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Zelkova carpinifolia (Pall.) K. Koch in Holocene sediments of Georgia – an indicator of climatic optima

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Abstract

Zelkova pollen has been found in Oligocene- to Pleistocene-aged deposits from many parts of Europe and northern Africa, but became extinct in mainland Europe prior to the last glacial maximum. This paper presents some observations on the ecology, pollen productivity and Holocene history of *Zelkova carpinifolia* to further understanding of Quaternary climatic trends. Georgia is one of the last refuges of this Tertiary relict tree.

Based on palynological data from 20 Holocene sediment profiles in Georgia, we have established that *Zelkova* pollen is almost always accompanied by elevated proportions of thermophilous taxa (*Castanea sativa, Quercus hartwissiana, Q. iberica* and *Pterocarya pterocarpa*) in pollen spectra. These spectra are associated with phases of climatic amelioration and humidification. *Zelkova carpinifolia* is characterised by low pollen productivity, and is underrepresented in pollen spectra by a magnitude of four to five. Because of this, even single grains of *Zelkova* pollen may play a significant role in pollen-based climatic reconstructions.

Six major climatic optima occurred in Georgia through the course of the Holocene, the longest and warmest of which was the mid-Holocene Atlantic period, reaching its maximum between 5200-4800 BP. During that period, *Zelkova* and

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Castanea forests were widespread. In Western Georgia the upper tree-line was elevated approximately 300m above its present-day level. In semi-arid Eastern Georgia, the tree-line was 500-600m higher. Other climatic optima are seen in late-Holocene pollen spectra dating to 3500-2400 BP and in the Middle Subatlantic period (1500-800 BP).

Keywords: *Zelkova carpinifolia*, pollen production, Holocene, Caucasus, climate change

1. Introduction

During past geological epochs, *Zelkova* trees were widespread in Europe, Eurasia and North Africa (van der Hammen et al., 1971; Wang et al., 2001; van Campo et al., 1964; Follieri et al., 1986; Ricciardi, 1961; Lona and Ricciardi, 1961a, 1961b; Follieri, 1958, 1962). They were present in many parts of Europe from the Oligocene until the terminal Pliocene (Manchester, 1989), in Italy until approximately 32000 BP (Follieri et al., 1986), and have modern populations in southeastern Sicily (*Zelkova sicula*), Crete (*Z. abelicea*), Iran and Caucasus (*Z. carpinifolia*), and Eastern Asia (*Z. schniederiana, Z. serrata* and *Z. sinica*) (Wang et al., 2001).

The discovery of *Zelkova* alongside *Pterocarya, Picea, Taxus, Ostrya, Tilia, Alnus, Quercus* and *Juglans* pollen in sediments from the Sahara led van Campo et al. (1964) to suggest that the desert was vegetated by a flora of 'essentially irano-caucasian' character (p.186) during an early Pleistocene 'pluvial'. The extinction of this flora was thought to be linked with subsequent phases of aridification and human impact (van Campo et al., 1964). Follieri et al. (1986) mention that macrofossils resembling *Zelkova carpinifolia* were found near Rome, supporting the existence of a 'Colchic' (West Georgian) forest there during the Riss interstadial (Follieri, 1958, 1962). They suggest that the cold and dry conditions of oxygen isotope stage two led to the demise of *Zelkova* in central Italy (Follieri et al., 1986). Likewise, Wang et al. (2001) argue that the fragmentation of *Zelkova* populations in Europe was the result of the cold and aridity associated with Pleistocene glaciations.

If we regard *Zelkova* as an example of Quaternary floral extinction, then the reasons for its disappearance from much of Europe are of considerable interest in understanding Quaternary climate changes. Why, for example, is *Zelkova* pollen less abundant in the later Pleistocene interglacials in Italy than the earlier ones? Little attention has been given to the present-day ecology and pollen productivity of *Zelkova* in the literature, and this impairs our ability to interpret palaeo-records in terms of temperature, precipitation, human impact, fire and edaphic factors.

Many of the fossil records of *Zelkova* in Europe are leaf imprints and fossil fruits (Kovats, 1856; Bůžek, 1971; Manchester, 1989), but it is interesting to note that fossil *Zelkova* fruits have not yet been found in any material from the Caucasus, the natural range of *Zelkova carpinifolia*, perhaps due to poor seed dispersal (Hoshino, 1993). Combined with the difficulties of identifying *Zelkova* species on leaf morphology (Wang et al., 2001; Nakagawa et al., 1998), pollen records are likely to provide a more robust source of information on the history of this taxon since *Zelkova carpinifolia, Z. sicula* and *Ulmus* pollen are all morphologically distinct (Nakagawa et al., 1986). The aim of this paper is to review the available data on the Holocene history of *Zelkova carpinifolia*, the Caucasian representative of the genus, as a means of determining its indicator value in fossil vegetation records, particularly pollen spectra.

2a. Distribution and ecology of **Zelkova carpinifolia**

The distribution of *Zelkova carpinifolia* in the Caucasus region has been considerably diminished by anthropogenic activity in recent centuries. This Tertiary-relict tree has been extensively logged for its valuable timber, which is prized for its attractiveness, lightness, flexibility and rot-resistance. Some small, isolated remnant stands of *Zelkova* are preserved in Western Georgia, in the Imereti and Megreli regions. A two-hectare grove of established *Zelkova* trees is preserved in the Ajameti Reservation (Figures 1 and 2). Unlike Western Georgia, in Eastern Georgia there are extensive stands of *Zelkova carpinifolia* in the Babaneuri Reservation (Figure 1). The Babaneuri Reservation was established expressly for the conservation of this living fossil, which was previously on the verge of complete disappearance in Georgia. The reserve contains approximately 210 ha of *Zelkova*-dominated forest.

Outside Georgia, *Zelkova carpinifolia* is found along the southern shores of the Caspian Sea, in Lenkoran, northern Iran and southwestern Nagorno-Karabakh (Vasiliev et al., 1961). Several isolated occurrences are recorded from Eastern Anatolia (Davis, 1965ff). It is cultivated, albeit rarely, as an ornamental tree in parks, gardens and cemeteries. Like *Ulmus*, its leaves (Figure 3) provide stock fodder, and its branches are often employed as stakes in vineyards.

Zelkova carpinifolia is a mesophilous tree, requiring warm conditions. It is light-demanding, always occurring as a canopy tree. It prefers moist, humus-rich soils, and will not tolerate waterlogging or swampy conditions. *Zelkova* is capable of growing on stony soils, but its growth is severely restricted on these sites and the tree often takes the form of a multi-branched shrub (Vasiliev et al., 1961). It will not tolerate cool summers, but can withstand winter minima of -20^{o}C.

In Georgia, *Zelkova carpinifolia* grows in the altitudinal range of 300-600m a.s.l. It is recorded at considerably higher elevations in Nagorno-Karabakh (see Figure 1), growing as a shrub (Sokolov et al., 1977). However, it reproduces from self-sown seed only at altitudes 100-400m where its growing conditions are optimal

(Vasiliev et al., 1961). *Zelkova carpinifolia* prefers sunny south-facing slopes and also grows on west-facing slopes. It forms pure stands, or may occur admixed with *Carpinus caucasica*, *Carpinus orientalis* and various species of *Quercus*. In Colchis (e.g. Ajameti Reservation), it forms *Quercus-Zelkova* associations, whereas in Eastern Georgia (e.g. Babaneuri Reservation), it is found in admixture with *Carpinus caucasica*. Zohary (1973) lists the following associations for *Zelkova carpinifolia* in Iran: *Quercus, Fagus, Carpinus, Pterocarya, Parrotia, Diospyros, Ulmus, Fraxinus, Acer* and *Juglans*.

Among trees, *Zelkova carpinifolia* is a relatively long-lived species, which accounts for its dominance in forests where human impact is minimal. A particularly large specimen was recorded in the Terjola district of Western Georgia in the 1950s. Located in Chkhari-Etseri Village, not far from the Ajameti Reservation, it was reportedly more than 800 years of age, with a trunk diameter of 3.3m and a height of 30m (Chikovani et al., 1990). Several large trees grow in the Babaneuri Reservation, one of which, known locally as *tqis beladi*, 'the Forest Chief', is 125cm in diameter and at least 25m tall. According to Grudzinskaya (1980), there are several *Zelkova carpinifolia* trees in the Talysh region (northern Iran), 800-850 years old, up to 40m in height and 3-4m in diameter.

2b. Climatic characteristics of **Zelkova carpinifolia** *habitats*

The climate of *Zelkova carpinifolia* habitats in Western Georgia is recorded at two meteorological stations located in the Ajameti Reservation at 107 and 200m a.s.l. The annual average temperature is 14^{o}C. Average January temperature is 4.4^{o}C, and 23.5^{o}C in July-August (Chikovani et al., 1990). The absolute minimum is 20^{o}C, and maximum 42^{o}C. The area is free of frost for about 278 days per year, and the growing period is 235 days in duration. Average annual precipitation is approximately 1500mm, most of which falls in the colder months. Approximately 538-570mm of precipitation falls during the growing period, although droughts sometimes occur in July and August.

The annual average temperature of the Babaneuri Reservation in Eastern Georgia is 12.4^{o}C. In July the temperature averages 23.7^{o}C, and in January 0.5^{o}C. The absolute maximum is 32^{o}C, and minimum -24^{o}C. The growing period lasts about 210 days. The annual rainfall is 914mm, and, of this, 633mm falls during the growing period (Chikovani et al., 1990). The climate of the Girkan Reservation (in the mountains of Lenkoran and Talysh) is similarly mild. In the *Zelkova* forests of this area, the annual temperature is 12-14^{o}C, 1.0-3.7^{o}C in January and 22-24.5^{o}C in July. The absolute minimum is -16^{o}C, and maximum 38^{o}C. Annual precipitation varies from 900 to 1400mm, depending on altitude (Gasanov, 1990).

3. Morphological characteristics of **Zelkova carpinifolia** *pollen grains*

The first descriptions of pollen morphology of the *Zelkova* genus appeared in the works of Samoilovich (1950) and Erdtman (1952), but the first detailed description of *Zelkova carpinifolia* pollen appears in Monoszon (1959). The species was also described more recently by Zavada (1983) and Nakagawa et al. (1998). In the latter work, both light-microscope and scanning electron microscope (SEM) microphotographs are presented (Nakagawa et al., 1998).

We obtained type material of *Zelkova carpinifolia* from flowering specimens in the Tbilisi Botanical Gardens. Over 500 pollen grains were measured and described. The equatorial diameter of these varied in size from 27-29µm to 39-45µm. Larger grains were also encountered, measuring up to 52µm. Most pollen grains possess four pores (62%) or five pores (33%). Nakagawa et al. (1998) obtained similar data from type material gathered in the Marseille Botanical Gardens. However, in the Tbilisi material, *Zelkova carpinifolia* pollen with six pores accounts for only 0.4%, whereas Nakagawa et al. (1998) report 2.8%. The Tbilisi material also contained pollen with three pores (Figure 4).

In terms of pollen morphology, we offer the following description using the terminology of Moore et al. (1991). *Zelkova carpinifolia* pollen is trizonoporate to hexazonoporate, oblate, with coarse rugulate sculpturing on the exine. On some grains the rugulae anastomose and intersect to form a semi-reticulate pattern, which is particularly prominent in the polar area (Figure 5). The sculpturing elements are generally larger and more prominent than those of *Ulmus*. The major distinguishing features of *Zelkova* pollen are the thickened pores. In polar view the exine thickens conspicuously towards each porus, and in equatorial view these thickened pores are surrounded by a broad area of psilate exine lacking the rugulate ornamentation of the body of the grain. Monoszon (1959) was the first to draw attention to this characteristic, which distinguishes *Zelkova* from species of the *Ulmus* genus. The thickened pores are clearly shown in the schematic diagram of Monoszon (Figure 6). We have also observed that the pores of *Zelkova* pollen tend to be elliptical, whereas *Ulmus* pores are usually circular.

No tetrad grains were observed in our material. Nakagawa et al. (1998) have shown that in the Sicilian species, *Zelkova sicula*, pollen of tetrad formation comprises 17.7% of its pollen production.

4. Pollen production and long-distance pollen transfer

The low pollen production of *Zelkova* has been previously noted in the literature (Gogichaishvili, 1988; Yazvenko, 1991; Stuchlik and Kvavadze, 1993; Garfi, 1998). The low representation of *Zelkova carpinifolia* pollen, both in subrecent spectra (Gogichaishvili, 1988; Stuchlik and Kvavadze, 1993) and in fossil spectra of the Tertiary and Quaternary periods, when *Zelkova* forests were widespread (Shatilova, 1967, 1984; Shatilova and Ramishvili, 1990; Mamatsashvili, 1975, 1991), also indicates that its pollen may be poorly preserved in most types of sediment.

Samples of surface mosses, soils, alluvium and wetland sediments were collected at various locations in the Babaneuri Reservation. In the mature forest, where *Zelkova* comprises 98% of the forest canopy, the *Zelkova* pollen content of soils amounts to only 13.3%. In moss polsters, where the preservation is better, *Zelkova* pollen is similarly under-represented, comprising 25.5% of the total pollen, and 37.5% of the arboreal pollen sum (Figure 7). The proportions are considerably lower in younger mixed *Quercus-Zelkova* forests: 1.0-2.9% in soil samples and 9.9% in moss polsters.

Regarding pollen transfer, it is noteworthy that *Zelkova* pollen was found in recent alluvium near Mukhura River in the chestnut forest belt, transported downstream by fluvial mechanisms from the Ajameti Reservation (Kvavadze, 1987). Fluvially-transported *Zelkova* pollen was also found in Colchis (lowland Western Georgia) and along the Inguri River in coniferous forests. However, *Zelkova* pollen was absent in terrestrial sediments near the same river (Mamatsashvili, 1975). *Zelkova* pollen is recorded in Black Sea marine sediments on the shelf of the Poti submarine canyon (Shatilova, 1974), where it was probably deposited by the waters of the Rioni River. Wind-transported *Zelkova* pollen has been found at an altitude of 2000m, in the alluvial silts of the Tskhenis Tskhali River, which runs through alpine meadow vegetation (Klopotovskaya, 1973).

Single *Zelkova* grains have been recorded in the humus-rich soils of the Eastern Georgian piedmont chestnut forests. It is occasionally encountered in Eastern

Georgia outside the present (restricted) distribution of *Zelkova carpinifolia*. Usually these pollen are found in mountain landscapes, where the role of wind transportation becomes important. Single grains of *Zelkova* are recorded in the recent wetland sediments of lakes on the Tsalka Plateau, Southern Georgia, at 1520-1700m elevation (Connor et al., 2004). Long-distance-transported *Zelkova* pollen was found in the Avchala wetlands of the Javakheti Uplands (2050m). *Zelkova* pollen was also recorded in forest clearings near Ivanovka and Nadarbazevi villages (1400m), in the sediments of lakes Cherepanov, Trialeti and Imera, and in sediments gathered from the centre of Lake Kumisi in the semidesert lowlands south of Tbilisi (Connor et al., 2004).

5. Pre-Holocene history of Zelkova *distribution in Georgia*

Zelkova fossils are widespread in Tertiary sediments of Europe and Asia. They occur in Georgia from the Miocene period (Table 1). Leaf imprints dating to the Upper Sarmatian and Meotian periods were found near Vale, in the mountains of southern Georgia (Chelidze, 1965). Upper Pliocene fossils were found in sediments near Sokhumi on the Black Sea (Kolakovski, 1951; Ratiani, 1959) and in Eastern Georgia in the Akchagyl layers of Kvavebi (Dolidze, 1965). More detailed data on *Zelkova* pollen and macrofossils are given in Table 1. Palynological evidence of *Zelkova* occurs as early as the Miocene, but thus far, no macrofossils of *Zelkova* fruit have been found in Georgia.

Table 1. Location and geological age of *Zelkova carpinifolia* fossils found in Georgia, presented in reverse stratigraphical sequence.

Site name	Geographical district	Fossil type	Geological stage (Caucasus stratigraphy)	Epoch	Reference
Vale	South Georgia	leaves	Upper Sarmatian-Meotian	MIOCENE	Chelidze, 1970
Chanitskali river	West Georgia	pollen	Sarmatian		Shatilova et al., 1991
Kisatibi	East Georgia	leaves	Meotian		Uznadze, 1965
Chochkhati village	West Georgia	pollen	Meotian		Purtseladze, 1968, 1977 Purtseladze and Tsagareli, 1974
Gejiri-river	Abkhasia	pollen	Meotian		Chelidze and Kvavadze, 1986
Gudou-river	Abkhasia	pollen	Meotan		Shatilova and Ramishvili, 1990
Pitsunda	Abkhasia	pollen	Pontian	PLIOCENE	Ramishvili, 1965, 1969
Gogoreti-village	West Georgia	pollen	Kimmerian, Kuyalnikian		Shatilova, 1967
Kobuleti	West Georgia	leaves	Kimmerian		Mchedlishvili, 1949
Duabi	Abkhasia	pollen	Kimmerian		Mchedlishvili, 1963
Tsikhisperdi	West Georgia	pollen	Kuyalnikian, Gurian		Shatilova, 1967
Khvarbeti village	West Georgia	pollen	Kuyalnikian, Gurian		Shatilova, 1967
Kuchkha River	West Georgia	leaves	Gurian		Mchedlishvili, 1956
Gogoreti village	West Georgia	leaves	Kuyalnikian		Mchedlishvili, 1954
Gogoreti village	West Georgia	pollen	Gurian		Shatilova, 1967
Ninoshvili village	West Georgia	pollen	Gurian		Shatilova,1967
Tsiagubani village	West Georgia	pollen	Gurian		Shatilova, 1967
Shava village	West Georgia	pollen	Gurian and Chaudian		Shatilova, 1967
Sakupre village	West Georgia	pollen	Chaudian	PLEISTOCENE	Shatilova, 1967
Tsvermagala	West Georgia	pollen	Chaudian		Shatilova and Ramishvili, 1990
Chakhvata	West Georgia	pollen	Chaudian		Shatilova, 1967
Patara Poti	West Georgia	pollen	Upper Chaudian		Mamatsashvili, 1975
Inguri River	West Georgia	pollen	Upper Chaudian		Mamatsashvili, 1975
Inguri River	West Georgia	pollen	Older Euxinian		Mamatsashvili, 1975
Patara Poti	West Georgia	pollen	Older Euxinian		Mamatsashvili, 1975
Ureki	West Georgia	pollen	Older Euxinian		Shatilova and Ramishvili, 1990
Tskaltsminda village	West Georgia	pollen	Uzunlarian		Shatilova and Ramishvili, 1990
Tskaltsminda village	West Georgia	pollen	Uzunlarian		Chochieva and Mamatsashvili, 1976
Patara Poti	West Georgia	pollen	Uzunlarian		Mamatsashvili, 1975
Kobuleti	West Georgia	pollen	Karangatian		Shatilova, 1974, 1984
Parata Poti	West Georgia	pollen	Karangatian		Mamatsashvili, 1975
Sukhumi	West Georgia	pollen	Lower Karangatian		Kvavadze and Rukhadze, 1999
Gulista river	West Georgia	leaves	Early Karangatian		Ratiani, 1970

Lechkop	Abkhasia	leaves	Early Karangatian		Kolakovski, 1952
Kobuleti	West Georgia	pollen	Karangatian		Shatilova and Badzoshvili, 1975
Inguri river	West Georgia	pollen	Karangatian		Mamatsashvili, 1975
Choloki river	West Georgia	pollen	Late Pleistocene		Kvavadze and Jeiranashvili, 1987
Kvabebi	East Georgia	leaves	Akchagyl		Dolidze, 1965,1968
Tsutskhvati	West Georgia	pollen	Paleolithic		Mamatsashvili, 1975
Sukhumi	West Georgia	pollen	New Euxinian		Kvavadze et al., 1984

6. Holocene history of **Zelkova carpinifolia** *in Georgia*

Zelkova pollen is found in various Holocene sediments in Georgia (Figure 8), including marine sediments (four profiles), alluvium (eight profiles), lake and mire deposits (four profiles), and in archaeological strata (three profiles).

However, first let us touch upon the question of the subdivision and geochronology of the Holocene. At present, there are several schemes for Holocene chronostratigraphy (e.g. Hafsen, 1970; Mangerud et al., 1974, 1982; Neustadt, 1952, 1985) and are the subject of considerable debate (see Mangerud et al., 1986). Whilst the various manifestations of the Blytt-Sernander scheme have fallen from favour in Western Europe (Roberts, 1998), the scheme was enthusiastically adopted and modified by Soviet scientists, such that it became a palaeoclimatic and relative dating tool removed from its original application in peat stratigraphy. Neustadt (1985) argues that the use of absolute chronology without comparing radiocarbon dates to the Blytt-Sernander periods is misleading and can result in chronological chaos. Rather than being a substitute for radiometric dating, the scheme is used as an aid to correlation and to differentiate regional climatic changes from other, more localised influences on palaeo-vegetation. It has been and continues to be successfully used as a reference scheme by many Holocene researchers throughout the former Soviet Union as well as in Eastern and Central Europe (Khotinsky, 1969, 1977).

In the interests of comparability, in this paper we adhere to the modified Blytt-Sernander scheme advocated by Mangerud et al. (1974) (see Figure 9). Although the climatic interpretation of the Blytt-Sernander scheme for separate periods in different regions is not always identical, the basic climatic trends are the same everywhere, i.e. a transition from cold conditions of the end of the last glaciation to the post-glacial climatic optimum, followed by subsequent cooling (Khotinsky, 1977). All dates given herein are in radiocarbon years before the present (yr ^{14}C BP).

In Georgia, the highest number of Holocene radiocarbon dates (about 30) has been obtained from sediments in the region of Abkhasia (northwestern Georgia, see Figure 8), where climatic conditions tend to favour peat formation. These deposits were also investigated palynologically (Kvavadze and Rukhadze, 1989; Kvavadze et al., 1992). More than 25 profiles from Abkhasia are located in different altitudinal belts and many of them below the present-day tree-line or higher. Of most interest are high mountain profiles since in the extreme conditions any slight climatic changes are clearly registered by pollen spectra. They also contain few anthropogenic indicator pollen because human settlements are largely absent in these highland areas, and this contributes to authenticity of palaeoclimatic reconstructions.

For quantitative reconstructions of climatic parameters, a mathematical method (Bukreeva et al., 1989) was employed. This made it possible to elaborate a model of vegetation and climate development for each Holocene period and sub-period (Kvavadze et al., 1992). A curve for upper tree limit oscillations, based on mathematical modelling of several dated pollen records, is shown in Figure 9 and reflects climatic fluctuations in Abkhasia. This curve shows that the climatic amelioration reached its maximum in the Late Atlantic period (6000-4800 BP) and middle Subatlantic period (2000 and 1200-900 BP). This curve for Holocene upper tree limit oscillations in Abkhasia correlates well with Holocene glacial retreat and advance stages in the Caucasus Mountains and with the Black and Caspian Sea level oscillations (Zubakov, 1992; Zubakov and Borzenkova, 1983).

6.1. Western Georgia

Sokhumi area. Two deep bores of marine sediments (bore #721 and #723) and one of alluvium (bore #36) were analysed palynologically. Bore #721 was taken from the continental shelf in a water depth of 14.9m. A 27m long sediment core was recovered. The deepest layers (27-26.5m) comprise of peat and are dated to 9310±80 BP (TB-346). At 25.5m these are overlain by marine sediments with fine sand with gravel-pebble inclusions and marine faunal remains. *Zelkova* pollen is recorded at 22.2m in a stratum dated palynologically to the Middle Boreal period (around 8500 BP), during a climatic optimum (Kvavadze and Rukhadze, 1989). The spectra belonging to this period are characterised by an abundance of broad-leafed taxa, particularly *Quercus, Castanea* and *Carpinus caucasica*. *Tilia, Rhus* and *Ulmus* also increase. The proportions of conifer pollen (*Picea, Abies* and *Pinus*) is lower compared to the previous and subsequent periods.

Bore #723 is located near bore #721, on the continental shelf in a water depth of 9.9m. The core is 26m long and consists of clay loams with marine fauna in its upper sections. *Zelkova* pollen occurs at a depth of 2.5m. A radiocarbon date of 3335±50 BP (TB-361) from 6.3m depth, suggests that the *Zelkova* pollen was deposited during the climatic optimum that occurred 1200-1000 years ago (Middle Subatlantic). This optimum followed the second cold period in this region (Kvavadze and Rukhadze, 1989). *Castanea* and *Alnus* are dominant among arboreal taxa in these pollen spectra. *Quercus* is also important, whereas coniferous species are very poorly represented.

Bore #36 was collected from continental deposits on the eastern part of the Sokhumi Peninsula, on the Black Sea coastal terrace at 4m above sea level. The core is 45m in length. Between 8.75 and 8.9m, a peat lens was dated to 6425±60BP (TB-352). Above this lens were compact grey clays containing significant quantities of *Zelkova* pollen (up to 3%). *Castanea, Quercus* and *Alnus* are predominant in these spectra, and significant quantities of *Carpinus* and *Pterocarya* pollen are recorded. *Fagus* and *Abies* occur in the lowest proportions (Kvavadze et al., 1984).

Akhali Ateni area. Bore #511 was obtained from the Black Sea shelf in 14.7m of water. The core is 28m long, consisting of dark grey compact clays. Single *Zelkova* pollen grains are found in Preboreal and Boreal layers, at depths of 21.8 and 17m respectively (Figure 10a). *Zelkova* proportions peak (up to 5%) in sediments of the first half of the Atlantic period (12-12.5m). By the terminal Late Atlantic (around 5000 BP), amounts of *Zelkova* pollen are considerably reduced (Kvavadze and Jeiranashvili, 1990). *Zelkova* pollen occurrences and peaks are accompanied by the increasing importance of *Castanea* and *Quercus*.

Bore #55 is located in the Aapsta River estuary (0.2 km from the coastline) on the first alluvial terrace. The profile is 24m thick. Lagoon sediments from 23-15m were studied palynologically (Figure 10b). These consist of dark grey clays with numerous fragments of wood and peat lenses (15.5-17.5m), aleurite deposits with layers of fine sand (17.5-22.6m), and grey clay with fine detritus, wood fragments and peat lenses (22.6-23.2m). This lower layer, sedimentologically similar to the upper layer, is dated to 6780±120 BP (Kiev Institute of Geological Research, KIGR-205). At 15.5m, the age is 5200±80 (KIGR-207). *Zelkova* pollen occurs throughout the entire profile. The pollen spectra are characterised by large proportions of broad-leafed taxa, especially *Castanea*. *Pterocarya* pollen also achieves comparatively high percentages.

Bore #182 is located in the same area at an altitude of 60m, on a landslip slope. The depth of the profile is 16m, and consists of clay loams with peat lenses. *Zelkova* pollen is recorded throughout the upper 5.85m of the profile. *Castanea* predominates in these spectra, and thermophilous broad-leafed taxa are common. *Pinus* and other conifers are observed in small quantities.

Gudauta area. Bore #521 was drilled in the shelf zone of the Black Sea in a water depth of 31.8m. The core depth is 21m. The upper 13m are of Holocene age and comprise clay loams with occasional fauna. *Zelkova* pollen is found in the lower and middle parts of the profile. Its representation increases in strata from the Preboreal and Atlantic periods. Alongside *Zelkova*, high proportions of other thermophilous taxa are recorded. *Castanea* pollen dominates the spectra during the Atlantic period.

Gagra area. Bore #603 was taken from the Black Sea shelf, south-east of the Zhvavakvara estuary. The water depth here was 15.2m, and the sediments are composed of clayey silts with small peat lenses. *Zelkova* pollen is recorded at a depth of 25.5m, dated palynologically to the Preboreal period. *Fagus* and *Quercus* are recorded in high proportions in these spectra, and *Tilia, Castanea, Ulmus, Juglans* and *Pterocarya* pollen are also important.

Kobuleti area. Bore #35 is located near Kobuleti, in the Choloki estuary (left tributary of the Natanebi River). The site is 7-8kms from the coast, and alluvial sediments were drilled to a depth of 120m. These consist of riverbed, lagoon and floodplain facies. The upper 45m is dated to the Holocene. The lower and middle sections of the profile consist of dark-grey silty clays. A layer of fine-grained sand occurs at 10-15.5m, overlain by loams. *Zelkova* pollen is found in layers dated to the Preboreal and Atlantic periods. The pollen spectra are dominated by *Castanea* and *Alnus*. *Quercus, Carpinus* and *Ulmus* are also important.

A 27m core of lacustrine clays and silts (Bore #39) was extracted near Bore #35, in the Choloki estuary. The upper profile is composed of clays. *Zelkova* pollen is recorded in layers assigned to the Late Atlantic period, which are dominated by *Castanea* and *Alnus*, and contain significant amounts of *Quercus, Ulmus* and *Tilia* pollen. These spectra are relatively poor in coniferous pollen, especially *Abies*, compared to subsequent spectra (Figure 11).

Supsa area. Three profiles of alluvial and lacustrine deposits have been studied in the lower reaches of the Supsa River, near Ormeti and Chochkhati villages. The Supsa River in this area has a meandering channel plan form, eroding fluvial terraces and exposing sections of alluvial deposits. On the left bank, the river forms three terrace levels, the highest of which is 1km long and up to 6.5m high. The Supsa 1 profile is located on this terrace. It consists of dark-grey loams grading to a dark brown matrix in the lower strata. Branches, stems and *in situ* tree stumps are found at a depth of 1.3m, and are radiocarbon dated to 1280±160 BP (Moscow State University, MSU-357). *Zelkova* pollen are found in layers of the Early and Middle Atlantic period and at the Boreal - Atlantic boundary (8000 BP) (Kvavadze, 1978). Besides *Zelkova*, the pollen spectra are characterised by significant quantities of other thermophilous taxa: *Tilia, Castanea, Quercus* and *Ilex*.

The Supsa 2 profile is located 2km downstream of Supsa 1, on the second fluvial terrace. This section is 8m in depth and consists of lacustrine and alluvial sediments. At a depth of 2.2m, standing tree stumps were dated 1260±120 BP (MSU-

358). *Zelkova* pollen is recorded at 1.9-4.9m depth, in dark-grey silts and sandy loams. In these samples, *Zelkova* pollen peaks considerably, and comprises 7-10% of the arboreal pollen sum. This is the only known case of such a significant participation of *Zelkova* in the pollen spectra of Georgia. The *Zelkova* peak coincides with increases in *Tilia* and *Hedera* pollen. *Pterocarya* and *Castanea* proportions also rise in layers dated to around 2000 BP (Figure 12).

The Supsa 3 profile is located near Supsa 1, on the lower (3rd) terrace. It is composed of brown sandy loams. *Zelkova* pollen is recorded between 1.0 and 1.9m depth, and is dated palynologically to the Middle Subatlantic. Here the *Zelkova* content is considerably lower than at Supsa 2, and does not exceed 3% of the arboreal pollen.

6.2. Eastern Georgia

Bazaleti B. Lake Bazaleti is situated in the foothills above the Aragvi Valley at an altitude of 874m. It is a closed lake, with a catchment area of 13.1 sq. km. and a surface area of 1.4 sq. km. Its maximum depth is 7m. A 3.25m core was taken in the northern part of the lake where the basin is gently-sloping and the water depth is 6.75m. The upper part of the core consists of lake gyttja with clay lenses, while the lower part is clay with occasional gyttja lenses. A radiocarbon date of 3190±60 BP was obtained from 3.17-3.20m depth. *Zelkova* pollen grains were found at various depths (Figure 13), and are highest in layers dated to approximately 4000-2000 BP (Middle and Late Subboreal) and the Middle Subatlantic. However, *Zelkova* pollen does not exceed 1.5-2% of the arboreal pollen sum. Its maximum values are accompanied by high proportions of *Quercus, Castanea* and *Pterocarya*, and minimum values of *Pinus, Betula* and *Abies.* These data are in accord with those produced by an earlier analysis of Lake Bazaleti sediments (Gogichaishvili, 1978).

Kumisi 1. Lake Kumisi is situated south of Tbilisi at an altitude of 470m. The lake is saline, and approximately 2km in diameter. It is a closed lake, but for the past two decades the water level has been artificially raised by river diversion. A 2.45m core was taken in the northern part of the lake where sediments were deepest. The water depth at the coring site was 2.9m. The sediments were dark-grey clays, with a basal date of 1150±40 BP (Australian Nuclear Science and Technology Organisation, OZG-616). *Zelkova* pollen is recorded from the upper and lower parts of the core, peaking at 2.20-2.44m. These spectra contain significant proportions of *Quercus* and *Juniperus*, as well as large quantities of aquatic *Ruppia* pollen, indicating a warm climate at this site 1150 years ago.

Tsavkisi 1. Wetland sediments have been studied from a small mire near Tsavkisi village, in the mountains above Tbilisi at an altitude of 1000m. The one-metre core yielded a basal age of 1890±40 BP (OZG-617). *Zelkova* pollen is recorded at depths of 18-22cm and 88-98cm. Maximum values of *Zelkova* are accompanied by an increase in *Quercus* pollen, as well as *Castanea* and *Pterocarya*.

Imera 1. Lake Imera is located to the east of Tsalka township, at an altitude of 1600m. A 247cm sediment core of alternating layers of clay and peat was extracted. Three radiocarbon dates have been obtained for this profile: 1010±40 BP (OZG-619) – 52-54cm; 1630±40 BP (OZG-642) – 112-115cm; and 4030±110 BP (OZG-623) – 197-198cm. *Zelkova* pollen is occasionally recorded in the middle and upper parts of the core (Figure 14). A small *Zelkova* peak at 106-108cm depth is accompanied by increased representation of *Quercus, Corylus* and *Carpinus* pollen, and decreased *Pinus, Picea* and *Abies* proportions. In the lower part of the profile, *Zelkova* reaches 7% of the arboreal pollen sum, suggesting that *Zelkova carpinifolia* trees were present near the lake at that time in a mixed forest and subalpine meadow vegetation. Pollen of thermophiles such as *Ephedra, Juniperus* and *Carpinus orientalis* is associated with this peak in *Zelkova*, while *Pinus, Picea* and *Abies* percentages are diminished.

Tkemlara 1 barrow. This ancient barrow is situated 5-6km southwest of Tetri-Tsqaro, at 1400m a.s.l. According to archaeological and palynological data, it is dated to the first stage of the Middle Bronze Age (29th –28th centuries B.C.) Large quantities of *Zelkova* pollen are found in the sediments of a tomb at a depth of 150-160cm. It amounts to 26.5% among arboreal taxa. Besides *Zelkova*, the spectra contain significant amounts of *Castanea*, as well as pollen of *Hedera* and *Smilax*. Such large quantities of *Zelkova* pollen in the burial chamber may be explained by the use of *Zelkova carpinifolia* branches in the construction of the chamber ceiling. The roofs of these chambers were constructed using large logs that were lined with branches and then covered with earth (Gobejishvili, 1980).

Tkemlara 2 barrow. This barrow is located nearby Tkemlara 1, but is archaeologically dated to the 24th century B.C., the ‘Bedeni’ culture (Gobejishvili, 1978). *Zelkova* pollen is found throughout the palynospectra of soils taken from earthenware pots. The pots were initially empty, and filled with soil once the ceiling of the burial vault began to collapse (Kvavadze et al., 2003).

Satsdeli 3 (Tkemlara). Near Tkemlara, 1.5km southwest of the barrows, a livestock-breeding site of the Feudal period has been found. Middle Bronze Age deposits are located beneath the Early Feudal layers, and *Zelkova* pollen is recorded at a depth of 70cm. It is accompanied by *Castanea sativa, Alnus barbata, Ophioglossum, Cryptogramma crispa* and other heat- and moisture-loving elements.

7. Discussion

The palynological data presented here indicates that the occurrence and increase in the amount of *Zelkova* pollen is almost always connected with the increasing role of thermophilous components of the pollen spectrum. From this we may consider *Zelkova* pollen as an indicator of climatic optimum conditions. The discussion below considers the role of *Zelkova* in relation to Holocene climatic fluctuations.

Preboreal period (10000-9000 BP). The Preboreal period was a time of climatic optimum. This is evident in the material from Western Georgia, where *Zelkova*, like other Tertiary relicts, survived the Younger Dryas probably in warm, protected gorges. This process occurred in both the northern and southern parts of Western Georgia (Figure 15). However, existing data do not record the occurrence of *Zelkova* pollen in Preboreal sediments of Eastern Georgia. Perhaps its distribution was fragmentary at this time. The warmer conditions of the Preboreal period near Tbilisi are expressed in the increasing role of arboreal pollen and particularly broad-leafed taxa (Kvavadze, 1999). The first maximum of *Carpinus caucasica* proportions is recorded at this time. The Preboreal climatic optimum is also noted in material from Southern Georgia. In the Bavra 1 and Bavra 2 archaeological sites (Akhalkalaki region), Preboreal layers overlie Late Pleistocene deposits and are characterised by an increasing role of arboreal species, especially *Pinus* (Gabunia et al., 1989).

Boreal period (9000-8000 BP). Against a background of pronounced climatic deterioration during the Boreal period, when tree-lines were depressed by 800m compared to their present-day altitude (Kvavadze and Rukhadze, 1989), one rather significant climatic amelioration is recorded in the Late Boreal period (Figures 15 and

9). In Western Georgia (Gudauta, Supsa, Akhali Ateni) at that time, *Zelkova* forests existed against a background of expanding *Carpinus-Fagus* forests.

Atlantic period (8000-5000 BP). This is the time of the most significant climatic optimum, the maximum phase of which falls during the period from 5200 to 4800 BP. The area of *Zelkova* forests expanded in suitable habitats throughout Georgia (Figure 15). In the low mountain forests, *Castanea, Quercus* and *Zelkova* became more important. *Pterocarya pterocarpa* expanded along river valleys and into many low mountain forests. In the districts of Shida Kartli and Kvemo Kartli (Eastern Georgia), *Castanea-Zelkova* forests probably occupied warm, south-facing slopes. The palynological data is also reinforced by palaeocarpological evidence. For example, near Tetri-Tsqaro at 1300-1400m a.s.l., large quantities of *Zelkova* pollen were found in Middle Bronze Age strata which yielded an abundance of *Castanea* fruit during an earlier excavation (Gobejishvili, 1978). The existence of *Zelkova* and *Castanea* forests in association with *Alnus barbata, Smilax* and *Hedera* on the Trialeti Ranges (near Tetri-Tsqaro) indicate that, in the second half of the Atlantic period, the upper tree-line was more than 500-600m higher than it is today. The climate of that period was comparable to that of Colchis today, where the mean annual temperature is approximately 15^{o}C, and the mean July temperature is around 24^{o}C (Lominadze and Chirakadze, 1971). Today the mean annual temperature in Tetri-Tsqaro is 8^{o}C, and 18.6^{o}C in July (Lominadze and Chirakadze, 1971). It may be concluded that at the height of the Atlantic climatic optimum, the mean annual temperature and mean summer temperature were up to 6^{o}C higher than at present. There was also considerably more rainfall in Eastern Georgia, perhaps no less than 1000-1200mm per annum near Tetri Tsqaro. The present annual precipitation there is 780-800mm (Lominadze and Chirakadze, 1971).

The Atlantic climatic optimum is recorded in the Anticaucasus Mountains, in palynological data from Lake Imera and Lake Sevan sediments and the cultural layers of the Norashen settlement (Sayadyan et al., 1977). There was a significant lake-transgressive phase at Lake Sevan caused by a humid climate 6270 years ago. The role of arboreal pollen increased markedly at that time, especially that of thermophilous elements such as *Quercus, Tilia* and *Ostrya* (Sayadyan et al., 1977). This occurred concurrently with the pronounced *Zelkova* peak in Imera Lake (Figure 14). The warm, humid climate favoured the afforestation of nearly the entire territory of Georgia, the South Caucasus region and the Near East generally, even where steppe landscapes are distributed today (Gogichaishvili, 1988; van Zeist and Bottema, 1991; Kvavadze, 1999).

Subboreal period (5000-2500 BP). In the early centuries of this period, a significant phase of climatic deterioration is recorded in Western Georgia, causing tree-lines to descend dramatically. Four thousand years ago, however, the climate became warmer, and an optimum occurred in the time interval of 3500-2400 BP. Both temperature and rainfall increased at this time, and the area of *Zelkova* and *Castanea* forests expanded in the lower mountain belt. Although this climatic optimum was weaker than the previous Atlantic one, it nevertheless had a significant effect on the vegetation cover and landscapes of the time. Tree-lines again began to ascend, but this process was curtailed by a second climatic deterioration at the end of the Subboreal period.

In Eastern and Southern Georgia, in contrast to Western Georgia, rainfall and temperature continued to increase up until 4000 BP, and it was not until 3500-3000 BP that climatic conditions deteriorated. The record from Lake Imera (Figure 14) shows that oak forests reached their maximum extent when lake levels in Lake Van were highest (Wick et al., 2003), indicating that the climatic optimum of the continental areas of the Caucasus came later than along the maritime-influenced coastlines.

Subatlantic period (2500 BP to the present). Western Georgian pollen spectra of the Subatlantic period show that the period began in a cold phase, but by 2200 BP, climatic amelioration commenced. The maximum phase of warming is observed in spectra from 2000 BP (Figure 15). It was probably a very favourable time for the expansion of *Zelkova* forests, as precipitation increased in tandem with temperature. A cooler phase occurred in Western Georgia about 1600-1550 years ago, when conditions were warmer in Eastern Georgia, and was followed by warmer climates in both regions from 1500 to 800 years ago. The area of *Zelkova* forest again broadened throughout Georgia (Figure 15).

Two subsequent phases of climatic deterioration (including the Little Ice Age), as well as extensive human impacts, saw an almost complete disappearance of *Zelkova* from Georgian forests in the last centuries of the Holocene.

8. Conclusions

This study has demonstrated that the pollen production of *Zelkova carpinifolia* is low and that its pollen is poorly preserved in sediments (particularly in soils). Importantly, it is clear that *Zelkova* pollen grains are poorly dispersed over long distances. Under current conditions, *Zelkova* pollen is rarely dispersed more than 80-100km from source plants in Georgia. Because of these factors, the occurrence of *Zelkova* pollen in fossil spectra likely indicates its local origin and a significant participation of *Zelkova carpinifolia* in palaeolandscapes. Its pollen representation is always 4-5 orders of magnitude lower than its canopy cover.

Since *Zelkova* species require heat and moisture during the growing period, the discovery of fossil remains in Holocene sediments is a good indicator of climatic optimum conditions, i.e. both of increased temperature and precipitation. An increase in *Zelkova* pollen proportions is almost always attended by the increasing role of *Castanea sativa, Pterocarya pterocarpa, Quercus hartwissiana* (in Abkhasia)*, Alnus barbata* (in Kartli and Southern Georgia)*, Hedera helix, Smilax excelsa* and others.

Six significant Holocene climatic ameliorations are recorded in Western Georgian pollen spectra based on the increasing importance of *Zelkova* and other thermophilous taxa. These periods are: Early Preboreal, Late Boreal, Early Atlantic, Late Atlantic, Middle Subboreal and Middle Subatlantic, of which the Atlantic climatic optimum was the most significant, beginning about 7500 BP. This amelioration was interrupted by a cold phase at 6000-5700 BP, after which a 1200-year period of warm, moist climate prevailed until the end of the Atlantic period. During that time, *Zelkova* and *Castanea* forests probably grew at altitudes up to 1300-1400m, whereas now *Zelkova* rarely ascends above 500-600m. Therefore, our material indicates that between 5200-4800 BP, tree-lines in the mountainous regions of Western Georgia were 300m higher. Eastern Georgian tree-lines were elevated approximately 500-600m above their present-day altitude in the subsequent period.

Though of a lower intensity than the late Atlantic climatic optimum, the warmer climate of the second half of the Subboreal period had a significant and positive effect on the expansion of *Zelkova* forests throughout Georgia. The same can be said of the amelioration associated with the Middle Subatlantic period (1500-800 BP), when tree-lines migrated upwards and the distribution of *Zelkova* broadened considerably. Although recent anthropogenic forest disturbance and fire have adversely affected *Zelkova* populations in Georgia, it is not yet known to what extent these impacts influenced *Zelkova* abundances through the Holocene and previous interglacials.

The extinction of species of *Zelkova* throughout much of Europe at the onset of the last glaciation undoubtedly relates to its sensitivity to cold and aridity, and its declining abundance through progressive interglacials follows the trend of European forest flora impoverishment related to increased aridity in the late Quaternary period (Bennett et al., 1991).

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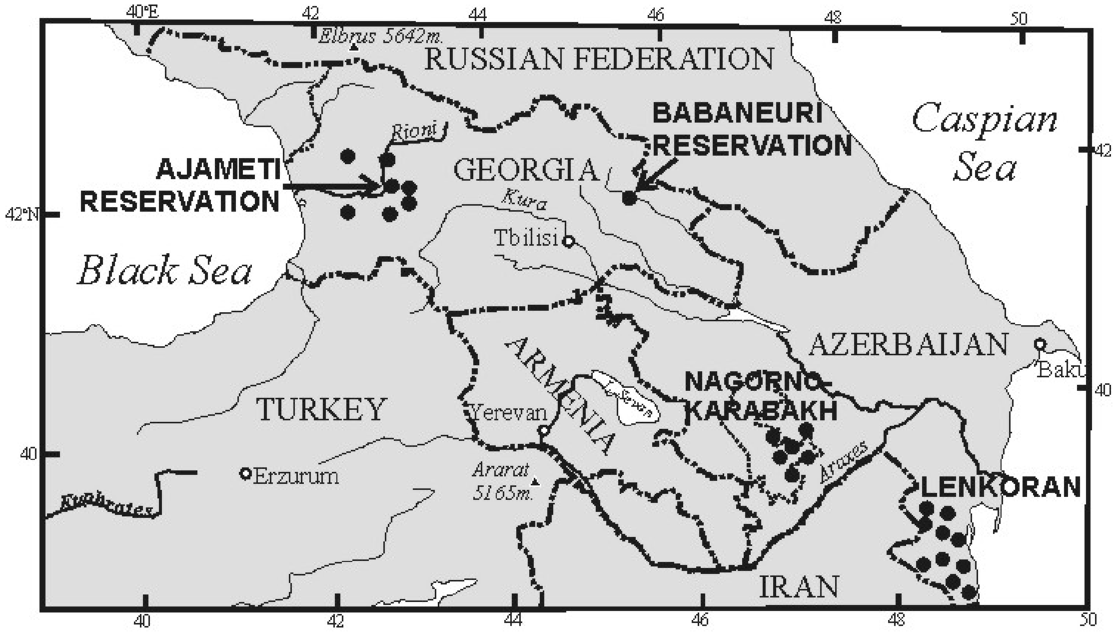

Figure 1. The distribution of *Zelkova carpinifolia* (Pall.) K. Koch in the Caucasus region, compiled with data from Sokolov et al. (1977) and Davis (1965). Dots denote *Zelkova* populations, and the locations of several important distributions are shown.

Figure 2. Photograph of *Zelkova carpinifolia* forest in the Ajameti Reservation, Western Georgia (photograph courtesy Dr. Eristo Kvavadze).

Figure 3. *Zelkova carpinifolia*: 1) flower, 2) inflorescences, 3) leaf, 4) branchlet, 5) fruit. Reproduced with permission from Grudzinskaia (1980).

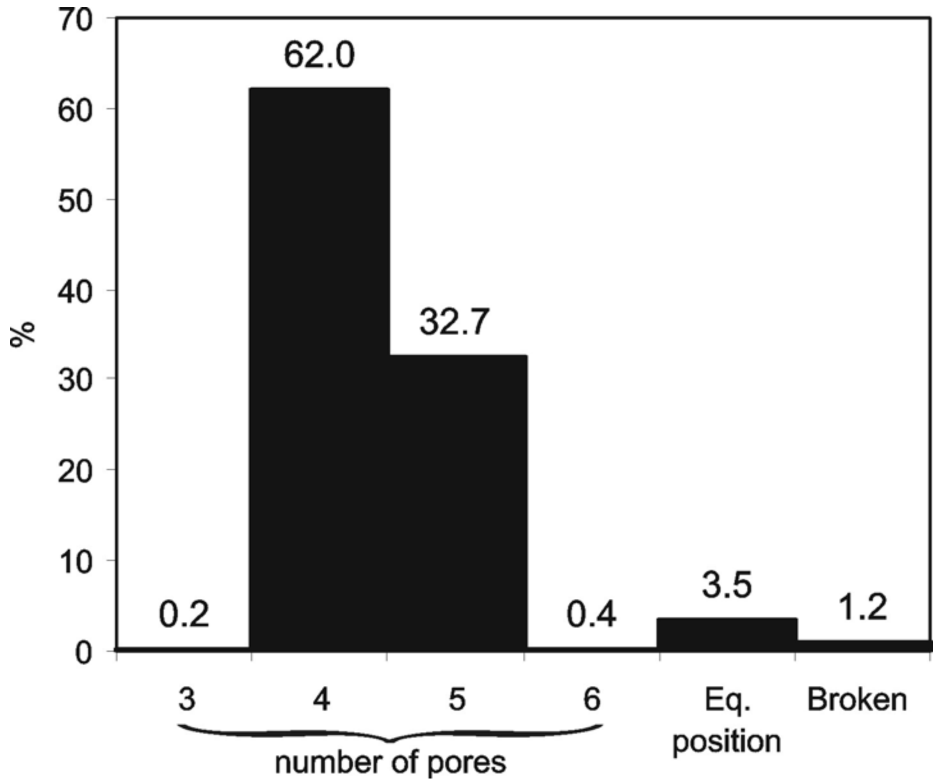

Figure 4. Graph of the number of pores possessed by *Zelkova carpinifolia* reference pollen from the Tbilisi Botanical Gardens. "Eq. position" refers to grains that were in the equatorial view and hence their number of pores was indeterminable.

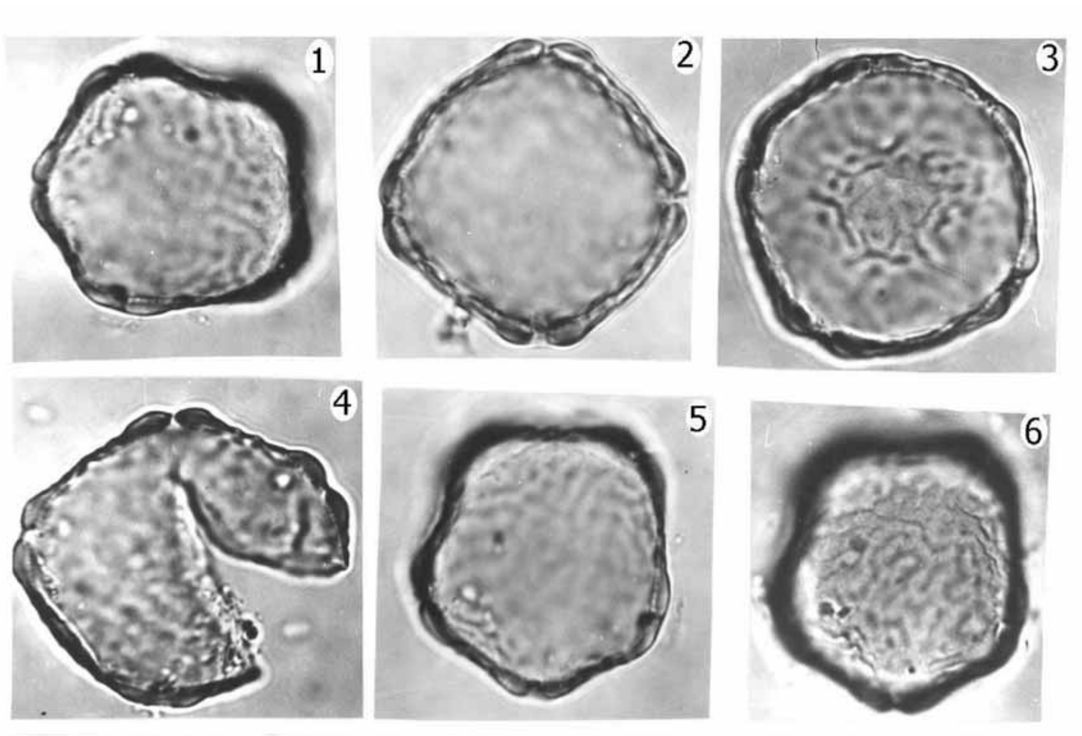

Figure 5. Microphotographs of *Zelkova* pollen from Tkemlara burial mound #1 (site no. 18, Figure 8), showing thickened pores and rugulate sculpturing.

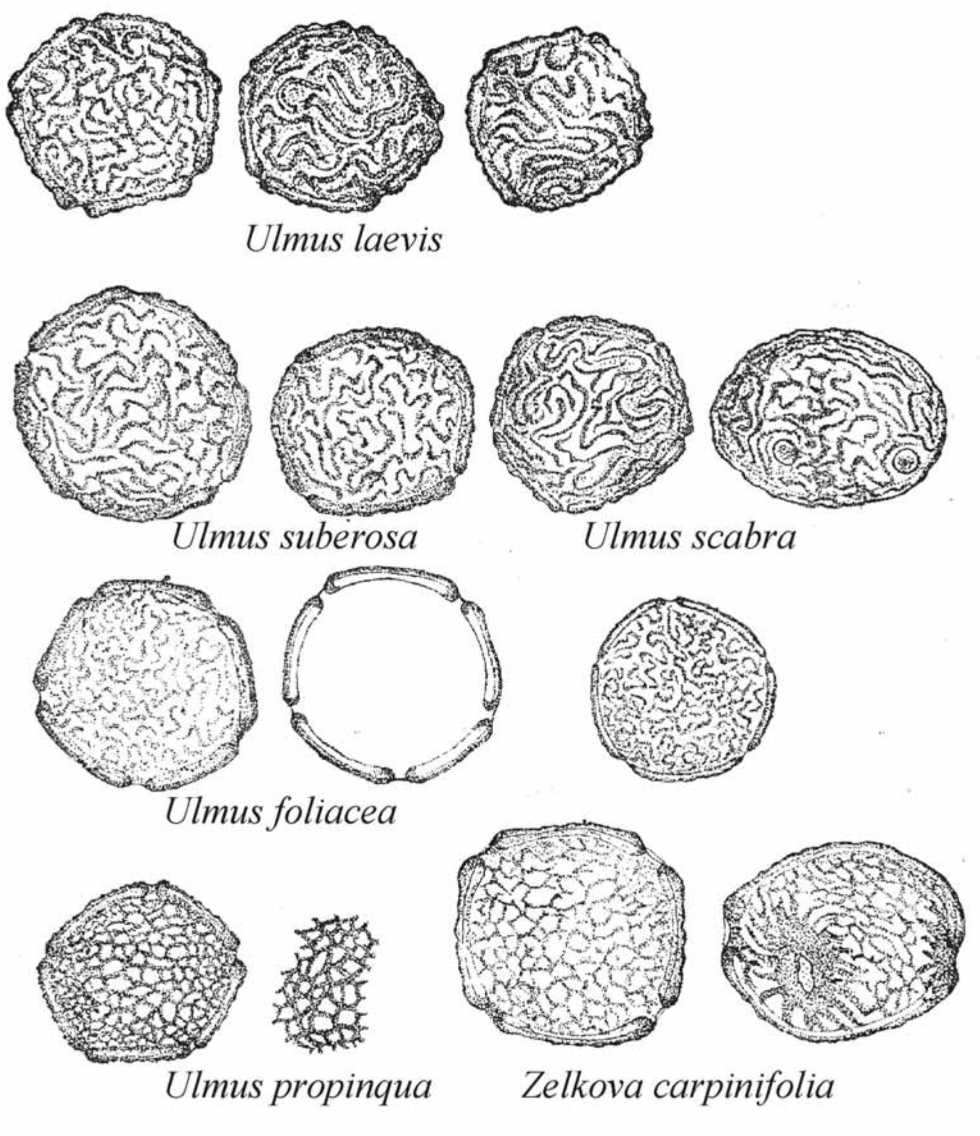

Figure 6. Diagrammatic comparison between *Zelkova carpinifolia* pollen (lower right) and various members of the *Ulmus* genus. Note the different pore structure of *Zelkova*. Adapted from Monoszon (1959).

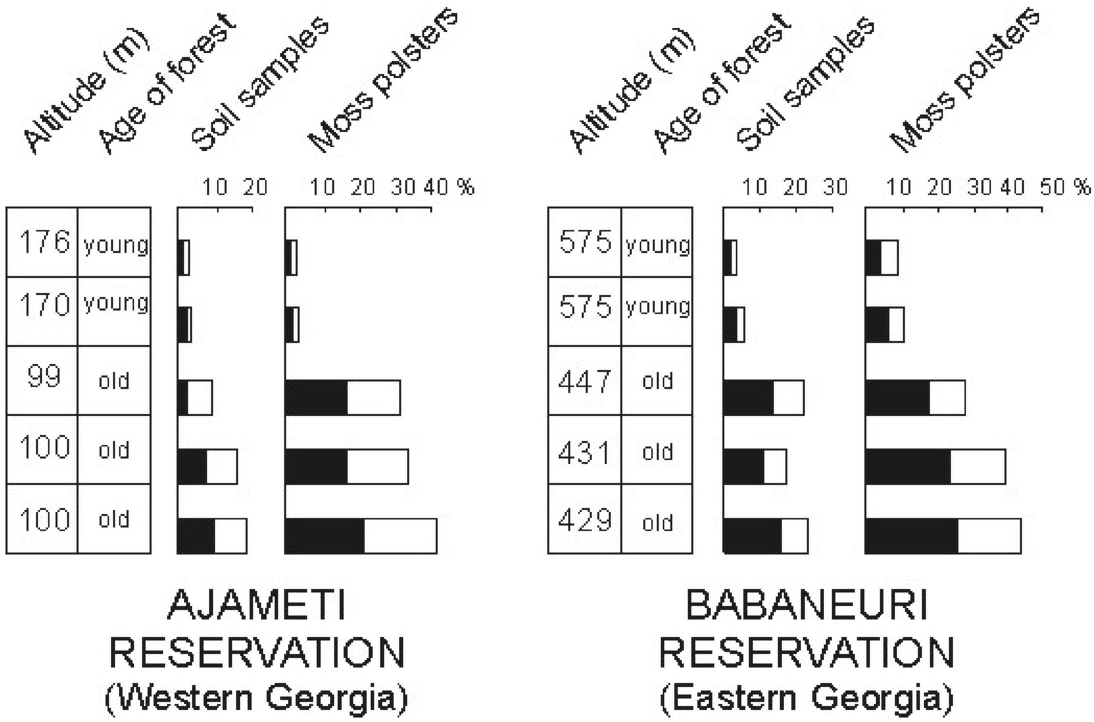

Figure 7. Graph showing the *Zelkova* pollen content of soils and moss polsters from two present-day *Zelkova carpinifolia*-dominated forests in Georgia. The black histograms indicate the *Zelkova* proportion of total pollen (TP), and the white histograms indicate its additional proportion of arboreal pollen (AP).

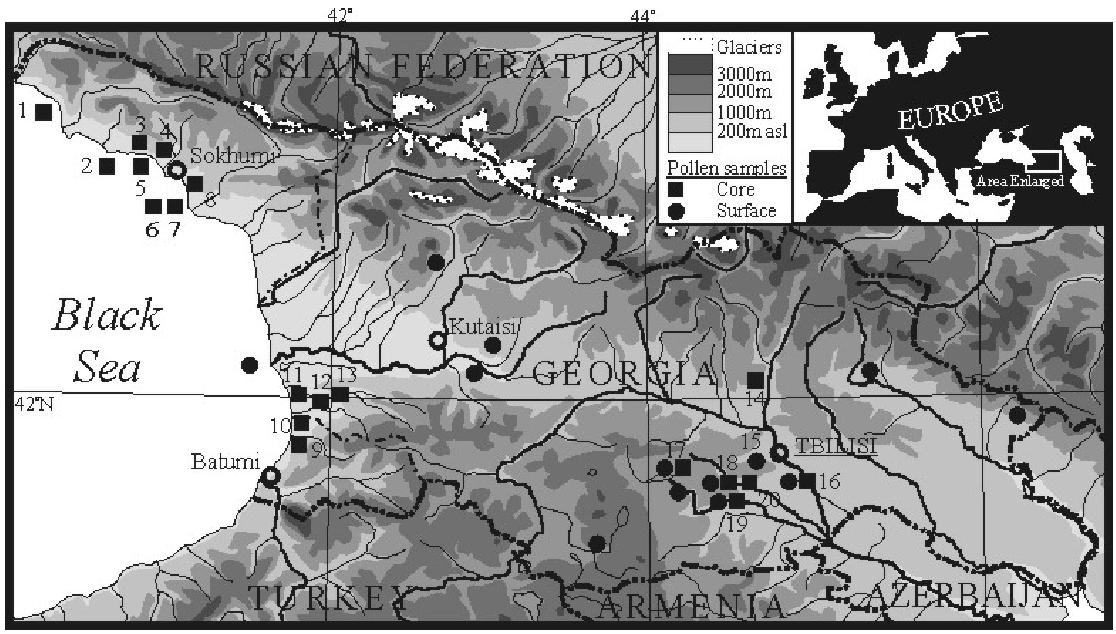

Figure 8. Topographic map of Georgia showing the locations of sediment profiles (numbered) and surface sediment samples (dots) discussed in the text. The names corresponding with the profile numbers may be found in Figure 15.

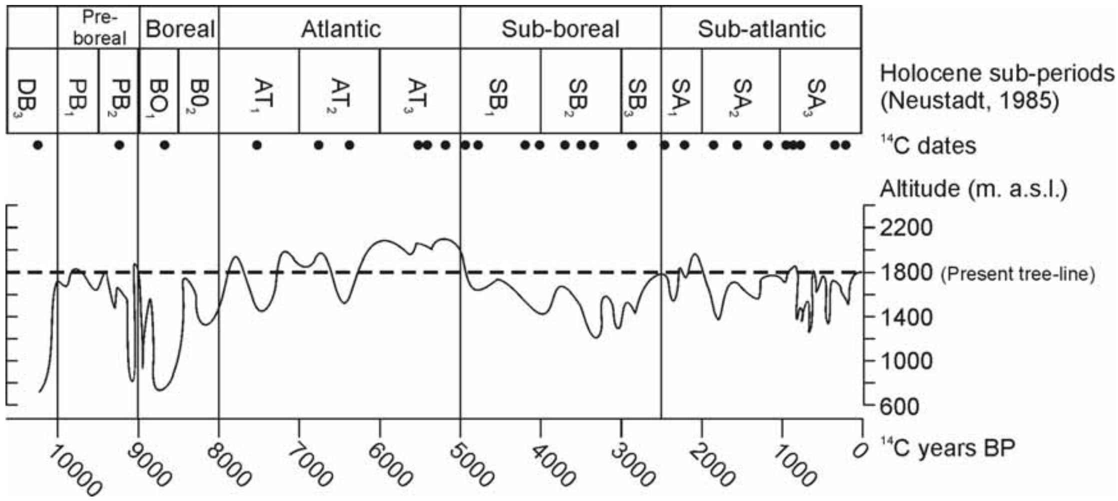

Figure 9. Curve of Holocene oscillations of the upper tree-line in Abkhasia based on mathematical modelling of palynological data (Kvavadze et al., 1992). Radiocarbon dates from the pollen diagrams used in modelling are denoted by dots. The chronostratigraphic scheme of Mangerud et al. (1974) is shown at top.

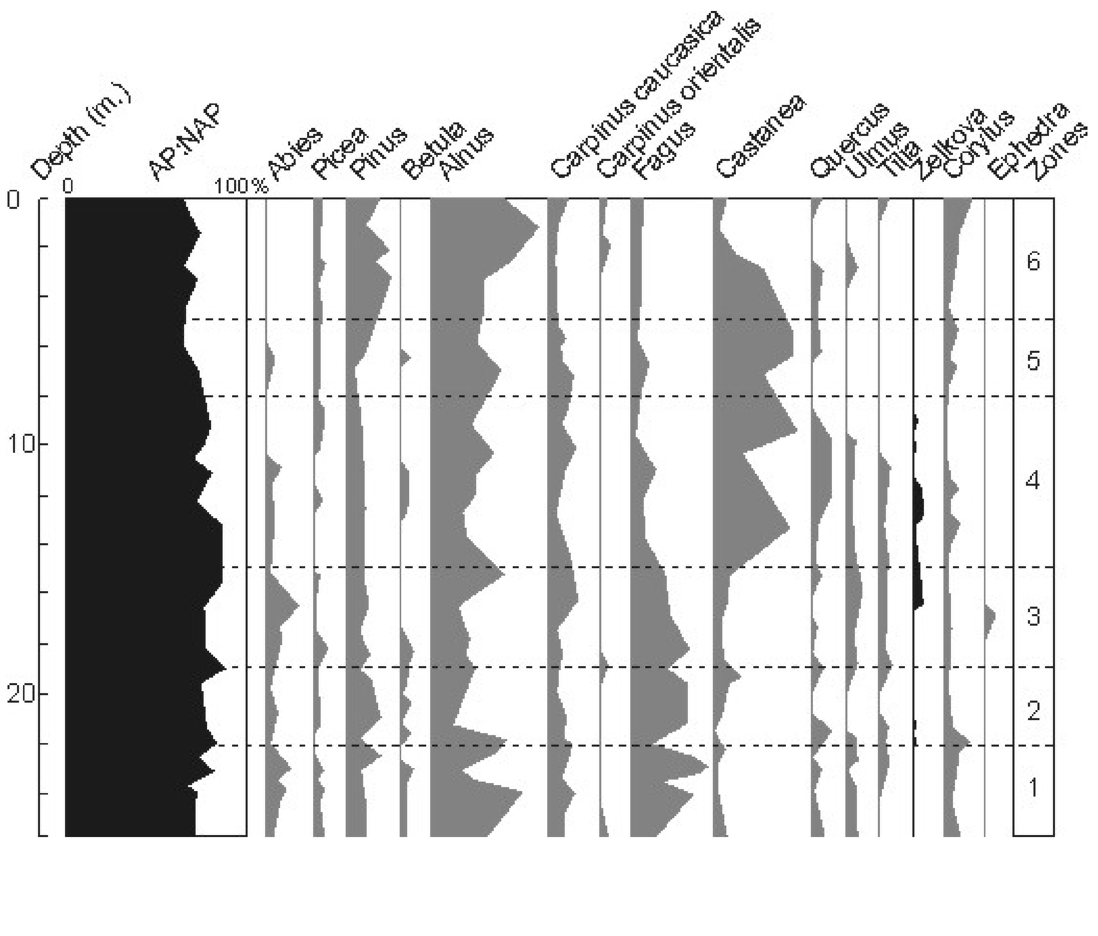

Figure 10a. Pollen diagram of Bore #511, from marine sediments off the coast of Akhali Ateni, Western Georgia (No. 5, Figure 8).

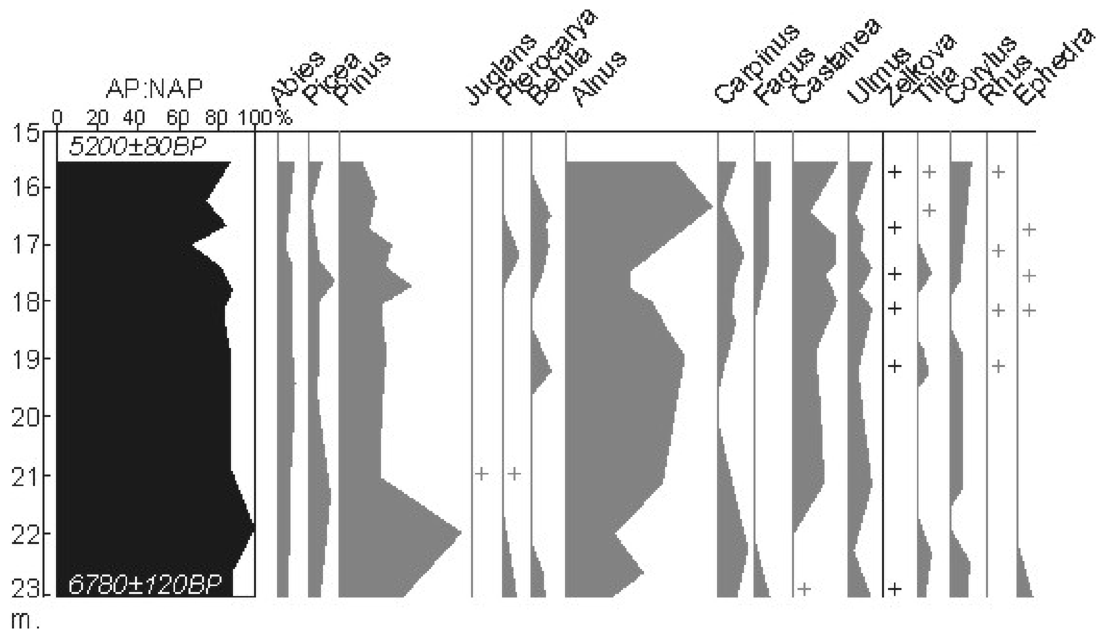

Figure 10b. Pollen diagram of Bore #55, from mid-Holocene terrestrial deposits at Akhali Ateni, Western Georgia (No. 3, Figure 8).

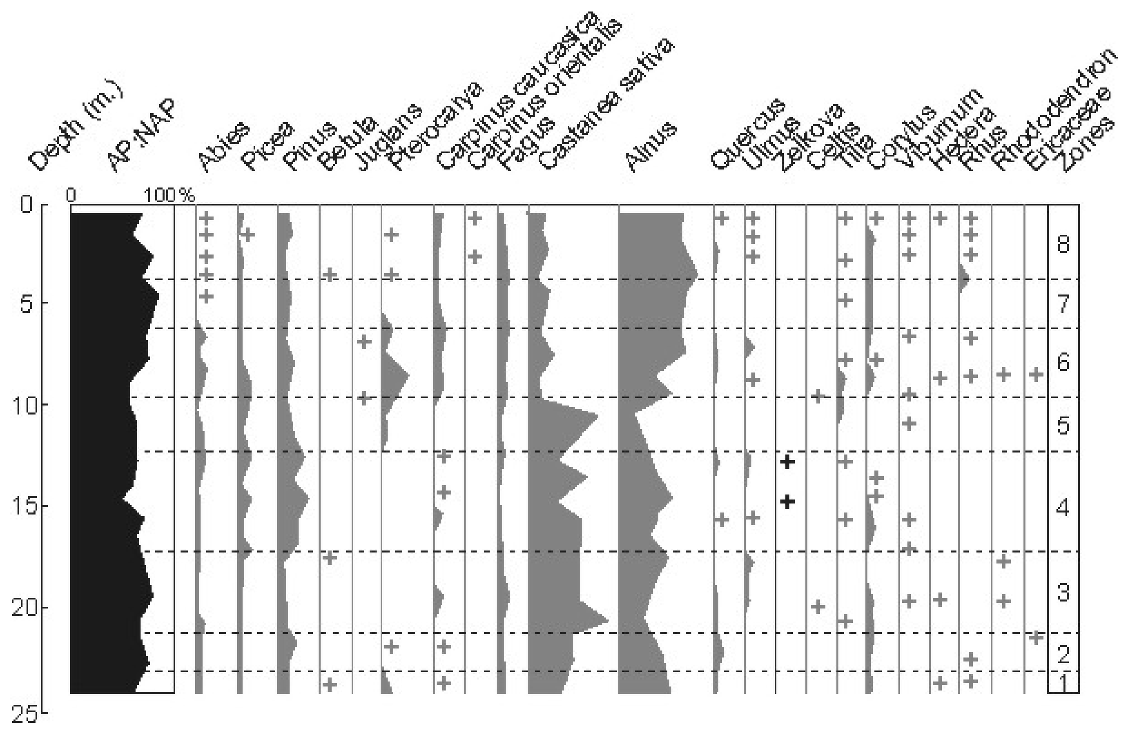

Figure 11. Pollen diagram of Holocene alluvial sediments of Bore #39, Kobuleti, coastal Western Georgia (No. 10, Figure 8).

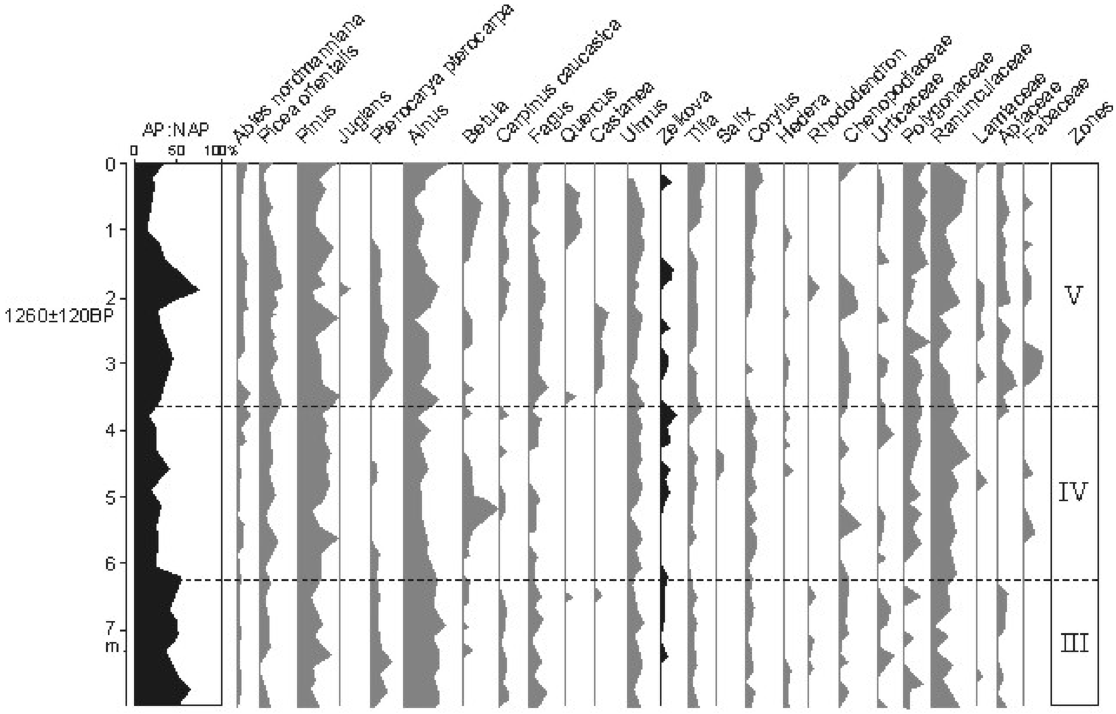

Figure 12. Pollen diagram of the Supsa 2 profile, from alluvial terraces in Western Georgia (No. 12, Figure 8).

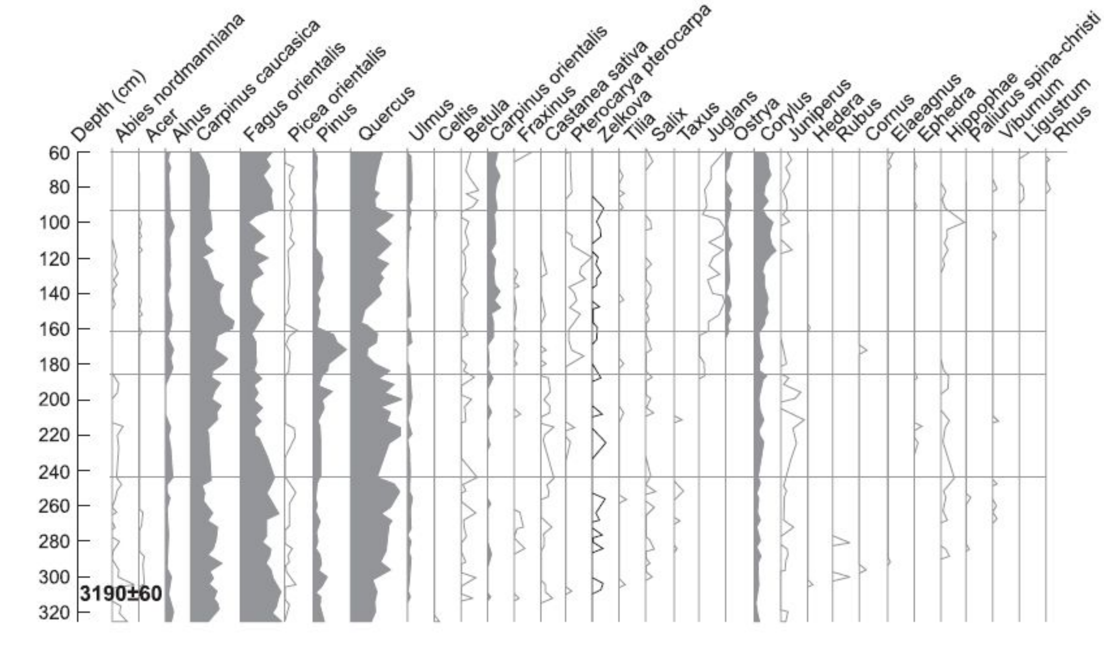

Figure 13. Late Holocene pollen diagram from Lake Bazaleti, Eastern Georgia (No. 14, Figure 8).

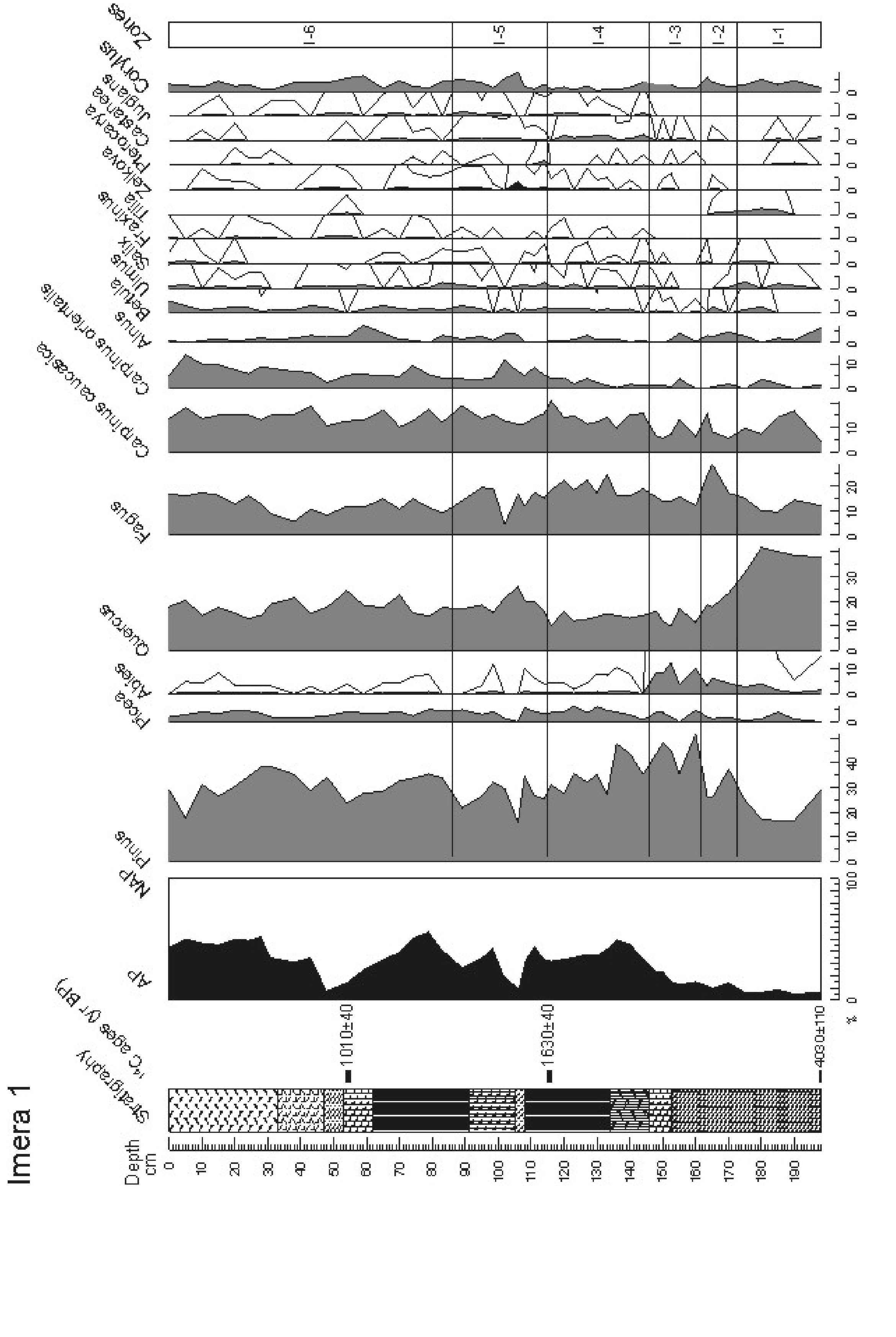

Figure 14. Pollen diagram of mid-late Holocene sediments of Imera Lake, Tsalka Plateau, Southern Georgia (No. 17, Figure 8).

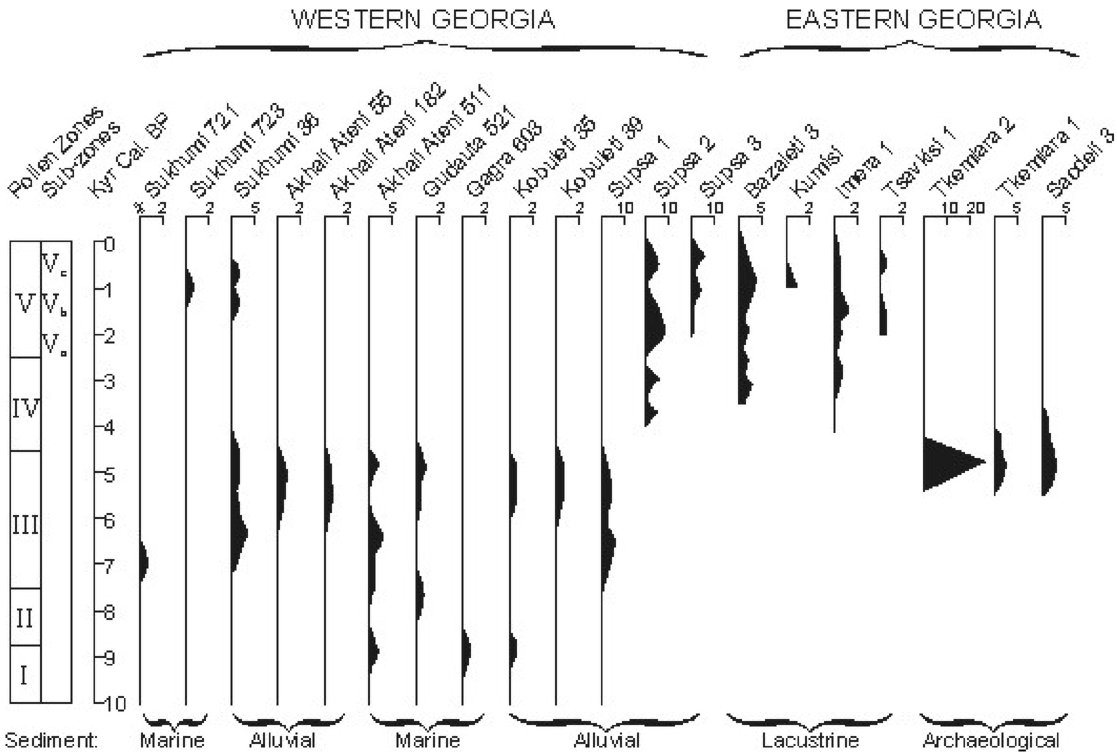

Figure 15. Correlation of all *Zelkova* pollen profiles mentioned in the text, with percentages expressed as a proportion of arboreal pollen (AP). Site numbers correspond to those in Figure 8. Dots to the left of individual profiles indicate radiocarbon date locations, and profiles not so marked were dated palynologically (based on taxa other than *Zelkova*).