GEORGIAN NATIONAL MUSEUM

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THE HISTORY OF THE FLORA AND VEGETATION OF GEORGIA

(South Caucasus)

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Paleobotanical investigations have been carried out in Georgia (South Caucasus) since the early 20th century. In this work, we bring together the great body of research on fossil material from Georgia's Phanerozoic deposits to provide descriptions of the floras, plant communities and paleogeographic conditions of past geological epochs.

The paleofloras of Western Georgia, from the stratotypical region of Eastern Paratethys, are considered in particular detail as the Black Sea deposits provide a continuous fossil record spanning the entire Neogene and Quaternary. These sediments, dated biostratigaphically using marine fauna, contain rich paleobotanical material of both macrobotanical remains and palynomorphs.

Pollen and spore assemblages from complete sections of various Upper Miocene, Pliocene, Pleistocene and Holocene stages have been interpreted using the landscape-phytocenological method, providing an almost uninterrupted reconstruction of vegetation and climate dynamics in Georgia.

The work also contains complete flora lists of various stratigraphical units, palynological diagrams, maps of fossil localities and paleogeographical maps of Georgia.

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INTRODUCTION

Georgia is situated in the central and western parts of the South Caucasus region, between the Black and Caspian Seas. It is a mountainous country with three major orographic systems within its borders: the mountain systems of the Greater and Lesser Caucasus; the intermontane depressions (Colchian, Kartlian and Alazanian); and the South Georgian volcanic highland (Fig.1).

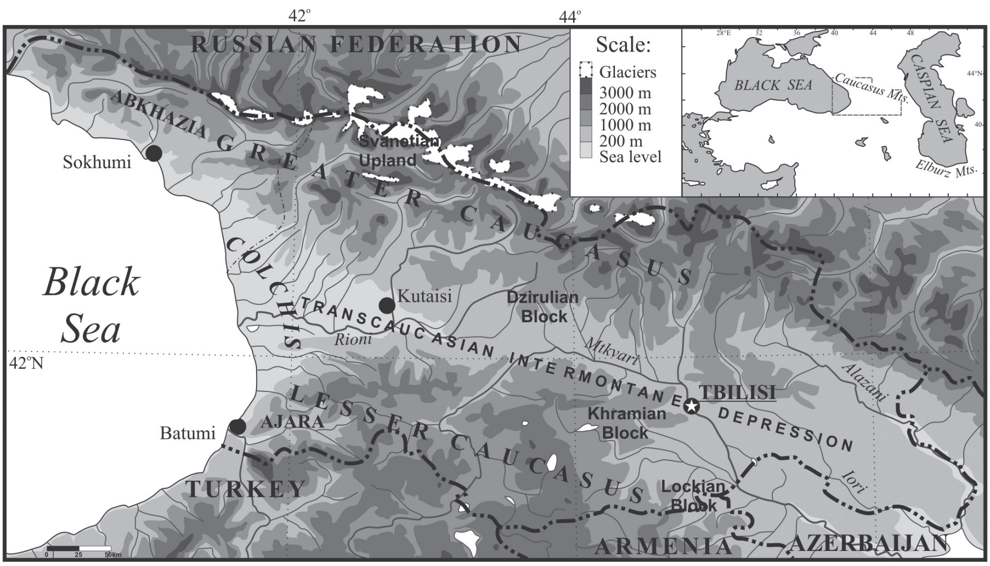

Fig.1. Topographic map of Georgia.

In spite of its diverse natural conditions, Georgia encompasses two principal regions – Western and Eastern – which differ markedly from each other. Western Georgia is characterized by a warm and humid climate, promoting the development of lush forest vegetation. This is the so-called Colchian botanical province, where some relicts of Tertiary floras are preserved even today. Quite a different picture can be seen in Eastern Georgia, where vegetation typical of a more arid, continental climate is distributed over large areas.

In 1990, the N. Ketskhoveli Institute of Botany of the Georgian Academy of Sciences published the "Materials on the History of the Flora and Vegetation of Georgia" (Shatilova, Ramishvili, 1990). This work provides an extensive review of factual data, although, owing to a lack of paleobotanical data, the floras of some stratigraphical units were not described in any great detail.

While subsequent investigations have not managed to fill all of the gaps in knowledge, and, from a paleobotanical point of view, our knowledge of Paleozoic and Paleocene floras is still relatively poor, rich palynological material from the Late Cenozoic has been collected over the last 20 years. These materials were interpreted using the landscape-phytocenological method, which allows the development of the flora and vegetation to be reconstructed. Under the influences of the abiotic and biotic factors, the fossil record indicates that changes in vegetation composition led to the formation of Georgia's current vegetation complex and its high biodiversity.

THE PALEOZOIC

THE CARBONIFEROUS

Within Georgian territory, Janelidze (1942) distinguished the labile folded zones of the Greater Caucasus and the Anticaucasus, separated by a stable zone called the Georgian Block. A scheme of Georgia's tectonic structure is given in Fig. 2.

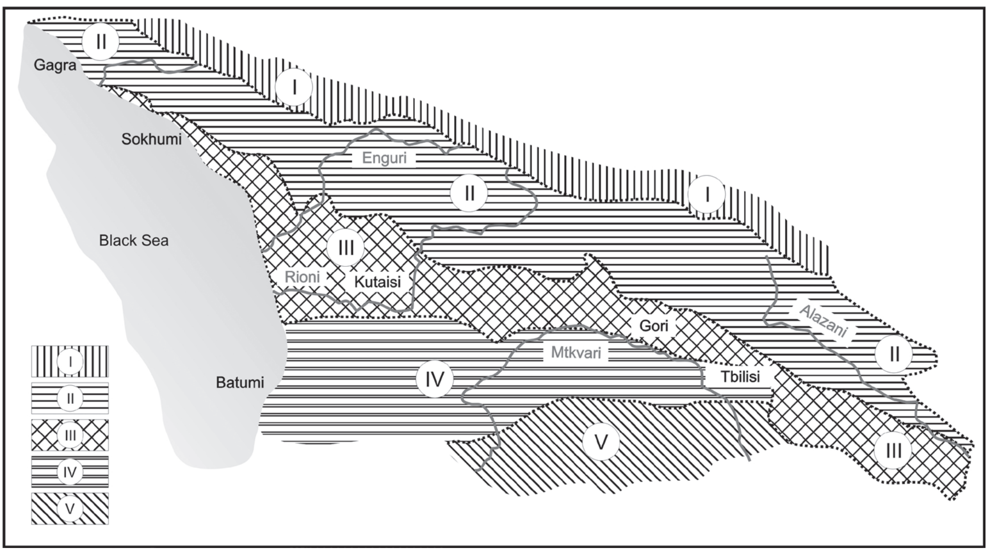

Fig.2. Scheme of tectonic structure of Georgia (after P. Gamkrelidze, 1964)
Key: I. The anticlinal Greater Caucasus; II. The folded system of the Greater Caucasus southern slope; III. The Georgian Block (intermontane depression); IV. The Adjara-Trialetian system; V. The Artvino-Bolnisian Block.

According to I. Gamkrelidze (2000), the following systems are found in Georgia: the folded system of the Greater Caucasus (*Kavkasioni*), the Transcaucasian (South Caucasus) intermontane region and the folded system of the Lesser Caucasus (*Antikavkasioni*).

In Georgia, sedimentary rocks are widely distributed and span the periods from the Paleozoic to the Holocene (Table I). The oldest deposits are outcrops in the crystalline and metamorphic rocks of the Dzirulian, Khramian and Lokian Blocks, representing a single formation (Fig.3). The lower part of this formation belongs to the Precambrian, while the upper part is Paleozoic (Adamia, 1968).

Table I. General scheme of stratigraphical division of Phanerozoic deposits in Georgia (after Borzenkova, 1992; Harland et al., 1985)

Ma	Group	System	Division/Stage	
0			Holocene	Modern
				Upper
		Quaternary	Pleistocene	Middle
				Lower
	Cenozoic		Neogene	Pliocene
				Miocene
		Tertiary		Oligocene
			Paleogene	Eocene
65				Paleocene
		Cretaceous	Upper	
			Lower	
			Upper - Malm	
		Jurassic	Middle - Dogger	
	Mesozoic		Lower - Lias	
			Upper	
		Triassic	Middle	
225			Lower - Scythian	
		Permian	Upper	
			Lower	
			Upper	
		Carboniferous	Middle	
			Lower	
			Upper	
		Devonian	Middle	
			Lower	
	Paleozoic	Silurian	Upper	
			Lower	
			Upper	
		Ordovician	Middle	
			Lower	
			Upper	
		Cambrian	Middle	
600			Lower	

Following long periods of denudation, in which most of the Lower-Middle Paleozoic deposits were washed away, the Dzirulian, Khramian and Lokian blocks became an area of sedimentation. During the Lower and Middle Carboniferous, volcanic-sedimentary rocks accumulated, preserving the remains of plants. The presence of these fossils, along with lenses of reef-derived limestone, indicates the near-shore and continental character of the sediments.

In Georgia the most ancient finds of fossil flora are dated to the Paleozoic. These plant remains from the Lower and Middle Carboniferous deposits of the Khramian Block were identified by Uznadze and Novak (Skhirtladze, 1964; Adamia, 1968).

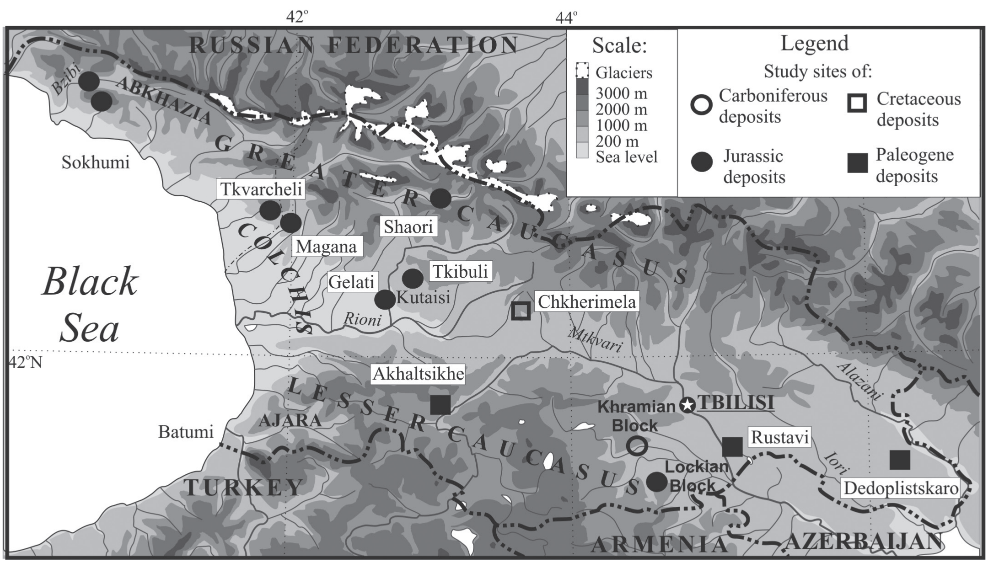

Fig.3. Study sites of Carboniferous, Jurassic, Cretaceous and Paleogene deposits in Georgia

Most of the plants listed in Table II are typical of the Paleozoic and only a few of them persisted through the Permian.

Representatives of the family Lepidodendraceae were large trees up to 40 m high and 2 m in diameter with dichotomous branching. The leaves were narrow and linear. The stele of lepidodendrons was weak and could not serve as the trees' main support. This structural function was instead performed multiple layers of tough bark. An analogous structure can be seen in grasses today, but is never present in modern trees (Davitashvili, 1949).

Table II. Plants from the Carboniferous deposits in Georgia (by macrofossils)

Class	Family	Species
Isoëtopsida	Lepidodendraceae	Lepidodendron dichotomum Sternb.
		Lepidophloios laricinus Sternb.
		Lepidophloios vsevolodii Zal.
	Sigillariaceae	Stigmaria ficoides Sternb..
Equisetopsida	Asterocalamitaceae	Asterocalamites scrobiculatus (Schl.) Zeill.
	Calamitaceae	Mesocalamites ramifer (Stur) Hirm.
Marattiopsida	Asterothecaceae	Asterotheca miltonii (Artis.) Zeill.
Lyginopteridopsida	Lyginopteridaceae	Lyginopteris bermudensiformis (Schl.) Patt. f.geinitzii Stur
		Lyginopteris bermudensiformis (Schl.) Patt. f.schlotheimii Stur
		Lyginopteris fragilis (Schln.) Patt.
		Lyginopteris hoeninghausii (Brongn.)Patt.
		Palmatopteris furcata (Brongn.)Pot.
Cordaitopsida	Cordaitaceae	Cordaites sp.

Representatives of the family Sigillariaceae were tall plants with a straight trunk, the upper part of which was dichotomously branched. They possessed a peculiar root structure called stigmaria and fossil remains of this are described under the name Stigmaria. The morphological function of stigmarias is not entirely clear. They may be considered stilt-roots or rhizophores, which are absent from recent Lycopodiaceae, but present in a more distinct form in the Selaginellaceae (Krishtofovich, 1957). According to Krasilov (1972), the superficial root system of recent hygrophilous trees is similar to Paleozoic stigmaria.

Asterocalamites and calamites were also large plants. Calamites had the capacity to produce secondary xylem. In terms of branching, they varied from abundantly branched to non-branched (Radchenko, 1963).

The genus Lyginopteris includes the seed ferns. These plants had a real seed-buds (ovules) located on the leaves, while the microphylls retained the appearance of sporiferous leaves. The trunk had secondary wood, peculiar for the Cycadales (Krishtofovich, 1957).

Remains of Cordaites were also found in Paleozoic deposits in Georgia. These trees had sturdy trunks, which had the anatomical structure of conifers, araucarioid tracheae and a well developed core (Krishtofovich, 1957).

THE MESOZOIC

THE JURASSIC

Jurassic deposits are distributed rather irregularly over Georgia (Fig.3). They occupy the greatest area in the folded system of the Greater Caucasus, while being poorly represented both in the Transcaucasian intermontane region (the Georgian Block) and the folded system of the Lesser Caucasus (Gamkrelidze, 2000). A scheme of stratigraphical division of Jurassic deposits is given in Table III.

Table III. Stratigraphical division of Jurassic deposits in Georgia (after Kakhadze, 1947; Topchishvili, 1969; Topchishvili et al., 2006).

Ma	System	Division	Stage
140	Jurassic	Upper - Malm	Tithonian
			Kimmeridgian
			Oxfordian
		Middle - Dogger	Callovian
			Bathonian
			Bajocian
			Aalenian
		Lower - Lias	Toarcian
			Pliensbachian
			Sinemurian
180			Hettangian

The Early Jurassic

During the Early Jurassic, the greater part of Georgian territory was covered by sea, except for the areas of the ancient blocks (Kakhadze, 1947; Vakhania, 1976).

In Southern Georgia, the Early Jurassic flora was preserved in Hettangian micaceous sandstones. Plant remains from the Dzirulian Block are also connected with "lower tuffites" of the Hettangian stage (Adamia, 1968; Svanidze, 1965, 1971;

Svanidze, Iakobidze, 1979 Topchishvili, 1969). Lias-aged deposits from several regions of Western Georgia have been studied palynologically (Karashvili, 1973, 1977).

In the Early Jurassic flora (Table IV), calamites were represented by one species: *Neocalamites hoerensis*. In Europe this form is known from Ret-Lias. Its fossils are rare in Georgian deposits and usually represented by stems found in bedding planes or perpendicularly to them (Svanidze, 1996).

Among the Jurassic Equisetopsida, the horsetail was the most widely distributed plant. A comparison of fossil and recent horsetails shows that there is no major difference between them. On this basis, Delle (1967) suggested a relationship between the remains of the Jurassic plant and the modern genus Equisetum. In the Early and Middle Jurassic floras, both small and large horsetail forms are represented. The latter group includes *Equisetum beanii,* the remains of which are rarely found in Jurassic deposits in Georgia, but usually alongside remains of Neocalamites. Both genera were probably plants of swampy terrestrial areas.

In the Early Jurassic paleofloras, ferns are represented by 25 forms, mainly differentiated on palynological grounds. Macroremains belong to the systematically uncertain taxon Cladophlebis, which is connected with the Osmundaceae family. Cladophlebis remains are abundant in Georgian Early Jurassic deposits and are usually well preserved, indicating that this fern's habitat was quite near to the sedimentary basin (Svanidze, 1996).

The Ginkgo genus is represented by two forms in the Early Jurassic: *Ginkgo mziae*, a species characteristic for Georgia, and *Ginkgo* ex gr. *huttonii*, which is known from many Jurassic flora localities. Svanidze avoided definitive identification of the remains of *G. huttonii* in light of taxonomic revisions, according to which, not all leaves described as *G. huttonii* belong to one and the same species (Doludenko, Lebedeva, 1972; Samylina, 1970).

The class Ginkgoopsida includes representatives of the family Czekanowskiaceae. By the Early Mesozoic these plants had already reached a high evolutionary level, with angiosperm-like preservation of the seed (Krasilov, 1968). Czekanowskia dominated in the Siberian Paleofloristic region from the Late Triassic until the Early Cretaceous. They played a lesser role in southern regions and disappeared entirely during the Late Jurassic. In Georgia, Czekanowskia were found in Lower and Middle Jurassic (Bathonian) deposits. As a rule, remains of these plants are very rarely and poorly preserved (Svanidze, 1996).

Jurassic spore-pollen assemblages include pollen of *Eucommidites troedssonii* Erdtman (Iakobidze et al., 1983). Initially this form was described by Erdtman from the Lias deposits and was thought to belong to the angiosperms. In 1958 Couper corrected this diagnosis and proved a relationship between *E. troedssonii* and gymnosperms on the basis of statistical analysis of pollen morphological features (Yaroshenko, 1965). Pollen of this species was later observed in gymnosperm seed ovules (Kotova, 1979).

Based on floral composition, Svanidze (1996) drew the conclusion that distinct plant communities existed in different topographic zones during Georgia's Early Jurassic. The climate was warm-temperate in the Middle Lias, after which the temperature fell. These data agree with the inference of a cool, wet Toarcian-Aalenian climate, contrasting starkly with the climates of subsequent stretches of the Jurassic (Yasamanov, 1980, 1985).

The Middle Jurassic

The middle Early Jurassic witnessed some significant downward tectonic movements in Georgia. Nearly all of Western Georgia was covered by sea, which approached the Dzirulian and Lockian Blocks and established shallow marine conditions around their margins. Marine regression took place in the Early Aalenian and, as a result of weak orographic uplift the mountain ranges were formed (Dzotsenidze & Skhirtladze, 1961; Kakhadze, 1947; Topchishvili et al., 2006).

In the Bajocian, the picture changed again. Late Liassic uplift was followed by intensive subsidence and, by the Early Bajocian, most of Georgia's territory was covered by sea. Large-scale subsidence continued during much of the Bajocian and finally came to a halt at the end of this stage, replaced by tectonic movements in the opposite direction. The sea retreated and only parts of Western Georgia remained inundated (Kakhadze, 1947; Vakhania, 1976).

The Late Bajocian regression continued in the Bathonian, when nearly the whole territory of Georgia terrestrialised. According to Adamia (Adamia et al., 1964), various freshwater basins appeared, providing conditions favorable to peat accumulation. Examples include the Tkibulian, Shaorian, Gelatian, Maganian, Tkvarchelian and Bzibian coal basins. On the basis of new data (Topchishvili et al., 2006), it is clear that each of these basins was part of a single, closed freshwater basin that had lost its connection to the sea. Sediments deposited in this basin contain abundant plant remains. Fossil remains have also been identified in Bathonian deposits of the Lockian Block (Svanidze et al., 1983; Zesashvili et al., 1977).

Compared to the Liassic flora, the Bathonian flora is very rich. It can be supposed that several plant communities were present in Georgia during this period, associated with both swampy and dry places:

1. Marsh and mangrove vegetation, in which Coniopteris, Pachypteris, Ctenozamites and Ptilophyllum were present.
2. Vegetation of swampy plains, in which representatives of the Selaginellaceae, Equisetaceae, Marattiaceae, Osmundaceae, Schizaeaceae, Gleicheniaceae, Hymenopyllaceae, Dicksoniaceae, Cycadaceae and Bennettitaceae were identified.
3. Vegetation of dry plains, in which Clathropteris, Matonidium, Pseudocycas, Ginkgoaceae, Podozamites, Podocarpus, Picea and Sciadopitys occurred.
4. Vegetation of piedmonts and shaded river gorges, including Dictyophyllum, Czekanowskia, Ginkgoaceae, Brachyphyllum, Classopolis and Pagiophyllum (Shengelia et al., 1987).

We should draw attention here to the question of mangrove fossilization raised by Doludenko (1984). Mangrove is a specific type of past vegetation, analogous to modern mangroves in terms of both systematic composition and specific ecological and morphological features. However, any tree- or shrub-dominated vegetation that grew in the intertidal zone is often attributed to a mangrove community (just as grass vegetation is linked to marsh communities).

This question was resolved by Teslenko (1979), who carried out research in India on the fossilization of various parts of mangrove plants in different sedimentary environments. These investigations showed that, in the intertidal zone inhabited by mangroves, conditions were not suitable for the fossilization of leaves. During high tide they float on the surface and are later carried out to sea by ebb tides. Plant remains caught between the roots of trees tend to be destroyed by wave action. Pollen and spores of mangrove plants are not fossilized in situ because waves and tides remove them from the intertidal zone. The only part of mangrove plants that tends to be fossilized is the root system. The discovery of fossil pneumatophores would enable us to draw important parallels between recent mangroves and the vegetation of past geological epochs.

The climate of Georgia in the Bathonian was humid and tropical. Some cooling took place at the end of the Early Jurassic and the sea temperature rose during the subsequent Bajocian. Similar conditions persisted into the Bathonian, when forests were dominated by Cycadales and Ginkgoales (Yasamanov, 1980).

The Callovian stage is the last part of the Middle Jurassic (Table III). It began with a transgression, the most significant one in the geological history of the Caucasus (Kakhadze, 1947; Topchishvili et al., 2006). Only the Svanetian Upland and some high places in Southern Georgia remained free of the sea (Vakhania, 1976).

Callovian deposits are rich in floral remains and have a composition quite different from those of the Bathonian (Svanidze, 1970a). Alongside these macrofossils, spore-pollen assemblages indicate the genus Classopolis increased to 40% (Karashvili 1973).

The boundary between Bathonian and Callovian was a time of radical changes in vegetation linked to marine transgression and the appearance of arid climatic zones in large swathes of the Northern Hemisphere. Analyses have revealed that a large number of Cheirolepidiaceae and a high percentage of Classopolis are found in deposits of regions where arid and semi-arid zones persisted into the Mesozoic. Under these conditions, Cheirolepidiaceae became dominant and are thought to have been capable of growing in various habitats, forming open woodlands (Alvin et al., 1978; Meien, 1987; Vakhrameev, 1980; Vakhrameev & Doludenko, 1976).

The boundary between the Bathonian and Callovian was also a turning-point in the development of the Jurassic flora in Georgia. The number of ferns decreased. The family Czekanowskiaceae went completely extinct and the number of genera in the Ginkgoaceae and Cycadaceae families declined. The diverse and luxuriant vegetation of the Bathonian was replaced by homogenous riparian communities. Cheirolepidiaceae became prevalent, indicating a tropical climate with low humidity (Doludenko & Svanidze, 1969).

According to Vakhrameev (1988), two paleofloristic regions existed in Eurasia during the Jurassic: the Siberian region in the north and the Indo-European in the south (the latter has since been renamed the 'Euro-Sinaian' region). The Indo-European region was split into three provinces: Eastern Asian, Central Asian and European, which includes the South Caucasus.

Svanidze (1996) noted that the Early Jurassic flora of Georgia had affinities to both the European and Central Asian provinces and hence avoided assigning Georgia to either of these provinces.

The Bathonian flora of Tkvarcheli was assigned to the European province by Delle (1967). She recognised the Caspian-Black Sea area as a transitional zone, but not as an independent phytogeographical unit. Svanidze, on the other hand, cites the presence of many new species in the Bathonian flora of Georgia as evidence for its independence.

According to Svanidze (1996), the Georgian Callovian flora was of mixed character. She thus proposed a separate province for Georgia, transitional between the European and Central Asian.

Georgia's Jurassic flora is listed in Table IV, based on materials analysed by Delle

(1960, 1960a, 1967); Doludenko (1984); Doludenko and Svanidze (1969), Iakobidze (1980, 1981); Iakobidze et al. (1983); Karashvili (1973, 1977); Kolakovsky (1973); Loladze (1979); Loladze et al. (1978); Prynada (1933); Shengelia et al. (1987); Svanidze (1960, 1965, 1969, 1970, 1970a, 1971; 1996); Svanidze and Iakobidze (1979); Svanidze and Shengelia (1979, 1987); and Svanidze et al. (1983). Taxonomy follows Takhtajan (Takhtajan, 1974; 1986; 1987; Takhtajan et al. 1963; Vakhrameev et al. 1963).

Table IV. Plants from the Lower and Middle Jurassic deposits in Georgia
Key: m – macrofossils; p – pollen

Class	Family	Species	Lower Jurassic	Middle Jurassic	
				Bathonian	Callovian
1	2	3	4	5	6
Lycopodiopsida	Lycopodiaceae	Lycopodiumsporites pseudolaterale Tralau	p		
		Lycopodiumsporites subrotundus (K.M.) Pocock	p		
		Lycopodium sp.	p	p	
Isoëtopsida	Selaginellaceae	Selaginella rostratus Burakowa		m	
		Selaginella sp.		p	p
Equisetopsida	Sorocaulaceae	Neocalamites hoerensis (Schimp.) Halle	m	m	
		Neocalamites aff.nathorsti Erdtman		p	
		Neocalamites sp.		m	
	Equisetaceae	Equisetum beanii (Bumb.) Harris	m	m	
		Equisetum columnare Brongn.		m	
		Equisetum laterale Phillips		m	
		Equisetum sp.	p	pm	p
Marattiopsida	Marattiaceae	Angiopteris iberica Delle et Dolud.			m
		Marattia muensterii (Goepp.) Delle		m	
		Marattisporites scabratus Couper	p		
		Marattisporites aff.hoerensis (Schimp.) Thomas		p	p
		Marattisporites sp.	p		p

1	2	3	4	5	6
Polypodiopsida	Osmundaceae	Osmunda papillata Bolch.			p
		Osmundacidites wellmanii Couper	p		
		Osmundacidites sp.		p	
		Osmundopsis prynadae Delle	m	m	
		Todites princeps (Presl.) Goth.		m	
		Todites williamsonii (Brongn.) Sew.		m	
	Schizaeaceae	Klukia exilis (Phill.) Racib.		m	p
		Klukia marginata Prynad.		m	
		Klukia sp.		p	
		Klukisporites variegatus Couper	p	p	
		Klukisporites sp.			p
	Lygodi-aceae	Lygodium sp.			p
	Pteri-daceae	Pteridaceae gen.indet.	p	p	p
	Gleicheni-aceae	Gleichenia delicata Bolch.		p	p
		Gleichenia sphenopteroides Brick.		p	
		Gleichenia sp.			p
		Gleicheniidites granulatus Grig.		p	p
	Matoniaceae	Matonidium goeppertii (Ett.) Schenk.		m	
		Matonisporites phlebopter-oides Couper	p	p	
		Matonisporites sp.	p	p	p
		Phlebopteris exornatus Bolch.	p		
		Phlebopteris polypodioides (Brongn.) Brongn.		m	
		Phlebopteris sp.		p	
	Dipteridaceae	Camptotriletes cerebri-formis Naum.			p
		Clathropteris obovata var. magna Tur.-Ket.	p	p	
		Clathropteris sp.		m	
		Dictyophyllum nilssonii (Brongn.) Goepp.	m	m	
		Dictyophyllum sp.	p		p
		Dictyophyllidites harrisii Couper	p	p	
		Dictyophyllidites vulgaris (Mal.) Sem.	p		
		Hausmannia sp.	p		p
		Thaumatopteris sp.		m	

1	2	3	4	5	6
Polypodiopsida	Polypodiaceae	Polypodites cladophleboides Brick.			p
		Polypodites harrisii Couper			p
		Polypodites sp.			p
		Polypodiaceae gen.indet.		p	
	Hymenophyllaceae	Hymenophyllum densigranulatum Vin.	p		
		Hymenophyllum sp.	p	p	
		Trichomanes sp.		p	
		Hymenophyllaceae gen. indet.			p
	Thyrsopteridaceae	Cibotium junctum K.-M.	p	p	p
		Cibotium sp.		p	
	Dicksoniaceae	Coniopteris angustiloba Brick.		m	
		Coniopteris georgica Iakob.		m	
		Coniopteris hymenophylloides (Brongn.) Sew.		pm	
		Coniopteris murrayana (Brongn.) Brongn.		m	
		Coniopteris aff.divaricata (K.-M.) Bolch.		p	
		Coniopteris sp.	p	p	p
		Dicksonia densa Bolch.			p
		Dicksonia aff.crocina Bolch.		p	
		Dicksonia sp.	p		p
		Eboracia sp.		p	p
		Gonatosorus lobifolius Bur.		m	
		Lobifolia lobifolia (Phill.) Rass.et Lebed.		m	
	Cyatheaceae	Cyathidites sustralis Couper		p	p
		Cyathidites minor Couper	p	p	p
		Cyathidites remalis Balme		p	
		Cyathidites sp.	p	p	
		Hemitelia sp.		p	p
		Cyatheaceae gen.indet.			p
The ferns of indeterminate systematical position		Calamospora mesozoica Couper			p
		Cladophlebis denticulata (Brongn.) Font.		m	m
		Cladophlebis denticulata var.caucasica Prynad.		m	
		Cladophlebis suluktensis Brick.		m	
		Cladophlebis haiburnensis (Lindl.et Hutt.) Goepp.	m		
		Cladophlebis whitbiensis (Brongn.) Brongn.	m	m	
		Cladophlebis williamsonii (Brongn.) Brongn.			m

1	2	3	4	5	6
The ferns of indeterminate systematical position		Cladophlebis aff.kamenkensis Thomas		m	
		Cladophlebis sp.	m		
		Raphaelia diamensis Sew.		m	
		Sphenopteris mokrynskyi Prynad.		m	
		Sphenopteris cf.gracillima Heer		m	
		Sphenopteris sp.			m
		Weichselia reticulata Stok. et Webb.		m	
Lyginopteridopsida	Caytoniaceae	Caytonanthus arberi (Thomas) Harris			p
		Caytonia oncodes Harris			p
		Caytonipollenites pallidus (Reiss.) Couper		p	p
		Sagenopteris colpodes Harris			m
		Sagenopteris heterophylla Dolud.et Svan.		m	m
		Sagenopteris latus Iakob.		m	
		Sagenopteris phillipsii (Brongn.) Presl.		m	m
		Sagenopteris sp.			m
The genera belong to Pteridospermae		Cycadopteris georgica Dolud.			m
		Cycadopteris jurensis (Kurr) Hirmer (= Pachypteris bendukidzeae Dolud.et Svan.)			m
		Ctenozamites uznadzeae Dolud.et Svan.			m
		Pachypteris lanceolata Brongn.		m	m
		Pachypteris multiformis Delle		m	
		Pachypteris aff.speciosa (Ett.) Andrea		m	
Ginkgoopsida	Ginkgoaceae	Baiera inaequilobata Delle		m	
		Eratmophyllum tomasii Dolud.et Svan.			m
		Ginkgo digitata (Brongn.) Heer		m	
		Ginkgo mziae Svan.	m		
		Ginkgo katcharavai Svan.		m	
		Ginkgo ex gr.huttonii (Sternb.) Heer	m		
		Ginkgo sp.		m	
		Ginkgocycadophytus sp.	p	p	p

1	2	3	4	5	6
Ginkgoopsida	Ginkgoaceae	Phoenicopsis ex gr.angustifolia Heer	m		
		Pseudotorellia cf.pulchella (Heer) Vassil.		m	
		Pseudotorellia sp.			m
		Sphenobaiera colchica (Prynad.) Delle		m	
		Sphenobaiera samylinae Dolud.et Svan.			m
		Sphenobaiera spectabilis (Nath.) Fl.	m		
		Sphenobaiera tsagarelii Svan.		m	
	Czekanowski-aceae	Czekanowskia latifolia Tur.-Ket.		m	
		Czekanowskia setacea Heer	m		
		Czekanowskia ex gr.rigida Heer	m	m	
		Czekanowskia sp.	m		
Pinopsida	Cheirolepidiaceae	Brachyphyllum expansum (Sternb.) Sew.			m
		Brachyphyllum aff.expan-sum (Sternb.) Sew.			m
		Brachyphyllum aff.mamil-lare Brongn.		m	m
		Brachyphyllum sp.			m
		Classopolis aff.classoides Pflug.em.Poc.et Jans.		p	p
		Classopolis sp.	p	p	p
		Elatides curvifolia (Dunk.) Nath.		m	
		Elatides williamsonii (Brongn.) Nath.			p
		Elatides sp.		m	
		Elatocladus ketovae Dolud.		m	
		Elatocladus subzamioides (Moell.)Tur.-Ket.		m	
		Elatocladus cf.curvifolia (L.et H.) Sew.		m	
		Elatocladus cf.indica Feistm.		m	
		Elatocladus sp.		m	m
		Haiburnia setosa (Phill.) Harris			m
		Pagiophyllum astrachan-ense Dolud.		m	m
		Pagiophyllum gracilis Svan. et Sheng.		m	
		Pagiophyllum peregrinum (L.et H.) Sew.		m	

1	2	3	4	5	6
Pinopsida	Cheirolepidiaceae	Pagiophyllum williamsonii (Brongn.) Sew.		m	m
		Pagiophyllum setosa (Phill.) Sew.		m	
		Pagiophyllum sp.		m	
		Tomharrisia sp.			m
		Walchites gradatus Bolkh.			p
	Podozamitaceae	Podozamites angustifolius (Eichw.) Heer		m	
		Podozamites eichwaldii Schimp.		m	
		Podozamites gramineus Heer	m		
		Podozamites lanceolatus (L.et H.) Schimp.	m	m	m
		Podozamites latifolia (Schenk.) Prynad.		m	
		Podozamites sp.	p	p	p
	Palissy-aceae	Stachyotaxus cf.elegans Nath.	m		
		Stachyotaxus sp.	m		
	Podocar-paceae	Podocarpus sp.			p
	Taxaceae	Taxites sp.		m	
	Araucariaceae	Araucariodendron angusti-folium Krassil.			m
		Araucarioxylon sp.		m	
		Araucarites macropteris Feistm.		m	
		Araucarites vassilevskiae Tur.-Ket.		m	
		Araucariaceae gen.indet.	p	p	p
	Pinaceae	Paleopinus sp.	p		
		Picea sp	p	p	
		Piceites latens Bolch.	p		p
		Piceites sp.	p	p	
		Pinus insignis Bolch.			p
		Pityophyllum latifolium Tur.-Ket.	m	m	
		Pityophyllum ex gr. nordenskioldii (Heer) Nat.	m	m	
		Pityostrobus sp.		m	
		Pseudopinus sp.			p
		Tsugaepollenites sp.			p
	Sciadopi-tyaceae	Sciadopitys mesozoicus (Couper) Zauer et Mtchedl.		p	p
		Sciadopitys sp.	p		p

1	2	3	4	5	6
Pinopsida	Taxodi-aceae	Taxodiaceae gen.indet.			p
	Cupres-saceae	Widdringtonites karataviensis Tur.-Ket.			m
		Widdringtonites sp.		m	
		Cupressaceae gen.indet.			p
Forma-taxa of conifers		Carpolithes aff.minor Prynad.		m	
		Carpolithes sp.		m	
		Paleoconiferus asaccatus Bolch.	p		
		Protoconiferus sp.			p
		Xenoxylon latiporosum (Cram.) Goth.		m	
Cycadopsida	Cycadaceae	Anthrophyopsis narulensis Dolud.et Svan.	m		
		Ctenis pontica Delle		m	
		Ctenis sp.		m	
		Cycadites rectangularis Brauns		m	
		Cycadites sp.		m	
		Cycadolepis gracilis Iakob.		m	
		Cycadolepis insignis Iakob.		m	
		Cycadolepis ovalis Dolud.		m	m
		Cycadolepis rugosa (Halle) Harris		m	m
		Cycadolepis sp.		m	
		Nilssonia grandifolia Delle		m	m
		Nilssonia grandifolia Delle f.rarinervis Delle		m	
		Nilssonia mediana Prynad.		m	
		Nilssonia princeps (Oldh.et Morr.) Sew.		m	
		Nilssonia variabilis Prynad.		m	
		Nilssonia vittaeformis Prynad. (=Nilssonia inouyei Yok.)		m	
		Nilssonia cf.kendalli Harris			m
		Nilssonia sp.			m
		Paracycas brevipinnata Delle		m	m
		Paracycas ctenis (Harris) Harris		m	
		Paracycas ctenis (Harris) Harris f.spinulata Dolud.		m	
		Paracycas intermedia Dolud.			m
		Paracycas raripinnata Dolud.			m

1	2	3	4	5	6
Cycadopsida	Cycadaceae	Pseudoctenis barulensis Dolud.			m
		Pseudoctenis latus Dolud.		m	m
		Pseudoctenis magnifolius Dolud.			m
		Pseudoctenis oleosa Harris			m
		Pseudoctenis weberi (Sew.) Prynad.		m	m
		Pseudoctenis aff.eathiensis (Rich.) Sew.			m
		Pseudoctenis aff.lanei Thomas			m
		Pseudoctenis aff. magnifolius Dolud.		m	
		Pseudoctenis sp.			m
Bennettitopsida	Williamsoniaceae	Williamsonia whitbiensis Nath.		m	
		Williamsonia sp.		m	
	Bennettitaceae	Anomozamites nitida Harris	m		
		Anomozamites minor (Brongn.) Nath.	m		
		Anomozamites variabilis (Prynad.) Iakob.		m	
		Anomozamites sp.		m	
		Bennettites sp.	p		
		Nilssoniopteris angustifolia Dolud.		m	m
		Nilssoniopteris longifolia Dolud.			m
		Nilssoniopteris muchlensis Dolud.		m	m
		Nilssoniopteris stenophylla Dolud.			m
		Nilssoniopteris tkibulensis Iakob.		m	
		Nilssoniopteris vulgaris Dolud.		m	m
		Nilssoniopteris vittata (Brongn.) Fl.		m	m
		Taeniopteris sp.cf.Nilssoniopteris vittata (Brongn.) Fl.		m	
		Otozamites beanii (L.et H.) Brongn.		m	
		Otozamites caucasicus Iakob.		m	
		Otozamites graphicus (Leck.) Schimp.		m	m
		Otozamites hislopii (Oldh.) Feistm.		m	

1	2	3	4	5	6
Bennettitopsida	Bennettitaceae	Otozamites latior Sap.		m	
		Otozamites obtusus (L.et H.) Brongn.		m	
		Otozamites sp.		m	m
		Pseudocycas cessiensis Dolud.		m	m
		Pseudocycas cf.saighanensis Jakob. et Shukla		m	
		Pterophyllum aequale (Brongn.) Nath.		m	
		Pterophyllum djanelidzei Svan.	m	m	
		Pterophyllum georgiense Dolud.			m
		Pterophyllum insigne Dolud.			m
		Pterophyllum kakhadzei Svan.		m	
		Pterophyllum magnum Dolud.			m
		Pterophyllum mirabile Dolud.			m
		Pterophyllum narulense Svan.	m		
		Pterophyllum papillatum Dolud.			m
		Pterophyllum paradoxum Dolud.			m
		Pterophyllum raripinnatum Dolud.			m
		Pterophyllum rionense Dolud.			m
		Pterophyllum aff.ptilum Harris			m
		Pterophyllum aff.subae-quale Hartz			m
		Pterophyllum cf.andreanum Schimp.	m	m	
		Pterophyllum sp.	m	m	m
		Ptilophyllum acutifolium Morr.		m	
		Ptilophyllum acutifolium Morr. f.latum Delle		m	
		Ptilophyllum caucasicum Dolud. et Svan.		m	m
		Ptilophyllum cutchense Morr.		m	
		Ptilophyllum longifolium Iakob.		m	

1	2	3	4	5	6
Bennettitopsida	Bennettitaceae	Ptilophyllum okribense Dolud. et Svan.		m	
		Ptilophyllum okribense f.ratchense Dolud. et Svan.			m
		Ptilophyllum vachrameevii (Dolud.) Dolud.			m
		Ptilophyllum cf.caucasicum Dolud. et Svan.	m		
		Zamites sp.		m	

THE CRETACEOUS

Deposits from the Cretaceous system are widely distributed in Georgia and divided into two parts – lower and upper (Table V).

In the Early Cretaceous there were three main sedimentary basins in Georgia: 1. a flysch basin, deposits of which now occur on the southern slope of the Greater Caucasus; 2. an epicontinental basin with carbonaceous deposits, which now outcrops in the Gagra-Djavian zone and in the Transcaucasian intermontane depression (Georgian Block); 3. a basin of synclinal type that developed at the end of the Early Cretaceous and was strongly affected by volcanic activity during the Albian. Deposits of the latter are found in the Adjara-Trialetian system.

By the end of the Jurassic, the Georgian Block (South Caucasian intermontane region) was transformed into dry land with low, but not fully peneplanated, relief. Higher elevations were to be found in the Kelasuri and Gumista basins, as well as on the Dzirulian Block.

A transgression over the syncline of the southern slope of the Greater Caucasus took place during the second part of the Kimmeridgian, reaching the Georgian Block in the Berriassian. By the middle Albian, this transgression had mostly receded. The Early Cretaceous ended with the Albian regression, which continued until the Cenomanian in some regions. On the Dzirulian Block, the Albian regression was interrupted by subsequent transgression (Eristavi, 1952; Kotetishvili, 1986).

Table V. Stratigraphical division of Cretaceous deposits in Georgia (after Gambashidze, 1984; Kotetishvili, 1986).

Ma	Division	Stage
65	Upper Cretaceous	Maastrichtian
		Campanian
		Santonian
		Coniacian
		Turonian
		Cenomanian
	Lower Cretaceous	Albian
		Aptian
		Barremian
		Hauterivian
		Valanginian
144		Berriassian

Paleobotanical material is known only from Aptian and Albian deposits in Georgia (Fig.3), the first data being contributed by Palibin (1940) and Mchedlishvili (1949). Later, Cretaceous paleobotanical material was studied by Svanidze (Svanidze & Sharikadze, 1973) and Loladze (1979; Loladze et al., 1978). Their findings are listed in Table VI.

Table VI. Plants from the Cretaceous deposits in Georgia (by macrofossils)

Class	Family	Species
Polypodiopsida	Matoniaceae	Phlebopteris rarinerve Lol.
	Dicksoniaceae	Gonatosorus dzirulensis Lol.
		Gonatosorus lobifolium Bur.
		Gonatosorus sp.
		Lobifolia lobifolia (Phill.) Rass.et Lebed.
		Lobifolia novopokrovskii (Pryn.) Rass.et Lebed.
		Lobifolia sp.
The ferns of unestablished systematical positions		Cladophlebis whitbiensis (Brongn.) Brongn.
		Cladophlebis aff.suluctensis Brick.
		Cladophlebis sp.
Lyginopteridopsida	Caytoniaceae	Sagenopteris colpodes Harris
		Sagenopteris heterophylla Dolud.et Svan.
		Sagenopteris sp.

Class	Family	Species
Pinopsida	Cheirolepidiaceae	Elatides curvifolia (Dunk.) Nath.
		Elatides sp.
		Haiburnia setosa (Phill.) Harris
		Pagiophyllum bellum Lol.
		Pagiophyllum stenocaulum Lol.
		Pagiophyllum setosum (Phill.) Sew.
	Araucariaceae	Araucarites charatishvilii Lol.
		Araucarites densicaulus Lol.
		Araucarites heterocaulus Lol.
		Araucarites latus Lol.
		Araucarites vassilevskiae Tur.-Ket.
		Araucarites sp.
	Taxodiaceae	Glyptostrobus stenocaulus Lol.
		Glyptostrobus aff.groenlandicus Heer
		Glyptostrobus vulgaris Lol.
		Glyptostrobus sp.
		Sequoia caucasica Lol.
		Sequoia colchica Lol.
		Sequoia delicate Lol.
		Sequoia sp.
	Cupressaceae	Thuites sp.
		Widdringtonites georgiense Lol.
		Widdringtonites karataviensis Tur.-Ket.
		Widdringtonites aff.subtilis Heer.
Bennettitopsida	Bennettitaceae	Pterophyllum magnum Dolud.

Compared to the Jurassic, the Early Cretaceous had much lower diversity in the Caytoniaceae, Cheirolepidiaceae, Cycadaceae and Bennettitaceae. On the other hand, the role of the Araucariaceae and Taxodiaceae increased.

According to Loladze (1979), Early Cretaceous Georgia was covered in forests with a predominance of the Araucarites and Pagiophyllum, which indicate a climate of low humidity. Nevertheless, changes in floral composition (i.e. an increase in fern and Taxodiaceae remains, the absence of the genus Brachyphyllum and declining species diversity in the genus Pagiophyllum) allow us to conclude that the climate of second half of the Lower Cretaceous was more humid than the Callovian, but with lower temperatures. Representatives of the genera Araucarites and Pagiophyllum occupied dry slopes, while ferns and Taxodiaceae grew in more humid habitats.

The two Early Cretaceous paleofloristic regions – the Siberian-Canadian and the European-Sinaian – are further divided into provinces: the Potomacian, Central Asian, Eastern Asian and European. The latter was characterized by the complete absence of Podozamitaceae and Czekanowskiaceae and the minor role of Ginkgoaceae in the flora. Arid and semi-arid conditions prevailed throughout the European province, which was reflected in xeromorphy and changing taxonomic composition (Meien, 1987). Vakhrameev (1988) included the Early Cretaceous flora of Georgia in the European province, while Loladze highlighted its strong affinities with the floras of both the European and Central Asian provinces.

The Aptian and Albian were times of major reorganization in the world's vegetation as angiosperms rapidly expanded their distribution. New coniferous forms also appeared at this time, including the Pinaceae, which were adapted to intense sunlight and dry conditions. The diversity of Ginkgoaceae decreased and Czekanowskia almost vanished. Dominants of Mesozoic forests such as Podozamites and Ptilophyllum became extinct; all Bennettitaceae and many Cycadaceae disappeared; the composition of fern assemblages changed significantly and Coniopteris was altogether absent; while the distribution of Gleicheniaceae and Schizaeaceae increased (Sinizin, 1980).

Data on the Late Cretaceous flora of Georgia are absent. Plant remains from Cenomanian deposits in the southeast of the South Caucasus region were described by Palibin (1930, 1935). The same collection was revised subsequently by Takhtajan (1966). The prevalence of Sequoia, Comptonia, Platanus and the presence of Fagaceae and Lauraceae was also noted by him.

Analysis of paleobotanical material from various Mesozoic deposits in Georgia shows that all forms in the Jurassic and Cretaceous floras can be split into two groups:

1. Genera that were vegetation dominants during the Jurassic. Only some persisted into the Early Cretaceous, after which most Mesozoic plants became extinct.
2. Plants with living relatives in various regions of the world. In the Mesozoic these taxa were subordinate, but progressive, elements of the flora, flourishing only later during the Cenozoic and becoming dominant in many Tertiary vegetation communities in Georgia alongside numerous angiosperms. Relict plants of this second group still survive in the flora of Colchis today.

THE CENOZOIC

THE PALEOGENE

Paleogene deposits are widely distributed in Georgia and are represented by various facies. Based on nummulites, planktonic foraminifers, nannoplankton and molluska, the Paleogene is subdivided into three epochs: the Paleocene, Eocene and Oligocene (Table VII). Each of these is divided into separate stages and horizons correlated with synchronous deposits in Southern Russia and Western Europe (I. Kacharava, 1964; M. Kacharava, 1977; Z. Kacharava, 2007; Kazachashvili, 1984; Salukvadze, 2000).

Table VII. Stratigraphical division of Paleogene deposits in Georgia (after I.Kacharava, 1964 and Kazachashvili, 1984).

Ma	Division	Stage	Layers
23.8	Miocene	Akvitanian	Uplistsikhian
	Oligocene	Chattian	
		Meskhetian	Lignitiferous multicoloured suite
			Lower Corbulian (Tori and Tsruta-Tsakhana sections)
			Solenoe
33.7		Chadumian	Karatubani
	Eocene	Priabonian	
		Biarrician	
		Lutetian	
54.9		Ypresian	
	Paleocene	Ilerdian	
		Thanetian	
65.0		Monian	

At the beginning of the Tertiary, the Caucasus formed part of the Tethys Sea (Alpine-Mediterranean orogenic region), which occupied a vast area from Gibraltar to the Himalayas. This huge synclinal basin, corresponing to the future Alpine folded zone, was characterized by a complex, rugged and changeable coastline. Numerous islands, the future mountains of the Alpine system, divided the Tethys into more-or-less distinct basins (Khain, 1984). The water of this great sea was warm, as indicated by coral reefs and thick deposits of nummulitic limestone. Water temperature had a profound influence on the plant life of coastlines and islands, especially during the Paleocene–Eocene. Branches of the Tethys later became the folded systems of the Greater and Lesser Caucasus, developing semi-independently under the influence of common orogenic phases. The most interesting Paleogene deposits are those of the Adjara-Trialetian zone, the southern part of which (Akhaltsikhian depression) includes the main Palaeogene flora localities (Fig.3).

The Paleogene was a critical period in the Cenozoic history of flora, forming a link between the ancient flora of the Mesozoic and the floras of the Neogene. Most of the ancient angiosperms went extinct to be replaced by new, progressive forms. By the end of Paleogene, vegetation communities similar to their Neogene counterparts had formed and geological processes, especially around the boundary of the Eocene and Oligocene, led to increasing floral differentiation. Distinct geobotanical provinces began to take shape within Eurasia's palaeofloristc regions, provinces that would anticipate their modern equivalents in several respects.

The Eocene

In Georgia, the most ancient Tertiary (Palaeogene and Neogene) deposits containing plants remains are the Eocene layers of the Akhaltsikhian depression. Data from Uznadze (1967) shows the fossil material to comprise mainly of leathery angiosperm leaf-imprints, amongst which the large, thick-veined leaves of *Artocarpidium latifolium* Uzn. are the most frequent. The presence of Rhizophora, Elaeodendron, Sapotacites and Artocarpidium, as well as the leathery structure of the fossil leaves, indicates evergreen vegetation growing in warm, humid conditions.

Eocene flora near the town of Akhaltsikhe was studied by Avakov (1989; 2010). Plant remains are preserved in sediment lenses dated Upper Eocene by nummulites and molluscs (Kacharava 2007; Kazachashvili, 1984).

Avakov (1989) grouped all of the Eocene taxa into genetic classes. One group was composed of forms characteristic of the Eocene, including plants that probably continued from the Palaeocene, but absent from younger floras. The next group was composed of forms that were judged to be more widespread on the basis of systematics and abudance: Myricaceae, Fagaceae and Juglandaceae.

These taxa were present in the Oligocene and persisted as relicts in Neogene floras. The Eocene flora also includes the ancestors of plants that make up the modern relict flora of Georgia. During the Tertiary they may have developed and changed their ecological tolerances, but the fact that the representatives of these taxa still exist today suggests that the vegetation complex that evolved during the Eocene would carry through the Neogene until the present.

The Middle and Upper Eocene deposits of the Akhaltsikhian depression have also been studied palynologically (Panova et al., 1984). Eocene deposits from boreholes in Eastern Georgia (Kakheti) were analyzed by Purtseladze (1988) and Shatilova & Mchedlishvili (2011).

In these pollen spectra, the dominant fern genera were Gleichenia, Anemia and Lygodium. Pteris and Polypodium, the characteristic components of Neogene floras, occur only as single spores. Conifers had a minor role, but were relatively diverse from a systematic point of view. Ginkgo, Pinus, Podocarpus, Dacrydium, Cedrus and Keteleeria pollen occured frequently, while taxa characteristic of a temperate climate – Picea, Tsuga, Abies – were relatively few.

The hallmark of spore-pollen assemblages in Georgia's Eocene deposits is the predominance of angiosperms over conifers and cryptogams. In Eocene deposits in Kakheti, 66% of the palynomorphs came from angiosperms, 25% from conifers and 9% from cryptogams (Fig. 4). This composition is typical of Paleogene palyno-complexes (Zaklinskaya, 1970).

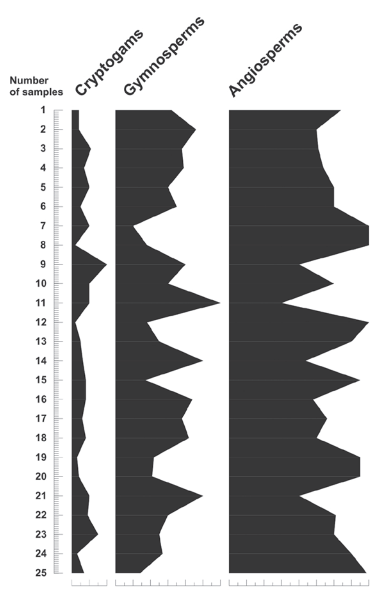

Fig. 4. Percentages of angiosperm, gymnosperm and cryptogam palynomorphs in spore-pollen assemblages of Eocene deposits in Eastern Georgia

It is quite difficult to reconstruct the type and structure of Eocene vegetation. Since the leaf imprints and pollen grains belong mainly to trees, the existence of forests as the main type of vegetation is beyond doubt. By drawing comparisons with modern altitudinal zonation in tropical and subtropical regions, Avakov (1989) suggested the following vegetation zones: 1) a zone of tropical (or subtropical) deciduous forest with some sclerophyll elements from the Myrtaceae and Myricaceae; 2) a zone of evergreen laurel rainforest; and 3) a zone of temperate climate with deciduous and coniferous forests.

According to Avakov, the first zone was made up of both monsoonal deciduous forests and sclerophyllous forests. Monsoon forests included *Celtis* sp., *Ailanthus gigas, Cedrela caucasica, Meliosma* sp., *Ziziphus paradisiacus* and others. Sclerophyll forests were composed of *Myrica bancksiaefolia, M. lignitum, M. longifolia, M. ungeri* and *Echitonum sophiae.*

Laurel rainforests of *Podocarpus isonervis, Engelhardia macroptera, Dryophyllum curticellense, Castanopsis decheni, Daphnogene sezannensis, Laurophyllum achalcichensis, Phoeba* cf. *pallida* and *Cinnamomum scheuchzeri* grew above the tropical deciduous-sclerophyllous zone.

The highest elevations were occupied by temperate deciduous and coniferous plants: Pinus, Picea, Abies, Keteleeria, Sciadopitys, Cedrus, Betula, Corylus, Cornus, Tilia and Acer. The forest understory was clothed mainly in ferns – Cyatheaceae, Schizaeaceae, Anemiaceae, Lygodiaceae and Gleicheniaceae.

The Oligocene

The modern relief of the Caucasus began to take shape during the Oligocene, when synclines began to form in folded systems. The Georgian Block, transformed into an intermontane depression, was covered by sea, in which the dark, non-carbonate Maikopian clays, often void of organic remains, accumulated. The Greater and Lesser Caucasus became erosional systems and basins of semi-marine or lagoon type remained only in some places. One such basin was the Akhaltsikhian depression (Adjara-Trialetian zone), where a full series of Paleogene deposits dated by fauna is represented. According to Kazachashvili (1984), they should be considered stratotypical (Table VII).

Oligocene deposits in Georgia rarely preserve fossil macrofloras. The most interesting is the Middle Oligocene flora of Corbulian layers near Tori village (Borjomi region). This flora was first discovered by Kozlovsky and kept in the Botanical

Institute of the Russian Academy of Sciences. Later this collection was studied by Mchedlishvili (1949a), who suggested that this unique flora represented the vegetation of a recent tropical xerophytic kingdom. Mchedlishvili's collection was subsequently revised by Avakov (1989), who distinguished *Dryophyllum curticellense* (Wat.) Sap., as the most interesting form.

Later the locality of Tori was re-investigated. Molluscs, confirming the Middle Oligocene age of the deposits, were studied, as well as imprints of leaves, pollen and spores (Kazakhashvili et al., 1983). Macroremains are composed of narrow and broad leathery leaves. On the whole, the macroflora and spore-pollen assemblages, as well as the presence of coal layers, indicate the existence of evergreen forests characteristic of a humid, subtropical climate.

Avakov (1989) also collected new material near Tori village, the most part of which was leaf impressions of *Dryophyllum curticellense* and a few fruit imprints of Leguminosae (Fabaceae).

Oligocene deposits of the Akhaltsikhian depression have been studied palynologically. In a section on the Abastumani River, the Upper Eocene is covered by sediments with molluska of Lower Oligocene age (Panova et al., 1984). A rich spore-pollen assemblage, transitional between the Eocene and Oligocene, was discovered in the lower part of this section. Among conifers the Pinaceae *(*Cedrus, Picea and Pinus*)* were predominant. Pollen grains of Taxodiaceae, Podocarpus and Ephedra were infrequent. As in the Eocene, the greater part of the assemblage was taken up by angiosperms.

Quite different spore-pollen assemblages characterize the upper layers of the section, where conifers are more prevalent – Pinus, Picea, Keteleeria, Cedrus and Taxodiaceae, with a small representation of Ginkgo and Podocarpus. Angiosperms are few, but diverse: Myrica, Platycarya, Quercus, Castanea and Castanopsis are represented by several species. Typical Oligocene taxa appear in this section, including *Carya* aff. *exelsa* Pan. and *Juglans compacta* Pan. Pollen grains of the former genera occur in low proportions. This assemblage dates to the Lower Oligocene. Subsequent layers are much poorer in floral remains and give little impression of the vegetation.

Pollen analysis was also carried out on Lower Oligocene deposits found near the villages of Ani and Karatubani. The section begins by yellow-gray sandstones with fauna characteristic of the Karatubani horizon, in which pollen and spores were not seen. Rich assemblages were discovered in overlying clay deposits. The palynoflora has an abundance of conifers and a diversity of angiosperms, mainly subtropical forms such as Comptonia, Platycarya, Engelhardia, *Castanopsis pseu-*

docingulum, Quercus gracillis, Liquidambar, Rhus, Nyssa, Myrtaceae, Sapindaceae, Sterculiaceae, Bombacaceae, Buxus, Oleaceae and Arecaceae. Another hallmark of these assemblages is the prominent role of warm-temperate plants, including Platanus, Corylopsis, Alnus, Carpinus, Juglans, Acer, Tilia, Ulmus and Fraxinus.

In the upper layers of this section, coniferous taxa are predominant in pollen spectra. Among angiosperms represented by great number of forms, the role of Juglans and Carya (especially *C. spackmaniana*) increases, while pollen of subtropical elements remains stable. The increasing role of spores is also noteworthy, among which the representatives of families Polypodiaceae, Pteridaceae predominate; Selaginella, Lycopodium, Cyathea, Gleichenia, Osmunda appear in fewer number.

Quite a different complex was found in the lower Corbulian sandstones of Tsruta-Tsakhana, dated to the Middle Oligocene. Among conifers, the pollen grains of Taxodiaceae dominate, while Pinaceae, Podocarpus, Cupressaceae and Ephedra also occur. Among angiosperms, the Juglandaceae (Platycarya, Carya, Engelhardia and Juglans) prevailed. Ulmus pollen was found in less abundance and both subtropical and warm-temperate plants were represented: Comptonia, Myrica, Salix, Ostrya, Acer, Tilia, Rhamnaceae, Sapindaceae, Sapotaceae and Corylopsis.

In this section, the upper part of the Middle Oligocene is represented by a multicoloured lignitiferous suite, dominated by conifer pollen. The assemblage of subtropical and warm-temperate plants is rich and diverse. The upper layers of multicolored suit are thick and homogenous, indicating the rapid growth of lush vegetation (Gamkrelidze, 1949).

Climatic changes on the boundary of the Eocene and Oligocene can be gauged from faunistic data. As a result of tectonic movements at the terminal Eocene, the sea basin was isolated from Tethys and later connected with the boreal province. With the commencement of the Oligocene transgression, Late Eocene thermophilous ecosystems were replaced by Early Oligocene boreal communities lacking large foraminifera (Kazachashvili, 1984). These data agree with palynological results that indicate an increasing role of conifers in Lower Oligocene deposits.

Pollen data indicate that the character of the flora changed after the Eocene. During the Oligocene, the number of conifers increased and the composition of warm-temperate plants became more diverse. These phenomena were probably linked to paleogeographical changes taking place in the Caucasus at the time, especially Early Oligocene orogenesis in the Greater and Lesser Caucasus. Mountain-building created bioclimatic conditions favorable to the development of temperate and warm-temperate vegetation.

A list of the Eocene and Oligocene floras is given below (Table VIII).

Table VIII. Plants from Eocene and Oligocene deposits in Georgia
Key: m – macrofossils; p – pollen

Class	Family	Species	Eocene	Oligocene
1	2	3	4	5
Bryopsida	Sphagnaceae	Sphagnum sp.	p	
Lycopodiop-sida	Lycopodiaceae	Lycopodium sp.	p	p
Isoëtopsida	Selaginellaceae	Selaginella sp.		p
Polypodiopsida	Osmundaceae	Osmunda sp.		p
	Schizaeaceae	Ruffordia subcretacea (Sap.)Barth.	m	
		Schizaeaceae gen.indet.	p	
	Anemiaceae	Anemia sp.	p	
	Lygodiaceae	Lygodium sp.	p	p
	Pteridaceae	Pteris sp.	p	p
		Polypodiaceoisporites potonie W.Kr. (Pteris)	p	
		Pteridaceae gen.indet.		p
	Gleicheniaceae	Gleichenia sp.	p	p
	Polypodiaceae	Polypodium sp.	p	p
		Polypodiisporites sellarius W.Kr. (Polypodium)	p	
		Polypodiisporites cf.tenella W.Kr. (Polypodium)	p	
		Polypodiaceae gen.indet.		p
	Dicksoniaceae	Dicksonia sp.	p	
	Cyatheaceae	Cyathea sp.	p	p
		Cyatheaceae gen.indet.	p	
Ginkgoopsida	Ginkgoaceae	Ginkgo sp.	p	p
Pinopsida	Podocarpaceae	Dacrydium sp.	p	
		Podocarpus isonervis Avak.	m	
		Podocarpus sp.	p	
	Araucariaceae	Araucaria sp.	p	
	Pinaceae	Abies sp.	p	p
		Cedrus sp.	mp	p
		Keteleeria sp.	p	p
		Picea sp.	mp	p
		Pinus sp.	mp	p
		Tsuga sp.	p	
		Pinaceae gen.indet.	p	p
	Taxodiaceae	Sciadopitys sp.	p	p
		Taxodiaceae gen.indet.	p	p

1	2	3	4	5
Gnetopsida	Ephedraceae	Ephedrites sotzkianus Ung.	m	
		Ephedra sp.	p	p
	Gnetaceae	Gnetaceoipollenites sp.	p	
Dicotyledoneae	Casuarinaceae	Casuarinidites cainosoicus Cook. et Pike	p	
		Casuarinidites sp.	p	
	Myricaceae	Comptonia acutiloba Brongn.		m
		Comptonia sp.	p	p
		Myrica acuminata Ung.	m	
		Myrica banksiaefolia Ung.	m	m
		Myrica esculentiformis Gladk.	p	
		Myrica hakeaefolia (Ung.) Sap.	m	
		Myrica lignitum (Ung.) Sap.	m	m
		Myrica longifolia Ung.	m	m
		Myrica pseudogranulata Gladk.	p	
		Myrica ungeri Heer	m	
		Myrica cf.carolinensis Gladk.	p	
		Myrica sp.	mp	p
		Myricacites sp.	p	
		Momipites sp. (Myricaceae)		p
		Myricaceae gen.indet.	p	
	Juglandaceae	Carya spackmaniana Trav.		p
		Carya cf.exilis Pan.		p
		Carya sp.	p	p
		Subtriporopollenites constans Pfl. (Carya)	p	
		Engelhardia macroptera (Brong.) Ung.	m	
		Engelhardia quieta (R.Pot.) Elsik	p	
		Engelhardia sp.		p
		Juglans acuminata A.Br.	m	
		Juglans compacta Pan.		p
		Juglans polyporata Vojc.	p	
		Juglans sp.	p	p
		Platycarya sp.	p	p
		Platycaryapollenites sp.	p	
		Pterocarya sp.	p	
		Momipites sp. (Juglandaceae)	p	p
		Plicatopollis plicatus (Pfl.)W.Kr. (Juglandaceae)	p	
		Juglandaceae gen.indet.	p	
	Salicaceae	Populus mutabilis Heer, var.lancifolia A.Br.	m	
		Populus sp.	m	
		Salix haidingeri Ett.	m	
		Salix varians Goepp.	m	

1	2	3	4	5
Dicotyledoneae	Betulaceae	Alnus sp.	p	p
		Betula subpubescens Goepp.	m	
		Carpinus sp.	p	p
		Corylus sp.	p	
		Ostrya sp.		p
	Fagaceae	Castanea crenataeformis Samig.	p	
		Castanea sp.	p	
		Castanopsis decheni (O.Web.) Kr. et Wld.	m	
		Castanopsis pseudocingulum (R.Pot.) Boitz.	p	p
		Castanopsis cf.tribuloides ADC	m	
		Castanopsis sp.		p
		Dryophyllum curticellense (Wat.) Sap.	m	m
		Dryophyllum dewalquei Sap.	m	
		Fagus sp.	p	
		Pasania sp.		p
		Quercus gracilis Boitz.	p	p
		Quercus lonchitis Ung.		m
		Quercus mauritanica Sap. et Mar.	m	
		Quercus neriifolia A.Br.		m
		Quercus sp.	p	
		Quercoides inamoenus Fred.	p	
		Tricolpopollenites liblarensis (R.Pot.) Pfl. (Fagaceae, Quercus?)	p	
		Tricolpopollenites sp. (Fagaceae?)		p
		Tricolporopollenites henrici (R.Pot.) Pfl. (Quercus)		p
		Tricolporopollenites sp. (Fagaceae?)		p
	Ulmaceae	Celtis sp.	m	
		Ulmus sp.	mp	
		Ulmaceae gen.indet.	p	
		Ulmoideipites planeraeformis Anders.	p	
	Moraceae	Artocarpidium latifolium Uzn.	m	
		Moraceae gen.indet.	p	
	Chenopodiaceae	Chenopodiaceae gen.indet.	p	
	Magnoliaceae	Liriodendron sp.	p	p
		Magnolia aff.megafigurata (W.Kr.) Ram.	p	
		Magnolia sp.	p	
	Lauraceae	Cinnamomum cinnamomeum (Rossm.) Holl.	m	
		Cinnamomum scheuchzerii Heer	m	

1	2	3	4	5
Dicotyledoneae	Lauraceae	Cinnamomum sp.	m	m
		Daphnogene sezannensis Wat.	m	
		Laurophyllum achalcichensis Avak.	m	
		Lindera antiqua (Heer) Lamotte		m
		Phoebe cf.pallida Nees	m	
		Lauraceae gen.indet.	p	
	Trochodendraceae	Trochodendron sp.	p	p
	Nymphaeaceae	Nelumbo sp.		p
	Platanaceae	Platanus sp.	mp	p
	Hamamelidaceae	Corylopsis sp.	p	p
		Hamamelis sp.	p	p
		Liquidambar sp.	p	p
	Rosaceae	Rosaceae gen.indet.	p	
	Fabaceae	Leguminosites cf. Brachiystegia eurycoma Harms.	m	
	Simarubaceae	Ailanthus gigas Ung.	m	
		Ailanthus sp.	m	
	Meliaceae	Cedrela caucasica Kutuzk.	m	
	Anacardiaceae	Rhus sp.	p	
	Sapindaceae	Sapindaceae gen.indet.	p	
	Sabiaceae	Meliosma sp.	m	
	Mimosaceae	Mimosites haeringiana Ett.		m
	Linaceae	Linum sp.		p
	Aceraceae	Acer sp.		p
	Aquifoliaceae	Ilex sp.	p	p
	Proteaceae	Proteacidites crassiporus subsp. pachysexinus Samoil.	p	
		Proteaceae gen.indet.	p	
	Celastraceae	Elaeodendron obovatifolium Engelh.	m	
	Olacaceae	Anacolosidites sp.	p	
	Rhamnaceae	Ceanothus cf.americanus L.	m	
		Zizyphus paradisiacus (Ung.) Heer	m	
		Zizyphus zizyphoides (Ung.) Heer	m	
	Melastomaceae	Astronia cf.cumingiana Vidal	m	
	Vitaceae	Parthenocissus sp.	p	p
	Tiliaceae	Tilia sp.	p	p
	Bombacaceae	Bombacaceae gen.indet.	p	p
	Rhizophoraceae	Rhizophora thinophylla Ett.	m	
	Sterculiaceae	Sterculiaceae gen.indet.		p
	Buxaceae	Buxus sp.		p
	Elaeagnaceae	Elaeagnus sp.		p
	Myrtaceae	Callistemophyllum speciosum Ett.		m
		Eucalyptus oceanica Ung.		m
		Myrtaceae gen.indet.	p	p

1	2	3	4	5
Dicotyledoneae	Alangiaceae	Alangium sp.		p
	Nyssaceae	Nyssa sp.	p	p
	Cornaceae	Cornus cf.platyphylla Sap.	m	
	Araliaceae	Araliaceae gen.indet.	p	p
	Sapotaceae	Chrisophyllum juglandoides Wat.	m	
		Sapotaceae gen.indet.	p	p
	Loranthaceae	Loranthaceae gen.indet.	p	
	Symplocaceae	Symplocos sp.	p	
	Rubiaceae	Cephalanthus sp.	p	
	Oleaceae	Fraxinus sp.		p
		Oleaceae gen.indet.	p	p
	Apocynaceae	Acerates veterana Heer		m
		Apocynophyllum achalcichensis Avak.	m	
		cf. Aspidodperma anomalum Muell.	m	
		Echitonium sophiae Web.	m	
	Asteraceae	Asteraceae gen.indet.		p
Monocotyledoneae	Potamogeton-aceae	Potamogeton sp.		p
	Poaceae	Phragmites provincialis Sap.	m	
	Arecaceae	Nipa sp.	p	
		Sabal sp.	p	
		Arecaceae (Phoenix sp.)	p	
		Arecipites convexus (Thierg.) W.Kr.	p	
		Arecipites cf.brandenburgensis W.Kr.	p	
		Palmaepollenites tranquilus R.Pot.	p	
		Monocolpopollenites dorogensis (R.Pot.) Pf. (Sabal)	p	
		Monocolpopollenites cf.magnus Pf. (Arecaceae)	p	
		Arecaceae gen.indet.		p
	Smilacaceae	Smilax sagittifera Heer	m	
	Sparganiaceae	Sparganium sp.		p
The forms of indeterminate taxonimical position		Leiotriletes sp.	p	
		Neogenisporites sp.	p	
		Trilites asolidus W.Kr.	p	
		Extratriporopollenites sp.	p	
		Fupingopollenites wackersdorfen-sis (Thiele-Pfeiffer) Liu Geng-wu.	p	
		Interpollis supplingensis W.Kr.	p	
		Nudopollis thiergarti (R.Pot.) Pfl.	p	
		Oculopollis sp.	p	
		Pollenites cingulum R.Pot.	p	
		Pollenites liblarensis Thoms.	p	
		Retitricolpites sp.	p	

1	2	3	4	5
The forms of indeterminate taxonimical position		Retitricolporopollenites sp.		p
		Rhoipites granulatus (Fred.) Boitz.	p	
		Rhoipites sp.	p	p
		Spinozonocolpites prominatus Kedv.	p	
		Subtrudopollis sp.	p	
		Triatriopollenites maculates Pfl.	p	
		Triatriopollenites sp.	p	
		Triporopollenites sp.	p	
		Trudopollis menneri (Mart.) Zakl.	p	
		Trudopollis pompeckji (R.Pot.) Pfl.	p	
		Trudopollis sp.	p	
		Verrutricolporites cf.tenuicrassus Pokrovskaja		p
		Verrutricolporites sp.	p	

THE NEOGENE

Neogene deposits are widely distributed in Georgia, their stratigraphical subdivision based on rich paleontological material. Most fossil floras are associated with faunal remains that provide the age of the sedimentary material. In our work, paleobotanical material from Neogene deposits is described in accordance with schemes devised for Georgia (Ananiashvili et al., 2000; Badzoshvili, 1986; Buleishvili, 1960; Chelidze, 1974; Taktakishvili, 1984).

In some of these schemes, the boundaries of regional stages conflict with those of the Neogene stratigraphic scheme for the Eastern Paratethys. Mainly it concerns the boundaries of Sarmatian. In particular, the Volkhinian substage and lower part of Bessarabian are put in Middle Miocene. Also the position of Pontian is changed, big part of which is put in Upper Miocene (Nevesskaya et al., 2003; Semenenko et al., 2009).

Lists of Neogene floras are given separately for every stretches of the Miocene and Pliocene. During our work we took into account changes in plant taxonomy after a revision of the fossil material (Takhtajan 1974).

THE MIOCENE

The Lower Miocene

Two areas of dry land existed in Georgia through most of the Miocene – the northern part and the southern part, including the small islands of the South Caucasus intermontane depression, which was mostly covered by sea (Fig. 5).

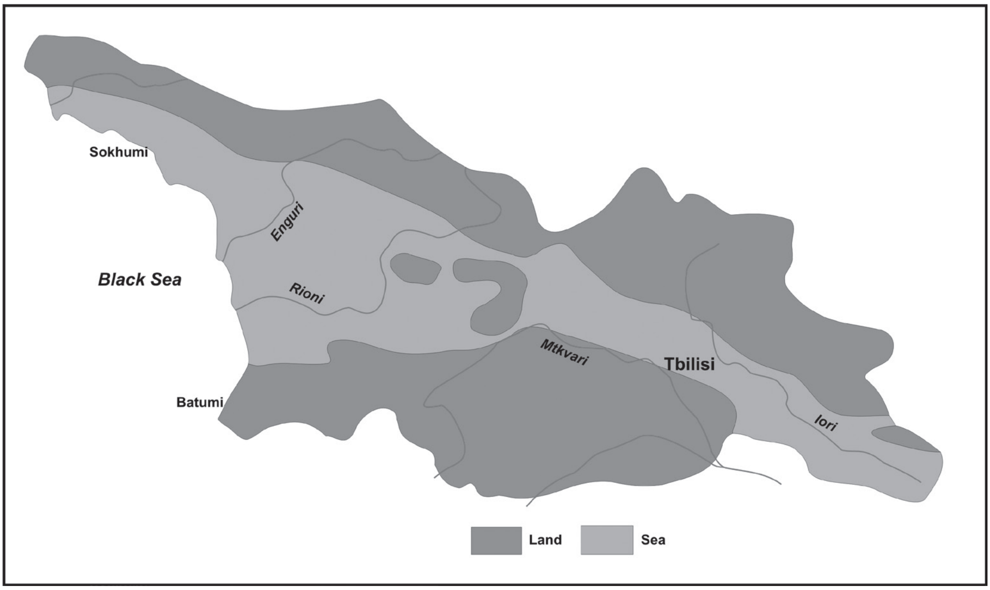

Fig. 5. Schematic paleogeographical map of Georgia during the Miocene (except the Late Sarmatian).

Clays containing foraminifers typical of the Lower Miocene accumulated in the deeper parts of this depression. Around the periphery, these clays are replaced by sandstones, which contain a rich fauna of mollusks (Adamia et al., 1964). In the Gori-Caspi region this fauna was studied by Davitashvili (1933, 1934), who distinguished two stratigraphical units – the Sakaraulian and Kotsakhurian (Table IX).

Table IX. Stratigraphical division of the Miocene deposits in Georgia (after Badzoshvili, 1986; Buleishvili, 1986; Ananiashvili et al., 2000; Nevesskaya et al., 2003; Semenenko et al., 2009; Zhgenti, 1981)

Ma	Division	Regional stage		Substage
7.1	Upper Miocene	Meotian		Akmanaian
9.5				Bagerovian
		Sarmatian		Khersonian
				Bessarabian
				Volhynian
13.0	Middle Miocene	Konkian		
		Karthvelian		
		Karaganian		
		Tschokrakian		
		Tharkhanian		
17.0	Lower Miocene	Maikopian series	Kotsakhurian	
			Sakaraulian	
23.8			Uplistsikhian (Akvitanian)	

Deposits with rich assemblage of stenohaline mollusks of the Mediterranean type were found near the village of Uplistsikhe (Gori region) below Sakaraulian levels. These deposits are considered equivalent to the Akvitanian of Eastern Paratethys and, on the basis of their fauna, are classed as an "Uplitsikhian stage" (Ananiashvili et al., 2000; Kurtskhalia et al., 1972).

A list of flora from Kotsakhurian deposits was published by Mchedlishvili (1955). In his opinion, the assemblages indicate hot and dry climatic conditions. According to Uznadze (1965), however, not all plants from this list are xerophytes, especially the various Lauraceae.

The Lower Miocene flora was studied in detail by Djaparidze (1982). All of the sites studied (Fig.6) were between Akvitanian (Uplistsikhian) and Sakaraulian deposits, dated by fauna and containing conifer needles, leaf imprints and seeds. The prevalence of narrow-leaved forms with leathery texture, which often obscures the details of fine venation, is a characteristic feature of this macroflora.

Most of the Early Miocene flora is composed of subtropical plants typical of dry sclerophyll forests. Leaf imprints of these plants have a xeromorphic appearance, distinguished by small leaf surfaces and a rough texture. The collections contain a large number of leathery leaves of the "Leguminosae" type, which was impossible to determine to greater taxonomic precision. Their presence, however, is indicative of a xeromorphic flora.

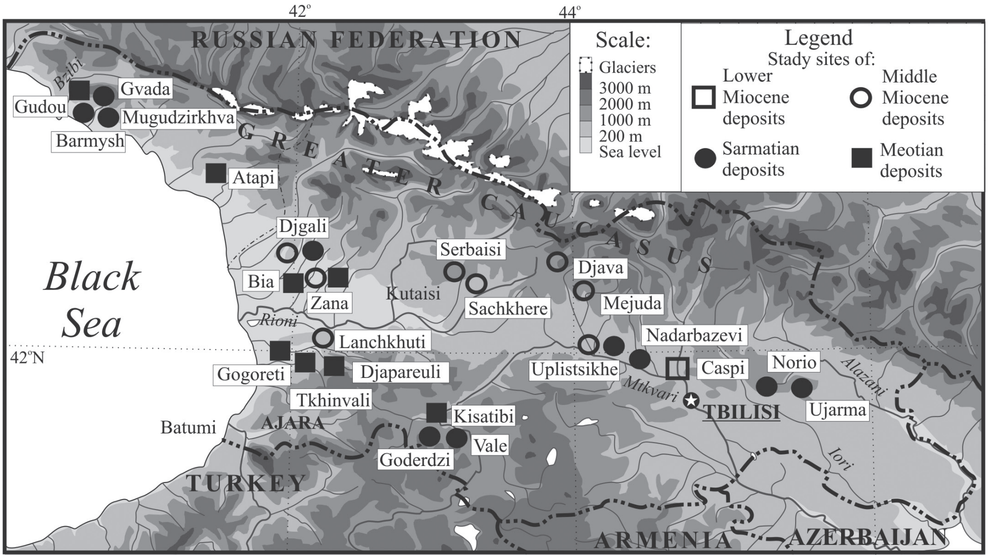

Fig.6. Study sites of Miocene deposits in Georgia

The laurels, evergreen Fagaceae and other thermophilous plants that formed moist subtropical Paleogene forests persisted in Eastern Georgia under conditions of low humidity. The fossil material indicates that they adapted to the arid climate and formed components of sclerophyll vegetation.

Riparian forests occurred in moist, poorly-drained areas and included species such as *Quercus neriifolia, Myrica lignitum* and *Pinus taedaeformis*. Plants of temperate climates occupied the upper mountain zones. This formation is rarely represented in macrofloras since its distribution was situated far from accumulation basins. Eastern Georgia's climate was subtropical during the whole Early Miocene, with a dry summer and a mild winter that did not interrupt the growing season (Djaparidze, 1982).

The Middle Miocene

At the beginning of the Middle Miocene (Table IX), the Greater and Lesser Caucasus formed into mountain systems. The Georgian Block subsided and slowly became the intermontane molassic depression.

From a paleobotanical point of view, the first half of Middle Miocene is poorly studied. Only a few lauraceous leaf imprints and leathery leaves of indeterminable evergreen dicotyledonous plants were found in Western Georgian Tschokrakian deposits (Uznadze, 1965). Floras of the Karaganian, Karthvelian and Konkian regional stages are much better studied. Plant macroremains (leaf imprints, seeds and flower parts) from the northern part of Kartli and some regions of Western Georgia (Fig.6) were described by Avakov (1967; 1979; 2008; 2010).

Middle Miocene deposits of Western Georgia have been studied by palynological methods (Ananiashvili & Purtseladze, 1976; Ramishvili, 1982). The spore-pollen assemblage reflects forest vegetation composed of deciduous warm-temperate and subtropical plants, as well as ferns (Fig.7).

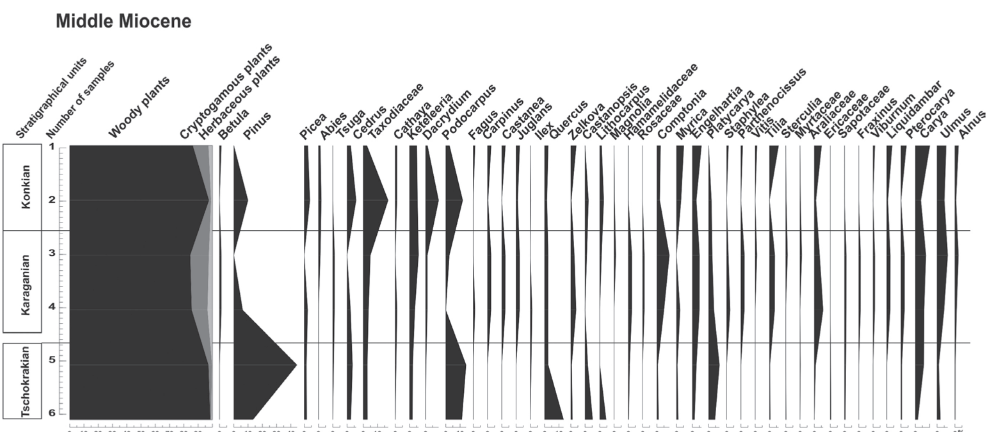

Fig.7. Composite palynological diagram of Middle Miocene marine deposits from Western Georgia

An abundance of ferns, their varied composition and their similarity with extinct taxa characteristic for the Paleogene and Early Miocene, give the Middle Miocene flora a somewhat ancient appearance. Some of them were determined by morphological system: *Toroisporites lusaticus, Clavifera triplex, Leiotriletes miocaenicus, L. wolffi, Divisiosporites* and others. A distinct group comprised ferns that were widely distributed in the past, but now have a narrow, relict area. Such include Anemia, Lygodium, Gleichenia, Hymenophyllum, Dicksonia, Cyathea and others.

The majority of gymnosperms were plants characteristic of subtropical mountain forests: Ginkgo, Podocarpus, Dacrydium, Cathaya, Pseudolarix, Keteleeria and Cedrus. Pinus pollen occurs in large quantities. As concerns Abies, Picea and Tsuga, plants typical of younger floras, their role in spore-pollen assemblages is quite small. Pollen of Sequoia, Cryptomeria and Taxodium numbers about the same as pollen from saccate conifers, however their macrofossil remains have not been found.

Angiosperms are distinguished by great systematic and ecological diversity. Pollen assemblages often include small, tricolporate grains of the "castanoid" type. Many of them are indeterminable, excluding grains of Castanea, Lithocarpus and Castanopsis. In some cases, "castanoid" pollen is referred to the forma-taxon *Tricolporopollenites cingulum*. Some pollen grains of the Fagaceae are similar to modern *Quercus*, but others probably belong to extinct oaks. They have been described as *Tricolporopollenites microhenrici* and *T. henrici,* characteristic taxa for Miocene pollen assemblages in the whole Mediterranean region.

The Middle Miocene flora of Georgia is distinguished by the occurrence of Myricaceae and Juglandaceae, both as macroremains and pollen. The genus Comptonia was represented by four species, of which three are morphologically similar to Comptonia pollen identified in Paleogene deposits in Siberia and Hungary (Gladkova, 1965; Kedves, 1974), i.e. *Comptonia grandis, C. imperfecta* and *C. pseudogranulata*. It would seem that these species were widely distributed during the Paleogene. Engelhardia and Platycarya are also very characteristic components, their pollen appearing in nearly in all outcrops of Middle Miocene deposits. Small grains are referred to as *Engelhardia wallichiana* and larger grains to the forma-taxa *Momipites punctatus* and *Triatriopollenites coryphaeus*.

Macrofossils and pollen indicate the existence of altitudinal vegetation zones with different climatic characteristics during the Middle Miocene. The coastal zone and the lower and middle mountain belts were covered by humid subtropical forests composed of Sterculiaceae, Araliaceae, Moraceae, Lauraceae, evergreen Fagaceae, Sapotaceae, Symplocaceae, Sycopsis, Mastixia, Magnolia, numerous Lauraceae, Engelhardia, Sapindus and Combretum. Arborescent ferns were represented, including Cyathea, Dicksonia and also Lygodium, Anemia, Hymenophyllum, some Polypodium and Pteris. The abundance of Myricaceae macrofossils in deposits of the Middle Miocene suggests that they grew along rivers, constituting the dominant species in riparian vegetation. Sclerophyll formation included myrtle, acacia, some species of oaks (*Quercus lonchites* and *Q. drymeja*), plants with narrow leaves of the Myrica- and Myrtus-type and lianas typical of humid subtropical climates, such as Smilax and Sabia (Avakov, 1967).

Deciduous warm-temperate and temperate communities were distributed at higher altitudes, comprised of Platanus, Comptonia, Juglans, Pterocarya, Platycarya, Castanea and Parthenocissus. Higher still, temperate cold-resistant plants like Betula, Carpinus, Fagus, Acer, Tilia and Ulmus were to be found. Broad-leaved species were intermixed with conifers: Dacrydium, Podocarpus, Cathaya, Keteleeria, and probably Abies, Picea and Tsuga.

The Middle Miocene climate throughout Georgia was subtropical and humid, as indicated by the abundance of Taxodiaceae in deposits of both western and eastern areas.

Comparing the Middle Miocene flora of Georgia with floras from adjacent regions (the flora of the eastern part of the South Caucasus and areas to the north of the Greater Caucasus) seem to have been poorer in ferns and thermophilous evergreen trees, with a lower diversity of conifers and broad-leaved trees (Ananova, 1974; Djabarova, 1976; Manukian, 1978).

The Middle Miocene flora of Georgia and contemporaneous floras of the Mediterranean developed evenly without major perturbations, especially during the Early and Middle Miocene (Nagy, 1985; 1992). Their development was not as monotonous as during the Paleogene, but more homogeneous than the floras of the periods to follow, when increasing differentiation led to the formation of separate phytogeographical provinces.

A list of Lower and Middle Miocene floras is given below (Table X).

Table X. Plants from Lower and Middle Miocene deposits in Georgia Key: m – macrofossils; p – pollen

Class	Family		Lower Miocene	Middle Miocene
1	2	3	4	5
Lycopodiopsida	Lycopodiaceae	Lycopodium sp.		p
Isoëtopsida	Selaginellaceae	Selaginella fusca N.Mtchedl.		p
		Selaginella sp.		p
		Echinatisporites miocaenicus W.Kr. (Selaginella sp.)		p
Ophioglossopsida	Ophioglossaceae	Ophioglossum sp.		p

1	2	3	4	5
Polypodiopsida	Osmundaceae	Osmunda heeri Gaud.	m	
		Osmunda sp.		p
	Anemiaceae	Anemia cf.hirta (L.) Swartz.		m
		Anemia cf.mexicana Klatsch		m
		Anemia sp.		p
		Mohria sp.		p
	Lygodiaceae	Lygodium digitatum Presl.		p
		Lygodium multivallatum (W.Kr.) Ram.		p
		Lygodium sp.		p
		Toroisporites lusaticus W.Kr.		p
	Pteridaceae	Pteris cretica L.		p
		Pteris parschlugiana Ung.		m
		Pteris sp.		p
		Polypodiaceosporites gracil-limus Nagy		p
		Polypodiaceosporites helveti-cus W.Kr.		p
		Polypodiaceosporites lusaticus W.Kr.		p
		Polypodiaceosporites mi-croverrucosus W.Kr.		p
		Polypodiaceosporites triangu-lus W.Kr.		p
	Adiantaceae	Anogramma sp.		p
		Onychium sp.		p
	Gleicheniaceae	Clavifera triplex Bolch.		p
		Gleichenia angulata Naum.		p
		Gleichenia sp.		p
	Polypodiaceae	Polypodium verrucatum Ram.		p
		Polypodium sp.		p
		Polypodiisporites potoniei Nagy		p
		Verrucatosporites alienus (R.Pot.) Th.et Pfl.		p
		Verrucatosporites favus (R.Pot.) Th.et Pfl.		p
		Verrucatosporites histiopteroi-des W.Kr.		p
	Hymenophyl-laceae	Hymenophyllum rotundum N.Mtchedl.		p
		Hymenophyllum sp.		p
	Thyrsopterida-ceae	Cibotium guriensis Purc.		p
	Dicksoniaceae	Dicksonia antarctica A.Br.		p
		Dicksonia reticulata Purc.		p
		Dicksonia unitotuberata Purc.		p
		Dicksonia sp		p

1	2	3	4	5
Polypodiopsida	Cyatheaceae	Cyathea sp.		p
		Divisisporites sp.		p
		Leiotriletes miocenicus Nagy		p
		Leiotriletes wolfii W.Kr.		p
	Aspleniaceae	Asplenium wegmanni A.Brongn.		m
	Aspidiaceae	Cyclosorus stiriacus (Ung.) Ching et Takht.	m	
		Cystopteris sp.		p
		Lastrea (Cyclosorus) fischeri Heer		m
	Blechnaceae	Woodwardia roessneriana (Ung.) Heer		m
Ginkgoopsida	Ginkgoaceae	Ginkgo sp.		p
Pinopsida	Podocarpaceae	Dacrydium sp.		p
		Podocarpus sp.		p
	Pinaceae	Abies sp.		p
		Cathaya sp.		p
		Cedrus sauerae N.Mtchedl.		p
		Cedrus sp.		p
		Keteleeria caucasica Ram.		p
		Picea metechensis Charat.	m	
		Picea sp.		p
		Pinus nikitini Budant.		m
		Pinus taedaeformis (Ung.) Heer	m	
		Pinus cf.engelhardti Menz.		m
		Pinus sp.	m	mp
		Pseudolarix aff.kaemferi Gord.		p
		Tsuga diversifolia (Maxim.) Mast.		p
	Taxodiaceae	Cryptomeria japonica Don		p
		Cryptomeria sp.		p
		Glytostrobus europaeus (Brongn.) Heer	m	
		Sequoia sp.		p
		Taxodium dubium (Sternb.) Heer	m	
		Taxodium sp.		p
	Cupressaceae	Libocedrus salicornioides (Ung.) Heer	m	m
Gnetopsida	Ephedraceae	Ephedra sp.		p
Dicotyledoneae	Myricaceae	Comptonia aborigena Glad.		p
		Comptonia acutiloba Brongn.	m	
		Comptonia grandis Glad.		p
		Comptonia imperfecta Glad.		p
		Comptonia sp.		p
		Myrica acuminata Ung.		m
		Myrica intermedia Glad.		p

1	2	3	4	5
Dicotyledoneae	Myricaceae	Myrica laevigata (Heer) Sap.		m
		Myrica lignitum (Ung.) Sap.	m	
		Myrica longifolia Ung.	m	
		Myrica pseudogranulata Glad.		p
		Myrica swanteviti (Ung.) Avakov		m
		Myrica ungeri Heer		m
	Juglandaceae	Carya sp.		p
		Cyclocarya sp.		p
		Engelhardia brongniartii Sap.	m	m
		Engelhardia gorensis Djap.	m	
		Engelhardia schlickumi Weyland		m
		Engelhardia wallichiana Lindl.		p
		Engelhardia sp.		p
		Juglans regia L.		p
		Juglans sp.		p
		Momipites punctatus Nagy (Engelhardia sp.)		p
		Platycarya miocenicus (Nagy) Ram.		p
		Platycarya sp.		p
		Triatriopollenites coryphaeus (R.Pot.) Th.et Pfl.		p
	Salicaceae	Populus latior A.Br.		m
		Populus sp.		m
		Salix angusta A.Br.		m
	Betulaceae	Alnus sp.		p
		Betula sp.		p
		Carpinus betulus L.		p
		Carpinus grandis Ung.	m	
		Carpinus neilreichii Kov.		m
		Carpinus sp.		mp
		Corylus sp.		p
		Ostrya sp.		p
	Fagaceae	Castanea sp.		p
		Castanopsis decheni (O.Web.) Kr.et Wld.		m
		Castanopsis cf.echidnocarpa A.DC		m
		Castanopsis brevicuspis Miq.		m
		Castanopsis sp.		p
		Lithocarpus sp.		p
		Fagus sp.		p
		Quercus accutissima Carruth.		m
		Quercus drymeja Ung.		m
		Quercus furcinervis (Rossm.) Heer		m

1	2	3	4	5
Dicotyledoneae	Fagaceae	Quercus lonchitis Ung.		m
		Quercus neriifolia A.Br.	m	m
		Quercus sp.		mp
		Tricolporopollenites cingulum (R.Pot.) Th.et Pfl.		p
		Tricolporopollenites henrici (R.Pot.) Th.et Pfl.		p
		Tricolporopollenites micro-henrici (R.Pot.)Th.et Pfl.		p
	Ulmaceae	Ulmus minuta Goepp.		m
		Ulmus pyramidalis Goepp.		m
		Ulmus sp.		p
		Zelkova sp.		p
	Moraceae	Ficus sp.		p
		Moraceae gen.indet.		p
	Loranthaceae	Viscum caucasicum Djap.	m	
	Magnoliaceae	Magnolia attenuata Web.		m
		Magnolia dianae Ung.		m
		Magnolia dzundzeana (Pal.) Takht.		m
		Magnolia megafigurata (Krutsch) Ram.		p
		Magnolia neogenica (W.Kr.) Ram.		p
		Magnolia sp.	m	m
	Lauraceae	Cinnamomum lanceolatum (Ung.) Heer	m	m
		Cinnamomum polymorphum Heer		m
		Cinnamomum scheuchzeri Heer		m
		Laurus agatophyllum Ung.	m	
		Lindera antiqua (Heer) Lamotte	m	
		Litsea primigenia (Ung.) Takht.	m	
		Ocotea heeri (Gaud.) Takht.	m	
		Ocotea kolakovskyi Harut.	m	
		Ocotea cf.pulchella Mart.		m
		Persea braunii Heer	m	
		Lauraceae gen.indet.		m
	Nymphaeaceae	Nuphar sp.		p
	Theaceae	Ternstroemia mocanerifolia Kol.		m
	Platanaceae	Platanus cf.orientalis L.		m
	Hamamelidaceae	Liquidambar europaeum A.Br.		m
		Liquidambar orientalis L.		p
		Liquidambar styraciflua L.		p
		Sycopsis colchica Ram.		p
	Rosaceae	Rosa sp.	m	

1	2	3	4	5
Dicotyledoneae	Rosaceae	Sorbus sp.	m	
		Rosaceae gen.indet.		p
	Fabaceae	Acacia colchica Avakov		m
		Dalbergia bella Heer	m	
		Dalbergia sp.	m	
		Wisteria fallax (Nath.) Tanai et Onoe	m	
		Leguminosites sp..	m	
	Caesalpiniaceae	Podogonium oehningense (Koen.) Kirch.	m	
	Meliaceae	Cedrela denticulata Djap.	m	
		Cedrela dorofeevi Djap.	m	
	Euphorbiaceae	Euphorbiaceae gen.indet.		p
	Anacardiaceae	Cotinus cf.coggygria Scop.		m
		Cotinus sp.	m	
		Rhus meriani Heer		m
		Rhus sp.	m	
	Sapindaceae	Cupania japonica Tanai	m	
		Sapindus bilinicus Ett.	m	
		Sapindus cupanoides Ett.		m
		Sapindus densifolius Heer		m
		Sapindus falcifolius (A.Br.) Heer	m	
		Sapindus cf.inaequilatera Rus-by		m
	Sabiaceae	Sabia cf.parvifolia Wall.		m
	Aquifoliaceae	Ilex cf.opaca Ait.		m
		Ilex sp.		p
	Staphyleaceae	Staphylea sp.		p
	Rhamnaceae	Berchemia multinervis (A.Br.) Heer		m
		Frangula cf.alnus Mill.		m
	Vitaceae	Parthenocissus quinquefoli-iformis Lub.		p
		Vitis sp		p
	Tiliaceae	Tilia sp.		mp
	Sterculiaceae	Sterculia sp.		p
	Elaeagnaceae	Elaeagnus sp.		p
	Myrtaceae	Eugenia haeringiana Ung.	m	
		Myrtophyllum armazii Avakov		m
		Myrtophyllum sp.		m
		Myrtus rectinervis Sap.		m
		Daplopollis mirtoides W.Kr.		p
		Myrtaceae gen.indet.		p
	Combretaceae	Combretum caucasicum Ava-kov		m
	Melastomaceae	Meriania vsatii Avakov		m
	Mastixiaceae	Mastixia sp.		p

1	2	3	4	5
Dicotyledoneae	Cornaceae	Aucuba cf.japonica Thunb.		m
		Cornus cf.capitata Wall.		m
	Araliaceae	Brassaiopsis sp.		p
		Araliaceae gen.indet.		p
		Tricolpopollenites edmundi (R.Pot.) Th.et Pf.		p
	Apiaceae	Apiaceae gen.indet.		p
	Clethraceae	Clethra iberica Djap.	m	
		Clethra maximoviczii Nat.	m	
	Myrsinaceae	Rapanea iberica Avakov		m
	Sapotaceae	Bumelia oblongifolia Ett.	m	
		Sapotaceae gen.indet.		p
		Sapotacepodaepollenites obscurus (Th.et Pf.) Nagy		p
	Symplocaceae	Symplocos paniculata Wall.		p
	Periplocaceae	Periploca sp.	m	
	Apocynaceae	Allamanda uacilai Avakov		m
		Apocynophyllum helveticum Heer		m
		Apocynophyllum sp.	m	
		Plumiera caucasica Avakov		m
		Tabernaemontana telaginensis Avakov		m
		Apocynaceae gen.indet.		m
		Phyllites sp. (Apocynaceae?)		m
	Oleaceae	Fraxinus sp.		mp
		Syringa cf.vulgaris L.		m
	Caprifoliaceae	Lonicera sp.		m
		Viburnum sp.		mp
	Lamiaceae	Lamiaceae gen.indet.		p
	Plantaginaceae	Plantago sp.		p
	Asteraceae	Artemisia sp.		p
		Asteraceae gen.indet.		p
Monocotyledoneae	Liliaceae	Smilax minuta Djap.	m	
		Smilax usanetensis Avakov		m
		Liliaceae gen.indet.		mp
	Poaceae	Poaceae gen.indet.		p
	Arecaceae	Arecipites monosulcoides W.Kr.		p
		Arecaceae gen.indet.		p
	Sparganiaceae	Sparganium sp.		p
	Typhaceae	Typha sp.		p

The Upper Miocene

In this section we provide an overview of the history of flora and vegetation during the Sarmatian and Meotian based on plant macroremains and palynological data. Palynological data were interpreted using the landscape-phytocenological method, which has as its foundation the zonal distribution of plant communities (Borzenkova, 1992). While this method does not provide exact paleoclimatic parameters, it reconstructs changes in landscape and vegetation zones effectively, making it a useful tool in palynological investigations. Paleoclimatic reconstructions were undertaken separately for each zone, depending on the paleovegetation (Shatilova et al., 2004a).

The same landscape-phytocenological method was applied to interpret spore-pollen assemblages for the remainder of the Cenozoic. Hence a continuous history of climate and vegetation, from the Sarmatian until the end of the Holocene, can be traced, characterized by several major stages of development (I-XIII).

The Sarmatian

Sarmatian deposits are found in the Transcaucasus intermontane depression and are divided into three substages: the Volhynian (Lower), the Bessarabian (Middle) and the Khersonian (Upper; see Table IX). Marine facies of the Lower and Middle Sarmatian are distributed throughout Georgia. Upper Sarmatian marine sediments have a much more limited distribution, especially in Eastern Georgia, where they are described from only one region of Kakheti (river Iori) as "marine strata" (Buleishvili, 1960; Grusinskaya et al., 1986).

Sarmatian leaf imprints from Western Georgia were researched by Uznadze (1965). Later, Kolakovsky (Kolakovsky & Shakryl, 1976) studied the rich Sarmatian floras of Abkhazia, near the villages Gvada, Mugudzirkhva and Barmish, and Ratiani (1972) investigated the small fossil locality near the village of Djirkhva (Fig.6). Sarmatian floras of Abkhazia are distinguished by systematic diversity, an abundance of subtropical plants and their unusual composition.

The remains of some conifers are found as lignitiferous phytolemma, which allowed the epidermis to be studied in detail, especially the stomatal structure. These observations indicated the presence of several taxa previously unknown in the palaeoflora of Georgia: the genus Colchidia and species *Sequoia corniculata, Cathaya europaea* and *C. abchasica* (Kolakovsky, 1970; Kolakovsky & Shakryl, 1968, 1974; Sveshnikova, 1964).

During the Sarmatian, the lower mountain belts in Abkhazia were clothed in evergreen subtropical forests with a predominance of Lauraceae and Myrsinaceae, the latter indicated in fossil material by the leathery leaves of Rapanea. A large area was covered by thermophilous deciduous plants: Ocotea, Persea and others, which now occur in Central and Southern America, the Mediterranean region and Southeast Asia. Warm-temperate and temperate plants occurred in varied assemblages. These plants were distributed on elevated dry land and possibly in cold valleys as well. Carpinus, Castanea, Fagus, Cryptomerya, Abies, Cathaya, and Colchidia were typical species. Hemixerophytes seem to have had a minor role and included *Arbutus elegans* f. *andrachne, Celtis magnifica, Smilax aspera, Thelycrania sanguinea, Quercus pseudorobur* and probably *Pinus paraeuxina*. The presence of subtropical and, in some cases, tropical plants in the Sarmatian flora of Abkhazia made it similar to the Oligocene-Miocene floras of Europe. This indicates a wide zonal distribution of some subtropical genera and species during the Neogene, which are now preserved only in disjunct botanical provinces. Mastixia, for example, as well as some other plants, are still to be found in the mountains of Malaya (Kolakovsky, Shakryl, 1976).

Rich macrofossil material from Lower-Middle Sarmatian deposits was collected by Chelidze (1972, 1979, 1987) near the town of Kaspi, Metekhi station, and Djava and Norio villages in Eastern Georgia. Her data (1979) indicate that Magnolia, Lauraceae, Podogonium, Myrtus and Apocynophyllum were prevalent in the Sarmatian flora of Kartli (Eastern Georgia). Sarmatian deposits of Kakheti (Norio village) contained at least 25 species, including one fern, two conifers and a large number of angiosperms. On the whole, the Sarmatian flora of Norio is subtropical. Eastern- and Southern-Asian and Atlantic elements from the Lauraceae and Myrsinaceae formed part of this composition (Chelidze, 1972).

The flora of Goderdzi deserves special mention because of its richness and diversity. Fossil material from this locality was studied by many paleobotanists, especially Uznadze. Nevertheless, the unique composition of Goderdzian flora is yet to be fully revealed (Uznadze & Tsagareli, 1979).

The fossil material is represented by wood and leaf imprints. The good preservation of leaves suggests that their fossilization occurred in situ during the accumulation of volcanic material. Study of fossilized wood supplemented the lists of flora with conifers and representatives of the Icacinaceae, leaves of which were absent (Shilkina, 1958).

Some ecological elements are distinguished in the composition of this flora: 1) a subtropical element, which comprised most of the fossil material; 2) a warm-temperate element - 17%; and 3) a temperate element - 15%.

Remains of subtropical plants are represented in great number and high diversity. The abundance of the family Lauraceae indicates a wide distribution of laurel forests, in which the other evergreen plants with laurel-like leaves also occurred.

The modern counterparts of plants of the Goderdzian flora are now distributed in SE Asia, NE India, N America, the Antilles, Canary Islands, Mediterranean and Caucasus (Uznadze & Tsagareli, 1979).

Plant remains from the lower part of the Goderdzi suite, found in limnic deposits near the village of Vale, were studied by Chelidze (1970). Warm-temperate deciduous plants were dominant in this flora; subtropical plants were represented by shrubs. The main feature of this flora was the prevalence of plants typical of dry, sunny slopes.

The Goderdzian suite was dated to the Upper Miocene (Sarmatian-Meotian) based on a petrographic analysis of fossil ash (Skhirtladze, 1958). The same conclusion was drawn later on the basis of hipparion faunal remains (Gabunia & Lasarashvili, 1962).

Until recently, most of our knowledge about the Sarmatian flora and vegetation was based on macrobotanical remains. Only some core samples from central Eastern Georgia were studied palynologically (P.Mchedlishvili & N.Mchedlishvili, 1953). These spore-pollen assemblages contained 28 identifiable forms, 3 of which were of cryptogamous plants, 7 of conifers and 18 of angiosperms.

Recent palynological studies of Sarmatian deposits in both Western and Eastern Georgia have greatly enriched our knowledge of this fossil flora (Kokolashvili & Shatilova, 2009; Maissuradze et al., 2008; Shatilova et al., 1999; 2004; 2004a; 2008; 2009; 2010). The pollen studies have revealed a suite of new taxa, especially ferns and conifers, for which palynomorphs fossilize better than macroremains.

Pollen and spore assemblages from Sarmatian deposits in Western and Eastern Georgia were interpreted using the landscape-phytocenological method. For every region, separate diagrams were constructed (Figs.8, 9). The curves on the left (A) correspond to the two major zonal vegetation formations of the Sarmatian: 1) polydominant forests of the plains, piedmonts and middle mountain belts, composed of subtropical and warm-temperate conifers, broadleafed plants and ferns; and 2) temperate forests of the upper mountain belt, composed of conifers. The curve of pine, an intrazonal plant indicative of humidity, is provided separately on these diagrams. The right-hand side of the diagrams (B) reflects plant-functional types of the Sarmatian in Western and Eastern Georgia.

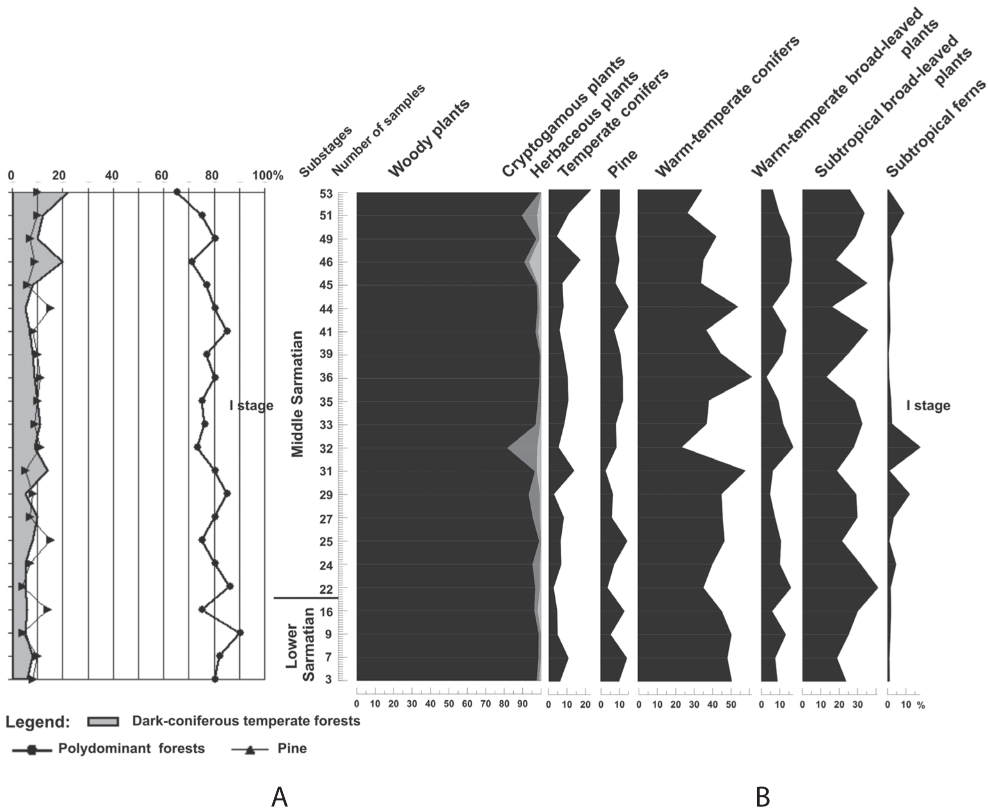

Fig. 8. Fluctuations in pollen percentages indicating changes in the major forest formations (A) and plant-functional types (B) of the Sarmatian in Western Georgia.

For Western Georgia, both parts of diagram (Fig.8: A, B) reflect a relatively stable development of vegetation and climate. Polydominant forest was the main formation, covering greater areas than coniferous communities. Only in the upper part of Middle Sarmatian, polydominant forests declined somewhat while dark coniferous communities expanded, a shift probably linked to paleogeographical changes at the boundary of the Middle and Upper Sarmatian. The role of herbaceous plants during whole Sarmatian was very small.

Vegetation dynamics in Eastern Georgia were quite different (Fig. 9: A, B). Lower-Middle Sarmatian palynological assemblages reflect variations in the distribution of polydominant and pine forests, probably as a result of humidity fluctuations. This process is especially pronounced during the Late Sarmatian, when herbaceous communities expanded on the plains. Woody plants probably formed riparian forests and open woodlands composed of warm-temperate and subtropical plants. Some of them probably occurred as shrubs. Pine dominated in the upper mountain belts. The Late Sarmatian forests saw a substantial decline in subtropical ferns compared to preceding periods. This suggests that one of the main factors in the development of Eastern Georgia's flora during this period was xerophytization. This is confirmed by pollen data and mammal assemblages from Upper Sarmatian and Post-Sarmatian deposits in Eastern Georgia (P.Mchedlishvili & N.Mchedlishvili, 1953; Meladze, 1967).

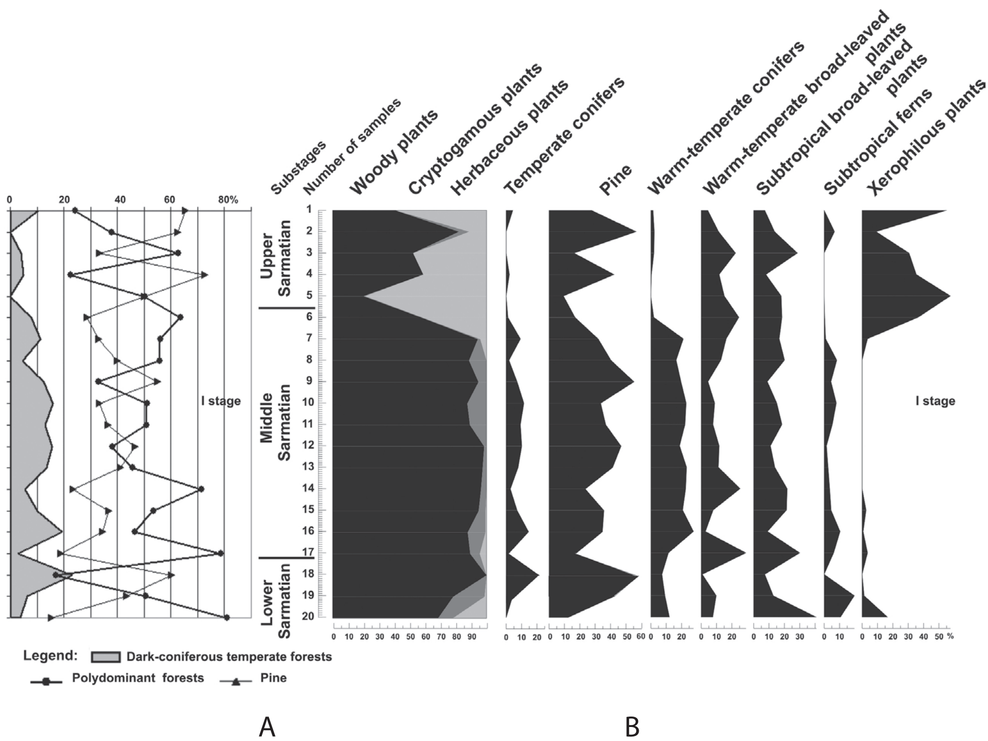

Fig. 9. Fluctuations in pollen percentages indicating changes in the major forest formations (A) and plant-functional types (B) of the Sarmatian in Eastern Georgia.

The end of the Middle Sarmatian was a turning-point in the geological history of the Caucasus. As a consequence of crustal movements, the Trancaucasian intermontane depression transformed into dry land, split into two sections (W and E) by the Dzirulian Block (Fig. 10). The Western part was linked with the Black Sea Basin, the so-called Rionian Bay, where marine deposits continued to accumulate until the end of the Pleistocene. The territory adjoining the Rionian Bay, hemmed in by high mountains, became isolated from the rest of the South Caucasus. A warm, humid climate prevailed here, helping to preserve rich forest vegetation. Thus, from the end of the Middle Sarmatian, the Colchis refuge took shape. Many

Tertiary species still survive there today.

Eastward of the Dzirulian Block, the Kurian Bay formed. In Late Sarmatian the territory of Georgia adjoining this bay became dry land with landscapes typical of a continental climate.

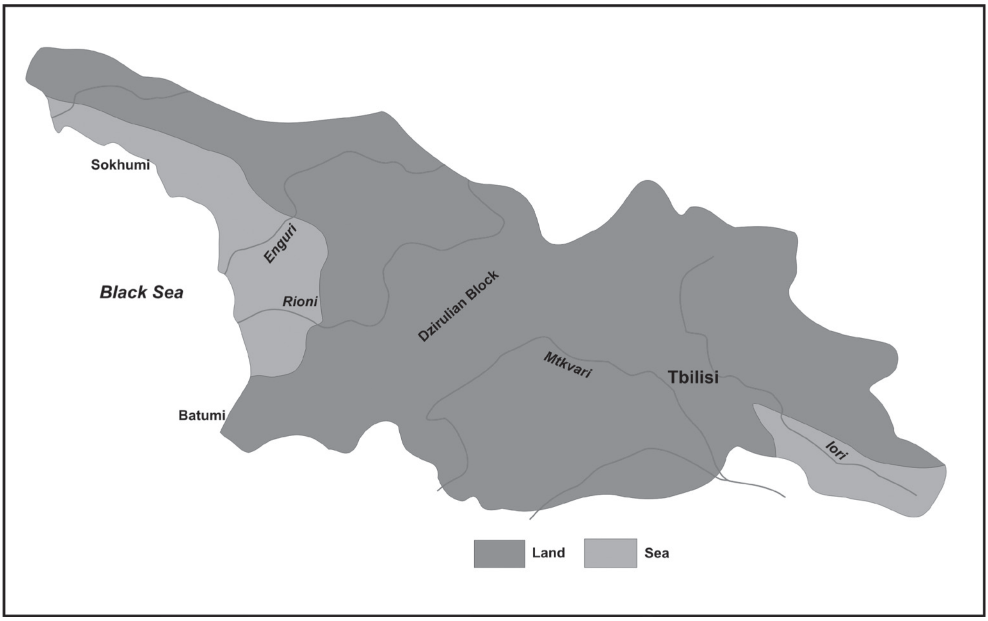

Fig. 10. Schematic paleogeographical map of Georgia during the Late Sarmatian.

So, from the Middle Sarmatian onwards, the vegetation of Western and Eastern Georgia developed along independent lines under the influence of quite different climatic conditions.

The Meotian (Western Georgia)

The Meotian deposits are only known from Western Georgia (Fig.6) and fall into two substages: the Lower or Bagerovian substage and the Upper or Akmanaian substage (Table IX). Data on plant macrofossils from this region have been published by Mchedlishvili (1956), Uznadze (1965), Kolakovsky et al. (1970), Tsagareli (Purtseladze & Tsagareli, 1974) and Chelidze (Chelidze, 1987; Chelidze & Kvavadze, 1983, 1986, 1987). A number of Meotian profiles in Western Georgia (Guria, Abkhazia and Megrelia) were also studied palynologically (Purtseladze, 1977; Purtseladze & Tsagareli, 1974; Shatilova et al., 1999, 2000, 2008a).

From the Kisatibi locality in Southern Georgia, Uznadze (1965) described plant macroremains from the upper levels of the Goderdzian suite, dated to the Meotian. The Kisatibian flora included 22 different forms, such as 3 ferns, 2 monocotyledons and the remainder deciduous trees, except Cinnamomum.

The Meotian flora of Western Georgia is distinguished by diversity amongst the conifers. Compared to the Sarmatian, there is a greater role of conifers ecologically associated with temperate climatic zones (i.e. Abies, Picea and Tsuga). In terms of composition, the subtropical conifers did not change. Podocarpus, Dacrydium, Cathaya, Araucaria, Keteleeria and Phyllocladus continued to occur into the Meotian (Fig.11).

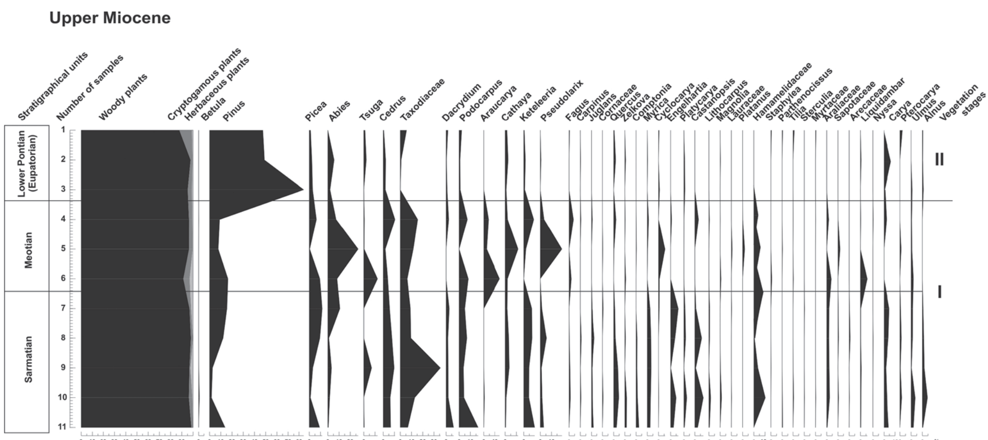

Fig.11. Composite palynological diagram of Upper Miocene (Sarmatian and Meotian) and Lower Pontian (Eupatorian) marine deposits from Western Georgia

In contrast, many of the subtropical angiosperms disappeared after the Sarmatian, especially from the Fagaceae, Lauraceae, Berberidaceae, Caesalpiniaceae, Fabaceae, Anacardiaceae, Sapindaceae, Icacinaceae, Rhamnaceae, Thymelaceae, Myrtaceae, Myrsinaceae, Symplocaceae and Apocynaceae. During the Meotian this group of thermophilous plants remained, however, systematically quite rich and represented mainly by taxa of humid-subtropical and warm-temperate climates (Kolakovsky at al., 1970).

One of the main features of Upper Miocene palynocomplexes in Georgia is a great diversity in the family Hamamelidaceae, represented by 24 forms, 14 genera and 3 subfamilies: Hamamelidoideae, Exbucklandioideae and Altingioideae (Shatilova, Stuchlik, 2001; Shatilova, Mchedlishvili, 2007; 2011a).

Three main stages occurred in the history of this botanical family in Georgia. The initial stage embraced the Eocene, Oligocene and Middle Miocene, when 4 genera are known to have existed: Hamamelis, Corylopsis, Sycopsis and Liquidambar (Ramishvili, 1982; Panova et al., 1984).

The Late Miocene was the second stage, a time when the Hamamelidaceae flourished. During the Sarmatian, Hamamelidaceae played a significant role in plant communities throughout Georgia. The same taxa continued into the Meotian, but the distribution of most genera was much smaller and generally restricted to Western Georgia.

The third stage of development of the Hamamelidaceae family saw their gradual decline and extinction in Eastern Georgia, followed somewhat later in Western Georgia, where the family persisted until the Middle Pleistocene.

Another taxon characteristic of the Sarmatian and Meotian is the genus Fupingopollenites (Shatilova & Mchedlishvili, 2009). This was an unidentified angiosperm that was distributed in Eurasia during the Cenozoic. Its fossil remains are known only from pollen and are often described using different names (Koreneva & Kartashova, 1978; Nagy, 1969, 1985, 1992; Rossignol-Strick, 1973; Shchekina, 1979). Thiele-Pfeiffer (1980) brought the many forms known in the literature together into a single taxon: *Tricolporopollenites wackersdorfensis.* Liu Geng-wu (1985; 1986) established a new genus, Fupingopollenites. In 1992 Nagy reffered the pollen grains of *Alangium sibiricum* Lubom., to the unidentified angiosperm plant and described it as *Tricolporopollenites sibiricum* (Lubom.) Nagy. Now this name is used by palynologists of Europe (Planderova, 1990; Jimenez-Moreno et al., 2007).

According to Liu Geng-wu (1985), the plant that produced the pollen grains of unidentified angiosperm lived in a subtropical, humid climate and was a component of an evergreen formation. The genus originated in the Middle Eocene, when its distribution was restricted to China. It began to spread during the Oligocene and prospered during the Miocene, when its distribution expanded to encompass most of the non-arid parts of Asia.

In Georgia, the genus Fupingopollenites is first known from the Eocene. At its apogee during the Sarmatian, it was represented by two species: *Fupingopollenites wackersdorfensis* Liu Geng-wu and *F. minutus* Liu Geng-wu. The genus Fupingopollenites disappeared from Eastern Georgia after the Middle Sarmatian, when the area of forests declined and vegetation typical of a continental climate became dominant.

In Western Georgia, the climate continued warm and humid well after the

Sarmatian and Fupingopollenites remained in the flora until the end of the Miocene. Along with many other subtropical plants, this genus became extinct on the boundary of the Meotian and Pontian, when conditions in Western Georgia became cooler and drier (Shatilova, Mchedlishvili, 2009).

The dynamics of Meotian vegetation and climate can be reconstructed using the landscape-phytocenological method. The uplift of high mountains toward the end of the Middle Sarmatian encouraged the development of more distinct altitudinal zonality than during previous stretches of the Miocene. While the structure of Meotian vegetation was the same as its Sarmatian counterpart, the distribution of each formation and the vegetation dynamics were different (Fig.12).

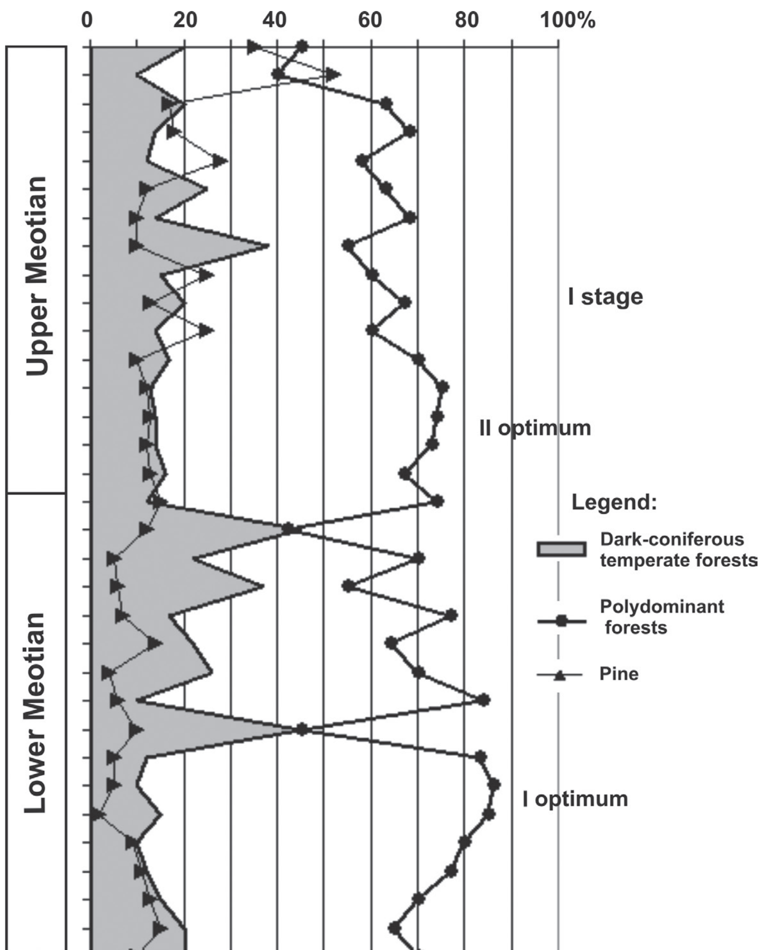

Fig. 12. Fluctuations in pollen percentages of ecological groups indicating changes in major forest types in Western Georgia during the Meotian.

In the Meotian, the dark conifers occupied the upper mountain belt and their area was significantly greater than it was during the Sarmatian.

Middle and lower mountain belts were covered with polydominant forests, which where composed of subtropical and warm-temperate conifers and broad-leaved trees: Podocarpus, Dacrydium, Cedrus, Keteleeria, Cathaya, Taxodiaceae, some species of Carya, Quercus, Fagus, Castanea, Juglans, Platanus, Nyssa and the family Hamamelidaceae. The forest understorey consisted of subtropical ferns such as Dicksonia, Gleichenia, Anemia, Polypodium and Pteris. Semi-hygrophilous broad-leaved forests were relatively widespread, composed of Castanopsis, some species of Carya, Pterocarya and Alnus, as well as *Libocedrus salicornioides* and Lauraceae (Kolakovsky et al., 1970).

As a whole, Meotian polydominant forests were more restricted and unstable compared to the Sarmatian. Conditions similar to those of the Middle Sarmatian occurred at the beginning of the Lower Meotian, when the polydominant forests had the greatest spread. This was probably the first climatic optimum. Changes in vegetation cover occurred during the second half of the Early Meotian, indicating a probable decrease in temperature and humidity.

The beginning of the Late Meotian can be considered as a second climatic optimum, although the area of polydominant forests was not as wide and stable as during the first optimum. By the end of Meotian, the decreasing role of dark conifers and increase of pine forests was brought on by abrupt climatic changes in Early Pontian – Eupatorian times (Fig. 11, 14, 15). According to Chepalyga (1987), the upper part of the Meotian can be correlated with a major regression in the marine basins of Paratethys – the so-called Messinian salinity crisis. According to others (Borzenkova, 1992; Zubakov, 1990), however, this phenomenon is synchronous with the Bosphorian substage of the Pontian.

Like the most epochs transitional between two major divisions in the geological timescale, the Meotian vegetation of Western Georgia preserved strong similarities with the vegetal landscapes of previous stretches of time on one hand, and, on the other, had already begun to assume some of the features typical of the ages to come. As a whole the Sarmatian and Meotian floras can be considered as a common developmental stage for the Upper Miocene vegetation of Georgia (stage I).

A list of Sarmatian and Meotian floras is given below (Table XI).

Table XI. Plants from Sarmatian and Meotian deposits in Georgia
Key: m – macrofossils; p – pollen

Class	Family	Species	Sarmatian	Meotian
1	2	3	4	5
Bryopsida	Sphag-naceae	Sphagnum sp.	p	p
Lycopodi-opsida	Lycopodi-aceae	Lycopodium alpinum L.	p	
		Lycopodium annotinum L.		p
		Lycopodium selago L.		p
		Lycopodium serratum Tunb.	p	p
		Lycopodium sp.	p	p
Isoëtopsida	Selaginel-laceae	Selaginella atrivirides Spring.	p	p
		Selaginella fusca N.Mtchedl.	p	p
		Selaginella selaginoides (L.) Link.		p
		Selaginella aff.eggersii Sodiro		p
		Selaginella sp.	p	p
Equisetop-sida	Equiseta-ceae	Equisetum sp.	mp	
Ophioglos-sopsida	Ophioglos-saceae	Botrychium sp.	mp	p
		Ophioglossum sp.		p
Polypodiopsida	Osmun-daceae	Osmunda cinnamomea L.		p
		Osmunda regalis L.		p
		Osmunda schlemnitziensis Pettko		m
		Osmunda strozzi Gaud.		m
		Osmunda sp.	mp	p
	Schizae-aceae	Schizaea sp.	p	p
	Anemiaceae	Anemia sp.	p	p
		Mohria sp.	p	p
	Lygodiaceae	Lygodium digitatum Presl.	p	p
		Lygodium japonicum Sw.	p	p
		Lygodium aff.multiwallatum (W.Kr.) Ram.	p	
		Lygodium sp.	p	p
	Pteridaceae	Cryptogramma crispa (L.) Br.		p
		Cryptogramma sp.	p	p
		Pteridacidites boerzoeniensis (Nagy) Shat., Stuch. (Pteris aff.quadriaurita Retz.)	p	p
		Pteridacidites dentatiformis Shat., Stuch. (Pteris dentata Forsk)		p
		Pteridacidites georgiensis Shat., Stuch. (Pteris sp.)		p
		Pteridacidites grandifoliiformis Shat., Stuch. (Pteris grandifolia L.)	p	p

1	2	3	4	5
Polypodiopsida	Pteridaceae	Pteridacidites helveticus (Nagy) St.et Sh. (Pteris sp.)	p	
		Pteridacidites longifoliiformis Shat., Stuch. (Pteris longifolia L.)		p
		Pteridacidites remotifolioides Shat., Stuch. (Pteris remotifolia Bak.)		p
		Pteridacidites venustaeformis Shat., Stuch. (Pteris venusta Kze.)	p	p
		Pteridacidites aff.verus (N.Mtchedl.) Shat., Stuch. (Pteris aff.crenata Sw.)	p	p
		Pteridacidites aff.vittatoides Shat., Stuch. (Pteris vittata L.)	p	
	Marsile-aceae	Marsilea sp.	p	
	Adiantaceae	Adiantum reniforme L.var.foss. Sap.et Mar.	m	
		Adiantum sp.	mp	p
		Anogramma sp.	p	p
		Onychium sp.	p	
		Pityrogramma sp.	p	p
	Gleicheni-aceae	Clavifera aff.tuberosa Bolch.	p	
		Clavifera sp.	p	
		Gleichenia angulata Naum.		p
		Gleichenia sp.	p	p
		Gleicheniaceae gen.indet.	p	p
	Matoni-aceae	Matonia sp.		p
	Polypodiaceae	Polypodium aureum L.	p	p
		Polypodium australe Fee	p	
		Polypodium palaeoserratum Kol.		m
		Polypodium pliocenicum Ram.		p
		Polypodium verrucatum Ram.	p	
		Polypodium sp.	mp	p
		Verrucatosporites histiopteroides W.Kr.	p	p
		Pyrrosia sp.	p	
		Polypodiaceae gen.indet.	p	p
	Hymeno-phyllaceae	Vandenboschia cf.radicans (Swartz) Copel.	m	
		Vandenboschia fomini (Pal.) Kol.	m	
		Hymenophyllum sp.	p	p
	Thyrsopteri-daceae	Cibotium guriensis Purc.		p
		Cibotium sp.	p	
	Dicksonia-ceae	Dicksonia antarctica R.Br.	p	p
		Dicksonia luculenta Purc.		p
		Dicksonia reticulata Purc.	p	p
		Dicksonia spanditocincta Purc.	p	p
		Dicksonia unitotuberata Purc.	p	p
		Dicksonia sp	p	

1	2	3	4	5
Polypodiopsida	Cyatheaceae	Alsophyla sp.	p	p
		Cyathea sp.	p	p
		Hemitelia sp.	p	
	Dennstaedtiaceae	Pteridium oeningense (Ung.) Kol.	m	
	Aspleniaceae	Asplenium wegmanni A.Brongn.		m
		Asplenium sp.	p	mp
	Aspidiaceae	Aspidium sp.		m
		Athyrium sp.		p
		Cyclosorus stiriacus (Ung.) Ching et Takht.	m	
		Cyclosorus sp.		m
		Cystopteris sp.	p	p
		Dryopteris sp.	p	p
		Lastrea (Cyclosorus) fischeri Heer	m	
		Lastrea sp.	m	
		Polystichum sp.		p
		Woodsia sp.	mp	
	Davalliaceae	Microlepia sp	p	
	Blechnaceae	Woodwardia roessneriana (Ung.) Heer	m	
	Salviniaceae	Salvinia sp.		p
	Filicales fam.indet.		p	
Ginkgoopsida	Ginkgoaceae	Ginkgo biloba L.	p	p
		Ginkgo occidentalis Samyl.	m	m
		Ginkgo sp.	p	p
Pinopsida	Podocarpaceae	Dacrydium sp.	p	p
		Podocarpus sp. (aff.javanicus Merril.)	m	
		Podocarpus sp.	p	p
	Phyllocladaceae	Phyllocladus sp.	p	p
	Taxaceae	Taxus grandis Kräus.		m
		Torreya sp.		m
	Araucariaceae	Araucaria sp.	p	p
	Pinaceae	Abies alba Mill.	p	p
		Abies cephalonica Loud.	p	p
		Abies ciliticaeformis N.Mtchedl.	p	p
		Abies nordmanniana (Stev.) Spach.	p	p
		Abies sp. cf.A.firma S. et L.	m	
		Abies sp.	mp	p
		Cathaya abchasica Sveshn.	m	m
		Cathaya europaea Sveshn.	m	
		Cathaya aff.argyrophylla C.et K.	p	p
		Cedrus atlantica Manetti	p	p
		Cedrus deodara Loud.	p	p
		Cedrus sauerae N.Mtchedl.	p	p
		Cedrus sp.	mp	

1	2	3	4	5
Pinopsida	Pinaceae	Colchidia angustissima Kol.et Schak.	m	
		Colchidia longicellulata Kol.et Schak.	m	
		Colchidia (?) ambigua Kol.	m	
		Keteleeria caucasica Ram.	p	p
		Picea complanataeformis N.Mtchedl.	p	p
		Picea minor N.Mtchedl.	p	p
		Picea mioorientalis Uzn.	p	
		Picea orientalis L.		p
		Picea sp.	mp	p
		Piceoxylon piceoides Schilk.	m	
		Pinus euxina Kol.		m
		Pinus halepensis Mill.		p
		Pinus irinae Kol.et Schak.	m	
		Pinus paraeuxina Kol.	m	
		Pinus pithyusa Stev.	m	p
		Pinus praepithyusa Palib.		m
		Pinus rjabinini Palib.	m	
		Pinus thomasiana (Goepp.) E.Reich.		m
		Pinus sp.	m p	mp
		Pityoxylon goderzicum Schilk.	m	
		Pseudolarix aff.kaemferi Gord.		p
		Pseudolarix sp.	p	
		Pseudotsuga sp.	p	
		Tsuga diversifolia (Maxim.) Mast.	p	p
		Tsuga canadensis (L.) Carr.	p	p
		Tsuga meierii Mched.		p
		Tsuga patens Downie		p
		Tsuga pattoniana Engelm.	p	p
		Tsuga shatilovae Mched.		p
		Tsuga sp.	mp	
	Sciadopity-aceae	Sciadopitys sp.	p	mp
	Taxodiaceae	Cryptomeria japonica Don	mp	mp
		Cryptomeria sp.		m
		Cunninghamia sp.	p	
		Glyptostrobus ungeri Heer	m	
		Glytostrobus sp.	mp	p
		Sequoia corniculata Kol.et Schak.	m	
		Sequoia langsdorfii (Brongn.) Heer	m	m
		Sequoia sp.	p	mp
		Sequoiadendron sp.	p	p
		Taxodium distichum foss. A.Br.		m
		Taxodium distichum miocenicum Heer	m	
		Taxodium dubium (Sternb.) Heer	m	m
		Taxodium sp.	p	mp
		Taxodiaceae gen.indet.	p	p

1	2	3	4	5
Pinopsida	Cupres-saceae	Cupressus palaeosempervirens Kol.et Schak.	m	
		Cupressus sempervirens L. foss.		m
		Cupressus sp.	p	p
		Helia salicornioides Ung.	m	
		Juniperus sp.	p	
		Libocedrus pliocenica Kink.	m	
		Libocedrus salicornioides (Ung.) Heer		m
		Libocedrus sp.	p	
		Thuja barmyschensis Kol.et Schak.	m	
		Thuja occidentalis L.		m
		Cupressaceae gen.indet.	p	p
Gnetopsida	Ephed-raceae	Ephedra distachya L.		p
		Ephedra aff.equisetina Bge.		p
		Ephedra aff.strobilaceae Bge.		p
		Ephedra sp.	p	p
Dicotyledoneae	Casuari-naceae	Casuarinaceae gen.indet.	p	
	Myricaceae	Comptonia sp.	p	mp
		Myrica banksiaefolia Ung.	m	
		Myrica laevigata (Heer) Sap.	m	
		Myrica lignitum (Ung.) Sap.	m	m
		Myrica palaeogale Pilar.	m	
		Myrica sismondae Mesch.	m	
		Myrica studeri Heer	m	
		Myrica sp. (cf. M.acuminata Ung.)	m	
		Myrica sp.	p	p
		Myricaceae gen.indet.	p	
	Juglandaceae	Carya aquatica (Michx.) Nutt.	p	p
		Carya bilinica Ung.	m	
		Carya cordiformis (Wangh.) C.Koch	p	p
		Carya denticulata (Web.) Iljinsk.	m	m
		Carya ovata (Mill.) C.Koch		p
		Carya serraefolia (Kr.) Goepp.	m	
		Carya aff.pecan (March.) Engl.		p
		Carya sp.	p	mp
		Cyclocarya sp.	p	p
		Engelhardia spicata Blume		p
		Engelhardia wallichiana Lindl.		p
		Engelhardia sp.	p	p
		Juglans cinerea L.	p	mp
		Juglans regia L.	p	p
		Juglans zaisanica Iljinsk.	m	m
		Juglans sp.	p	
		Platycarya sp.	p	p
		Pterocarya castaneifolia (Goepp.) Schlecht.	m	

1	2	3	4	5
Dicotyledoneae	Juglandaceae	Pterocarya paradisiaca (Ung.) Iljinsk.	m	
		Pterocarya pterocarpa (Michx.) Kunth.	p	p
		Pterocarya rhoifolia Sieb.et Zucc.		p
		Pterocarya stenoptera DC.	p	p
		Pterocarya sp.	p	p
	Salicaceae	Populus balsamoides Goepp.	m	m
		Populus populina (Brongn.) Knobl.	m	
		Populus sp.	m	
		Salix coriacea Uzn.et Tsag.		m
		Salix integra Goepp.	m	
		Salix macrophylla Heer	m	
		Salix media A.Br.	m	
		Salix varians Goepp.	m	m
		Salix sp.	mp	mp
	Betulaceae	Alnus angustifolia Kol.		m
		Alnus feroniae (Ung.) Czecz.	m	
		Alnus subcordata C.A.M.	m	m
		Alnus sp.	mp	p
		Betula caudata Goepp.	m	
		Betula macrophylla (Goepp.) Heer		m
		Betula sp.	p	p
		Carpinus betulus L.	p	p
		Carpinus caucasica Grossh.	p	p
		Carpinus colchica Kol.	m	
		Carpinus grandis Ung.	m	m
		Carpinus orientalis Mill.	p	p
		Carpinus pliofauriei Rat.		m
		Carpinus subcordata Nath.	m	m
		Carpinus uniserrata (Kol.) Rat.et Kol.	m	m
		Carpinus subyedoensis Konno	m	
		Carpinus sp.	p	p
		Corylus aff.colurna L.		p
		Corylus aff.ferox Wall.		p
		Corylus sp.	p	p
		Ostrya angustifolia Andr.	m	
		Ostrya atlantides Ung.	m	
		Ostrya sp.	p	p
	Fagaceae	Castanea atavia Ung.	m	m
		Castanea pliosativa Kol.		m
		Castanea sp.	p	p
		Castanopsis abchasica Kol.	m	
		Castanopsis adjarica Kol.	m	
		Castanopsis bifurcata Kol.	m	
		Castanopsis decheni (O.Web.) Kr.et Wld.	m	
		Castanopsis elisabethae Kol.	m	
		Castanopsis furcinervis (Rossm.) Kr.et Wld.		m

1	2	3	4	5
Dicotyledoneae	Fagaceae	Castanopsis guriaca (Ung.) Iljinsk.	m	m
		Castanopsis aff.pavlodarensis Macul.	m	
		Castanopsis sp. (cf. C.echidnocarpa A.DC)	m	
		Castanopsis sp.	p	p
		Lithocarpus longifolia (Kol.) Kol.		m
		Lithocarpus sp.	p	
		Fagus attenuata Goepp.	m	
		Fagus orientalis Lipsky	p	p
		Fagus orientalis Lipsky var.palibinii Iljinsk.	m	m
		Fagus cf.sylvatica Schilk.	m	
		Fagus sp.	mp	p
		Quercus cerris Kol.		m
		Quercus cruciaca A.Br.	m	
		Quercus drymeja Ung.	m	
		Quercus euboea Palib.	m	
		Quercus ilex L.	m	m
		Quercus kubinyi (Kov.) Cz.	m	
		Quercus lonchitis Ung.	m	
		Quercus neriifolia A.Br.	m	m
		Quercus pseudocastanea Goepp.	m	
		Quercus pseudorobur Kov.	m	
		Quercus sosnowskyi Kol.		m
		Quercus sp.	mp	mp
		Quercinium lithocarpoides Schilk.	m	
	Ulmaceae	Celtis japetii Ung.	m	
		Celtis magnifica Kol.	m	
		Celtis sp.	p	p
		Ulmus bronii Ung.		m
		Ulmus carpinoides Goepp.	m	
		Ulmus foliacea Gilib.	p	p
		Ulmus longifolia Ung.	m	
		Ulmus sp.	p	p
		Zelkova carpinifolia (Pall.) Dipp.	mp	p
		Zelkova ungeri Kov.	m	m
		Zelkova zelkovifolia (Ung.) Büzek et Kotlaba	m	m
		Zelkova sp.	p	p
	Eucommi-aceae	Eucommia ulmoides Oliv.	p	p
	Moraceae	Ficus insignis Ett.	m	
		Ficus lanceolata Heer	m	
		Ficus sp.	p	p
		Morus sp.		p
		Moraceae gen.indet	p	p
	Canna-baceae	Cannabis sp.	p	

1	2	3	4	5
Dicotyledoneae	Polygonaceae	Polygonum sp.	mp	p
		Polygonaceae gen.indet.	p	
	Caryophyllaceae	Stellaria sp.		p
		Caryophyllaceae gen.indet.	p	p
	Chenopodiaceae	Atriplex sp.		p
		Kochia sp.		p
		Chenopodiaceae gen.indet.	p	p
	Magnoliaceae	Liriodendron tulipifera L.	p	p
		Magnolia attenuata Web.	m	
		Magnolia dianae Ung.	m	
		Magnolia dzundzeana (Pal.) Takht.	m	
		Magnolia euxina Palib.	m	m
		Magnolia grandiflora L.		p
		Magnolia megafigurata (Krutsch) Ram.	p	p
		Magnolia mirabilis Kol.	m	
		Magnolia sinuata Kirchh.		m
		Magnolia sp.	p	mp
	Annonaceae	Annona sp.	p	p
	Schizandraceae	Kadzura irregularinervia Kol.	m	
		Schizandra grossheimii Kol.		m
		Schizandra sp. cf.S.propinqua Hook et Thoms.	m	
	Lauraceae	Actinodaphne dolichophylla Takht.	m	m
		Appolonias barbusana (Cav.) A.Br.		m
		Apollonias georgica Uzn.et Tsag.	m	
		Cinnamomum cinnamomeum (Rossm.) Holl.	m	m
		Cinnamomum japonicum Kol.et Schak.		m
		Cinnamomum lanceolatum (Ung.) Heer	m	m
		Cinnamomum sp.	p	p
		Cinnamomophyllum cf. lanceolatum (Ung.) Kol.		m
		Cinnamomophyllum marginatum Kol.et Schak.		m
		Cryptocarya abchasica Schak.	m	
		Daphnogene abchasica Schak.	m	
		Daphnogene cinnamomifolia (Brongn.) Ung.	m	
		Daphnogene kolakovskyi Schak.	m	
		Daphnogene sp.	m	
		Laurinum cinnamomoides Schilk.	m	
		Laurinum hufelandioides Schilk.	m	
		Laurinum goderdzicum Schilk.	m	

1	2	3	4	5
Dicotyledoneae	Lauraceae	Laurophyllum aniboides Kol.et Schak.		m
		Laurophyllum perseoides Kol.et Schak.		m
		Laurophyllum princeps (Heer) Kr.et Wld.	m	
		Laurus lalages Ung.	m	
		Laurus nobilis L.		m
		Laurus pliocenica (Sap.et Mar.) Kol.	m	m
		Laurus sp.	mp	m
		Lindera antiqua (Heer) Lamotte		m
		Lindera neglecta Web.	m	
		Litsea barmyschensis Schak.	m	
		Litsea dermatophyllon Web.	m	
		Litsea magnifica Sap.		m
		Litsea pontica Kol.		m
		Litsea primigenia (Ung.) Takht.	m	m
		Machilus ugoana Huzioka		m
		Neolitsea magnifica (Sap.) Takht.	m	m
		Neolitsea sp.(cf.N.palaeosericea Takht.)	m	m
		Ocotea curviparia Kol.et Schak.	m	
		Ocotea givulescui Kol.et Schak.	m	
		Ocotea heeri (Gaud.) Takht.	m	m
		Ocotea pulchella Mart.		m
		Ocotea sp.(cf.O.rhombifolia Kol.)	m	
		Persea colchica Kol.		m
		Persea pliocenica (Laur.) Kol.	m	m
		Persea sarmatica Schak.	m	
		Persea schakrylii Kol.	m	
		Persea sp.	p	
		Lauraceae gen.indet.	p	p
	Berberi-daceae	Berberis sp.	m	
		Mahonia marginata (Lesq.) Arnold	m	
		Mahonia cf.aquifolium Nutt.	m	
		Berberidaceae gen.indet.	p	
	Ranuncu-laceae	Ranunculus sp.	p	p
	Menisper-maceae	Cocculus frangonervis Uzn.et Tsag.	m	
		Cocculus laurifolium DC foss.Uzn.et Tsag.		m
		Cocculus sp.	m	
		Menispermites sp.		m
		Menispermum sp.	p	p
	Nymphae-aceae	Nuphar luteum (L.) Smith		p
		Nuphar sp.	p	p
		Nymphaea polyrhiza Sap.	m	
		Nymphaea sp.	p	
		Nymphaeaceae gen.indet.	p	p

1	2	3	4	5
Dicotyledoneae	Aristolochiaceae	Aristolochia colchica Kol.		m
		Aristolochia sp.	m	m
	Theaceae	Camellia abchasica Kol.	m	
		Camellia sp.		p
	Brassicaceae	Brassicaceae gen.indet.	p	
	Papaveraceae	Papaver sp.	p	
	Platanaceae	Platanus aceroides Goepp.		m
		Platanus leneariloba Kol.	m	m
		Platanus platanifolia (Ett.) Knobl.	m	
		Platanus sp.	p	p
	Eupteleaceae	Euptelea sp.	p	p
	Hamamelidaceae	Altingia aff.excelsa Nor.		p
		Chunia aff.bucklandoides H.T.Chang	p	p
		Corylopsis aff.cordata Merill et Li	p	p
		Corylopsis aff.pauciflora Sieb.et Zucc.	p	p
		Disanthus aff.cercidifolius Maxim.	p	p
		Disanthus aff.cercidifolius Maxim. var. minor Shat. et Mched.	p	
		Distylium aff.racemosum Sieb.et Zucc.		p
		Distyliopsis aff.dunii (Hamsl.) P.K.Endr.	p	p
		Eustigma aff.oblongifolium Gard.et Champ.	p	p
		Fortunearia aff.sinensis Rehd.et Wils.	p	p
		Fothergilla aff.gardenii Murr.	p	p
		Hamamelis aff.japonica Sieb.et Zucc.	p	p
		Hamamelis meschetiensis Uzn.	m	
		Liquidambar europaea A.Br.	m	m
		Liquidambar formosana Hance	p	p
		Liquidambar orientalis Mill.	p	p
		Liquidambar styraciflua L.	p	p
		Liquidambar aff.turgaica Kupr.	p	p
		Parrotia fagifolia Heer	m	
		Parrotia pristina (Ett.) Stur.		m
		Parrotia aff.persica (DC) C.A.M.	p	p
		Parrotiopsis jaquemontiana (Decne) Rehd.		m
		Sycopsis colchica Ram.	p	p
		Hamamelidaceae gen.indet.	p	p
	Cercidiphyllaceae	Cercidiphyllum sp.	p	
	Hydrangeaceae	Hydrangea maeotica Tsag.		m
	Saxifragaceae	Ribes cf.orientalis Desf.	m	
		Saxifragaceae gen.indet.		p

1	2	3	4	5
Dicotyledoneae	Rosaceae	Amelanchier vulgaris Moench.		m
		Crataegus sp.		m
		Eriobotrya miojaponica Hu et Chaney		m
		Malus parahupensis Hu et Chaney		m
		Malus sp.	m	
		Photinia serrulata Lindl.	m	
		Prunus officinalis (cf.P.laurocerasus) Roem.		m
		Pyracantha coccinea Roem.foss.		m
		Pyrus malus L.		m
		Pyrus theobroma Ung.	m	
		Robinia regeli Heer	m	
		Rosa canina L.	m	
		Rosa pimpinellifolia L.	m	
		Rubus sp.		m
		Sorbus aucuparia L.	m	
		Spiraea cf.salicifolia L.	m	
		Rosaceae gen.indet.	mp	mp
	Caesalpiniaceae	Caesalpinites schaparenkoi Kol.	m	
		Cassiophyllum berenices (Ung.) Kr.	m	m
		Cassiophyllum magnum Kol.	m	
		Cassiophyllum phaseolites (Ung.) Kol.	m	
		Cassia ambigua Ung.	m	
		Cassia lignitum Ung.	m	
		Cassia phaseolites Ung.	m	m
		Cassia sp.	m	
		Cercis sp.		m
		Podogonium knorrii Heer	m	m
		Caesalpiniaceae gen.indet.	p	
	Fabaceae	Acacia sp.	p	
		Dalbergia bella Heer	m	
		Dalbergia derrisaecarpa Kol.	m	
		Dalbergia rectinervis Ett.		m
		Dalbergia sarmatica Kol.	m	
		Dalbergia sp.		m
		Colutea orientalis Mill.	m	
		Gleditschia allemanica Heer	m	
		Pithecolobiophyllum sarmatica Kol.	m	
		Sophora miojaponica Hu et Chaney	m	
		Sophora europaea Ung.	m	m
		Sophora sarmatica Pimen.	m	
		Fabaceae gen.indet.	mp	p
	Geraniaceae	Geranium sp.	p	p
	Euphorbiaceae	Sapium germanicum Kirchh.		m
	Rutaceae	Rutaceae gen.indet.		m
	Simarou-baceae	Ailanthus dryandroides Heer		m
		Simaroubaceae gen.indet.	p	

1	2	3	4	5
Dicotyledoneae	Anacardiaceae	Pistacia miocenica Sap.	m	m
		Rhus fatalievii Kol.	m	
		Rhus herthae Ung.	m	
		Rhus meriani Heer	m	
		Rhus noeggerathii Web.	m	
		Rhus sp.	p	mp
	Aceraceae	Acer integrilobum Web.	m	
		Acer integerrimum (Viv.) Mass.	m	
		Acer laetum C.A.M.		m
		Acer cf.pseudoplatanus L.	m	m
		Acer santagatae Mass.	m	
		Acer subcampestre Goepp.		m
		Acer trilobatum A.Br.	m	m
		Acer sp.	mp	p
	Sapindaceae	Sapindus cupanoides Ett.	m	
		Sapindus falcifolius (A.Br.) Heer	m	m
		Sapindus graecus Ung.	m	
		Sapindus heliconius Ung.	m	
		Sapindus radobojanus Ung.	m	
		Sapindus undulatus Heer	m	
		Sapindus ungeri Ett.	m	
		Sapindus sp.	p	p
	Sabiaceae	Sabia parvifolia Wall.var.foss.	m	
	Hippocastanaceae	Aesculus sp.	p	p
	Cyrillaceae	Cyrilla sp.	p	
	Aquifoliaceae	Ilex colchica Pojark.var.foss.	m	m
		Ilex falsani Sap.et Mar.	m	m
		Ilex simile Kol.		m
		Ilex sp.	p	p
	Icacinaceae	Citronella aff.mucronata D.Don	m	
		Icacinoxylon citronelloides Schilk.	m	
		Icacinoxylon goderdzicum Schilk.	m	
		Icacinaceae gen.indet.	p	
	Celastraceae	Celastrus barmischensis Kol.	m	
		Celastrus sp.	m	
		Euonymus sp.	p	p
	Staphyleaceae	Staphylea sp.	p	p
	Buxaceae	Buxus pliocenica Sap.et Mar.		m
		Buxus sempervirens L.	m	p
		Buxus sp,	p	
	Rhamnaceae	Berchemia cuspidata Kol.	m	
		Berchemia multinervis (A.Br.) Heer	m	m
		Frangula alnus Mill.		m
		Hovenia thunbergii (Nath.) Baik.		m
		Hovenia sp.	m	

1	2	3	4	5
Dicotyledoneae	Rhamnaceae	Paliurus spina-christi Mill.	m	
		Rhamnus deperdita Ung.	m	
		Rhamnus gaudini Heer	m	
		Rhamnus graeffii Heer		m
		Rhamnus mioalaternus Uzn.	m	
		Rhamnus rectinervis Heer	m	
		Rhamnus sp. cf.R.vinogradovii Palib.	m	
		Rhamnus sp.	p	mp
		Sageretia caucasica Pal.	m	
		Ventilago sp.	m	
		Ziziphus tiliaefolius Heer	m	
		Zizyphus sp.	m	
	Vitaceae	Cissus sosnowskyi Kol.	m	
		Parthenocissus quinquefolia (L.) Planch.	p	p
		Parthenocissus sp.	p	p
		Vitis cf.subintegra Sap.	m	
		Vitis teutonica A.Br.	m	
		Vitis sp.	p	p
	Tiliaceae	Tilia caucasica Rupr.	p	p
		Tilia cordata Mill.	p	p
		Tilia aff.platyphyllos Scop.	p	
		Tilia aff.taquetii C.K.Schneid.	p	p
		Tilia sp.	p	p
	Malvaceae	Hibiscus splendens Baik.		m
		Malvaceae gen.indet.		p
	Sterculi-aceae	Sterculia sp.	p	p
		Sterculiaceae gen.indet.	p	p
	Thymelaceae	Daphne kimmerica Kol.		m
		Daphne minima Kol.	m	
		Daphne sp.		p
		Pimelia adjarica Palib.	m	
		Pimelia crassipes Heer	m	
	Elaeagnace-ae	Elaeagnus argentea Push.		p
		Elaeagnus sp.	p	p
	Violaceae	Viola sp.	p	
	Cucurbita-ceae	Trichosanthes sp.	m	
	Myrtaceae	Eugenia aizoon Ung.	m	
		Eugenia haeringiana Ung.	m	
		Myrtophyllum warderi Jasq.	m	
		Myrtophyllum sp.	m	
		Myrtus sp.	mp	p
		Myrtaceae gen.indet.	mp	p
	Onagraceae	Epilobium sp.	p	p
		Onagra sp.	p	p
	Punicaceae	Punica granatum L.		m

1	2	3	4	5
Dicotyledoneae	Alangiaceae	Alangium aff.kurzii Craib.	p	p
		Alangium aff.simplex Nagy		p
		Alangium sp.	p	
	Mastixiaceae	Mastixia microphylla Kol.	m	
		Mastixia sp.	p	
	Nyssaceae	Nyssa disseminata (Ludw.) Kirchh.		m
		Nyssa longifolia Uzn.et Tsag.		m
		Nyssa punctata Heer.		m
		Nyssa sp.	p	p
	Cornaceae	Cornus sp.		p
		Svida graeffi (Heer) Steph.	m	
		Thelycrania sanguinea (L.) Fourr.	m	m
		Cornaceae gen.indet.	p	p
	Araliaceae	Acanthopanax mirabilis (Kol.) Kol.	m	
		Acanthopanax serratus Kol.	m	
		Acanthopanax sp.	p	p
		Aralia hispida Michx.		p
		Aralia sp.	p	p
		Brassaiopsis sp.	p	
		Dendropanax sp.	p	p
		Fatsia sp.	p	
		Hedera colchica C.Koch, var.foss.	m	
		Hedera sp.	p	p
		Schefflera colchica Kol.		m
		Schefflera integrifolia Kol.	m	
		Schefflera sarmatica Kol.	m	
		Tricolpopollenites edmundi (R.Pot.) Th. et Pf.	p	
		Araliaceae gen.indet.	p	p
	Apiaceae	Bifora sp.		p
		Hydrocotyle reniforma Tsag.		m
		Turgenia sp.	p	
		Apiaceae gen.indet.	p	p
	Ericaceae	Arbutus guriense Uzn.	m	m
		Arbutus elegans Kol.forma andrachne	m	
		Epigaea baikovskaja Iljinsk.		m
		Leucothoe protogaea (Ung.) Schimp.	m	
		Rhododendron sp.	mp	p
		Vaccinium integerrimus Uzn.et Tsag.		m
		Vaccinium longifolium Uzn.		m
		Vaccinium protoarctostaphyllos Kol.	m	
		Ericaceae gen.indet.	p	
	Myrsinaceae	Ardisia snigerevskaiae Takht.	m	
		Myrsine centraurorum Ung.	m	
		Myrsine doryphora Ung.	m	
		Myrsine radobojana Ung.	m	

1	2	3	4	5
Dicotyledoneae	Myrsinaceae	Myrsine spatulata Palib.	m	
		Rapanea caucasica Pashkov	m	
		Rapanea kubanensis Pashkov	m	
	Sapotaceae	Bumelia minor Ung.	m	
		Bumelia cf.lanuginosa (Michx.) Pers.	m	
		Sapotaceae gen.indet.	p	p
	Ebenaceae	Diospyros anceps Heer	m	
		Diospyros brachysepala A.Br.	m	m
		Diospyros colchica Uzn.et Tsag.		m
		Diospyros lotoides Uzn.	m	m
		Diospyros sp.	m	
	Styracaceae	Styrax neiburgi (Pal.) Baik.	m	
		Styrax parrotiaefolia Uzn.	m	
		Styrax pseudoofficinale Baik.		m
	Symplo-caceae	Symplocos bzybica Kol.	m	
		Symplocos palaeotheifolia Kol.	m	
		Symplocos paniculata Wall.		p
		Symplocos simile Kol.	m	
		Symplocos sp.	p	p
	Periplo-caceae	Periploca helenae Kol.	m	
		Periploca sp.	m	
	Verben-aceae	Vitex goderdzica Tsag.	m	
	Apocyn-aceae	Apocynophyllum ibericum Palib.	m	
		Apocynophyllum linearifolium Kol.	m	m
		Apocynophyllum wrightianum Kol.	m	
		Apocynophyllum sp.	m	
		Echitonium sophiae Web.	m	
		Dryoxylon symplocoides Schilk.	m	
		Apocynaceae gen.indet.	p	
	Oleaceae	Fraxinus sp.	p	mp
		Jasminum pliocenicum Laur.		m
		Ligustrum sp. (cf.L.vulgare L.)	m	
		Osmanthus kolakovskyi Takht.	m	
		Phillyrea media L.		m
		Oleaceae gen.indet.	p	
	Scrophulari-aceae	Paulownia caucasica Pal.	m	
	Caprifoli-aceae	Lonicera similifolia Kol.	m	
		Lonicera sp.	p	p
		Viburnum sp.	p	mp
	Lamiaceae	Lamiaceae gen.indet.	p	
	Plantagi-naceae	Plantago sp.	p	
	Valerian-aceae	Valeriana sp.		p

1	2	3	4	5
Dicotyledoneae	Campanulaceae	Campanulaceae gen.indet.		p
	Dipsacaceae	Cephalaria sp.		p
		Dipsacus sp.		p
		Knautia sp.	p	p
		Scabiosa sp.	p	p
	Asteraceae	Achillea sp.	p	
		Artemisia sp.	mp	p
		Aster sp.	m	
		Centaurea sp.		p
		Asteraceae gen.indet.	p	p
Monocotyledoneae	Potamogetonaceae	Potamogeton crispus L.		p
		Potamogeton pectinatus L.		m
		Potamogeton sp.		p
	Liliaceae	Smilax aspera L.	m	
		Smilax excelsa L.var.foss.		m
		Smilax grandifolia (Ung.) Heer	m	
		Smilax protolancaefolia Kol.	m	
		Smilax sp.	m	
		Liliaceae gen.indet.	p	p
	Poaceae	Phragmites oenigensis Heer	m	m
		Sasa kodorica Kol.	m	m
		Poaceae gen.indet.	p	p
	Arecaceae	Livistona palibinii Takht.	m	
		Nipa sp.	p	p
		Palmophyllum sp.	m	
		Arecaceae gen.indet.	p	p
	Sparganiaceae	Sparganium sp.	p	p
	Typhaceae	Typha latifolia L.		p
		Typha latissima A.Br.	m	m
		Typha sp.	p	p
	Cyperaceae	Cyperaceae gen.indet.	p	p
The forms of indeterminate systematical position		Fupingopollenites wackersdorfensis (Thiele-Pfeiffer) Liu Geng-wu	p	p
		Fupingopollenites minutus Liu Geng-wu	p	

THE PLIOCENE AND EOPLEISTOCENE (WESTERN GEORGIA)

The Pliocene

According to the stratigraphic scheme developed for the Black Sea, the Georgian Pliocene stretched from the Pontian to the Kuyalnician stage (Table XII; Taktakishvili, 1984).

Table XII. Stratigraphical division of Pliocene and Eopleistocene deposits in Georgia (after Buleishvili, 1986a; Nevesskaya et al., 2003; Semenenko et al., 2009; Taktakishvili, 1984)

<table>
<tr><th rowspan="2">Ma</th><th rowspan="2">Division</th><th rowspan="2">Regiostage</th><th colspan="2">Western Georgia</th><th colspan="2">Eastern Georgia</th></tr>
<tr><th colspan="2">Horizon</th><th colspan="2">Stage</th></tr>
<tr><td rowspan="2">1.8</td><td rowspan="2">Eopleistocene</td><td rowspan="2">Gurian</td><td colspan="2">Naderbazetian</td><td rowspan="2">Apsheronian</td><td rowspan="5">Alazanian</td></tr>
<tr><td colspan="2">Khvarbetian</td></tr>
<tr><td rowspan="3">3.4</td><td rowspan="9">Pliocene</td><td rowspan="3">Kuyalnician (Egrissian)</td><td colspan="2">Tsikhisperdian</td><td rowspan="3">Akchagilian</td></tr>
<tr><td colspan="2">Etserian</td></tr>
<tr><td colspan="2">Skurdumian</td></tr>
<tr><td rowspan="2">5.3</td><td rowspan="2">Kimmerian</td><td colspan="2">Kamyshburunian</td><td colspan="2" rowspan="2">Redwellian suite</td></tr>
<tr><td colspan="2">Azovian</td></tr>
<tr><td rowspan="4">7.1</td><td rowspan="4">Pontian</td><td colspan="2">Bosporian</td><td colspan="2" rowspan="5">Dushetian (Shirakian) suite</td></tr>
<tr><td colspan="2">Portaferian</td></tr>
<tr><td rowspan="2">Novorossian</td><td>Odessian</td></tr>
<tr><td>Eupatorian</td></tr>
<tr><td></td><td>Miocene</td><td>Meotian</td><td colspan="2">Upper</td></tr>
</table>

The Pliocene of Western Georgia is of particular interest because the full spectrum of Pliocene stratigraphical units is represented, containing rich faunal and floral assemblages. The same cannot be said of other parts of the Black Sea region. Hence the biostratigraphical scheme of Pliocene marine deposits in Western Georgia is considerably more detailed.

The Pontian

Pontian deposits are widely distributed throughout Western Georgia. They contain a rich molluscan fauna, which forms the basis for subdividing the Pontian stage into substages and horizons (Table XII).

Plant remains from Pontian deposits were first described by Palibin (1930a) and Mchedlishvili (1954). The fossils were found in Guria (southern part of Western Georgia) and in Abkhazia, around the Bichvinta (Pitsunda) Peninsula. The Bichvinta flora was later studied by Kolakovsky (1962), who also undertook an analysis of a rich Pontian flora locality by the Kodori River (Kolakovsky, 1964), near Meore-Atara village (Fig.13).

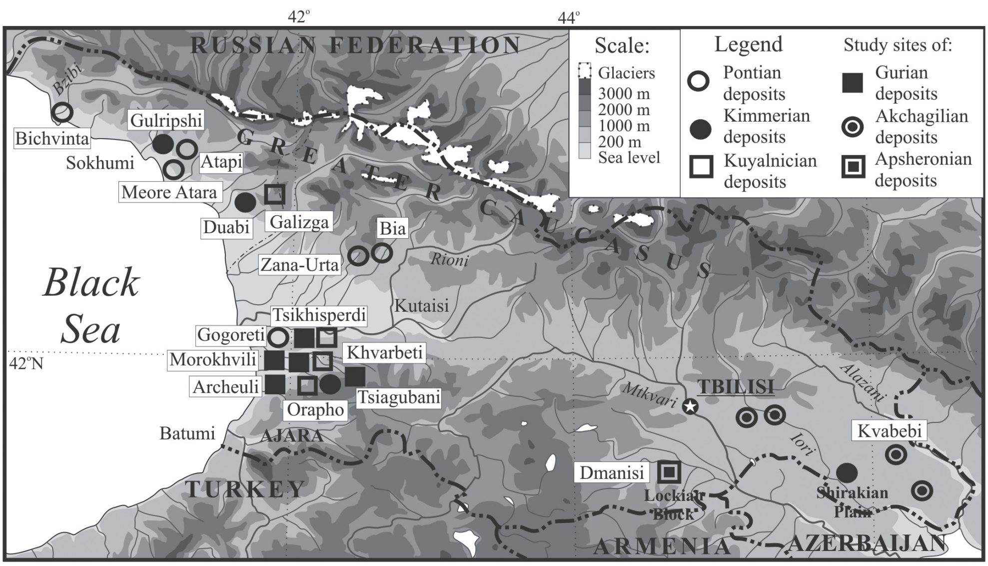

Fig.13. Study sites of Pliocene and Eopleistocene deposits in Georgia

According to Kolakovsky, this Kodorian flora is unique and one of the richest in Eurasia. The subtropical character of the vegetation of its lower mountain belt "confirms the existence in Colchis of a major refugium for Tertiary species that gradually died out" (Kolakovsky, 1964, p.5). The Kodorian flora was mainly composed of subtropical plants (30.5%), especially in riparian forests and lower mountain belt communities. One such community was formed of *Quercus nerifolia, Salix varians, Alnus subcordata* and *Myrica lignitum*. On coastal plains and in river gorges, *Quercus kodorica* and *Carya denticulate* formed another community. Swamp forests were composed of *Alnus subcordata* and *Salix varians,* judging from the distinct layers of leaves and catkins present in the deposits.

Kolakovsky classified the forests of lower mountain belt into moist forests and hemi-xerophilous woods. The flora of moist subtropical forests was very rich, including *Tectocarya lusatica,* Symplocos, Ocotea, Pasania, Cyclobalanopsis, Castanopsis and members of the Araliaceae. Vast areas were covered by laurel communities. Sclerophyll communities with elements of maquis also grew in the lower mountain belt, while a pine community was restricted to cliffy sites on calcareous ridges.

Pontian deposits were studied palynologically by Ramishvili (1969). She described the pollen complexes of the upper part of the Lower Pontian (Odessian horizon) and of the Bosporian substage. More recently, rich palynological material has been collected from complete Pontian sections (Shatilova et al., 2000; 2001; 2007).

Pollen analysis revealed some clear differences between macrofloras and palynofloras. The macroscopic remains of ferns and herbs found in the Kodorian and Bichvintian floras are almost absent and temperate conifers are represented with much less frequency. Subtropical evergreen taxa, especially the Lauraceae, are better reflected in macrofloras because their pollen grains preserve less well than their leathery leaves. But the major difference between these two paleofloras is in the volume of information. Macroremains were fossilized either in situ or brought into the Rionian Bay from nearby forests. Kolakovsky regarded the Kodorian material as mainly representative of riparian or swamp forests, which, being communities of azonal character, cannot be used as indicators of climatic conditions. Even laurels, the macroremains of which are typical for the Kodorian flora, provide limited palaeoclimatic information and reflect neither tropical climatic conditions nor the existence of evergreen forests over large areas.

Palynological complexes of the Pontian marine deposits contain the pollen production of forests growing on the whole territory of Paleo-Colchis, from the plains to the upper mountain belt. Pollen and spores are preserved in nearly in all layers of Pontian-aged outcrops, allowing us to reconstruct vegetation changes through the whole period of sediment accumulation. The same can be said for subsquent stages in Western Georgia – the Pliocene and Pleistocene – as well.

Lower Pontian deposits are known from Abkhazia, Megrelia and Guria, but only in three localities (on the Atapi and Zana rivers) is the Novorossian substage represented by a full series of sediments (Fig.13). In all other sections the Eupatorian is absent and the Lower Pontian begins with the Odessian horizon (Chelidze, 1974; Shengelia, 1976; Taktakishvili, 1984).

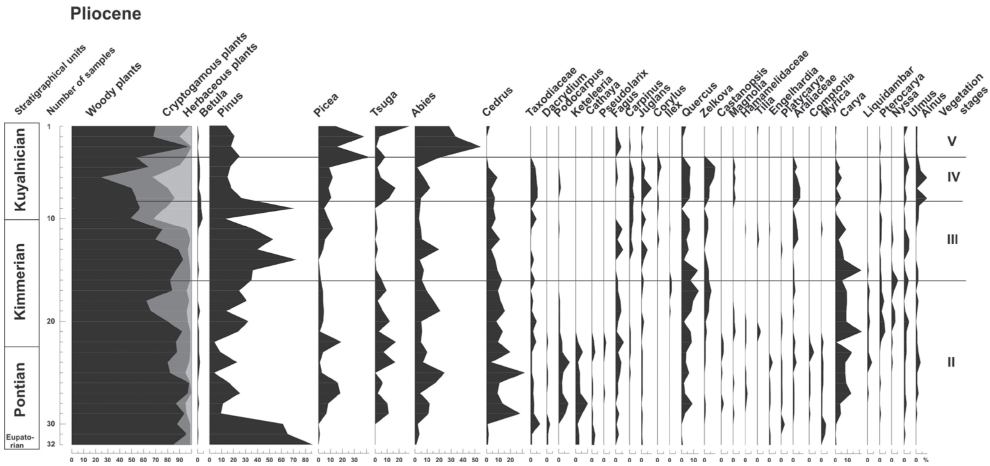

Fig.14. Composite palynological diagram of Pliocene marine deposits from Western Georgia

The analysis of samples from the Atapi and Zana deposits revealed that the changes in pollen assemblages at the boundary of the Miocene and Pliocene were similar at both sites (Fig.11). They show a transition from the rich and diverse pollen flora of the Meotian to poor assemblages with a predominance of pine. In upper part of the Odessian the pine was replaced by dark-conifer communities (Fig. 14, 15), occupying almost all altitudes. This suggests that after the Eupatorian a decrease in temperature took place, possibly linked with Early Pontian cooling around the North Hemisphere (Borzenkova, 1992; Zubakov, 1990).

After the Odessian the climate again became warm and humid, especially during the Middle part of Portaferian, when polydominant forests stabilised. It was probably during this climatic optimum that the Kodorian macroflora accumulated.

The later stretches of the Middle Pontian and the beginning of the Late Pontian were characterized by repeated shifts in forest boundaries. Polydominant formations became predominant toward the end of Late Pontian, probably as a second climatic optimum, corresponding to the accumulation of the Bichvintian flora, took place.

When we compare the Pontian spore-pollen assemblages of Western Georgia with those from synchronous deposits of Northern part of Black Sea coast, the rhythmic changes of epochs with different climates can be traced. However, in Western Georgia the frequency and amplitudes of these changes were weaker. The main difference between the northern Black Sea coast and Western Georgia was in terms of humidity. In the north, the Pontian was a time of declining temperatures and xerophytisation (Shchekina, 1979), while in Colchis precipitation increased side by side with gradually lowering temperatures.

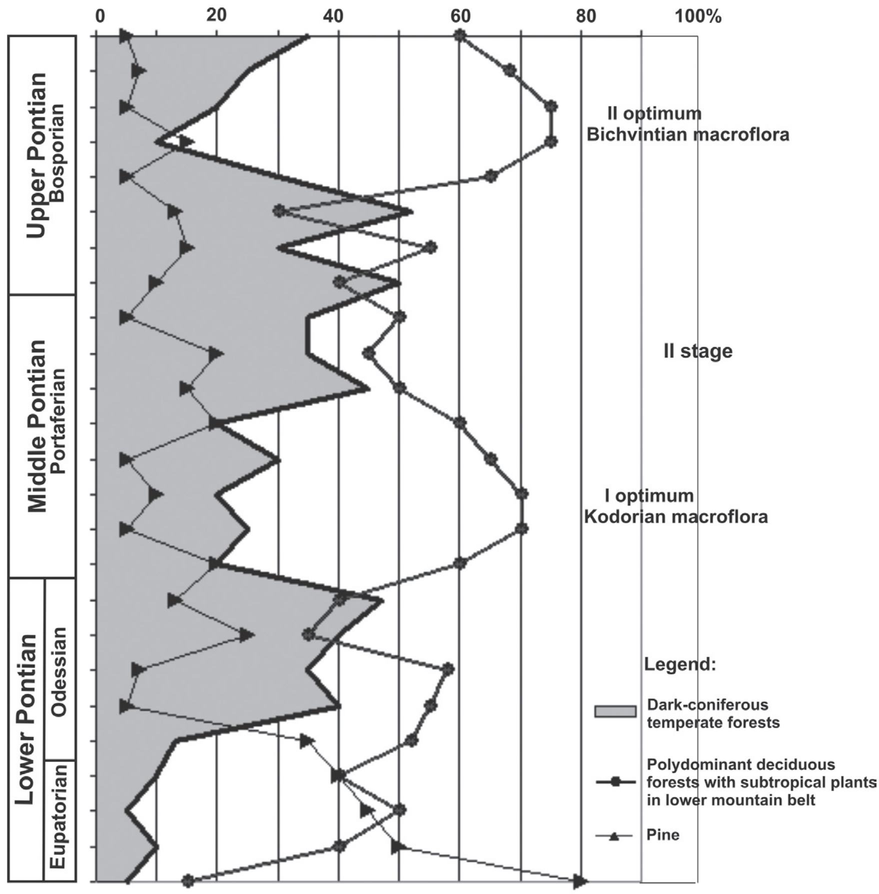

Fig. 15. Percentage fluctuations in palynological groups in Western Georgia during the Pontian, reflecting changes in the distribution of the major forest communities.

The Kimmerian

The area of Western Georgia under the sea became considerably smaller during the Kimmerian. Sea-level fluctuations also occurred on top of this overall regression in the Rionian Bay, leading to the bedding unconformity of the Kimmerian over more ancient deposits (Chelidze, 1964). Kimmerian deposits are distributed in same regions of Western Georgia as the Pontian, but occupied a comparably smaller area (Fig.13). The primary difference between these two stages is in the character of the facies: Kimmerian deposits are usually shallow-water facies that indicate marine regression and the expansion of terrestrial areas (Taktakishvili, 1984).

There are two main schemes for the subdivision of Kimmerian deposits. Davitashvili (1933) identified three horizons: the Azovian, Ampilacian and Panticapeian. This division was later adopted by Gabunia (1953), although the original horizon names were not retained. Taktakishvili (1984) changed the scheme and divided the Kimmerian into two parts – the Azovian and Kamyshburunian – the later stage combining Davitashvili's Ampilacian and Panticapeian horizons (Table XII).

Palibin (1930a), Mchedlishvili (1949a) and Uznadze (1965) were the first researchers to describe the plant remains of Kimmerian deposits. A rich location of Kimmerian fossil flora was found by the Duabi River and dated using fauna to the Kamishburunian (Taktakishvili, 1984). Contemporaneous with the Duabian flora is the flora of Gulripsh (Fig.13); both locations were described by Kolakovsky (Kolakovsky, 1956, 1958; Kolakovsky & Shakryl, 1978). Mchedlishvili (1963) first investigated Kimmerian deposits using palynological methods and, during recent years, a large body of rich palynological material has been collected from Kimmerian deposits in Abkhazia, Guria and Megrelia (Shatilova et al., 2000; 2002; Shatilova & Mchedlishvili, 2007a).

This palynological material was analyzed by the landscape-phytocenological method to trace the dynamics of climate and vegetation during the Kimmerian (Fig. 16).

The warmest climate, close to subtropical, occurred at the end of the Azovian and beginning of the Kamyshburunian. Data from this period indicate a decreasing role for conifer forests, which came to be dominated by Abies, Tsuga and Cedrus. This indicates a temperature rise during these stretches of the Kimmerian, agreeing with the proposition of a global Pliocene optimum in the Azovian-Kamyshburunian interval (Zubakov, 1990; Borzenkova, 1992). This period saw the accumulation of the Duabian flora in Western Georgia, an assemblage with poorer taxonomic diversity compared to the Kodorian flora. Cooling climates during the upper part of the Portaferian and the beginning of the Bosphorian, which led to the extinction of a large number of angiosperms from the plains and lower mountain belt, may explain the depauperate composition of the Duabian flora. The number of genera making up the Fagaceae, Lauraceae, Berberidaceae, Aristolochiaceae, Hamamelidaceae, Araliaceae, Fabaceae, Anacardiaceae, Aquifoliaceae and Arecaceae decreased. In spite of this, Kolakovsky (Kolakovsky & Shakryl, 1978) states that evergreen plants still occupied first place in Kimmerian landscapes. This conclusion was made on the basis of macrofossils and interpreted as reflecting a climatic optimum. On the whole it is possible to suppose that pol-

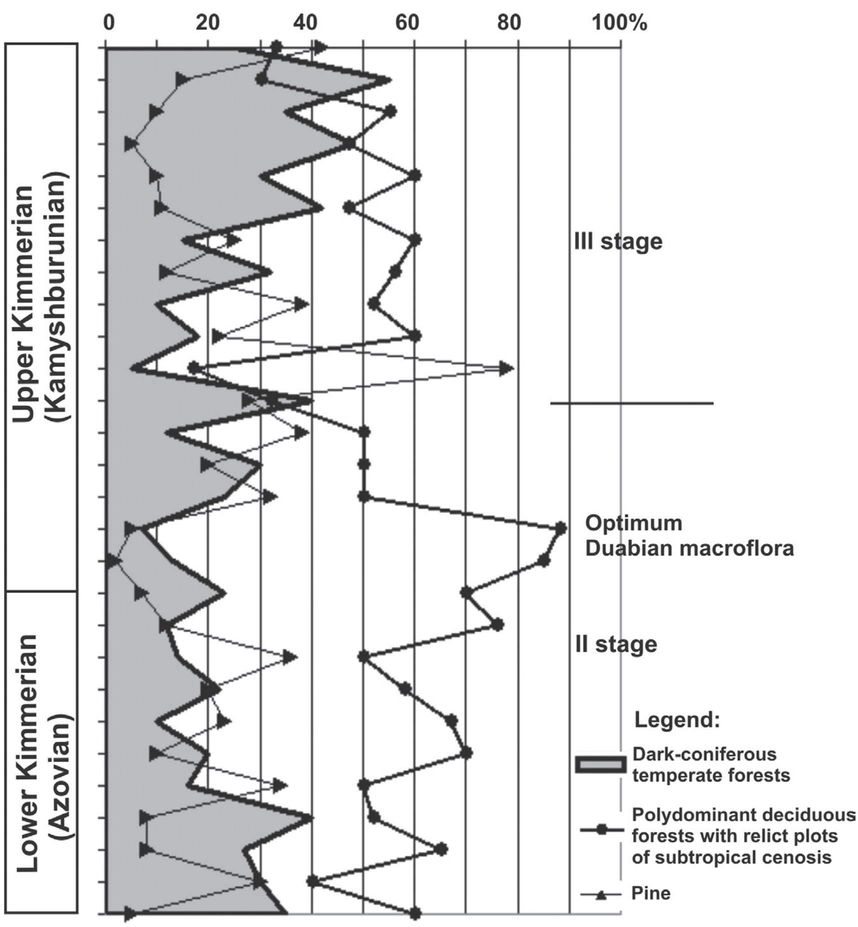

Fig. 16. Percentage fluctuations in palynological groups in Western Georgia during the Kimmerian, reflecting changes in the distribution of the main forest formations.

ydominant deciduous forests existed on the plains and in the lower mountain belt, with relict subtropical communities in refugia, the area of which changed depending on climatic conditions. According to Kolakovsky (1956), the composition of these forests was very variable. He distinguished three groups of plants: 1) those of a humid monsoonal climate; 2) hygrophilous plants with ecological similarities to species of Atlantic North American lowland and riparian forests; and 3) sclerophyllous, cold-hardy species, tolerant of high summer temperatures and with ecological similarities to components of sub-xerophilous Mediterranean forests. At higher elevations, warm-temperate forests were replaced by temperate broadleaf and coniferous formations.

The subsequent stretch of the Kamyshburunian had a cooler, drier climate and pine became dominant in the vegetation cover. The end of Kamyshburunian was warm, but distinguished by a floral composition nearly devoid of subtropical elements and with periodic shifts in dark-coniferous and pine forest areas.

Hence the floras of the Pontian, Azovian and lower part of Kamyshburunian may be combined into a single stage (II) of development in Western Georgian vegetation, although the vegetation complex of the Pontian reflects cooler conditions than the beginning of the Kimmerian. The upper part of Kamyshburunian and the lower part of subsequent Kuyalnician stage (Scurdumian horizon) have fossil floras of somewhat different character and can be combined into stage III.

Kimmerian-aged deposits also occur in Eastern Georgia, where the Shirakian suite contains 34 angiosperm forms. The taxa indicate a riparian forest community, including *Alnus hoernesi, Populus populina, Acer saliense, Ulmus carpinoides* and *Zelkova ungeri*. Vegetation of dry plains and slopes was represented by maquis, shibliak and open woodlands composed of evergreen and deciduous plants: laurels, sclerophyllous and saxicolous oaks, Phillyrea, Viburnum, pistachio, storax, nettle tree, etc.

On the Shiraki plain (Eastern Georgia's Kakheti region) in the Pliocene occurrence of two different types of vegetation (riparian forests and an arid formation) with a prevalence of microphyllous plants indicates the presence of a hot, dry season, characteristic of a Mediterranean climate (Kolakovsky & Ratiani, 1967).

A list of Pontian and Kimmerian floras is given below (Table XIII).

Table XIII. Plants from Pontian and Kimmerian deposits in Georgia
Key: m – macrofossils; p – pollen

Class	Family	Species	Pontian	Kimmerian
1	2	3	4	5
Bryopsida	Sphagnaceae	Sphagnum sp.	p	p
Lycopodiopsida	Lycopodiaceae	Lycopodium alpinum L.	p	p
		Lycopodium annotinum L.	p	p
		Lycopodium clavatum L.	p	p
		Lycopodium densum Sw.		p
		Lycopodium selago L.	p	p
		Lycopodium serratum Tunb.	p	p
Isoëtopsida	Selaginellaceae	Selaginella atrivirides Spring.	p	p
		Selaginella fusca N.Mtchedl.	p	p
		Selaginella pliocenica Dorof.	m	m
		Selaginella selaginoides (L.) Link.	p	p
		Selaginella sp.		p
Equisetopsida	Equisetaceae	Equisetum sp.		p
Ophioglossop-sida	Ophioglos-saceae	Botrychium sp.	p	p
		Ophioglossum lusitanicum L.	p	
		Ophioglossum sp		p
Polypodiopsida	Osmundaceae	Osmunda cinnamomea L.	p	
		Osmunda claytoniana L		p
		Osmunda heeri Gaud.		m
		Osmunda regalis L.	p	p
		Todea sp.	p	p
	Schizaeaceae	Schizaea sp.		p
	Anemiaceae	Anemia	p	
	Lygodiaceae	Lygodium japonicum Sw.	p	p
		Lygodium sp.	p	
	Pteridaceae	Cryptogramma acrostichoides R.Br.	p	
		Cryptogramma crispa (L.)R.Br.	p	p
		Cryptogramma sp.	p	p
		Pteridacidites boerzoenyensis (Nagy) St., Sh. (Pteris aff.quadriaurita Retz.)	p	p
		Pteridacidites dentatiformis Sh., St. (Pteris dentata Forsk)	p	p
		Pteridacidites grandifoliiformis St., Sh. (Pteris grandifolia L.)	p	p
		Pteridacidites guriensis Sh., St. (Pteris aff.togoensis Hieron)	p	p
		Pteridacidites kimmeriensis Sh., St. (Pteris sp.)	p	p

1	2	3	4	5
Polypodiopsida	Pteridaceae	Pteridacidites longifoliiformis Sh., St. (Pteris longifolia L.)	p	p
		Pteridacidites rarotuberculatum Sh., St. (Pteris sp.)		p
		Pteridacidites remotifolioides Sh., St. (Pteris remotifolia Bak.)	p	p
		Pteridacidites spiniverrucatum St., Sh. (Pteris pellucida Pr.)		p
		Pteridacidites variabilis St.et Sh. (Pteris cretica L.)	p	p
		Pteridacidites venustaeformis St., Sh. (Pteris venusta Kze.)	p	p
		Pteridacidites verus (N.Mtchedl.) Sh., St. (Pteris aff.crenata Sw.)	p	p
		Pteridacidites vittatoides Sh., St. (Pteris vittata L.)		p
	Parkeriaceae	Ceratopteris duabensis Kol.		m
	Adiantaceae	Anogramma sp.	p	p
		Pityrogramma sp.	p	p
	Gleicheniaceae	Gleichenia angulata Naum.	p	
		Gleichenia sp.		p
	Polypodiaceae	Polypodium aureum L.	p	p
		Polypodium palaeopectinatum Kol.	m	
		Polypodium palaeoserratum Kol.	m	
		Polypodium pliocenicum Ram.	p	p
		Polypodium serratum (Wild.) Futo (=P.australe Fee)		p
		Polypodium verrucatum Ram.	p	p
		Polypodium tuberculatum N.Mtchedl.		p
		Polypodium vulgare L.	p	p
		Polypodium sp.	p	p
		Verrucatosporites histiopteroides W.Kr.	p	p
		Pyrrosia sp.	p	p
	Hymenophyllaceae	Hymenophyllum rotundum N.Mtchedl.	p	p
		Hymenophyllum sp.	p	
	Thyrsopteridaceae	Cibotium glaucum (Sw.) Hr.et Arn.	p	
		Cibotium sp.	p	
	Dicksoniaceae	Dicksonia antarctica R.Br.	p	p
		Dicksonia luculenta Purc.	p	p
		Dicksonia reticulata Purc.	p	p

1	2	3	4	5
Polypodiopsida	Dicksoniaceae	Dicksonia unitotuberata Purc.	p	p
		Dicksonia aff. fibrosa Col.		p
	Cyatheaceae	Alsophylla sp.	p	p
		Cyathea sp.	p	p
	Aspleniaceae	Asplenium sp.		p
	Aspidiaceae	Athyrium sp.	p	p
		Cyclophorus sp.		p
		Cyclosorus (Lastrea) fischeri Heer	m	
		Cystopteris sp.	p	p
		Dryopteris sp.	p	p
		Gymnocarpium sp.		p
		Lastrea sp.		m
		Struthiopteris filicastrum All.		m
		Woodsia alpina (Bolton) S.F.Gray		p
		Woodsia sp.	p	
	Blechnaceae	Woodwardia radicans (L.) Smith.	p	
		Woodwardia roessneriana (Ung.) Heer	m	
		Woodwardia sp.	m	p
	Salviniaceae	Azolla sp.		p
		Salvinia palaeopilosa Shap.	m	
		Salvinia sp.		p
Ginkgoopsida	Ginkgoaceae	Ginkgo biloba L.	p	p
		Ginkgo occidentalis Samyl.	m	m
Pinopsida	Podocarpaceae	Dacrydium sp.	p	p
		Podocarpus sp.	p	mp
	Phyllocladaceae	Phyllocladus sp.	p	
	Taxaceae	Cephalotaxux sp.		p
		Taxus sp.	p	p
		Torreya nucifera Sieb.et Zucc. foss. Kink.	m	
	Araucariaceae	Araucaria sp.	p	p
	Pinaceae	Abies alba Mill.	p	p
		Abies cephalonica Loud.	mp	p
		Abies ciliticaeformis N.Mtchedl.	p	p
		Abies nordmanniana (Stev.) Spach.	p	p
		Abies sp. cf. A. protofirma Tanai		m
		Abies sp.	mp	m
		Cathaya abchasica Sveshn.		m
		Cathaya argyrophylla C. et K.	p	p
		Cathaya sp.	p	
		Cedrus atlantica Manetti	p	p
		Cedrus deodara Loud.	p	p
		Cedrus libani Laws.	p	p
		Cedrus sauerae N.Mtchedl.	p	p
		Keteleeria caucasica Ram.	p	p

1	2	3	4	5
Pinopsida	Pinaceae	Picea complanataeformis N.Mtchedl.	p	p
		Picea minor N.Mtchedl.	p	p
		Picea orientalis L.	p	p
		Picea sp.	p	mp
		Pinus euxina Kol.	m	m
		Pinus geanthracis (Goep.) E.Reich.	m	
		Pinus hordaceae (Rossm.) Engelm. et Menzel.	m	
		Pinus longisquama Kol.	m	
		Pinus palaeopentaphylla Tanai et Onoe	m	
		Pinus pithyusa Stev.	p	
		Pinus pontica Kol.	m	
		Pinus sp.	mp	mp
		Pseudolarix sp.	p	p
		Pseudotsuga sp.	p	p
		Tsuga aculeata Anan.	p	p
		Tsuga canadensis (L.) Carr.	p	p
		Tsuga diversifolia (Maxim.) Mast.	p	p
		Tsuga inordinata Mched.		p
		Tsuga korenevae Mched.		p
		Tsuga meierii Mched.	p	p
		Tsuga patens Downie	p	p
		Tsuga pattoniana Engelm.	p	p
		Tsuga shatilovae Mched.	p	p
		Tsuga sivakii Mched.		p
		Tsuga tortuosa Mched.	p	p
		Tsuga aff. blaringhemi Flous		p
	Sciadopityaceae	Sciadopitys sp.	p	p
	Taxodiaceae	Cryptomeria japonica Don	mp	mp
		Cunninghamia sp.		p
		Glyptostrobus europaeus (Brongn.) Heer	m	m
		Glyptostrobus sp.	p	p
		Metasequoia sp.	p	p
		Sequoia sp.	mp	p
		Sequoiadendron sp.	p	
		Taxodium distichum foss. A.Br.	m	
		Taxodium sp.	p	p
		Taxodiaceae gen. indet.	p	p
	Cupressaceae	Cupressus cf.sempervirens L.	m	
		Libocedrus salicornioides (Ung.) Heer	m	m
		Juniperus sp.	p	p
		Thuja cf.occidentalis L.	m	
		Cupressaceae gen. indet.	p	p

1	2	3	4	5
Gnetopsida	Ephedraceae	Ephedra sp.	p	p
Dicotyledoneae	Myricaceae	Comptonia sp.	p	p
		Myrica carolinensis Mill.	p	p
		Myrica lignitum (Ung.) Sap.	m	
		Myrica palaeogale Pilar.		m
		Myrica salicina Ung.		m
		Myrica sp.	p	p
	Juglandaceae	Alfaroa sp.	p	p
		Carya aquatica (Michx.) Nutt.	p	p
		Carya bilinica Ung.	m	
		Carya cordiformis (Wangh.) C.Koch	p	p
		Carya denticulata (Web.) Iljinsk.	m	
		Carya minor Sap.et Mar.	m	
		Carya mirabilis Kol.	m	
		Carya ovata (Mill.) C. Koch	p	p
		Carya serraefolia (Goepp.) Krausel	m	m
		Carya aff. glabra (Mill.) Sweet.		p
		Carya aff. pecan (Marh.) Engl.		p
		Carya sp.	p	p
		Cyclocarya aff. paliurus (Batalin) Iljinsk.		p
		Engelhardia sp.	p	p
		Platycarya sp.	p	p
		Pterocarya pterocarpa (Michx.) Kunth.	p	mp
		Pterocarya rhoifolia Sieb. et Zucc.	p	p
		Pterocarya stenoptera DC	p	p
		Juglans cinerea L.	p	mp
		Juglans colchica Kol.	m	
		Juglans regia L.	p	p
		Juglans zaisanica Iljinsk.	m	m
	Salicaceae	Populus balsamoides Goepp.	m	m
		Populus leucophylla Ung.		m
		Populus populina (Brongn.) Knob.	m	m
		Salix cinerea L.		m
		Salix integra Goepp.	m	m
		Salix varians Goepp.	m	m
		Salix sp.	p	p
	Betulaceae	Alnus angustifolia Kol.		m
		Alnus hoernesi Stur		m
		Alnus cordata Desf.	m	
		Alnus subcordata C.A.May	m	m
		Alnus ducalis (Gaudin) Knob.		m
		Alnus aff. barbata C.A.May		m
		Alnus sp.	p	mp
		Betula pubescens Ehrh.	p	p

1	2	3	4	5
Dicotyledoneae	Betulaceae	Betula subpubescens Goepp.	m	
		Betula sp.	p	mp
		Carpinus betulus L.	p	p
		Carpinus caucasica Grossh.	p	p
		Carpinus cuspidens (Sap.)Kol. var. breviserrata Kol.	m	
		Carpinus grandis Ung.	m	m
		Carpinus duabensis Dorof.		m
		Carpinus orientalis Mill.	p	p
		Carpinus pliofauriei Rat.	m	
		Carpinus uniserrata (Kol.) Rat. et Kol.	m	m
		Carpinus sp.	p	p
		Corylus avellana L.	mp	p
		Corylus protocolchica Kol.	m	
		Corylus sp.	p	p
		Ostrya angustifolia Andrean.	m	m
		Ostrya sp.	p	p
	Fagaceae	Castanea atavia Ung.	m	m
		Castanea pliosativa Kol.	m	
		Castanea sativa Mill.	p	p
		Castanopsis bifurcata Kol.	m	
		Castanopsis elisabethae Kol.	m	m
		Castanopsis decheni (O.Web.) Kr. et Wld.		m
		Castanopsis furcinervis (Rossm.) Kr. et Wld.	m	m
		Castanopsis sp.	p	p
		Cyclobalanopsis kryshtofovichii Kol.	m	
		Lithocarpus palaeouncinata (Kol.) Kol.	m	
		Lithocarpus sp.	p	
		Fagus attenuata Goepp.	m	m
		Fagus orientalis Lipsky	p	mp
		Fagus orientalis Lipsky var. palibini Iljinsk.	m	m
		Quercus castaneifolia C.A.M.	m	
		Quercus cerrisicarpa Kol.	m	
		Quercus iberica Stev.	m	
		Quercus kodorica Kol.	m	m
		Quercus kubinyi (Kol.) Cz.	m	
		Quercus microcerrisicarpa Kol.	m	
		Quercus neriifolia A.Br.	m	m
		Quercus pliovariabilis Kol.	m	
		Quercus pseudocastanea Goepp.	m	m
		Quercus sosnowskyi Kol.	m	m

1	2	3	4	5
Dicotyledoneae	Fagaceae	Quercus sp.	p	p
	Ulmaceae	Celtis magnifica Kol.	m	
		Celtis japetii Ung.	m	
		Celtis sp.	p	p
		Ulmus carpinoides Goepp.	m	m
		Ulmus foliacea Gilib.	p	p
		Ulmus laevis Pall.		p
		Ulmus longifolia Ung.	m	m
		Ulmus paralaciniata Hu et Chaney		m
		Ulmus sp.	p	p
		Zelkova carpinifolia (Pall.) Dipp.	p	p
		Zelkova ungeri Kov.	m	
		Zelkova zelkovifolia (Ung.) Buzek et Kotlaba		m
		Zelkova sp.	p	p
	Eucommiaceae	Eucommia ulmoides Oliv.	mp	p
	Moraceae	Artocarpus kimmerica Kol.	m	
		Ficus kolakovskyi Dorof. et Negru		m
		Ficus sp.	p	p
		Morus alba L.	p	p
		Moraceae gen.indet.	p	p
	Cannabaceae	Cannabis sp.		p
		Humulus lupulus L.	p	
	Polygonaceae	Polygonum lapathifolium L.		m
		Polygonum sp.	p	p
	Caryophyllaceae	Stellaria sp.	p	
		Caryophyllaceae gen.indet.	p	p
	Chenopodiaceae	Chenopodiaceae gen.indet.	p	p
	Magnoliaceae	Liriodendron tulipifera L.	p	p
		Magnolia denudata Desr.	p	p
		Magnolia georgica Kol.	m	m
		Magnolia grandiflora L.	p	p
		Magnolia kobus DC		m
		Magnolia mirabilis Kol.	m	
		Magnolia vittae Kol.	m	
		Magnolia cf.accuminata L.	p	
		Magnolia sp.	p	mp
	Schizandraceae	Kadsura palaeojaponica Kol.	m	
		Schizandra grossheimii Kol.	m	m
	Lauraceae	Aniba longifolia Kol. et Schak.		m
		Cinnamomophyllum cinnamomeum (Rossm.) Kol.	m	m
		Cinnamomophyllum lanceolatum (Ung.) Kol.	m	m
		Cinnamomophyllum radobojanum (Ung.)Kol.	m	

1	2	3	4	5
Dicotyledoneae	Lauraceae	Cinnamomophyllum cf.Cinnamomum loureieii Nees	m	
		Cinnamomum japonicum Kol.et Schak.	m	
		Cinnamomum sp.	p	p
		Daphnogene buchii (Heer) Kol. et Schak.	m	m
		Daphnogene marginatum (Kol. et Schak.) Kol. et Schak.	m	m
		Daphnogene polymorpha (A.Br.) Etting.		m
		Daphnogene sp.		m
		Laurophyllum abchasicum Kol. et Schak.		m
		Laurophyllum duabense Kol. et Schak.		m
		Laurophyllum nobile Kol.et Schak.	m	
		Laurophyllum ocoteafolium (Ett.) Kol.	m	
		Laurophyllum pithyusum Kol.et Schak.	m	
		Laurophyllum ponticum Kol.et Schak.	m	
		Laurophyllum simile Kol. et Schak.		m
		Laurophyllum primigenia (Ung.) Kol.	m	m
		Laurophyllum sp.	m	
		Laurus pliocenica (Sap.et Mar.) Kol.	m	
		Laurus sp.	p	p
		Lindera antiqua (Heer) Lamotte	m	
		Lindera ovata Kol.	m	
		Litsea magnifica Sap.	m	m
		Litsea pontica Kol.	m	
		Nectandra euxina Kol.	m	
		Nectandra sp.	m	
		Oreodaphne heeri Gaud.	m	
		Oreodaphne rhombifolia Kol.	m	
		Persea braunii Heer		m
		Persea colchica Kol.	m	
		Persea pliocenica (Laur.) Kol.	m	
		Persea styracifolia (Weber) Kol.		m
		Persea sp. aff. P. superta Sap.		m
		Persea sp.	p	p
	Saxifragaceae	Saxifragaceae gen.indet.	p	p
	Ranunculaceae	Ranunculus reidii Szafer		m
		Ranunculus sp.	p	mp
	Berberidaceae	Mahonia heterophylla Kol.	m	
		Mahonia spinulosa Kol.	m	

1	2	3	4	5
Dicotyledoneae	Menispermaceae	Menispermum sp.	p	p
		Sinomenium cantalense (E.M. Reid) Dorof.		m
	Nymphaeaceae	Nelumbo sp.	p	p
		Nuphar luteum (L.) Smith	p	p
		Nymphaea sp.	p	p
	Ceratophyllaceae	Ceratophyllum cf.demersum L.	m	
	Aristolochiaceae	Aristolochia africanii Kol.	m	
		Aristolochia colchica Kol.	m	
		Aristolochia sp.	m	
	Actinidiaceae	Actinidia arguta (S. et Z.) Planch.		m
		Actinidia faveolata C. et E.M. Reid		m
	Theaceae	Camellia abchasica (Kol.) Kol.	m	
		Eurya cf. japonica Thunb.		m
		Schima wallichii (DC) Choisy		m
		Ternstroemia mocanerifolia Kol.	m	
	Hypericaceae	Hypericum sp.		m
	Platanaceae	Platanus aceroides Goepp.	m	
		Platanus linearifoba Kol.	m	
		Platanus orientalis L.		p
		Platanus platanifolia (Ett.) Knob.		m
	Hamamelidaceae	Corylopsis aff.cordata Merrill et Li	p	p
		Fortunearia colchica Kol.	m	
		Fothergilla aff.gardenii Murr.	p	p
		Hamamelis cachetica Kol.		m
		Hamamelis miomollis Hu et Chaney		m
		Parrotia pristina (Ett.) Stur	m	
		Sycopsis colchica Ram.	p	p
		Altingia aff.excelsa Nor.	p	p
		Liquidambar europaea A.Br.	m	m
		Liquidambar formosana Hance	p	p
		Liquidambar orientalis Mill.	p	mp
		Liquidambar styraciflua L.	p	p
		Liquidambar aff.turgaica Kupr.	p	
	Cercidiphyllaceae	Cercidiphyllum sp.	p	
	Rosaceae	Cerasus sp.	m	
		Cotoneaster palaeobacillaris Kol.	m	
		Crataegus sp.		m
		Laurocerasus pliocenicum Kol.	m	
		Photinia kodorica Kol.	m	
		Photinia cf.integrifolia Lindl.	m	
		Rosa sp.		p
		Rubus kodorica Kol.	m	
		Rubus meriani (Heer) Kol.	m	

1	2	3	4	5
Dicotyledoneae	Rosaceae	Rubus sp.		m
		Spiraea salicifolia L.	m	
		Rosaceae gen. indet.	p	p
	Caesalpiniaceae	Caesalpinia macrophylloides Kol.	m	
		Cassiophyllum berenices (Ung.) Kr.		m
		Ceratonia emarginata A.Br.	m	
	Fabaceae	Acacia sp.		p
		Dalbergia bella Heer	m	
		Dalbergia derrisaecarpa Kol.	m	
		Dalbergia rectinervis Ett.	m	
		Desmodium maximum (Ung.) Kol.	m	
		Gleditchia allemanica Heer	m	
		Gymnocladus meoreatharica Kol.	m	
		Pithecolobiophyllum abchasica Kol.	m	
		Sophora europaea Ung.	m	
		Sophora miojaponica Hu et Chang	m	
	Geraniaceae	Geranium sp.	p	p
	Euphorbiaceae	Croton ratianii Kol.	m	
	Rutaceae	Phellodendron amurense Rupr.		mp
		Phellodendron sp.	p	
	Simaroubaceae	Ailanthus sp.		m
	Meliaceae	Cedrela sarmatica Kov.	m	m
		Melia sp.		p
	Anacardiaceae	Cotinus coggygria (L.) Scop.	m	
		Pistacia miochinensis Hu et Chang	m	
		Pistacia terebinthus L.	m	
		Pistacia sp.		p
		Rhus cf.rhomboidalis Sap.	m	
		Rhus sp. cf.R.chinensis Mill.	m	
		Rhus sp.	p	p
		Toxicodendron quercifolia (Michx.) Greene		m
	Aceraceae	Acer integerrimum (Viv.) Mass.		m
		Acer laetum CAM pliocenicum Sap.et Mar.	m	
		Acer pseudomonospessulanum Ung.		m
		Acer trilobatum (Sterb.) A.Br.		m
		Acer sp.	mp	mp
	Sapindaceae	Sapindus falcifolium (A.Br.) Heer	m	
	Sabiaceae	Meliosma caucasica Dorof.		m
		Meliosma kimmerica Kol.		m
	Aquifoliaceae	Ilex cassineformis Kol.	m	
		Ilex colchica Pojark.	p	
		Ilex falsani Sap.et Mar.	m	

1	2	3	4	5
Dicotyledoneae	Aquifoliaceae	Ilex georgica Kol.	m	
		Ilex gracilis Kol.	m	
		Ilex horrida Sap.	m	
		Ilex microcassine Kol.	m	
		Ilex palaeotriflora Kol.	m	
		Ilex (?) parschlugiana Ung.	m	
		Ilex raridentata Kol.	m	
		Ilex simile Kol.	m	
		Ilex cf.diplosperma Hu Shiu Ying	m	
		Ilex sp.	p	p
	Celastraceae	Celastrus curvinervia (Kol.) Kol.	m	
		Euonymus sp.	p	p
	Staphyleaceae	Staphylea colchica Stev.	mp	p
		Staphylea protocolchica Kol.	m	
	Buxaceae	Buxus sempervirens L. foss. Englh. et Kinkelin		m
		Buxus sp.	p	
	Rhamnaceae	Berchemia multinervis (A.Br.) Heer	m	
		Ceanothus abchasica Kol.	m	
		Ceanothus ebuloides O.Weber	m	m
		Ceanothus tiliaefolium Ung.	m	
		Ceanothus sp.		m
		Frangula rectinervis (Heer) Kol.	m	
		Hovenia dulcis Thunb.	m	
		Rhamnus sp.	p	p
	Vitaceae	Ampelopsis abchasica Kol.	m	
		Ampelopsis europaea Dorof.		m
		Ampelopsis ludwigii (A.Br.) Dorof.		m
		Cissus sp. cf. C. adnata Plench.		m
		Parthenocissus quinquefolia (L.) Planch.	p	p
		Vitis subintegra Sap.	m	
		Vitis sp.	p	p
	Leeaceae	Leea vladimerii (Kol.) Kol.	m	
	Elaeocarpaceae	Elaeocarpus palaeolanceolata Kol.	m	
		Elaeocarpus palaeolittoralis Kol.	m	
	Tiliaceae	Tilia caucasica Rupr.	p	p
		Tilia cordata Mill.	p	p
		Tilia platyphyllos Scop.	p	p
		Tilia aff. taqueti C. Schneid.	p	p
		Tilia tomentosa Moench.	p	
		Tilia sp.	p	p
	Malvaceae	Malva sp.	p	
	Sterculiaceae	Sterculia ramesiana Sap.		m
		Sterculia rarinervis Kol.	m	
		Sterculia sp.	p	p
	Thymellaceae	Daphne kimmerica Kol.	m	

1	2	3	4	5
Dicotyledoneae	Thymellaceae	Daphne odora Thunb.	m	
		Daphne cf. pontica L.		m
	Elaeagnaceae	Elaeagnus sp.	p	
	Violaceae	Viola sp.	m	
	Cucurbitaceae	Trichosanthes fragilis Reid.		m
		Trichosanthes kodorica Kol.		m
	Trapaceae	Trapa sp.		m
	Haloragaceae	Myriophyllum sp.	m	
	Myrtaceae	Myrtus rectinervis Sap.	m	
		Myrtaceae gen.indet.	p	p
	Onagraceae	Chamaenerium sp.		p
		Epilobium sp.	p	
		Ludwigia sp.		p
		Onagra sp.	p	p
	Alangiaceae	Alangium aff. kurzii Craib.	p	p
	Nyssaceae	Nyssa dissemonata (Ludw.) Kirchh.		m
		Nyssa europaea Ung.	m	
		Nyssa sylvatica L.	p	p
		Nyssa sp.	p	p
	Cornaceae	Bothrocaryum controversum (Hemsl.) Pojark.		m
		Cornus sp.	p	p
		Thelycrania sanguinea (L.) Fourr.	m	m
		Thelycrania lusatica Kirchh		m
	Araliaceae	Acanthopanax mirabilis (Kol.) comb. nov.		m
		Acanthopanax kimmericus Kol.		m
		Acanthopanax sp.	p	p
		Aralia cf. hispida Michx.		mp
		Aralia cf. continentalis Katagawa		m
		Aralia cf. cordata Thunb.		m
		Aralia cf. hypoleuca Presl.		m
		Aralia (Brassaiopsis) abchasica Kol.	m	
		Aralia (Brassaiopsis) angustiloba Kol.	m	
		Aralia sp.	p	p
		Boerlagiodendron grandidentatum Kol.	m	
		Brassaiopsis mirabilis Kol.	m	
		Brassaiopsis sp. cf. B. glomeratula (Bl.) Regel.		m
		Brassaiopsis sp.	p	p
		Dendropanax sp.	p	p
		Hedera multinervis Kol.		m
		Hedera sp.	p	p
		Fatsia sp.	p	p
		Pentapanax fibriatum Kol.	m	

1	2	3	4	5
Dicotyledoneae	Araliaceae	Pentapanax simile Kol.		m
		Schefflera colchica Kol.	m	
		Schefflera integrifolia Kol.	m	
		Schefflera pontica Kol.	m	
		Araliaceae gen.indet.		p
	Apiaceae	Caucalis sp.	p	p
		Heracleocarpum protoponticum Kol.		m
		Turgenia latifolia Hostm.	p	p
		Apiaceae gen. indet.	p	p
	Ericaceae	Arbutus elegans Kol.	m	
		Rhododendron sp.	p	p
		Vaccinium minimum Kol.	m	
		Vaccinium protoarctostaphyllos Kol.	m	
		Vaccinium raridentatum Sap.		m
		Ericaceae gen. indet.	p	p
	Myrsinaceae	Myrsine colchica Kol.	m	
		Rapanea kubanensis Pashkov		m
	Sapotaceae	Bumelia minor Ung.	m	
		Sapotaceae gen.indet.	p	p
	Ebenaceae	Diospyros anceps Heer.	m	
		Diospyros brachysepala A.Br.	m	
	Styracaceae	Halesia crassa (C. et E.M.Reid) Kirchh.		m
		Halesia aff. diptera Ellis		m
		Halesia kodorica Kol.	m	
		Styrax raridentata Kol.		m
		Styrax aff. japonica S. et L.		m
	Symplocaceae	Symplocos abchasica Kol.		m
		Symplocos antiqua Kol.		m
		Symplocos kimmerica Kol.	m	
		Symplocos lidiae Kol.	m	
		Symplocos paniculata Wall.	p	p
		Symplocos tinctoria (L.) L. Her	p	p
		Symplocos sp.	p	p
	Periplocaceae	Periploca graeca L.	m	
	Apocynaceae	Apocynophyllum apocynophyllum (Web.)Wld.	m	
		Apocynophyllum decheni (Web.) Wld.	m	
		Apocynophyllum kimmericum Kol.		m
		Apocynophyllum linearifolium Kol.	m	
		Apocynophyllum sp.	m	
	Oleaceae	Forsythia cf.viridissima Lindl.	m	

1	2	3	4	5
Dicotyledoneae	Oleaceae	Fraxinus sp.	p	p
		Ligustrum vulgare L.	mp	
		Phillyrea media L.	m	
	Convolvulaceae	Convolvulus sp.	p	
	Callitrichaceae	Callitriche sp. cf.C.verna L.	m	
	Caprifoliaceae	Lonicera sp.	m	p
		Viburnum lantana L.		m
		Viburnum pliocenicum (Sap. et Mar.) Kol.	m	m
		Viburnum tenuilobatum (Sap.) Kol.		m
		Viburnum sp.	p	p
		Sambucus ebulus L.		m
		Sambucus sp.		m
	Lamiaceae	Ajuga antiqua C.et E.M.Reid		m
		Lycopus sp.		p
		Lamiaceae gen. indet.		p
	Solanaceae	Solanum sp.		m
	Dipsacaceae	Cephalaria sp.	p	p
		Dipsacus sp.		p
		Knautia sp.	p	p
		Scabiosa sp.	p	p
	Plantaginaceae	Plantago sp.	p	p
	Campanulaceae	Campanulaceae gen.indet.	p	
	Asteraceae	Artemisia sp.	p	p
		Asteraceae gen.indet.	p	p
Monocotyledoneae	Potamogeton-aceae	Potamogeton crispus L.	m	
		Potamogeton pectinatus L.		m
		Potamogeton sp.		m
		Ruppia maritima L.		m
	Liliaceae	Smilax aspera L.	m	
		Smilax minima Kol.	m	
	Poaceae	Phragmites oeningensis Heer	m	
		Sasa kodorica Kol.	m	
		Poaceae gen. indet.	p	p
	Arecaceae	Chamaerops humilis L.	m	
		Nipa sp.	p	
		Arecaceae gen.indet.	p	p
	Sparganiaceae	Sparganium nanum Dorof.		m
		Sparganium sp.	p	p
	Typhaceae	Typha latifolia L.	p	p
		Typha latissima A.Br.		m
	Cyperaceae	Cladium mariscus (L.) R.Br.	m	m
		Cyperaceae gen. indet.		p

The Kuyalnician (Egrissian)

Kuyalnician deposits in Western Georgia are considerably thicker than their counterparts in the type locality near Odessa, Ukraine. On the basis of this, the Kuyalnician of Western Georgia was distinguished by Taktakishvili (1978; 1978a) as a separate stratigraphical unit named the “Egrissian stage” and divided into three horizons: the Scurdumian, Etserian and Tsikhisperdian (Table XII). Most of what we know of the Egrissian flora is based on pollen data (Shatilova, 1967, 1984; Shatilova et al., 1998; 2005).

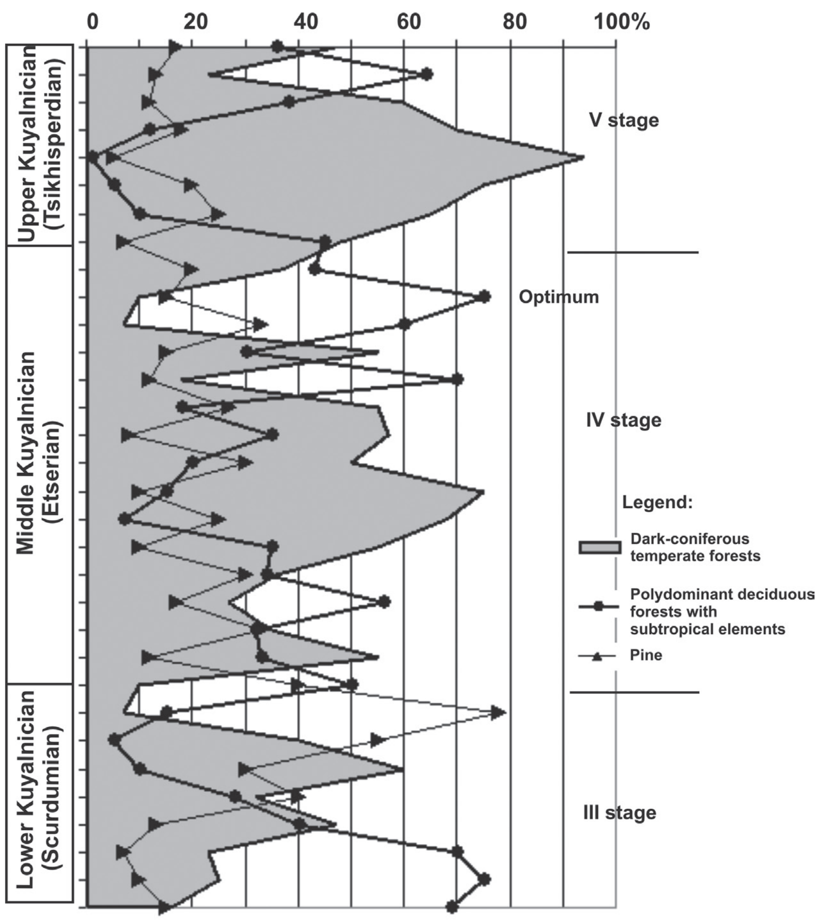

Fig. 17. Percentage fluctuations in palynological groups in Western Georgia during the Kuyalnician, reflecting changes in the distribution of the main forest formations.

The reconstruction of Kuyalnician palynological assemblages through the landscape-phytocenological method shows how the vegetation and climate developed during the Egrissian. The flora of the beginning of the Scurdumian retained some features of the Upper Kimmerian flora, following a wave of dry climate when the bulk of subtropical elements died out. The next dry period took place in the upper part of the Scurdumian, leading to the disappearance of evergreen forest communities altogether. Pine pollen was dominant in the Kamyshburunian (following the Duabian optimum) and in the upper part of Scurdumian (Fig.14, 16, 17). This indicates that humidity was lower than in previous and subsequent stretches of the Pliocene. Several authors (Milanovsky, 1968; Tsagareli & Astakhov, 1971) have suggested that the peneplanation of the Greater and Lesser Caucasus took place around this time. These events could have modified regional climatic patterns such that the unique bioclimatic characteristics of Colchis were lost, resulting in a mass extinction of drought- and cold-sensitive subtropical plants. Polydominant forests through the remainder of the Upper Pliocene were composed of deciduous trees, although subtropical relicts of the ancient floras continued to be constituents of this flora. According to palynological data the boundary between the Kimmerian and Egrissian sits above the Skurdumian, since the upper Kamyshburunian and lower Egrissian reflect a common stage (III) in the development of Western Georgian flora. Such a position for the Kimmerian-Kuyalnician boundary was proposed by Davitashvili (1933).

Climatic conditions again changed in the Middle Egrissian (Etserian time). Humidity increased and the temperature regime became more unstable (stage IV). This was reflected in successive changes from periods dominated by dark-conifer forest to periods dominated by polydominant communities. This phenomenon became especially apparent in the middle Etserian when the distribution area of dark conifers exceeded that of previous stretches of the Pliocene. The main components of these dark-conifer forests were Picea, Abies and Tsuga. There were many reasons for this change, but two of them stand out. The first relates to orogenic movements taking place at the end of the Neogene (Antonov et al., 1977; Kogoshvili, 1977; Milanovsky, 1977; Tsagareli, 1980). Uplift favored the wide distribution of dark conifers, which today develop most fully in a temperate and humid zone from 1400 to 1900 m in elevation. The second reason was a widespread fall in temperatures and increasing humidity, allowing dark-conifer forest to expand in the middle and even lower mountain belts. Abies and Picea have considerable ecological plasticity and it is possible that, in the past, their populations could easily have migrated up and down (Dolukhanov, 1989).

By the upper Etserian the temperature had risen and conditions became favourable for wide distribution of warm-temperate forests. Polydominant communities occupied the whole middle and lower mountain belts during what was probably a climatic optimum. These communities contained Taxodiaceae, Fagus, Quercus, Zelkova, Carya and Carpinus. The role of Cedrus, so characteristic of Kimmerian and Pontian vegetation, decreased and cedar occurred only in admixture among coniferous and broad-leaved forests. The role of other thermophilous conifers - Podocarpus, Dacrydium and Keteleeria - was also minor. Riparian and swamp forests included Carya, Taxodium, Pterocarya, Ulmus and Alnus, while Nyssa and Liquidambar were very infrequent.

The vegetation of Upper Egrissian (Tsikhisperdian) time was quite different as the area of broadleafed plants shrank and dark-conifer forests rose to prominence, continuing to dominate until the Early Gurian (stage V).

Hence we can conclude that the vegetation of the Egrissian differed significantly from that of previous Pliocene epochs, both in the absence of evergreen communities and in the frequency and amplitude of climatic fluctuations. During the Middle Kuyalnician, climate change related to both increasing humidity and lowering temperatures. The first evidence for this comes from the beginning of Etserian time (stage IV), but it was not so strong and long as the second wave of cold, humid climate that embraced the whole Upper Kuyalnician and lower Early Gurian. For this reason we join these two stretches of time into one stage (V) and relate it tentatively to the Danube glaciations in Europe during the Upper Pliocene (Venzo, 1964).

THE EOPLEISTOCENE

The Gurian

Outcrops of the Gurian horizon are known only from the region of the same name in SW Georgia (Fig.13). The so-called Gurian beds encompass two suites, the Khvarbetian and Naderbazetian (Ilijn, 1930). The stratigraphical scheme of the Gurian was often changed by later authors (Kitovani, 1976; Kitovani et al., 1991). Taktakishvili (1984) found it expedient to retain the original two-part division (Table XII).

The Khvarbetian suite (or Pirgulian-Micromelanian beds) are usually conformably bedded on the Tsikhisperdian horizon (Upper Egrissian) and are represented by a thick clayey-sandstone series with Pyrgula and Micromelania. The Khvarbetian suite is distributed only in southern Guria and is conformably overlapped by the Naderbazetian, known throughout Guria.

Knowledge about the Gurian flora is based on palynological data (Shatilova, 1967, 1974; 1984; Shatilova et al., 2002a). In terms of composition, it is the same as the Egrissian flora (Table XIV); the main difference was in the character of vegetation, specifically the increasing representation of mesophytes.

In the first half of the Early Gurian, dark-conifers had a wide distribution and occupied the upper and probably middle mountain belts. The area of warm-temperate forest was reduced. Spore-pollen assemblages from the beginning of the Gurian reflect the same stage (V) of development of vegetation as Upper Kuyalnician assemblages, which were probably related to the Danube glaciation (Fig. 14, 18, 19).

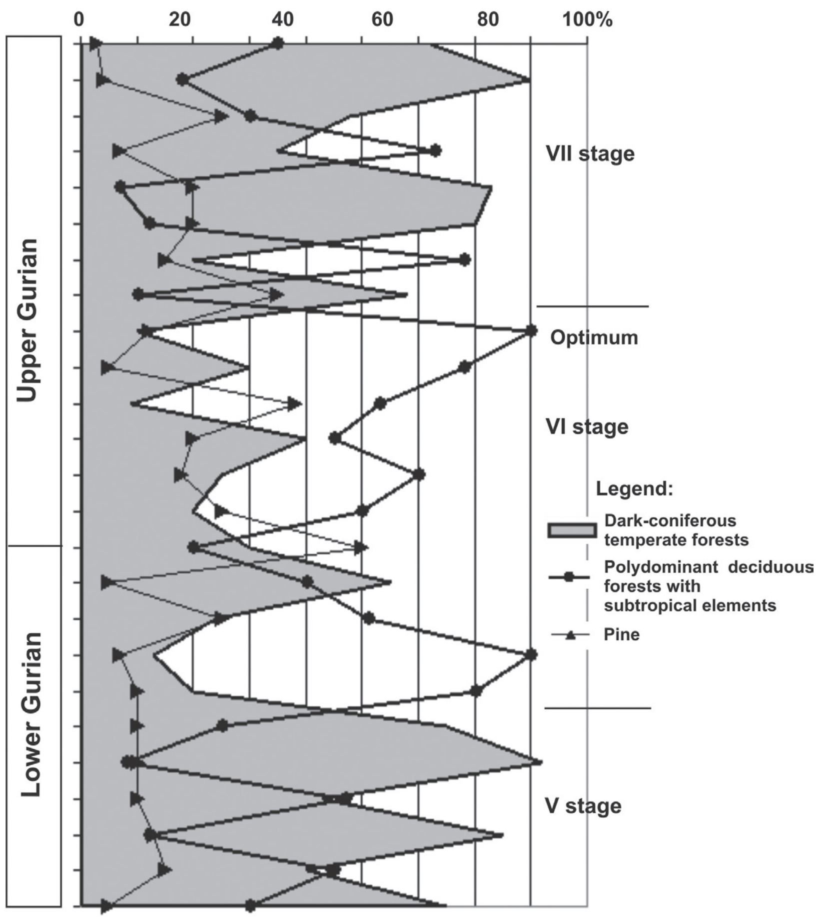

Fig. 18. Percentage fluctuations of palynological groups in Western Georgia during the Gurian, reflecting changes in the distribution of the main forest formations.

The second half of the Early Gurian and beginning of Late Gurian (stage VI) were characterized by repeated shifts in two main formations – warm-temperate polydominant communities and dark-coniferous temperate forests. Conditions were more stable during the first half of the Late Gurian, which was characterized by polydominant forests, including Fagus, Quercus, Carya, Juglans, subtropical plants such as Liquidambar, Aralia, Engelhardia, Platycarya, Eucommia, Magnolia, Alangium, Symplocos and Fortunearia, conifers including Tsuga, Abies, Picea, Sciadopitys, Taxodiaceae, Cupressaceae, Podocarpus, Dacrydium and Phyllocladus. This period can be considered a climatic optimum.

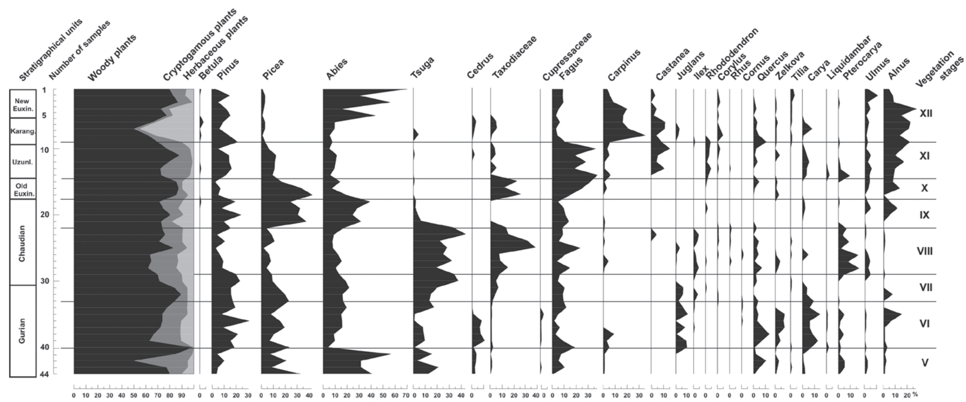

Fig.19. Composite palynological diagram of Eopleistocene and Pleistocene marine deposits from Western Georgia

In general, the climate of stage VI, from the upper Early Gurian to the beginning of the Late Gurian, was warm-temperate and humid, suggesting that it was synchronous with the Danube-Günz interglacial.

This picture changed at the end of the Late Gurian (stage VII), when the area of dark-coniferous forest increased. Among broadleafed trees, a dominant position was occupied by Fagus and Juglans. The expansion of temperate plants indicated cooling climatic conditions, probably connected with the Günz glaciation.

Climatic fluctuations at the end of Gurian were probably responsible for major changes in floral composition. Amongst the ferns, conifers and angiosperms, many Pliocene relicts disappeared. During the Late Gurian, radical changes also occurred in vegetation structure and zonal communities took on an appearance resembling their modern equivalents. Polydominant warm-temperate deciduous forests of rich floristic composition were distributed across the lower mountain belts and the plains. The middle mountain belt was occupied by beech, which began to form separate communities from the end of the Gurian. Abies, Picea and Tsuga formed forest communities in the upper mountain belts.

A list of the Kuyalnician (Egrissian) and Gurian floras is given in Table XIV.

Table XIV. Plants from Kuyalnician (Egrissian) and Gurian deposits in Georgia
Key: m – macrofossils; p – pollen

Class	Family	Species	Kuyalnician	Gurian
1	2	3	4	5
Bryopsida	Sphagnaceae	Sphagnum aff.cuspidatum Ehrh. et Hoffm.		p
		Sphagnum sp.		p
Lycopodiopsida	Lycopodiaceae	Lycopodium alpinum L.	p	p
		Lycopodium annotinum L.	p	p
		Lycopodium clavatum L.	p	p
		Lycopodium selago L.	p	p
		Lycopodium serratum Tunb.	p	p
Isoëtopsida	Selaginellaceae	Selaginella fusca N.Mtchedl.	p	p
		Selaginella sanguinolenta (L.) Spring.	p	
		Selaginella selaginoides (L.) Link.	p	p
		Selaginella aff.sibirica (Milde) Hieron		p
Ophioglossopsida	Ophioglossaceae	Botrychium sp.	p	p
		Ophioglossum sp	p	p
Polypodiopsida	Osmundaceae	Osmunda cinnamomea L.	p	p
		Osmunda aff.claytoniana L	p	p
		Osmunda regalis L.	p	p
	Pteridaceae	Cryptogramma arctostichoides R.Br.	p	p
		Cryptogramma crispa (L.) R.Br.	p	p
		Cryptogramma sp.	p	p
		Pteridacidites boerzoenyensis (Nagy) St., Sh. (Pteris aff.quadriaurita Retz.)	p	p
		Pteridacidites dentatiformis Sh., St. (Pteris dentata Forsk)	p	
		Pteridacidites grandifoliiformis St., Sh. (Pteris grandifolia L.)	p	
		Pteridacidites guriensis Sh., St. (Pteris aff.togoensis Hieron)	p	p
		Pteridacidites kimmeriensis Sh.,St. (Pteris sp.)	p	
		Pteridacidites longifoliiformis Sh., St. (Pteris longifolia L.)	p	

1	2	3	4	5
Polypodiopsida	Pteridaceae	Pteridacidites rarotuberculatum Sh., St. (Pteris sp.)	p	
		Pteridacidites remotifolioides Sh., St. (Pteris sp.)	p	p
		Pteridacidites spiniverrucatum St., Sh. (Pteris pellucida Pr.)	p	
		Pteridacidites variabilis St., Sh. (Pteris cretica L.)	p	p
		Pteridacidites venustaeformis St., Sh. (Pteris venusta Kze.)	p	p
		Pteridacidites verus (N.Mtchedl.) Sh., St. (Pteris aff.crenata Sw.)	p	p
		Pteridacidites vittatoides Sh., St. (Pteris vittata L.)	p	p
	Adiantaceae	Anogramma sp.	p	p
		Pityrogramma sp.	p	
	Polypodiaceae	Polypodium aureum L.	p	p
		Polypodium australe Fee.	p	p
		Polypodium pliocenicum Ram.	p	p
		Polypodium verrucatum Ram.	p	p
		Polypodium vulgare L.	p	p
		Polypodium sp.	p	p
		Verrucatosporites histiopteroides W.Kr.	p	p
	Hymenophyllaceae	Hymenophyllum sp.		p
	Dicksoniaceae	Dicksonia antarctica R.Br.	p	
		Dicksonia reticulata Purc.	p	p
		Dicksonia unitotuberata Purc.	p	p
		Dicksonia aff. fibrosa Kol.	p	
		Dicksonia sp.	p	p
	Cyatheaceae	Cyathea sp.	p	p
	Thelypteraceae	Thelypteris sp.	p	p
	Aspleniaceae	Asplenium sp.	p	p
	Aspidiaceae	Athyrium sp.	p	p
		Cystopteris sp.	p	p
		Dryopteris sp.	p	p
		Gymnocarpium sp.	p	p
		Polystichum sp.		p
		Woodsia alpina (Bolton) S.F.Gray	p	p
		Woodsia aff.polystichoides Eaton.	p	

1	2	3	4	5
Pinopsida	Podocarpaceae	Dacrydium sp.	p	p
		Podocarpus sp.	p	p
	Phyllocladaceae	Phyllocladus sp.	p	p
Polypodiopsida	Pinaceae	Abies alba Mill.	p	p
		Abies aff.cephalonica Loud.	p	p
		Abies ciliticaeformis N.Mtchedl.	p	p
		Abies nordmanniana (Stev.) Spach.	p	p
		Cedrus deodara Loud.	p	p
		Cedrus aff.libani Laws.	p	
		Cedrus sauerae N.Mtchedl.	p	p
		Keteleeria caucasica Ram.	p	p
		Picea complanataeformis N.Mtchedl.	p	p
		Picea minor N.Mtchedl.	p	p
		Picea orientalis L.	p	p
		Picea aff.schrenkiana F.et M.	p	p
		Pinus sp.	p	p
		Pseudotsuga sp.	p	p
		Tsuga aculeata Anan.	p	p
		Tsuga canadensis (L.) Carr.	p	p
		Tsuga diversifolia (Maxim.) Mast.	p	p
		Tsuga inordinata Mched.	p	p
		Tsuga korenevae Mched.	p	p
		Tsuga meierii Mched.	p	p
		Tsuga patens Downie	p	p
		Tsuga pattoniana Engelm.	p	p
		Tsuga shatilovae Mched.	p	p
		Tsuga sivakii Mched.	p	p
		Tsuga tortuosa Mched.	p	p
		Tsuga aff. blaringhemi Flous	p	p
		Tsuga aff.yunnanensis Mast.	p	p
	Sciadopityaceae	Sciadopitys verticillatiformis Scht. et Ram.	p	p
	Taxodiaceae	Cryptomeria japonica Don	p	p
		Cunninghamia sp.		p
		Glyptostrobus sp.		p
		Metasequoia sp.	p	p
		Sequoia sp.	p	p
		Taxodium sp.	p	p
		Taxodiaceae gen. indet.	p	p
	Cupressaceae	Juniperus sp.		p
		Libocedrus sp.		p
		Cupressaceae gen. indet.	p	p
Gnetopsida	Ephedraceae	Ephedra distachya L.	p	p
		Ephedra sp.	p	p

1	2	3	4	5
Dicotyledoneae	Myricaceae	Comptonia sp.	p	
		Myrica sp.	p	p
	Juglandaceae	Carya aquatica (Michx.) Nutt.	p	p
		Carya cordiformis (Wangh.) C.Koch	p	p
		Carya ovata (Mill.) C.Koch	p	p
		Carya aff. glabra (Mill.) Sweet.	p	p
		Carya aff.texana DC		p
		Carya sp.	p	p
		Cyclocarya aff. paliurus (Batalin) Iljinsk.	p	p
		Engelhardia sp.	p	p
		Juglans cinerea L.	p	p
		Juglans nigra L.	p	p
		Juglans regia L.	p	p
		Juglans aff.rupestris Engelm.		p
		Platycarya sp.	p	p
		Pterocarya pterocarpa (Michx.) Kunth.	p	p
		Pterocarya aff.rhoifolia Sieb. et Zucc.	p	p
		Pterocarya aff.stenoptera DC	p	p
		Pterocarya sp.	p	p
	Salicaceae	Salix sp.	p	p
	Betulaceae	Alnus sp.	p	p
		Betula sp.	p	p
		Carpinus betulus L.	p	p
		Carpinus caucasica Grossh.	p	p
		Carpinus orientalis Mill.	p	p
		Corylis avellana L.	p	p
		Corylus sp.	p	p
	Fagaceae	Castanea sativa Mill.	p	p
		Fagus orientalis Lipsky	p	p
		Quercus sp.	p	p
	Ulmaceae	Celtis sp.	p	p
		Ulmus foliacea Gilib.	p	p
		Ulmus laevis Pall.	p	p
		Ulmus propinqua Koidz.		p
		Ulmus sp.	p	p
		Zelkova carpinifolia (Pall.) Dipp.	p	p
		Zelkova serrata (Thunb.) Macino	p	
		Zelkova sp.	p	p
	Eucommiaceae	Eucommia aff.ulmoides Oliv.		p
	Moraceae	Morus alba L.	p	p
	Polygonaceae	Polygonum persicaria L.	p	p
		Polygonum sp.	p	p
	Caryophyllaceae	Caryophyllaceae gen.indet.	p	p

1	2	3	4	5
Dicotyledoneae	Chenopodiaceae	Chenopodiaceae gen.indet.	p	p
	Magnoliaceae	Liriodendron tulipifera L.	p	p
		Magnolia denudata Desr.	p	p
		Magnolia grandiflora L.	p	p
		Magnolia sp.	p	p
	Annonaceae	Annona sp.	p	p
	Ranunculaceae	Helleborus sp.		p
	Menispermaceae	Menispermum sp.	p	
	Nymphaeaceae	Nymphaeaceae gen.indet.		p
	Platanaceae	Platanus orientalis L.	p	p
	Hamamelidaceae	Altingia aff.excelsa Nor.		p
		Fortunearia aff.sinensis Reid.et Wils.		p
		Liquidambar formosana Hance	p	p
		Liquidambar styraciflua L.	p	p
		Parrotia persica (DC) C.A.M.		p
	Rosaceae	Kerria sp.	p	
		Rosaceae gen. indet.	p	p
	Geraniaceae	Geraniaceae gen.indet.	p	p
	Anacardiaceae	Rhus toxicodendron L.	p	p
		Rhus sp.	p	p
	Aceraceae	Acer aff.platanoides L.	p	p
	Aquifoliaceae	Ilex sp.	p	p
	Celastraceae	Euonymus sp.	p	p
	Staphyleaceae	Staphylea colchica Stev.	p	p
	Vitaceae	Parthenocissus quinquefolia (L.) Planch.		p
		Vitis aff.forestalensis Trav.		p
	Tiliaceae	Tilia caucasica Rupr.	p	p
		Tilia cordata Mill.	p	p
		Tilia ledebourii Borb.		p
		Tilia platyphyllos Scop.	p	p
		Tilia tomentosa Moench.	p	p
		Tilia aff.grandipollinia Trav.	p	p
		Tilia aff. taqueti C. Schneid.	p	p
	Elaeagnaceae	Elaeagnus sp.	p	
	Onagraceae	Epilobium sp.	p	p
	Alangiaceae	Alangium aff. kurzii Craib.	p	p
	Nyssaceae	Nyssa sylvatica L.	p	
		Nyssa aff.ingentipollinia Trav.		p
		Nyssa sp.	p	p
	Cornaceae	Cornus sp.	p	p
	Araliaceae	Aralia aff.hispida Michx.	p	p
		Hedera colchica C.Koch.		p
		Fatsia sp.		p

1	2	3	4	5
Dicotyledoneae	Apiaceae	Turgenia latifolia Hoffm.		p
		Apiaceae gen. indet.	p	p
	Ericaceae	Rhododendron sp.	p	p
	Symplocaceae	Symplocos cf.paniculata Wall.	p	p
		Symplocos cf.tinctoria (L.) L' Her	p	p
		Symplocos sp.	p	p
	Oleaceae	Fraxinus sp.	p	p
		Ligustrum vulgare L.		p
	Convolvulaceae	Convolvulus sp.		p
	Caprifoliaceae	Lonicera sp.	p	p
		Viburnum sp.	p	
	Lamiaceae	Lamiaceae gen. indet.		p
	Plantaginaceae	Plantago sp.	p	p
	Dipsacaceae	Cephalaria sp.	p	p
		Knautia sp.	p	p
		Scabiosa sp.	p	p
	Asteraceae	Artemisia sp.	p	p
		Asteraceae gen.indet.	p	p
Monocotyle-doneae	Liliaceae	Liliaceae gen.indet.		p
	Poaceae	Poaceae gen. indet.	p	p
	Sparganiaceae	Sparganium sp.	p	p
	Typhaceae	Typha latifolia L.	p	p

THE PLIOCENE AND EOPLEISTOCENE (EASTERN GEORGIA)

THE PLIOCENE

The Akchagilian

During the majority of the Pliocene, Eastern Georgia was dry land and thick continental sediments accumulated. These facies have great geographic variability, and therefore the same-aged sediments of different regions are often described using different names. Meotian-Pontian deposits in Kartli are referred to as the Dushetian suite, which changes to the east into the freshwater-continental Shirakian suite. Around the Iori River the Shirakian suite is overlapped by deposits of Akchagilian and Apsheronian stages (Table XII). They are represented by marine facies and the continental Alazanian series, composed primarily of conglomerate (Buleishvili, 1960).

Akchagilian deposits in Eastern Georgia are distributed mainly on the Iori Upland and are represented by shallow-water sediments with fossilized mollusks, plants and terrestrial vertebrates (Fig.13). They are divided into three parts on the basis of faunal stratigraphy. The Lower Akchagilian contains a monotonous fauna, becoming rich and diverse in the Middle Akchagilian and changing to indicate shallowing of the basin during the Upper Akchagilian (Djikia, 1977).

The first data on the Akchagilian flora was provided by Palibin (Palibin & Tsyrina, 1934; Palibin et al., 1934). Later, macroremains of plants from some localities were described by Uznadze (1965), Ratiani (1972a) and Dolidze (1970, 1999).

According to Ratiani, the number of Mediterranean elements increased significantly in the Akchagilian flora. Xerophytisation, which began in the Upper Miocene, intensified in the Pliocene and the vegetation took on characteristic Mediterranean features.

In the work of Dolidze (1999), devoted to the general characteristics of Akchagilian flora, a list of fossil plants is given. In Eastern Georgia these plants are thought to have formed several communities: riparian forests; mesophilous formations on the plains; a subtropical xerophilous formation of steppes and open woodlands; broad-leaved forests of the lower and middle belts; and conifer forests, the composition of which was determined through palynological analysis by Kvavadze (Dolidze, 1999).

Relicts of ancient floras are still to be observed in the Lower Akchagilian, e.g. *Cyclosorus fisherii, Tsuga* sp.*, Alnus ducalis, Cinnamomum cinnamomeum, Liquidambar europea,* Hamamelidaceae gen. indet.*, Ilex horrida, Acer saliens* and *A. decipiens*. In the Upper Akchagilian, however, these relicts are entirely absent.

Akchagilian deposits of the Iori Upland were studied palynologically (Vekua & Kvavadze, 1981; Kvavadze & Vekua, 1993). Samples were collected from Middle Akchagilian deposits linked to the Kvabebi locality of vertebrate fauna.

The pollen data indicate that during the Middle Akchagilian the greater part of the Iori Upland was covered by forest-steppe vegetation like savanna. Herb steppe was distributed mainly on the plains, while forests spread along the rivers and large areas were covered by Alnus and Platanus. Beech, oak and walnut occurred on drier soils. These forests had rich shrub layer of Ilex, Rhododendron, *Carpinus orientalis* and others. The presence of pollen grains of Betula and conifers such as Pinus, Cedrus, Abies, Sequoia and Picea provides some indication of the vegetation of the middle and upper mountain belts.

The climate of the Middle Akchagilian was close to Mediterranean, with a mild, humid winter and hot, dry summer (Vekua & Kvavadze, 1981).

THE EOPLEISTOCENE

The Apsheronian

The distribution of Apsheronian deposits is confined to the east part of Kakheti, where they are conformably bedded on the Akchagilian (Buleishvili, 1960). Plant macroremains were described by Uznadze (1965) and includes a list of 12 elements, amongst which only *Acer pseudomonospessulanum* Ung. is no longer represented in the modern flora of Georgia.

Most of what we know about the Apsheronian flora and vegetation is based on palynological data. Coprolites from the bone-beds of Dmanisi (Fig.13), which contain hominid remains dated 1.8 Ma (in the Black Sea region this corresponds to the lower boundary of the Gurian stage), were studied by Kvavadze (Kvavadze & Vekua, 1993).

Pollen spectra from these hyena coprolites are characterized by a large number of taxa belonging to quite different ecological groups. Herbaceous pollen is predominant (60-52%), while arboreal pollen makes up 32-38% and has no particular dominant taxon. Pinus, Alnus and Fagus are the principal arboreal types, occurring in more-or-less equal abundance. Pollen of Castanea, Tilia and Carpinus is found in relatively high quantities, along with single grains of Ulmus and Salix. Among shrubs, the pollen of Rhododendron, Corylus and Vaccinium is prevalent. The herbaceous group is represented by Chenopodiaceae, Asteraceae, Poaceae, Cyperaceae, Artemisia, Fabaceae, Caryophyllaceae, Polygonaceae, Plumbaginaceae, Ranunculus, Onagraceae and Geraniaceae.

Taxa representing sporiferous plants are unusually abundant and diverse. Monolete spores without perisporium are predominant, but there are also many spores with preserved ectexine, allowing determination to genus level, e.g. Asplenium, Athyrium, Blechnum, Dryopteris and Polystichum. Club mosses were also significant, including *Lycopodium alpinum, L. clavatum, L. selago* and *Lycopodium* sp. Spores of *Botrychium* sp., *Selaginella selaginoides* and *Sphagnum* sp. were also identified.

Ecological analysis of the palynological data indicates the presence of several vegetation formations in different altitudinal zones. The presence of elements such as *Selaginella selaginoides, Lycopodium alpinum* and Botrychium suggests the existence of alpine, and possibly subnival, vegetation belts. Montane forests consisted mainly of Abies, Betula and Pinus with some admixture of Fagus. The middle mountains were covered by broad-leaved forests of Fagus, Carpinus and

Ulmus. In the lower mountain belt, Castanea, Tilia and Quercus were prevalent. All these communities could have occurred along the ridges of the Javakheti Range and on the Dmanisi Plateau, while meadow-steppe vegetation probably grew at lower altitudes on the adjacent plains.

The pollen data permit the conclusion that the climate of the southern part of Eastern Georgia in Apsheronian time was rather mild and warm, with high rainfall in the mountains and very dry conditions in the lowlands (Kvavadze & Vekua, 1993; Kvavadze, 1997).

A list of Akchagilian and Apsheronian floras is given in Table XV.

Table XV. List of plants from the Akchagilian and Apsheronian deposits in Georgia
Key: m – macrofossils; p – pollen

Class	Family	Species	Akchagilian	Apsheronian
1	2	3	4	5
Bryopsida	Sphagnaceae	Sphagnum sp.	m	p
Lycopodiopsida	Lycopodiaceae	Lycopodium alpinum L.		p
		Lycopodium aquifolium Scop.	m	
		Lycopodium clavatum L.		p
		Lycopodium selago L.		p
		Lycopodium serratum Tunb.		p
		Lycopodium sp.		p
		Selaginella fusca N.Mtchedl.		p
		Selaginella selaginoides (L.) Link.		p
		Selaginella aff.sibirica (Milde) Hieron	m	
		Selaginella sp.	m	
Ophioglossopsida	Ophioglossaceae	Bothrychium sp.		p
Polypodiopsida	Pteridaceae	Pteris sp.		p
	Polypodiaceae	Polypodiaceae gen.indet.	mp	p
	Dennstaedtiaceae	Pteridium aquilinum (L.) Kuhn.	m	
		Pteridium sp.	m	p
	Aspleniaceae	Asplenium sp.		p
	Aspidiaceae	Athyrium sp.		p
		Cyclosorus (Lastrea) fischeri (Heer) Kol.	m	
		Dryopteris mediterranea Fomin	m	
		Dryopteris sp.		p
		Polystichum sp.		p
		Woodsia aff.polystichoides Eaton		p
	Blechnaceae	Blechnum spicata With.	m	
		Blechnum sp.		p

1	2	3	4	5
Pinopsida	Pinaceae	Abies sp.	m	p
		Cedrus sp.	mp	p
		Picea orientalis L.	mp	m
		Picea sp.	mp	p
		Pinus eldarica Medw.	m	
		Pinus pithyusa Stev.	m	
		Pinus sp.	mp	p
		Pseudotsuga sp.		p
		Tsuga sp.	mp	
	Taxodiaceae	Sequoia langsdorfii (Brongn.) Heer	m	
	Cupressaceae	Juniperus sp.	mp	p
		Cupressaceae gen. indet.	mp	
Gnetopsida	Ephedraceae	Ephedra sp.	mp	
Dicotyledoneae	Myricaceae	Myricaceae gen.indet.	mp	
	Juglandaceae	Carya sp.	mp	
		Juglans acuminata A.Br.	m	
		Juglans regia L.	m	mp
		Juglans sp.	m	p
		Pterocarya paradisiaca (Ung.) Iljinsk.	m	
		Pterocarya pterocarpa (Michx.) Kunth.	m	m
	Salicaceae	Populus alba L.	m	
		Populus nigra L.	m	
		Populus populina (Brongn.) Knobl.	m	
		Populus tremula L.	m	m
		Salix alba L.	m	
		Salix apoda Trautv.	m	
		Salix caprea L.	m	
		Salix caucasica L.	m	
		Salix cinerea L.		m
		Salix integra Goepp.	m	
		Salix pentandra L.	m	
		Salix purpurea L.	m	
		Salix triandra L.	m	
		Salix varians Goepp.	m	
		Salix sp.	m	p
	Betulaceae	Alnus ducalis (Gaud.) Knobl.	m	
		Alnus glutinosa (L.) Gaerth.	m	
		Alnus hoernesi Stur	m	
		Alnus subcordata C.A.M.		m
		Alnus sp.	p	p
		Betula alba L.	m	
		Betula raddeana Trautv.	m	
		Betula sp.	p	p

1	2	3	4	5
Dicotyledoneae	Betulaceae	Carpinus grandis Ung.	m	
		Carpinus caucasica Grossh.	p	p
		Carpinus orientalis Mill.	mp	p
		Corylis avellana L.	m	m
		Corylus colurna L.		m
		Corylus sp.	mp	p
		Ostrya carpinifolia Scop.	m	
	Fagaceae	Castanea sativa Mill.	m	
		Castanea sp.	p	p
		Fagus orientalis Lipsky	mp	p
		Fagus orientalis Lipsky var. palibini Iljinsk.	m	m
		Fagus sp.	m	
		Quercus cerris L.	m	
		Quercus iberica Stev.	m	
		Quercus pseudocastanea Goepp.	m	
		Quercus robur L.	m	
		Quercus sosnowskyi Kol.	m	
		Quercus sp.	mp	
	Ulmaceae	Celtis sp.	m	p
		Ulmus campestris L.	m	
		Ulmus foliacea Gilib.	m	
		Ulmus longifolia Ung.	m	
		Ulmus suberosa Moench.	mp	
		Ulmus sp.		p
		Zelkova carpinifolia (Pall.) Dipp.	m	
		Zelkova crenata Spath.	m	m
		Zelkova zelkovifolia (Ung.) Buzek et Kotlaba	m	
	Moraceae	Morus alba L.	m	
		Morus andrussowii Palib.et Zyr.	m	
		Moraceae gen.indet.	m	
	Urticaceae	Urtica sp.		p
	Polygonaceae	Polygonum persicaria L.	mp	p
		Polygonaceae gen.indet.	m	p
	Plumbaginaceae	Plumbago sp.		p
	Caryophyllaceae	Caryophyllaceae gen.indet.	mp	mp
	Chenopodiaceae	Chenopodium sp.	p	p
		Chenopodiaceae gen.indet.	mp	mp
	Lauraceae	Cinnamomum cinnamomeum (Rossm.) Holl.	m	
	Ranunculaceae	Ranunculaceae gen.indet.		p
	Platanaceae	Platanus sp.	mp	p

1	2	3	4	5
Dicotyledoneae	Hamameli-daceae	Liquidambar europaea A.Br.	m	
		Liquidambar sp.	m	
		Hamamelidaceae gen.indet.	m	
	Rosaceae	Amelanchier vulgaris Moench.	m	
		Cotoneaster racemiflora (Desf.) C.Koch	m	
		Crataegus sp.	m	
		Laurocerasus officinalis Roem.	m	
		Laurocerasus pliocenica (Laur.) Kol.	m	
		Rosa sp.	m	
		Prunus mahaleb L.	m	
		Prunus persica S.et L.	m	
		Prunus spinosa L.	m	
		Pyracantha coccinea Roem.	m	
		Pyrus caucasica Fed.	m	
		Pyrus communis L.	m	m
		Sorbus caucasigena Kom.	m	
		Spiraea salicifolia L.	m	
		Rosaceae gen. indet.		p
	Geraniaceae	Geraniaceae gen.indet.		p
	Caesalpini-aceae	Cercis siliquastrum L.	m	
	Fabaceae	Gleditschia caspica Desf.	m	
		Lespedeza bicolor Trun.	m	
		Onobrychis radiata N.B.	m	
		Fabaceae gen.indet.	m	p
	Anacardiaceae	Cotinus coggygria (L.) Scop.	m	
		Pistacia lentiscus L.	m	
		Pistacia terebinthus L.	m	
	Aceraceae	Acer decipiens A.Br.	m	
		Acer ibericum N.B.		m
		Acer insigne Boiss.et Buhse	m	
		Acer saliense (Andr.) Kol.et Rat.	m	
		Acer tataricum L.	m	m
	Aquifoliaceae	Ilex horrida Sap.	m	
	Celastraceae	Euonymus latifolia Scop.	m	
		Euonymus sp.	m	
	Rhamnaceae	Frangula alnus Mill.	m	
		Frangula grandifolia (F.etM.) Grub.	m	
		Paliurus aculeatus LAM.	m	
		Rhamnus cathartica L.	m	
		Rhamnus microcarpa Boiss.	m	
		Ziziphus jujuba Mill.	m	
		Ziziphus sp.	m	

1	2	3	4	5
Dicotyledoneae	Vitaceae	Vitis silvestris Gmel.	m	
	Tiliaceae	Tilia caucasica Rupr.	p	p
		Tilia platyphyllos Scop.	m	
		Tilia sp.	mp	p
	Elaeagnaceae	Hippophaë sp.	m	
	Onagraceae	Onagraceae gen.indet.	m	p
	Punicaceae	Punica granatum L.	m	
	Cornaceae	Cornus mas L.	m	
		Cornus sp.		p
	Araliaceae	Hedera colchica C.Koch.	m	
	Apiaceae	Apiaceae gen. indet.	p	
	Ericaceae	Rhododendron sp.	mp	p
		Vaccinium sp.		p
		Ericaceae gen.indet.	m	
	Myrsinaceae	Myrsinaceae gen.indet.	m	
	Ebenaceae	Diospyros lotus L.	m	
	Periplocaceae	Periploca graeca L.	m	
	Oleaceae	Fraxinus excelsior L.	m	
		Ligustrum vulgare L.	m	
	Caprifoliaceae	Sambucus racemosa L.	m	
		Viburnum orientalis Pall.	m	
		Viburnum opulus L.	m	
		Caprifoliaceae gen.indet.	m	
	Lamiaceae	Lamiaceae gen. indet.	mp	p
	Scrophulari-aceae	Linaria sp.	m	
	Plantagi-naceae	Plantago sp.	mp	p
	Valerianaceae	Valeriana sp.	m	
		Valerianaceae gen.indet.	m	
	Asteraceae	Artemisia sp.	mp	p
		Asteraceae gen.indet.	mp	p
Monocotyle-doneae	Poaceae	Phragmites communis Trin.	m	
		Poaceae gen. indet.	mp	p
	Typhaceae	Typha latifolia L.	m	
	Cyperaceae	Carex sp.	mp	
		Cyperaceae gen.indet.	mp	p

THE PLEISTOCENE (WESTERN GEORGIA)

The Pleistocene marine deposits are known only from Western Georgia and are divided into the following stratigraphical units based on faunal stratigraphy: Chaudian, Old Euxinian, Uzunlarian, Karangatian and New Euxinian (Table XVI).

Table XVI. Stratigraphical division scheme for Pleistocene deposits in Georgia (after Kitovani et al., 1991)

Ma	Division	Regiostage	Layers
0.01	Pleistocene	New Euxinian	
		Karangatian	Upper
0.1			Lower
		Uzunlarian	
		Old Euxinian	Omparetian
0.4			Urekian
		Chaudian	Tsvermagalian
0.9			Natanebian

The most outstanding and characteristic feature of the Pleistocene was repeated glaciation. Ideas about the number of glaciations in the Caucasus are somewhat inconsistent, however. According to Maruashvili (Maruashvili et al., 1991), traces of Riss (Middle Pleistocene) and Wurm (Upper Pleistocene) are most evident, while Tsereteli (1966, 1977) considered the moraines of three glaciations beginning from the Mindelian to be part of the same cycle of glaciations as those of the Russian Plain, but not fully synchronous.

The Chaudian

In Western Georgia the Chaudian basin was of similar size to the Gurian basin and somewhat more extensive than modern Black Sea; its coastline lay 2 km from the current one. Chaudian outcrops are distributed throughout Guria and in the Colchis depression they can reach great depth (Imnadze, 1975; Kitovani & Imnadze, 1986; Tsereteli, 1966). The Chaudian horizon is divided on the basis of fauna into the Lower Chaudian (Natanebian) and Upper Chaudian (Tsvermagalian) layers (Kitovani et al., 1982; 1991).

Palibin collected the first material on the Chaudian flora (1930a, 1931) and the fossil flora was described by Kara-Mursa (1941). Of the 21 plants identified, only *Acer velutinum* is absent from the modern flora of Western Georgia. At present two main localities (Fig.20) are known – from the Chakhvata River and near Khvarbeti village – and both were described by Chochieva (1965, 1975, 1985).

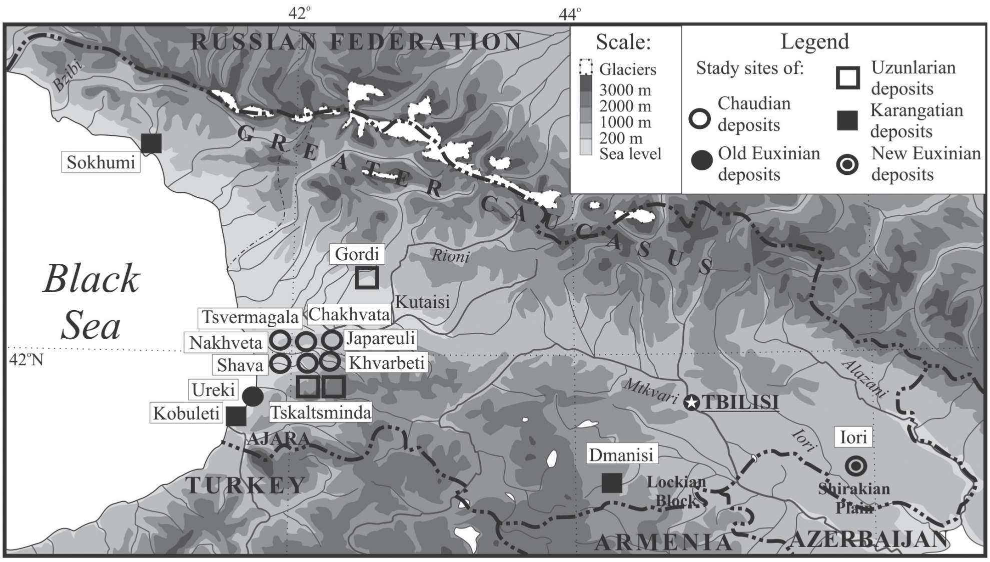

Fig.20. Study sites of Pleistocene deposits in Georgia

Chaudian deposits are very rich in pollen and spores. Nearly all outcrops, as well as borehole samples from the Colchian plain, have been studied palynologically (Mamatsashvili, 1975; Mchedlishvili, 1984; Shatilova, 1967, 1974; Shatilova & Mchedlishvili, 1980; Shatilova et al., 2006). The Chaudian has been reconstructed using landscape-phytocenological analysis and three main stages in its climatic and vegetational history elucidated (Fig. 21).

In the Late Gurian and beginning of the Early Chaudian (Fig.18, 19, 21), the dominant plant community was dark-conifer forest with Tsuga, Abies and Picea. The climate in their distributional area was temperate and humid. The area of warm temperate and beech forest was less (stage VII).

By the upper part of the Early Chaudian, the character of vegetation had changed somewhat (stage VIII). The middle mountain belt was covered by beech forests, which had begun to form in the Late Gurian as new ecological niches appeared as a result of tectonic uplift (Kogoshvili, 1977; Tsagareli, 1980). The long-term development of beech forests was rather sporadic. At the beginning of the Chaudian (stage VII), beech was a component of dark-coniferous or coniferous-broadleaved forests. Later (stage VIII), it formed a distinct community, but its area was changeable. We suppose that the reduction of beech forests was caused mainly by cooling, since today the upper boundary of *Fagus orientalis* is determined by temperature and winter precipitation. Oriental beech forests achieve maximum productivity when the temperature of the warmest month is 17-20°C and annual precipitation is not less than 700-1400 mm (Dolukhanov, 1989). Similar conditions accompanied the maximum development of beech communities during the Chaudian.

The Taxodiaceae family reached great abundance during stage VIII. They occupied a large and stable area at the time when the Chakhvatian and Khverbetian floras were laid down. The Khvarbetian can be considered as a climatic optimum, as also indicated by the presence of some subtropical Pliocene relicts in this macroflora (Chochieva, 1975, 1985).

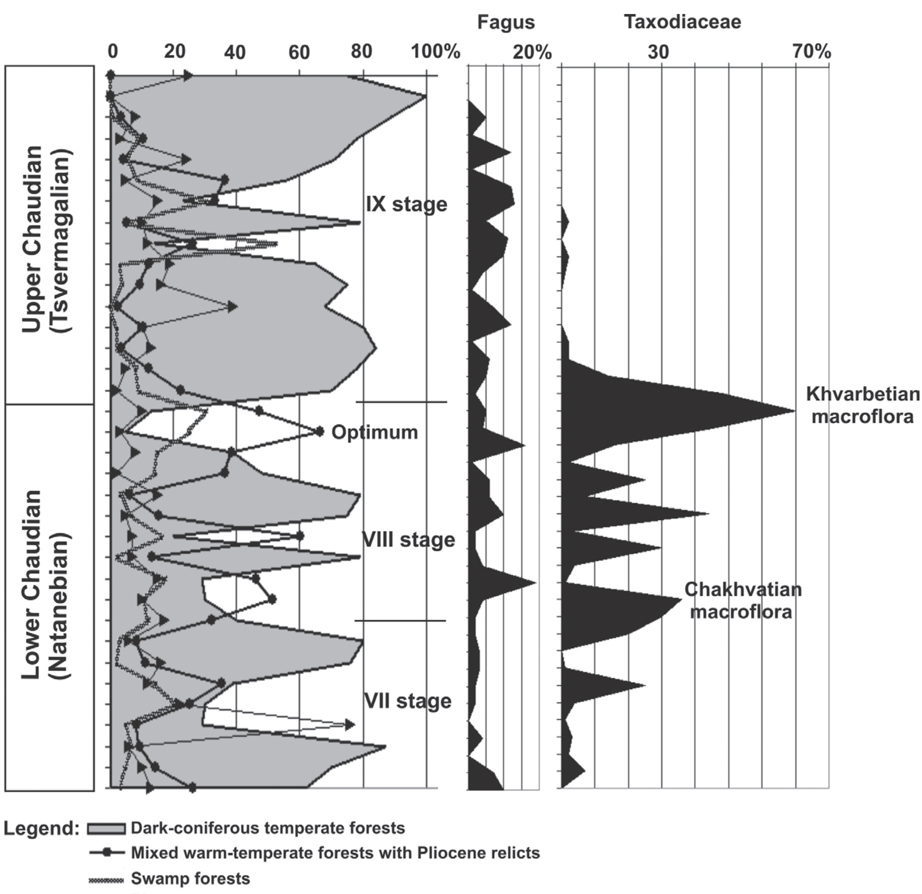

Fig. 21. Percentage fluctuations of palynological groups in Western Georgia during the Chaudian, reflecting changes in the distribution of the main forest formations.

According to Dolukhanov (1989), Taxodiaceae were pushed down nearly to sea level by cooling temperatures at the time of the Khvarbetian flora. However, we think that the main reason was orogenic movements, which created habitats favorable for beech forest in the middle mountain belt. Beech forced Taxodiaceae and other thermophilous plants down into the lower mountain belt, where they formed mixed communities made up of Juglans, Quercus, Zelkova, Acer, Tilia and Pliocene relicts such as Myrica, Platycarya, Engelhardia, Magnolia, Nyssa, Liquidambar, Symplocos and Carya.

During the Late Chaudian (stage IX), significant changes in the composition of flora and character of the vegetation took place. The number of Pliocene relicts and the diversity of the Taxodiaceae family and genus Tsuga decreased and their dominant role in coniferous forests was lost. Broadleafed plants remained only at lower altitudes, while other elevations were covered by coniferous forests in which Abies and Picea prevailed.

The Chaudian climate was temperate in the upper and middle forest belts, and warm-temperate in the lower. Humidity was generally high. The Early Chaudian climate was warmer and altitudinal zonation more distinct than in the Late Chaudian, which appears to have been temperate at most elevations.

Connections between the Chaudian and the Pleistocene glaciations have been considered by many researchers (Fedorov, 1978; Tsereteli, 1966; Zubakov, 1986). According to Borzenkova (1992), the Early Pleistocene included the classic Günz and Mindel glaciations, separated by the Günz-Mindelian interglacial.

On the basis of our data, we can relate stage VII (upper part of Gurian and lower part of the Early Chaudian) to the Günz glaciations, stage VIII (the upper part of Lower Chaudian - the warmest period) to the Günz-Mindelian interglacial, and stage IX (the whole Upper Chaudian or Tsvermagalian layers) to the Mindelian glaciation.

A list of plant remains from Chaudian floras is given in Table XVII.

Table XVII. Plants from Chaudian deposits in Georgia
Key: m – macrofossils; p – pollen

Class	Family	Species	Lower Chaudian	Upper Chaudian
1	2	3	4	5
Lycopodiopsida	Lycopodiaceae	Lycopodium clavatum L.	p	p
		Lycopodium selago L.	p	p
		Lycopodium sp.	p	

1	2	3	4	5
Isoëtopsida	Selaginellaceae	Selaginella fusca N.Mtchedl.	p	
		Selaginella selaginoides (L.) Link.	p	
		Selaginella sp.	p	
Ophioglossopsida	Ophioglossaceae	Bothrychium sp.	p	p
		Ophioglossum sp	p	
Polypodiopsida	Osmundaceae	Osmunda cinnamomea L.	p	p
		Osmunda regalis L.	p	p
	Pteridaceae	Cryptogramma arctostichoides R.Br.	p	
		Cryptogramma crispa (L.) R.Br.	p	p
		Pteris cretica L. (Pteridacidites variabilis St.et Sh.)	p	p
	Polypodiaceae	Polypodium aureum L.	p	
		Polypodium australe Fee.	p	p
		Polypodium vulgare L.	p	p
		Polypodium sp.	p	
	Cyatheaceae	Cyathea sp.	p	
	Thelypteridaceae	Thelypteris sp.	p	
	Aspleniaceae	Asplenium sp.	p	
	Aspidiaceae	Athyrium sp.	p	
		Cystopteris fragilis (L.) Bernh.	p	
		Dryopteris sp.	p	
		Gymnocarpium sp.	p	
		Polystichum sp.	p	
Pinopsida	Podocarpaceae	Podocarpus sp.	p	
	Taxaceae	Taxus sp.	mp	
	Pinaceae	Abies aff.cephalonica Loud.	p	p
		Abies ciliticaeformis N.Mtchedl.	p	p
		Abies nordmanniana (Stev.) Spach.	mp	p
		Cedrus deodara Loud.	p	p
		Cedrus sauerae N.Mtchedl.	p	
		Picea minor N.Mtchedl.	p	
		Picea orientalis L.	mp	p
		Pinus sosnowskyi Nakai	p	
		Pinus sp.	p	p
		Pseudotsuga sp.	p	
		Tsuga aculeata Anan.	p	
		Tsuga canadensis (L.) Carr.	mp	p
		Tsuga diversifolia (Maxim.) Mast.	mp	p
		Tsuga europaea (Menzel) Szafer	m	

1	2	3	4	5
Pinaceae	Pinaceae	Tsuga inordinata Mched.	p	
		Tsuga korenevae Mched.	p	p
		Tsuga meierii Mched.	p	p
		Tsuga patens Downie	p	p
		Tsuga shatilovae Mched.	p	p
		Tsuga sivakii Mched.	p	
		Tsuga tortuosa Mched.	p	
		Tsuga aff. blaringhemi Flous	p	
		Tsuga aff.yunnanensis (Frangh.) Mast.	p	
	Taxodiaceae	Athrotaxis annae Choch.	m	
		Athrotaxis sp.	m	
		Cryptomeria japonica Don	p	p
		Cryptomeria sp.	mp	
		Cunninghamia sp.	p	
		Metasequoia cf.glyptostroboides Hu et Cheng	m	
		Metasequoia sp.	mp	
		Sequoia langsdorfii (Brongn.) Heer	m	
		Sequoia cf.sempervirens (Lamb.) Endl.	m	
		Sequoia sp.	mp	p
		Sequoiadendron sp.	mp	
		Taxodium sp.	p	p
	Cupressaceae	Cupressus cf.sempervirens L.	m	
		Cupressus sp.	mp	
		Chamaecyparis obtusa Sieb. et Zucc.	m	
		Chamaecyparis cf.pisifera Sieb.et Zucc.	m	
		Chamaecyparis nootkatensis (Lamb.) Spach	m	
		Chamaecyparis sp.	m	
		Juniperus sp.	mp	
		Libocedrus sp.	p	
		Thuja occidentalis L.	m	
Gnetopsida	Ephedraceae	Ephedra distachya L.	p	
		Ephedra sp.	p	p
Dycotyledoneae	Myricaceae	Myrica sp.	p	
	Juglandaceae	Carya aquatica (Michx.) Nutt.	p	p
		Carya aff.texana DC	p	
		Carya sp.	mp	
		Engelhardia sp.	p	
		Juglans cinerea L.	mp	
		Juglans nigra L.	p	

1	2	3	4	5
Dycotyledoneae	Juglandaceae	Juglans regia L.	p	p
		Platycarya sp.	p	
		Pterocarya pterocarpa (Michx.) Kunth.	mp	p
		Pterocarya rhoifolia Sieb. et Zucc.	p	
		Pterocarya stenoptera DC	p	
		Pterocarya sp.	p	
	Salicaceae	Populus tremula L.	m	
		Salix caprea L.	m	
		Salix sp.	p	
	Betulaceae	Alnus glutinosa (L.) Gaerth.	m	
		Alnus sp.	mp	p
		Betula sp.	mp	p
		Carpinus betulus L.	m	
		Carpinus caucasica Grossh.	p	p
		Carpinus orientalis Mill.	mp	p
		Carpinus sp.	m	
		Corylis avellana L.	mp	p
		Corylus cf.colurna L.	m	
		Corylus aff.maxima Mill.	p	
		Ostrya carpinifolia Scop.	m	
	Fagaceae	Castanea sativa Mill.	mp	
		Fagus orientalis Lipsky	p	p
		Fagus orientalis Lipsky var. palibini Iljinsk.	m	
		Quercus cerris L.	m	
		Quercus hartwissiana Stev.	m	
		Quercus aff.castaneifolia C.A.Mey	p	
		Quercus aff.petraea Liebl.	p	
		Quercus aff.pontica C.Koch	p	
		Quercus aff.pseudorobur Kov.	m	
		Quercus sp.	mp	p
	Ulmaceae	Ulmus foliacea Gilib.	mp	
		Ulmus laevis Pall.	p	
		Zelkova carpinifolia (Pall.) Dipp.	p	p
		Zelkova serrata (Thunb.) Macino	p	
	Moraceae	Ficus sp.	p	
		Morus alba L.	p	
	Polygonaceae	Polygonum sp.	mp	
		Rumex sp.	m	
	Caryophyllaceae	Stellaria sp.	p	
		Caryophyllaceae gen.indet.	p	

1	2	3	4	5
Dycotyledoneae	Chenopodiaceae	Chenopodiaceae gen.indet.	p	
	Magnoliaceae	Magnolia denudata Desr.	p	
		Magnolia aff.acuminata L.	p	
	Ranunculaceae	Ranunculus sp.	mp	
		Thalictrum sp.	p	
	Nymphaeaceae	Euryale ferox Salisb.	m	
		Nuphar sp.	p	
	Theaceae	Eurya cf.stigmosa (Ludw.) Mai	m	
		Stuartia emarginata Choch.	m	
	Papaveraceae	Papaver sp.	m	
	Hypericaceae	Hypericum sp.	m	
	Platanaceae	Platanus orientalis L.	p	
	Hamamelidaceae	Liquidambar styraciflua L.	p	
	Rosaceae	Laurocerasus officinalis (L.) Roem.	m	
		Prunus sp.	m	
		Rosa canina L.	p	
		Rosa sp.	p	
		Rubus cf.idaeus L.	m	
		Rubus sp.	m	
		Sanguisorba sp.	p	
	Geraniaceae	Geranium sp.	p	p
	Rutaceae	Phellodendron aff.amurense Rupr.	p	
	Anacardiaceae	Rhus sp.	p	
	Aceraceae	Acer campestre L.	m	
		Acer ibericum M.B.	m	
		Acer polymorphum pliocenicum Sap.	m	
		Acer pseudoplatanus L.	m	
		Acer cf.velutinum Boiss.	m	
		Acer sp.	mp	
	Hippocastanaceae	Aesculus hippocastanum L.	mp	
	Aquifoliaceae	Ilex colchica Pojark,	p	p
		Ilex cf.aquifolium L.	m	
		Ilex sp.	p	
	Celastraceae	Euonymus sp.	p	
	Staphyleaceae	Staphylea colchica Stev.	p	
	Buxaceae	Buxus sempervirens L.	m	
	Vitaceae	Parthenocissus quinquefolia (L.) Planch.	p	
		Vitis silvesrtis Gmel.	m	
	Tiliaceae	Tilia caucasica Rupr.	p	p
		Tilia cordata Mill.	mp	
		Tilia ledebouri Borb.	p	

1	2	3	4	5
Dycotyledoneae	Tiliaceae	Tilia platyphyllos Scop.	p	
		Tilia tomentosa Moench.	p	
		Tilia aff.grandipollinia Trav.	p	
	Violaceae	Viola sp.	p	
	Onagraceae	Epilobium sp.	p	
		Chamaenerium aff. angustifolium (L.) Scop.	p	
	Trapaceae	Trapa lydiae Choch.	m	
		Trapa sp.	m	
	Nyssaceae	Nyssa sp.	p	
	Cornaceae	Cornus sp.	p	
	Araliaceae	Hedera colchica C.Koch.	mp	
		Hedera helix L.	mp	
		Fatsia aff.japonica (Thunb.) Decne et Planch.	p	
	Apiaceae	Bifora sp.	m	
		Heracleum guriensis Choch.	m	
		Heracleum sp,	m	
		Turgenia latifolia Hoffm.	p	
	Ericaceae	Rhododendron ponticum L.	m	
		Vaccinium sp.	p	
	Ebenaceae	Diospyros lotus L.	m	
	Symplocaceae	Symplocos chvarbetica Choch.	m	
		Symplocos cf.paniculata Wall.	p	
		Symplocos cf.tinctoria (L.) L'Her	p	
		Symplocos sp.	p	
	Oleaceae	Fraxinus oxycarpa Willd.	p	
		Fraxinus sp.	p	
		Ligustrum vulgare L.	p	
	Convolvulaceae	Convolvulus sp.	p	
	Lamiaceae	Lycopus europaeus L.	m	
		Lycopus exaltatus L.	m	
		Lycopus sp.	p	
	Plantaginaceae	Plantago sp.	p	p
	Caprifoliaceae	Lonicera sp.	p	
		Sambucus sp.	m	
	Valerianaceae	Valeriana sp.	p	p
	Dipsacaceae	Cephalaria sp.	p	p
		Knautia sp.	p	p
		Scabiosa sp.	p	p
	Asteraceae	Artemisia sp.	p	p
		Eupatorium cannabinum L.	m	

1	2	3	4	5
Monocotyledoneae	Najadaceae	Najas marina L.	m	
	Liliaceae	Liliaceae gen.indet.	p	p
	Iridaceae	Iris sp.	p	p
	Poaceae	Phragmites communis Trin.	m	
		Poaceae gen. indet.	p	p
	Sparganiaceae	Sparganium sp.	p	p
	Typhaceae	Typha latifolia L.	p	
	Cyperaceae	Carex cf.riparia Currtt.	m	
		Carex sp.	m	
		Dulichium spathaceum Pers.	m	
		Dulichium vespiforme Reid.	m	
		Scirpus sp.		p

The Old Euxinian and Uzunlarian

The Upper Chaudian (Tsvermagalian) deposits of Western Georgia are overlapped by Old Euxinian layers on marine terraces, in natural outcrops and in boreholes from the Colchis plain (Fedorov, 1978; Imnadze, 1975; Imnadze et al., 1975; Kitovani et al., 1982, 1991; Laliev, 1957; Mamaladze, 1975; Tsereteli, 1966).

Data on the flora of the Old Euxinian is based on palynological analysis (Chochieva & Mamatsashvili, 1977, 1991; Chochieva et al., 1982; Mamatsashvili, 1975; Shatilova, 1974; Shatilova & Mchedlishvili, 1980; Shatilova & Ramishvili, 1990; Shatilova et al., 2010a). In borehole records and natural outcrops (Fig.20), Old Euxinian deposits contain high percentages of Picea, Abies and Taxodiaceae pollen, the latter comprising only three genera that remained after the Chaudian: Taxodium, Cryptomeria and Sequoia. Among broadleafed trees, Fagus and Alnus were predominant (Fig.19).

Old Euxinian deposits are overlapped by Uzunlarian layers. The flora of Uzunlarian was studied from both macroremains and pollen (Chochieva, 1980; Shatilova, 1982; Shatilova & Mchedlishvili, 1980). Uzunlarian palynological assemblages differ from those of the Old Euxinian in the small number of Taxodiaceae pollen, the high percentage of broad-leaved deciduous plants and in the increasing representation of Pliocene relicts, i.e. Cedrus, Tsuga, Carya, Liquidambar and Magnolia (Fig.19).

A Middle Pleistocene vegetation reconstruction using the landscape-phytocenological method is given in Figure 22 and indicates a two-stage development in the vegetation: the Old Euxinian (X) and the Uzunlarian (XI).

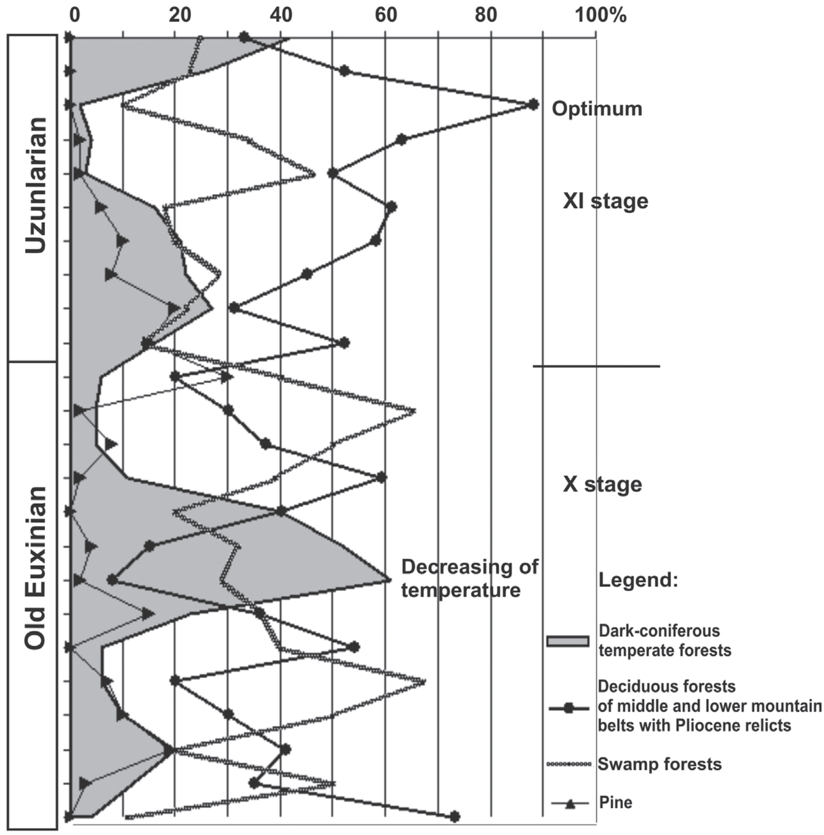

Fig. 22. Percentage fluctuations of palynological groups in Western Georgia during the Middle Pleistocene, reflecting changes in the distribution of the main forest formations.

The great prevalence of Taxodium pollen in Old Euxinian deposits (Fig.19) is indicative of the extensive riparian and swamp forests that occurred along the sea shore (Mamatsashvili, 1975; Shatilova, 1974). Alnus, Pterocarya and Ulmus were also to be found in these forests. Mixed coniferous-broadleaved communities were distributed through the lower mountain belt and included Sequoia and Cryptomeria as their main components. The majority of the middle belt was occupied by monodominant beech forests, indicated by a high percentage of Fagus pollen grains in palynological assemblages. In the upper mountain belt, dark coniferous forests of Picea and Abies predominated. Tsuga was also present in this community, as indicated by single pollen grains. The middle stretches of the Old Euxinian were distinguished by the expansion of dark-coniferous forests, probably as a result of temperature reductions.

In the Uzunlarian, the character of vegetation again changed (Fig. 19, 22). Among broadleaved plants, *Fagus orientalis, Castanea sativa, Carpinus caucasica* and Alnus were most prevalent, the latter forming the main component of riparian and swamp forests. The area of mixed coniferous-broadleaved forests declined and Taxodiaceae decreased, yet on the whole Uzunlarian forests were much more diverse than those of the Old Euxinian.

In general the climate of the Middle Pleistocene was warm and humid. The Old Euxinian was rather cold compared to the climatic optimum of the Uzunlarian. The two stages correspond to the Mindel-Riss interglacial (stage X) and the Riss-Wurmian interglacial (stage XI), respectively.

Lacustrine deposits near Gordi village, dated to the Middle Pleistocene, also contain Taxodiaceae pollen grains (Maruashvili et al., 1975; 1991). A list of the Old Euxinian and Uzunlarian floras is given in Table XVIII.

The Karangatian and New Euxinian

The Karangatian and New Euxinian horizons are represented by deep-water deposits and marine terraces.

The Karangatian flora was studied from plant macroremains (Ratiani, 1979) and palynological complexes (Arslanov et al., 1976; Cherniuk, 1986; Kvavadze & Rukhadze, 1999; Shatilova & Badzoshvili, 1966; Shatilova 1974).

After the Uzunlarian, the number of Tertiary-relict taxa declined so that by the Karangatian they are represented only by a handful of species: *Cedrus deodara, Carya aquatica, Parrotia pristina* and Taxodiaceae, macroremains of which were preserved in Karangatian peat on the Colchis plain (Sluka, 1978). Following the Karangatian, the Taxodiaceae family disappeared from Georgia and the whole Black Sea region (Koreneva & Kartashova, 1978).

In the Early Karangatian, the upper mountain belt was occupied by dark-coniferous forests of Abies and Picea (Fig.19, 23). Beech forests were distributed through the middle mountain belt, grading into mixed broadleaved communities at lower altitudes. Swamp forests with *Alnus barbata, A. hoernesi, A. glutinosa, Pterocarya pterocarpa, Ulmus foliacea, U. scabra* and some Taxodiaceae occurred in the coastal lowlands.

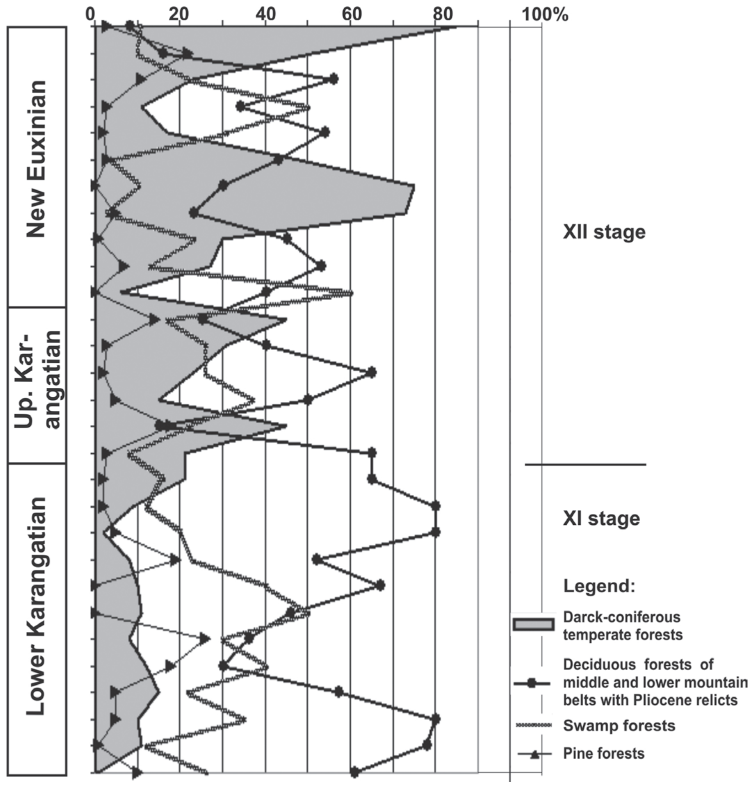

Fig. 23. Percentage fluctuations of palynological grounps in Western Georgia during the Late Pleistocene, reflecting changes in the distribution of the main forest formations.

The Early Karangatian, as well as the Uzunlarian, correlates with the Riss-Wurmian interglacial (stage XI), characterized by a warm climate with low humidity (Maruashvili et al., 1991).

By the Late Karangatian the situation had changed somewhat, as dark-coniferous forests began to migrate to lower elevations. Probably these were the first effects of the Wurm glaciation, which was followed by three stages of decreasing temperatures in the New Euxinian (stage XII).

Evidence for lower temperatures during the New Euxinian comes from palynological analyses of sediments from the Black Sea floor. New Euxinian assemblages contain a high percentage of Chenopodiaceae and Artemisia pollen grains (Neishtadt et al., 1965). The presence of these taxa in the Black Sea region during the Late Pleistocene indicates cold climatic conditions and glacial activity. During periods of extensive glaciations, the sea level fell, allowing the former sea bed to be colonised by halophytes.

Neishtadt's data are in accordance with materials analysed by Koreneva (1980;

1983). In her opinion, Pleistocene regressions in the Black Sea were mainly triggered by glaciations. The reduction in the Black Sea's area resulted in changes to the regional climate system, leading to low atmospheric humidity and low temperatures. These conditions promoted a particular type of periglacial vegetation dominated by Chenopodiaceae and Artemisia. Decreasing temperatures in the New Euxinian were also noted by Sluka (1978).

The large extent of climatic changes during the New Euxinian is confirmed by palynological analysis of limnic-alluvial deposits found on the terraces of the Iori River in Eastern Georgia (Tumajanov & Gogichaishvili, 1969). Spore-pollen assemblages dated to the Late Pleistocene (Wurm) indicate cold forest-steppe communities and treeless areas. These cold climatic conditions are further suggested by archeological and lithological data (Tsereteli & Maisuradze, 1980).

On the basis of new data and published materials, it can be concluded that the climate of Georgia during the second half of the Late Pleistocene was colder than during previous stretches of the Quaternary. According to Velichko (1973), a particular type of treeless landscape originated during the New Euxinian in response to dry and cold climatic conditions and spread over vast areas, including to the Black Sea region. In Georgia such a type of vegetation appeared only in the eastern part. In Colchis, where temperature and humidity were higher, the colder climate manifested as a downward migration of dark-coniferous forests, while broadleaved plants sought refuge in warm gorges. In the favorable conditions of interstadials, broadleaved species expanded and deciduous forests occupied areas left after glacial retreat.

In the history of development of Western Georgia's vegetation during the Middle and Upper Pleistocene, three stages can be distinguished (X-XII). These stages differed mainly in terms of temperature, as the global climate oscillated between interglacials and glacials. The warm stages, X and XI, correspond to the Old Euxinian, Uzunlarian and Lower Karangatian, and are chronologically linked to the Mindel-Riss and Riss-Wurm interglacials. The colder stage, XII, from the Upper Karangatian and whole New Euxinian, is linked to the Wurm glacial. Fossil traces of the flora of the Riss glaciation in Western Georgia have not been found.

A list of floras is given in Table XVIII.

Table XVIII. Plants from Old Euxinian, Uzunlarian, Karangatian and New Euxinian deposits in Georgia
Key: m – macrofossils; p – pollen

Class	Family	Species	Old Euxinian	Uzun-larian	Karan-gatian.	New Euxin-ian
1	2	3	4	5	6	7
Bryopsida	Sphagnaceae	Sphagnum sp.			p	
Lycopodiop-sida	Lycopodiaceae	Lycopodium clava-tum L.	p	p	p	p
		Lycopodium selago L.	p	p	p	p
		Lycopodium sp.		p		
Isoëtopsida	Selaginellaceae	Selaginella fusca N.Mtchedl.		p		
		Selaginella selagi-noides (L.) Link.	p	p	p	p
Ophioglos-sopsida	Ophioglos-saceae	Bothrychium sp.	p	p	p	p
		Ophioglossum sp.		p	p	p
Polypodiopsida	Osmundaceae	Osmunda cin-namomea L.		p		
		Osmunda regalis L.	p	p	p	p
	Pteridaceae	Cryptogramma crispa (L.)R.Br.		p	p	p
		Pteris cretica L. (Pteri-dacidites variabilis St., Sh.)	p	p	p	p
	Polypodiaceae	Polypodium australe Fee.	p	p	p	p
		Polypodium plioceni-cum Ram.		p		
		Polypodium vulgare L.	p		p	p
		Polypodium sp.	p	p	p	
		Polypodiaceae gen. indet.			p	
	Dennstaedti-aceae	Pteridium sp.		p	p	
	Thelypteri-daceae	Thelypteris sp.		p	p	p
	Aspleniaceae	Asplenium tricho-manes L.			p	
		Asplenium sp.	p			
		Onoclea sp.	p			
	Aspidiaceae	Athyrium filix femina (L.) Röth	p	p		
		Cystopteris sp.	p			
		Dryopteris filix-mas (L.) Schott			p	
		Dryopteris sp.	p			

1	2	3	4	5	6	7
Polypodiop-sida	Aspidiaceae	Woodsia aff.alpina (Bolt.) Grey		p		
		Woodsia glabella R.Br.		p		
Pinopsida	Taxaceae	Taxus sp.	p			
	Pinaceae	Abies cephalonica Loud.			m p	p
		Abies ciliticaeformis N.Mtchedl.	p	p		
		Abies nordmanniana (Stev.) Spach.	p	p	m	
		Cedrus deodara Loud.	p	p	p	
		Picea orientalis L.	p	p	p	p
		Picea sp.		m		
		Pinus sosnowskyi Nakai			mp	
		Pinus sp.	p	p	p	p
		Tsuga diversifolia (Maxim.) Mast.	p	p		
		Tsuga shatilovae Mched.	p	p		
	Taxodiaceae	Cryptomeria japonica Don	p	p		
		Glyptostrobus sp.		p		
		Sequoia sp.	p	p		
		Taxodium sp.	p	p	p	
		Taxodiaceae gen. indet..			p	
	Cupressaceae	Juniperus sp.	p			
		Cupressaceae gen. indet.	p	p		
Gnetopsida	Ephedraceae	Ephedra sp.	p	p	p	p
Dicotyledoneae	Juglandaceae	Carya aquatica (Michx.) Nutt.	p	p	p	
		Carya aff.texana DC		p		
		Juglans regia L.		p	p	p
		Pterocarya pterocar-pa (Michx.) Kunth.	p	p	mp	p
	Salicaceae	Populus tremula L.	m		m	
		Salix alba L.	m		m	
		Salix caprea L.			m	
		Salix triandra L.			p	
		Salix sp.	p	p	p	
	Betulaceae	Alnus barbata C.A.M.		mp	mp	
		Alnus glutinosa (L.) Gaerth.			p	p
		Alnus hoernesi Stur			m	

1	2	3	4	5	6	7
Dicotyledoneae	Betulaceae	Betula pubescens Ehrh,		p		
		Betula litwinowii A.Dol.		m	m	
		Betula cf. verrucosa Ehrh.		m		
		Betula sp.	p	p	p	p
		Carpinus betulus L.			m	
		Carpinus caucasica Grossh.		m	p	p
		Carpinus orientalis Mill.	p	mp	p	p
		Corylus avellana L.	p	mp	p	p
		Corylus colchica Alb.		m		
		Corylus sp.			p	
		Ostrya carpinifolia Scop.			m	
	Fagaceae	Castanea atavia Ung.			m	
		Castanea pliosativa Kol.	m			
		Castanea sativa Mill.	p	mp		p
		Fagus antipovii Heer			m	
		Fagus orientalis Lipsky		p	mp	p
		Fagus orientalis Lipsky var. palibini Iljinsk.	m			
		Quercus aff.hartwissi-ana Stev.	p			
		Quercus aff.iberica Stev.	p		p	p
		Quercus aff.pontica C.Koch		p	p	p
		Quercus pseudor-obur Kov.			m	
		Quercus sp. (cf.Q.sosnowskyi Kol.)		m		
		Quercus sp.	p	p		
	Ulmaceae	Ulmus foliacea Gilib.	p	p	mp	p
		Ulmus scabra Mill.	p		p	p
		Ulmus sp.		m	p	
		Zelkova carpinifolia (Pall.) Dipp.	p	p	p	p
	Moraceae	Ficus sp.			p	
		Morus alba L.	p	p	p	p
		Moraceae gen.indet.			p	
	Urticaceae	Urtica sp.	p	p	p	

1	2	3	4	5	6	7
Dicotyledoneae	Polygonaceae	Polygonum persicaria L.		p	p	p
		Polygonum viviparum L.	p	p	p	p
		Polygonum sp.			p	
	Caryophyllaceae	Caryophyllaceae gen. indet.	p	p	p	p
	Chenopodiaceae	Chenopodiaceae gen.indet.	p	p	p	p
	Magnoliaceae	Magnolia sp.		mp		
	Ranunculaceae	Ranunculaceae gen. indet.			p	
	Lauraceae	Laurus nobilis L.			m	
		Laurus sp.		m		
	Nymphaeaceae	Nuphar luteum L.			p	p
		Nuphar sp.		p		
		Nymphaeaceae gen. indet.			p	
	Papaveraceae	Papaveraceae gen. indet.			p	
	Brassicaceae	Brassicaceae gen. indet.		p		
	Hypericaceae	Hypericum inodorum Willd.			p	
	Platanaceae	Platanus sp.			p	
	Hamamelidaceae	Corylopsis aff.cordata Merrill et Li		p		
		Liquidambar styraciflua L.		p		
		Parrotia pristina Ett.			m	
	Rosaceae	Pyracantha coccinea Roem.	m		m	
		Rosa canina L.		p		
		Rosa sp.	p	p	p	
		Rubus sp..		m		
		Sanguisorba sp.		p	p	p
		Sorbus aucuparia L.			m	
		Sorbus subfusca (Ledeb.) Boiss.			m	
		Sorbus sp.	p		p	
	Fabaceae	Fabaceae gen.indet.	p	p	p	
	Geraniaceae	Geranium sp.	p	p	p	p
	Anacardiaceae	Rhus toxicodendron L.		p		
		Rhus sp.	p	p	p	p
	Aceraceae	Acer laetum CAM pliocenicum Sap.et Mar.			m	

1	2	3	4	5	6	7
Dicotyledoneae	Aceraceae	Acer trautvetteri Medw.			m	
		Acer aff.platanoides L.			p	p
		Acer sp.	p	p	p	
	Aquifoliaceae	Ilex colchica Pojark.	p	p	p	p
		Ilex sp.	p	p		
	Celastraceae	Euonymus sp.	p	p	p	p
	Staphyleaceae	Staphylea sp.	p	p	p	
	Buxaceae	Buxus colchica A.Pojark.			m	
		Buxus sp.	p	p		
	Rhamnaceae	Frangula cf.alnus Mull.		m		
		Rhamnus sp.		p	p	
	Tiliaceae	Tilia caucasica Rupr.	p	p	p	p
		Tilia cordata Mill.	p			
		Tilia ledebouri Borb.			p	p
		Tilia platyphyllos Scop.	p	p		
		Tilia tomentosa Moench.		p		
	Thymellaceae	Daphne sp.			p	
	Violaceae	Viola sp.		p	p	
	Malvaceae	Malva sp.			p	p
	Elaeagnaceae	Elaeagnus sp.			p	p
	Onagraceae	Epilobium sp.	p	p	p	p
	Trapaceae	Trapa lydiae Choch.				
		Trapa cf.colchica N.Alb.			p	p
	Cornaceae	Cornus sp.		p	p	p
	Araliaceae	Hedera colchica C.Koch.		mp	mp	
		Hedera sp.	p	p		
		Fatsia aff.japonica (Thunb.) Decne et Planch.	p			
	Apiaceae	Turgenia latifolia Hostm.	p	p	p	p
		Apiaceae gen.indet.	p	p	p	p
	Ericaceae	Rhododendron ponticum L.	p	p		
		Rhododendron sp.			p	p
		Vaccinium sp.	p			
		Ericaceae gen.indet.			p	

1	2	3	4	5	6	7
Dicotyledoneae	Oleaceae	Fraxinus ornus L.		p		
		Fraxinus oxycarpa Willd.		p		
		Fraxinus sp.	p	p	p	
		Ligustrum sp.			p	
	Convolvulaceae	Convolvulus sp.		p		
	Plantaginaceae	Plantago sp.	p	p	p	p
	Caprifoliaceae	Lonicera sp.			p	
		Viburnum sp.		p		
	Lamiaceae	Lycopus sp.	p	p		
		Lamiaceae gen. indet.	p	p	p	p
	Valerianaceae	Valeriana sp.	p	p	p	p
	Dipsacaceae	Cephalaria sp.	p	p	p	p
		Dipsacus sp.	p	p		
		Knautia sp.	p	p	p	p
		Dipsacaceae gen. indet.			p	
	Asteraceae	Achillea sp.			p	
		Artemisia sp.	p	p	p	p
		Asteraceae gen.indet.	p	p	p	p
Monocotyledoneae	Liliaceae	Smilax excelsa L.			m	
		Liliaceae gen.indet.	p	p	p	p
	Iridaceae	Iris sp.		p		
	Poaceae	Arundo sp.		m		
		Poaceae gen. indet.	p	p	p	p
	Sparganiaceae	Sparganium sp.	p	p		
	Typhaceae	Typha latifolia L.		p		
	Cyperaceae	Cyperaceae gen. indet.			p	

THE HOLOCENE

Palynological studies of marine, lagoon, alluvial and bog sediments from the Black Sea coastline of Georgia include 26 profiles of Holocene sediments (Fig.24). Analysis and synthesis of pollen diagrams allowed us to make a stratigraphic subdivision of Holocene sediments and reveal climatic fluctuations for the last 11 500 years.

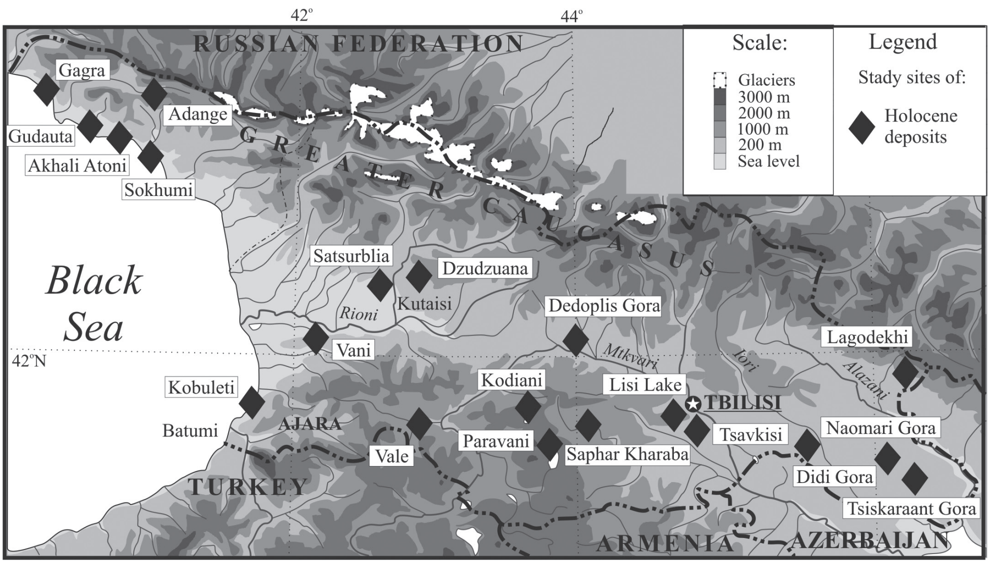

Fig.24. Locations of the profiles and archaeological sites studied from Georgia

In Georgia, palynological study of Holocene marine sediments began in the early 1970s (Shatilova, 1974). Extensive drilling of the Black Sea shelf and estuarine sediments was performed as part of engineering-geological surveys near coastal resorts and sanatoriums (Fig.24). Drilling was performed from the scientific ship "Geochimik" and during 1978-1984 a substantial body of core material was collected and studied using many methods of the natural sciences, including palaeogeographical, paleontological, geomorphological, geochronological and climatostratigraphical methods (Ostrovsky et al.,1977; Balabanov et al., 1981; Balabanov & Gei, 1981; Kvavadze & Dzheiranashvili, 1985; Balabanov& Kvavadze, 1985; Fedorov, 1988).

Palynological and sedimentological results showed that the Black Sea reached its lowest level 18 – 17 thousand years BP. During this regression, corresponding to the last phase of the Würm Ice Age, the sea level was some 120m lower than today. Cooling was followed by intensive warming, glaciers began to melt and the New Black Sea transgression began. By the onset of the Holocene (11.5 thousand years ago) the sea-level rose by nearly 70 m (Tvalchrelidze et al., 2004). Subsequent sea-level changes, the climate of each of the Holocene transgression phases and human activity throughout the Holocene have all been topics for recent research in Georgia. The Caucasus, and Georgia in particular, is a region in which the manufacturing economy that forms the basis of modern civilization originated during the first stages of the Holocene (Trifonov & Karakhanyan, 2004). According to radiocarbon dates, early agricultural settlements in the southern part of Georgia date to the early 6^{th} millennium B.C. (Hansen et al., 2007).

The Black Sea shelf sediments studied comprise mostly fine grained sands, silt and clay (Kvavadze & Rukhadze, 1989). The depth of Holocene sediments in the region varies from 17 m (borehole 120) to 27.8 (borehole 511). Material from 26 boreholes was studied palynologically: 7 of these were located in the Gagra area (boreholes 603, 607, 609, 613, 424 and Gagra-1), while borehole 471 was drilled nearby in the continental zone (Table XIX).

To the south-west of Gagra lies the Gudauta shelf zone, where boreholes 120 and 521 were drilled to a depth of 9.5 and 31.8 m respectively.

In the Akhali Atoni area, borehole 511 (at a depth of 21.1 m) was collected. Boreholes 55, 39, 182, 128 and 149 were drilled nearby on the alluvial-marine terrace.

Boreholes 732 and 721 come from the Sokhumi coastal area, at a depth of 9.8 and 14.9 m on the shelf, where Holocene sediments are represented most completely. Borehole 36 was drilled here in the continental part near the shelf (Table XIX).

Table XIX. Database of Holocene profiles studied

Profile name	**Date and sampling frequency**	**Lower depth of profiles**	**Number of samples**	**Sediment type**
Gagra area:				
Gagra-603	1981, every 50 cm	25.5m	5	Marine
Gagra-1	1971, every 10 cm	70cm	10	Marine + peat
Gagra-607	1981, every 50 cm	37m	12	Marine
Gagra-609	1981, every 50 cm	15m	12	Marine
Gagra-613	1981, every 50 cm	32m	9	Marine
Gagra-424	1978, every 50 cm	12m	5	Marine
Gagra-471	1978, every 10 cm	28m	66	Peat

Gudauta area:				
Gudauta-120	1983, every 50 cm	9.5m	17	Marine
Gudauta-521	1983, every 50 cm	31.8m	20	Marine
Akhali Atoni area:				
Akhali Atoni-511	1984, every 10 cm	21.1m	35	Marine
Akhali Atoni-55	1982, every 50 cm	24m	12	Alluvial
Akhali Atoni-128	1983, every 50 cm	9m	6	Alluvial
Akhali Atoni-182	1983, every 50 cm	16m	7	Alluvial
Akhali Atoni - 49	1983, every 50 cm	17m	4	Alluvial
Akhali Atoni -39	1983, every 50 cm	12.5m	8	Alluvial
Sokhumi area:				
Sokhumi-721	1980, every 10 cm	21m	60	Marine
Sokhumi-723	1980, every 10 cm	26m	50	Marine
Sokhumi-36	1980, every 10 cm	45m	120	Alluvial + peat
Kobuleti area:				
Kobuleti-22	1984, every 10 cm	22.6m	99	Marine
Kobuleti-35	1984, every 10 cm	120m	120	Alluvial + peat
Kobuleti-39	1984, every 10 cm	27m	25	Alluvial + peat
Ispani II	2003, every 10 cm	9.5m	47	Peat
Supsa-1	1972, every 20 cm	6.5m	33	Alluvial + lake
Supsa-2	1972, every 20 cm	7.8m	42	Alluvial + lake
Supsa-3	1972, every 20 cm	3m	17	Alluvual
Supsa-4	1972, every 20 cm	2.1m	17	Alluvial

The Kobuleti area lies on the southernmost sector of the Georgian coastline. Here borehole 22 was drilled between the Choloki and Kintrishi river mouths at a depth of 7.3 m on the shelf. Boreholes 35 and 39 come from the continental area. Profiles Ispani II, Supsa 1, 2, 3, 4 were also studied in this area.

Table XX provides the results of radiocarbon dating of organic remains found in these marine and continental sediments (Uncalibrated age, ^{14}C yr. BP).

Table XX. Radiocarbon dating of borehole sediments on the shelf of the Black Sea (eastern part)

Borehole	**Core depth (m)**	**Material analyzed**	**Age (^{14}C yr $_{BP}$**
Gagra-416	4.5	Peat	2450±80
Sokhumi-723	6.4	Shell	3335±50
Sokhumi-723	7.5	Archaeolog.	3500±50
Gagra-1	6.5	Peat	3690±120
Gagra-609	24.4	Shell	4000±140
Gagra-607	21.1	Shell	4140±160
Akhali Atoni-55	15	Shell	5200±80
Gagra-607	34.5	Shell	5410±320
Sokhumi-723	11.2	Shell	5540±60
Akhali Atoni-55	23	Shell	6780±120

Sokhumi-723	14	Shell	7630±250
Sokhumi-723	20.1	Shell	8690±300
Sokhumi-722	26	Peat	9310±80
Gudauta-120	17	Shell	11000±150
Supsa-1	2.20	Wood	1260±120
Ispani-II	5.20	Wood	1940±40
Ispani-II	6.95	Wood	4060±40
Ispani-II	9.45	Wood	4900±40

Palynological analysis of Holocene sediments in 5 study areas showed that, in the more complete pollen diagrams, 5 regional palynozones can be distinguished (Fig. 25, 26, 27, 28). Palynozone I is assigned to the Pre-Boreal period, palynozone II to the Boreal period, palynozone III to the Atlantic period, palynozone IV to the Sub-Boreal period and palynozone V covers the Subatlantic period.

Palynozone I differs from the underlying Younger Dryas sediments its greater representation of thermophilous arboreal taxa such as chestnut and oak (Fig.25). The zone itself is indicated by a Fagus-Carpinus-Abies association. Note, for comparison, that during the Younger Dryas only high-mountain vegetation elements prevailed. Palynozone I is divided into two subzones, the first reflecting more arid climatic conditions compared to the second. Redeposited pollen is found in significantly less quantity (up to 25 - 27% of the total pollen) in Pre-Boreal strata compared to the Younger Dryas (up to 46%).

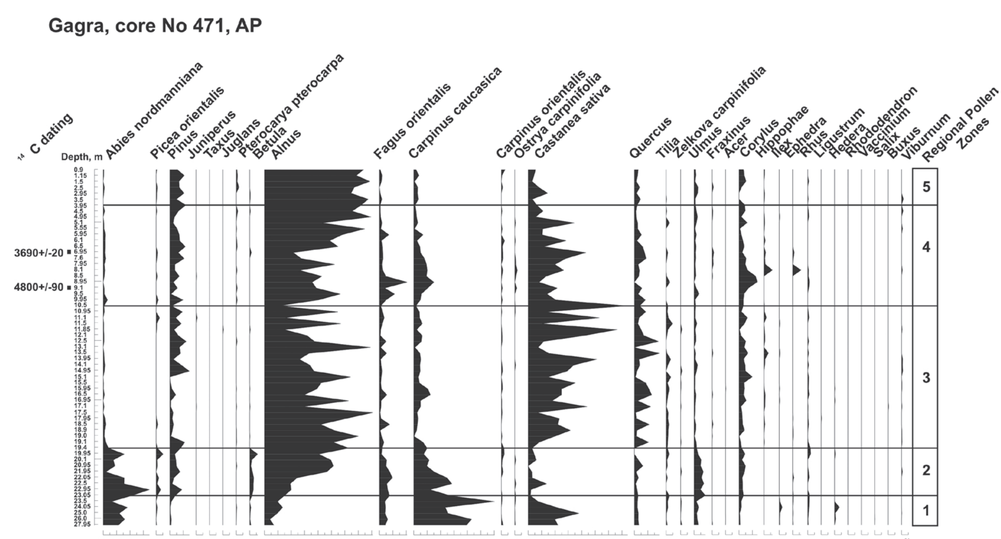

Fig.25. Palynological diagram of lagoon and mire sediments from the Kolkhidka river mouth (Gagra area) exposed in borehole 471.

Palynozone II covers the Boreal period and is indicated by an Abies-Fagus-Picea association. In all diagrams, pollen representing piedmont forest elements decreases, while high mountain forest indicators increase. In the Gagra area, where high mountains front the coast, subalpine vegetation (e.g. birch) is also clearly reflected in the spectra. This is the "coldest" palynozone, and is divided into three subzones. The first and the third subzone exhibit stronger climatic aridity than the second subzone. It should be mentioned that in this palynozone redeposited pollen reaches maximum values – up to 60-62% of the total pollen sum.

Palynozone III reflects radical changes in pollen assemblages and corresponds to the Atlantic period. In almost all the study area, pollen diagrams show a prevalence of chestnut and oak pollen. This zone is indicated by Castanea-Alnus-Quercus throughout Georgia. The occurrence of thermophile species, such as *Pterocarya pterocarpa, Juglans regia, Tilia caucasica* and *Zelkova carpinifolia*, increases significantly. This palynozone is divided into three subzones, the second exhibiting some climatic cooling represented in the diagrams by an increase in high mountain forest elements (fir, beech and spruce). As a whole, the Atlantic period was the warmest and most humid period during the Holocene in this region. Maximum warmth and humidity occurred during its second half. The amount of redeposited pollen in sediments of the Atlantic period decreases significantly (<20%).

Palynozone IV in the study area has no equivalent in the Blytt-Sernander terminology. This may be explained by a stronger anthropogenic effect with spatially variable impact. Nevertheless, the diagrams clearly show an increase in the pollen of cold-tolerant vegetation components and a decrease in the pollen of thermophilous species. The spectra also suggest an increase in aridity. Alnus pollen becomes dominant along the coast, which together with an increasing role of *Pteridium aqulinum* and *Rhododendron luteum*, indicates forest felling and swamp drainage. Subdominants include beech and fir, while pine is also prevalent. The climate of the first half of the Sub-Boreal period on the Black Sea coast of Georgia was more arid compared both to the previous and subsequent periods. The palynozone is divided into two subzones in some diagrams, where the first half is distinguished by higher aridity than the other. Rredeposited pollen occurs up to 45%.

Palynozone V corresponds to the Subatlantic period. It is indicated by an Alnus-Pinus-Castanea association in the northern part and Pinus-Alnus-Castanea in the southern part (Kobuleti area). High mountain vegetation indicators decrease to minimum values in palynozone V. Fir, spruce and birch pollen is found only as single grains. In the Gagra area, which has been more thoroughly investigated, palynozone V is divided into three subzones, the second reflecting warmer and more humid climatic conditions. *Pterocarya pterocarpa* pollen content increases rather significantly and redeposited pollen are few throughout the whole palynozone (up to 20%).

The occurrence of distinct palynozones is due to vegetation and climate dynamics in the eastern part of the Black Sea coast during the Holocene. The close proximity of mountain ranges facilitated a detailed and clear reflection of change in all the altitudinal vegetation belts of the region. This is explained by the specific character of pollen spectra of marine sediments in which regional vegetation is more clearly reflected compared to spectra from continental deposits.

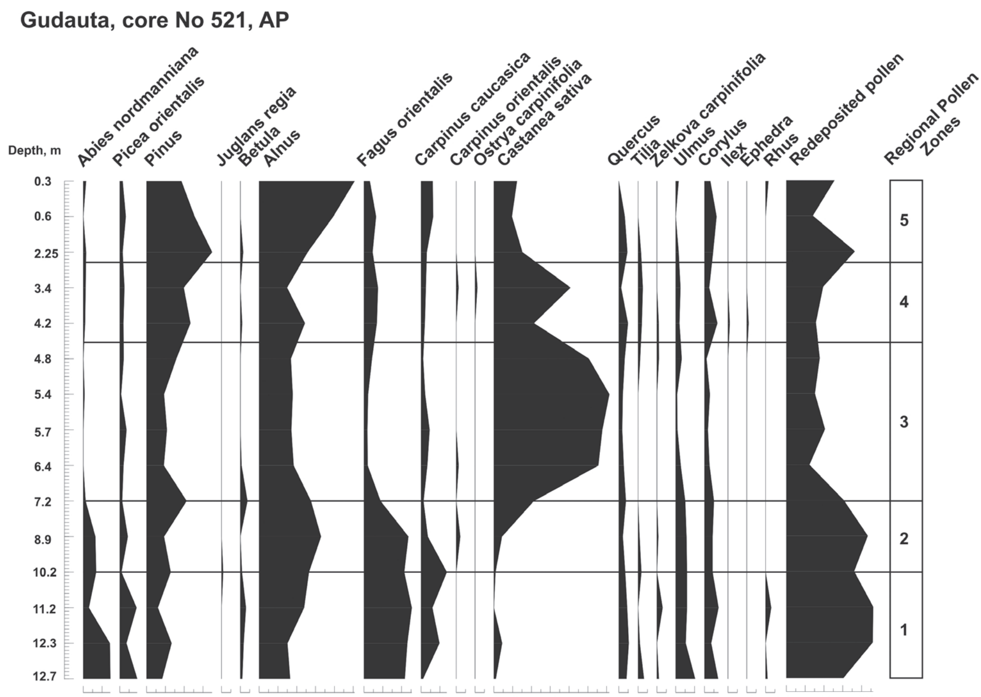

Fig.26. Palynological diagram of marine sediments from the Gudauta shelf exposed in borehole 521.

Regional paleozones derived from analysis of marine, lagoon and alluvial sediments represent the major events in the Holocene development of vegetation in the Caucasus region. Marine sediments, in particular, show major shifts in species dominance that reflect changes in vegetation in all altitudinal belts, thanks to the proximity of mountain ranges to the Black Sea. In this case the Black Sea can be regarded as a natural pollen trap in which pollen accumulated for the last ten thousand radiocarbon years. Importantly, there are no gaps in the record and therefore we have a complete and detailed picture of palaeoecological events. Statistical processing of the palynological material using the software "Paleoclimate 1" (Bukreeva, 1990) allowed us to reconstruct quantitative indices of the climate and to reconstruct oscillations of the upper tree limit in response to climatic fluctuations (Kvavadze et al. 1992, 1994). In addition to marine palynospectra, palaeoecological reconstruction also incorporates pollen data from alluvial and lagoon sediments along the coastline and from the high mountains of Abkhasia (Kvavadze et al., 1992).

In the first stage, very early in the Holocene, sedimentological data (Tvalchrelidze et al., 2004) indicate that the Black Sea level was 50-60 m lower than nowadays. The timberline was 800-850 m lower than now (Kvavadze & Connor, 2005). Comparing the earliest Holocene pollen spectra with those of the Younger Dryas, it is clear that broad-leaved forests of hornbeam, oak, chestnut and wingnut expanded. This process was due to warmer, wetter climatic conditions. During the Younger Dryas, July mean temperature on the coast was reconstructed as 18.3°C, while in the Preboreal it rose to 23.3°C.

The second stage of landscape development corresponds to the Boreal period when the long-term process of warming was interrupted by short-term cooling. The sea-level lowered by approximately 1-1.5 m. The timberline also descended significantly. Forests of beech and fir broadened. Reconstructed temperatures on the coastline were 19.4°C in July and 3.3°C in January (mean annual temperature 10.7°C). Precipitation was about 1827 mm per year.

The third stage occurred during the warming of the Atlantic period. This stage was quite long and resulted in rather substantial changes in altitudinal vegetation zones. Rapid ascent of all vegetation belts began during this stage. Upper mountain belts of dark coniferous forests migrated upslope and narrowed in their altitudinal range. At the same time, the area of broad-leaved chestnut, oak, wingnut and zelkova forests expanded substantially (Kvavadze & Connor, 2005). Paludification of the coastline led to the expansion of boggy areas. Temperatures and humidity increased, reaching maximum 6000-5500 years ago. Compared with the Boreal, winter temperatures on the coastline nearly doubled and reached 6-6.5°C. In mountains far from the sea, climatic warming was particularly intensive. In Abkhazia, Adjara and Svaneti, the timberline ascended 300 m during the peak of the Holocene climatic optimum (Kvavadze & Rukhadze, 1989; Connor et al., 2007; Margalitadze, 1995), while in the mountains of the South Georgian Upland it ascended no less than 400-500 m.

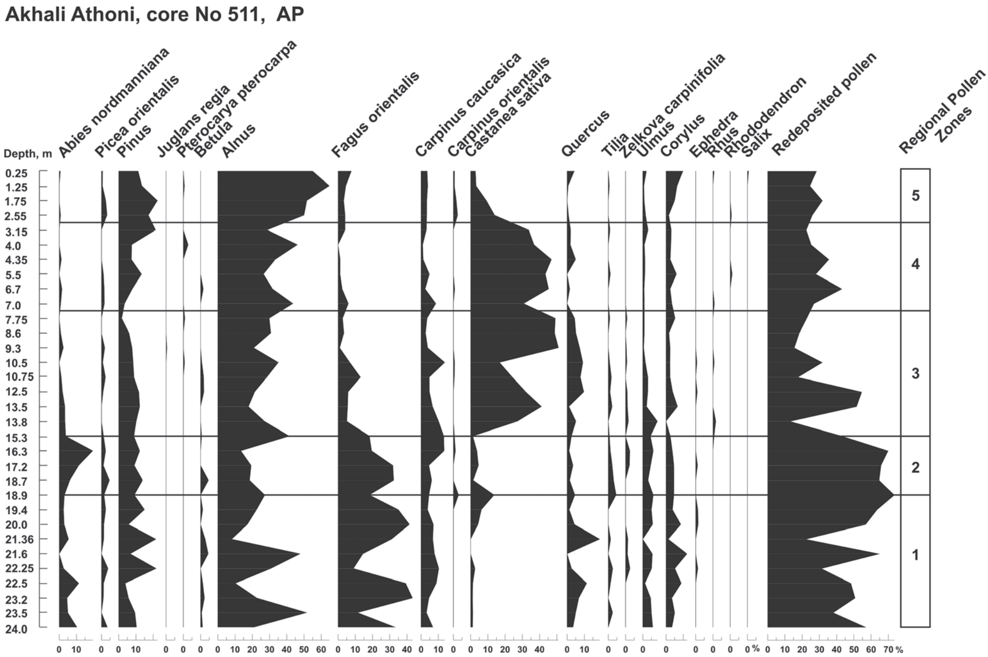

Fig.27. Palynological diagram of marine sediments from the Akhali-Atoni shelf exposed in borehole 511.

The sea level during the Atlantic period rose rapidly and, between 6000-5500 years, exceeded its present-day level by some meters (Tvalchrelidze et al., 2004).

It was under the warm and humid conditions of the Atlantic period that the first early agricultural settlements appeared in the south-east of Georgia. Palynological studies of cultural layers in the settlement mounds of Gadachrili Gora and Arukhlo, dated to the 6th-5th millennia B. C., indicated a warmer, more humid climate. In place of present-day steppes there grew forests of alder, wing-nut, hornbeam and oak (Gogichaishvili, 1984; 1990). Humans, besides grain-growing, were engaged in viticulture. In the lower layers of Gadachrili Gora, a piece of loom-woven flax fabric was found and imprints of hand-knitted flax fabric were discovered in ceramic vessels. These finds, as well as macroremains of toadflax seeds (Rusishvili, 1990), suggest the existence of local weaving. Toadflax, *Linum usitatisimum,* grows only under humid climatic conditions (Zohary & Hopf, 1993). Microremains of numerous flax fibres and woollen fabric, including coloured fibres, were also revealed during palynological study of material (cultural layers and pot contents) from Neolithic layers at these sites. Pollen analysis of organic material found in ceramic vessels provides evidence of beekeeping.

Data from the investigation of archaeological monuments in the South Georgian Uplands are also very interesting. Material from the Early Kurgan epoch of Javakheti (beginning of the third millennium B.C.) shows the existence of agriculture at an altitude of 2000-2800 m. In this period forest vegetation with oak and lime occurred at these altitudes (Kvavadze et al., 2007), whereas today these forests occur at lower altitudes: 1700-1800 m (Dolukhanov, 1989; Nakhutsrishvili, 1999).

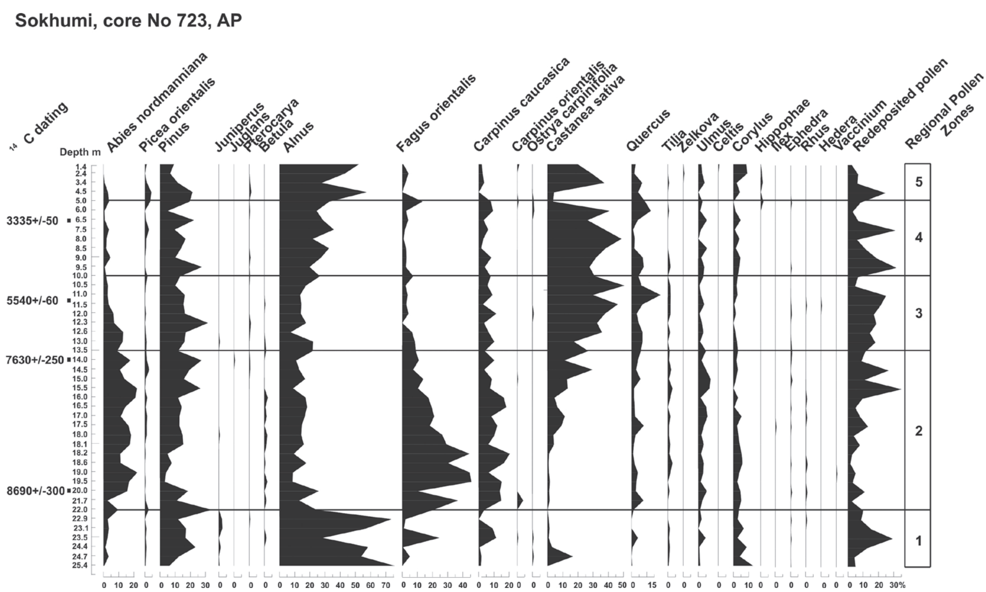

Fig.28. Palynological diagram of marine sediments from the Sokhumi shelf exposed in borehole 723.

During the Atlantic period, the process of warming was interrupted twice by mild, short-lived cooling. This process is seen in the curves of both timberline oscillations and Black Sea fluctuations (Kvavadze et al.,1992; Tvalchrelidze et al.,2004).

The fourth stage in landscape development is characterised by significant climate cooling, causing the Phanagorian regression in the Black Sea. In the Subboreal period, erosion processes accelerated, indicated by the increase in redeposited pollen in marine sediments. This increased erosion is explained by base-level lowering in Colchic river systems.

This period witnessed a lowering of zonal vegetation belts. The timberline was 600-550 m lower than nowadays. At the same time, the area of chestnut and other thermophilous species decreased, as indicated in all pollen diagrams. Cooling was accompanied by a moderate decrease in humidity.

In the second half of the Subboreal period, between 3800-2500, a change in climatic conditions is observed. The Black Sea rose to levels somewhat higher than today. This warming manifested itself clearly, not only in the lowland territories adjacent to the sea (Kvavadze & Connor, 2005; Connor et al., 2007, 2007a; Arabuli et al., 2007), but also on the mountain plateaux of Southern Georgia. Palynological studies of archaeological sites (Safar-Kharaba and Imera burials) indicate that, during the 15th-14th centuries B.C., agriculture, horticulture and viticulture were practised at an altitude of 1700-1800 m. Forests comprised oak, lime, zelkova and other species (Kvavadze et al., 2007). Here, for the first time, cotton fabric and fibres were discovered, indicating a well-developed trade between India and the Caucasus (Kvavadze & Narimanishvili, 2006, 2006a). In Colchis and regions more remote from the Black Sea, signs of forest destruction can be observed in this stage (Connor et al., 2007).

The fifth stage coincides with the Subatlantic period. Around 2500 years ago, a short-term, but pronounced, cooling took place, resulting in a Black Sea regression. The sea-level lowered nearly 20 m compared to the end of the Subboreal. In high mountain areas, agriculture was replaced by stock-breeding. Viticulture went into decline at high altitudes and was not even developed in the middle mountains (Bieniek & Licheli, 2007). The timberline descended nearly 350-400 m compared to the present-day level. Then, five centuries later (2000 years ago), significant climate warming occurred, resulting in the Nymphaean transgression in the Black Sea. The sea-level again rose some metres higher than nowadays. Climate warming was accompanied by an increase in humidity on the Black Sea coast. In antiquity, according to palynological and palaeoethnobotanical studies of cultural layers in the Eshera and Nokalakevi settlements, flax-growing was very intensively developed (Rukhadze et al., 1988; Bokeria et al., 2009). Moreover, the population of Colchis of the time was engaged in grain-growing, gardening and viticulture. Cultivation of olives imported from Greece began.

Intensive deforestation took place as agriculture developed on the coastal lowlands and in the piedmonts of Colchis. This process is indicated in palynological spectra by the increasing role of pollen from secondary vegetation.

The 3th - 4th centuries A.D. were rather cool, followed by a period of warming from the 7th to 11th centuries. At that time, human population density increased in the high mountains and agriculture, including viticulture, occupied a prominent place in the economy (Kvavadze et al., 2007, 2007a; Arabuli et al., 2008). Areas under olive plantation increased, as indicated by the pollen record (Connor & Kvavadze, 2005).

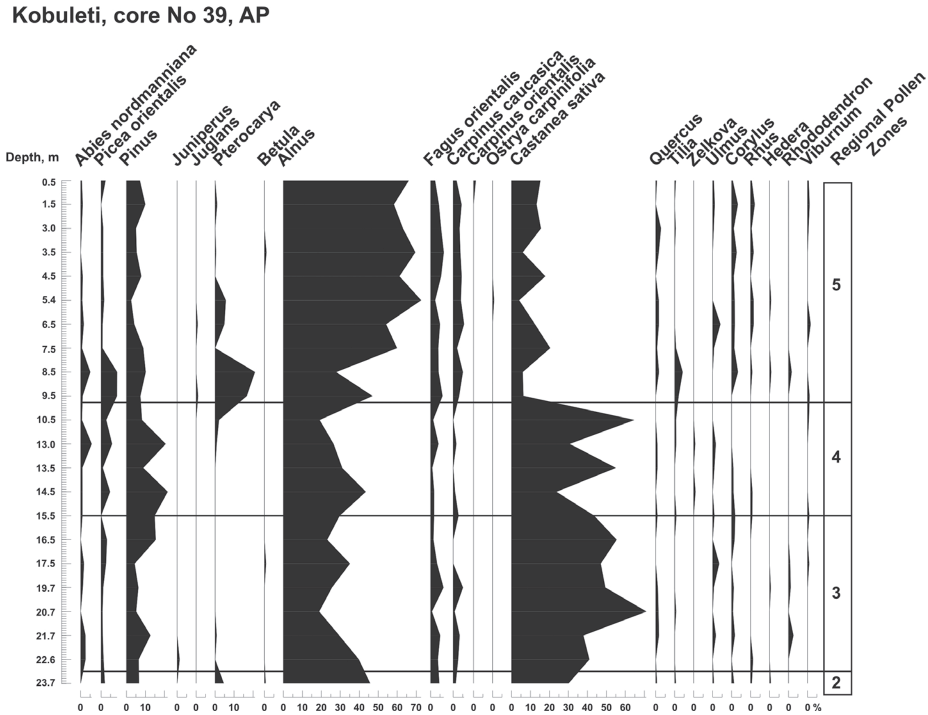

Fig.29. Palynological diagram of marine sediments from the Kobuleti shelf exposed in borehole 39.

During the 12th-14th centuries, climatic conditions again deteriorated, but switched back during the 15th-16th centuries, according to palynological data. Viticulture and wine-making developed intensively in the mountains of Southern Georgia. A palynological study of material from cultural layers and vessels from the Atskuri settlement at 1200 m altitude showed that, here, besides the vine, olives were also cultivated (Kvavadze & Licheli, 2009). According to historical documents, olive plantations were also to be found in the gorge of the Khrami River, in its headwaters, and in many places in the Colchis lowlands (Ketskhoveli, 1959).

This rather significant and long-term warming lasted nearly 200 years. In the second half of the 17th century, the short-term, but very strong, global cooling of the Little Ice Age took place. Though it lasted perhaps only 40 years (1675 – 1715) (Grove, 1997), it exerted a strong influence on landscapes. Since that time, in Atskuri and in other mountains settlements, viticulture was no longer practised (Kvavadze & Licheli, 2009). Olive plantations were completely destroyed by frost everywhere in Georgia (Ketskhoveli, 1959).

The comparison of our scheme of Holocene climate changes with similar schemes from mountainous territories in southern Europe and the Near East shows a very good agreement, especially for the second half of the Holocene (Le Roy Ladurie, 1971; Grove, 1997; Ramezani et al., 2008). It demonstrates the global character of climatic fluctuations that had feedback effects on sea-levels in Southern Europe, including the Black Sea (Fig.30).

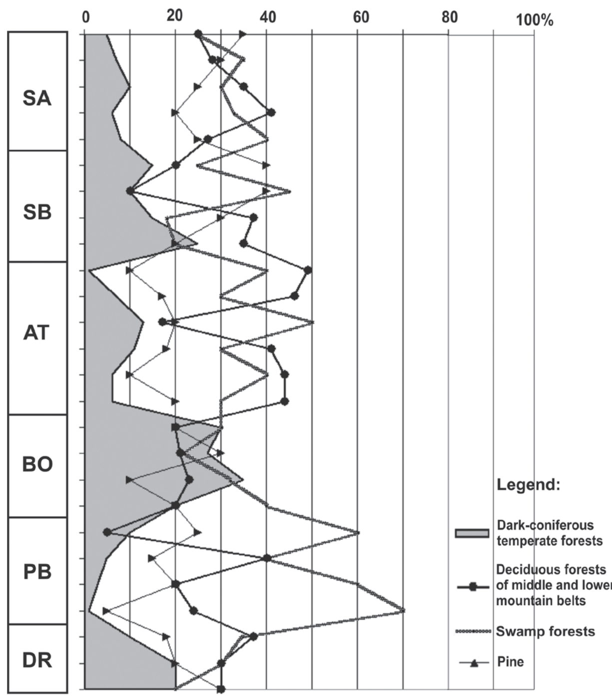

Fig.30. Percentage fluctuations in palynological groups in Western Georgia during the Holocene, reflecting changes in the distribution of the main forest formations.

The palynological study of numerous profiles of Holocene sediments at different altitudes in the Georgian mountains, as well as the study of cultural layers of archaeological monuments, indicated the occurrence of six major climatic optima during the Holocene. The three most significant were the Atlantic optimum, Subboreal optimum and the Medieval optimum. The Atlantic optimum lasted between 6000 and 5500 Cal. yr BP. In Western Georgia, the upper tree line was elevated by as much as 300 m above its present-day level. In the South Georgian Uplands the tree line may have been 500-600 m higher (Kvavadze et al., 2007). The contrasting topography of this area, from the extensive volcanic plains to the abrupt craters and cones of the ranges, allows both climate and human impact to be reconstructed, since the plains were the main loci of human activity, while the peaks were left relatively undisturbed. In pollen diagrams, human impact does not suppress the climatic signals, but, on the contrary, it enhances them. At that time both grain farming and gardening, including wine-growing, were developed on high mountain plateaux. Intensive agricultural development here was facilitated not only by climatic warming, but also by fertile mountain soils formed over volcanic alkaline rocks. Anthropogenic indicator pollen types increased during this period, including Cerealia, *Juglans regia,* Corylus and *Vitis vinifera*. This feature manifests most vividly in material from archaeological sites of the Early Bronze Age (Kura-Araxes culture) at altitudes of 1450-1800m. The combination of maximum Juglans-Corylus-Vitis pollen coincides witha *Quercus iberica* maximum, indicating a relatively warm climate in this area.

A second significant optimum is recorded in Late Holocene pollen spectra dating to 3800-2500 Cal. yr BP (Subboreal). In Western Georgia the area of chestnut forests increased, whereas in Eastern Georgia Zelkova and oak forests expanded. Humans again engaged in high mountain agricultureand agriculture, viticulture, horticulture and apiculture developed in the mountains at altitudes of 1600-1700 m. Mountain forest patches existed side-by-side with human settlements.

The latest significant optimum is recorded around 1350-800 Cal. yr BP and the impact of human activity on vegetation becomes more perceptible at this time. Deforestation took place not only on the plains and lowlands, but also on steeper mountain slopes. During this period semi-forested landscapes appear in many areas, which, during the past few centuries, were converted into completely deforested cultural landscapes (Connor & Kvavadze, 2008).

A list of the Holocene flora of Georgia is given in Table XXI.

Table XXI. Plants from Holocene deposits in Georgia
Key: m – macrofossils; p – pollen

Class	Family	Species	W.Georgia	E.Georgia
1	**2**	**3**	**4**	**5**
Bryopsida	Sphagnaceae	Sphagnum sp.	p	p
Lycopodiopsida	Lycopodiaceae	Lycopodium alpinum L.	p	p
		Lycopodium annotinum L.	p	p
		Lycopodium clavatum L.	p	p
		Lycopodium innundatum L.	p	p
		Lycopodium selago L.	p	p
		Lycopodium sp.	p	p
Isoëtopsida	Selaginellaceae	Selaginella helvetica (L.) Link.	p	p
		Selaginella selaginoides (L.) Link.	p	p

1	2	3	4	5
Equisetopsida	Equisetaceae	Equisetum sp.		p
Ophioglossopsida	Ophioglossaceae	Bothrychium lunaria (L.) Sw.	p	p
		Bothrychium sp.		p
		Ophioglossum vulgatum L.	p	p
		Ophioglossum sp.	p	p
Polypodiopsida	Osmundaceae	Osmunda regalis L.	p	p
	Pteridaceae	Cryptogramma crispa (L.) R.Br.		p
		Cryptogramma sp.	p	
		Pteris cretica L.	p	
	Adiantaceae	Adiantum sp.	p	p
		Anogramma sp.	p	
	Polypodiaceae	Blechnum sp.		p
		Polypodium serratum (Willd.) Futo	p	
		Polypodium vulgare L.	p	p
		Polypodium sp.	p	p
		Polypodiaceae gen.indet.		p
	Dennstaedtiaceae	Pteridium aquilinum (L.) Ruhn.	p	p
		Pteridium sp.	p	p
	Aspleniaceae	Asplenium sp.	p	p
	Aspidiaceae	Athyrium filix femina (L.) Röth	p	p
		Athyrium sp.		p
		Cystopteris sp.		p
		Dryopteris filix –mas (L.) Schott.		p
		Dryopteris thelypteris L.	p	
		Dryopteris sp.		p
		Polystichum sp.	p	p
		Woodsia sp.	p	
Pinopsida	Taxaceae	Taxus baccata L.	mp	p
		Taxus sp.		p
	Pinaceae	Abies nordmanniana (Stev.) Spach.	p	p
		Abies sp.		p
		Cedrus libani Laws.		p
		Cedrus sp.		p
		Picea orientalis L.	p	
		Picea sp.		p
		Pinus kochiana Klotzsch.	p	
		Pinus pithyusa Strangw.	p	
		Pinus sp.		p
	Cupressaceae	Juniperus communis L.	p	p
		Juniperus sp.		p
		Cupressaceae gen.indet.	p	

1	2	3	4	5
Gnetopsida	Ephedraceae	Ephedra distachia L.		P
		Ephedra procera Fisch. et Mey		p
		Ephedra sp.	p	p
Dicotyledoneae	Juglandaceae	Juglans regia L.	mp	p
		Juglans sp.	p	
		Pterocarya pterocarpa (Michx.) Kunth.	mp	p
		Pterocarya sp.	p	p
	Salicaceae	Populus sp.		p
		Salix sp.	mp	p
		Salicaceae gen.indet.	p	
	Betulaceae	Alnus barbata C.A.M.	mp	p
		Alnus incana (L.) Moench.	p	
		Alnus sp.	mp	p
		Betula sp.	p	p
		Carpinus betulus L.		p
		Carpinus caucasica Grossh.	mp	p
		Carpinus orientalis Mill.	mp	p
		Corylus avellana L.	mp	
		Corylus colurna L.	p	
		Corylus iberica Wittm.et Ket.-Nath.	p	
		Corylus sp.	p	p
		Ostrya carpinifolia Scop.	p	p
	Fagaceae	Castanea sativa Mill.	p	p
		Castanea sp.	p	p
		Fagus orientalis Lipsky	mp	p
		Fagus sp.		p
		Quercus hartwissiana Stev.	m	
		Quercus sp.	p	p
	Ulmaceae	Celtis caucasica Willd.	p	
		Celtis sp.		p
		Ulmus sp.	p	p
		Zelkova carpinifolia (Pall.) Dipp.	p	p
		Zelkova sp.	p	
	Moraceae	Ficus carica L.	mp	
		Morus alba L.	m	p
		Morus sp.	p	p
	Cannabaceae	Cannabis sp.		p
		Humulus sp.	p	
	Urticaceae	Parietaria sp.		p
		Urtica sp.	p	p
		Urticaceae gen.indet.	p	
	Loranthaceae	Viscum sp.	p	
		Loranthaceae gen.indet.	p	

1	2	3	4	5
Dicotyledoneae	Polygonaceae	Fagopirum sp.		p
		Oxyria sp.	p	
		Polygonum alpestre C.A.Mey		p
		Polygonum amphibium L.	p	p
		Polygonum aviculare l.	m	
		Polygonum bistorta L.		p
		Polygonum convolvulus L.		p
		Polygonum hydropiper L.	m	
		Polygonum lapathifolium L.	m	
		Polygonum minus Huds.	m	
		Polygonum persicaria L.	m	p
		Polygonum viviparum L.		p
		Polygonum sp.	p	p
		Rumex alpestris Jacq.	m	
		Rumex crispus L.	m	
		Rumex obtusifolium L.	m	
		Rumex sp.	p	p
		Polygonaceae gen.indet.	p	p
	Portulacaceae	Portulaca oleracea L.	m	
	Caryophyllaceae	Agrostemma githago L.		p
		Agrostemma sp.		p
		Arenaria serpillifolia L.		m
		Cerastium sp.		p
		Dianthus sp.		P
		Gypsophila sp.		P
		Herniaria sp.		p
		Moehringia trinervia (L.) Clairv.	m	
		Saponaria officinalis L.	m	
		Silene italica (L.) Pers.	m	p
		Silene sp.	p	
		Spergularia campestris (L.) Aschers		m
		Stellaria nemorum L.	m	p
		Caryophyllaceae gen.indet.	mp	p
	Chenopodiaceae	Chenopodium album L.	m	
		Chenopodium polyspermum L	m	
		Chenopodium sp.		p
		Kochia sp.		p
		Salsola sp.	p	
		Chenopodiaceae gen.indet.	p	p
	Amaranthaceae	Amaranthus retroflexus L.	m	m
		Amaranthus sp.	p	
	Lauraceae	Laurus sp.	p	
		Lauraceae gen.indet.	p	

1	2	3	4	5
Dicotyledoneae	Ranunculaceae	Adonis vernalis L.		P
		Adonis aestivalis L.		P
		Anemone sp.		p
		Aconitum sp.		P
		Caltha sp.	p	p
		Ranunculus acer L.	m	
		Ranunculus arvensis L.	m	p
		Ranunculus bulbosus L.	m	m
		Ranunculus chius DC	m	
		Ranunculus lingua L.	m	
		Ranunculus repens L.	m	
		Ranunculus sceleratus L.	m	
		Ranunculus subtilis Trautv.	m	
		Ranunculus sp.	p	p
		Thalictrum minus L.		m
		Thalictrum sp.	p	p
		Trollius sp.		p
		Ranunculaceae gen.indet.	p	p
	Saxifragaceae	Chrysosplenium sp.		p
		Parnassia palustris L.		p
		Ribes sp.		p
		Saxifraga folia L.		p
		Saxifragaceae gen.indet.		p
	Crassulaceae	Sedum sp.		p
		Crassulaceae gen.indet.		p
	Berberidaceae	Berberis cf. vulgaris L.		m
		Berberis sp.	mp	p
	Nymphaeaceae	Nuphar sp.	p	
		Nymphaea alba L.		p
		Nymphaea sp.	p	
		Nymphaeaceae gen.indet.	p	
	Aristolochiaceae	Asarum caucasicum (Ducharte) Kolak.	m	
	Ceratophyllaceae	Ceratophyllum sp.	m	
	Papaveraceae	Chelidonium sp.		P
		Corydalis sp.		P
		Fumaria officinalis L.		m
		Glaucium sp.		p
		Papaver dubium L.		m
		Papaver sp.		p
		Papaveraceae gen.indet.	p	
	Brassicaceae	Alyssum parvifolium M.B.		m
		Camelina sp.		p
		Neslia paniculata (L.) Desv.		m
		Sinapis sp.	p	p
		Brassicaceae gen.indet.	p	p

1	2	3	4	5
Dicotyledoneae	Hypericaceae	Hypericum caucasicum (Woron.) Goraschk.	m	
		Hypericum perforatum L.		p
		Hypericum sp.		P
	Platanaceae	Platanus sp.		p
	Rosaceae	Agrimonia eupatoria l.	m	p
		Alchemilla caucasica Bus.	m	
		Alchemilla sericea Willd.	m	
		Alchemilla sp.		p
		Cerasus avium (L.) Moench.	m	
		Cerasus vulgaris Mill.	m	
		Crataegus microphylla C.Koch.	m	
		Crataegus pentagyna Wald. et Kit.	m	m
		Crataegus sp.	p	p
		Filipendula sp.	p	p
		Fragaria sp.		p
		Geum sp.		p
		Malus orientalis Uglitzk.	m	
		Malus silvestris Mill.	p	
		Potentilla anserina L.		m
		Potentilla brachypetala Fisch.	m	
		Potentilla crantzii (Crantz) Beck.	m	
		Potentilla elatior Willd.ex Schlecht.	m	
		Potentilla erecta (L.) Hampe	m	m
		Potentilla micrantha Ramond.	m	
		Potentilla ruprechtii Boiss.	m	
		Potentilla sp.	p	p
		Prunus divaricata Lebed.	m	
		Prunus spinosa L.	m	
		Prunus sp.		p
		Pyrus caucasica Fed.	m	
		Pyrus sp.		p
		Rosa canina L.	m	
		Rosa sp.		p
		Rubus anatolicus Focke	m	
		Rubus arcticus L.		P
		Rubus caesius L.	m	
		Rubus candicans Weiche	m	
		Rubus caucasica Focke	m	
		Rubus saxatilis L.	m	
		Rubus sp.	p	p
		Sanguisorba officinalis L.		p
		Spiraea sp.		P
		Sorbus sp.	m	p

1	2	3	4	5
Dicotyledoneae	Rosaceae	Rosaceae gen.indet.	p	p
	Fabaceae	Astragalus stevenianum DC		p
		Lathyrus hirsutus L.	m	
		Lathyrus pratensis L.	m	
		Lathyrus sativus L.	m	
		Lens culinaris Medik	m	
		Lotus sp.	m	p
		Medicago arabica (L.) Hudson	m	
		Medicago minima Grufberg	m	
		Medicago sativa l.	m	
		Onobrychis viciifolia Scop.		m
		Onobrychis sp.	p	p
		Pisum sativum L.	m	
		Serratula sp,		P
		Trifolium campestre Schreb.		m
		Trifolium pratense L.	p	p
		Trifolium repens L.	p	p
		Trifolium sp.		p
		Vicia ervilia (L.) Willd.	m	
		Vicia faba L.	m	
		Vicia hirsuta (L.) S.F.Gray	m	
		Vicia tetrasperma (L.) Moench.	m	
		Vicia sp.	p	p
		Fabaceae gen.indet.	mp	p
	Geraniaceae	Geranium sp.		p
		Geraniaceae gen.indet.	p	
	Linaceae	Linum bienne Mill.	m	
		Linum catharticum L.		m
		Linum sp.		p
		Radiola sp.		p
	Zygophyllaceae	Tribulus terrestris L.	mp	m
	Euphorbiaceae	Euphorbia helioscopia L.	m	
		Euphorbia nutans Lag.	m	
		Euphorbia oblongifolia C.Koch.	m	m
		Euphorbia platyphyllos L.	m	m
		Mercurialis sp.	p	p
		Euphorbiaceae gen.indet.	p	
	Anacardiaceae	Cothinus sp.		p
		Pistacia sp.		p
		Rhus sp.	p	p
	Aceraceae	Acer campestre L.	m	
		Acer sp.	p	p
	Aquifoliaceae	Ilex colchica Pojark,	m	
		Ilex sp.	p	p
	Celastraceae	Euonymus sp.	p	p

1	2	3	4	5
Dicotyledoneae	Staphyleaceae	Staphylea colchica Stev.	m	
	Buxaceae	Buxus colchica A.Pojark.	mp	p
		Buxus sp.	p	p
	Rhamnaceae	Frangula alnus Mill.	mp	p
		Frangula sp.		p
		Paliurus spina-Christi Mill.		p
		Rhamnus imeretina Booth.	m	
		Rhamnus sp.	p	p
	Vitaceae	Vitis sylvestris Gmel.	m	
		Vitis vinifera L.	mp	p
		Vitis sp.	p	p
	Tiliaceae	Tilia caucasica Rupr.	mp	
		Tilia sp.	p	p
	Thymelaeaceae	Daphne sp.	p	
		Thymelaea passerina (L.) Coss. et Germ.		p
		Thymelaea sp.		p
	Violaceae	Viola alba L.	m	
		Viola arvensis Murr.		p
		Viola biflora L.	m	
		Viola canina L.	m	
		Viola palustris L.		p
		Viola reichenbachiana Jord.	m	
		Viola sp.		p
		Violaceae gen.indet..	p	p
	Cucurbitaceae	Trichosantes sp.	m	
		Cucurbitaceae gen.indet.	m	p
	Malvaceae	Abutilon theophrasti Medic.	m	
		Althea officinalis L.	m	
		Lavatera sp.		p
		Malva sp.		p
	Elaeagnaceae	Elaeagnus sp.	p	p
		Hippophaë rhamnoides L.	p	
		Hippophaë sp.	p	p
	Cistaceae	Helianthemum sp.		p
	Resedaceae	Reseda sp.		p
	Tamaricaceae	Myricaria sp.		p
		Tamarix sp.	p	
	Lythraceae	Lythrum sp.	m	p
	Onagraceae	Chamaenerium sp.	p	
		Epilobium algidum M.B.	m	
		Epilobium sp.		p
		Ludwigia sp.	p	
		Onagraceae gen.indet.	p	
	Trapaceae	Trapa colchica Albov	p	
		Trapa natans L.	p	
	Haloragaceae	Myriophyllum sp.	p	p

1	2	3	4	5
Dicotyledoneae	Cornaceae	Cornus mas L.	m	p
		Cornus sp.	p	
		Swida australis (C.A.M.) Pojark.	m	
	Araliaceae	Hedera colchica C.Koch.	p	
		Hedera helix L.	m	
		Hedera sp.	p	p
	Apiaceae	Aegopodium podagraria L.		m
		Aethusa cynapium l.	m	
		Ammi sp.		p
		Anethum graveolens L.	m	
		Antriscum sp.		P
		Astrantia maxima Pall.		P
		Astrantia sp.	p	p
		Bupleurum sp.	p	p
		Chaerophyllum sp.		p
		Daucus sp.		p
		Eryngium campestre L.		m
		Eryngium sp.	p	p
		Falcaria sp.	p	P
		Heracleum apiifolium Boiss.	m	
		Heracleum sp.	p	P
		Peucedanum palustre (L.) Moench.		p
		Peucedanum sp.	p	p
		Petroselinum crispum (Mill.) Nym.		m
		Pimpinella sp.	p	P
		Smirnium sp.		p
		Apiaceae gen.indet.	p	P
	Ericaceae	Calluna vulgaris (L.) Hill.	p	
		Erica sp.	p	
		Rhododendron caucasicum Pall.	p	p
		Rhododendron luteum Sweet.	p	
		Rhododendron ponticum L.	p	
		Rhododendron sp.	p	p
		Vaccinium sp.	p	p
		Ericaceae gen.indet.		p
	Phytolaccaceae	Phytolacca americana L.	m	
	Primulaceae	Androsace septentrionalis L.		m
		Cortusa sp.		P
		Glaux maritima L.		P
		Lysimachia vulgaris L.		p
		Primula farinosa L.	p	p
		Primula veris L.		p
		Primula sp.	p	p
		Samolus sp.		p
		Soldanella sp.		P

1	2	3	4	5
Dicotyledoneae	Primulaceae	Primulaceae gen.indet.	p	
	Plumbaginaceae	Armeria sp.		p
		Limonium vulgare L.		P
		Plumbago sp.		p
		Plumbaginaceae gen.indet.	p	p
	Verbenaceae	Verbena officinalis L.		m
		Verbena sp.		p
	Apocinaceae	Apocinum sp.	p	
	Gentianaceae	Gentiana campestris L.		p
		Gentiana detonsa Rottb.		p
		Centaurium sp.		p
	Oleaceae	Fraxinus sp.	p	p
		Jasminum sp.	p	
		Ligustrum vulgaris L.		p
		Ligustrum sp.	p	p
		Olea cf.europaea L.	p	p
	Rubiaceae	Galium aparine L.	m	
		Galium palustre L.		m
		Galium sp.	p	mp
		Rubiaceae gen.indet.	p	
	Boraginaceae	Echium vulgare L.		m
		Echium sp.		p
		Heliotropium suaveolens M.B.		m
		Lappula echinata Gilib.		m
		Nonea versicolor (Stev.) Sweet.		p
		Pulmonaria sp.	p	p
		Symphytum sp.	p	p
		Boraginaceae gen.indet.	p	p
	Solanaceae	Datura stramonium L.	m	
		Hiosciamus niger L.		p
		Physalis alkekengi L.	m	
		Solanum nigrum L.	m	p
		Solanum persicum Willd.	m	
		Solanaceae gen.indet.	p	
	Scrophulariaceae	Digitalis purpurea L.	p	p
		Digitalis sp.		p
		Melampirum pratense L.		p
		Melampirum sp.		P
		Pedicularis sp.	p	p
		Scrophularia sp.		p
		Veronica sp.	m	p
		Scrophulariaceae gen.indet.	p	p
	Convolvulaceae	Calystegia sepium (L.) R.Br.	m	
		Convolvulus arvensis L.	m	p
		Convolvulus sp.		p
	Cuscutaceae	Cuscuta sp.		p
	Polemoniaceae	Polemonium sp.		p

1	2	3	4	5
Dicotyledoneae	Plantaginaceae	Plantago lanceolata L.	p	p
		Plantago major L.	m	p
		Plantago maritima L.	p	p
		Plantago media L.		p
		Plantago sp.	p	
		Plantaginaceae gen.indet.	p	
	Lentibulariaceae	Pinguicula sp.		p
		Urticularia sp.	p	p
	Caprifoliaceae	Lonicera sp.	p	p
		Viburnum lantana L.	m	p
		Viburnum sp.	p	p
		Sambucus ebulus L.	mp	
		Sambucus nigra L.	mp	p
		Caprifoliaceae gen.indet.	p	
	Adoxaceae	Adoxa sp.		p
	Lamiaceae	Ajuga chia Schreb.	m	m
		Ajuga reptans L.	m	m
		Galeopsis bifida Boenn.	m	
		Lycopus europaeus L.	m	m
		Marrubium sp.	p	P
		Mentha sp.	p	p
		Prunella vulgaris L.		m
		Prunella sp.		p
		Salvia aethiopis L.	m	
		Salvia nutans L.	m	
		Salvia verticillata L.	m	
		Scutellaria sp.		p
		Sideritis sp.		p
		Stachys annua L.	m	m
		Stachys silvatica L.	m	p
		Stachys sp.		p
		Theucrium sp.	p	p
		Thymus caucasicus Willd.	m	
		Lamiaceae gen. indet.	p	p
	Valerianaceae	Valeriana sp.	p	p
		Valerianaceae gen.indet.	p	
	Dipsacaceae	Cephalaria sp.	p	
		Dipsacus sp.		p
		Knautia sp.	p	p
		Scabiosa sp.	p	p
		Dipsacaceae gen.indet.	p	p
	Callitrichaceae	Callitriche polymorpha Lönr.		p
	Campanulaceae	Campanula sp.	mp	p
		Phyteuma sp.		p
	Asteraceae	Achillea sp.	p	p
		Ambrosia sp.	P	p
		Anthemis sp.	P	p

1	2	3	4	5
Dicotyledoneae	Asteraceae	Arctium sp.		p
		Artemisia sp.	P	
		Aster sp.	P	
		Carduus sp.	p	mp
		Centaurea cyanus L.		p
		Centaurea phrigia L.		p
		Centaurea scabiosa L.		P
		Centaurea solstitialis L.	p	p
		Centaurea sp.		p
		Cichorium sp.	p	p
		Cirsium vulgare (Savi) Ten.		p
		Cirsium sp.	p	p
		Echinops sp.		p
		Grossheimia sp.		p
		Jurinea sp.		p
		Lapsana communis L.		m
		Rhinanthus sp.	p	
		Serratula sp.		p
		Siegesbeckia orientalis L.	m	p
		Taraxacum sp.		p
		Xanthium strumarium L.	m	
		Xanthium cf.spinosum L.		m
		Xanthium sp.	p	p
		Asteraceae gen.indet.	p	p
Monocotyledoneae	Alismataceae	Alisma plantago-aquatica L.		p
		Alisma sp.	p	p
		Alismataceae gen.indet.	p	
	Butomaceae	Butomus sp.		p
		Butomaceae gen.indet.	p	
	Hydrocharitaceae	Hydrocharitaceae gen.indet.	p	
	Juncaceae	Juncus filiformis L.	m	
		Juncus effusus L.	m	
		Juncus sp.	mp	
	Potamogetonaceae	Potamogeton natans L.	m	
		Potamogeton sp.	p	p
		Ruppia sp.		p
	Liliaceae	Allium sp.		p
		Colchicum speciosum Stew.		p
		Lilium sp.		p
		Gagea sp.		p
		Ornithogalum pyrenaicum L.		m
		Tulipa silvestris L.		p
		Smilax excelsa L.	m	
		Smilax sp.		p
		Liliaceae gen.indet.	p	p

1	2	3	4	5
Monocotyledoneae	Amaryllidaceae	Amaryllidaceae gen.indet.	p	
	Iridaceae	Iris pseudacorus L.	mp	
		Iridaceae gen.indet.	p	p
	Poaceae	Avena fatua L.		m
		Avena sp.		p
		Deschampsia caespinosa	m	
		Digitaria sanguinalis (L.) Scop.	m	
		Echinochloa crus-galli (L.) R.et Sch.	m	
		Echinochloa frumentacea (Roxb.) Link.	m	
		Eleusine indica (L.) Gaertn.	m	
		Hordeum distichum L.	m	
		Hordeum sp.		p
		Lolium remosum Schrenk.	m	
		Panicum cappilare L.	m	
		Panicum miliaceum L.	m	
		Panicum sp.	p	p
		Paspalum paspaloides (Michx.) Scribn.	m	
		Phragmites sp.		p
		Poa nemoralis L.		m
		Secale cereale L.		p
		Secale sp.		p
		Setaria glauca (L.) Beauv.	m	
		Setaria italica (L.) Beauv.	m	
		Setaria verticillata (L.) Beauv.		m
		Setaria viridis (L.) Beauv.	m	
		Setaria sp.	p	p
		Sorghum halepense (L.) Pers.		m
		Tragus racemosa (L.) Desf.		m
		Triticum aestivum s.l.	m	
		Triticum dicoccum Shubl.	m	
		Triticum monococcum L.	m	
		Triticum sp.	mp	p
		Zea mays L.		p
		Poaceae gen. indet.	p	p
	Sparganiaceae	Sparganium neglectum Beeby.	m	
		Sparganium sp.		p
		Sparganiaceae gen.indet.		p
	Typhaceae	Typha angustifolia L.		p
		Typha latifolia L.	mp	p
		Typha sp.	m	p
	Cyperaceae	Carex acutiformis Ehrh.	m	
		Carex canescens L.	m	

1	2	3	4	5
Monocotyledoneae	Cyperaceae	Carex capitellata Boiss.et Bal.ex Boiss.	m	
		Carex dacica Heuff.	m	
		Carex elongata L.	m	
		Carex inflata Huds.	m	
		Carex leporina L.	m	
		Carex micropodioides V.Krecz.	m	
		Carex oreophila C.A.M.	m	
		Carex pallescens L.	m	
		Carex panicea L.	m	
		Carex remota L.	m	
		Carex vesicaria L.	m	
		Carex sp.1, sp.2	m	
		Dichostylis micheliana (L.) Nees.		m
		Scirpus lacustris L.	m	
		Scirpus tabernaemontani C.C.Gmel.	m	
		Cyperaceae gen.indet.	p	p

CONCLUSION

In Georgia, the most ancient finds of fossil flora date back to the Palaeozoic. Lower and Middle Carboniferous deposits of the Khramian block contain the remains of 13 plant taxa.

Among Mesozoic deposits, Jurassic sediments are the richest archives from a paleobotanical viewpoint. Application of various methods of study has allowed the rich composition of the flora to be reconstructed, with three main stages of development.

By the Early Jurassic, almost all of Georgian territory was covered by sea except for the ancient blocks. Various vegetation formations grew on these elevated areas, composed mainly of ferns and conifers.

In the Middle Jurassic (Bathonian), the recession of the sea, rising temperatures and increasing humidity provided favorable conditions for the expansion of lush, diverse vegetation consisting mainly of ferns, Caytoniales, Cycadales, Bennettitales and conifers.

In upper part of the Middle Jurassic (Callovian), the vegetation cover changed conspicuously in response to widespread aridification in Eurasia. A great number of ferns, conifers, Cycadales and Bennettitales disappeared. The rich vegetation of the Bathonian was replaced by a community of relatively low species diversity, dominated by Cheirolepidiaceae.

In the Early Cretaceous (Aptian, Albian), a great mass of Jurassic ferns disappeared and the systematic diversity of Caytoniales, Cheirolepidiaceae, Bennettitales and others declined, while the role of Araucaria and Taxodiaceae increased. Data on the subsequent Late Cretaceous vegetation of Georgia are absent thus far.

Eocene deposits constitute Georgia's most ancient Tertiary sediments containing fossil plant remains. The flora of this time was dominated by angiosperms, especially Myricaceae, Juglandaceae and evergreen Fagaceae. Ferns and conifers occupied a subordinate place.

During the Oligocene, the uplift of mountain chains led to fundamental changes in the character of the vegetation: conifers increased and the group of subtropical and warm-temperate plants became more variable.

The majority of plant macroremains from the Early Miocene can be attributed to angiosperms, predominantly Myricaceae, Juglandaceae and Lauraceae.

Evergreen Fagaceae, Lauraceae and other thermophilous plants that made up the moist-subtropical forest communities of the Paleogene continued to exist under the drier conditions of the Early Miocene. They were part of a sclerophyll community that grew in close proximity to the depositional basin.

Paleobotanically, the Karaganian, Konkian and Kartvelian deposits are studied in detail. They include abundant plant macrofossils as well as pollen and spores. The ferns are mainly of taxa now extinct. It is notable that Pinus and Taxodiaceae were the most prevalent conifers at that time, while others typical of younger floras, such as spruce and fir, were hardly represented. Angiosperms were distinguished by particular systematic and ecological diversity. The vegetation of the Middle Miocene throughout Georgia was more or less homogenous, dominated by elements characteristic of subtropical climates with high humidity.

Sarmatian deposits in various regions of Georgia contain rich paleobotanical material, both as plant macroremains and palynomorphs. Macrofloras in Western Georgia reflect the existence of a Lauraceae-dominated evergreen community on the plains and in the lower mountain belt. The role of hemixerophilous elements was minor. Macroremains from Eastern Georgia suggest that both sclerophyllous and moist-subtropical communities were broadly distributed.

In Southern Georgia, plant remains were identified in the Goderdzi suite, the greatest part of which dates to the Sarmatian. The Goderdzi flora contains a great abundance and variety of well-preserved fossils and indicates hygrophilous evergreen and deciduous forests. These communities occupied different areas of relief with distinct microclimatic conditions. The fossil flora of Vale was found in the lower part of the Goderdzian suite and was predominantly made up of plant remains indicative of a subtropical or warm-temperate climate. Subtropical plants are represented mainly by shrubs, while the Lauraceae occur as narrow-leaved xerophilous forms.

In recent years, a rich body of palynological material has been collected from Upper Cenozoic deposits in Georgia. The interpretation of this data using landscape-phytocenological analysis provides new insights into the history of vegetation and climate in Georgia and distinguishes 13 (I-XIII) stages of development (Table XXII).

Table XXII. Climatic events during the Upper Neogene, Pleistocene and Holocene in Georgia

Ma	Western Georgia: Stratigraphical units			Probable correlation with climatic phenomena	Vegetation stages		Eastern Georgia
0	Holocene	Upper		Subatlantic	XIII	3	Subatlantic
				Subboreal			Subboreal
		Middle		Atlantic			Atlantic
				Boreal			Boreal
		Lower		Preboreal			Preboreal
0.01	Pleistocene	New Euxinian		Wurm glaciation	XII		
		Karangatian	Upper				
			Lower	Riss-Wurm interglacial	XI		
0.1		Uzunlarian		Optimum			
		Old Euxinian		Decreasing of temperature Mindel-Riss interglacial	X		
0.4		Chaudian	Upper	Mindelian glaciation	IX		
			Lower	Günz-Mindelian interglacial, optimum	VIII		
0.9	Eopleis-tocene	Gurian	Upper	Günz glaciation	VII		
			Lower	Danube-Günz interglacial, optimum	VI	2	Apsheronian flora
1.8	Pliocene	Kuyalnician (Egrissian)	Upper	Danube glaciation	V		
			Middle	Optimum Increasing of humidity and fall of temperature	IV		Akchagilian flora
			Lower	Decreasing of temperature and humidity	III		
3.4		Kimmerian	Upper	Optimum (Duabian flora)	II	1	
			Lower				
5.3		Pontian	Upper	Optimum (Bichvintian flora)			
			Middle	Optimum (Kodorian flora)			
			Lower	Decreasing of humidity and temperature			
7.1	MIocene	Meotian	Upper	Optimum Decreasing of temperature	I		Dushetian (Shirakian) suite
			Lower	Optimum			Natskhorian (Eldarian) suite
9.5		Sarmatian	Upper				
			Middle	Optimum			
13.0			Lower				

The details of each of these stages are clearly portrayed in the landscape-phytocenological diagrams for separate geological epochs. Even so, there are a number of turning points worth mentioning for their profound influence on the composition of the flora and dynamics of the vegetation.

Palynological assemblages from Lower and Middle Sarmatian deposits in Western Georgia indicate a prevalence of polydominant forests with subtropical and warm-temperate elements. The territory occupied by conifers was much smaller. The distribution of polydominant forests remained stable, indicating a climate with no or muted fluctuations. Similar forest communities occurred in Eastern Georgia, but their vegetation dynamics were quite different on account of unstable climatic conditions. This difference became even more acute after the Middle Sarmatian, when orogenic movements transformed the Transcaucasian intermontane depression into dry land with two regions – Western and Eastern – separated by the Dzirulian Block. The western territory adjoining the Black Sea, the so-called Colchian refugium, became geographically isolated and its warm, humid climate favoured the development of lush forests. At the same time, Eastern Georgia saw the development of vegetation typical of a dry climate. The Sarmatian therefore was the period in which the vegetation of Western and Eastern Georgia began to develop independently under the influence of different climate conditions.

The history of subsequent geological epochs is reconstructed from materials from Western Georgia. Today this is the stratotypical region of Eastern Paratethys, where all the stratigraphical units of the Neogene and Pleistocene are represented by a full series of deposits with rich assemblages of fauna and flora.

Evidence for the Pliocene flora of Eastern Georgia is restricted to Akchagilian and Apsheronian time, when marine transgressions covered the region and laid down the deposits that contain plant remains.

After the Sarmatian, the first turning-point in Western Georgia's vegetation history occurred at the boundary between the Miocene and Pliocene (between stages I - II), when a sharp fluctuation of climate occurred in Western Georgia during whole Lower Pontian time. The result was a mass extinction of many thermophilic plants and changes to Western Georgia's vegetation dynamics. Nevertheless, the main part of the Pontian and Kimmerian flora continued to be subtropical and warm-temperate. In terms of climate, the Kimmerian was somewhat warmer than the Pontian, under the influence of a global Pliocene optimum.

The second turning-point occurred from the upper part of the Kimmerian until the end of the Lower Kuyalnician (stage III). It began and ended with the domination of pine, indicating a decrease in humidity and probably temperature. It is likely that these changes related to the lowering elevation of the Greater and Lesser Caucasus suggested by many researchers. This phenomenon could explain the reduced isolation of Colchis and related changes in climatic conditions, which caused the mass extinction of subtropical plants and the demise of evergreen communities.

After stage III, subtropical communities disappeared from Western Georgia as independent vegetation units.

The third turning-point corresponds to the boundary between the Lower and Middle Kuyalnician (between stages III - IV), when climatic trends in Western Georgia reversed, resulting in increased humidity. Fluctuations in temperature were taking place alongside this phenomenon, as a consequence of orogenic movements that led to Colchis again being transformed into an isolated region, as well as the global climatic fluctuations of the Upper Pliocene.

The forth turning-point came in the Late Gurian and Early Chaudian (stage VII), when a large number of Pliocene relicts became extinct in Western Georgia. Only a few of them went on to appear in the floras of the Pleistocene. Radical changes in vegetation structure also took place during the Late Gurian. Once the Greater and Lesser Caucasus had formed into huge mountain ranges, conditions became favorable for temperate and warm-temperate plants. They were distributed in altitudinal zones and gradually produced a new vegetation structure close to the modern one. Three forest belts with different climatic conditions appeared: an upper belt with dark-coniferous forest, a middle belt occupied by beech forest and a lower belt with mixed forest containing more thermophilous plants.

After the forth turning-point the evolution of flora in Western Georgia continued with a gradual extinction of Pliocene relicts, a process that continued through the Pleistocene. As for vegetation dynamics, the migration of vegetation zones under the influences of glacial and interglacial periods is evident from glaciations from the Günz to the Wurm, while evidence for the Riss has yet to be seen in fossil floras from Georgia.

During the Holocene, according to palynological data, Black Sea transgressive phases can be clearly identified by the combination of a vast number of pollen of thermophilous arboreal species and low values of redeposited pollen in shelf sediments. Conversely, during Black Sea regressions, the role of thermophilous elements decreases and there is a sharp increase in the quantity of redeposited pollen due to enhanced erosion from base-level lowering.

Holocene transgressive phases with warm climatic conditions lasted longer than regressive phases. The most significant warming and sea transgression took place in the Atlantic period, lasting nearly three millennia (8000-5500 BP). The climatic trend was toward increased temperatures and precipitation. This process reached its peak 6000-5500 years ago, when the sea-level in Colchis exceeded its present-day level by several meters for the first time for the whole post-glacial period.

At the beginning of the Atlantic period, with the establishment of humid, warm conditions, the first Neolithic agricultural settlements appeared on the alluvial plains of Southern Georgia, where, besides grain-growing, horticulture, viticulture, apiculture and weaving developed. During the Eneolithic period, this warming process continued and mild climatic conditions facilitated the rise of new cultures and allowed agriculture to penetrate into mountainous areas.

A second significant ingression of the Black Sea took place at the end of the Subboreal period (3800 -2400 years ago), also due to climate warming. The sea level was again higher than nowadays. Broad-leaved forests with chestnut, lime, wing-nut and zelkova expanded. In the high mountains, traditional stock-breeding was replaced by agriculture, viticulture and horticulture. Trade may have developed at this time, judging by the presence of traded goods, such as cotton, in archaeological material from the 15-14th centuries B.C.

The last 2000 geological years are characterized by more frequent transgressions and climatic fluctuations, among which the rather long climatic optimum of the Middle Ages (7th-11th centuries) is noteworthy. The last warming and significant transgression of the Black Sea lasted for 200 years and occurred during the 15th and 16th centuries.

Human impact on landscape development in Georgia can be observed from as early as the Subboreal period, when deforestation is evident not only on the Colchis lowland, but also in the mountains of Western and Southern Georgia.

The comparison of our scheme of climatic changes with similar schemes from mountain territories in Southern Europe and the Near East shows a strong correspondence, explained by the global character of these palaeoclimatic events.

As a whole, the history of vegetation development during the Late Cenozoic can be divided into three main intervals (Table XXII).

The first interval is characterized by a prevalence of subtropical forest vegetation. In Eastern Georgia this formation existed only through the Early and Middle Sarmatian, whereas in Western Georgia it persisted during the Sarmatian, Meotian, Pontian and the main part of the Kimmerian (stages I-II).

The second interval covers a transitional period (stages III-VI), when the vegetation retained many old features but also obtained new ones. At this time the division of broadleaved and coniferous polydominant forests as separate entities began and they came to be distributed according to altitudinal zonality.

The third interval (stages VII-XIII) was a time when a vegetation structure of modern character arose. During this interval, the extinction of Tertiary-relict taxa was completed, with the exception of a handful of ancient species that still grow in Western Georgia and other Caucasian refugia today.

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ლუარა რუხაძე, ელისო ყვავაძე

საქართველოს ფლორისა და მცენარეულობის ისტორია

რეზიუმე

1990 წელს საქართველოს მეცნიერებათა აკადემიის ნ. კეცხოველის სახ. ბოტანიკის ინსტიტუტის მიერ გამოიცა ი.შატილოვასა და ი.რამიშვილის ნაშრომი – "მასალები საქართველოს ფლორისა და მცენარეულობის ისტორიის შესახებ". წიგნში წარმოდგენილია მდიდარი ფაქტიური მასალა, თუმცა არასაკმარისი მონაცემების გამო ყველა სტრატიგრაფიული ერთეულის ფლორა დეტალურად არ არის განხილული. სამწუხაროდ, ყველა ამ ხარვეზის შევსება ვერც შემდგომში მოხერხდა, რადგან პალეოზოური და პალეოცენური ფლორები ჯერ კიდევ არ არის სრულად გამოკვლეული. ბოლო 20 წლის განმავლობაში მდიდარი პალინოლოგიური მასალა იქნა მოპოვებული ნეოგენური და პლეისტოცენური ნალექებიდან. ამ მასალის ინტერპრეტაციამ ლანდშაფტურ-ფიტოცენოლოგიური მეთოდის გამოყენებით საშუალება მოგვცა აღგვედგინა ფლორისა და მცენარეულობის განვითარების თითქმის უწყვეტი პროცესი. დადგინდა ბიოტური და აბიოტური ფაქტორების შედეგად გამოწვეული მნიშვნელოვანი ცვლილებები, რომლებმაც გავლენა იქონია საქართველოს თანამედროვე მცენარეულობის ფორმირებაზე.

საქართველოში ნამარხი ფლორის უძველესი ნაშთები პალეოზოურით თარიღდება. ხრამის მასივის ქვედა და შუა ქვანახშირის ნალექებიდან განსაზღვრულია მცენარეთა 13 ტაქსონი.

მეზოზოურიდან, პალეობოტანიკური თვალსაზრისით, ყველაზე მდიდარი იურული ნალექებია. ამ ნალექებიდან, კვლევის სხვადასხვა მეთოდების გამოყენებით, აღწერილია მდიდარი ფლორა, რომლის ევოლუციაში სამი მთავარი ეტაპია გამოყოფილი. ადრე იურულში საქართველოს თითქმის მთელი ტერიტორია, გარდა ლოქის, ხრამისა და ძირულის უძველესი მასივებისა, ზღვით იყო დაფარული. რელიეფის ამ ამაღლებულ უბნებზე ხარობდა მრავალფეროვანი ტყეები, რომელთა კომპონენტებს გვიმრები

და წიწვოვნები შეადგენდნენ. შუა იურულში (ბათური) ხმელეთის გაფართოებამ, აგრეთვე ტემპერატურისა და ტენიანობის მატებამ განაპირობა მდიდარი და მრავალფეროვანი მცენარეულობის ფართოდ გავრცელება. ფლორის უმთავრესი კომპონენტები იყო გვიმრები, Caytoniales, Cycadales, Bennettitales და წიწვოვნები. ზედა იურულში (კალოვიური) მოხდა მცენარეული საფარის მკვეთრი ცვლილება, რაც გამოწვეული იყო ევრაზიის ტერიტორიაზე არიდული ჰავის ზონის წარმოქმნით. გვიმრების, Caytoniales, Cycadales, Bennettitales-ისა და წიწვოვნების უმეტესობა მოისპო. ბათურის მდიდარი მცენარეულობა შეიცვალა ერთფეროვანი ასოციაციებით, სადაც დომინირებდა Cheirolepidiaceae.

ადრე ცარცულში (აპტური, ალბური) იურული გვიმრების უდიდესი ნაწილი გადაშენდა; Caytoniales, Cheirolepidiaceae, Bennettitales-თა და სხვათა სისტემატიკური მრავალფეროვნება მოისპო. საქართველოს გვიანცარცული მცენარეულობის შესახებ მონაცემები არ მოგვეპოვება.

ეოცენური ნალექები მესამეული ასაკის ყველაზე ძველი შრეებია საქართველოში, რომლებიც მცენარეულ ნაშთებს შეიცავს. ამ დროის ფლორა ღარიბია გვიმრებითა და წიწვოვნებით; დომინანტური პოზიცია უჭირავს ფარულთესლიან მცენარეებს, განსაკუთრებით, Myicaceae, Juglandaceae და მარადმწვანე Fagaceae-ს.

ოლიგოცენურში რელიეფის ამაღლებამ გამოიწვია მცენარეულობის შემადგენლობის ცვლილება, კერძოდ, მოიმატა წიწვოვანთა რაოდენობამ, ხოლო სითბოს მოყვარულ მცენარეთა ჯგუფი უფრო მრავალფეროვანი გახდა.

ადრემიოცენური ფლორის უმეტესი ნაწილი, რომელიც მცენარეთა მსხვილი ნაშთებით არის შესწავლილი, წარმოდგენილია ფარულთესლიანებით. მათ შორის დომინირებს Myricaceae, Juglandaceae, ასევე Lauraceae. თერმოფილური ჯიშები, რომლებიც პალეოგენურში ნოტიო სუბტროპიკულ ტყეებს ქმნიდნენ, ადრე მიოცენურშიც განაგრძობდნენ არსებობას შედარებით დაბალი ტენიანობის პირობებში. ისინი შედიოდნენ ხეშეშფოთლიანი ფორმაციების შემადგენლობაში, რომლებიც გავრცელებული იყო ნალექდაგროვების აუზის სიახლოვეს.

კარაგანული, კონკური და ქართველური შრეები დაწვრილებით არის შესწავლილი პალეობოტანიკური თვალსაზრისით. ამ შრეებში უხვად მოიპოვება მცენარეთა როგორც მსხვილი ნაშთები, ასევე მტვრის მარცვლები და სპორები. გვიმრები ძირითადად გადაშენებული ტაქსონებითაა წარმოდგენილი. წიწვოვნებს შორის დომინირებს ფიჭვი და Taxodiaceae–ს ოჯახის წარმომადგენლები, რაც შეეხება ნაძვს, სოჭსა და ცუგას, რომ-

ლებიც უფრო ახალგაზრდა ფლორებისთვისაა დამახასიათებელი, მათი როლი კომპლექსებში უმნიშვნელოა. ფარულთესლიანები გამოირჩევიან სისტემატიკური და ეკოლოგიური მრავალფეროვნებით. ზოგადად, საქართველოს ტერიტორიაზე შუამიოცენური მცენარეულობა მეტ-ნაკლებად ერთფეროვანი იყო და სუბტროპიკული და ტენიანი ჰავის ელემენტების სიჭარბით ხასიათდებოდა.

სარმატული ნალექები შეიცავს მდიდარ პალეობოტანიკურ მასალას, რომელიც წარმოდგენილია როგორც მცენარეთა მსხვილი ნაშთების, ასევე პალინომორფების სახით. დასავლეთ საქართველოს მაკროფლორები ასახავს დაბლობისა და მთის ქვედა სარტყლის მარადმწვანე ფორმაციების არსებობას, დაფნისებრთა დომინირებით; ჰემიქსეროფილური ელემენტების როლი უმნიშვნელოა. აღმოსავლეთ საქართველოს ტერიტორიაზე, როგორც მცენარეთა მსხვილი ნაშთები გვიჩვენებს, ფართოდ იყო გავრცელებული ორივე ფორმაცია – ტენიანი სუბტროპიკულიც და სკლეროფილურიც.

სამხრეთ საქართველოში მცენარეთა მაკრონაშთებს შეიცავს გოდერძის წყება, რომლის უმეტესი ნაწილი სარმატულად თარიღდება. გოდერძის ფლორა გამოირჩევა კარგი დაცულობის ნამარხი მასალის სიუხვითა და მრავალფეროვნებით. იგი ჰიგროფილური მარადმწვანე და ფოთოლმცვენი ტყეების არსებობას ასახავს. ამ ფორმაციებს ეკავათ რელიეფის სხვადასხვა დონეები, რომლებიც ერთმანეთისაგან მიკროკლიმატური პირობებით განსხვავდებოდა. გოდერძის წყების ქვედა ნაწილს შეესაბამება ვალეს ფლორა, რომლის გაბატონებული ელემენტებია სუბტროპიკული და ზომიერად თბილი ჰავის მცენარეები. სუბტროპიკული მცენარეები ძირითადად ბუჩქებითაა წარმოდგენილი, ხოლო დაფნისებრნი – წვრილფოთლიანი ქსეროფილური ფორმებით.

უკანასკნელ წლებში მდიდარი პალინოლოგიური მასალა იქნა მოპოვებული საქართველოს ზედაკაინოზოური ნალექებიდან. მისი ინტერპრეტაცია ლანდშაფტურ-ფიტოცენოლოგიური მეთოდის გამოყენებით ახლებურად აშუქებს საქართველოს მცენარეულობისა და ჰავის ისტორიას და საშუალებას გვაძლევს გამოვყოთ განვითარების 13 ეტაპი (გვ 167, Table XXII). ჩვენ ამ ეტაპებს დაწვრილებით არ განვიხილავთ, რადგან ისინი დატანილია დიაგრამებზე, რომლებიც ცალკეული გეოლოგიური სართულების მცენარეულობის აღწერას ახლავს თან. აქ ჩვენ შევეხებით, მხოლოდ გარდატეხის იმ ძირითად მომენტებს, რომლებმაც ზეგავლენა მოახდინა საქართველოს ფლორასა და მცენარეულობაზე.

დასავლეთ საქართველოს ქვედა- და შუასარმატული ნალექების პალი-

ნოსპექტრები გვიჩვენებს პოლიდომინანტური სუბტროპიკული და ზომიერად თბილი ჰავის ტყეების ბატონობას. წიწვოვნებით დაკავებული ფართობი გაცილებით მცირეა. პოლიდომინანტური ტყეების არეალი თითქმის უცვლელია, რაც ერთგვაროვანი კლიმატური პირობების არსებობაზე მიუთითებს. მსგავსი შემადგენლობის ტყეები აღმოსავლეთ საქართველოშიც ხარობდა, მაგრამ მცენარეულობის დინამიკა იქ სრულიად განსხვავებული იყო. აღმოსავლეთ საქართველოს ქვედა- და შუასარმატული ნალექების პალინოსპექტრები არასტაბილური კლიმატური პირობების არსებობაზე მეტყველებს. მცენარეულობის დინამიკამ უფრო მკვეთრი ხასიათი მიიღო შუა სარმატულის შემდეგ, როდესაც ოროგენული მოვლენების შედეგად ამიერკავკასიის მთათაშუა დეპრესია ხმელეთად გადაიქცა. ეს ხმელეთი ძირულის მასივით დასავლეთისა და აღმოსავლეთის რეგიონებად გაიყო. დასავლეთით შავი ზღვის მიმდებარე ტერიტორია ჩამოყალიბდა იზოლირებული რეგიონად – ე.წ. კოლხეთის რეფუგიუმად, სადაც თბილი და ნოტიო ჰავა ხელს უწყობდა მდიდარი ტყის მცენარეულობის განვითარებას. სულ სხვაგვარი პირობები იყო აღმოსავლეთ საქართველოს ტერიტორიაზე, სადაც შუა სარმატულის შემდეგ დაიწყო მშრალი ჰავის მცენარეულობის გაბატონება. ამგვარად, სარმატულის შემდეგ დასავლეთ და აღმოსავლეთ საქართველოს მცენარეულობა, სხვადასხვა კლიმატური პირობების ზეგავლენით, ერთმანეთისაგან დამოუკიდებლად ვითარდებოდა.

გეოლოგიური დროის შემდგომი მონაკვეთების ისტორია აღდგენილია დასავლეთ საქართველოდან მოპოვებული მასალის მიხედვით. როგორც ცნობილია, დასავლეთ საქართველო აღმოსავლეთ პარატეთისის სტრატოტიპული რეგიონია. აქ ნეოგენურისა და პლეისტოცენურის ყველა სტრატიგრაფიული ერთეული წარმოდგენილია ნალექების სრული სერიით, რომლებიც ფაუნისა და ფლორის მდიდარი კომპლექსებით ხასიათდება.

აღმოსავლეთ საქართველოს პლიოცენური ფლორის შესახებ არსებული მონაცემები შემოისაზღვრება მხოლოდ აღჩაგილური და აფშერონული დროით, როდესაც მიმდინარეობდა ზღვის ტრანსგრესია და მცენარეთა ნაშთების შემცველი შრეების აკუმულირება.

დასავლეთ საქართველოს მცენარეულობის განვითარების პროცესში, სარმატულის შემდეგ, გარდატეხის პირველი მომენტი შეესაბამება მიოცენურისა და პლიოცენურის საზღვარს (I და II ეტაპების საზღვარი), როდესაც მოხდა თერმოფილურ მცენარეთა მასობრივი გადაშენება. მიუხედავად ამისა, პონტური და კიმერიული ფლორის უდიდესი ნაწილი კვლავ სუბტროპიკული და სითბოს მოყვარული ფორმებისაგან შედგებოდა, რაც

ამ რეგიონში მაღალ ტემპერატურასა და ტენიანობაზე მიუთითებს.

გარდატეხის მეორე მომენტი შეესაბამება დროის ინტერვალს კიმერიულის ზედა ნაწილიდან სკურდუმულის (ქვედაკუიალნიკური) ბოლომდე (III ეტაპი). მცენარეულობის განვითარების ეს ეტაპი იწყება და მთავრდება ფიჭვის დომინირებით, რომელიც ტენიანობისა და, შესაძლოა, ტემპერატურის შემცირების მაჩვენებელიც იყოს. მკვლევართა ვარაუდით, ეს ცვლილებები დიდი და მცირე კავკასიონის რელიეფის პენეპლენიზაციაზე მიუთითებს. ეს მოვლენა, სავარაუდოდ, კოლხეთის იზოლაციის დარღვევისა და კლიმატური პირობების შეცვლის მიზეზს წარმოადგენდა, რამაც, თავის მხრივ, სუბტროპიკულ მცენარეთა მასობრივი გადაშენება გამოიწვია. III ეტაპის შემდეგ დასავლეთ საქართველოს მცენარეულობაში სუბტროპიკული ცენოზები, როგორც დამოუკიდებელი ერთეული, აღარ არსებობდა. შემდეგი IV ეტაპის (შუაკუიალნიკური) პოლიდომინანტური ტყეები უკვე ფოთოლმცვენი ჯიშებისაგან იყო აგებული, თუმცა მათ შორის ჯერ კიდევ გვხვდებოდა უძველესი ფლორების რელიქტები.

გარდატეხის მესამე მომენტი, სავარაუდოდ, შეესაბამება ქვედა და შუა კუიალნიკურის საზღვარს (III და IV ეტაპების საზღვარი), როდესაც დასავლეთ საქართველოს ტერიტორიაზე კლიმატის ევოლუციამ მიმართულება შეიცვალა, რაც ტენიანობის შემცირებაში გამოიხატებოდა; ამავე დროს აღინიშნებოდა ტემპერატურის ფლუქტუაციაც. ეს ცვლილებები ძირითადად გამოწვეული იყო ახალი ოროგენული მოვლენებით, რომლებმაც კოლხეთი კვლავ იზოლირებულ ოლქად გადააქცია, ხოლო ზედა პლეისტოცენურის ჰავაზე მკვეთრი ზეგავლენა მოახდინა.

გარდატეხის მეოთხე მომენტი შეესაბამება გვიან გურიულს და ადრე ჩაუდურს (VII ეტაპი), როდესაც დასავლეთ საქართველოს ტერიტორიაზე პლიოცენური რელიქტების უდიდესი რაოდენობა გადაშენდა. მხოლოდ რამდენიმე რელიქტური სახეობა იყო შემორჩენილი გვიანპლეისტოცენურ ფლორაში. გვიან გურიულში რადიკალური ცვლილება მოხდა მცენარეულობაშიც. მცირე და დიდი კავკასიონის მაღალ მთებად ფორმირების შემდეგ ჩამოყალიბდა ხელშემწყობი პირობები ზომიერი და სითბოზომიერი ჰავის მცენარეებისათვის. ისინი რელიეფის მაღალ დონეებზე ხარობდნენ და თანდათანობით მცენარეულობის ახალ, თანამედროვე ტიპის, სტრუქტურას ქმნიდნენ. წარმოიქმნა განსხვავებული კლიმატური პირობების მქონე ტყის სამი სარტყელი: ზედა — მუქწიწვოვანი ტყეების სარტყელი, შუა სარტყელი, რომელიც წიფლის ტყეებს ეკავა, და ქვედა — შერეული ტყის სარტყელი, რომელშიც შემორჩენილი იყო თერმოფილური მცენარეები.

გარდატეხის მესამე მომენტის შემდეგ (V—XII ეტაპები), რომელიც შეესაბამება დროის ინტერვალს ქვედა კუიალნიკურიდან პლეისტოცენურის ბოლომდე, დასავლეთ საქართველოს მცენარეულობის განვითარების ძირითადი განმსაზღვრელი ფაქტორი იყო ტემპერატურა. მის ცვლილებას, სავარაუდოდ, განაპირობებდა გამყინვარებებისა და გამყინვარებათშორისი პერიოდების მონაცვლეობა გიუნცურიდან ვიურმულამდე; გამონაკლისს წარმოადგენს რისული გამყინვარება, რომლის აშკარა კვალი ვერ იქნა ნაპოვნი საქართველოს ნამარხ ფლორაში.

ჰოლოცენური დროის განმავლობაში (ეტაპი XIII), პალინოლოგიური მონაცემების თანახმად, შავი ზღვის ტრანსგრესიული ფაზები თანხვდებოდა შელფურ ნალექებში თერმოფილური ხე-მცენარეების მტვრის რაოდენობის მატებას და გადალექილი მტვრის მარცვლების მცირე შემცველობას. რეგრესიული ფაზების დროს კი პირიქით, თერმოფილური ელემენტების როლი მცირდებოდა და მკვეთრად მატულობდა გადალექილი მტვრის მარცვლების რაოდენობა. ეს მიუთითებს ზღვის დონის დაწევასთან დაკავშირებულ ეროზიულ პროცესებზე. ტრანსგრესიული ფაზები თბილი კლიმატური პირობებით უფრო ხანგრძლივი იყო, ვიდრე რეგრესიული. ტრანსგრესიასთან დაკავშირებული ყველაზე მნიშვნელოვანი დათბობა მოხდა ატლანტიკურ პერიოდში და დაახლოებით 3 მილიონ წელს გასტანა (8000-5500 BP). კლიმატური ტრენდი მიმართული იყო ტემპერატურისა და ნალექების მატებისაკენ. ამ პროცესმა მაქსიმუმს მიაღწია 6000-5500 წლის წინ, როდესაც გამყინვარების შემდგომ პერიოდში კოლხეთში ზღვის დონემ პირველად გადააჭარბა თანამედროვეს რამდენიმე მეტრით.

ატლანტიკური პერიოდის დასაწყისში ნოტიო და თბილი ჰავის ჩამოყალიბებისთანავე, სამხრეთ ქართლის ალუვიურ დაბლობებზე პირველი ნეოლითური სასოფლო-სამეურნეო დასახლებები გაჩნდა. აქ მემარცვლეობის გარდა, განვითარებული იყო მებაღეობა, მევენახეობა, მეფუტკრეობა და ფეიქრობა. დათბობის პროცესი ენეოლითის განმავლობაშიც გრძელდებოდა. თბილი ჰავა ხელს უწყობდა ახალი კულტურების წარმოქმნას და სოფლის მეურნეობის განვითარებას მთიან ოლქებში.

შავი ზღვის მეორე მნიშვნელოვანი ინსგრესია მოხდა სუბბორეალური პერიოდის ბოლოს (3800-2400 წლის წინ), რაც ასევე ჰავის დათბობასთან იყო დაკავშირებული. ზღვის დონე თანამედროვეზე მაღალი იყო. გაიზარდა ფოთლოვანი ტყეების არეალი, სადაც წაბლი, ლაფანი და ძელქვა ხარობდა. მაღალ მთებში ტრადიციული მეცხოველეობა მევენახეობით და მებაღეობით შეიცვალა. ამ დროს განვითარებული უნდა ყოფილიყო ხელოსნობაც, რაზეც მიუთითებს ძვ.წ. მე-15-14 საუკუნეების არქეოლო-

გიურ მასალაში ბამბის ბოჭკოების აღმოჩენა.

ბოლო 2000 წელი უფრო ხშირი ტრანსგრესიებით და კლიმატური ფლუქტუაციებით ხასიათდება, რომელთა შორის ყველაზე ხანგრძლივი კლიმატური ოპტიმუმი შუა საუკუნეებზე (მე-7-11 სს.) მოდის. ყველაზე დიდი დათბობა და შავი ზღვის დიდი ტრანსგრესია აღინიშნებოდა მე-15-16 საუკუნეებში და 200 წელს გრძელდებოდა.

ადამიანის მოღვაწეობის ზემოქმედება ლანდშაფტის განვითარებაზე ნათლად ჩანს სუბბორეალურ პერიოდში, როდესაც გაუტყეურდა არა მარტო კოლხეთის დაბლობი, არამედ დასავლეთ და სამხრეთ საქართველოც. კლიმატური ცვლილებები გარკვეულ მსგავსებას იჩენს სამხრეთ ევროპისა და ახლო აღმოსავლეთის მთიანი ტერიტორიების ჰავასთან, რაც ზემოაღწერილი პალეოკლიმატური მოვლენების გლობალური ხასიათით აიხსნება.

ამგვარად, გვიანკაინოზოური მცენარეულობის განვითარების ისტორია შეიძლება სამ ძირითად ნაწილად გაიყოს:

პირველი ინტერვალი ხასიათდება სუბტროპიკული მცენარეულობის დომინირებით. აღმოსავლეთ საქართველოში ეს ფორმაცია არსებობდა მხოლოდ ადრეულ და შუა სარმატულში. დასავლეთ საქართველოში იგი შენარჩუნებული იყო სარმატულ, მეოტურ, პონტურ საუკუნეებსა და კიმერიულის უმეტეს ნაწილში (I—II ეტაპები).

მეორე ინტერვალი მოიცავს გარდამავალ პერიოდს (III—VI ეტაპები), როდესაც მცენარეულობა ჯერ კიდევ ინარჩუნებდა ძველ თვისებებს, მაგრამ უკვე იძენდა ახალს. ამ დროს დაიწყო ფოთლოვანი და წიწვოვანი პოლიდომინანტური ტყის ცალკეულ ცენოზებად დაყოფა და მათი გავრცელება რელიეფის შესაბამისად.

მესამე ინტერვალში (VII—XIII ეტაპები) დომინირებდა ისეთი მცენარეულობა, რომლის სტრუქტურა დღემდე შენარჩუნებულია. დროის ამ პერიოდში ძირითადად დამთავრდა მესამეული რელიქტების გადაშენების პროცესი, თუმცა ზოგიერთი რელიქტური სახეობა დღემდე განაგრძობს არსებობას დასავლეთ საქართველოს თანამედროვე ფლორაში.

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