Acta Palaeobot. 42(1): 63–92, 2002

Relationship between biodiversity of recent pollen spectra and vegetation of beech forests in Caucasus and Carpathian Mountains*

ELISO KVAVADZE[1] and LEON STUCHLIK[2]

[1] L. Davitashvili Institute of Palaeobiology, Georgian Academy of Sciences, Potochnaya Str. 4, 380004 Tbilisi, Republic of Georgia; e-mail: eliso@paleobi.acnet.ge
[2] W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz Str. 46, 31-512 Krakow, Poland; e-mail: stuchlik@ib-pan.krakow.pl

Received 9 October 2000; accepted for publication 14 May 2002

ABSTRACT. The palynological diversity of surface samples from beech forests (*Fagus orientalis* in the Caucasus and *Fagus sylvatica* in the Carpathians) is characterized and its relationships to the species composition of modern vegetation is discussed. Some problems of beech ecology, relevant for the reconstructions of palaeovegetation are considered. The problems of long-distance transport of beech pollen as well as the pollen productivity of the two beech species in various ecological conditions are discussed.

KEY WORDS: *Fagus orientalis, Fagus sylvatica*, pollen spectra, Caucasus, Carpathian Mountains

INTRODUCTION

The beech genus is a typical representative of a moderate mesophilous flora and is nowadays widespread in the northern hemisphere (Fig. 1). Most of the 10 species occur in the mountains within the altitudinal range 1000–2000 m a.s.l. (Fig. 2). The origin of the genus is East Asia, where the first primitive ancestors were found, evolving to the North-American and Euro-Caucasian species (Takhtadjan 1981).

The closest species of this genus are *Fagus sylvatica* L. and *Fagus orientalis* Lipsky. The latter is somewhat intermediate between *Fagus sylvatica* L. and *Fagus sieboldii* Engl. which grows in Japan (Dolukhanov 1989).

In fossil floras beech is known in the Caucasus and Europe since the Neogene (Kolakovski 1964, Środoń 1985). In Poland beech was widespread twice: in the Tertiary and in the Holocene (Ralska-Jasiewiczowa 1983, Środoń 1990). However, in the Caucasus beech forests occurred in the Quaternary period (Shatilova 1974, 1977, Shatilova & Ramishvili 1990, Chochieva 1980).

In the northern part of the area beech species are spread essentially on the plains, and in the southern part in a particular mountain belt (Fig. 2). In Europe the northern boundary of beech is limited, first of all, by low winter temperatures, but the southern boundary is connected with the summer humidity and temperature regime. A similar situation is also observed in the mountains, where the upper limit of beech forests is mainly controlled by winter temperatures and precipitation and the lower limit by summer precipitation.

In the Caucasus beech forests containing *Fagus orientalis* exhibit maximum development and productivity at those altitudes where the mean temperature of the warmest month reaches 17–19°C, with the annual temperature amplitude is no more than 21.5°C, most frequently 18–21°C, and where the annual rainfall is no less than 700 mm (Dolukha-

* This research was supported in part by the Mianowski Fund (in 2000).

Fig. 1. Distribution area of the genus *Fagus* (after Boratyńska & Boratyński 1990, emended)

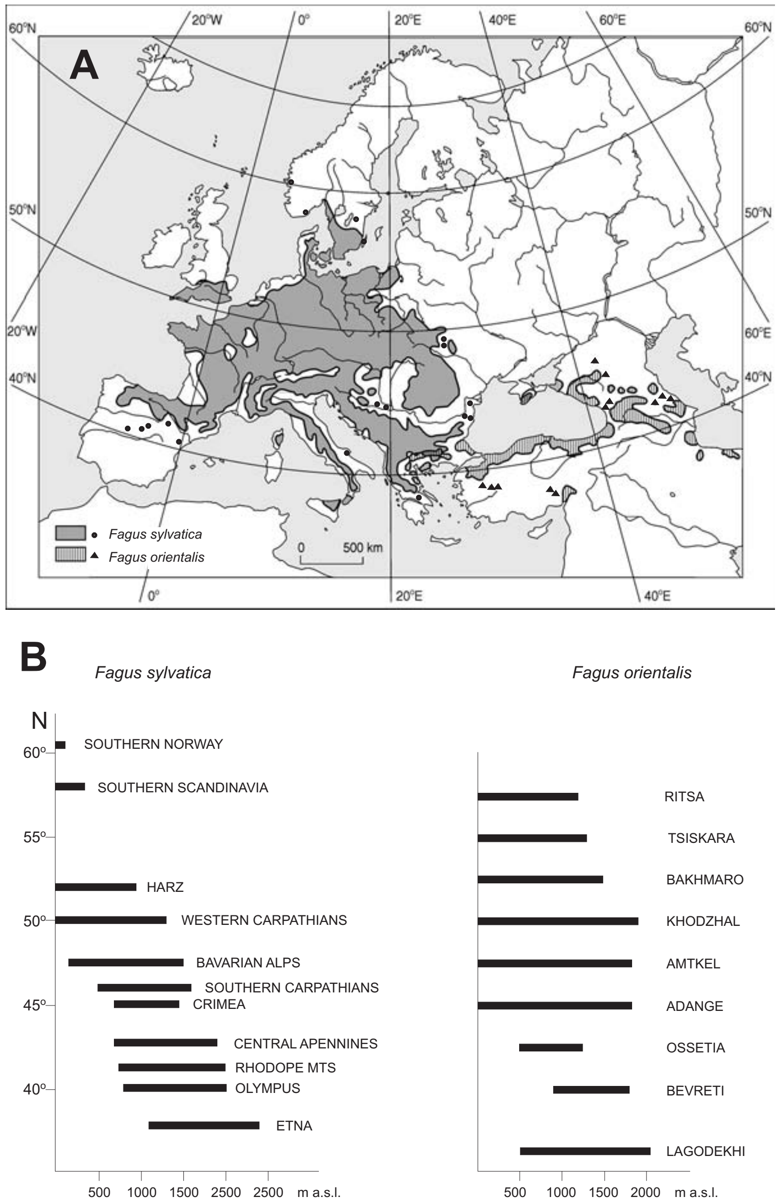

Fig. 2. Distribution area of *Fagus sylvatica* L. (after Boratyńska & Boratyński 1990, emended) and *Fagus orientalis* Lipsky (after Browicz 1982, Sokolov et al. 1977, and Dolukhanov 1989, emended). **A** – horizontal spreading, **B** – vertical spreading

nov 1989). In the mountains of West Georgia this optimum is within 700–1400 m, in more humid regions of East Georgia within 1000–1450 m, while in more arid regions within 1300–1600 m. The upper limit of beech forests is 2000–2100 m, almost the same in both parts of the region under consideration. Beech can grow as elfin woodland only in humid climate, where a long period of snow cover protects the elfin woodland against winter colds and spring frosts. Under these conditions beech elfin woodland ascends the mountains nearly up to the places with January isotherms -7 to -8°C and August isotherms 11–12°C (Dolukhanov 1989).

In the Carpathians the beech forest belt is situated as a whole much lower than in the Caucasus. In the Ukrainian Carpathians on the north-eastern ridges with the cool climate, the altitudinal range of *Fagus sylvatica* is 700–800 m (Stoyko & Odinak 1988). In the Polish Carpathians beech forests grow at an altitude from 850 to 1100 m. The upper limit coincides with the mean annual temperature isotherm of 4°C and July temperature of 13°C (Dzwonko 1990).

In the Caucasus as a whole, as well as in Georgia, beech forests occupy half of the area of all forests. In the Ukrainian Carpathians they account for 55% of the forest area. In the

High Tatra Mountains beech forests account only for 2.2% (Trampler et al. 1990). Throughout Poland beech forests occupy only 4.1% of all forests (Boratyńska & Boratyński 1990). In Europe beech forests of *Fagus sylvatica* reach their maximum values in the Balkans (up to 42% of the whole forest area). Beech forests are also well developed in Austria, Switzerland, France, and Italy (Sokolov 1951).

The investigation carried out by Rudolf and Firbas in 1926 should be considered as the very first work devoted to the study of subfossil pollen spectra of mountain beech forests in Poland. In the Sudetes in the Karkonosze Mts. the above-mentioned authors studied recent soil samples in beech forests at an altitude from 740 to 950 m. The amount of beech pollen reached maximum values directly under beech trees (up to 43%). However, even at some distance from the beech forest this index dropped sharply (to 6%).

In the Caucasus the investigations of subfossil spectra of beech forests began much later (Mamatsashvili 1972, Klopotovskaya 1973, Kvavadze 1974). According to Klopotovskaya (1973), in beech forests the maximum percentage of *Fagus orientalis* pollen was recorded in the pollen spectra of moss cushions (up to 64.7%).

The aim of our investigation is: 1) to establish exact criteria for distinguishing fossil spectra of Caucasian and Carpathian beech forests and their comparison with vegetation; 2) to reveal the dependence of the quantitative content of beech pollen in the spectra in different ecological conditions associated with the vertical climatic gradient.

MATERIAL AND METHODS

The material was gathered during Polish-Georgian expeditions from 1980 to 2000 (Fig. 3). Georgian beech forests and pollen spectra formed here were studied on 12 sites from 40 spots. In the Tatra Mountains 8 pol-

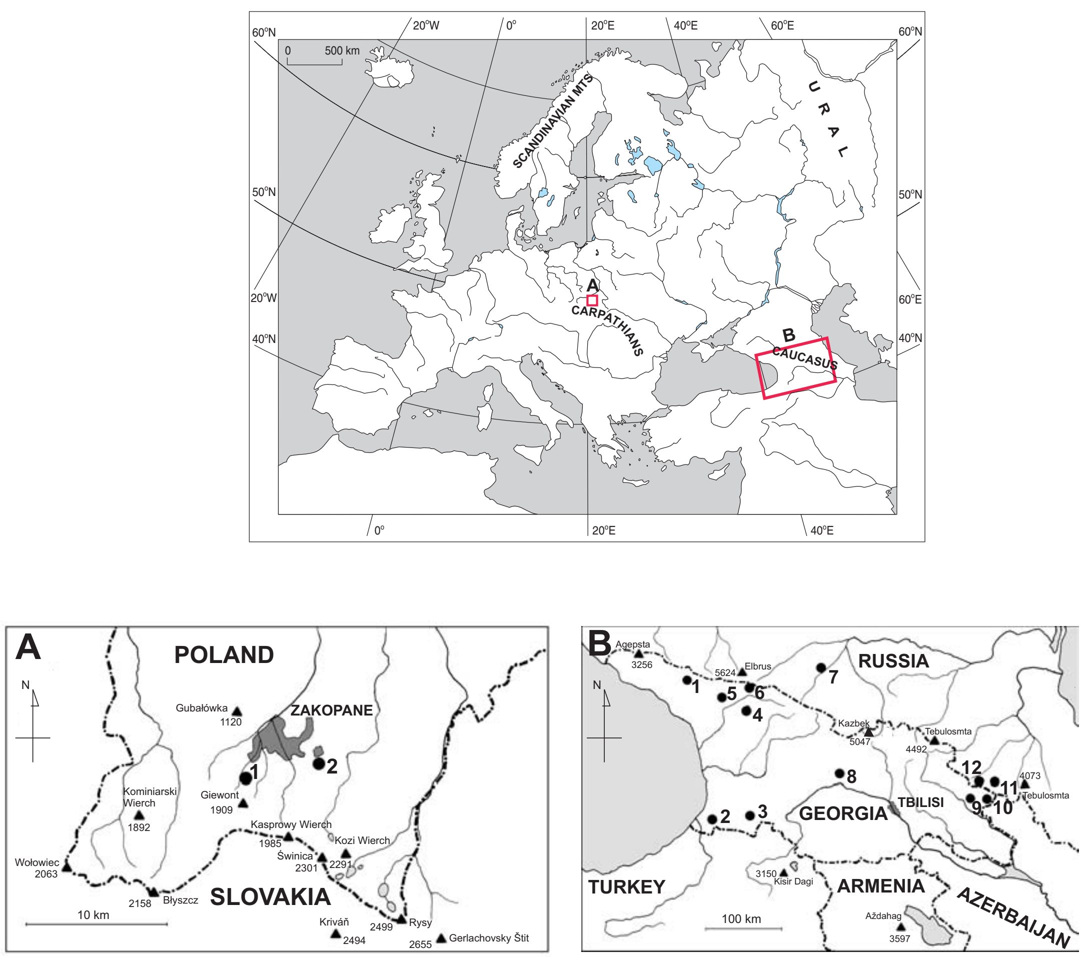

Fig. 3. Regions of beech forest studied: **A** – High Tatra Mountains: **1** – Stążyska valley, **2** – Olczyska valley; **B** – Caucasus Mountains: **1** – Ritsa, **2** – Tsiskara, **3** – Pontic Reservation, **4** – Khodzhal, **5** – Adange, **6** – Amtkel, **7** – Ossetia, **8** – Bevreti, **9–12** – Lagodekhi Reservation

len spectra from 2 sites were studied. In Ojców National Park (south Poland) one site in the beech forest was studied. In some places, for comparison, soils, moss cushions, Tauber pollen trap samples were studied. The material taken in the Caucasus was treated in the laboratory of the Institute of Palaeobiology, Georgian Academy of Sciences, (Tbilisi) using the Ertdman (1943) and Grichuk (Grichuk & Zaklinskaya 1948) methods, while samples from Polish beech forests were studied in the laboratory of the W. Szafer Institute of Botany, Polish Academy of Sciences (Kraków), using the Ertdman method (Erdtman 1943, 1960).

Detailed description of the subfossil spore-pollen spectra taken in beech forests are made on the basis of the AP pollen group, taking into account also the general pollen sum of NAP. Most diagrams were plotted on the same principle. In some cases, when the pollen spectrum of one or another sample had already been described in detail in the earlier work, we repeated this spectrum description (Kvavadze & Stuchlik 1990b, 1991, 1996). These were the spectra of Ritsa and Lagodekhi Reservations and those of beech forests of Trialeti.

RESULTS

CAUCASUS. WEST GEORGIA

In West Georgia, depending of climate humidity, beech forests are often situated above the dark coniferous forest belt. A similar picture is mostly observed in Abkhazia, where at lower levels the climate is dry and unfavourable for beech forests. In areas where beech forest grows above dark coniferous forests, the tree limit is formed by beech elfin woodland. This situation is observed in the headwaters of the Adange, Amtkel, Kelasuri, and Big Khodzhal rivers. However, also in Abkhazia on the southern spurs of the Greater Caucasus in the region of Lake Ritsa, beech forest grows below the spruce-pine belt. Here in the Ritsa Reservation a test site of the primary beech forests was studied. A similar site in the natural beech forest below the belt of dark coniferous forests was studied in Adzharia in the Tsiskari Reservation and in Guria on the way to the Bakhmaro resort in the beech forest (Pontic Reservation).

RITSA RESERVATION. The Ritsa Reservation (about 16 132 ha.) situated on the southern slopes of the Main Caucasian Range around Lake Ritsa, is mostly covered by forest vegetation. At lower altitudes (300–1200 m a.s.l.) in the forest the leading role is played by hornbeam, lime, and box tree. At higher altitudes are pine and oriental beech. High mountain forests consist of the Caucasian fir and beech, with a small admixture of the Sosnovski pine, spruce, and birch. The description of vegetation and pollen spectra in three altitudinal belts, lower, middle and high (Fig. 4) follows Kvavadze and Stuchlik (1990b).

Lower belt (800 m a.s.l.) represents sample No. 21 taken from a site about 30 km west from Lake Ritsa in a beech forest with under-

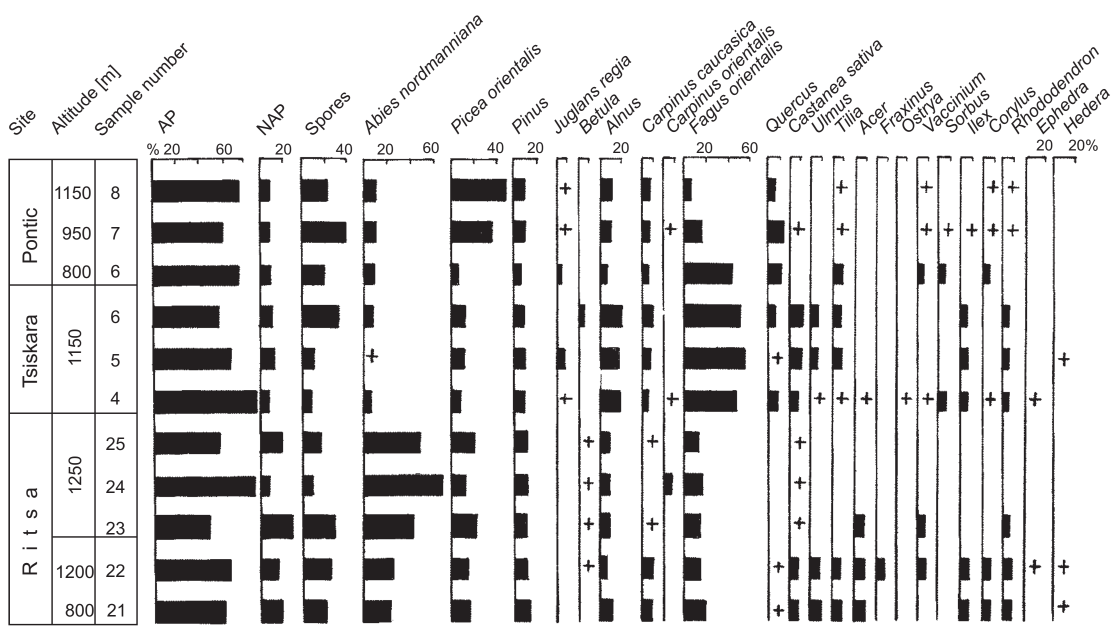

Fig. 4. Subfossil spore-pollen spectra of beech forest from the Ritsa Reservation (samples 21–25); Tsiskara (samples 4–6); Pontic Reservation (samples 6–8)

growth consisting mainly of *Buxus colchica* and *Rhododendron mucronatum*. The spore-pollen spectra of the sample are characterized by arboreal pollen of 64% and herbaceous and spore-bearing species of 18% each. 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 maximum values. The content of *Pinus*, *Picea*, and *Alnus* pollen ranges from 8 to 12%. Pollen of *Taxus*, *Quercus*, *Carpinus caucasica*, *Castanea*, *Tilia*, *Acer*, and *Ulmus* is found in single grains. Among shrubs *Ilex*, *Corylus*, and *Rhododendron* play a considerable role. The group of herbaceous species is marked by a great diversity. Pollen of Apiaceae, Asteraceae, Ranunculaceae, Boraginaceae, and Chenopodiaceae is most abundant, but other groups (Plantaginaceae, Geraniaceae, Lamiaceae, *Artemisia*, and others) are found occasionally. Spore-bearing species are mostly represented by monolete spores of Polypodiaceae (up to 65%). The content of *Hupertia selago* and *Botrychium lunaria* spores is considerable as well. Among monolete spores *Athyrium* and *Polystichum* are identified to the level of genus.

The forest of site 1 (sample 21) is characterized as a well developed more or less natural mountain forest with absolute dominant of *Fagus orientalis* covering more than 75% of the spot area. Other trees *Carpinus caucasica* *Acer sonsnovskyi* and *A. campestre* as an admixture cover less than 25% of the spot area. Phytosociological description of the studied sites was carried out by the Braun-Blanquet method (1951) and is presented on Table 1.

Comparison of the pollen spectrum of sample No. 21 with the botanical description of the site shows that the content of beech pollen is considerable underrepresented compared to its actual participation in the vegetation cover, while the amount of fir pollen suggests that it belongs not only to the trees growing on the given site but mostly blown in from a bordering belt. The *Alnus barbara* pollen (up to 11%) is also blown in from the neighbouring alder stands. *Buxus*, *Laurocerasus*, *Philadelphus*, *Rubus*, and *Smilax* growing in the sample plot are not represented in the spectra, probably because poor preservation of their pollen in soils. As to the herbaceous stratum, only its main components are reflected in the spectra.

Middle belt (1200 m a.s.l.) represents sample No. 22 taken from a spruce-beech forest. 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, *Abies* (up to 33%), *Fagus* (up to 16%), and *Picea* (up to 15%) are dominant. The amount of the *Pinus* and *Alnus* pollen is smaller, 12% and 5%, respectively. *Betula*, *Carpinus*, *Castanea*, *Acer*, *Ulmus*, *Tilia*, and *Fraxinus* are represented only by a few pollen grains. Pollen grains of shrubs (*Corylus*, *Ilex*, *Rhododendron*, *Vaccinium*, and *Ephedra*) are found in insignificant quantities. The herbaceous species group is distinguished by a large variety of plants: Apiaceae, Asteraceae, Boraginaceae, Chenopodiaceae, Fabaceae, Geraniaceae, Plantaginaceae, Plumbaginaceae, Poaceae, Polygonaceae, Ranunculaceae, Silenaceae, Violaceae, and others. Among spore-bearing species Polypodiaceae prevail, partially identified to the species level (*Polypodium vulgare*), while others (*Athyrium*, *Dryopteris*) are identified to the generic level. The spores of *Botrychium* are present in a rather large amount.

The beech-spruce forest (Tab. 1, site 2) of the middle belt is quite different from that of the lower belt. It differs by lower representation of *Fagus orientalis* in the forest (under 25% of area) and a considerable high amount of *Picea orientalis* about 25% of the area). The most characteristic feature of this forest is well developed undergrowth stratum formed by *Hedera colchica* and *Laurocerasus officinalis* covering more than 60% of the plot area, and *Ilex colchica*, *Fraxinus excelsior*, *Philadelphus caucasicus*, *Sambucus nigra*, and *Ulmus* sp. as admixture. The sample plot is situated in a rocky location and comprises trees of uneven age.

As one can see, the spectrum of sample No. 22 reflects better than of sample No. 21 the existing vegetation. *Picea*, *Fagus*, and *Acer*, as well as some representatives of shrubs (*Fraxinus*, *Ilex*, and *Rhododendron*) are adequate represented in the pollen spectrum. *Abies*, *Alnus*, *Pinus*, *Carpinus*, *Ulmus*, and *Tilia* are overrepresented mainly by long-distance pollen from other mountain belts.

In the higher belt (1250 m a.s.l.) samples Nos 23–25 from the beech-fir forest have pollen spectra also distinguished by a high concentration and good preservation of pollen. The pollen of arboreal species attains a maxi-

Table 1. Ritsa Reservation

Number of site		1	2	3
Sample numbers		21	22	23–25
Date		17.06. 1986	17.06. 1986	17.06. 1986
Altitude a.s.l. in m		800	1200	1250
Exposure		–	–	NW
Slope degree		0	0	15
Height of trees (maximum) in m		20–25	25–30	30
Diameter of tree stem in cm		100	100	110
Cover of tree layer %	a	90	60	50
Cover of shrub layer %	b	30	40	5
Cover of herb layer %	c	70	80	70
Trees:				
Fagus orientalis	a	5.5	2.2	1.1
	b	+	1.1	+
	c	+	–	1.1
Carpinus orientalis a		1.1	–	–
	b	+	–	–
	c	+	+	–
Abies nordmanniana	a	+	+	3.3
	b	–	+	+
Picea orientalis	a	–	2.2	+
	b	–	1.1	–
Acer pseudoplatanus	a	–	–	2.2
	b	–	–	–
	c	–	–	1.1
A. sosnovskyi	a	1.1.	–	–
	b	1.1	–	–
A. trautvetteri	a	–	1.1	–
	b	+	–	–
	c	+	–	–
A. campestre	b	1.1	–	–
	c	+	–	–
Quercus iberica	b	+	+	–
Taxus baccata	a	–	1.1	–
	b	+	–	–
Tilia caucasica	a	–	1.1	–
	b	–	+	–
Ulmus sp.	a	–	+	–
	b	–	1.1	–
Fraxinus excelsior	b	–	+	–
Shrubs:				
Buxus colchica		1.1	–	–
Rhododendron mucronatum		1.1	–	–
Ilex colchica		+	2.2	–
Philadelphus caucasicus		+.	1.1	–
Laurocerasus officinalis		+	3.3	–
Rubus caesius		+	–	–
Sambucus nigra		–	+	–
Hedera colchica		2.2	4.4	–
Smilax excelsa		1.1	–	–

Number of site	1	2	3
Herbs:			
Asarum europaeum	2.2	–	–
Fragaria vesca	2.2	+	–
Sanicula europaea	2.2	–	2.2
Alliaria officinalis	–	–	+
Aristolochia sp.	1.1	–	–
Asperula odorata	1.1	–	3.3
Borago officinalis	–	–	+
Carex sp.	1.1	–	–
Cephalanthera rubra	1.1	–	–
Ichenomene indica	–	+	1.1
Mycelis muralis	1.1	–	–
Phyllitis scolopendrium	1.1	+	–
Salvia sp.	1.2	–	–
Symphytum grandiflorum	1.3	+	2.2
Asplenium trichomanes	+.2	1	–
Athyrium filix-femina	+	1.1	3.3
Calystegia sepum	+	–	–
Cardamine hirsuta	–	+	1.3
Carex sylvatica	+	–	–
Cerastium dahuricum	+	–	–
Convallaria majalis	+	–	–
Dentaria bulbifera	–	+	+
Dryopteris filix-mas	–	+	3.3
Epipactis latifolia	+	–	+
Euphorbia oblongifolia	–	–	+
Festuca gigantea	–	+	–
Galium rotundifolium	–	+	–
Geranium robertianum	+	+	+
Geum urbanum	–	–	+
Lathraea squamaria	–	–	+
Lathyrus niger	+	–	–
Luzula pilosa	–	+	+.2
Melica nutans	–	–	+
Myosotis amoena	–	–	1.3
Oxalis acetosella	–	+	+
Paris incompleta	–	–	+
Platanthera bifolia	+	–	–
Polygonatum multiflorum	–	+	–
Polypodium vulgare	–	+	–
Polystichum sp.	+	+	–
Prunella grandiflora	+	–	–
Ranunculus sp.	–	–	+
Rubus sp.	–	–	+
Ruscus colchica	–	+	–
Sedum stoloniferum	–	–	+
Senecio platyphylloides	–	–	2.2
Urtica dioica	–	–	+
Vaccinium arctostaphylos	–	–	+
Veratrum lobelianum	–	–	+
Vincetoxicum scandens	–	–	+
Viola sp.	+	+	–

mum of 80%, with *Abies* predominant (41, 49 and 73%, respectively). The beech pollen takes second place (17%). Pine pollen is less significant (10–15%). The pollen content of the alder is also small (4–5%). Then come *Carpinus orientalis, C. caucasica, Betula, Castanea, Tilia, Acer, Vaccinium,* and *Rhododendron*. Herbaceous species are represented by pollen of Poaceae, Asteraceae, Fabaceae, *Campanula,* Geraniaceae, Dipsacaceae, Polygonaceae, Boraginaceae, Ranunculaceae, and others. Quantitatively the Silenaceae pollen is predominant. 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 is situated in the Auadkhara region in a well developed beech-fir forest of uneven age form very young to old and big trees (Tab. 1, site 3). 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.

TSISKARA RESERVATION. At an altitude of 1150 m, 1 km south of the meteorological station near the Mtirala mountain, with the highest amount of precipitation reaching up to 3000 mm a year, the test site has a well-developed natural forest (Kvavadze & Stuchlik 1990a). The first stratum consists only of *Fagus orientalis*. Its trees reach here 35m in height and 150 cm in diameter. However, the area of cover does not exceed 40%. The stratum of shrubs is also well-developed and is characterized by diversity of species, among which *Laurocerasus officinalis*, covering 50% of the area, is predominant. There is much *Daphne, Rhododendron ponticum,* and *Vaccinium arctostaphylos* here. *Fagus, Hedera Rhododendron luteum,* and *Sorbus* are also found. *Castanea sativa, Ilex colchica, Rubus,* and *Viburnum,* are met occasionally. The stratum of herbs is poorly developed and covers up to 5% of the area. These are mainly ferns.

For spore-pollen analysis three soil samples were studied. The pollen spectra (Fig. 4) have the following peculiarities. In the common group arboreal pollen prevails (91–61%). The content of herbaceous species is not high. Monolete spores of ferns are predominant. Among arboreal species beech pollen prevails (up to 53%). Alder is the second dominant (up to 20%). There are high quantities of chestnut (up to 13%) and pine (up to 10%). Low amounts of spruce and fir are found. *Carpinus caucasica, Quercus, Ulmus, Tilia, Betula,* and *Juglans* occur even in smaller quantities. The shrub group is represented by *Corylus, Hedera, Ilex, Laurocerasus, Rhododendron, Sorbus,* and *Vaccinium*. The group of herbaceous species is poor and contains single pollen grains of Apiaceae, *Artemisia*, Asteraceae, Chenopodiaceae, Poaceae, Polygonaceae and Silenaceae. Spore-bearing species consist only of ferns.

As is evident, pollen spectra in this region more adequately reflect the existing vegetation. The role of beech in the spectrum is not reduced at all, as was observed in the spectra of beech forests of the Ritsa Reservation. The transported pollen of dark coniferous species growing in the upper belt is found in lower quantities. However, here the amount of pollen transported from the lower belt of chestnut-hornbeam forests is somewhat higher (especially *Alnus*).

PONTIC RESERVATION. In the beech forest belt at an altitude from 900 to 1200 m three samples in lower, middle and upper parts on the way from Chochkhati to the Bakhmaro resort were studied (Nos 6, 7, 8 in Fig. 4).

The first sample (No. 6) was taken at the lowest level of the belt under consideration in the thicket of *Quercus pontica*. In the pollen spectra the content of arboreal species is 78%. In the group of herbaceous plants spore-bearing species containing monolete spores of ferns prevail. In arboreal pollen beech is predominant (42%), and *Quercus pontica,* widespread in the undergrowth, is the second dominant (10%). The group of conifers consists of *Abies, Picea,* and *Pinus* pollen. They are contained in equal quantities of no more than 7–8%. There is little lime and Caucasian hornbeam pollen. *Juglans regia* and *Alnus barbata* are found in rather small quantities. Shrubs are represented by *Corylus, Sorbus, Rubus,* and *Vaccinium* pollen. As a whole, their amount here is not high. Among herbaceous species Apiaceae, *Artemisia*, Asteraceae, Chenopodiaceae, Polygonaceae, and *Scabiosa* are met in single pollen grains. Spore-bearing species are represented by *Dryopteris* and *Pteridium* spores.

In the vegetation on the test site under consideration the first stratum (trees) is absent, the second stratum consists of *Quercus pontica* shrubs and covers more than 75% of the plot area. The maximum shrub height reaches 3 m. Under the oak thickets a lower shrub stratum composed of *Laurocerasus officinalis* and *Rhododendron ungernii,* which cover area is 100%. *Ilex colchica, Vaccinium arctostaphylos* and *Viburnum orientalis* cover 35% of the surface, grow sporadically under *Rhododendron* and cherry-laurel thickets. Herbaceous species are absent under shrub thickets. *Fagus orientalis, Acer trautvetteri, Sorbus aucuparia, Rubus* sp., and *Dryopteris filix-mas* are recorded only in the marginal areas.

In the middle part of the beech forest belt sample 7 was taken. Here, unlike the above-mentioned test site, the first stratum is present and consists entirely of *Fagus orientalis.* However, here the beech pollen content in pollen spectra hardly reaches 19%. Among arboreal species *Picea orientalis* is predominant. In other respects the spectrum is the same as that of sample 6.

In the upper part even lover quantities of beech pollen are recorded in the spectrum of sample 8, taken at the upper beech forest limit. Here it accounts only for 4%. And the spruce growing in the upper belt reaches 48% in the spectrum of sample 8. Fir pollen is the second dominant (10%).

At the upper limit of beech forests the vegetation has the following peculiarities. The description was made on the uneven-aged forest site, on the eastern slope of the Bakhmaro mountain. The tree height reaches 30m, diameter up to 110 cm. The first stratum consists of beech and fir, which cover 50–75% and 25% of the area, respectively. The undergrowth consists only of young specimens of *Fagus, Abies* and *Picea,* covering 75% of the area.

The herbaceous stratum is taxonomically rich but represented occasionally. Beech, fir, and spruce seedlings are predominant. Here typical representatives of the herbaceous stratum of beech forests (*Asperula odorata, Galium rotundifolium, Paris incompleta, Dentaria bulbifera, Salvia glutinosa, Carex sylvatica, Sanicula europaea, Dryopteris filix-mas,* and *D. dilatata*) are found. These plants are more important than those characteristic for spruce forests. The latter are represented by the following species: *Gentiana schistocalyx, Oxalis acetosella, Cardamine hirsuta, Melandrium album, Vaccinium arctostaphylos, Cerastium vulgatum,* and others.

In the lower part of their extent the beech forests of Bakhmaro are reflected in the pollen spectra much better than at the border with dark-coniferous forests (Stuchlik & Kvavadze 1987, Kvavadze & Stuchlik 1988).

BIG KHODZHAL HEADWATERS. The river Big Khodzhal is situated in the eastern part of the Kodori Range and originates from the spurs of the Khodjal mount (maximum height 3313 m). Here forests with predominance of beech at an altitude of 1170–1800 m have been studied. It should be mentioned that in the region under investigation the dark-coniferous forest of spruce and fir does not form a continuous belt. It is discontinuous and is almost completely replaced by the beech forest.

Pollen spectra from the beech forest belt (Fig. 5, samples 2, 3, 4, 5, and 6) were studied in three parts of the belt: lower part at altitude 1170–1200 m a.s.l. (samples 2, 3), middle part at 1400–1500 m a.s.l. (samples 3, 4), and higher part at 1800 m a.s.l. (sample 6).

In the lower part beech is predominant in the forest, but rather large quantities of chestnut on slopes (sample 2) and alder in a floodplain (sample 3) are also recorded, and *Carpinus caucasica, Tilia caucasica,* and *Acer trautvetteri* are admixed. In the undergrowth *Rhododendron, Vaccinium,* and *Ilex* prevail. In the pollen spectrum of sample No. 2 the content of arboreal pollen is as a maximum (84%). In this group the beech and chestnut also play an essential role (25% each). The content of hornbeam and lime pollen does not exceed 9%, while that of alder, which does not grow near the site mentioned, is as high as 14%. The amount of pollen of fir, spruce, pine, elm, oak, and walnut is small. Among shrubs the nut-tree and *Rhododendron* are prevalent. The amount of the bilberry pollen is less. *Ilex* is not reflected in the pollen spectra at all. Among herbaceous species only pollen grains of Asteraceae are found in greater amount. Spore-bearing plants are represented only by monolete spores of Polypodiaceae (16%).

In the pollen spectrum of sample 3 the features vegetation cover is adequately reflected. Among arboreal plants alder and beech are predominant, constituting 34% and 18%, respectively. The pollen content of spruce and

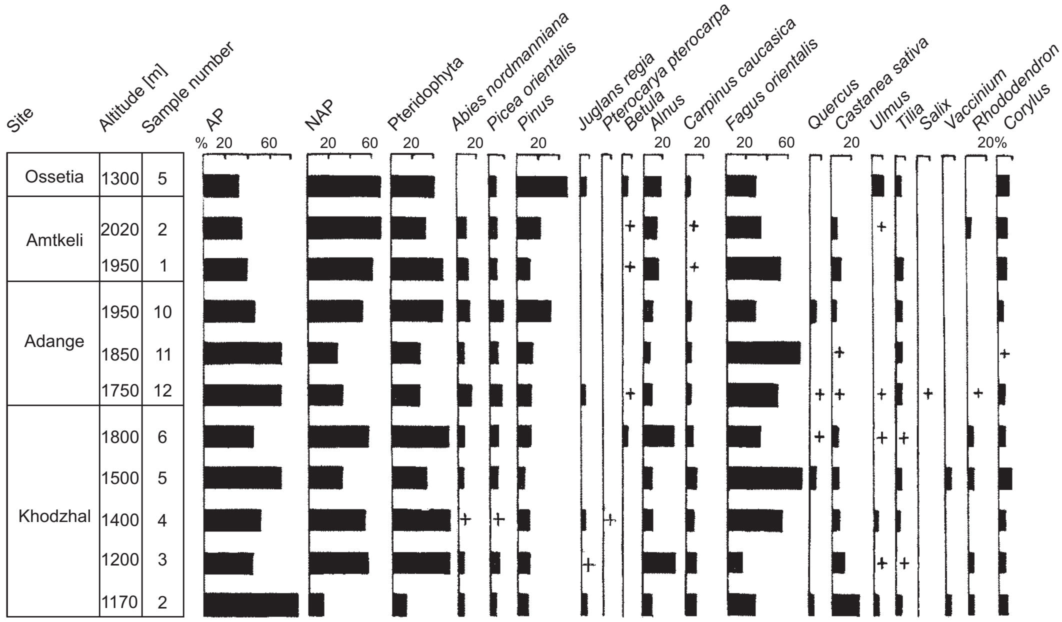

Fig. 5. Subfossil spore-pollen spectra of beech forest along the river Big Khodzhal valley (samples 2–6); Adange river valley (samples 10–12); Amtkeli river valley, beech elfin woodland (samples 1,2); Ossetia (sample 5)

pine is prevalent (up to 10%), but there is little pollen of fir (2%). Other arboreal plants are represented by single pollen grains of lime, elm, and walnut. There is little pollen of *Rhododendron* and *Corylus*.

There are very few herbaceous species and many spore-bearing ones (56%). The abundance of ferns results from higher humidity of soils in the flood-plains of rivers. Apart from the monolete spores of ferns, trilete spores of *Pteridium aquilinum* and *Lycopodium alpinum* occur.

In the middle part, samples 4 and 5 taken from pure beech forests, have pollen spectra with up to 53–71% beech pollen, and 9–18% of alder pollen. The role of hornbeam, chestnut, pine, and nut-tree is insignificant. Occasionally occur pollen of spruce, fir, *Pterocarya,* walnut, elm, and bilberry. Herbaceous species are rather poorly represented as single pollen grains of Apiaceae, Asteraceae, Chenopodiaceae, Fabaceae, Poaceae, and Polygonaceae. Spore-bearing species (31–51%) are represented by the monolete spores of ferns.

In the higher part sample 6 was taken from the beech elfin woodland of the subalpine belt at an altitude 1800 m a.s.l. Its pollen spectrum is distinguished by the following features. The amount of arboreal species is about 45% and of herbaceous species only 6%. Spore-bearing plants reach the highest amount (49%). Among arboreal plants the leading role is played by pollen of beech (33%) and alder (27%). It should be noted that in the belt of beech elfin woodland, which forms impassable thickets, beech pollen in soil does not exceed 40%, while in the pure beech forest it is as high as 71%. Probably being suppressed, the crawling form of arboreal plants produce much less pollen. In the pollen spectra of the soils under the beech elfin woodland one can also see pollen of 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. Pollen of *Artemisia,* Boraginaceae, Plumbaginaceae, Ranunculaceae, and Silenaceae is reflected in the spectrum as well as that of Apiaceae, Asteraceae, Chenopodiaceae Lamiaceae, Polygonaceae, and others. Monolete ferns represent almost all the spore-bearing plants. *Lycopodium alpinum* occurs as isolated spores.

Thanks to the absence of the dark coniferous forest belt, pollen spectra reflect a real picture of vegetation existing here.

HEADWATERS OF THE ADANGE RIVER VALLEY. The Adange River is the right tributary of the river Chkhalta and is in the region of the Marukhi Pass, where the spurs of the Greater Caucasus, Chkhalta, and the eastern margin of Bzyb Range converge. The climate here is very humid, so beech forests grow together with dark – coniferous forests, and at the tree limit they form the belt of pure beech forests, changing into the beech elfin woodland. Three pollen samples, from the lower, middle, and upper part of the belt have been taken in various type of forest. The pollen spectra are presented on Fig. 5.

The lower sample No. 12 comes from an altitude of 1750 m in the beech-fir forest. Here the admixture of spruce is very low. For spore-pollen spectra of arboreal species, beech pollen (43%) is prevalent. As in the vegetation, the subdominant is fir (19%). Single pollen grains of birch, oak, willow, and hazel result from a small admixture of these species in this altitudinal belt. Pollen of other arboreal species has been transported in low quantities from the lower belts. Herbs are not numerous, only single pollen grains of *Artemisia*, Asteraceae, Chenopodiaceae, Poaceae, and Polygonaceae are present. Many monolete spores of ferns (21%) are recorded, including *Athyrium*.

The middle sample No. 11 comes from an altitude 1850 m in the belt of pure beech forests, where beech pollen accounts for 69%. Pollen of other arboreal species is transported from long distance. The composition of herbaceous plants is richer than in sample 12. Pollen of Apiaceae, Geraniaceae, Plumbaginaceae, Silenaceae, and others is also found. The spore contents is rather high (18%). Besides monolete spores of ferns, *Botrychium lunaria* spores are present.

The upper sample No. 10 comes from an altitude 1950 m in the belt of beech elfin woodland above the timberline. The pollen spectrum is distinguished by abundance of monolete spores of ferns (up to 50%). There are many *Botrychium* spores here. Among arboreal species the transported pine pollen prevails, while beech pollen amounts only to 28%, somewhat less than in the beech elfin woodland in the Big Khodzhal valley. There is a lot of transported pollen of *Alnus* here. Among herbaceous plants Asteraceae and Silenaceae are predominant. Pollen of Apiaceae, *Artemisia,* Chenopodiaceae, Lamiaceae, Onagraceae, and others is present.

THE RIVER AMTKELI HEADWATERS. The trough valley of the river Amtkeli at its headwaters is separated from the Adange valley by a narrow mountain strip. Sample 1 comes from the border of beech elfin woodland and beech forest at an altitude 1950 m and sample 2 from the very elfin woodland at an altitude 2020. In sample 1 beech pollen (56%) among arboreal species is predominant (Fig. 5). The second dominant here is pine (16%) and alder, chestnut, fir, lime, and spruce pollen is recorded in low quantities. Birch and hornbeam are met in single grains. The group of herbaceous plants is characterized by a rather great diversity, but as a whole their amount is not high. There are many spore-bearing species here (46%), entirely represented by monolete spores of ferns.

The pollen spectrum of sample 2 is characterized by a slight decrease in the beech pollen content (41%) among arboreal species and an increase in the herbaceous pollen content. The pollen content of arboreal, herbaceous, and spore-bearing species here is almost the same. In the herb group Asteraceae are predominant. Spore-bearing species are mainly represented by monolete spores of ferns. *Lycopodium* and *Pteridium* are recorded as single spores.

Thus the considered beech elfin woodland spectra suggest that here, as in the headwaters of Big Khodzhal and Adange, the pollen productivity of the shrub form of beech is much lower.

NORTH CAUCASUS

OSSETIA. Soil sample 5 comes from basin of the river Ardon in the Koban gorge at an altitude 1300 m in the beech forest (Fig. 5). High-mountain maple grows in low quantities together with beech. Arboreal pollen occurs in lower quantities than herbaceous pollen, and spore-bearing species prevail. These are essentially ferns (*Dryopteris, Phyllitis*), amounting to 40% of the whole quantity of counted sporomorphs. Arboreal species and shrubs account for 35% of the spectrum. Among them the transported pollen of pine (41%) prevails. The second dominant is beech (up to 26%). Rather high amounts of alder, elm, and hazel pollen (14–9%) are recorded. Birch, hornbeam, lime, and spruce are of less importance.

In the herbaceous group pollen of ruderal plants from long-distance transport prevails. These are mainly Asteraceae and Chenopodiaceae. As local elements Apiaceae, Boraginaceae, Brassicaceae, Poaceae, and others are met. Pollen of Cerealia (up to 3%) is also found.

The spore-pollen spectra as a whole adequately reflect regional peculiarities of the Ardon gorge, where at an altitude 1200–1600 m pine and pine-birch forests prevail. The local vegetation is also characterized by the abundance of ferns typical for highland beech forests and by the predominance of beech pollen among broad-leaved species. In the pine and pine-birch forests ferns are found in very low quantities both in the vegetation and in pollen spectra (no more than 8–9%).

EAST TRANSCAUCASIA

TRIALETI RANGE. Beech-oak forests occur on the extreme eastern spurs of the Trialeti Range in the neighbourhood of the village Bevreti, and beech-spruce forests near the village Mskhaldidi Phytosociological description of the studied sites carried out by the Braun-Blanquet method (1951) is presented after our previous paper (Kvavadze & Stuchlik 1991) on Table 2.

Samples 3, 4, 5 were taken at an altitude of 1200 m in an uneven-aged beech-spruce forest, plot 2. Description of the spore-pollen spectra comes from Kvavadze and Stuchlik (1991). The spore-pollen spectra are distinguished by maximum content of the arboreal species (82–87%). Herb content is 10–18% and spores do not exceed 2–3% (Fig. 6). Among trees pollen of *Picea* (up to 41%) and beech (up to 35%) prevail. *Carpinus caucasica* can be considered as the third dominant (up to 19%). The participation of *Quercus* and *Carpinus orientalis* is also significant, up to 7% and 6% respectively. A few pollen of *Acer*, *Alnus*, *Betula*, *Juglans*, and *Tilia* were found. Among shrubs only *Corylus* occurs in small amounts. Among herbs adventitious pollen of *Artemisia* and Chenopodiaceae is predominant. There is little pollen of Apiaceae, Asteraceae, *Carex*, *Plantago*, Poaceae, Polygonaceae, and Ranunculaceae. In the spectrum of the soil sample taken on the bank very close to the river, pollen of aquatic-paludal vegetation was revealed (*Sparganium* and *Myriophyllum*). Sporiferous species are represented by *Polypodium vulgare* and *Dryopteris filix-mas* and monolete spores of ferns without perisporium. The pollen spectrum composition compares well with that of the vegetation growing on the experimental plot.

The test site 2a with beech-oak forest is situated at an altitude 1150 m. Spore-pollen

Table 2. Bevreti

Number of site (field)		2	2a
Sample number		3,4,5	6,7,8
Date		27.05.1989	13.06.1989
Altitude a.s.l. in m		1200	1150
Exposure		E	E
Slope degree		45	15
Height of trees (maximum) in m		25	15
Diameter of tree stem in cm		50	50
Cover of tree layer %	a	80	100
Cover of shrub layer %	b	30	10
Cover of herb layer %	c	20	30
Trees:			
Fagus orientalis	a	3.3	4.4
	b	1.1	2.2
	c	+	–
Quercus iberica	a	–	4.4
Carpinus caucasica	a	1.1	2.2
	b	–	+
C.orientalis	a	–	+
Acer campestre	a	+	+
	b	–	1.1
A. laetum	a	–	+
	b	1.1	+
Tilia caucasica	b	+	–
Ulmus sp.	b	+	–
Shrubs:			
Lonicera caucasica		1.1	+
Euonymus europaeus		+	+
Rubus hirtus		1.1	+
Crataegus sp.		–	+
Herbs:			
Asperula odorata		+	1.1
A. taurica		–	1.1
Dentaria bulbifera		2.2	2.2
Geranium robertianum		–	+
Sanicula europaea		2.2	–
Polygonatum multiflorum		+	+
Poa nemoralis		–	1.1
Primula macrocalyx		–	1.1
Viola mirabilis		+	+
Lathraea squamaria		+	–
Lathyrus hirsutus/niger		+	1.1
Luzula sylvatica		+	–
Melica nutans		1.1	1.1
Anthriscus sp.		–	1.1
Fragaria vesca		–	+
Cephalanthera rubra		–	+
Platanthera bifolia		–	+
Galium aparine		–	+
Chaerophyllum aromaticum		–	+
Polypodium vulgare		1.1	–
Dryopteris filix-mas		+	–
D. carthusiana		–	+
Serratula sp.		–	+
Silene italica		–	+

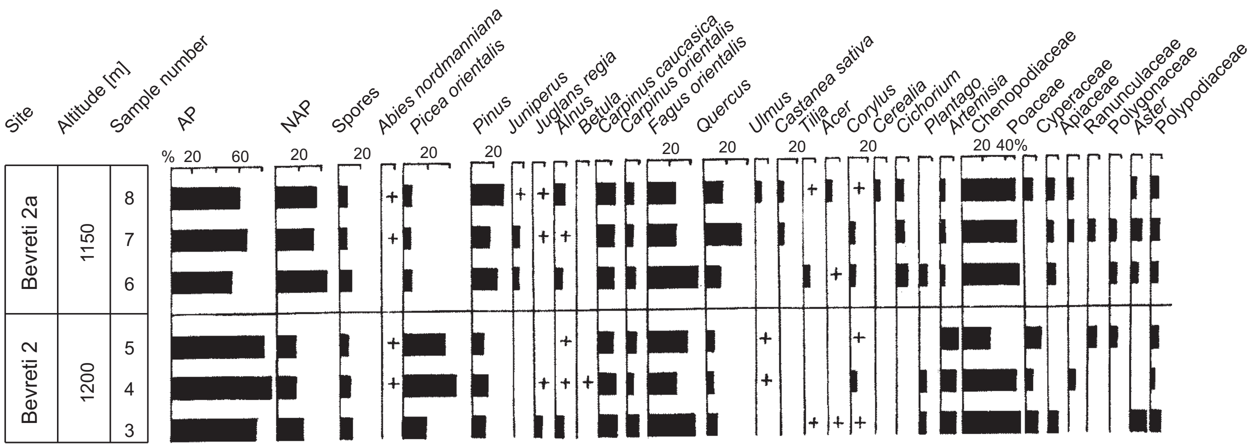

Fig. 6. Subfossil spore-pollen spectra of beech forests of Bevreti (samples 3–8)

spectra of samples 6, 7, and 8 taken here are characterized by predominance of arboreal plants (56–68%) The proportion of herbs is 30–38% and that of spores 1–5% (Fig. 6). Among arboreal species the following are predominant: *Fagus* (up to 39%), *Carpinus* (up to 19%), and *Quercus* (up to 35%). Pollen of *Pinus* (up to 26%), which in all samples probably comes from long-distance transport, is of adventitious character. The content of the *Picea* pollen reaches 3–4%. *Abies* is represented by single pollen grains. *Acer, Alnus, Carpinus orientalis, Castanea, Juglans, Tilia,* and *Ulmus,* are distinguished by low content of pollen. Shrubs are represented by *Corylus* and *Juniperus.* Among herbs three groups are predominant: *Artemisia* (up to 2,9%), Asteraceae (up to 5.2%), and Chenopodiaceae (up to 50%), There is some pollen of Apiaceae, *Carex, Plantago,* Poaceae, Polygonaceae, Ranunculaceae, Silenaceae, and others. Single pollen grains of *Sparganium* are encountered. Sporiferous taxa include *Ophioglossum, Polypodium vulgare* and other Polypodiaceae.

LAGODEKHI RESERVATION. This reservation is in the extreme north-eastern part of Georgia. It is one of the oldest reservations with rich vegetation containing many Tertiary relicts and high endemism. However, here dark coniferous forests are absent. Only *Pinus hamata* is recorded in very low quantities. Beech forests occupy two thirds of the forest area. Here optimal conditions for beech are only at altitudes from 800 to 1500m (Dolukhanov 1941). More detailed information on the history and nature of the reservation is given in our earlier work (Kvavadze & Stuchlik 1996).

We studied more comprehensively the beech forests situated on the reservation territory than in other regions. Besides soil samples, moss cushions were investigated. In 1996 pollen monitoring began here. In the beech forests 5 modified Tauber traps were placed, where the pollen rain collected in these traps for each calendar year is studied (Kvavadze 2001). Material of the last three years can be compared with those of soils and mosses.

At the altitudes from 690 to 2035 m and within the forest regions with participation of beech the vegetation has been recorded by the Braun Blanquet method (1951) on 9 test sites (Tab. 3).

In the Lagodekhi Reservation surface samples of soils have been studied in three altitude forest belts:

The lower mountain belt — **beech-chestnut forest** (690–720 m a.s.l.), site 1 and 2 (field numbers 2 and 3, Tab. 3), samples 2–8;

The middle mountain belt — **beech-hornbeam forest** (950 – 1650 m a.s.l.), site 3–7 (field numbers 10–12 and 20–21, Tab. 3), samples 24–32 and 56–60;

The high mountain belt — **beech-maple forest** (1720–2035 m a.s.l.), site 8 and 9 (field numbers 16 and 19, Tab. 3), samples 45–47 and 52–54.

The description of the vegetation and spectra is elaborated on the basis of data taken from the previous work (Kvavadze & Stuchlik 1996). The main component of the forest in all three belts is *Fagus orientalis,* but pure beech

Table 3. Description of the beech forests in the Lagodekhi Reservation

Ordinal number		1	2	3	4	5	6	7	8	9
Number of site (field)		(3)	(4)	(10)	(11)	(12)	(21)	(20)	(19)	(16)
Sample number		2,3	4–8	24–26	27–29	30–32	58–60	55–57	52–54	45–47
Date		05.06. 1989	05.06. 1989	07.06. 1989	07.06. 1989	07.06. 1989	09.08. 1989	09.08. 1989	09.06. 1989	08.09. 1989
Altitude a.s.l. in m		690	720	950	1220	1400	1650	1675	1720	2035
Exposure		SE	SW	S	N	N	SE	W	S	N
Slope degree		15	30	30	45	45	15	20	45	60
Height of trees (maximum) in m		30	30	25	35	30	25	30	35	30
Diameter of tree stem (maximum) in cm		120	100	80	100	80	80	90	150	100
Cover of tree layer %	a	80	90	80	90	80	90	90	80	80
Cover of shrub layer %	b	40	60	30	10	20	5	30	40	70
Cover of herb layer %	c	30	20	5	30	60	80	70	60	60
Trees:										
Fagus orientalis	a	4.4	5.5	3.3	3.3	2.2	3.3	3.3	2.2	5.5
	b	3.3	3.3	3.3	1.1	2.2	1.1	2.2	3.3	4.4
	c	1.1	1.1	1.1	–	1.1	–	–	+	–
Castanea sativa	a	1.1	2.2	–	–	–	–	–	–	–
	b	+	–	–	–	–	–	–	–	–
	c	+	–	–	–	–	–	–	–	–
Carpinus caucasica	a	2.2	1.1	3.3	1.1	3.3	3.3	3.3	–	–
	b	+	–	+	–	–	+	+	–	–
	c	+	+	+	–	–	–	–	–	–
Fraxinus excelsior	a	2.2	1.1	–	–	–	–	–	–	–
	b	+	–	–	–	–	–	–	–	–
	c	+	–	–	–	–	–	–	–	–
Tilia caucasica	a	1.1	+	3.3	2.2	1.1	1.1	1.1	–	–
	b	+	+	–	–	–	–	1.1	–	–
Quercus iberica/	a	1.1	+	–	–	–	2.2	*1.1	–	–
**Q. macranthera*	b	+	–	–	–	–	–	+	–	–
	c	–	+	–	–	–	–	–	–	–
Acer velutinum	a	–	–	–	–	–	–	–	–	–
	b	–	+	–	–	–	–	–	–	–
	c	–	–	+	1.1	–	–	–	–	–
A..campestre	b	1.1	–	–	–	–	–	–	–	–
A.. pseudoplatanus	a	–	–	–	–	–	–	–	–	–
A. trautvetteri	a	–	–	–	–	–	2.2	2.2	3.3	1.1
	b	–	–	–	–	–	–	–	1.1	–
	c	–	–	–	–	1.1	+	1.1	1.1	–
A. laetum	a	–	+	–	1.1	1.1	–	2.2	–	–
	b	1.1	+	–	–	+	–	+	+	–
	c	+	–	–	1.1	1.1	–	–	–	–
Corylus avellana	b	3.3	1.1	–	–	–	–	+	–	–
	c	–	–	+	–	–	–	–	–	–
C. colurna	a	–	–	–	–	–	1.1	–	–	–
Shrubs:										
Rubus caesius		2.2	–	–	–	–	–	–	–	–
R. .idaeus		–	–	–	–	–	–	–	+	+
R. serpens		1.1	–	–	–	–	–	–	+	+
Rubus sp.		–	+	–	2.2	2.2	+	+	–	+
Ulmus elliptica	b	+	–	–	–	–	–	–	–	–
Hedera helix	b	+	–	+	–	–	–	–	–	–
	c	+	+	1.1	–	–	–	–	–	–

Table 3. Continued

Ordinal number		1	2	3	4	5	6	7	8	9
Sambucus nigra	b	–	–	–	–	+	–	–	–	+
Rhododendron flavum	b	–	1.1	–	–	–	–	–	–	–
Sorbus cancasigena			–	–	–	–	–	–	–	1.1
Herbs:										
Asperula odorata		1.1	–	+	+	3.3	3.3	3.3	3.3	1.1
A. taurica		–	–	–	–	–	+	1.1	+	1.1
Festuca sylvatica		2.2	2.2	+–	–	–	+	1.1	2.2	–
Dryopteris filix-mas		+	+	+	3.3	1.1	3.3	3.3	3.3	3.3
D. carthusiana		–	–	–	–	–	–	–	+	+
Polygonatum multiflorum		+	–	–	–	–	–	+.3	–	+
P. verticillatum			–	–	+	–	–	–	–	+
Salvia glutinosa		+	–	–	–	–	–	–	+	+
Viola mirabilis		+	+	–	–	–	–	–	–	–
V. sylvestris		–	–	+	–	+	+	+	+	–
Euphorbia macrocarpa		+	–	–	+	+	1.1	1.1	1.1	+
Pteridium aquilinum		+.2	+	–	–	–	–	–	–	–
Circea lutetiana		+	+	–	–	–	–	–	–	–
Geranium robertianum		–	–	–	–	–	1.1	1.1	1.1	–
Dentaria bulbifera		–	–	+	2.2	+	+	1.1	–	1.1
Moehringia trinervia		–	–	–	–	+	1.1	1.1	+	+
Polystichum braunii		–	–	–	+	+	–	–	—	–
Stellaria holostea		–	–	–	–	–	3.3	3.3	2.2	–
Poa nemoralis		–	–	–	–	–	+	1.1	–	–
Athyrium filix femina		–	–	–	–	–	1.1	+	–	–
Neottia nidus-avis		–	–	–	+	–	+	–	–	–
Astrantia maxima		–	–	–	–	–	+	+	–	+
Gentiana schistocalyx		–	–	–	–	–	–	1.1	+	1.1
Carex brizoides		–	+	–	–	–	–	–	–	–
C. sylvatica		–	–	–	–	–	–	–	+	–
Stachys sylvatica		–	+	–	–	+	+	+	–	–
Primula macrocalyx		–	–	–	–	–	1.1	1.1	+	+
Galeopsis tetrachit		–	–	–	–	–	–	+	–	–
Geum urbanum		–	–	–	–	–	+	+	+	+
Phyllitis scolopendrium		–	–	–	–	+	–	–	–	–
Urtica dioica		–	–	–	–	+	–	+	–	–
Anthriscus nemorosa		–	–	–	–	–	+	–	+	–
Calamagrostis arundinacea		–	–	–	–	4.4	–	–	–	2.2
Impatiens noli-tangere		–	–	–	–	+	3.3	3.3	1.3	–
Sedum stoloniferum		–	–	–	–	–	+	+	+	1.1
Asteraceae										
(cf. *Telekia speciosa*)		–	–	–	–	–	+	1.1	1.1	1.1
Lapsana communis		–	–	–	–	–	+	–	+	+
Mycelis muralis		–	–	–	–	–	–	–	+	+
Veronica chamaedrys		–	–	–	–	–	+	–	+	–
Symphytum grandiflorum		–	–	–	–	–	+	–	+	–
Senecio sp.		–	–	–	–	–	–	–	1.1	+

Sporadic species: in site nr 3: +, *Aristolochia iberica* +, *Crataegus* sp. +, *Lathyrus* sp. +, *Salix caprea* +, *Vicia cracca* +; 4: *Carex digitata* +, *Hypericum androsacaeum* +, *Vicia crocea* +; 10: *Cephalantera* sp.+; 12: *Lathyrus* sp. +; 16: *Aruncus silvester* 1.1, *Asplenium adiantum-nigrum* +, *Athyrium distentifolium* +, *Betula litvinovii* (b) +, *Epilobium* sp.+, *Myosotis* sp. +, *Oxalis acetosella* +, *Ranunculus* sp. +, *Rumex arifolius* +, *Salix caprea* +; 19: *Cardamine hirsuta* +, *Galeobdolon luteum* +, *Galium* sp.+; 20: *Lamium album* +, *Mespilus germanicus* (b)+, *Senecio macrophyllus* 1.1, *Solidago virga-aurea* +; 21: *Colchicum speciosum* 2.2, *Rumex tuberosus* +, *Scrophularia divaricata* +, *S. lateriflora* +, *Silene wallichiana* +, *Stellaria nemorum* +; 21: *Hesperis voronovii* +. *Rosa* sp.+.

forest is very rare in the Lagodekhi Reservation. Mostly these are mixed deciduous beech (*Fagus orientalis*) forests with admixture of *Castanea sativa, Carpinus caucasica, Tilia caucasica*, and various *Acer* species.

The lower mountain belt is characterized by considerable prevalence of *Fagus oreintalis*, which covers from 60% to more than 75% of the area of sites 3 and 4 respectively, and a significant admixture of *Castanea sativa, Tilia caucasica, Carpinus caucasica*, and *Fraxinus exelsior*. Under the canopy of trees a shrub layer with components of the tree layer and *Corylus avellana, Hedrea helix, Rhododendron flavum* and various species of *Rubus* is well developed covering 40–60% of the described site areas. In the forest studied seven soil samples were taken and analysed: samples 2 and 3 from site No. 3 and samples 4–8 from site No. 4. The pollen spectra are shown on Fig. 7. The content of arboreal and shrub pollen (AP) is high (up to 80%). The percentage of pteridophytes is 3–13%. In the AP group pollen of *Fagus* predominates (up to 45%), and the second subdominant is *Castanea* (up to 30%). *Carpinus* pollen is to 27%, and *Tilia* is always present in small amounts. Sample No. 8, taken directly under a lime tree, is distinguished by an abundance of *Tilia* pollen (up to 45%). Pollen of *Alnus, Pterocarya, Pinus* and *Quercus* is found in small amounts. Very few pollen grains of *Fraxinus, Juglans, Picea*, and *Ulmus* occur, and among shrubs *Corylus* is dominant. *Hedera* occurs as single pollen grains.

As already mentioned, *Fagus orientalis* dominated here in the past, and subdominants were *Castanea sativa, Carpinus caucasicus*, and *Tilia caucasica*. The undergrowth includes *Corylus avellana, Rhododendron flavum, Rubus caesius, Hypericum androsaemum, Crataegus*, and *Ulmus*. In the herb cover *Festuca sylvatica* and *Asperula odorata* were predominant. Ferns were represented by *Dryopteris filix-mas* and *Pteridium aquilinum*.

As one can see, the AP pollen spectra in general adequate reflect the structure of the forest, but they show considerable underrepresentation of *Fraxinus* and do not show *Acer* pollen in them at all.

In the **middle mountain belt** five sites of beech-hornbeam forest were studied (field numbers 10, 11, 12, 20, 21). At lower altitude (950–1220 m a.s.l.) these forests grew only in admixture with *Tilia caucasica* which role in higher altitudes till 1675 m a.s.l. was reduced. From 1220 m a.s.l. appeared *Acer laetum* which in higher altitudes at about 1650–1675 m a.s.l. was accompanied by *A. trautvetteri, Quercus macranthera*, and *Corylus colurna*. All sites represent a well developed and good restoring forest of uneven age, with all group of trees from juvenile to old aged big trees up to 35 m high and 100 cm stem diameter. The cover degree of the tree layer in all sites is rather high, varies from 80% to 90%, while

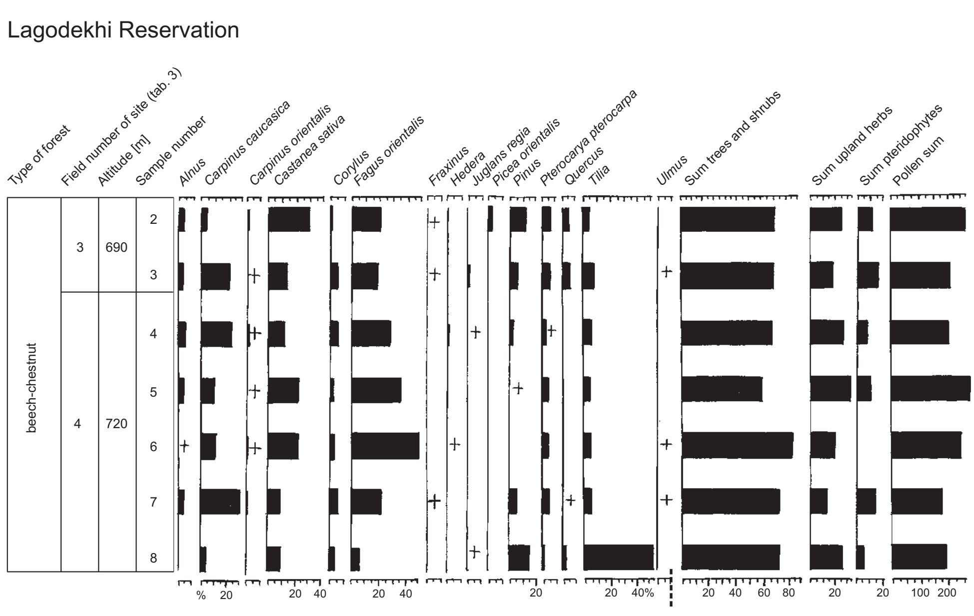

Fig. 7. Subfossil spore-pollen spectra of beech-chestnut forest of the Lagodekhi Reservation (samples 2–8)

that of the shrub layer is rather low and varies from 5% to 30%.

From the site No. 10 samples 24, 25, and 26 were taken for pollen analysis. In spite of the fact that the three forest components contained similar numbers of individuals, the pollen spectra (Fig. 8) show a considerable dominance of *Fagus* (up to 50% of sum of trees and shrubs). *Carpinus* and *Tilia* (20% and 15% respectively) were second subdominants. The AP group is characterized by large quantities of *Pterocarya pterocarpa* pollen (up to 20%), which has been carried here from below. This has evidently been caused by the southern exposition of the slope and its great steepness. Vertical slopes of the mountains serve as a screen where the pollen of many plants transported from lower belts is trapped. In addition to *Pterocarya*, the spectra contain *Alnus, Castanea, Juglans, Ulmus*, and *Corylus*. Some pollen has been carried from the higher mountain belts too, for example, pollen of *Betula* and *Pinus*. As a result of the long-distance transport from the west pollen of *Picea* and *Abies* occur, while pollen grains of *Artemisia*, Chenopodiaceae, and *Ephedra* have been brought in from the steppes and forest-steppes of the lowland parts of East Georgia. There are also many spores of ferns (up to 45%).

In pollen spectra of soil samples 27, 28, and 29 taken in site 11 (Fig. 8) local pollen is very well represented. *Fagus* pollen prevails (up to 43%) with *Tilia* (up to 22%) as second dominant, what is adequate to the representation in the forest. Only *Carpinus* as a subdominant is recorded in lower amounts than it is represented in the forest composition. The other components of the spectra present a very interesting picture. Here there is very little pollen of plants growing in the lower belts, much less than in site 10. However, the amount of *Pinus* pollen increases sharply, mainly coming from the pine forests on the northern slopes of the Greater Caucasus in Daghestan.

Pollen spectra (Fig. 8) of samples 30, 31, and 32 taken from the site 12 are distinguished by a large *Carpinus caucasica* pollen content (up to 67%), followed by *Fagus* (up to 52%), and *Tilia* (up to 20%), what adequately reflect the forest composition. *Acer* does not appear in the spectra at all, while *Acer laetum* plays a considerable role in the forest composition. The spectra do not show such shrub elements as *Rubus*, which grows extensively, covering up to 20% of the brushwood layer (b) in the forest. However, there is pollen of forest species from neighbouring belts, namely *Alnus, Castanea, Corylus, Juglans, Pterocarya*, and *Ulmus*. From higher altitudinal belts pollen of *Pinus* and *Betula* has been transported, while from the steppe regions of the eastern and south-eastern Georgia, pollen of *Artemisia* and Chenopodiaceae has been brought in. The spectra adequately register the local herbs and

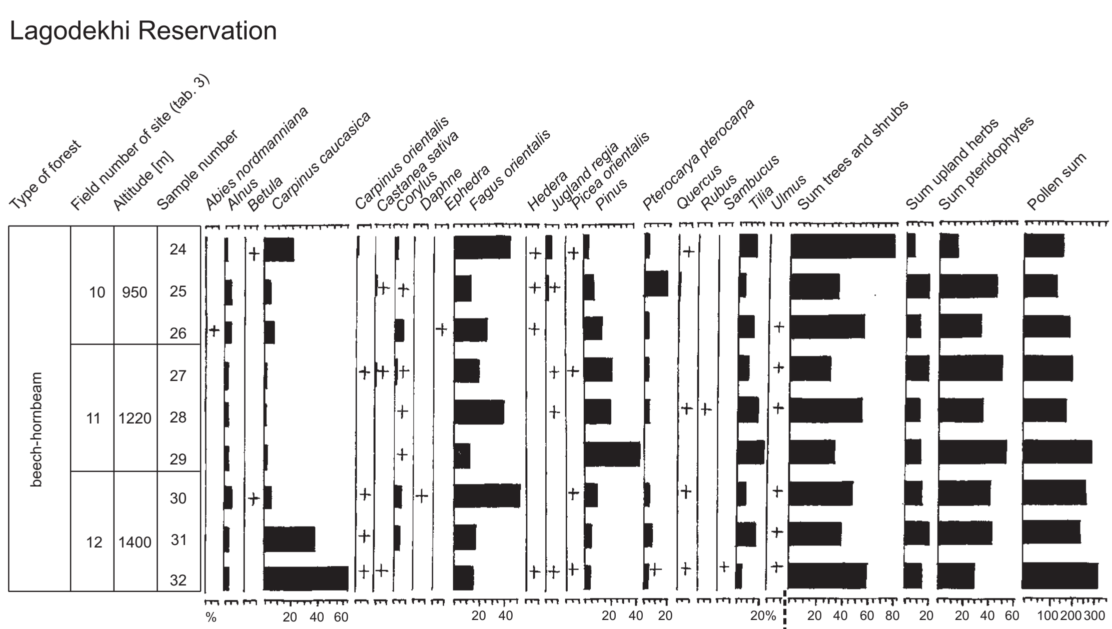

Fig. 8. Subfossil spore-pollen spectra of beech-hornbeam forest of the Lagodekhi Reservation (samples 24–32)

pteridophytes, with the amounts of the latter fully matching the quantities in the present-day communities.

At the uppermost border of the beech-hornbeam forest, in both sites 21 and 20, *Fagus orientalis* and *Carpinus caucasica* were dominants covering over 25% each of the area, and *Acer trautvetteri* with *Tilia caucasica* subdominant. As subdominants were also *Quercus iberica*, and *Corylus colurna* in site 21, and *Quercus macranthera* and *Acer laetum* in site 20.

In pollen spectra of samples 58, 59, and 60 from the site 21 (Fig. 9) *Carpinus* and *Fagus* are dominants just as in the forest, and all the subdominants are represented as well. The slope aspect has limited the availability of pollen from the south of the region to that of *Artemisia*, Chenopodiaceae, *Juglans regia*, and others. Pteridophytes and other local herbaceous plants are adequately represented in the spectra.

The spore-pollen spectra of samples 56 and 57 from the site 20 are characterized by the predominance of *Fagus* (up to 26%) and *Carpinus* (20%) pollen, and subdomince of *Tilia*, what adequately reflect the composition of forest. High amount of *Pinus* pollen (19%), was transported from pine forests of Daghestan, since the slope is of north-western aspect here. From the higher belts there was also transported pollen of *Betula* and *Rhododendron*, and spores of *Botrychium lunaria*, whereas single pollen grains of *Abies* and *Picea* were transported by the wind from north-western Georgia. The spectra also show elements from the lower belts, including *Alnus*, *Juglans*, *Pterocarya*, and *Ulmus*. However, elements of the steppe region are much more poorly represented than on the south-facing slopes. Thus there is no pollen of *Ephedra* and very little of *Artemisia*, Cerealia, and others. There are many fern spores in the spectra.

In the **upper mountain belt** at altitudes of 1720 and 2035 m, two sites of beech forest were studied (Nos 19 and 16), with dominance of *Fagus orientalis* and *Acer trautvetteri* in the tree and undergrow layers, with the covering degree more than 75% of the area. As subdominant in site 19 was also *Acer laetum*. *Rubus idaeus and R. serpens* were the only additional undershrub in both sites, while in site 16 additional *Sorbus caucasigena* and *Betula litwinowii* are playing a considerable role in the forest. The herb layer in both sites was very rich with *Asperula odorata* and *Stellaria holostea* and many ferns (*Dryopteris filix-mas* and *D. carthusiana*), as well as representatives of mountainous tall forb communities (Asteraceae, *Gentiana schistocalyx* and others) as predominant.

Soil samples 52, 53 and 54 were taken from the site 19 and samples 45, 46, and 47 from the site 16 at the upper limit of the beech-

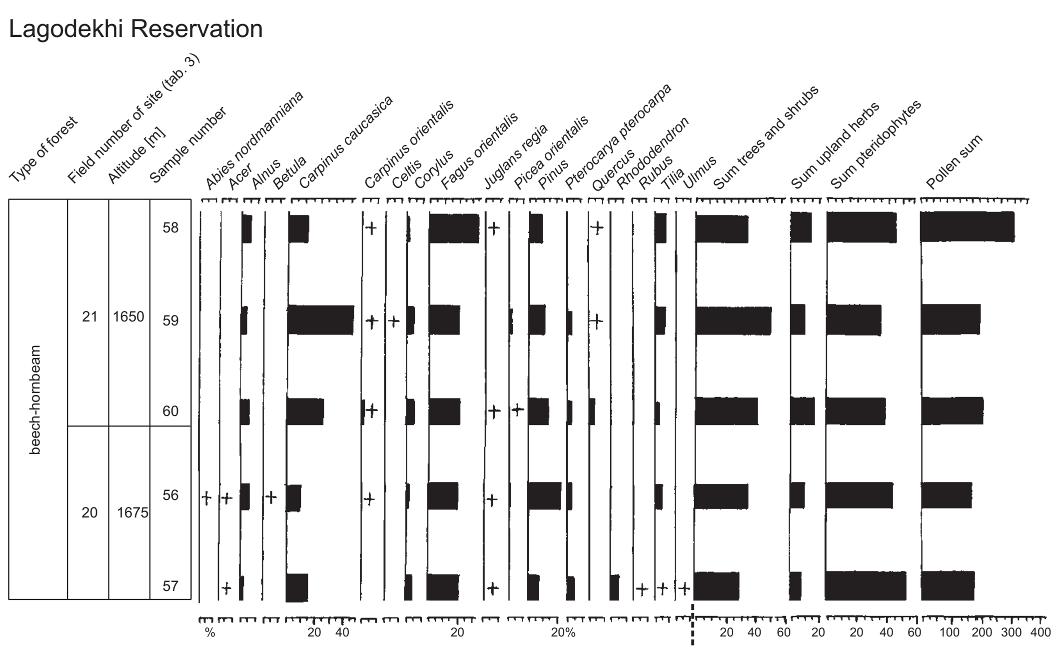

Fig. 9. Subfossil spore-pollen spectra of beech-hornbeam forest of the Lagodekhi Reservation (samples 56–60)

hornbeam forest. The spore-pollen spectra (Fig. 10) of samples from the both site are characterized by a dominance of sporiferous plants (Pteridophytes) reaching their maximum value (62.5%).

In pollen spectra from the site 19 among the AP group pollen of *Fagus*, *Pinus*, and *Carpinus* predominates. The amount of *Acer* occurs only as single grains. Among the conifers pollen of *Picea orientalis* is always present, while that of *Abies nordmanniana* occurs only in one sample. The elements of the lower belts are represented by fairly significant amounts of *Alnus barbata* and *Pterocarya pterocarpa*. *Castanea sativa*, *Juglans regia*, *Quercus iberica*, *Tilia caucasica*, and *Ulmus glabra* occur only sporadically. Among the shrubs pollen of *Corylus* and *Ephedra* is found only in two samples.

In the NAP group Chenopodiaceae (up to 21%), *Artemisia*, and Asteraceae predominate here on the southern slope. Among sporiferous plants, apart from *Dryopteris*, there are spores of *Botrychium* and *Ophioglossum*. The former has most probably been carried in from the upper belts, while the latter has come from below. Pollen of many NAP taxa is found in small amounts, included elements of synanthropic vegetation.

Pollen spectra of samples 45, 46, and 47 from the site 16 are characterized by dominance of *Fagus* (up to 36%), *Carpinus* (up to 18%), and *Betula* (up to 15%), in the AP group (Fig. 10). The large amount of *Betula* indicates the proximity of the tree limit. The spectra do not contain pollen of *Abies* and *Picea*, most probably because of the northern exposition of the slope. However, *Pinus* is always present, with a high percentage of pollen (up to 10%), coming mainly from long distance transport. The quantities of *Alnus*, *Corylus*, and *Pterocarya* are fairly significant (up to 2.7%, 4% and 2.2% respectively), and pollen grains of *Acer*, *Carpinus orientalis*, *Castanea*, *Ephedra*, *Juglans*, *Quercus*, *Tilia*, and *Ulmus* are coming from long-distance transport.

In the NAP group Polypodiaceae (up to 60%) are dominants, while Chenopodiaceae (up to 5%), *Artemisia* (up to 1.1%), and other Asteraceae (up to 1.1%), can be considered as subdominants, other herbaceous plants (Apiaceae, Euphorbiaceae, Poaceae, Ranunculaceae, *Taraxacum* and others) are represented in less than 1% of pollen in the spectra. There are many spores of *Dryopteris* and *Asplenium* (up to 12.4% and 5.5% respectively). Pollen of synanthropic plants occurs only sporadically.

Thus the factual material presented above suggests that the maximum beech content in the spectra is recorded at an altitude 720–950 m. The same is the case for the soil spectra of beech forests within the altitude range 1230–1400 m. However, in spite of the absence of the dark coniferous forest belt at its upper growth limit, beech was not adequately re-

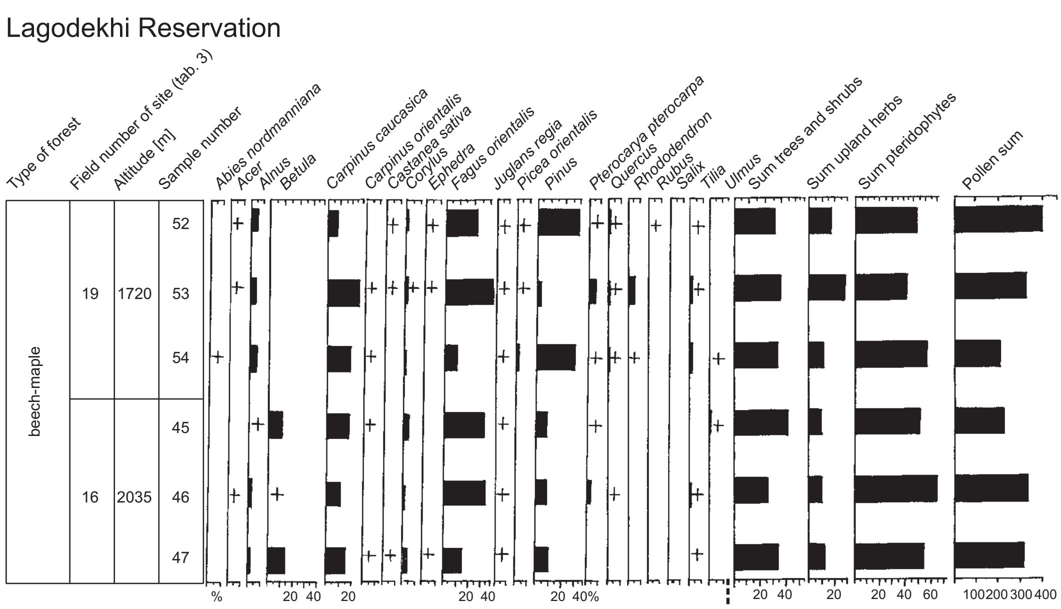

Fig. 10. Subfossil spore-pollen spectra of beech-maple forest of the Lagodekhi Reservation on the upper limit of *Fagus orientalis* (samples 52–57)

flected (underrepresented) in the pollen spectra of soil samples.

POLISH CARPATHIANS

In the High Tatra Mountains the beech forest belt (Carpathian beech forests, *Dentario glandulosae-Fagetum* of the *Querco-Fagetea* class) is situated at altitudes from 550 (600) m to 1150(1250) m a.s.l.. Besides dominating *Fagus sylvatica*, *Abies alba* and *Acer pseudoplatanus* are occasionally admixed.

Along the river Strążyska in Tatra National Park three sites with beech forests (site 14, 15, 16) at the altitude 800, 930, and 1000 m and one site along of the Olczyska valley at altitude 870 m have been studied (more comprehensive material is under study, Obidowicz personal communication). From each site three soil samples were taken, while in the Olczyska valley both soil samples and moss were taken for analysis. However, not all the samples appeared to be suitable for analysis. Sufficient quantities of pollen and spores could be counted in 8 samples, whose spore-pollen spectra are given in Fig 11. The description of the forest along the Strążyska valley made by the Braun Blanquet (1951) method is presented on Tab. 4.

Soil sample 31 was taken from site 14 situated at an altitude of 1000 m, where beech and low and equal admixtures of spruce, fir, and maple grow. In the pollen spectra (Fig. 11) some predominance of herbaceous plants (55%) over arboreal species is characteristic. In the group of arboreal pollen, despite the predominance of beech in the forest, beech pollen accounts for 6% only. In the pollen spectra alder (25%) and pine (20%) pollen prevails. They do not grow not only on test site 14, but even throughout the whole beech forest belt. The transported birch pollen accounts for 18% of the arboreal group and should be considered as the third dominant. However, spruce, fir, and maple growing on the test site are reflected in the spectra rather poorly. The spruce pollen content hardly reaches 14%, fir up to 1%, and maple no more than 1%. The content of beech pollen at only 6% is also very reduced. Among other broad-leaved species oak, hornbeam, and elm, whose pollen was transported here from the lower belts, are also present. From these belts *Corylus* pollen reaches rather large quantities (up to 14%), transported from long distance. Among herbaceous species only Poaceae prevails. The second dominants are Asteraceae species (*Artemisia, Aster, Cirsium,* and *Cichorium*). Quite large amounts of Chenopodiaceae and other ruderal elements are found. Apiaceae, Cerealia, *Plantago,* and Ranunculaceae occur as single grains. Spore-bearing species are fully represented by monolete spores of ferns (*Dryopteris, Athyrium*). The description of vegetation presented

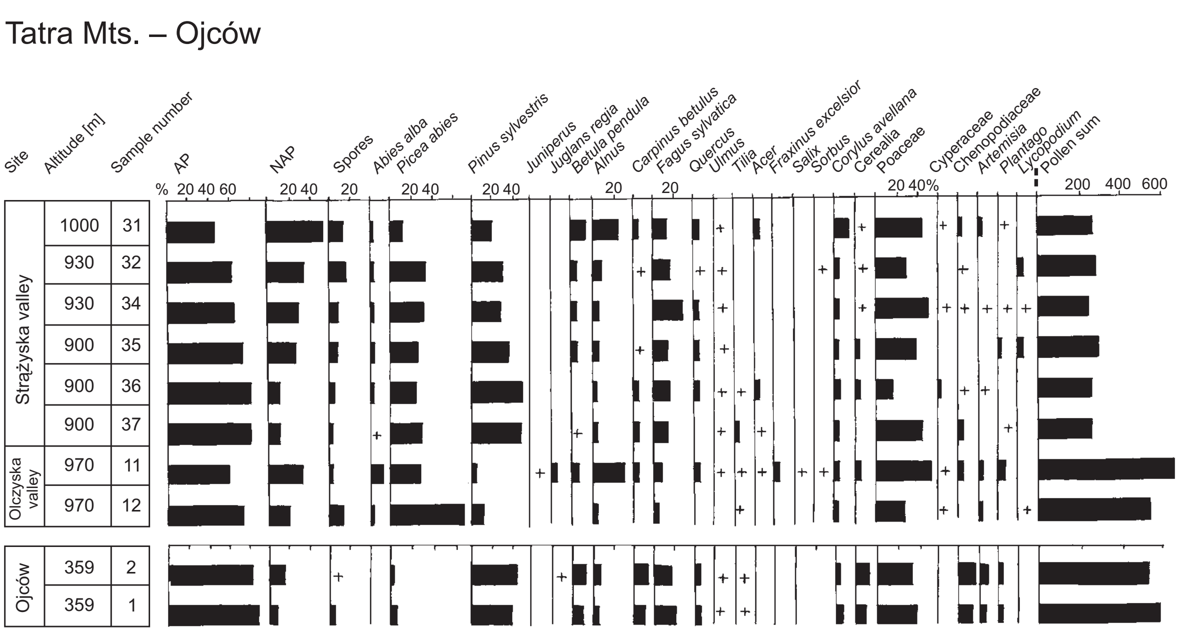

Fig. 11. Subfossil spore-pollen spectra of *Fagus sylvatica* forest in the High Tatra Mountains: Strążyska valley (samples 31–37); Olczyska valley (samples 11, 12); and in the Ojców National Park (samples 1, 2)

Table 4. Description of the beech forest in the Tatra Mts. (all records are made in the Stążyska valley)

Number of site		14	15	16
Sumple number		31	32,34	35–37
Date		13.09. 1989	13.09. 1989	13.09. 1989
Altitude a.s.l. in m		1000	930	900
Exposure		W	E	E
Slope degree		45	60	60
Height of trees (maximum) in m		30	25	30
Diameter of tree stem in cm		100	50	50
Cover of tree layer %	(a)	90	100	80
Cover of shrub layer %	(b)	60	20	30
Cover of herb layer %	(c)	90	30	90
Trees:				
Fagus sylvatica	a	4.4	5.5	4.4
	b	1.1	1.1	2.2
	c	–	+	+
Abies alba	a	1.1	1.1	2.2
	b	1.1	1.1	1.1
	c	–	+	+
Picea abies	a	1.1	–	+
	b	2.2	1.1	+
	c	–	–	+
Acer pseudoplatanus	a	1.1	+	+
	b	1.1	+	+
	c	–	–	+
Larix decidua	a	–	–	1.1
Fraxinus excelsior	b	–	–	+
Shrubs:				
Sorbus aucuparia		–	+	+
Rubus hirtus		–	–	+
R. idaeus		–	–	+
Herbs:				
Geranium robertianum		3.3	+	–
Asarum europaeum		2.2	–	+
Cardamine trifolia		2.2	2.2	–
Sanicula europaea		2.2	–	1.1
Galeobdolon luteum		1.1	–	–
Fraxinus excelsior		1.1	1.1	1.1
Veronica montana		1.1	–	–
Oxalis acetosella		3.3	2.2	3.3

Number of site	14	15	16
Stellaria nemorum	2.2	–	–
Athyrium filix-femina	1.1	+	+
Chrysanthemum rotundifolium	1.1	–	–
Crepis paludosa	1.1	–	–
Mycelis muralis	1.1	–	–
Phyteuma spicatum	–	+	+
Petasites albus	1.1	+	+
Primula elatior	1.1	–	–
Ranunculus lanuginosus	1.1	–	–
Actea spicata	+	–	–
Ajuga reptans	+	1.1	–
Anthriscus sylvestris	+	–	
Calamagrostis arundinacea	+	+	4.4
Dryopteris filix-mas	+	–	+
Epilobium montanum	+	–	+
Fragaria vesca	+	+	1.1
Luzula sylvatica	+	–	*flaves-cens*+
Myosotis sylvatica	+	–	–
Gymnocarpium dryopteris	+	–	–
Polygonatum verticillatum	+	–	–
Polystichum braunii	+	–	–
Prenanthes purpurea	+	2.2	1.1
Pulmonaria officinalis	+	–	–
Senecio fuchsii	+	–	–
Dentaria glandulosa	–	+	–
Gentiana asclepiadea	–	+	+
Hieracium lachenalii	–	+	*muro-rum* 1.1
Lapsana communis	–	+	1.1
Mercurialis perennis	–	+	–
Paris quadrifolia	–	+	
Solidago virga-aurea	–	+	–
Streptopus amplexicaule	–	+	–
Viola reichenbachiana	–	1.1	1.1
Prunella vulgaris	–	–	+
Astrantia major	–	–	+
Dryopteris carthusiana	–	–	+
Soldanella carpatica	–	–	+
Vaccinium myrtillus	–	–	+
Poa nemoralis	–	–	+

in Table 4 shows that local vegetation and especially participation of beech in the spectra is very reduced. However, the content of transported pollen is nearly 80% of the arboreal spectrum.

Soil samples 32 and 34 were taken on test site 15, situated at altitude of 930 m. The peculiarity of the pollen spectra is the predominance of arboreal pollen (69–67%), among which spruce (37–38%) and pine (27–28%) should be regarded as dominants. The third dominant is beech (18–26%). The quantity of fir (2%) somewhat increased. However, here the pollen content of alder and birch compared to the spectra of sample 31 sharply decreases. In the spectra of samples 32 and 34 the oak, hornbeam, elm, and hazel pollen is recorded in low quantities. In the group of herbaceous species, like the spectra of sample 31, Poaceae (27–50%) prevail. Rather small quantities of Asteraceae, Chenopodiaceae and Ranunculaceae are found. Among spore-bearing species ferns are predominant. *Lycopodium clavatum* spores are recorded as single spores.

For spore-pollen spectra of samples 35, 36 and 37, taken at the altitude of 900 m (site 16), the following features are characteristic. The pollen of arboreal species (76–84%) becomes more important. Among arboreal species the transported pine pollen is predominant (39–52%). Spruce is the second dominant (25–31%). The content of beech, as in previous spectra, takes the third place and reaches up to 11–14%. Here hornbeam, lime, and maple become more important. The content of fir pollen as a whole also increases. However, birch, alder, and oak are of less importance. In the group of herbaceous plants Poaceae also predominates. The importance of Cerealia and ruderal elements also increase. Among spore-bearing species ferns prevail. *Athyrium* and *Dryopteris* are identified up to the generic level. In sample 35 *Lycopodium clavatum* spores are found.

On site 15 in the middle of the beech forest the spectra reflected coenosis peculiarities better than on site 14. Here the beech pollen content reaches maximum values. Spruce and fir are also represented in higher quantities. The role of transported pollen is much lower than in site 14 and accounts here for no more than 35%. For site 16 the beech pollen content in the spectra again is strongly reduced with respect to the existing vegetation, while the transported pollen of arboreal species is up to 50%.

As has already been noted, along the Olczyska valley in the High Tatra Mountains a longitudinal profile was examined from the lower to the upper limit of spruce forests. In the beech forest belt samples 11 (moss) and 12 (soil) at an altitude of 970 m besides beech there are small quantities of fir, spruce, and maple and, as a whole, the vegetation character is similar to that of site 14. In the spore-pollen spectrum (Fig. 11) of moss sample 11 arboreal species account for 64%. Transported pollen of alder is predominant (35%). The second dominant is spruce (26%) and the third is fir (13%). The beech pollen content does not exceed 5%. Thus the portion of local pollen in moss spectra is 44%. Rather insignificant quantities of transported pollen of pine (4%), birch (6%), and willow (1%) are found here. Among broad-leaved species, besides beech, oak (3%), hornbeam (0.6%), ash (0.4%), elm (0.2%), maple (0.1%), nut-tree (1%), and lime (0.1%) are recorded, as well as hazel (2%), and juniper (0.1%) of shrubs.

The group of herbaceous pollen is also characterized by a rich composition, with prevailing of Poaceae, and large quantities of Asteraceae, Ranunculaceae, *Plantago,* and Cerealia. Of lower importance are Cyperaceae, Chenopodiaceae, and *Artemisia* as single grains. There are very low quantities of spore-bearing species, mainly monolete spores of ferns.

Pollen spectra of soil sample 12, taken from the same site of the beech forest, are characterized by the following peculiarities. The portion of arboreal species is 78% with predominance of spruce pollen (85%). The second dominant is not alder, as in sample 11, but pine pollen (10%). The amount of beech does not exceed 2%, though it is the third dominant. The pollen of fir and alder is met even in smaller quantities. Lime and hazel are recorded only as single grains. The portion of local arboreal pollen in the spectra of soil samples is 87%.

The group of herbaceous plants is represented by abundance of Poaceae and ferns. It should be noted that in moss spectra spores of ferns are recorded in very low quantities. A similar regularity were observed in the material from Lagodekhi Reservation. In general *Fagus* is underrepresented in pollen spectra of soil from the Tatra Mts. and pollen of coniferous trees is abundant thanks a high amount of pollen from long-distance transport. While local pollen mainly of Poaceae is strongly overrepresented in the spectra. So, we should say that in general pollen spectra of soil in beech forest of Tatra Mts. not quite adequately reflect the forest composition.

For comparison we also studied one site in the beech forest in Ojców National Park. Beech forests here occupy nearly one third of the forested area (Medwecka-Kornaś & Kornaś 1963). However, in the spectra of soil samples beech-pollen content is also reduced. Pine pollen is predominant (43–45%), in spite of the fact that pine forests play a insignificant role in the park. In the pollen spectra (Fig. 11) among arboreal species the third dominant is the transported pollen of birch (15%) which does not grow in beech forest at all (Medwecka-Kornaś & Kornaś 1992), but is common in open landscape (Michalik 1978). Much pollen of hornbeam, alder, oak, and hazel is observed. Spruce, lime, elm and nut-tree are recorded in low quantities.

Among herbaceous species, like the spectra of beech forests in the Tatra Mountains, Poaceae and Asteraceae are predominant. A lot of Chenopodiceae and Cerealia pollen is found. Apiaceae, Brassicaceae, Polygonaceae, Ranunculaceae, *Plantago,* and *Typha* are recorded. Spore-bearing species are met in single monolete spores of ferns.

DISCUSSION

The factual material presented in this work suggests that in most cases the pollen spectra of beech forest reflect the real picture of beech in the coenosis. In these spectra the beech content reaches up to 60–70%, which indicates the presence of highly productive forests that are usually situated in the middle part of the beech forest belt. However, in the marginal areas, where the beech forest is adjacent to other vegetation belts, strong distortion of the pollen spectra often takes place. In these cases reliable criteria to characterize the beech forest spectra should be found what will allow one to identify similar fossil pollen spectra.

In the humid marine climatic conditions of West Georgia, where the beech forest belt is situated below the dark coniferous forests, extensive infestation of the spectra with coniferous pollen takes place. This process is most pronounced, for example, in spectra of the Ritsa and Pontic Reservations. In this case, in spite of spectra distortion, in all spectra of beech forests in the group of broad-leaved species beech pollen still prevails (Figs 4, 5). The same phenomenon is also observed in the spectra of beech forests of other regions of the Caucasus. This phenomenon may be a reliable criterion for identification of fossil spectra of beech forests due to the fact that in the Caucasus within the mountain forest zone beech pollen is not transported in large quantities from one belt to another. Therefore predominance of beech pollen among broad-leaved species means its real prevalence in the coenosis forming the spectrum under consideration. Typical is also the fact that in beech forest spectra of the western part of the Caucasus the total amount of arboreal species, as a whole, exceeds herbaceous plants considerably.

To establish the upper tree limit in high mountains it is very important to identify fossil spectra. Because in the western part of the Caucasus the beech elfin woodland often forms a tree line, it is necessary to identify the spectrum of beech elfin woodland thickets in the palaeospectrum and to distinguish it from that of the beech forest growing at lower altitudes. As is evident from our material, the typical feature of the beech elfin woodland spectrum is the predominance of the pollen of 3 spectrum components (Tab. 5). Only the sequence of dominant and subdominant can change. However, the prevailing complex is always the same and consists of *Fagus-Alnus-Pinus,* or *Pinus-Fagus-Alnus,* or *Fagus-Pinus-Alnus.* High content of the transported pine and alder pollen in the Caucasus conditions is characteristic for open landscapes within the upper tree limit (Klopotovskaya 1973, Kvavadze 1993). Besides, for spectra being formed under thickets of beech elfin woodland the predominance of spore-bearing species (especially ferns) in the group of herbaceous plants (Tab. 5) is characteristic. Noteworthy is also the nearly equal ratio of arboreal pollen to spore-bearing species. The content of other herbaceous species in the spectra considered is much lower than that of Pteridophyta representatives.

As seen in Table 5, unlike elfin woodlands the spectra of beech forests have, besides beech, which is almost always the spectrum dominant, the second and third subdominants are usually representatives of the neighbouring belts, both of the lower and upper belts. In most cases this is either spruce and fir from above or such broad-leaved species as hornbeam, oak, and chestnut from below. It is also important that the pollen content of beech itself reaches high values (up to 60–70%) in the upper part as it passes into the beech elfin woodland. And in the beech elfin woodland this index is no more than 28–40%.

Noteworthy is also the fact that on the territory of the Ritsa Reservation both in pollen spectra of beech-spruce and in beech-fir forests the fir pollen is predominant (60%). Beech in the beech-spruce forest is the second dominant, while spruce, covering 25% of the arboreal stratum, occupies the third place in the

Table 5. The dominant pollen in beech elfin spectra and beech forest spectra in western Georgia

Altitude	Site name	Dominant AP pollen	Dominant NAP pollen	Dominant forest composition
Beech elfin				
1800 m	Big Khodzhal	*Fagus-Alnus-Pinus*	Polypodiaceae-Asteraceae -Apiaceae	*Fagus orientalis* elfin – *Rhododendron caucasicum*
1950 m	Adange	*Pinus-Fagus-Alnus*	Polypodiaceae-Silenaceae -Asteraceae	*Fagus orientalis* elfin
1950 m	Amtkel	*Fagus-Alnus-Pinus*	Polypodiaceae-Polygonaceae -Asteraceae	*Fagus orientalis* elfin – *Rhododendron caucasicum*
Beech forest				
1500 m	Big Khodzhal	*Fagus-Alnus-Carpinus*	Polypodiaceae-Polygonaceae -Asteraceae	*Fagus orientalis*
1750 m	Adange	*Fagus-Pinus-Abies*	Polypodiaceae-Asteraceae -Polygonaceae	*Fagus orientalis* – *Picea orientalis*
1600 m	Kelasuri	*Fagus-Alnus-Abies*	Polypodiaceae- Asteraceae -Polygonaceae	*Fagus orientalis* – *Abies nordmanniana*
1150 m	Tsiskara	*Fagus-Alnus-Castanea*	Polypodiaceae- Asteraceae -Polygonaceae	*Fagus orientalis* – *Lauro-cerasus officinalis*
1150 m	Bakhmaro	*Fagus-Quercus-Picea*	Polypodiaceae-Asteraceae -Apiaceae	*Fagus orientalis* – *Abies nordmanniana*
800 m	Ritsa Reserv.	*Abies-Fagus-Alnus*	Polypodiaceae-Asteraceae -Apiaceae	*Fagus orientalis-Acer* – *Buxus* – *Hedera-herbs*

spectra. In the beech-fir forest the importance of beech pollen is strongly reduced. However, among the broad-leaved species beech is still the first dominant. The predominance of fir pollen in the spectra can be attributed to regional peculiarities of the reservation under consideration, where as a whole the area of fir forests considerably predominates. However, on the territory of the Pontic Reservation in the beech-fir forest, where beech covers 75% and fir 25% of the forest area in the spectra, the spruce pollen prevails (up to 55%), and the portion of fir is only 10%, while beech accounts here for 6%. And in this case the beech pollen is also predominant among broad-leaved species. High content of transported spruce pollen is also explained by a prevailing role of spruce forests on the Bakhmaro Range. According to our observations, the area of fir forests here is several times smaller than that of spruce forests.

In the conditions of East Georgia, on the Trialeti Range, where the climate as a whole is more arid, beech at its lower limit is more poorly reflected in the spectra (Fig. 6, samples 10, 11), than, for example, in the Lagodekhi Reservation with more humid climate. In mixed broad-leaved forests with participation of beech on the Trialeti Range the beech pollen content in the spectra hardly reaches 2–4% (Kvavadze & Stuchlik 1991). However, in similar broad-leaved forests with beech participation in the lower mountain belt of Lagodekhi the beech content in the spectra reaches 24–25%.

The peculiarity of the spectra of beech-oak forests with low participation of hornbeam on the Trialeti Range is the predominance of beech pollen (up to 39%). The second subdominant is hornbeam pollen, accounting for 19% rather than oak, which is recorded here in large quantities. The oak content in the spectra accounts only for 14%, which is also explained by predominance of hornbeam forests on the eastern margin of the Trialeti Range.

Very plausible and informative are pollen spectra of beech-chestnut forests in the humid climate of the Lagodekhi Reservation. They most faithfully reflected the coenosis structure, where, for example, on site 4 all forest dominants are represented in the pollen spectra. Beech accounts for 45%, chestnut 30%, and hornbeam 27% of the total arboreal species, similar to the test site. As for beech-hornbeam forests of the Lagodekhi Reservation, they perfectly reflect the existing vegetation. There beech is a dominant and hornbeam a subdominant.

However, beech forests situated above 1650 m are of somewhat different character. Though they almost fully consist of *Fagus orientalis*, the role of the beech pollen in the spectra is strongly reduced compared to the spectra of beech-hornbeam or beech-chestnut forests. The amount of beech pollen at an altitude from 1675 to 2053 m, though being predominant in the pollen spectra, hardly reaches 14–42% of the total amount of arboreal pollen. We thought that this phenomenon might have been caused by increasing importance of transported pollen both from upper and lower vegetation belts, characteristic for uplands (Kvavadze & Stuchlik 1996). However, according to the results of pollen monitoring at the upper limit of beech forests, besides the increasing the role of transported pollen, the beech pollen influx is also very important in formation of pollen spectra. At these altitudes beech produces 5–6 times less pollen than at lower levels (Kvavadze 1999).

The comparison of peculiarities of the pollen spectra of beech forests in the Caucasus and Tatra Mountains showed a number of specific features of recent spectra of soils being formed in the belt of beech forests of the High Tatra Mountains. While in the Caucasian spectra a distortion of actual spectrum content takes place essentially with the arboreal pollen transport from the adjacent belts, in the spectra of beech forests of the Tatra Mountains large quantities of arboreal pollen from the whole region are found. In no one studied pollen spectrum in the beech forest spectrum is beech the first dominant, since its quantity does not exceed 18–26%. It should be noted that this maximum is observed exactly in the spectra of the middle part of the beech forest belts, where, as has already been mentioned, a similar index in the Caucasian mountains can reach 60–70%. As for the marginal areas of the beech belt, in the Tatra Mountains the role of beech pollen is so much reduced that its pollen cannot even be regarded as the third subdominant. It is evident from the quantitative beech content in spectrum of sample 31 at an altitude of 1000 m a.s.l. in the Strążyska valley. Here the beech content in the spectrum is 7%. Even smaller amounts of beech pollen (2–5%) are in spectra 11, and 12, obtained at an altitude of 970 m along the Olczyska valley, where beech reaches its upper limit, as in the Strążyska valley. Little beech pollen is also in Ojców National Park, where conditions for beech forests are more favourable. After Obidowicz (1996) low quantities of beech are recorded in subfossil spectra of the Tatra Mountains. According to his data the amount of beech pollen in the middle part of the beech forest does not exceed 34.7%, while in the marginal areas its percentage drops to 4.7%. Not so much beech pollen is also in the spectra of beech forests of the Roztocze National Park in south-eastern Poland, where pollen monitoring is now being undertaken (Pidek & Bałaga 2000). According to this author the influx of *Fagus sylvatica* pollen here is very low and accounts only for 500 gr/cm^2 year.

Researchers also report low *Fagus sylvatica* pollen productivity and its reduced role in recent spectra, compared with other broad-leaved species in other European regions. The detailed discussion of this problem is given in the work by Schneider (1984), according to which in the Kalabri Mountains in the south of Italy at altitudes of 1000, 1400, and 1800 m, the beech pollen content in the beech forest spectra does not exceed 14–40%. Stefanova (1996) reported low pollen productivity of *Fagus sylvatica* at altitudes of 1640 and 1740 m. According to Stefanova, in the Northern Pirin Mountains in Bulgaria recent spectra of moss cushions in the pure beech forest the amount of beech pollen in the spectrum hardly reaches 21%. In this case the forest under investigation is at the upper limit of beech.

It should be mentioned that at the same time in the literature there are quite different data. For example according to Arap (1984), in the belt of beech forests of the Ukrainian Carpathians on the Polonin Range, the beech content of recent spectra reaches 78–84% of the total arboreal pollen. A lot of beech pollen (up to 60%) is also recorded in other regions of the Ukrainian Carpathians (Arap 1984). Big quantities of beech pollen are observed in the South Carpathians. In the moss pollen spectra in the belt of beech forests of the Retezat National Park in Romania at an altitude of 1110–1200 m the beech pollen content reaches 70–90% (Pop 1967).

Rather different results on the influx of beech pollen have been obtained in the studies of pollen rain from pollen traps and moss cushions. For example, productivity of *Fagus orientalis* is twice as low as that of *Fraxinus, Tilia,* and *Quercus* and is from 5600 to 6900 grains/cm^2/year in mosses (Andersen 1970) and from 8500 to 11500 grains/cm^2/year in pollen traps (Andersen 1974). As has already been mentioned, the beech pollen influx in south-eastern Poland amounts to only 500 grains/cm^2/year. However, the data on pollen productivity of various arboreal species in the Caucasus Mountains show that, on the contrary, *Fagus orientalis* produces the highest quantity of pollen among all broad-leaved plants. Its maximum pollen influx at an altitude of 1250 and 1500 m is up to 120 000–130 000 grains/cm^2/year. For comparison it should be mentioned that in the mountains of the Lagodekhi Reservation the maximum influx of *Quercus iberica* pollen is 83 000 grains/cm^2/year *Tilia caucasica* up to 60 000 grains/cm^2/year, and *Carpinus caucasica* 45 000 grains/cm^2/year (Kvavadze 1999, 2000a). Thus, according to our data *Fagus orientalis* produces twice as much pollen as lime and oak and three times as much as *Carpinus caucasica*. As has already been mentioned, at its upper limit the beech pollen productivity significantly decreases, and in the mountains of the Lagodekhi Reservation at an altitude of 2000 m it reaches no more than 20 000 grains/cm^2/ year.

The comparison of pollen spectra of soil samples and moss cushions under the canopy of beech forests both in the Caucasus and Tatra Mountains showed that the pollen spectrum of moss cushions is richer in its taxonomic composition. In mosses the total content of pollen is represented. For example, in the moss spectra of sample 11 (Fig. 11) from the Olczyska valley in Tatra Mts. the amount of counted pollen is much higher than in soils. In addition, in these spectra the pollen of those plants was recorded that are rather rarely met here in the soil spectra (*Acer*, *Juniperus*, *Sorbus*, and *Salix*). However, it should also be mentioned that moss cushion spectra do not adequately reflect, for example, the role of spore-bearing species and especially monolete spores of ferns that are abundant in the coenosis. And in soil spectra spore-bearing species are properly reflected. A similar situation is also observed from the comparison of soil and moss spectra in the Lagodekhi Reservation. As to the comparison of the pollen content of beech itself in soil, moss, and pollen-trap spectra, the following regularities are observed. As a whole, in soil samples there is less beech pollen than in mosses and pollen traps (Fig. 12). This phenomenon is quite explicable, since in soils, under influence of biological and various mechanical and chemical processes, fossilisation and the following destruction of pollen grains begins as soon as pollen enters the soil (Tyuremnov & Berezina 1965). However, in moss cushions and pollen traps, which have ideal conditions due to the absence of mineral basis and other biotic and abiotic factors, pollen is well conserved, and the process of fossilisation here does not take place. Therefore these traps have much pollen of plants with thinner exine (*Acer*, *Juniperus*, *Larix*, *Populus*, etc.) which is easily destroyed in soils.

Analysis of our data suggests that the pollen spectrum of the beech forest can be mainly distorted for two reasons: 1) inadequate ecological conditions for highly-productive beech

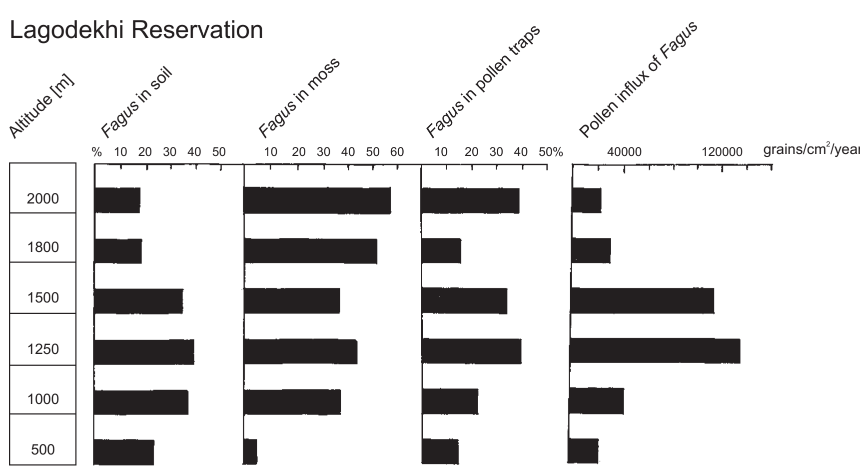

Fig. 12. Comparison of recent spore-pollen spectra of soils and moss cushions with pollen spectra from Tauber pollen traps in beech forest of the Lagodekhi Reservation

forests, leading to a decrease in the pollen productivity; 2) an increase in the amount of transported pollen of other arboreal species both from the neighbouring mountain belts and from more distant regions, thus changing drastically the character of the beech-forest spectrum.

The simultaneous action of the above-mentioned two factors can explain the strong distortion of beech forest spectra in the Tatra Mountains. Here the beech forests, compared to other regions of the Carpathians, have the least extent. The area of beech forests in the Tatra Mountains is only 2.2%, while, for example, in Bieszczady Mts. their area reaches 40.9% and in the Beskides 27% (Trampler et al. 1990). Such an insignificant development of beech forests in the Tatra Mountains might be explained by the absence of optimal conditions for growth of highly productive forests with high pollen productivity. Our analysis showed that the actual role of beech pollen in the Tatra Mountains spectra is also reduced due to mass pollen transport from other regions. The process of pollen transport from one vegetation belt to another by strong winds in the Carpathians is described in other works (Kvavadze 1988, 2000b, Stuchlik & Kvavadze 1995). It should be mentioned here that very complex circulation of air masses not only in the Carpathians but throughout the whole territory of Poland, where during the year quite different air masses prevail, facilitating the formation of rather peculiar and complex wind regimes. Only by winds of different directions, including north can one explain, for example, too high a percentage of pine pollen in the Tatra Mountains spectra (Stuchlik & Kvavadze 1995), since the area of pine forests in the belts of beech or spruce forests on the territory of the Tatra Mountains and West Carpathians does not exceed 17%. However, in the pollen spectra the content of pine pollen in the belt of beech and spruce forests can reach up to 50%, and in alpine and subalpine belts up to 60% and higher. Of course here we deal with long-distance transport of pine pollen from the plains of Poland, where the area of pine forests accounts for 71.6% of the whole forest area.

In the Tatra Mountains the local pollen transport from one belt to another is higher than in the Caucasus. In the belt of beech forests, apart from pine, much pollen of spruce, birch, and alder is found. This phenomenon is also explained by the regime of local winds, whose force and duration reach significantly higher values than in the Caucasus (Hess 1965, Lominadze & Chirakadze 1971).

As for pollen spread of beech itself, both in conditions of the Tatra Mountains and in the studied regions of the Caucasus beech pollen in big quantities cannot be transported from one belt to another. Beech pollen also does not distort pollen spectra of open landscapes of subalpine and alpine meadows. However, the situation changes drastically in the Ukrainian Carpathians, where most ridges have meridional position towards west winds which have high force and duration, and the area of beech forests is half of the forest area. Intensive beech transport begins already in spruce forests, and in the alpine spectra the beech content can reach up to 70% of arboreal pollen.

CONCLUSION

The detailed analysis of regularities of formation of pollen spectra of two types of beech forests in various geographical and ecological conditions of the Caucasus and Carpathians allows us to draw a number of important conclusions for each region, and they should be taken into account in interpretation of fossil spore-pollen spectra.

1. In conditions of humid marine climate of West Transcaucasia, in pure beech forests situated in the middle part of the beech belt, adequate pollen spectra are being formed, where the beech content can reach 60–70%. In these spectra the second and third subdominants are usually representatives of the neighbouring vegetation belts.

2. In those spectra, where the beech role is very reduced, the criterion for establishing a beech pollen spectrum is the predominance of beech pollen in the group of other broad-leaved species. In the same spectrum the total amount of arboreal pollen prevails over herbaceous species among which only representatives of Pteridophyta can reach high values.

3. The criterion for establishing the spectrum of beech elfin woodland is the presence of the following three dominating components in different ratios in the pollen spectrum complex. These are either *Fagus-Alnus-Pinus*, or

Pinus-Fagus-Alnus, or *Fagus-Pinus-Alnus*. The pollen content of beech itself in soils under the elfin woodland thickets does not exceed 28–40%. In the group of herbaceous plants spore-bearing species and especially ferns are predominant. It should also be mentioned that the total content of fern spores approaches quantitatively the total amount of arboreal pollen.

4. At the lower limit of forests with beech participation in conditions of the more arid climate of East Georgia (eastern margin of the Trialeti Range) the percentage of beech pollen in spectra is lower (2–4%) than in the regions of East Georgia with the more humid climate where, for example, in the low-mountain forests even with the insignificant admixture of beech in the Lagodekhi Reservation its content reaches 24–25%.

5. Among spectra of mixed beech – broad-leaved forests most adequate are pollen spectra of beech-chestnut and beech-hornbeam forests of the Lagodekhi Reservation, where each coenosis component is precisely reflected in pollen spectra of soil samples. In these spectra the beech pollen content is 40–50%.

6. Pollen monitoring showed that at the upper limit of pure beech forests in cold climatic conditions of the Lagodekhi Reservation, *Fagus orientalis* produces 6–7 times less pollen than in the middle of the belt at an altitude 1400–1580 m. The percentage of beech pollen in the spectra above 1800 m hardly reaches 14–22%, while even in mixed beech – broad-leaved forests at lower levels the beech pollen content is much higher.

7. In the Tatra Mountains the maximum content of European beech pollen is recorded in the middle part of beech forest belt, where the beech amount in the pollen spectra does not exceed 26–35% of the total amount of arboreal pollen. In the marginal areas and especially at the upper limit of beech forests this index drops to 2–5%. There as in the Caucasus the main criterion according to which a similar fossil spectrum can be assigned to the beech forest spectrum is the predominance of beech pollen in the group of broad-leaved species.

8. A particularly complex wind regime in the Tatra Mountains causes strong averaging of the pollen spectra of beech forests, where regional vegetation features are fixed and better reflected, while in the Caucasus the spectra better reflect basic features of local vegetation.

9. A very low content of *Fagus sylvatica* pollen in the belt of beech forests in the High Tatra Mountain can be explained by two reasons. These are the absence of optimal conditions for the development of highly productive forests producing high quantities of pollen, and intensive transport of arboreal pollen both from lower belts and from more distant regions.

10. Unlike the Ukrainian Carpathians, both in the Tatra and the Caucasus, beech pollen is not transported in large quantities to the neighbouring vegetation belts. It does not also distort pollen spectra of subalpine and alpine meadows.

11. The high content of beech pollen in the fossil pollen spectra indicates the existence of optimal climatic conditions for beech forests. In Transcaucasia it means that temperatures in the warm season reached 17–19^{o}, and in the Tatra Mountains this index is at least 13–15^{o}. Thus the character of the quantitative participation of beech pollen in the spectrum can also be a reliable criteria for paleoclimatic reconstruction.

REFERENCES

ANDERSEN S.T. 1970. The relative pollen productivity and pollen representation of North European trees, and correlation factors for tree pollen spectra. Danm.Geol. Unders. II, 96: 1–99.

ANDERSEN S.T. 1974. Wind conditions and pollen deposition in a mixed deciduous forest II. Seasonal and annual pollen deposition 1967–1972. Grana, 14: 57–77.

ARAP R. YA. 1984. Palinologichni doslidzheniya subfosilnikh prob z Ukrains'kikh Karpat (summary: Palynological analysis of subfossil assays from the Ukrainian Carpathians). Ukrain. Botan. Zhurn., 41(l): 73–77. (in Ukrainian).

BORATYŃSKA K. & BORATYŃSKI A. 1990. Systematyka i geograficzne rozmieszczenie (summary: Systematics and geographic distribution): 27–75. In: BIAŁOBOK S. (ed.) Buk zwyczajny – *Fagus sylvatica* L. PWN, Warszawa-Poznań. BRAUN-BLANQUET J. 1951. Pflanzensoziologie. Grundzüge der Vegetationskunde. Springer Verl., Wien.

CHOCHIEVA K.I. 1980. Uzunlarskaya flora Tskaltsminda (The Uzunlarian flora of Tskaltsminda). Metsniereba, Tbilisi. (in Russian).

DOLUKHANOV A.G. 1941. Kratky ocherk rastitel'nosti Lagodekhskovo zapovednika (A brief description of the Lagodekhi Reservation): 11–23. ln: Zaitsev F.A. (ed.) Lagodekhsky zapovednik (The Lagodekhi Reservation) lssue 1. lzdat. Akad. Nauk Gruzinskoy SSR, Tbilisi. (in Russian).

DOLUKHANOV A.G. 1989. Lesnaya rastitel'nost' Gruzii, I (Forest vegetation of Georgia, Part 1). Metsniereba, Tbilisi. (in Russian).

DZWONKO Z. 1990. Ekologia: 237–328. In: BIAŁOBOK S. (ed.) Buk zwyczajny. – *Fagus sylvatica* L. PWN, Warszawa-Poznań. (in Polish).

ERDTMAN G. 1943. An introduction to pollen analysis. Chronica Botanica, Waltham, Massachusetts.

ERDTMAN G. 1960. The acetolysis method. Svensk. Botan. Tidskr., 54(4): 561–564.

GRICHUK V.P. & ZAKLINSKAYA E.D. 1948. Analiz iskopaemykh pyl'tsy i spor i evo primenenie v paleogeografii (Analysis of fossil pollen and spores and its application in palaeogeography). Geographizd, Moskva. (in Russian).

HESS M. 1965. Piętra klimatyczne w Polskich Karpatach Zachodnich. Nakładem Uniwersytetu Jagiellońskiego, Kraków. (in Polish).

KLOPOTOVSKAYA N.B. 1973. Osnovnye zakonomernosti formirovanya sporovo-pyl'tsevykh spektrov v gornykh rayonakh Kavkaza (Basic regularities of spore-pollen spectra formation in the Caucasian uplands). Metsniereba, Tbilisi. (in Russian).

KOLAKOVSKY A.A. 1964. Pliotsenovaya flora Kodori (The Pliocene flora of Kodori). lzdat. Akad. Nauk Gruzinskoy SSR, Sukhumi. (in Russian).

KVAVADZE E.V. 1974. Dannye rezul'tatov sporovo-pyl'tsevovo analiza donnykh otlozheniy reki Khobi-Zapadnay Gruzya (Data of the spore-pollen analysis of bottom sediments of the river Khobi). Deponirovanie VINITI (Vsevoiuznii Institut Nauchnoi i Tekhnicheskoi Informatsii). N 1810-74, 10 p. (in Russian).

KVAVADZE E.V. 1988. Soderzhanie privnosnoi pyl'tsy drevesnykh v sporovopyl'tsevykh spektrakh Kavkaza i Karpat (summary: The content of transported arboreal pollen in spore-pollen spectra of the Caucasus and Carpathians). Bull. Acad. Sc. Georg. SSR, 132(1): 193–196.

KVAVADZE E.V. 1993. On the interpretation of subfossil spore-pollen spectra in the mountains. Acta Palaeobot., 33(l): 347–360.

KVAVADZE E.V. 1999. The first results of the Pollen Monitoring Programme in the Caucasus mountains (Georgia). Acta Palaeobot., 39(1): 171–177.

KVAVADZE E.V. 2000a. The results of the investigation carried out under Pollen Monitoring Programme in the Caucasus mountains on the territory of Georgia. Abstracts of 3-rd Meeting of EPMP (12–17 April 2000), National Museum & Gallery, Cardiff, Great Britain.

KVAVADZE E.V. 2000b. The role of pollen transport by wind in the formation of pollen spectra from the Ukrainian Carpathians. Acta Palaeobot., 40(2): 207–214.

KVAVADZE E. 2001. Annual modern pollen deposition in the foothills of the Lagodekhi Reservation (Caucasus, East Georgia), related to vegetation and climate. Acta Palaeobot., 41(2): 355–364.

KVAVADZE E.V. & STUCHLIK L. 1988. Znachenie izuchenya subretsentnykh sporovo-pyl'tsevykh spektrov dlya vosstanovleniya istorii razvitiya golotsenovoy rastitel'nosti Kolkhidy (summary: On the role of subrecent spore-pollen spectra in the reconstruction of the history of the Holocene vegetation in Colchis), lzvest. Akad. Nauk Gruzinskoi SSR, Ser.Biolog. 4(4): 250–257.

KVAVADZE E.V. & STUCHLIK L. 1990a. Sporovo-pyl'tsevye spektry poverkhnostnykh prob iz shirokolistvennykh lesov Kintrishskovo i Tsiskariyskovo zapovednikov – Adzhariya (summary: Sporo-pollen spektra of the surface samples from the broad-leaved forests of the Kintrishian and Tsiskarian Forest Reserves, Adzharia). Bull.Acad. Sci. Georgian SSR, l37(2): 425–428.

KVAVADZE E.V. & STUCHLIK L. 1990b. Subrecent spore-pollen spectra and their relation to recent vegetation belts in Abkhazia (North-Western Georgia, USSR). Acta Palaeobot., 30(2): 227–257.

KVAVADZE E. & STUCHLIK L. 1991. Correlation of subfossil pollen spectra with recent vegetation of the eastern border of the Trialeti Range (The Tbilisi environs). Acta Palaeobot., 31(l, 2): 273–288.

KVAVADZE E.V. & STUCHLIK L. 1996. Recent pollen spectra of the mountain forests of the Lagodekhi Reservation (East Georgia). Acta Palaeobot., 36(1): 121–147.

LOMINADZE V.P. & CHIRAKADZE G.L. (ed.). 1971. Klimat i klimaticheskie resursy Gruzii (Climate and climatic resources of Georgia). Gidrometeoizdat Leningrad. (in Russian).

MAMATSASHVILI N.S. 1972. Sporovo-pyl'tsevye spektry poverkhnostnykh otlozheny doliny reki Inguri (Spore-pollen spectra of surface samples of the Ingur river). Soobscheniya Akademii Nauk Gruzinskoi SSR, 68, 1: 105–108. (in Russian).

MEDWECKA-KORNAś A. & KORNAŚ J. 1963. Mapa roślinności Ojcowskiego Parku Narodowego (summary: Vegetation map of the Ojców National Park). Ochr. Przyr. 28: 16–87.

MEDWECKA-KORNAŚ A. & KORNAŚ J. 1992. The Ojców National Park (S. Poland). ln: Veröffentlichungen des Geobotanischen Institutes der Eidg.Tech-Hochschule, Stiftung Rübel,in Zürich, 107: 60–82.

MICHALIK S. 1978. Rośliny naczyniowe Ojcowskiego Parku Narodowego (summary: Vascular plants of the Ojców Natioanl Park). Studia Naturae, A, 16: 1–171.

OBIDOWICZ A. 1996. A late Glacial-Holocene history of the formation of vegetation belts in the Tatra Mts. Acta Palaeobot., 36(2): 159–206.

PIDEK A. & BAŁAGA K. 2000. Pollen rain deposition in the region of Roztocze National Park (SE Poland) – preliminary results. Abstracts of 3-rd Meeting EPMR (12–17 April 2000), National Museum & Gallery, Cardiff, Great Britain.

POP E. 1967. Some aeropalynological remarks and conclusions on the South Carpathian Mountains (Romania). Rev. Palaeobot. Palynol., 4(1–4): 233–242.

RALSKA-JARIEWICZOWA M. 1983. Isopolen maps of Poland: 0–11 000 years B.P. New Phytol., 94: 133–175.

RUDOLPH K. & FIRBAS F. 1926. Pollenanalitische Untersuchung subalpiner Moore des Riesengebirges. Ber. Deutsch. Botan. Gesell., 44: 227–238.

SCHNEIDER R. 1984. Vergleich des Pollengehaltes von Oberflächenproben mit der rezenten Vegetation in Aspromonte, Kalabrien Italien. Dissertationes Batanicae, 72 (Festschrift Welten): 275–318.

SHATILOVA I. I. 1974. Palinologicheskoe obosnovanie geokhronologii verkhnevo pliotsena i pleistotsena Zapadnoi Gruzii (summary: The palynological base of the geochronology of the Upper Pliocene and Pleistocene of Western Georgia). Metsniereba, Tbilisi.

SHATILOVA I.I. 1977. Ob istorii formirovaniya bukovykh lesov Kolkhidy (On the history of the Colchis beech forest formation). Isvest. Akad. Nauk Gruzinskoy SSR, ser. biol., 3, N 5: 458–464. (in Russian).

SHATILOVA 1. 1. & RAMISHVILI I.Sh. 1990. Materialy po istorii flory i rastitel'nosti Gruzii (Materials on the history of flora and vegetation of Georgia). Metsniereba, Tbilisi.

SOKOLOV S. YA. 1951 (ed.). *Fagus*-buk. In: Derev'ya i kustarniki SSSR, 2, lzdat. Akad. Nauk SSSR, Moskva.

SOKOLOV S.Ya., SVIAZEVA O.A. & KUBLI V.A. 1977. Areali derev'ev i kustarnikov SSSR tom 1 (Areal of trees and shrubs of the USSR) vol. 1. Nauka, Leningrad. (in Russian).

STEFANOVA I. 1996. Relationship between recent pollen deposition and vegetation in Northern Pirin Mountains. Phytologia Balcanica, 2/2: 61–65.

STOYKO S.N. & ODINAK YA.P. 1988. Bukovye lesa (Beech forests): 72–77. In: Golubets M.A. (ed.) Ukrainskie Karpaty. Priroda (Ukrainian Carpathians. Nature). Naukova Dumka, Kiev.

STUCHLIK L. & KVAVADZE E.V. 1987. Subrecent spore-pollen spectra and their relation to recent forest vegetation of Colchis (Western Georgia, USSR). Palaeontographica B, 207(l-6): 133–151.

STUCHLIK L. & KVAVADZE E.V. 1995. On the problem of actuopalynology in the Carpathians and Caucasus. Acta Palaeobot., 35(1): 73–83.

ŚRODOŃ A. 1985. *Fagus* in the forest history of Poland. Acta Palaeobot., 25(1–2): 119–137.

ŚRODOŃ A. 1990. Buk w historii lasów Polski (summary: beech in the forest history of Poland): 7–27. In: Bialobok S. (ed.) Buk zwyczajny – *Fagus sylvatica* L. PWN, Warszawa-Poznań.

TAKHTADJAN A. 1981. Flowering plants origin and dispersal. Oliver and Boyd, Edinburg.

TRAMPLER T., KLICZKOWSKA A., DMYTERKO E. & SIERIPIŃSKA A. 1990. Regionalizacja przyrodniczo-leśna na podstawach ekologiczno-fizjograficznych (Natural-forestry regionalisation of Poland on the ecological-physiographical basis). PWRiL, Warszawa. (in Polish).

TYUREMNOV S.N. & BEREZINA N.A. 1965. O razrushenii pyl'tsy drevesnikh porod v razlichnikh usloviakh vodno-mineral'novo rezhima (On pollen destruction of various tree genera in different water-mineral conditions). Vest. Moskov. Gosudarst. Univer. Ser. Biolog.-Pochvennaya, 5: 62–71. (in Russian).