History of the Flora and the Vegetation

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The history of the flora and, especially, the vegetation of Georgia is very complicated and, despite the intensive paleobotanical investigations of the recent past, still needs to be studied.

The earliest records of fossil flora stem from the Paleozoic. Species of *Lepidodendron* (large trees reaching a height of nearly 40 m), *Sigillaria* (high plants with erect stems and characteristic rhizophore system: stigmarias), *Asterocalamites* were determined from the Lower and Middle Carboniferous deposition of the Khrami crystalline massif (South Georgia). Cordaitales – a group with anatomical structures (tracheids, well-developed pith) very similar to that of conifers (Shatilova et al. 2011) – are known from the same period.

In the Early Jurassic, almost the entire territory of Georgia was covered by sea, except for Khrami, Loki and Dzirula ancient massifs.

The climate of this period was warm-temperate. Water temperature in the sea reached 23–24 °C, but in Late Toarcian it decreased considerably (7–15 °C). Calamitales are of special interest with the only species *Neocalamites hoerensis* present in the early Jurassic depositions. The above mentioned period was characterized by the wide-spread occurrence of equisetoids, which were restricted to marshes as it is nowadays (Svanidze 1972).

Pteridophytes were represented by 25 taxa. Microfossils found belong mainly to the genus *Cladophlebis* (Osmundaceae). At the same time *Ginkgo* was represented by two species: *G. mziae* (specific to Georgia) and *G. huttonii*. The species *Sphlenobaiera spectabilis* and *Phoenicopsis angustifolia* also belong to Ginkgoaceae. In the early Jurassic, a considerable group was formed by Bennettitales – the ancestors of the flowering plants (according to the viewpoint of several botanists). *Eucommiidites troedssonii* (gymnosperms pollen) and many other plants were present in the same period too.

In the Bajocian (Middle Jurassic) the entire territory of Georgia was under the sea; by the end of it, first the eastern part and afterwards (in Bithonian) the whole territory has emerged. The appearance of freshwater basins was characteristic to that period, as well as the process of peat accumulation (Kakhadze 1947). The Early Jurassic flora is much richer than that of the Early Jurassic. Today nearly 175 plant

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species are known from the Middle Jurassic. 55 of them are ferns (*Coniopteris,* Cyatheaceae*,* Osmundaceae*,* Gleicheniaceae) and representatives of *Paracycas* (Cycadaceae)*, Ptilophyllum* (Benettitaceae), etc. The climate of the Middle Jurassic was probably tropical; representatives of Cycadales and Ginkgoales dominated the woodlands (Svanidze 1972).

In the Late Jurassic the territory of Georgia was covered by sea, except the Svaneti Elevation, as well as the southern parts.

The occurrence of remnants of the new species *Angiopteris iberica (*Marattiaceae) in the Late Jurassic fossiliferous deposits is of great importance. It underlies the opinion that these archaic living ferns disappeared from the floras of the Northern Hemisphere after the Middle Jurassic.

According to Vakhrameev (cited by Shatilova et al. 2011), the Late Jurassic paleofloristic province of the Caucasus was a part of the Euro-Sinian region.

The flora of the above-mentioned province could be characterized by the presence of occasional equisetoids, a few ferns, Ginkgoales, the absence of *Czekanowskia* and the predominance of Cycadales*,* Bennettitales as well as *Pachypteris, Sagenopteris, Pagiophyllum.*

2.1 The Tertiary

In the **Paleocene** and **Eocene** a long island was formed on the territory of the Caucasus as a basis for further development of mountain range. In the Eocene, the dominant position was occupied by the Angiosperms, representatives of evergreen Fagaceae and *Myrica*.

At the same time the process of migration of the Boreal cold-resistant plants, which had begun previously in the Cretaceous, resumed at the end of the Eocene.

At the Eocene/Oligocene boundary, the folded structure of the Alpine system started to form in the Mediterranean orogenetic band. It comprised the (geosynclinal) regions of the Southern Slope of the Greater Caucasus range and Ajara-Trialeti, the main part of today's Georgia. Uplift caused a change in the climatic conditions; the latter determined the character of the vegetation: the number of conifers increased and warm-temperate plants became more numerous (Tumajanov 1955; Shatilova et al. 2011).

During the **Oligocene**, the Caucasus was a small island surrounded by a vast basin with scattered islands, where the tropical flora of the Poltava type (palms, laurels, etc.) was well developed. In West Georgia (near the town Chiatura), in the Oligocene deposits remnants of conifers (species of *Pinus*) were found, indicating the penetration of northern taxa into the Caucasus.

The Oligocene plant world was greatly influenced by the Arcto-Tertiary or Turgay flora, formed in the eastern and northern parts of modern Asia. Representatives of this flora, especially pines, penetrated into the Caucasus. Many botanists consider that migration of the Turgay elements became more intensive after the Turgay Strait had become dry by the end of the Oligocene.

According to Grossheim (1948), Turgay migrants began to change and gave rise to the ancient mesophytic forest flora, called Mediterranean-Turgay flora by this author.

During the **Miocene** the Caucasian island started to expand. Fossil assemblages from different parts of Georgia, especially from Western Georgia (Guria), confirm the subtropical nature of the Miocene flora with the predominance of evergreen woody plants, accompanied by the deciduous *Castanea sativa*, as well as by conifers of northern origin *(Pinus neptuni)*.

The following plants have been known since the Early Miocene deposites of Kartli (East Georgia): *Myrica neriifolia* (=*M. lignitum*), *Laurophyllum primigenium,* species of *Apocynophyllum*. Of the 46 taxa two are pteridophytes and five gymnosperms. The dominant position is occupied by Angiosperms, namely *Comptonia acutiloba, Myrica neriifolia* (=*M. lignitum*), etc. The greatest part of the Early Miocene flora, studied by macrofossils, is represented by Angiosperms. Among them the predominance of Myricaceae, Juglandaceae and Lauraceae should be noted, whose role has somewhat increased since the Paleogene. Evergreen Fagaceae, Lauraceae and other thermophilous plants, contributing to the formation of moist-subtropical forests in the Paleogene, adapted to the reduced humidity of the Early Miocene.

In the Middle Miocene plants of warm and dry climate participated in sclerophyllous formations. *Myrica* species covered river banks. Sclerophyllous plants were represented by the species of *Myrtus, Callistemophyllum, Acacia, Quercus (Q. drymeja)*. Several species of Lauraceae, *Sapindus, Smilax* and *Magnolia* formed moist-subtropical forests.

It is possible to suggest that an altitudinal differentiation of vegetation already existed in the Middle Miocene. Coastal and low mountainous areas were covered by subtropical forests with high numbers of Sterculiaceae, Araliaceae, Lauraceae, evergreen Fagaceae, arborescent ferns, *Hymenophyllum*, etc. The next altitudinal belt was occupied by mesophilous deciduous forests of *Platanus, Comptonia, Juglans, Pterocarya*, etc. Cold-resistant plants occurred even higher; mention should be made of species of *Betula, Fagus, Acer, Tilia, Ulmus,* accompanied by *Cathaya, Keteleeria,* etc. (Shatilova et al. 2011).

During the Sarmatian (Upper Miocene), the Caucasian island, known in the literature as Jephethis, was situated close to Iranian and Central Asian land. This encouraged the immigration of xerophilous elements into the Caucasus. It is suggested that the forestless formations of xerophytic plant communities were widely distributed during the Early Miocene. According to Grossheim (1946), *Pelargonium endlicherianum*, the fern *Ceterach*, etc., are relicts of the ancient xerophytic flora of this period.

The close position of Jephethis to the Iranian mainland, separated as a cape, caused a division of the mesophytic Mediterranean-Turgay flora into western and eastern parts. In the west, the Colchic flora began to form, while the Hyrcanian elements evolved in the eastern part. Both were of mesophytic nature. The analysis of the contemporary vegetation makes many botanists suggest the existence of a third xerophytic flora.

Based on the fossils, it is possible to build up a picture of the Sarmatian flora: evergreen *Magnolia dianae,* species of Lauraceae (*Cinnamomum, Laurophyllum primigenium, Laurophyllum pseudoprinceps,* etc.), as well as the representatives of the Mediteranean-Turgay and Turgay deciduous flora, such as *Salix, Pyrus, Carpinus, Juglans, Ulmus,* etc. Conifers (*Pinus saturi, Sequoia langsdorfii*) and xerophytic species of *Myrica* have been known from the same age.

Kolakovsky and Shakril (1976) pointed out that the richest Sarmatian floras occurred in Abkhazeti (Colchis). They were closely related to the southern subtropical and tropical floras (*Melastomites* sp., *Mastixia microphylla, Ventilago* etc.). The Sarmatian floras of Abkhazeti are very similar to Oligocene-Miocene European floras. These floras indicate the wide distribution of subtropical evergreen plants, mainly Lauraceae, such as *Ocotea, Persea, Aniba,* and many others, and the deciduous arborescent plants of warm climate which have survived until now only in Central and South America, partly in the Mediterranean area and in South-Eastern Asia. These forests show a great similarity to the vegetation, confined to mountainous Japan during the Miocene-Pliocene. It is suggested that this vegetation is similar to that now found in the mountain systems of South-Eastern Asia, Himalaya and China, where relic forests of *Ulmus, Fagus, Quercus, Abies* and *Cryptomeria* were well represented.

The Tertiary-relic species of Colchic type, such as species of *Buxus, Pterocarya*, etc. and the hemixerophytic Mediterranean plants *Arbutus, Celtis, Smilax, Thelycrania (Cornus), Quercus*, have been found in the Sarmatian deposites of Abkhazeti.

The territory of East Georgia, where steppes and semi-deserts are distributed now, is considered to have been covered with both sclerophyllous and moist-subtropical forests.

In South Georgia the shrubs of subtropical and temperate climate dominated by Lauraceae, were represented by narrow-leaved xerophytic elements.

In the Meotian, after the regression of the Mediterranean Sea, the strait separating the Jepethis from the southern mainland disappeared and the Caucasus became a peninsula. The formation of the main folded systems reached the final point, and the vegetational belts were formed. The Meotian macrofossils included *Cryptomeria japonica*, species of Lauraceae*, Salix coriacea, Myrica neriifolia* (=*M. lignitum*). Ferns, especially *Dicksonia*, were represented by a large number of species. Palynological data attest to the fact that the following genera of conifers were present: *Abies, Picea, Tsuga* (five species), *Cedrus,* as well as *Carya, "Castanopsis furcinervis"* (leaf remnants of *Quercus),* representatives of Hamamelidaceae or Altingiaceae *(Liquidambar*, etc.).

According to the composition of the fossiliferous deposits, in this period, coniferous and broad-leaved forests *(Taxodium, Cryptomeria, Magnolia,* species of Hamamelidaceae, etc.) with the species of *Quercus, Carya, Fagus, Castanea* and *Platanus* began to prevail.

Relatively dry habitats were occupied by the following hemixerophytes: *Quercus drymeja, Celtis punica, Pistacia miocenica, Sophora europaea, Pyracantha coccinea*. At the same time the following plants began to crop up (present-day

members of the Georgian flora): *Rhododendron caucasicum, Fagus orientalis, Zelkova crenata (=Z. carpinifolia)*. During the period of Pontian Sea expansion, the Caucasus and Transcaucasia became consolidated.

The fossil flora of Goderdzi pass (South-Western Georgia) was distinguished by the features characteristic of Sarmatian flora; in Pontic it had already been a relic flora.

Taking into account fossil deposits of this region, mesophytic flora obviously prevailed here. Representatives of Annonaceae, Hamamelidaceae and Lauraceae are known from this period which was characterized by a warm maritime climate. Ferns, distributed in Georgia during the Pontian, can now be found only in the tropics.

During the Pontian, gymnosperms were widespread. Nowadays, they occur in montane forests of tropical and subtropical countries. In the beginning of the Pliocene, *Pinus pithyusa* was widely distributed.

Investigations carried out by Kolakovsky (1964) in Kodori (Abkhazeti) point to the existence of lowland and low-mountain forests with *Myrica lignitum, Salix varians, Alnus subcordata*. Coastal lowlands were covered with forests of *Quercus kodorica* and *Carya denticulata*, while the riversides were occupied by species of *Liquidambar, Taxodium, Nyssa, Tectocarya, Ocotea,* evergreen Fagaceae like *Pasania, Castanopsis*, etc., which were characteristic of the subtropical forests of the Pontian. In the lower montane zone, considerable areas were populated by Laurisilva with tree ferns *(Cyathea, Alsophila, Dicksonia).*

In the lower montane zone sclerophyllous formations were distributed with the elements of maquis. Pines occupied rocky habitats.

Kolakovsky (1974) pointed out that an important change in the flora of the warm-temperate climate took place during the Pontian. The mid-mountain belt was populated by *Fagus, Castanea, Acer, Tilia* species. The presence of conifers – *Ginkgo, Keteleeria* – , ferns like *Polypodium*, etc., lianas like *Vitis betulifolia, Parthenocissus quinquefolia* becomes fairly possible.

Dark coniferous forests (with species of *Abies, Tsuga, Picea, Cedrus,* etc.) occupied relatively higher altitudes.

On the territory of West Georgia a great number of angiosperms has vanished since the Pontian.

In Cimmeridian (Middle Pliocene), the shrinking of the Tethys led to the exposure of new land, fit for colonization by xerophytic vegetation, such as semi-desert vegetation, shibliak, light forests, maquis, etc., so characteristic of the Mediterranean. Meanwhile, taxa of Araliaceae, as well as ferns were well represented. The dominant position was occupied by species of *Pteris* and *Polypodium*. According to Kolakovsky and Shakril (1978), forests of warm-temperate climate began to prevail in Cimmeridian; they were composed by the species of moist monsoon climate, now peculiar of the mountains of Eastern Asia and xerophytes, ecologically similar to the plants of xerophytic forests of the Mediterranean. Above the warm-temperate forest zone hardwood and coniferous forests grew.

During the Kuyalnitskian-Akchagylian (Upper Pliocene), a large part of East Georgia lay under the sea. The Greater and Lesser Caucasus were connected by a land bridge to the Near East (Asia Anterior–South-West Asia) in the south. The

most striking feature of the fossil floras of this period is the absence of Poltava floral elements and evergreen plants. The following plants are known from this period: species of *Populus, Ostrya, Fagus, Zelkova, Tilia, Pyrus, Ligustrum, Salix, Prunus, Acer, Quercus, Pterocarya*, together with representatives of *Carex* and *Phragmites*. All these plants are members of the present-day flora of Georgia, though they have changed their habitats. For example, remains of *Fagus orientalis* and *Ostrya carpinifolia* have been found in Akchagyl deposits of the Shiraki steppe. Due to increasing aridity, these trees are no longer there.

According to Grossheim (1948) the Akchagylian flora by its nature is closely connected with that of the Quaternary. To quote his words: "The period between Sarmatian and Akchagylian was the turning-point in the floristic history of the Caucasus; the tropical flora had been replaced by that of temperate climate" (Grossheim 1948: 171). Broad-leaved forests were replaced by conifers, namely species of *Picea, Abies,* and *Tsuga*. In general, during the late Pliocene, the role of polydominant forest vegetation was reduced and, instead, the formation of communities with one or two dominant species was stimulated. These changes in the vegetational cover were probably provoked by the intensification of cold at the end of the Miocene and in the Pliocene.

The existence of a dry and hot climate between the cold periods encouraged the enrichment of the Caucasian flora with xerophytes. In Akchagylian times, many recent Mediterranean plants penetrated into the present area from the west.

Therefore, in the **Pliocene**, the piedmonts and the lower montane zone were clothed by subtropical forest vegetation. Forests of warm-temperate climate were situated higher up. Many species known from this period are still members of the modern forest flora. In the beginning of the Pliocene, within the territory of West Georgia and adjacent areas (e.g., Turkey), a Colchic refuge was formed for many relics of mesophytic forest flora. This was a direct result of the warm and humid climate of this territory. The Colchic refuge was of great importance as one of the most stable "shelters" for relic species during the Late Pliocene and especially in the Pleistocene, including the Ice Ages. Many species, which continue to exist in the Colchis died out many millions of years ago on the territory of West Eurasia. Members of the Colchic flora are such relics and/or neoendemics as *Betula medwedewii, Quercus pontica, Rhamnus imeretina, Hedera colchica, Pterocarya pterocarpa, Laurocerasus officinalis, Arctostaphylos caucasica, Rhododendron ponticum, Rh. ungernii* and *Rh. smirnowii*. At present, their relatives with a similar autecology have mainly survived in the mountains exposed to the summer monsoon in eastern and south-eastern Asia, in the Appalachians of North America, etc.; for instance, the genus *Epigaea* is represented now by just three species, one of which is distributed in Japan, the second in North America and the last in Ajara (Georgia) and Lazistan (N. Turkey).

2.2 The Quaternary

Thus, having surveyed the Tertiary history of the Georgian flora, we now come to the **Pleistocene**. During the Pleistocene, most of the thermophilic elements vanished from the flora of Georgia. The role of cold-resistant plants considerably increased, at the same time vertical shifts of the vegetational belts appeared, especially during the glacial periods.

Another event, which might have occurred during the Pleistocene is the development of boreal elements. Though the flora of Georgia was strongly influenced by the neighbouring floristic centres of Eastern Mediterranean and SW. Asia (Near East, Anterior Asia), the process of autochthonous development provided a large number of endemic species, including present-day local endemics.

In the Early Chaudian (the **Early Pleistocene**) deposits the highest taxonomical diversity and an abundance of Taxodiaceae and Cupressaceae could be observed; these families were manifested by the following genera: "*Athrotaxis*" (=extinct Taxodiacea), *Cryptomeria, Metasequoia, Sequoia, Sequoiadendron, Taxodium; Cupressus, Chamaecyparis, Libocedrus, Juniperus*.

The dominant position was occupied by *Abies nordmanniana, Tsuga diversifolia*, whereas *Abies alba, Cedrus* aff. *libani* and some others had vanished.

In the Chaudian flora, Juglandaceae were represented by several genera: *Pterocarya, Carya, Juglans*, etc. Pollen of *Zelkova* was found in the Chaudian of Georgia.

In the Chaudian, beech forests were as widely spread as the representatives of the genus *Tilia*. Chaudian pollen assemblages contained pollen of plants very closely allied to evergreen shrub *Fatsia japonica*, which is now confined to the forests of Japan, as well as that of *Symplocos* which is largely distributed in tropical areas. Obviously, the prevailing types of vegetation in the Early Chaudian were monodominant forests of *Tsuga, Abies,* representatives of Taxodiaceae and *Fagus*. Lower montane and piedmont belts were covered by the forests of *Juglans, Carpinus, Quercus, Zelkova*, and also by subtropical species of *Magnolia, Fatsia, Symplocos,* etc.

At the same time, many ferns and spore-bearing plants vanished together with the most thermophilic elements. In the Late Chaudian, almost all the plants of subtropical and temperate climate died out. The representatives of *Tsuga* and Taxodiaceae lost their leading position in forests.

The second half of the Chaudian was characterized by the predominance of *Picea-Abies* communities in almost all the mountain belts, whereas the lower parts were covered with broad-leaved forests (Tchotchieva 1965).

Middle Pleistocene. Many ferns, which can be found in the contemporary flora of Georgia, have been known since the old Euxine period. During that period, taxonomic diversity of *Abies*, *Cedrus*, *Picea* and *Tsuga* was reduced. Members of the Taxodiaceae family prevailed in forest communities. Within the territory of Georgia, only 6 out of 66 taxa, known from the Old Euxine became extinct.

In West Georgia, the old Euxinian depositions are covered by that of Uzunlar (Shatilova et al. 2011). The Uzunlarian ferns were represented by those species which continue to exist in present-day Georgia. A dominant position in forests was

occupied by widely spread *Abies nordmanniana, Picea orientalis* with an admixture of *Cedrus deodara, Tsuga diversifolia* and *T. shatilova*. *The* Taxodiaceae family was represented by *Taxodium, Cryptomeria, Sequoia,* and *Glyptostrobus*. Hardwood forests consisted of the following species which have become members of the modern Georgian flora: *Fagus orientalis, Castanea sativa, Carpinus caucasica,* etc. It should be mentioned here that mesophytic species were substituted in East Georgia by those of *Pinus, Carpinus, Quercus,* etc.

In the **Late Pleistocene**, there were still a number of species which have since disappeared from the territory of Georgia. Mention should be made of the representatives of Taxodiaceae, of *Cedrus deodara* and *Carya aquatica*. Except for *Carya*, angiosperms were represented by species which are characteristic of modern Georgian flora.

Man introduced considerable changes into the vegetational cover of Georgia. Forest destruction, development of secondary meadows, cultivated lands are the results of human activities. At the same time, the Georgian flora was enriched both by cultivars and adventive weeds.