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SUBRECENT SPORE-POLLEN SPECTRA AND THEIR RELATION TO RECENT VEGETATION BELTS IN ABKHAZIA (NORTH-WESTERN GEORGIA, USSR)

Sporowo-pyłkowe spektra prób powierzchniowych i ich związek ze współczesnymi piętrami roślinnymi w Abchazji (Półn.-Zach. Gruzja, ZSRR)

ABSTRACT. Results of palynological studies of subrecent surface samples in Abkhazia, the north-western part of Colichis are presented. Regularities of spore-pollen spectra formation have been established for each individual vertical belt. The problems associated with distribution of pollen of the predominating species of trees and shrubs are discussed as well as those of pollen productivity. The extent of preservation of the pollen in various sediments from different hypsometric levels is determined. Such investigations will make it possible to correctly decode not only the Holocene spore-pollen spectra, but more ancient ones as well.

CONTENTS

INTRODUCTION

The present paper is a continuation of the series of investigations devoted to analyses of recent deposits in well known refugia of the Teriary elements of Eurasia, according to the program of scientific collaboration between the L. Sh. Davitashvili Institute of Palaeobiology, Academy of Sciences of the Georgian SSR (Tbilisi) and the W. Szafer Institute of Botany, Polish Academy of Sciences (Kraków). In the paper concerning subrecent spore-pollen spectra of Colchis (Stuchlik & Kvavadze 1987) the central and southern part of this province was investigated in detail. The present paper deals with the results of studies on subfossil spore-pollen spectra of Abkhazia, the north-western part of Colchis characterized by strong dissection of the relief with great altitudinal range and remarkable diversity of vegetation cover.

Subrecent spore-pollen spectra formation in the mountains is characterized by a number of peculiarites differing from those of lowland territories. This, in particular, relates to the problem of pollen transfer. In the mountain regions force and direction of the wind are of extremely complex character depending on numerous dynamic factors which are determined by topography and thermal conditions of a locality (Barry 1981). The most complex and variable field of the wind in the mountain region is responsible for the fact that pollen transfer by air takes place not only in one direction, but more or less equally from belts lying below up to those lying above and vice versa. This seems to be valid for mountains with marine climate where the wind field is imposed by breeze action. However, in most cases both the mountain and valley winds have a highly pronounced diurnal range: in the daytime these winds blow upwards, while at night they blow downawards along gorges and mountain valleys. When studying regularities of subfossil spore-pollen spectra formation, apart from pollen transfer problems, it is necessary to clarify those of pollen productivity, preservation, volatility of pollen grains of predominant plants. In the case of the territory of Abkhazia where for a distance of only few fens of kilometers a lot of vegation associations relieve each other with altitude starting from broad-leaved forests with prevalence of the oak and chestnut up to alpine meadows. it is very important to know the characteristics of subfossil spectra of each vegetation belt and the role of pollen blown in them from other territories. Without exact criteria for characterization of recent vertical belts based on subfossil spectra, it is impossible to trace all those migration processes between altitudinal belts which took place repeatedly for the space of the Late Glacial and Holocene periods.

MATERIAL AND METHODS

More than 100 samples have been taken and analyzed. The sites of sampling are localized at various hypsometric levels and lithologically the samples of recent deposits are represented by various genetic types. All the vegetation belts have been investigated starting from bottom deposits of the Black Sea (shelf deposits) up to the subnival belt. The pollen spectra of the samples taken from reservation territories are investigated most thoroughly.

The material was treated by the alkaline (KOH) method with subsequent acetolysis according to the Erdtman method (Erdtman 1943). The plotting of pollen diagrams is based on the same principle as in the previous paper (Stuchlik & Kvavadze 1987), however, here the herbaceous species group is represented to full extent.

The material was collected during joint expeditions to Abkhazia in July, 1980, and in June, 1986.

CHARACTERISTICS OF NATURAL CONDITIONS OF ABKHAZIA

Abkhazia is characterized by rather unique and contrast natural conditions. The area of Abkhazia is about 8,665 sq. km. It is situated in the north-western part of Georgia (48° 85' – 42°27' N; 40° –42°08' E) occupying 12.34% of its territory.

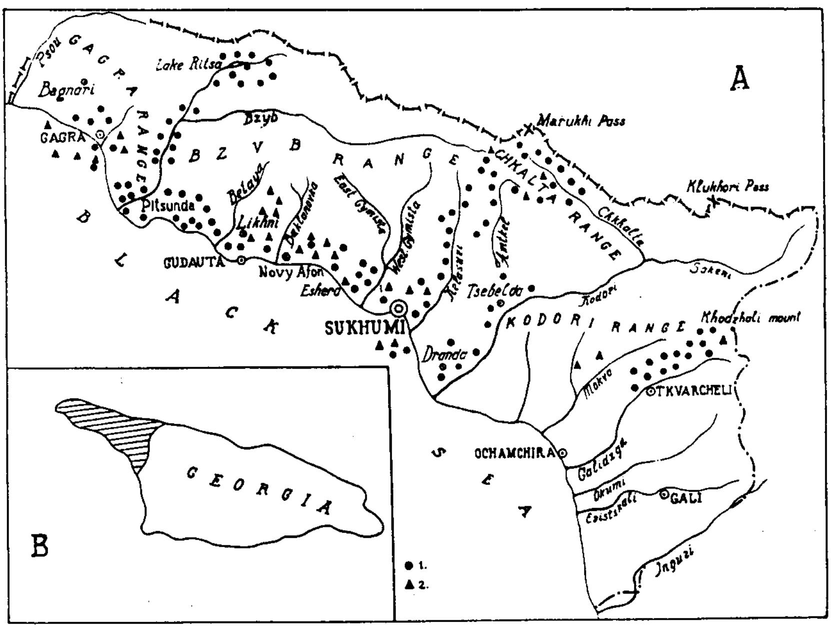

Fig. 1. A — Map of Abkhazia showing localities of analyzed surface samples (1) and Holocene profiles (2): B — Abkhazia in the map of Georgia

The relief of Abkhazia comprises a lowland coastal plain which occupies about 25% of its territory, transitory band of hilly piedmonts (10%) and the region of high mountains (65%). It is a typical mountain coastal land whose orographic axis is the MainCaucasian Range extending from the north-west to the south-east and rising high from 2000 m a.s.l. to 4000 m a.s.l. (Fig. 1). In the north-western part of mountainous Abkhazia there is the Gagra Range, a meridional limestone range with widely developed karst topography. Ancient glacial circuses clints, and glacial troughs can be seen here as well. To the east of it the sublatitudinal Bzyb Range is located whose western part is also limestone, while the eastern one, porphyritic, is marked out by mountain-valley eroded and glacial forms of the relief.

Between the Kodori and Inguri rivers there are the Svaneti — Abkhazian Range, characterized by typical alpine relief and covered with permanent snow and glaciers, and the Kodori Range which is much lower and marked out by relatively smoothed relief. Its western part is limestone with karst forms. In the north the Chkhaltinian and Chedyni Ranges extend parallel to the Main Caucasian Range. Mountainous Abkhazia is distinguished by extremely deep dissection of the surface: longitudinal tectonic-eroded valleys are wide and gentle, while transverse ones are narrow and steep. There are a lot of canyons and gorges there.

The history of relief formation in Abkhazia is extremely complicated. Tectonic uplifts intensified the processes of wash-out and drift of the material resulting in dissection of the ancient relief surface. At the same time in the regions which underwent sinking, accumulation of thick sedimentary rocks arose and surface levelling took place. In one and the same places over a long period of geological development these processes repeatedly changed the direction of movements, complex processes of erosion and denundation being alterated by the processes of accumulation and imposed on each other (Kuftyreva et al. 1961, Maruashvili 1971).

Geology. Geological history of territory evolution in Abkhazia is complicated, too. However, in spite of general complexity of geological structure, one can observe a kind of regularity in space arrangement of the deposits which is expressed in zonal alteration of young rocks by ancient ones in the south-north direction. Quaternary deposits of the coastal lowlands are represented by loams, sandy clays, sands, gravels, poorly cemented conglomerates, loose sandstones. Oligocene and Neogene rocks of the hilly piedmonts are composed of the material originated from wash-out of rocks of the Main Caucasian Range. Paleocene-Eocene and Cretaceous rocks are well developed in the southern part of Abkhazia. They are represented by marl-stones and limestones having thickness up to 2 km. Jurassic deposits constituting the uplands to the south of the axial zone of the Main Caucasian Range are most widely spread. Paleozoic rocks outcrop also in the northern part of Abkhazia on the Main Caucasian Range. They are represented by various crystalline shales and granitoides. Besides, Precambrian and Cambrian rock masses represented by gneisses, shales, phyllites, quartz, etc. are also well developed. Among them Paleozoic formations (granites, granodiorites, gabbro, porphyrites, diabases, etc.) are distinguishable.

Climate. Complex orographic structure of Abkhazia as well as its geographic position are responsible for extremely diverse climatic conditions. The most important climate factor is the Black Sea exerting influence on the climate to be more moderate especially on that of the coast. Since Abkhazia undergoes the action of atmospheric circulation of moderate and subtropical latitudes, the weather conditions here are more unstable than those in a typical subtropic zone. As to the climate as a whole, it is characterized by a well pronounced vertical differentiation.

Winter in the coastal lowland part of Abkhazia is the warmest in the USSR. The mean winter temperature decreases from the north-west to the south-east depending on the arrangement of mountain ranges which come quite close to the sea in the north-west, thus protecting the region from invasion of cold air masses, and retire more and more inland to the south. In this connection the mean temperature of January in Gagra is about +7,3°C, in Pitsunda +6,2°C, in Gudauta +5°C for the same reason in Novy Afon it again rises almost up to the values characteristic of those of Gagra and then lowers down to +6,3°C in Sukhumi and Gulripshi, +4,1°C in Ochamchira, and +4,4°C in Gali (Fig. 2).

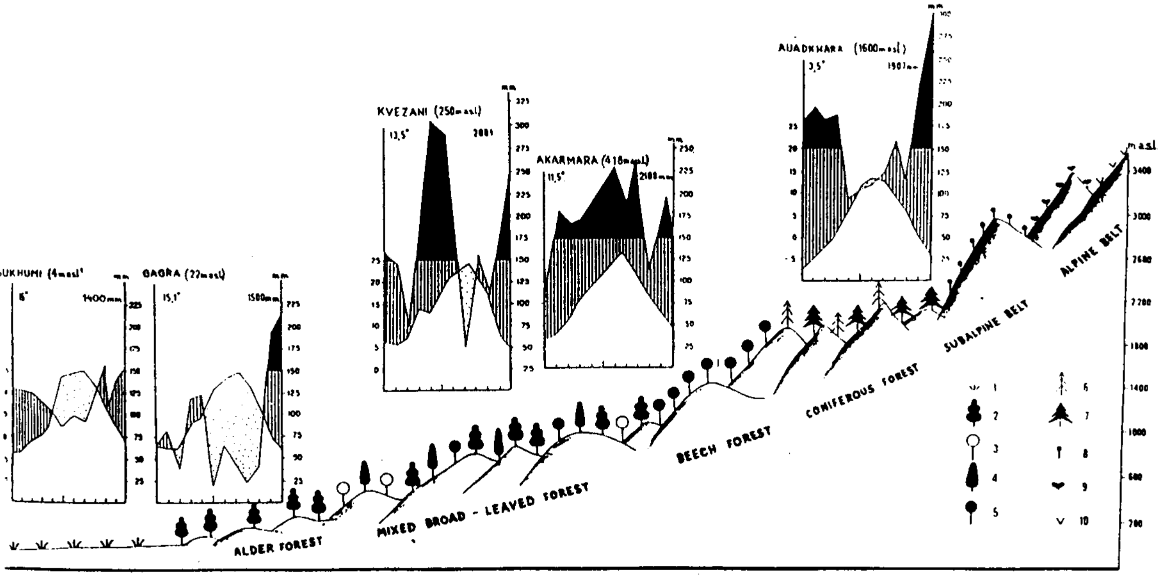

Fig. 2. Mountain relief with climatic diagrams. 1 — treeless landscape (meadows vegatation), 2 — alder, 3 — hornbeam, 4 — chestnut, 5 — beech, 6 - spruce, 7 — fir, 8 — tall grasses, 9 — alpine meadows, 10 — subnival herbaceous vegetation

As altitudinal level of a terrain rises, the mean temperature of January gradually decreases. Up to 200-250 m a.s.l. this lowering of temperature is insignificant. Above 250 m it is associated both with altitude and with distance from the sea. Thus, in Tsebelda (426 m a.s.l., the dinstance from the sea being 25 km) the mean temperature of January is +2,3°C, in the village of Lata (450 m a.s.l., the distance from the sea being 55 km) it lowers down to +1,9°C and in the southern branch of the Gagra Range (1.940 m a.s.l.) — down to –3,2°C. At the same altitude in locations situated far from the sea the mean temperature of winter is much lower. In the Main Caucasian Range it falls down to –15°C, –19°C.

The amount of rainfall and its distribution depends on the distance from the Black Sea, direction of prevailing air masses and diversity of the relief. In the coastal region the mean annual rainfall varies from 1310 mm (Ochamchira) to 1500 mm (Leselidze). With hypsometric elevation of the location the amount of rainfall rieses sufficiently: Duripi (250 m) - 1980 mm, Lake Ritsa (1640 m) — 2280 mm, Auadkhara (1600 m) — 2280 mm. On the southern slopes of the Bzyb and Kodori Ranges the rainfall level exceeds 3000 mm, and on the Abkhazian Kavkasioni it reaches 4000 mm (Fig. 2). In intermontain depressions the amount of rainfall is less (on the average, 1500-1800 mm per annum).

In the most part of the territory of the Republic the maximum of precipitations falls within the autumn-winter perod, when the sea is warmer than the land, except for South Abkhazia, where the maximum rainfall takes place in the summer-autumn period. In the coastal zone it snows rather seldom, now cover thikness being 10 cm, but it is unstable due to the positive radiation balance. In the mountains thickness of snow cover attains 2-4 m.

Proceeding from the above data it is possible to distinguish five main types of the climate: a) marine humid warm temperate climate with warm winter and hot summer (up to 300-400 m a.s.l.): b) humid temperate climate with moderately cold winter and long warm summer (from 300-400 to 1000-1100 m a.s.l.): e) humid cool temperate climate with cold winter and long cool summer (from 1000-1100 to 2000-2100 m a.s.l.): d) high-mountain humid and cool climate (from 2000-2100 to 2800-2900 m a.s.l.): high-mountain nival climate (above 2800-2900 m a.s.l.) (Lashkhia 1982).

Hydrology. As was mentioned above, the territory of Abkhazia is washed by the Black Sea playing an important part in formation of its climate and landscapes. The coastal line length is 204 km. Regularity and general rectilinearity of the coast is determined by its fault type, large linear fractures, absence of tides due to remoteness from the World Ocean.

Internal waters are represented by mountain glaciers, rivers, lakes, springs, swamps, whose distribution and regime stem from the whole complex of climatic orographic, lithological and soil-vegetation conditions.

The total area of glaciation in Abkhazia is 77 sq. km. All the glaciers feed the system of two rivers: the Kodori and the Bzyb. Out of 131 glaciers only 5 belong to the first category, and the rest ones — to the second category. The lower line of permanent snow (snow-line) runs at an altitude 2700 m a.s.l. in the west and 2800-2900 m a.s.l. in the east, being the lowest in the Caucasus.

In Abkhazia there are 120 rivers whose total extent is equal to 5000 km (Barach 1960). They are characterized by a high runoff coefficient, but at the same time they are not very large due to scantiness of the territory across which they flow. Two rivers can be considered as comparatively large (more than 100 km long): the Kodori (with the Sakeni river) and the Bzyb originating from the mountain-meadow zone near glaciers and making their way along tectonic structures. The rivers Gumista, Kelasuri, Khipsta, Galidzga (more than 50 km long) originate from foremost ranges. All the rivers mentioned form canyon-like almost impassable gorges. Coming out to lowlands they preserve, more or less, the character of mountain rivers. The rivers of south-eastern Abkhazia are quite different. Flowing through the Abzhuga and Samurzakani lowlands they become similar to rivers of plain and form meandres.

Characteristic of Abkhazia as of all the Colchis lowland are small rivers fed by swamp waters and rainfall. Also rather peculiar to this region are rivers which partly flow undeground in karst cavities. Large rivers of Abkhazia carry away a lot of sediments forming small deltas at river mounths. There are floods in spring and at the beginning of summer and drought periods in winter. In autumn during heavy rains floods can occasionally occur.

In Abkhazia there are 186 lakes (Abkhazava 1975), however, their total area is not large -only 0,06% of the whole territory. Most of them are shollow ones. They are situated in the high-mountain zone. The lakes are of various origin: glacial, volcanic, karst and rockwell. Such are Lakes Bolshaya and Malaya Ritsa, Amtkel, Goluboe, Mzi, etc. In the lowland the lakes are of lagoon type: Bebesyri, Inkit, Apyshkhtsara and others. Also flood-plain (dead) lakes can occasionally occur.

Geographical distribution of the main types of soils as well as of other components in Abkhazia also follows the altitudinal zonality. In the territory of Abkhazia the following soil zones are distinguished (see Sabashvili 1969):

1) the lowland zone with prevalence of boggy alluvial and podzolic soils,

2) the zone of yellow and red soils of hilly piedmonts,

3) the zone of mountain-frest soils most widely spread, it is represented by humus carbonate and carbonate soils on lime-stones and soils of medium and small thickness as well as by light and podzolized brown forest soils on noncarbonate rocks,

4) the zone of mountain-meadow soils in the subalpine belt which are represented by mountain meadow sod and sod-peat soils, while in the alpine belt — by raw sod-peat mountain-meadow soils.

Thus, the peculiarity of nature in Abkhazia is mainly determined by ist geographical position and arrangement of its territory among altitudinal zones where each natural component plays an important role in forming landscapes.

GENERAL CHARACTERISTIC OF THE VEGETATION IN ABKHAZIA

Vegetation cover in Abkhazia is extremely rich and variegated, which is due to diversity of the character of the relief, altitude, climate and soils in different part of the country. Long hisotry of flora and vegatation development also have played a considerable role, in particular, the fact that Abkhazia was a part of a well-known Colchis refugium where the main body of Tertiary relict floras survived up today. Here it is natural that the coastal and high-mountain zones of vegetation are the richest in Tertiary relicts.

Acoding to Kolakovskij (1980) the flora of Abkhazia numbers about 2000 species of vascular plants. Among them there are more than 150 species of trees and shrubs and more than 1800 species of herbaceous plants. This flora is original in many aspects: it comprieses 319 endemic Colchis species (out of total 450 species) including 133 Abkhazian endemics which corresponds to 30%. A lot of species can be distinguished here which are peculiar to the flora of Abkhazia and characteristic of lime-stones. Among endemic species there are some which represent young endemism.

By its origin the vegetation of Abkhazia is closely connected with that of the Mediterranean Sea. That is why it comprises a large group of Mediterranean flora representatives which is assigned to the lower vegetation belt and concentrated mainly in the region of Pitsunda-Myussera.

Among the Abkhazian flora it is worth noting a relatively small number of arcto-alpine and boreal species with wide areals which came here later and are mainly related to the secondary vegetation type. Finally, the flora of Abkhazia includes numerous introduced species whose number at present amounts to 486 against 50 which were indicated by Maleev in 1936. Therefore, according to Kolakovskij (1980), today the nativ flora of Abkhazia is represented by 1492 species.

Such a remarkable factor of affecting the flora and vegetation of Abkhazia as activity of man who is intensively reconstructing nature can not be neglected. An essential part of vegetation cover, mainly that of lowland regions of the country, is represented by widely spread artificial stands of various introduced species (*Eucalyptus*, palm, cypress, pine, *Cryptomeria*, *Acacia*, etc.) forming thickets here and there.

An important peculiarity of the Abkhazian flora consists in that, it mostly belongs to sylvan and apline meadow plants with obvious prevalence of forest vegetation, locally spread from the seashore up to an altitude 2000 m a.s.l., where due to unfavorable natural conditions it gives way to mountain meadow and alpine vegetation.

As in any mountain country, the vegetation in Abkhazia is arranged according to vertical zonation which is determined first of all by altitude above the sea level complicated by local changes of the relief: e.g. slope steepness and exposure with corresponding microclimate and soil conditions.

Vertical zonation of vegetation cover has been accomplished by the authors on the basis of the data presented by Kolakovskij (1947, 1958) and Maleev (1936) with allowance for geographic distribution of vegetation associations in different regions of the country (Kuftyreva et al. 1961).

1. The belt of lowland vegetation (from O to 30 m a.s.l.)
   a) seashore-growing psammophilous littoral vegetation on gravel-sandy littoral sediments almost deprived of soil cover
   b) the region of maritime pine forests at the Pitsunda Cape
   c) Lowland predominantly paludal forests of Abkhazia on boggy and podzolic soils.
2. The belt of piedmont Colchis forests (from 30 to 650-700 m a.s.l.) on various soils red, yellow soils and their podzolized differences, brown forest soils and humus carbonate soils.
3. The belt of mountain forests (from 650-700 to 1800-2200 m a.s.l.)
   a) The Gagra-Gudauta limestone region with soil cover consisting of dark brown forest soils and podzolized humus carbonate soils
   b) Sukhumi-Gali noncarbonate soils with mountain brown forest soils, pale podzolic and podzolic soils.
4. The belt of subalpine elfin woodland, shrubs, tall grasses (from 1800 to 2200-2400 m a.s.l.)
   a) the Gagra-Bzyb subalpine limestone region
   b) the Abkhazian subalpine nonlimestone region.
5. The belt of alpine meadows, dense sod formation and carpets (from 2200 to 2800 m a.s.l.) on thin rocky mountain meadow soils
   a) the Gagra-Bzyb alpine limestone region
   b) the Abkhazian alpine nonlimestone region
   c) Abkhazian-Svanetian alpine nonlimestone region.

It is natural that the borders dividing these belts do not correspond to one and the same altitudinal levels, their deviation being dependent on relief. It should be noted here that in Abkhazia (as in West Transcaucasia in general) along with vegetation species more or less related to certain belts, there are lots of plants which are spread from the sea level up to the upper forest border. The main reason for such „altitudianal cosmopolitism" is high humidity of the climate which is to a certain degree characteristic of all the territory of the Abkhazia.

SUBRECENT SPORE-POLLEN SECTRA OF SURFACE SAMPLES

The Myussera Reservation

Six soil smples were taken for spore-pollen analysis. Sample No. 1 was taken from a mixed broad-leaved forest with obvious prevalence of the hornbeam (see diagram in Fig. 3). It is characterized by a high frequency of pollen with predominance of trees and shrubs. Among them *Carpinus caucasica* pollen is predominant (54%), *Carpinus orientalis, Quercus, Castanea, Alnus* are found in various amounts (6-9%). Among broad-leaved plants isolated pollen grains of Fagus, *Pterocarya, Juglans* and *Ulmus* occur. Conifers are represented by *Pinus* (8%), *Abies* (4%), and *Picea* (isolated grains), while the group of shrubs is represented by pollen of *Rhododendron* (3%), *Corylus* (2%), *Erica* and *Laurocerasus* (isolated grains). Pollen of herbaceus species is found in small quantities (*Chenopodiaceae, Plantago, Caryophyllaceae, Compositae, Artemisia* and others. Among spore-bearing species *Pteridium aqulinum* is prevalent. *Ophioglossum, Lycopodium* as well as perisporeless monolete spores of *Polypodiaceae* are found in lesser amounts.

Location 1 is situated in a hornbeam forest on a hill 50 m a.s.l. The forest consists of trees of uneven age. Stratification is expressed rather well. The first stratum covers almost 100% of the surface and includes *Carpinus orientalis* (predominantly) and *C. caucasica* with a small admixture of *Castanea sativa* and *Quercus iberica*. This stratum is up to 14 m high with trees having up to 50 cm in diameter. The well-defined second stratum consists of *Rhododendron ponticum* (100%) whose height amounts to 4 m. Young plants of the species comprising the first stratum occur as isolated individuals. Shrubs growing under the rhododendron form dense impenetrable thickets with the latter. They cover 100% of the surface. Apart from *Rhododendron ponticum*, these thickets consist of *Rh. luteum, Crataegus sp., Mespilus germanica, Cistus tauricus, Carpinus caucasica, Corylus avellana, Erica arborea, Cornus mas, Ruscus aculeatus, Swida australis* and others. The herbaceous stratum is not rich. It covers 20-40% of the surface an comprises young specimens of all the strata, as well as *Pteridium aquilinum, Athyrium filix-femina, Luzula forsteri, Primula sp., Viola reichenbachiana, V. alba, Hypericum androsaemum, Lathyrus sylvestris*. These strata are interweaved by lianas: *Tamus communis, Smilax excelsa* and *Hedera colchica*. Beyond this sampling site we found *Juglans regia, Malus orientalis, Pyrus domestica, Ficus carica, Diospyros lotus, Frangula alnus, Pyracantha coccinea*, and *Epimedium colchicum*.

Comparison of the spore-pollen spectra with the geobotanical description reveals that as a whole the former have reflected the principal features of the forest (a small quantity of herbs and prevalence of the hornbeam). Elements of a mixed forest (chestnut,oak) can also be found in the spectra. Prevalence of the hornbeam-wood however (*Carpinus orientalis*), is not reflected in the spectra, which can be explained by lower pollen producitvity of *Carpinus orientalis* campared to that of *C. caucasica* rather than by different degree of their pollen preservation. Most likely the same is the reason for a small amount of the *Rhododendron ponticum* pollen in the spectra (up to 3%), though it is prevalent among shrubs. At the same time in the high-mountain zone under the thickets of *Rhododendron caucasicum* which also form the second stratum, the proportion of its pollen in the spectra is relatively high (36-40%), which can be seen from the diagram of the Ritsa Reservation and the region of the town Khodzhali.

Sample No. 2 was taken from a flood-plain overflowed during high water. Here a flood-plain forest grows consisting of *Pterocarya pterocarpa* and *Alnus barbata*. The pollen spectra of the sample are characterized by a high pollen concentration (AP — 78%, NAP — 22%). Among arboreal species *Pterocarya* (40%) and *Alnus* (24%) are prevalent. The pollen of the hornbeam, lime, pine is found in equal quantities (up to 6%). There is little pollen of the beech, chestnut, oak, fir, and spruce. The walnut, maple, willow are represented by isolated pollen grains. Among shrubs *Corylus, Rhododendron, Cornus*, occur most frequently, *Hedera* and *Rubus* are found occasionally. Among the herbaceous species group *Gramineae, Chenopodiaceae* and *Plantago* are most prevalent. There is little pollen of the nettle, sedge, *Compositae*, and *Labiatae*. Spore-bearing species are represented by *Dryopteris, Ophioglossum, Lycopodium* and monolete spores of *Polypodiaceae* without perisporium.

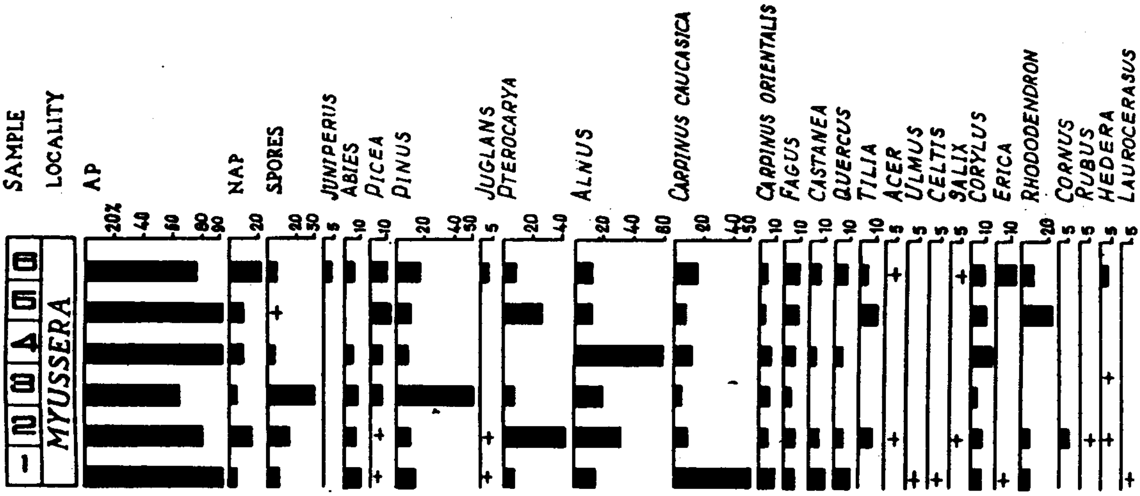

Fig. 3. Spore-pollen diagram of surface samples from the Myussera Reservation

In the flood-plain forest where sample No. 2 was taken the first stratum consists of *Pterocarya pterocarpa* (75%) up to 25 m high with stem diameter 80 cm as well as of *Alnus barbata* and *Tilia caucasica*. The second stratum is well developed and includes *Pterocarya* and in lesser quantity, *Corylus avellana, Acer campestre, Sambucus nigra, Cornus mas* and *Diospyros lotus.* There are not many lianas: *Smilax excelsa, Hedera colchica* and *Rubus*. The shrub stratum covers 80% of the surface. The herbaceous layer is also well developed. The main components are *Salvia glutinosa, Glechoma hederaceae, Chrysosplenium, alternifolium, Dryopteris oreopteris, Symphytum grandiflorum, circea lutetiana, Commelina communis*. As admixture in small quantities are growing *Urtica dioica, Poa palustris, Paris incompleta, Aegopodium podagraria, Geum urbanum, Impatiens noli-tangere, Rumex conglomeratus, Lamium purpureum* and others.

Comparison of the pollen spectra of sample No. 2 with the vegetation has revealed their adequancy. The spectra fully reflected the dominants of each group, growing at the site. These are: *Pterocarya, Ulmus, Tilia, Corylus, Cornus, Dryopteris*. Pollen from long distance transport of *Abies, Picea, Fagus* and others is present in small quantities.

In the Myussera territory soil samples taken from forest openings (samples Nos. 3, 4, 5) were analyzed. Here the pollen concentrtion is low, probably, because unlike samples Nos. 1 and 2, humus horizon is not thick. As was already mentioned (Stuchlik & Kvavadze 1987), the pollen concentration and preservation in West Georgia is directly dependent on humus horizon thickness. Nevertheless, the pollen spectra of samples Nos. 3, 4, 5 as a whole reflect the existing vegetation.

The pollen spectra of sample No. 3 are characterized by prevalence of arboreal and shrub species (62%) with predominating *Pinus* (57%) and *Alnus* (16%). There is little pollen of hornbeam, beech, *Pterocarya*, spruce, and fir. Occasionally are found *Fraxinus* *excelsior* and *Carpinus caucasica*. Also here one can sea pollen of cedar and *Tsuga*, transported from cultural stands in the parks and public gardens. There are only two herbaceous groups: *Chenopodiaceae* and *Compositae*. Sporebearing species are represented most widely. First of all they include the monolete spores of *Polypodiaceae* and trilete of *Pteris cretica, Pteridium aquilinum* and *Ophioglossum* which occur as isolated spores.

The sample plot where from sample No. 3 was taken can be described as follows. It is a secondary forest at a brook on a precipice above the sea. *Alnus barbata* predominates. There grow single trees of *Pinus pithyiusa, Carpinus caucasica* and *Ulmus*. The undergrowth is poorly developed. It consists of single individuals of *Corylus avellana Crataegus, Rubus*. In a distance grows *Ficus carica*. Herbs are represented by *Urtica dioica, Phyllitis scolopendrium Tussilago farfara* and others.

The above material has shown that the existing composition of arboreal species is somewhat distorted in the spectra: they reflect prevalence od *Pinus* pollen rather than that of *Alnus,* though the latter is predominant in the vegetation cover of the plot. This can be accounted for not only by high productivity of the pine, but by better conditions of pollen preservation compared to those of *Pinus. Ulmus, Rubus, Crataegus* are not reflected in the spectra which should also be considered as a consequence of poor conditions of pollen preservation in thin soils.

Sample No. 4 was taken from a forest meadow of a terrace above the flood-plain of the river Djidjuar. The soil is sandy-loam, thin. Herbaceous cover consists of *Oxalis acetosella, Trifolium sp., Stellaria* sp., ferns, etc. The mountain slopes are covered by rather a closed forest comprising *Alnus barbata* and *Carpinus orientalis*. Occasionally *Castanea sativa* can occur. The undergrowth consists of *Corylus* and *Rhododendron ponticum*. At some distance downstream grow *Laurocerasus officinalis, Smilax, Rubus, Crataegus*, and *Rhodeodendron luteum* occur sporadically.

The pollen spectra of sample No. 4 reflect the vegetation of locality more fully than those of sample No. 3. Among arboreal species in the spore-pollen spectra the content of the *Alnus* pollen is the highest (66%). The amount of *Capinus* and *Castenea* is less. The undergrowth is well represented by *Corylus*, though there is no pollen of *Rhododendron* because of poor conditions of preservation of its pollen.

Sample No. 5 was taken from a meadow in a hornbeam forest. As the previous samples, it is characterized by a low concentration and poor preservation of the pollen.

Taxonomically sample No. 6 has a richer pollen spectrum since it was taken in a forest on the ridge of a small range. The first strtatum consists of *Quercus*, the second one — of *Carpinus orientalis, Crataegus*. The third stratum is formed by *Rhododendron ponticum* and *Rh. luteum, Erica arborea.* At a distance from the sample plot there grow isolated trees of *Castanea sativa* in shadowy spots (the first stratum).

All the above mentioned taxa have been reflected in the spore-pollen spectra of sample No. 6. However, quantitatively the oak and hornbeam content is underestimated. There is little pollen of *Rhododendron*. As was already mentioned, this can be explained by low pollen productivity.

Lowland treeless landscapes

The spore-pollen spectra of the lowland part of Abkhazia (Fig. 4), where almost no natural forest vegetation is preserved, are characterized by the following featurs. In the vicinity of the Gagra town, where the mountains come close to the sea, the pollen spectra mostly reflect vegetation of piedmonts and middle mountains. The pollen content of the alder, chestnut, oak, and hornbeam, — i.e. the elements of piedmont and middle mountain forests — reaches maximal values. The arboreal pollen attains 66%. However, in the regions where wooded mountains are far away, the spectra reveal prevalence of pollen of herbaceous plants. Samples Nos. 3,4 were taken at the sea shore near the settlement of Dranda. The pollen spectra of the sample are characterized by abundance of herbaceous species. In the group of arboreal species pollen of alder and pine prevail which is very peculiar for open

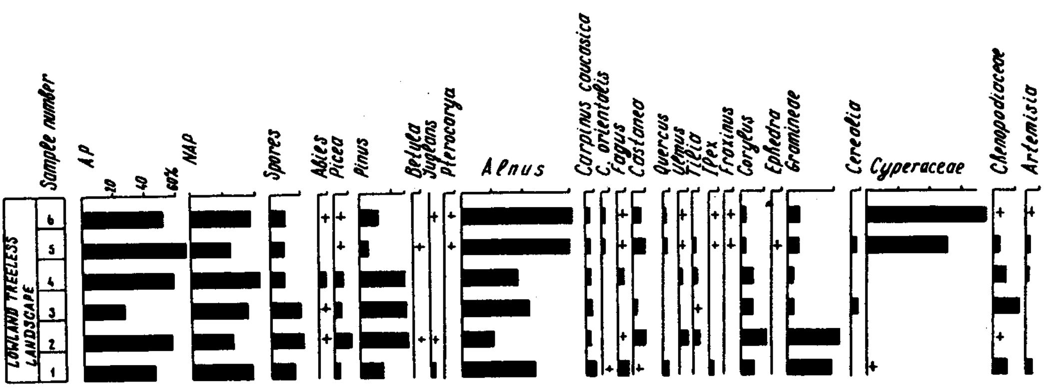

Fig. 4. Spore-pollen diagram of surrface samples from lowland treeless landscape

landscapes of Colchis. Among shrubs the *Corylus* pollen prevails which is marked out by high volatility due to its morphological features. The spectra of open landscapes in the lowland part of the Republic show rather a high content of the spores of *Pteridium aquilinum*, — a harmful weed of farm crops.

Similar properties are characteristic for the pollen spectra of soils from Sukhumi, Eshera,Novy Afon, Gudauta (samples Nos. 1, 2, 4, 5).

Thus the analysis of the pollen spectra of the samples taken in open landscapes of the lowland part of Abkhazia and their comparison with existing vegetation allows us to conclude that prevalence of *Pinus, Alnus, Corylus* in the spectdra with a wide participation of various herbs as well as substantial content of the *Pteridium aquilinum* spores point to occurrence of treeless landscapes in the region under study.

Marine deposits

Pollen spectra of bottom sediments of the Black Sea (Fig. 5, samples Nos. 1-5) were taken from a shelf near the town of Sukhumi (bore-holes Nos. 721 and 723). These samples are characterized by prevalence of arboreal pollen (74-79%). The proportion of harbaceous species is less than that of spore-bearing ones. In the arboreal group *Alnus* pollen predominates (up to 55%). In these samples the amount of all the broad-leaved trees rises, particular'y this refers to the pollen of *Fagus* (up to 9%). In contrast to this, the role of the pollen of conifers becomes less important compared to the spectra of soils. The amount of herbaceous species is small, with *Cyperaceae* being prevalent. The pollen of *Chenopodiaceae*, *Gramineae*, and *Compositae* is registered in minute quantities. Spore-bearing species are represented only by ferns with *Pteridium aquilinum* constituting a considerable part of them.

The marine deposits are marked out by presence of redeposited pollen and spores. In the Sukhumi region there is much pollen of *Taxodiaceae, Carya, Cedrus, Tsuga* and Mesozoic spore-bearing species are found occasionally.

Uniqueness of subfossil spectra of the marine depostis can be explained by the fact that first of all rivers bring to the sea pollen of plants growing in flood-plains. In Abkhazia it is mainly the alder. Though the area occupied by alder forests here is negligible small, the amount of the alder pollen in the spectra attains high values which is explained not only by abundant pollen producitivity, high volatility, but by a better resistance to destruction. Proceeding from the analysis of other elements of arboreal vegetation it can be cocluded that the marine depostis spectra mostly reflect elements of the first stratum of the Abkhazian forests: *Abies, Picea, Pinus, Fagus, Alnus, Castanea, Carpinus caucasica, Quercus, Tilia, Pterocarya, Ulmus, Juglans.* The undergrowth is represented only by *Corylus* pollen. To a certain degree this can be accounted for by absence of large allochtonous rivers in the Sukhumi region.

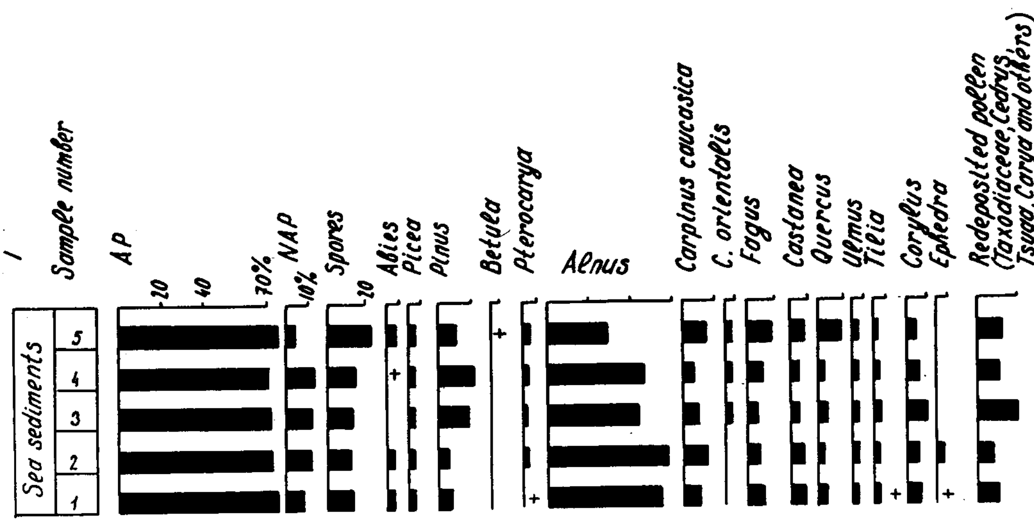

Fig. 5. Spore-pollen diagram of samples taken from the surface of marine deposits

Downstream of the River Bzyb

In the Bzyb valley above Lake Goluboye in the zone of mixed broad-leaved forests, soils and alluvial sediments have been investigated. Samples Nos. 15 and 16 were taken from small terraces of the Bzyb river not far from a *Sequoia* grove, while sample No. 17 was taken in the alluvium of a small meander of the Bzyb below the grove mentioned. Soil sample No. 18 was taken at the site of confluence of the rivers Yupshara and Bzyb.Samples Nos. 19 and 20 were taken in the Yupshara valley from the sites which are hypsometrically highest. There dark coniferous species are admixed with broad-leaved ones.

As shown in the diagram (Fig. 6), the pollen of arboreal plants exhibits obvious prevalence among all the plants (from 55 to 92%). The herbaceous species content does not exceed 10%: spore-bearing plants amount to 30%. It should be mentioned that pollen preservation and concentration differ from sample to sample. In this respect alluvial sample No. 17 consisting of spring floods deposits of very fine fraction appeared to be the best one. Samples Nos. 19, 20 taken from thin soils are characterized by a less concentration of pollen and spores.

The subfossil spectra of samples Nos. 15, 16, 17 (the river Bzyb valley) show prevalence of broad-leaved species among arboreal plants, while those of samples Nos. 19, 20 (the river Yupshara valley) reveal prevalance of conifers: *Pinus, Abies* and *Picea*. It is not unexpected, since in the forest of the river Yupshara valley broad-leaved species have already been mixed with conifers producing a large amount of pollen which is more transportable and resistant to destructions. These reasons are also responsible for an abrupt increase of conifer pollen in thin soil spectra, though in the existing vegetation their role is less significant. That is why when interpreting fossil spectra with a similar complex (prevalence of dark coniferous species) one should pay attention to the role of spore-bearing species. The spectra of dark coniferous forests are distinguished by a small amount of spore-bearing species (15%), with *Botrychium* and *Lycopodium* being predominant. Quite a different situation is characteristic of the broad-leaved forests spectra in which the total content of spore-bearing species is rather high and mostly represented by monolete ferns. The regularities mentioned become more pronounced after comparison of the diagrams in Figs 6-9. Some peculiarities of the subfossil spectra of broad-leved forests growing in the Bzyb gorge were stated. The pollen contens of the lime, alder, chestunt are prevalent there being equal to 33%, 26%, and 18%, respectively. The pollen content of the hornbeam does not exceed 10%. The beech pollen grains are only found in samples Nos. 17 (alluvium) and 20 where the beech is the principal component of the forest. We can see, however, that its participation in the spectrum is rather understimated (2-3%), perhaps, due to poor preservation and low volatility of its pollen in that type of sediments. Bearing in mind actual participation of *Carpinus caucasica* and *C. orientalis* in the local vegetation cover, we suppose that the data concerning their pollen content in the spectra are also understated.

The local vegetation of the sites where the samples were taken from is mostly characterized by the lime, chestnut, alder, and hornbeam. All the four dominants are reflected in the spectra. Besides the spectra permanently show the pollen of *Sequoia* and *Cedrus* planted on the terraces of the Bzyb river. When analyzing the role of only natural vegetation in the pollen spectra we do not present quantitative characteristics of introduced plants, this being the subject of another paper (Kvavadze 1988a). There are no data on herbaceous species in the diagram either, since the herbs pollen is mentioned only occasionally. These are in the main pollen grains of *Chenopdiaceae, Gramineae*, sedges, *Compositae, Polygonaceae, Polemoniaceae* and others. Spore-bearing species are represented only by monolete spores without preisporium of the family *Polypodiaceae*.

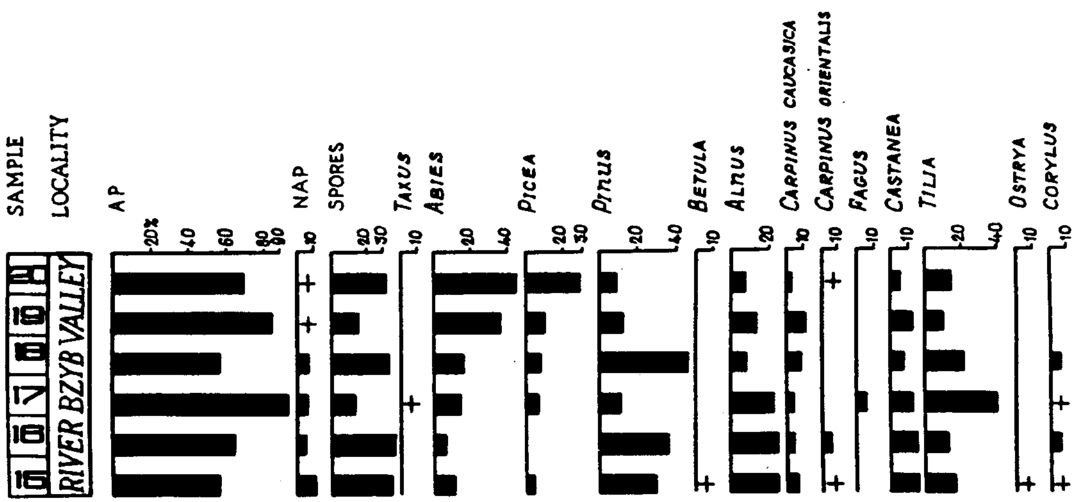

Fig. 6. Spore-pollen diagram of surface samples from the River Bzyb Valley

The Ritsa Reservation

The Ritsa reservation is situated on the southern offshoot of the Main Caucasian Range around Lake Ritsa. Almost all the area of the reservation (about 16.132 ha) is covered by forest vegetation. At lower altitudes (300-1200 m a.s.l.) in the forests the leading role is played by hornbeam, lime and boxtree. At the higher altitude there grow pine and oriental beech. High-mountain forests consists of the Caucasian fir and beech with a small admixture of the Sosnovski pine, spruce and birch.

We have examined surface samples of soils under the canope of beech (sample No. 21), spruce-beech (sample No. 22), fir (samples Nos. 23, 24, 25) forests as well as under thickets of the *Rhododendron caucasicum* in the subalpine belt (samples Nos. 26 and 27). A detailed geobotanical description is made of those sites in the forest where samples Nos. 21, 22 and 23 were taken from.

As can be seen on the pollen diagram (Fig. 7), the spectra of the samples taken from high-mountain forests are characterized by prevalence of arboreal pollen, aspecially of *Abies* (up to 73%). *Fagus* should be considered as the next dominant (up to 21%). The following species permanently take part in the spore-pollen spectra: *Alnus* (up to 30%), *Picea* (up to 14%), *Pinus* (up to 10%), *Betula* (up to 1%). All the broad-leaved species (*Castanea, Carpinus, Quercus, Tilia, Ulmus, Acer, Fraximus*) are represented in small quantities. Among the undergrowth elements pollen of *Rhododendron caucasicum* shows obvious prevalence, while participation of *Vaccinium, Corylus, Ephedra* and *Ilex* is insignificant.

The following detailed characterization of the vegetation and pollen spectra on the sample plots under study can be presented.

Sample No. 21 was taken from a site at an altitude 800 m a.s.l. 30 km of Lake Ritsa somewhat below it in the belt of beech forests with undergrowth consisting of *Buxus colchica*. The spore-pollen spectra of the sample are marked out by the following features. Arboreal pollen accounts for 64%. Herbaceous and spore-bearing species are represented in equal amounts (18%). Among arboreal plants pollen of the fir (31%) and beech (21%) is prevalent. Here in the beech forest belt the amount of beech pollen attains its maximal values. The content of the *Pinus, Picea* and *Alnus* pollen ranges from 8 to 12%. The pollen of *Taxus, Quercus, Carpinus caucasica, Castanea, Tilia, Acer, Ulmus* is found in isolated grains. Among shrubs one can see *Ilex, Corylus, Rhododendron* and *Hedera*. The group of herbaceous species is marked out by a great diversity. The pollen of *Umbelliferae, Compositae, Ranunculaceae, Boraginaceae, Chenopodiaceae* is the most abundant, other groups *Plantaginaceae, Geraniaceae, Labiatae, Artemisia*, etc. are found occassionally. Spore-bearing species are mostly represented by monolete spores of *Polypodiaceae* (up to 65%). The content of *Lycopodium selago* and *Botrychium lunaria* spores is considerable as well. Among monolete spores *Athyrium* and *Polystichum* are identified up to the level of genus.

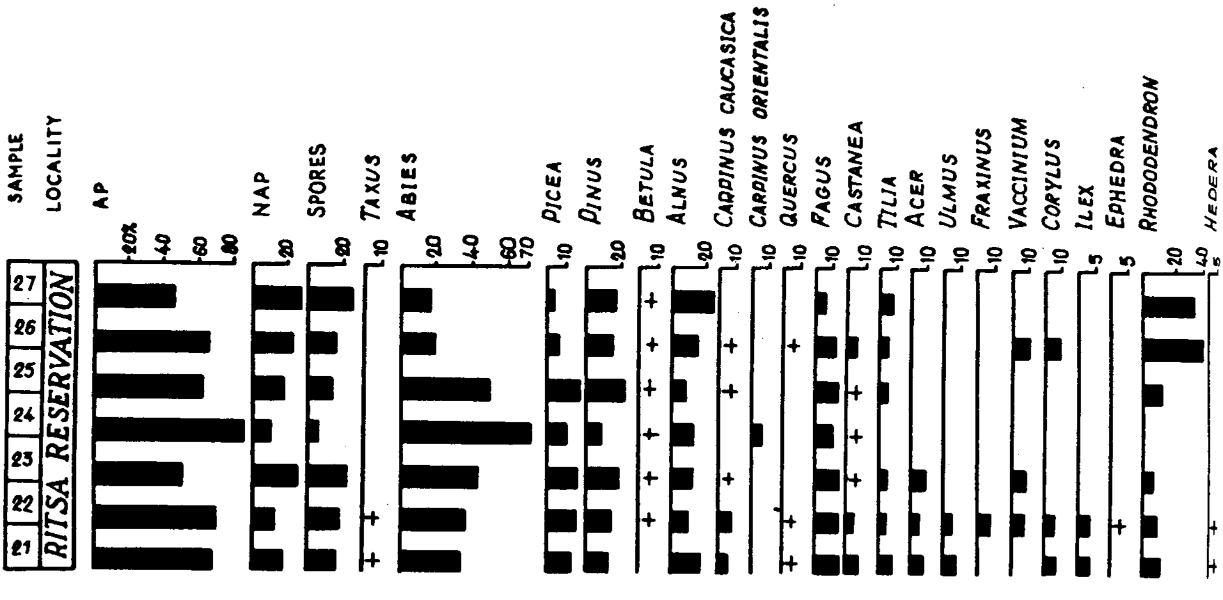

Fig. 7. Spore-pollen diagram of surface samples from the Ritsa Reservation

The forest of the sample 21 site can be characterized as follows. In the well developed more or less natural mountain forest two strata of trees can be distinguished. The first stratum comprieses *Fagus orientalis* covering 75% of the surface. The tallest trees are 20-25 m high and 100 cm in diameter. Apart from the beech, there grow *Carpinus orientalis, Tilia caucasica* with admixture of *Abies* and *Acer*. In the second stratum *Buxus colchica* prevails, covering more than 20% of the area. The plants are 5 m high. The undergrowth stratum is represented by a large number of shrubs covering not more than 30% of the area. This stratum includes *Fagus orientalis, Buxus colchica, Ilex colchica, Carpinus orientalis, Laurocerasus officinalis, Taxus, Rhododendron, Acer, Corylus avellana, Rubus caesius, Jasminum* and *Quercus iberica.* Lianas are only represented by *Smilax excelsa* and *Hedera colchica*. The herbaceous stratum is rich, well developed and covers up to 70% of the surface. The principal elements of herbaceous species are: *Sanicula europaea, Asarum europaeum, Aristolochia iberica, Phyllitis scolopendrium, Salvia glutinosa, Mycelis muralis, Cephalanthera rubra, Symphytum grandiflorum, Asperula odorata.* As to *Cerastium tauricum, Calystegia sepium, Lathyrus vernus, Asplenium trichomanes, Geranium robertianum, Athyrium filix-femina, Carex sylvlatica, Prunella vulgaris, Convallaria transcaucasica, Geum urbanum*, they occur sporadically.

Comparison of the pollen spectra of sample No. 21 with the botanical description of the site shows that the content of the beech pollen in the spectra is somewhat lower compared to ist actual participation in vegetation cover, while the amount of the fir pollen suggests that it belongs not only to the trees growing on the given site, but most part of it might be blown in from a bordering belt. The same picture can be observed everywhere at the borders of belts not only in Abkhazia, but in high-mountain forests of Adzharia as well. At the beech-dark coniferous forests border the pollen of conifers is always prevalent which, as was already mentioned, is due to its higher productivity and volatility as compared to the beech pollen. The *Alnus barbata* pollen (up to 11%) is also blown in from the neighbouring alder stands. *Buxus, Laurocerasus, Rubus, Jasminum, Smilax* growing in the sample plot are not reflected in the spectra which can probably be attributed to poor preservation of their pollen in soils. As to the herbaceous stratum, only its main components are reflected in the spectra.

Sample No. 22 was taken from a spruce-beech forest (above the site where sample No. 21 was taken). It is characterized by a high pollen and spore concentration and a good preservation of the material. In the arboreal group constituting 66% of the spectrum predominant is pollen of *Abies* (up to 33%), *Fagus* (up to 16%), *Picea* (up to 15%). The amount of the *Pinus* and *Alnus* pollen is smaller — 12% and 5%, respectively. *Betula, Carpinus, Castanea, Acer, Ulmus, Tilia, Fraxinus* are represented only by few pollen grains. Pollen grains of shrubs (*Corylus, Ilex, Rhododendron, Vaccinium, Ephedra*) are found in insignificant quantities. The herbaceous species group is distinguished by a large variety of plants: *Gramineae, Boraginaceae, Umbelliferae, Leguminosae, Ranunculaceae, Plantaginaceae, Caryophyllaceae, Compositae, Chenopodiaceae, Polygonaceae, Violaceae, Plumbaginaceae, Geraniaceae* and others. Among spore-bearing species *Polypodiaceae* are prevailing, partialy identified up to the species level (*Polypodium vulgare*), while others (*Athyrium, Dryopteris*) are identified up to the generic level. The spores of *Botrychium* are present in rather a large amount.

The sample plot of the spruce-beech forest is situated in a rocky location and comprieses trees of uneven age. The first stratum is formed by *Picea* and *Fagus*, each covering 25% of the area. The trees are 25-30 m high and 100 cm in diameter. In the first stratum there also grow *Acer trautvetteri* and *Ulmus scabra*. The undergrowth stratum is well developed and taxonomically rich, covering up to 50% of the area. Its main elements are *Laurocerasus officinalis, Ilex colchica*, covering more than 25% of the area, as well as *Philadelphus caucasicus, Ulmus, Picea orientalis,Fagus, Abies nordmanniana Fraxinus exelsior, Tilia caucasica, Quercus iberica, Sambucus nigra, Hedera colchica* and *Ilex colchica*. The herbaceous stratum is well developed too and covers 80% of the surface. It mostly consists of ferns:

Asplenium trichomanes, Phyllitis scolopendrium, Athyrium filix-femina, Polypodium vulgare, Dryopteris filix-mas. Among other herbs there are *Polygonatum multiflorum, Dentaria bulbifera, Lactuca muralis, Salvia glutinosa, Ruscus colchicus, Viola, Galium rotundifolium, Luzula multiflora, Geranium robertianum* and others.

As one can see, the spectra of sample No. 22 (like those of sample No. 21) reflect the existing vegetation, but they also include a lot of blown in pollen of *Abies* covering the mountain slopes at a higher altitude. Thus, the soil spectra as well as the spectra of other deposits give information not only on local vegetation, but they reveal peculiarities of regional vegetation as well.

At a higher altitude in the belt of fir-beech forests samples Nos. 23, 24, 25 were taken, whose pollen spectra are also distinguished by a high concentration and good preservation of pollen. The pollen of arboreal species predominates attaining its maximum 80%) with the *Abies* pollen showing obvious prevalence (41, 49, and 73%, respectively). The beech pollen takes the second place (17%). The content of the pine and fir pollen is less significant (10-15%). The pollen content of the alder is also small (4-6%). Then come *Carpinus orientalis, C. caucasica, Betula, Castanea, Tilia, Acer, Vaccinium, Rhodedendron*. Herbaceous species are represented by the pollen of *Graminaeae, Compositae, Leguminosae, Campanula, Geraniaceae, Dipsacaceae, Polygonaceae, Boraginaceae, Ranunculaceae* and others. Quantitatively the *Caryophyllaceae* pollen is prevalent. The group of spore-bearing plants has its own peculiarities. In this group the role of *Botrychium* and *Lycopodium* becomes more essential, while that of the monolete spores of ferns in the spectra decreases.

The sample plot of a fir-beech forest is situated in the Auadkhara region. The forest is well developed. The age of the trees is rather uneven from very young individuals to old and big ones, e.g. 30 m high and 110 cm in diameter. The first stratum is not closed. It covers 50% of the surface. Here *Abies nordmanniana* is prevalent. It covers 25% of the area. *Fagus orientalis* and *Acer pseudoplatanus* admix to *Abies*. The two former species cover 25% of the area. The second stratum is formed only by isolated young individuals belonging to the species of the first stratum. The herbaceous layer is well developed and cover more than 70% of the surface. In the main they are ferns: *Dryopteris filix-mas* covering 50% of the surface: *Symphytum grandiflorum, Sanicula europaea, Asperula odorata, Senecio platyphylloides* covering more than 25% of the area. The following species occur in smaller quantities: *Asperula caucasica, Cardamine hirsuta, Ranunculus lanuginosus, Myosotis amoena, Urtica dioica, Aegopodium podagraria, Rubus, Geum urbanum, Abies, Acer, Fagus, Melica nutans, Borago officinalis, Dentaria bulbifera, Luzula multiflora, Vincetoxicum albovianum, Paris incompleta, Euphorbia oblongifolia, Vaccinum arctostaphylos, Lathraea squamaria, Veratrum lobelianum, Sedum stoloniferum, Oxalis, Urtica* and others.

Comparison of the pollen spectra with the vegetation described reveals that the former reflect not only the principal forest formations, but elements of isolated associations as well.

Samples Nos. 26 and 27 were taken in thickets of *Rhododendron caucasicum* in the subalpine belt. The amount of NAP rises markedly, while that of AP falls to a minimum (46%). Here the *Rhododendron* pollen is prevalent. The amount of pollen from a long distance transport increases. Thus, the *Alnus* pollen reaches 24%, *Pinus* — up to 15%, *Abies* — up to 16%, other taxons (*Picea, Fagus, Castanea, Tilia* and *Carpinus*) are found sporadically. The group of herbaceous species is characterized by a number of specific features. The spectra are enriched in pollen of plants belonging to the families *Plumbaginaceae, Legumi-*

nosae, Caryophyllaceae, Plantaginaceae, Geraniaceae, Compositae, Polygonaceae. Spore-bearing species are mostly represented by the spores of *Lycopodium selago* (up to 70%), *Botrychium lunaria* (9%), *Polypodiaceae* (21%). For the first time the spores of *Selaginella selaginoides* occur which is generally characteristic of the high-alpine and subnival belts.

Longitudinal profile of the River Bolshoy Khodzhali Valley

Regularities of formation of subfossil spore-pollen spectra have been also analyzed in the regions of base sections of the Holocene deposits.

The studied section of fluvioglacial deposits with streaks of peats is situated in the eastern highest part of the Kodori Range (Mount Khodznali, 3313 m) in the highstream of the river Maly Khodzhali (the right tribute of the river Galidzga) at an altitude 2030 m a.s.l. The section is in the subalpine belt. To clear up peculiarities of the polen spectra of surface deposits and their relation to recent vegetation in the Bolshoy Khodzhali and Mezevara rivers valleys, we have taken and analyzed soil samples starting from the broad-leaved forest belts to the subnival one (Fig. 8).

Sample No. 1 was taken from a broad-leaved forest consisting of *Tilia, Castanea, Carpinus, Fagus* at an altitude 1030 m a.s.l. Conditionally this forest can be named a chestnut forest due to prevalence of the chestnut tree. Besides, there are many lime-trees and beeches there. The hornbeam and maple are admixed in small quantities. In the undergrowth *Corylus* and *Rhododendron* are prevalent.

The spore-pollen spectra of sample No. 1 adequately reflect the vegetation of the mentioned altitudinal belt. In the whole group of vegetation the major part is formed by arboreal pollen (70%) with the pollen of *Castanea* and *Tilia* being prevalent (26% in each case). There is much blown pollen of *Alnus* (11%). The amount of the beech pollen does not exceed 8% and that of the hornbeam is equal to 7%. Among other arboreal plants pollen of *Picea* (6%), *Pinus* (5%) and sporadic of *Juglans* and *Quercus* should be mentioned. The *Acer* pollen is absent from the spectra. Among the elements of the undergrowth only *Rhododendron* — (8%) and *Corylus* as single grains are found. The amount of herbaceous pollen represented by isolated grains of *Chenopodiaceae, Compositae, Cyperaceae, Gramineae* and others is not large. Among spore-bearing plants monolete spores of ferns are prevalent. The spores of *Botrychium* occur in small quantities.

Hypsometrically, sample No. 2 was taken somewhat higher in the belt of broad-leaved forests in which *Fagus orientalis* is predominant. There are a lot of chestnut trees, too. The hornbeam, lime, and maple occur in less quantities. In the undergrowth *Rhododendron*, bilberry, and *Ilex* are prevalent. In the pollen spectra of sample No. 2 the content of arboreal pollen reaches its maximum (84%). In this group the beech and chestnut also play an essential role (25% each). The content of the hornbeam and lime pollen does not exceed 9%, while that of the alder which does not grow near the site mentioned is as high as 14%. The amount of pollen of the fir, spruce, pine, elm, oak, and walnut is small. Among schrubs the nut-tree and *Rhododendron* are prevalent. The amount of the billberry pollen is less. *Ilex* is not reflected in the pollen spectra at all. Among herbaceous species only pollen grains of *Compositae* are found in biger amount. Spore-bearing plants are represented only by monolete spores of *Polypodiaceae* (16%)

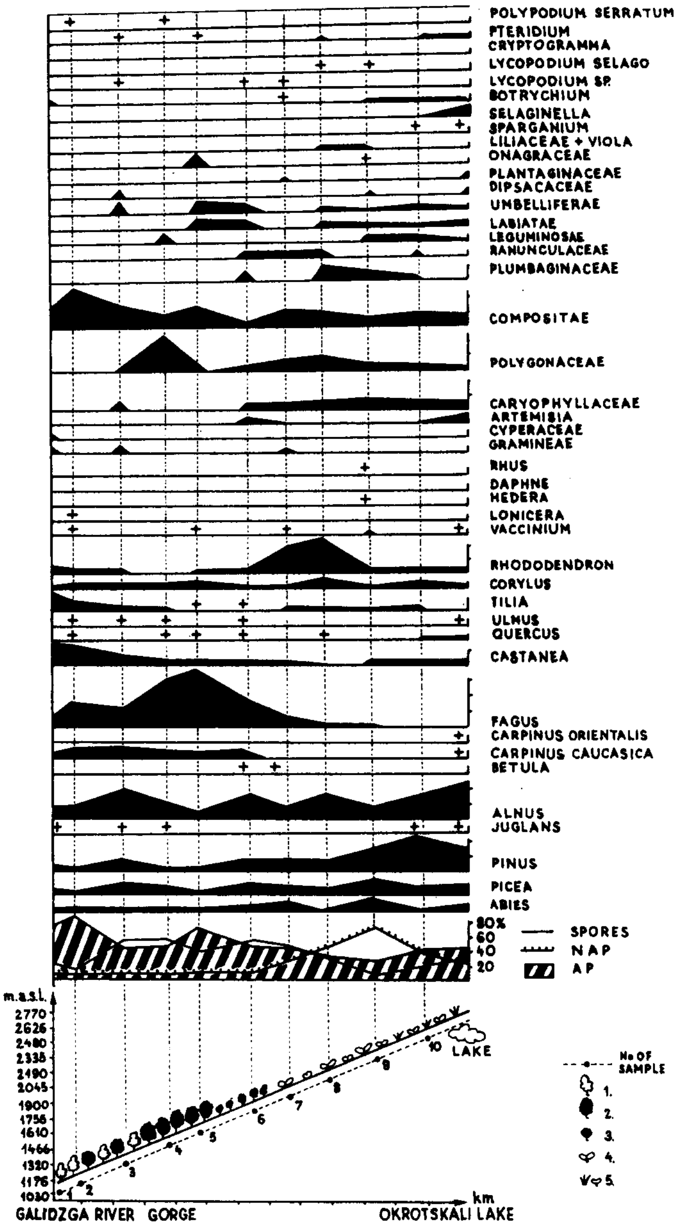

Fig. 8. Spore-Pollen diagram of surface samples taken from the longitudinal profile of the River Bolshoy Khodzhal Valley. 1 — chestnut, 2 — beech, 3 beech elfin woodland, 4 — subalpine tall grasses, 5 — alpine meadows

Sample No. 3 was taken from the same broad-leaved forest belt in which the beech is predominant. The site was situated in a flood-plain where apart from the hornbeam and chestnut, the admixture of the alder is rather essential. These features of vegetation cover have adequately been reflected in the pollen spectra. Among arboreal plants the alder and beech are predominant constituting 34% and 18%, respectively. The pollen content of hornbeam and chestnut is equal (6%). Among conifers the pollen of spruce and pine is prevalent (up to 10%), but there is little pollen of the fir (2%). Other arboreal plants are represented by single pollen grains of the lime, elm, and walnut. There is little pollen of rhododerdron and nut-tree. *Cryptomeria japonica* occurs as isolated pollen grains blown from cultural stands of settlements. There are very few herbaceous species and many spore bearing ones (56%). The abundance of the ferns results from elevated humidity of soils in the flood-plains of rivers. Apart from the monolete spores of ferns, the trilete spores of *Pteridium aquilinum* and *Lycopodium alpinum* occur.

Still higher, in the belt of pure beech forests samples Nos. 4 and 5 ware taken whose pollen spectra comprise up to 53-71% of beech pollen, 9-18% of alder pollen. The role of the hornbeam, chestnut, pine, and nut-tree is insignificant. Occasionally occur pollen of the spruce, fir, *Pterocarya*, walnut, elm, and bilberry. The spectra of herbaceous species are rather poor. Only single pollen grains of *Chenopodiaceae, Compositae, Leguminosae, Gramineae, Umbelliferae, Polygonaceae* are found. There is a lot of spore bearing species (31-51% represented by the monolete spores of ferns.

Samplel No. 6 was taken from the beech elfin woodland of the subalpine belt at an altitude 1800 m a.s.l. Its pollen spectra are distinguished by the following features. About 45% falls to the share of arboreal species, 6% — to the share of herbaceous species with spore-bearing plants having the highest content (49%). Among arboreal plants the leading role is played by the pollen of the beech (33%) and alder (27%). It should be noted that in the belt of beech elfin woodland, which forms impassable thickets, the beech pollen amount in soils does not exceed 40%, while in the pure beech forest it is as high as 71%. Probably, being suppressed, crawling forms of arboreal plants produce much less pollen. In the pollen spectra of the soils under the beech elfin woodland one can also see pollen from long distance transport (*Pinus* 13%, *Picea* 9%, *Abies* 4%, *Carpinus* and *Castanea* in small quantities and isolated pollen grains of *Tilia, Quercus* and *Ulmus*). Taxonomically the composition of herbaceous plants is extremely diverse. The pollen of *Caryophyllaceae, Plumbaginaceae, Boraginaceae, Ranunculaceae, Artemisia* is reflected in the spectra as well as that of *Compositae, Polygonaceae, Umbelliferae, Labiatae, Chenopodiaceae* and others. Monolete ferns represent almost all the spore-bearing plants. *Lycopodium alpinium* occurs as isolated spores.

Again in the subalpine belt though in another vegetation association samples Nos. 7 and 8 were taken in which vegetation peculiar for the *Rhododendron caucasicum* thickets is reflected. In the vegetation group as a whole the role of arboreal pollen decreases (38-39%). On the contrary, the amount of herbaceous and spore-bearing species increases reaching 13-39% and 23-47%, respectively. Among arboreal plants prevalent is the pollen of alder (17-29%) and pine (12-13%). Among shrubs the content of *Rhododendron* is 28-41%. Prevalence of the *Rhododendron caucasicum* pollen under its thickets is revealed in all the regions of Abkhazia. Among other trees and shrubs in the spectra it should be mentioned the pollen of alder, spruce, beech (where at a close distance there are thickets of a beech elfin woodland its pollen content amounts to 17%), lime, oak, chestnut, birch, bilberry and nut-tree. The dominants among herbaceous species are *Plumbaginaceae* and *Caryophyllaceae* (17% each), *Compositae* and *Polygonaceae* (16% each). *Boraginaceae, Gramineae, Artemisia, Plantaginaceae, Labiatae, Chenopodiaceae, Ranunculaceae, Umbelliferae, Liliaceae, Cyperaceae* and others occur regularly. Apart from monolete ferns, spore-bearing species are represented by *Lycopodium alpinum* (in large quantities) and *L. selago, Botrychium, Pteridium aquilinum* (as isolated spores).

Sample No. 9 was taken at an altitude 2300 m a.s.l. in subalpine tall herbage. In its pollen spectra the amount of herbaceous pollen reaches its maximum (60%). The percentage of arboreal plants does not exceed 33%. The role of spore-bearing plants is comparatively negligible (7%). Among herbaceous species pollen of the following taxons is prevalent: *Compositae* (14%), *Ranunculaceae* (13%), *Caryophyllaceae* (11%), *Plumbaginaceae* (7%). As to *Liliaceae, Boraginaceae, Viola, Leguminosae, Dipsacaceae, Onagraceae, Umbelliferae, Gramineae, Cyperaceae* and *Chenopdiaceae* their content is less. Among spore-bearing plants there are a lot of monolete ferns, while *Botrychium* and *Lycopodium selago* occur occasionally.

Sample No. 10 was taken in the alpine meadows belt at an altitude 2510 m a.s.l. The pollen spectra of this sample are characterized by the following features. The content of arboreal, herbaceous, and spore-bearing species is equal to 49%, 33%, and 18%, respectively. Such a high precentage of arboreal plants in the spectra of the sub-alpine belts indicates an important role of pollen from a long distance transport especially *Pinus* (48%) and *Alnus* (26%). Similar pollen spectra are characteristic for treeless landscapes not only in the mountains, but in lowlands as well. Among other arboreal plants pollen of the fir (3%), spruce (10%), oak (2%), chestnut (3%), should be mentioned, as well as beech, lime and walnut which occur occasionally. Among shrubs hazel-nut pollen constitutes 5%, while that of *Rhododendron caucasicum* — 2%. Pollen of herbaceous plants is abundant and taxonomically rich. The peculiarity of these spectra consists in absence of a dominant. Equally abundant are *Caryophyllaceae, Ranunculaceae, Polygonaceae, Chenopodiaceae, Umbelliferae, Plumbaginaceae, Chenopodiaceae, Compositae, Umbelliferae, Plumbaginaceae, Leguminosae*. Whereas pollen of *Cyperaceae, Artemisia, Sparganium, Labiatae, Gramineae* and *Dipsacaceae* is found in small quantities. The composition of spore-bearing species is also rather peculiar. Apart from monolete ferns, spores of *Botrychium* are present in quantities exceeding those of the lower altitudinal belts. *Selaginella selaginoides* is marked in the form of isolated spores. *Pteridium aquilinum* spores come in small quantities from lower altitudinal belts with a long distance transport.

Sample No. 11 was taken in the subnival belt at an altitude 2630 m a.s.l. from the bottom of a lake. Genetically it is represented by deposits of spring floods. The spore-pollen spectra have a number of peculiarities. As in the alpine belt, here an important part is palyed by arboreal pollen from a long distance transport (52%). The content of herbaceous species is 22%, while that of spore-bearing ones is 26%. Among arboreal plants there is much pollen of the alder (41%) and pine (27%). High-mountain forest elements are represented by the fir (7%) and spruce (10%). But there is little pollen of the broad-leaved beech and chestnut (3% each). Pollen of the hornbeam, oak, elm, *Carpinus orientalis*, walnut, bilberry and rhododendron is found sporadically. The herbaceous pollen spectra are peculiar enough. Here *Artemisia* (22%) and *Compositae* (13%) are predominant, *Caryophyllaceae, Dipsacaeae, Chenopodiaceae, Plantaginaceae, Umbelliferae, Labiatae, Polygona-*

ceae are found in less quantities. *Gramineae* und *Sparganium* occur occasionally. Spore-bearing vegetation is marked out by the following features. In the spectra of alpine meadows *Botrychium* is the second dominant after *Polypodiaceae*. As to the subnival belt, by the amount of spores the second place is taken by *Selaginella selaginoides* and then comes *Botrychium*. thus, in sample No. 11 monolete ferns account for 77% while *Selaginella* and *Botrychium* for 18% and 1%, respectively. Spores of *Pteridium aquilinum* from a long distance transport correspond to 4%.

Longitudinal profile of the Adange River

Surface samples taken from the valleys of the rivers Amtkal, Adange, Sibista where a series of the Holocene sections is situated were studied. The most interesting subfossil spectra are those of the samples taken from the valley of the river Adange (the right tribute of the river Chkhalta) in the region of the Marukhi pass, where the offshoots of the Main Caucasian and Chkhaltinian Ranges as well as the eastern margin of the Bzyb Range meet. Unlike the vegetation of the river Bolshoy Khodzhali, the high-mountain vegetation of the region under study has a number of peculiarities. Here due to high humidity, the belt of dark coniferous forests is very well developed. The beech forests belt changes gradually into beech-dark coniferous forests with prevalence of the beech and fir. In this case the fir admixture is insignificant. Close to the upper border of forests the fir and spruce disappear and pure beech forests are relieved by beech elfin woodland. Altogether 12 surface samples were taken starting from the belt of beech-dark coniferous forests and up to the subnival belt (see diagram Fig. 9). Since the material was collected in the up-down direction, starting from lakes located at the source of the Adange river the sample numbers mentioned below are given in the descending order.

Sample No. 12 was taken in the lowest belt at an altitude 1750 m a.s.l. in a beech-dark coniferous forest. Its pollen spectra are characterized by prevalence of arboreal species (69%). The herbaceous species content does not exceed 9%, while that of the spore-bearing species is equal to 21%. Among arboreal plants pollen of beech and fir is predominant (43% and 19%, respectively). The content of the spruce pollen does not exceed 6%. Pollen from a long distance transport is represented mostly by pine (12%) and alder (7%) and in small quantities by chestnut, hornbeam, walnut, lime and elm. Isolated pollen grains of birch, oak, willow, and hazel-nut are revealed in the spectra due to individual trees growing as an insignificant admixture in the mentioned altitudinal belt. The group of herbaceous species is not very rich. It comprises isolated pollen grains of *Compositae, Polygonaceae, Gramineae, Artemisia* and others. The only representatives of spore-bearing species are monolete ferns among which *Athyrium* is identified up to the genetic level.

In the above-lying belt of pure beech forests sample No. 11 was taken. In the pollen spectra the arboreal pollen predominates (74%). The contents of the herbaceous and spore-bearing species are 14% and 11%, respectively. Among arboreal species the beech is an obvious dominant (69%). There is much pollen of pine (16%) and sporadic of fir, chestnut, alder, hornbeam, lime, all from a long distance transport. The herbaceous species are represented better than in the lower altitundinal belt in small quantities is found pollen of *Caryophyllaceae, Plumbaginaceae, Geraniaceae, Umbelliferae, Artemisia, Polygonaceae* and others. In the spore-bearing group in addition to monolete spores of ferns and trilete spores of *Botrychium lunaria* appear (8%).

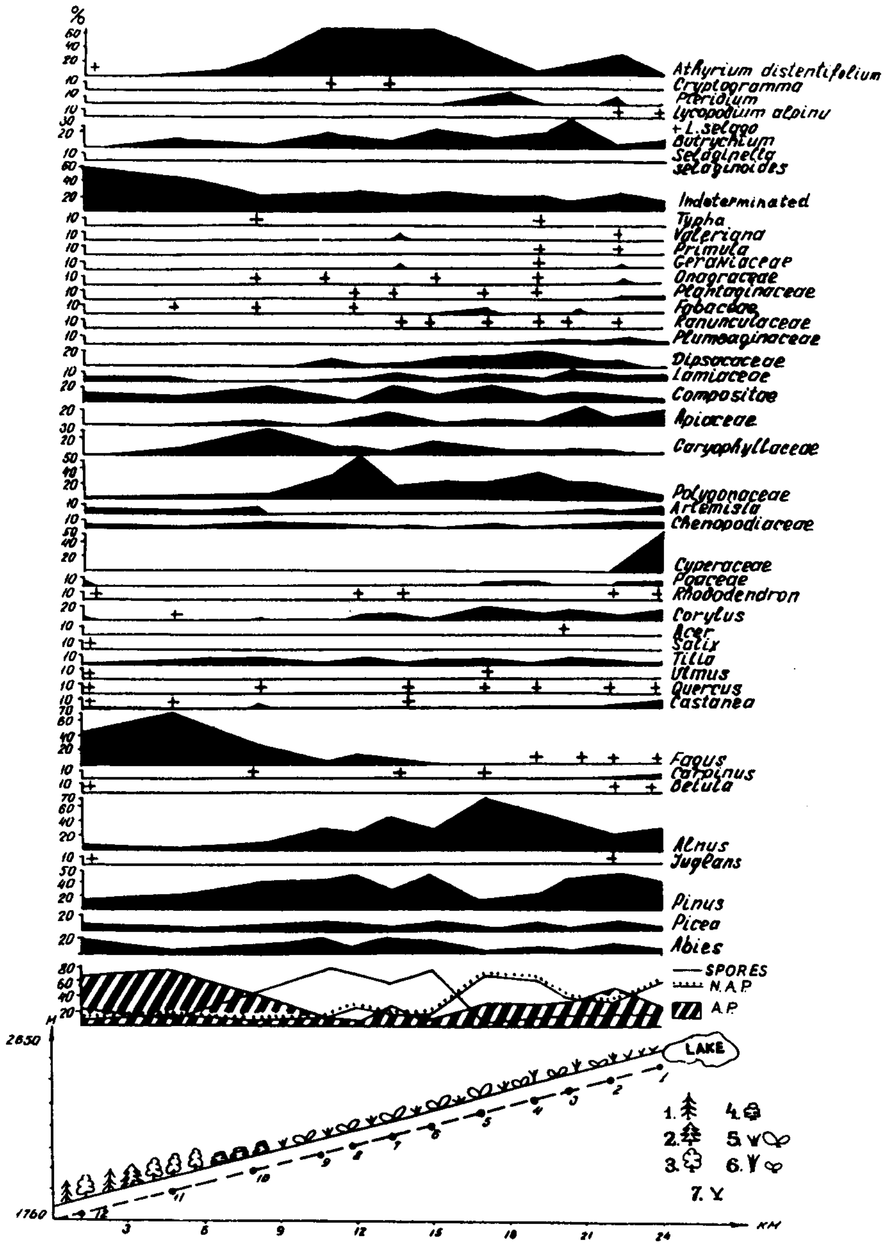

Fig. 9. Spore-pollen diagram of surface samples taken from the longitudinal profile of the River Adange Valley. 1 — spruce, 2 — fir, 3 — beech, 4 — beech elfin woodland, 5 — subalpine thicket of *Athyrium distentifolium*, 6 — alpine meadows, 7 — subnival herbaceous vegetation

Sample No. 10 was taken in a beech elfin woodland. The content of the arboreal species in the pollen spectra is 47%. The herbaceous species proportion is as low as 9%. At the same time the spore-bearing plants occur in abundance (42%). Among arboreal species pine and beech pollen is prevalent (35% and 28%, respectively). In smaler amount appear pollen of alder (12%, fir (8%), spruce (5%) and isolated pollen grains of chestnut, oak, lime and hornbeam. Among shrubs *Corylus* pollen is mentioned. Among herbaceous plants *Caryophyllaceae* and *Compositae* are prevalent (36% and 23%, respectively). *Chenopodiaceae, Labiatae, Umbelliferae, Artemisia, Cyperaceae*, and others are found in less quantities. Spore-bearing plants are represented by monolete ferns and spores of *Botrychium lunaria*.

Samples Nos. 9, 8, 7 were taken in the subalpine belt in thickets of *Athyrium distentifolium*. The spore-pollen spectra of this belt in this region are characterized by prevalence of spore-bearing species (from 55 to 71%). Arboreal plants account for 5-25%, herbaceous plants — for 11-23%. In the group of arboreal plants consisting solely of pollen from a long distance transport, the alder and pine predominate (43% and 45%, respectively). The fir, hazel-nut, and spruce pollen is present in small quantities (10%, 7% and 5%, respectively). The beech, chestnut, lime, hornbeam, oak and rhododendron are represented by isolated pollen grains. Among herbaceous species marked out by taxonomic diversity, *Compositae, Polygonaceae, Umbelliferae* are predominant. There is much pollen of *Labiatae, Plumbaginaceae, Dipsacaceae, Onagraceae*. The pollen of *Chenopodiaceae, Plantaginaceae, Valeriana, Geranium* and others is registered in small quantities. Among spore-bearing species there are mostly spores of *Athyrium distentifolium*, though the spores of *Botrychium* and *Cryptogramma* are also found in rather large quantities (up to 16% and 3%, respectively). It should be noted that *Cryptogramma* growing in the high mountains occurs only in Abkhazia owing to mild climate and high humidity (Kolakovskij 1980).

Samples Nos. 5, 4, 3 were taken in alpine meadows belt. Their pollen spectra are marked out by prevalence of herbaceous species (up to 66%). The amount of arboreal pollen all from a long distance transport is 29-33%, while that of spores — 4-10%. The pollen of the alder and pine is prevalent among arboreal plants, whereas the fir, spruce and hazel-nut are of minor importance. The beech, maple, chestnut, hornbeam, oak and elm are represented by isolated pollen grains. In sample No. 3 two pollen grains of *Cedrus* were found, which seem to have been brough from cultivated stands. The group of herbaceous species is the most rich taxonomically. Pollen of *Compositae, Polygonaceae, Umbelliferae, Onagraceae* and *Labiatae* is, equally abundant, *Caryophyllaceae, Artemisia, Plumbaginaceae, Dipsacaceae* are presented in considerable quantities, whereas *Valeriana, Chenopodiaceae, Gramineae, Ranunculaceae* and others are registerd as isolated grains. Spore-bearing species include monolete spores of ferns as well as a large amount of *Botrychium* (from 12% to 35%).

Samples Nos. 2 and 1 were taken in the subnival belt near the lake close to a snow-patch at an altitude about 2750 m a.s.l. Their pollen spectra are marked out by an increase of arboreal pollen from a long distance transport (25% to 50%). The content of herbaceous species is 32%-56%, that of spore-bearing ones — 17-18%. Among arboreal plants the pine pollen is prevalent (39%-47%). The amount of the alder polen somewhat decreases and does not exceed 20-28%. In sample No. 1 the spruce pollen content amounts up to 12%, fir to 82%, hazel-nut to 6%. The birch, beech, oak, walnut, chestnut, lime, rhododendron are found as isolated pollen grains. Herbaceous species are diverse and their pollen is abundant. The following taxons are predominant in sample No. 1: *Polygonaceae* (15%), *Umbelliferae* (10%), *Compositae* (8%). There is much pollen of *Plumbaginaceae, Dipsacaceae, Chenopodiaceae, Caryophyllaceae, Geraniaceae, Labiatae, Onagraceae, Ranunculaceae*, other groups *Cypera-*

ceae, Plantaginaceae, Gramineae, Artemisia are found in less quantities. In spore-bearing species a lot of monolete spores of ferns can be seen and a considerable amount of *Botrychium* and *Pteridium aquilinum*. In samples Nos. 1 and 2 for the first time in the case of this profile spores of *Selaginella selaginoides, Lycopodium alpinum*, and *L. selago* are observed.

Longitudinal profile of the River Amtkel Valley

The trough of the river Amtkel is separated from the river Adange valley by a narrow band of mountains. Here the longitudinal profile extends from the beech elfin woodland up to the upper border of the alpine meadows. Six samples of recent deposits have been studied.

As is seen from the diagram (Fig. 10), here the same trends can be traced as in the valleys of the rivers Adange, Malyi Kodzhali and others. Only in the pollen spectra of samples Nos. 5 and 6, taken under thick well developed thickets of *Rhododendron caucasicum*, the quantitative ratio of some elements of arboreal species is of slightly different character. It is natural in this case that the amount of the rhododendron pollen reaches high values and hence provalence of the alder and pine is not so much pronounced.

Longitudinal profile of the Kelasuri River Valley from Sukhumi to the Marukhi Pass

In the diagram (Fig. 11) are shown the results of spore-pollen analysis of surface samples taken from the bottom sediments of Black Sea and different sediments from lowland up to the subnival zone. Samples Nos. 1 and 2 are described on page 238 and samples 3 and 4 have been taken into consideration in the description of lowland treeless landscape. Sample 5-7 were taken from a flood plain alder forest up to 800 m a.s.l. The main component in the pollen spectra is *Alnus*, which reaches in this vertical belt its maximum (60%). Considerable high values in the pollen spectra have conifers (*Pinus* 20%, *Picea* 10%, *Abies* 5%) pollen of which come mainly with the long distance transport. Other components of the spectra are found in small quantities only. Pollen spectra of samples 8 and 9 taken from the chestnut forest belt rather adequately reflect the type of vegetation. *Castanea* reaches its maximum (up to 50%), whereas other components of the forest having the status of admixture (*Tilia, Carpinus, Fagus, Corylus* and *Rhododendron*) are represented in the pollen spectra only by insignificant values. In wet places on the river banks grow some alder stands what is reflected in the pollen spectra by the amount of 15% *Alnus*. Similar values of alder pollen occur in the spectra of all higher vertical belts, what means, that small alder forests along the river banks can be observed till the timber line in the Abkhazian mountains. Only in the spectrum of sample 9 taken near the border of beech-dark coniferous forest the amount of *Abies* is somewhat higher. Samples 10-12 are taken from the beech-dark coniferous forest belt. In the pollen spectra *Abies* reaches its maximum (44%) value. The second dominant is *Fagus* (24%). This reflects very well the actual forest vegetation of this belt, where predominant are *Abies* and *Fagus* forests with some admixture of *Tilia, Castanea*, and *Carpinus* (5%, 12%, 5%, respectively in pollen spectra). The undergrowth composed of *Rhododendron ponticum, Laurocerasus officinalis, Corylus avellana, Vaccinium arctostaphylos* is also well reflected in the pollen spectra. Spores of *Botrychium* and *Lycopodium* appear here for the first time. Samples 13-16 were taken from pure beech forest

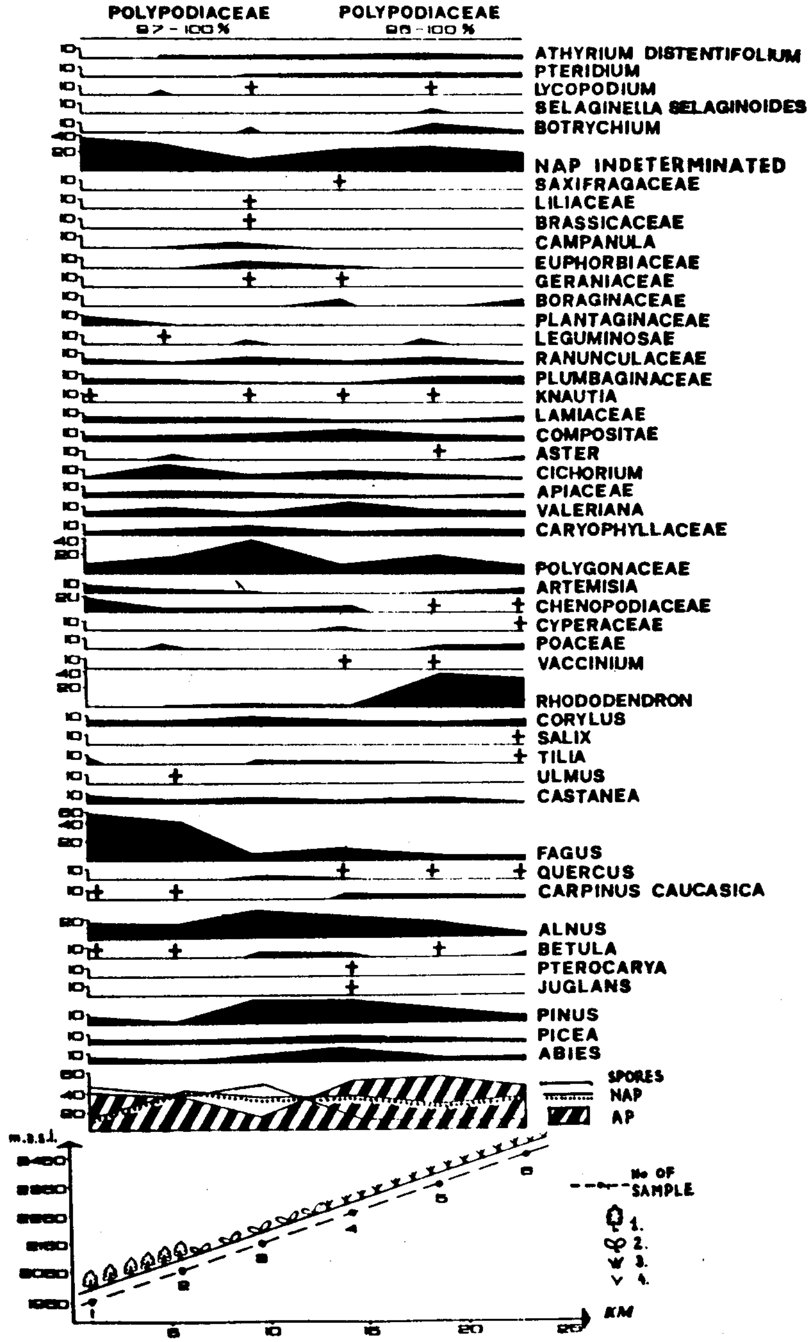

Fig. 10. Spore-pollen diagram of surface samples taken from the longitudinal profile of the River Amtkel Valley. 1 — beech elfin, 2 — tall grasses, 3 — *Rhododendron caucasicum* thickets, 4 alpine meadows

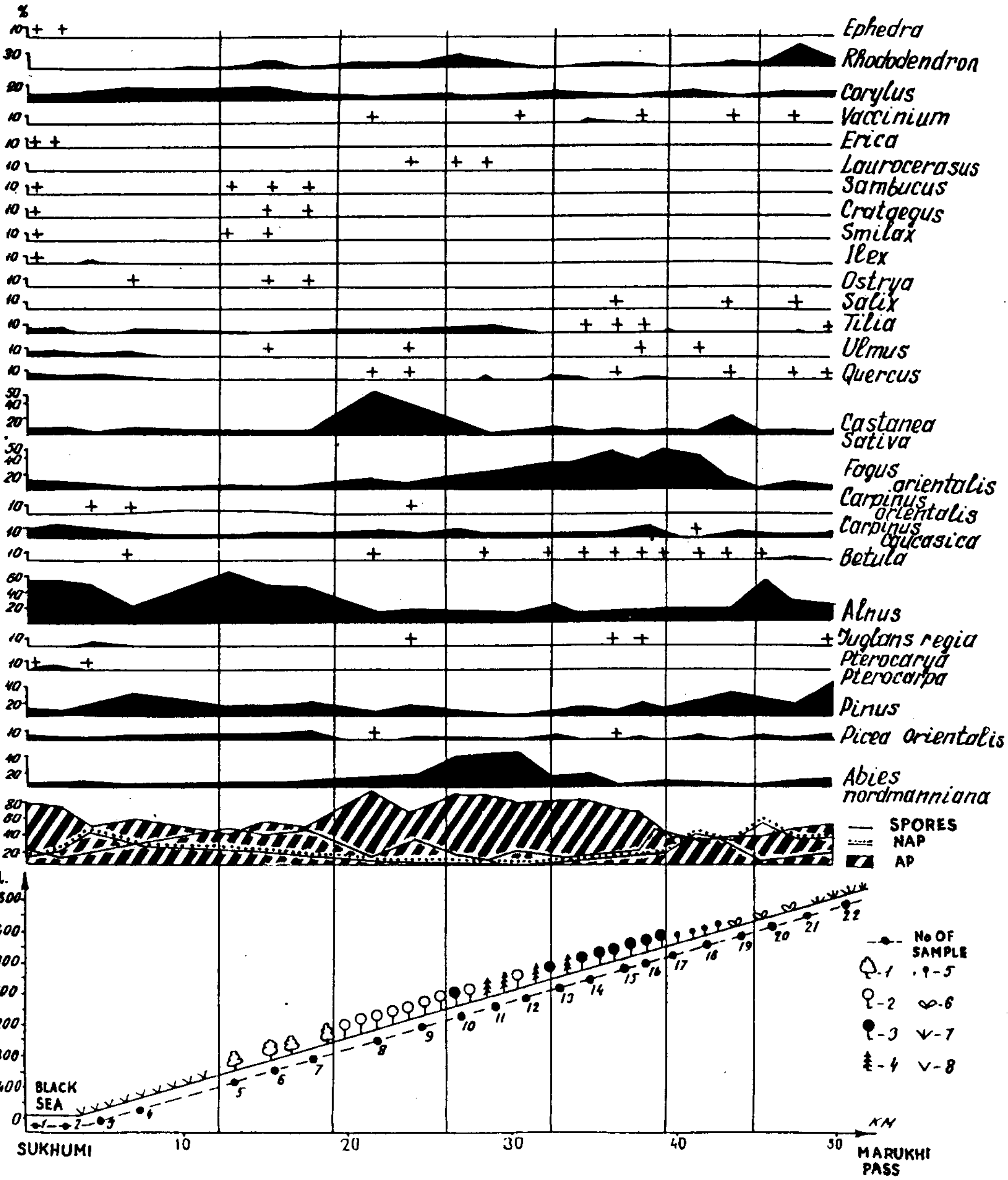

Fig. 11. Spore-pollen diagram of surface samples taken from the longitudinal profile of the River Kelasuri Valley from Sukhumi to the Marukhi Pass. 1 — alder, 2 — chestnut, 3 — beech, 4 — conifers, 5 — beech elfin woodland, 6 — subalphine tall grasses, 7 — alpine meadows, 8 — sea shore vegetatopm and lowland meadows

only with some admixture of *Abies* in lower altitudes. *Fagus* reaches its maximum in pollen spectra (47%) whereas other admixture elements such as *Abies, Carpinus, Castanea* and *Quercus* are found in smaller quantities (15%, 13%, 5% and 2% respectively). In samples 17 and 18 taken from sediments in the beech elfin belt *Fagus* is also predominant (40%), and pollen from long distance transport become more important, especially *Pinus* 12% and *Castanea* 21%. In general, in the spectra of samples 19-22 taken from subalpine and alpine vegetation belts the role of NAP is increasing up to 57%, as well as arboreal pollen from long distance transport. *Alnus* has its second maximum here (53%). Also *Rhododendron* pollen reaches its maximum (30%) what reflects the *Rhododendron caucasicum* thickets very well. Spores of *Selaginella selaginoides* and *Lycopodium alpinum* appear here for the first time.

CONCLUSIONS

1. In most cases the studied spore-pollen spectra adequately reflect vegetation of the vertical belts.

2. Pollen concentration and preservation in recent deposits of Abkhazia is quite good. In soils these factors directly depend on thickness of the humus horizon, and a certain predominance of arboreal pollen in the alpine spectra compared to the spectra of treeless regions at lower altitudes can be caused simply by better conditions of pollen preservation in deposits of the subalpine and alpine zones which first of all results from the soil acidic reaction.

3. Extremely complicated and changeable wind field in the mountain region depending on dynamic factors determined by topography and temperature conditions of a locality (Barry 1981) results in that pollen transportation by air proceeds more or less equally from lower altitudinal belts to the higher ones and vice versa, rather than in one direction, for example to the alpine zone (cf. Klopotovskaya 1985).

4. An interesting phenomenon is observed at the border between the beech and dark coniferous belts. If the beech belt is situated at hypsometrically lower altitudes, the spectra always show prevalence of the coniferous species pollen. However if the beech forest is above the dark coniferous one, there is no distortion in the spectra. The beech content amounts to 70% and more.

5. In the belt of beech elfin woodland forming impenetrable thickets, the beech pollen amount in soils does not exceed 25-40%, while in beech high forests attains 50-70%. An abrupt reduction of pollen amount in subalpine elfin woodland is also marked for *Pinus mugo* in the Carpathians (Kvavadze 1988b) and for *Betula nana* in the Khibini Mountains (Kvavadze & Rukhadze 1989). Being suppressed, crawling forms of arboreal plants seem to produce much less pollen. Morphologically the pollen grains of crowling forms are distinguished by small size, thicker exine: besides there are a lot of underdeveloped (ugly) and sterile individuals among them.

6. In the spore-pollen spectra of open landscapes the amount of arboreal pollen from a long distance transport is prevalent, while in forests it decreases abruptly. The pollen spectra of treeless regions of the lowland are characterized by predominance of *Alnus, Pinus,* and *Corylus* pollen from a long distance transport. These spectra reflect a high content of pollen of herbaceous species and spores of *Pteridium aquilinum*. In the spectra of treeless landscapes of high-mountains pollen of arboreal species predominates also (alder and pine pollen). However, taxonomic composition of herbaceous species here is different — much richer and much more diverse. Spores of *Botrychium* and *Selaginella* are present permanently.

7. The soil spectra, like the spectra of other deposits, give information not only on narrow and local vegetation, but they reveal features of regional and more general one and in this case the local vegetation is reflected in them much more completely.

8. The soil spectra have not reflected prevalence of *Carpinus orientalis* over *C. cauca-sica* in corresponding regions, as it is in the vegetation cover, what can be explained by lower pollen producitivity of *Carpinus orientalis* compared to that of *C. caucasica*, rather than by different degrees of preservation of their pollen.

9. It should be noted that the participation of *Rhododendron ponticum* in the spectra is very low (about 5%) even where it is a stratum forming element. However, under thickets of *Rhododendron caucasicum* in acidic soils in the high-mountain zone participation of its pollen in the spectra corresponds to much higher values (36-40%).

10. The amount of pollen of the oak, willow, maple, *Ilex*, heath, *Taxus* and juniper is usually somewhat understated in the soil spectra compared to their actual participation in vegetation cover. As for the boxtree playing an important part in low-mountain forests of Abkhazia, its pollen is not preserved in soils. It can be found only as isolated grains in the spectra of lake and boggy deposits.

11. In the spectra of marine deposits (like in the spectra of open landscapes) percent-age of the pine and particularly alder pollen is over-estimated. The large amount of the latter can be explained by the fact that rivers bring to the sea first of all pollen of flood-plain vegetation. One of the peculiarities of the marine spectra is that they reflect mainly ele-ments of wind-pollinated plants. There is little pollen of herbaceous species in them.

12. The marine deposits spectra are characterized by presence of large quantities of redeposited pollen. In this connection it is worth nothing that one cannot have an idea abouth real taxonomic composition of vegetation which grew in this or that territory in the past without correlation between marine and continental spectra of the same age (enclosed lakes, soils, high-mountain peats and peats of lowlands a great distance away from flood-plains and mouths of large rivers) in which pollen redeposition is practically excluded.

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