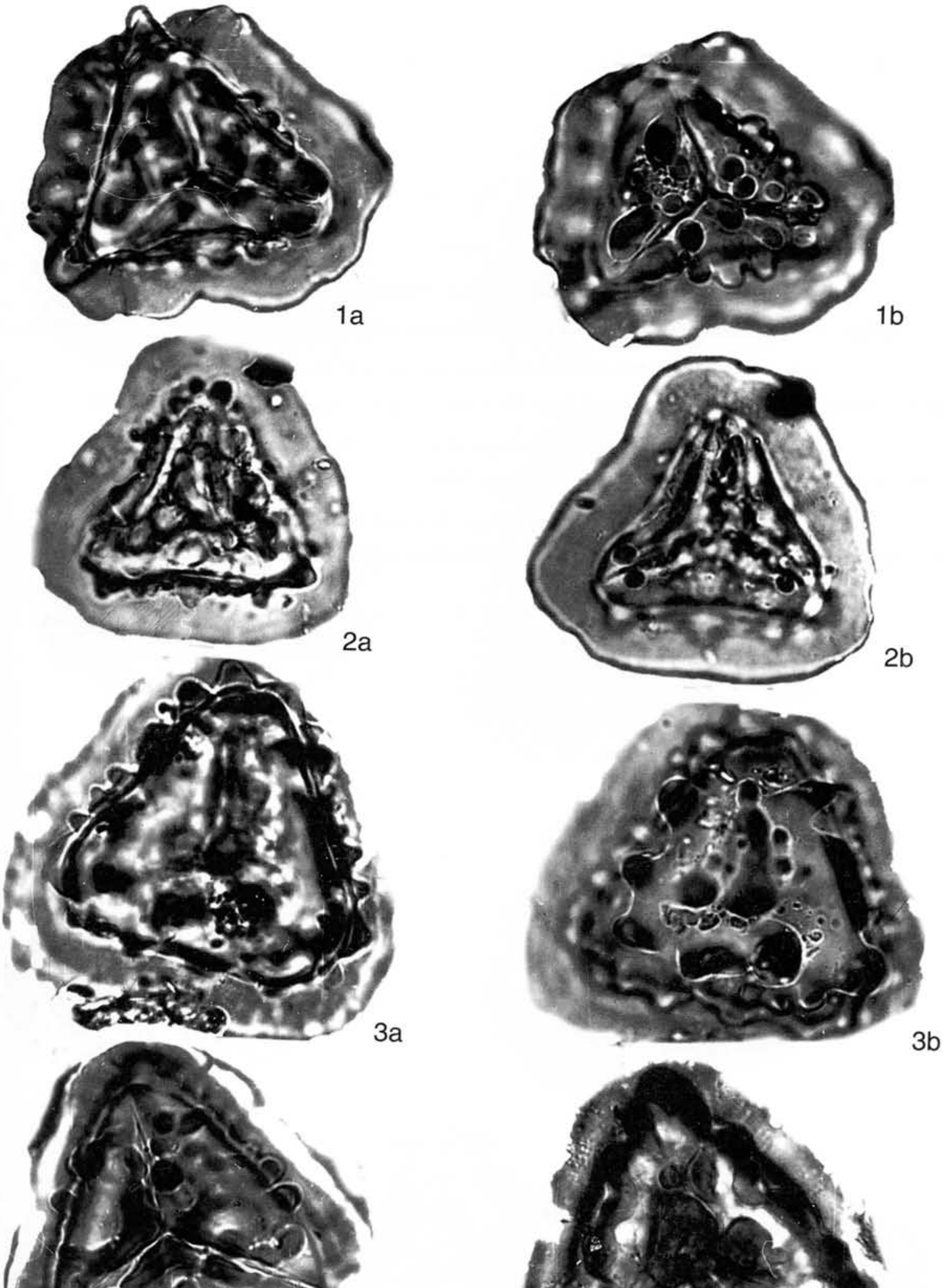

1a
1b
2a
2b
3a
3b
4a
4b

Plate 18

× 1000

Pteridacidites pseudocreticus Stuchlik & Shatilova **sp. nov.**

1. a – surface, b – proximal face, c – distal face, Western Georgia, Tsikhisperdi village, Kuyalnikian

Pteridacidites kimmeriensis Shatilova & Stuchlik **sp. nov.**

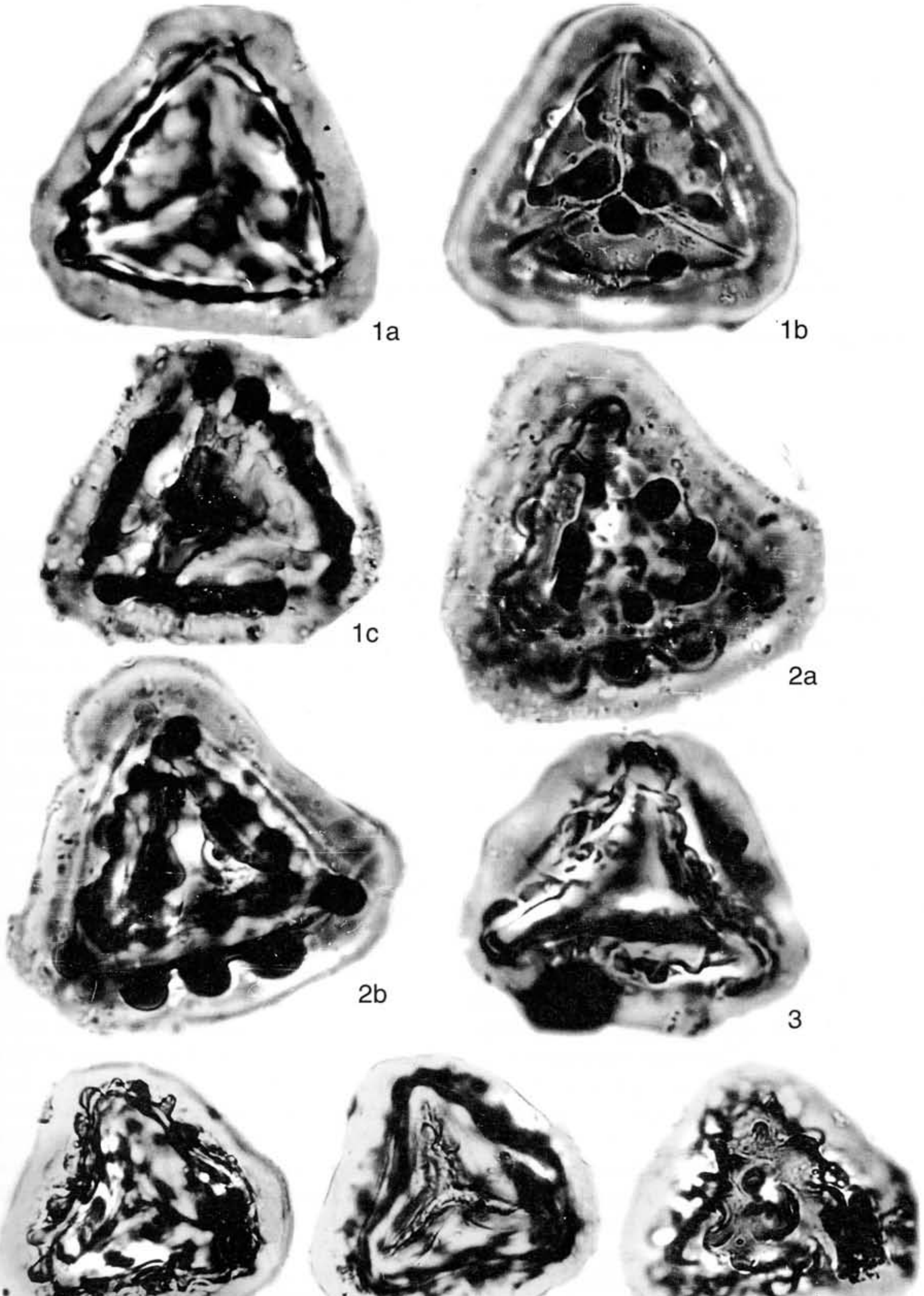
2. a, b – two optical sections of proximal face, Western Georgia, Gogoreti village Kuyalnikian

Pteridacidites georgensis Stuchlik & Shatilova **sp. nov.**

3. proximal face, Western Georgia, Gogoreti village, Meotian

Pteridacidites helveticus (Nagy) Stuchlik & Shatilova **comb. nov.**

4. a – surface, b – proximal face, c – distal face, Western Georgia, Djgali village, Sarmatian


1a
1b
1c
2a
2b
3
4a
4b
4c