Quaternary International 661 (2023) 34–48

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Middle to late Holocene lake level changes of Lake Sevan (Armenia) – Evidence from macro and micro plant remains of Tsovinar-1 peat section

Narine Hayrapetyan[a,*], Elen Hakobyan[a,b], Eliso Kvavadze[c], Edoardo Martinetto[b], Ivan Gabrielyan[a], Angela A. Bruch[d]

[a] A. Takhtajan Institute of Botany, National Academy of Sciences of the Republic of Armenia, 0063, Yerevan, Armenia
[b] University of Turin, Department of Earth Sciences, 10124, Turin, Italy
[c] Georgian National Museum, 0105, Tbilisi, Georgia
[d] ROCEEH Research Centre, Senckenberg Research Institute, 60325, Frankfurt/M, Germany

ARTICLE INFO

Keywords:
Pollen
NPP
Carpoflora
Aquatic plants
Ceratophyllum

ABSTRACT

In the Caucasus, peat deposits exposed near Lake Sevan (Armenia) provide a Middle to Late Holocene record of lake level fluctuations. The Tsovinar-1 section at the southern shore of Lake Sevan in the Armenian Highlands reveals a well-dated and divers pollen and carpo-flora covering a time span from 6000 BC to 900 AD. The abundances of pollen of forest taxa in relation to steppe vegetation indicate climatic changes through time. In parallel, the presence and number of fossils of aquatic and wetland plants, both in micro and macro floras, provide information about the presence of water and allows estimating changes of water depth. Characteristic taxa pointing to deeper water at Tsovinar-1 are *Myriophyllum* sp., *Ceratophyllum demersum*, and several species of *Potamogeton*. In shallow water, *Persicaria amphibia, Sparganium* sp., and *Typha* sp. dominate. In fluctuating water and wetlands those plants are replaced by *Menyanthes trifoliata, Ceratophyllum submersum, Alisma* sp., and others. High lake levels can be inferred at 6000−5000 BC, 1700−900 BC and 200−900 AD and are associated with humid climate and the development of forest vegetation. Low lake levels occurred at 4000−2600 BC and 600 BC−100 AD corresponding to epochs of decreased humidity and expanded steppe vegetation. Macro and micro remains of plants from the Tsovinar-1 site serve as reliable sources of information for determining environmental changes over time, which are in accordance with archaeological data from the region showing the effects of lake level changes on human activities.

1. Introduction

In the Caucasus, at the crossroads between Europe and Asia, the largest lake is Lake Sevan with a surface area of 1241 km^2. It is situated in the northern part of the Armenian Volcanic Highland, in Gegharkunik province, 60 km north of Yerevan, the capital of Armenia (Fig. 1). The lake is located today at an altitude of 1900 m a.s.l. (Statistical Committee of the Republic of Armenia, 2019) and constitutes an important freshwater source. Before the artificial lowering of the water level during the 20th century, 80% of the republic's freshwater resources were accumulated here. The unique and rich flora and fauna of Lake Sevan constitutes an important part of the Armenian biodiversity. Also, the lake has an important economic value as a food resource as well as touristic and recreation area. (Avagyan, 2003). The whole basin that hosts the lake, the Sevan hydrological catchment area, covers an area of 4891 km^2 (Karakhanyan et al., 2016; Gabrielyan, 1978). About 1660 species of vascular plants have been registered in this region (Tamanyan and Fayvush, 2009), which is part of the Caucasus biodiversity hotspot (Myers et al., 2000).

The history of Lake Sevan, the causes of changes, and their consequences are crucial to be known to make accurate predictions about its state. Thus, this work focuses on the effects of natural impacts on Lake Sevan's water level changes. The continuous and significant fluctuations in Lake Sevan water level, caused by changes in geological and climatic conditions, have inevitably led to changes in the flora surrounding the lake. The sediment record of Tsovinar-1 (Fig. 1) provides important evidence of natural changes in Lake Sevan water level during the Holocene. Our aim is to partially reconstruct this history and gain a better understanding of Lake Sevan's future development.

Between 1933 and 1960s, the lake level was lowered artificially by

---

* Corresponding author.
E-mail address: narine.hayrapetyan1993@gmail.com (N. Hayrapetyan).

https://doi.org/10.1016/j.quaint.2023.03.013
Received 14 December 2022; Received in revised form 8 March 2023; Accepted 11 March 2023

about 18 m, from originally 1916 m a.s.l., as a result of intermittently increasing lake outflow for irrigation and hydroelectric power generation (Hovhannisyan, 1994). Accordingly, there has been a reduction of the total lake surface area by 12%, the average depth was lowered by 34.2% and the lake volume by 42.2% (Deheryan, 2005). As a result of those artificial changes of the lake level, various Holocene deposits and lakeshore terraces are now exposed in the basin (Sayadyan, 2000), and became informative sources for paleoenvironmental reconstructions.

Especially, the fluctuations of Lake Sevan water level during the late Holocene have been investigated in multiple studies based on the research of geology, archaeology, fossil pollen and mollusks in the area (e.g., Sayadyan, 2000, 2009; Leroyer et al., 2016; Gorbatov et al., 2019). For example, Sayadyan (2000) studied lake terraces and distinguished four natural regressive/transgressive phases in the history of Lake Sevan over the past ten thousand years. Moreover, Leroyer et al. (2016) reconstruct the Middle Holocene climatic history of the Sevan basin with its implications on lake level.

The Tsovinar-1 peatbog at the southern shore of Lake Sevan provides an excellent archive to study Holocene lake level changes and their relation to climate and anthropogenic influences. According to the map of morphogenetic types of relief (Kazakova, 1958), the modern Tsovinar-1 peatland is located on lake-alluvial accumulative terraced plains. The section Tsovinar-1 appears to be the best dated Holocene section in the region for now and is of major scientific interest as a paleoenvironmental archive. Here, well preserved fossil plant remains provide a great opportunity to reconstruct changes of the Lake Sevan shoreline due to the fact that the distribution of aquatic macrophytes in lakes often depends on water depth (Leira and Cantonati, 2008).

For that reason, in order to fully understand the fluctuations of the lake level and estimate the water cover at Tsovinar-1, we combine palynological and carpological data on fossil remains with a specific focus on aquatic and wetland plants, which can inform about past water depth and quality. For example, *Myriophyllum* sp. frequently grows at 1–6 m water depth, while the preferred habitat of *Ceratophyllum demersum* is at 2–3 m water depth, but it can occur up to 10 m depth (Gaillard and Birks, 2007). Also, such taxa as *Myriophyllum* sp., *Ceratophyllum* sp., and *Persicaria amphibia* could inform about the level of eutrophication of the lake. *P. amphibia* is relatively tolerant to pollution and increasing eutrophication and it is often one of the last aquatic macrophytes to survive (Partridge, 2001; Gaillard and Birks, 2007).

The combination of data from macro and micro plant remains in our study offers the unique possibility to detect Sevan lake level fluctuations over the Middle to Late Holocene in high temporal resolution.

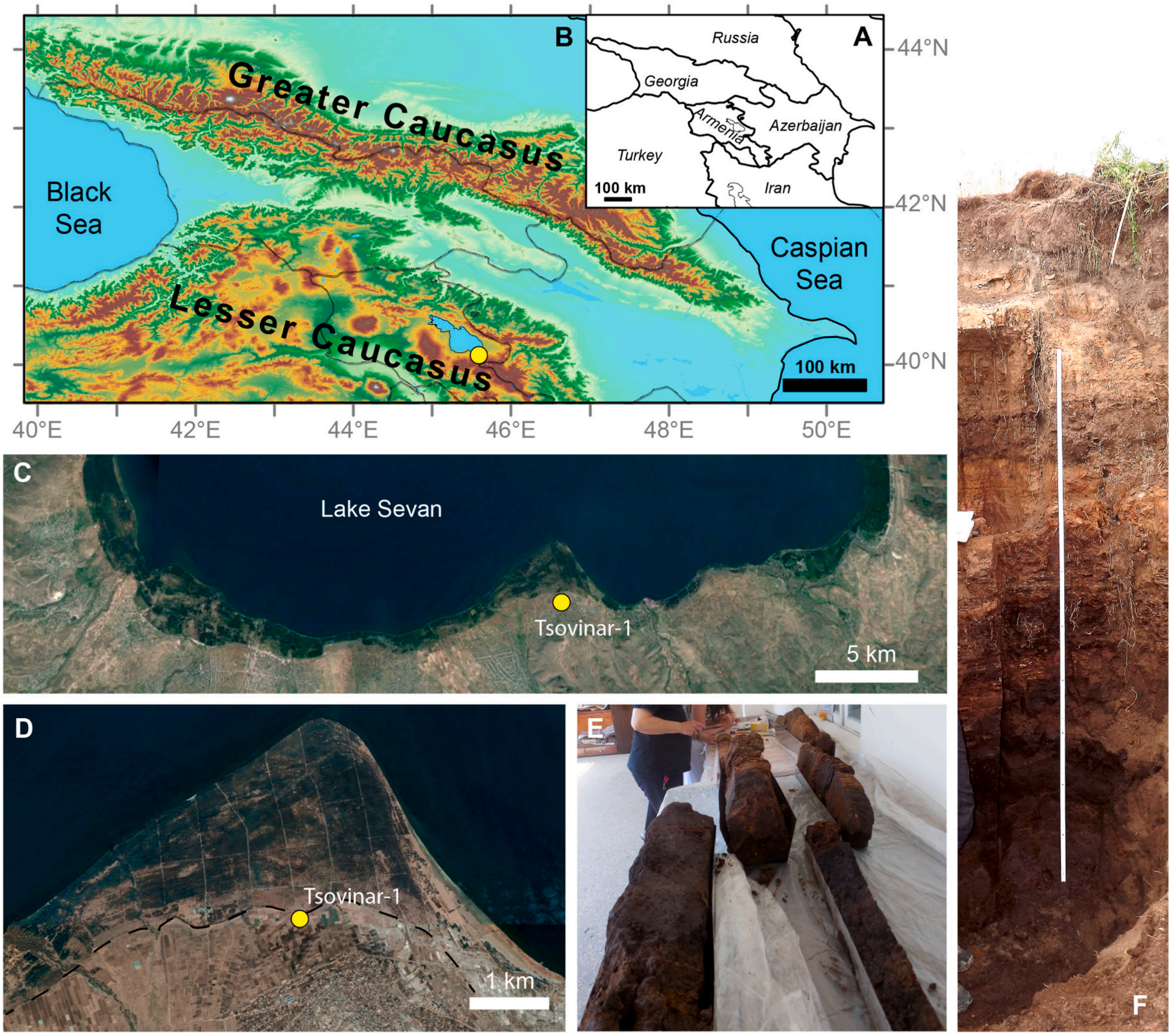

Fig. 1. Geographic position of the study site Tsovinar-1 (yellow dot) in Armenia south of Lake Sevan. A – Political boundaries in the Caucasus; B – Geographic overview of the Caucasus region; C – Southeastern shore of Lake Sevan (picture from Google Earth); D – Close-up of the study area with the location of Tsoviar-1 near the former shoreline (dashed line) before the artificial lowering of the lake level (picture from Google Earth); E – Sampling of Tsovinar-1 sediments in the Department of Paleobotany of A. Takhtajan Institute of Botany, Yerevan, Armenia (photo: A. Bruch); F – Outcrop of section Tsovinar-1, scale is 2 m (photo: I. Gabrielyan).

2. The Lake Sevan basin

2.1. Geological history

The Caucasus is part of the Alpine-Himalayan orogenic belt where the Eurasian and African-Arabian plates are still converging. In this context, the Sevan basin is an intramontane depression, which was part of the Eastern Paratethys during the Late Sarmatian (12.7−8.3 Ma) that started to regress from Meotian (8.3−6.04 Ma) and later formed the Black Sea and the Caspian Sea (Krijgsman et al., 2019). During the Pliocene, the rise of the Lesser Caucasus and the Armenian Highland caused a high level of volcanic activity in the region. As a result, the lake basin is mainly composed of lava and volcanic sediments from Pleistocene to Holocene ages (Wilkinson, 2020). Although the volcanoes in Armenia are not active anymore, there is still regular tectonic activity until today as expressed by the devastating 1988 earthquake in northern Armenia.

Lake Sevan itself developed, after a brackish phase since the Early Pliocene, into a freshwater lake at the end of the Pliocene. At the end of the Pleistocene, volcanic activity blocked the outflowing river paleo-Hrazdan and the modern lacustrine environment of Lake Sevan was established (Wilkinson, 2020).

2.2. Modern climatic characteristics

Today's climate in the vicinity of Lake Sevan is very contrasting. The region is characterized by a mountain climate with mild summers and extremely cold and snowy winters (Climate Handbook of the, 1966; 1969). According to the Köppen–Geiger climate classification system, the data collected from the Martuni meteorological station in the southern part of the lake (1991–2020, 30 years series) corresponds to the Dfb class, which is a cold climate with no dry seasons and warm summers (Peel et al., 2007). Seasons here are expressed very clearly. Winters are cold, and the average January temperature is about −4,6 °C, with a mean minimum temperature of −38 °C. The average July temperature is 17 °C (according Martuni meteorological station) and the maximum temperature is about 34 °C (Vardanyan, 2007). Water temperatures of Lake Sevan reach 18−19 °C in July and August, and in some protected places up to 20−22 °C (Gabrielyan, 1978).

Most of the precipitation is provided during spring, partly in autumn, and originates from the North Atlantic transported by the Westerlies (Berg, 1950). The lowest number of cloudy days in Armenia (20−25 days) is observed in the southern part of Lake Sevan basin (Climate Handbook of the, 1968). Mean annual precipitation ranges from 540 mm (according Martuni meteorological station) at the western, southern and south-eastern shore of the lake to 1000 mm in the mountains (Vardanyan, 2007).

2.3. Flora and vegetation

The diversity of landscapes is striking, due to the rugged relief and the diversity of elevation (Babayan et al., 2003). The flora of the Sevan basin is rich and typical for the Armenian Highlands, which are located at an altitude of 1900–3600 m a.s.l. (Afrikyan, 1987). The Sevan hydrological catchment area covers the Sevan and Areguni floristic regions Sevan (Fayvush and Aleksanyan, 2016). The vegetation of these floristic regions is represented mainly by steppes, meadow-steppes and meadows. Only on the northeastern coast of the lake also residual oak forests and juniper woodlands occur (Tamanyan and Fayvush, 2009). Aquatic vegetation is abundantly developed in shallow coves, bogs and ponds. In Lake Sevan, aquatic vascular plants like *Ceratophyllum* sp., *Potamogeton* sp., *Myriophyllum* sp. are ample to depths of 2–5 m (Babayan et al., 2003; Avetisyan, 1973).

After the artificial lowering of the water level, the dried-up areas of the former lake bottom have been forested by alien plant species, which form the largest artificial woodland of the country. These forests consist of pine (*Pinus caucasica*), acacia (*Caragana brevispina*, *Caragana trutex*), poplar (*Populus canadensis*, *Populus simonii*), and willow (*Salix viminalis*). Also, sea buckthorn *(Hippophae rhamnoides*) forms impenetrable bushes (Garibyan, 2007).

3. Material and methods

3.1. Sampling

The section Tsovinar-1 (N 40.166, E 045.459) is located south of Lake Sevan (Fig. 1), 3 km from the modern shoreline and some 100 m south of the pre-1930 shore (before the artificial lowering of Sevan lake level). The elevation of the section was measured to be approximately 17 m higher than the current lake level. Besides several GPS measurements also the altitude of the site in relation to the pre-1930 coastline was estimated in the field. The effects of erosion at the pre-1930 shore is clearly visible in the landscape as well as on the satellite images (Fig. 1D). Field work was conducted in June 2017, when a 3 m thick sequence of peat bog sediment was dug out. The whole section was measured and 18 sediment layers visually described in the field.

For palynology and dating purposes the exposed sediment has been sampled from the upper part of L3 to the lower part of L17 (from 77 to 270 cm profile depth) with three metallic boxes (66 cm × 7 cm x 6.5 cm) in overlapping sections. The uppermost layers L1 (top soil) and L2 (silty sand) as well as the lowermost part of the profile at the contact to layer L18 (sand with coarse gravel) have not been sampled. Thus, 193 cm of continuous sediment record could be recovered from the profile.

In the laboratory of the A. Takhtajan Institute of Botany, National Academy of Sciences of the Republic of Armenia, Yerevan, the three sediment sections were correlated based on the corresponding sediments. A detailed description of the combined sequence together with field observations provided the full sedimentary succession as given in Table 1 and Fig. 2. From this material ten samples were taken for AMS ^{14}C dating and sent to Leibniz Laboratory for Radiometric Dating and Stable Isotope Research at Christian-Albrechts-University, Kiel, Germany. Subsequently, for pollen and NPP analyses, continuous sampling took place from the sediment in the boxes between 77 and 270 cm profile depth, resulting in 198 individual palynological samples of maximum one cm thickness each.

For the analysis of carpological fossils, samples were taken in the field following the lithology of the described sedimentary layers (Fig. 2).

Table 1
Description of the sedimentary sequence of Tsovinar-1.

Profile depth (cm)	Layer	Thickness of layer (cm)	Sediment description
1–40	L1	40	modern soil
40–65	L2	25	light grey silty sand
65–95	L3	30	light grey sandy clay
95–108	L4	13	dark brown peat
108–117	L5	9	brown peaty clay
117–127	L6	10	light brown peaty clay
127–141	L7	14	reddish brown peaty clay
141–166	L8	25	dark brown laminated clayish peat
166–186	L9	20	dark brown laminated peat, hard, brittle, with lots of roots
186–195	L10	9	dark brown laminated clayish peat with layers of white mineral deposits
195–200	L11	5	reddish brown (weathered) clayish peat
200–211	L12	11	dark brown clayish peat
211–216	L13	5	reddish brown (weathered) clayish peat
216–226	L14	10	black peaty clay
226–236	L15	10	dark brown peaty clay
236–256	L16	20	dark grey peaty clay
256–281	L17	25	light grey sandy clay
end of profile	L18		grey sand with coarse gravel

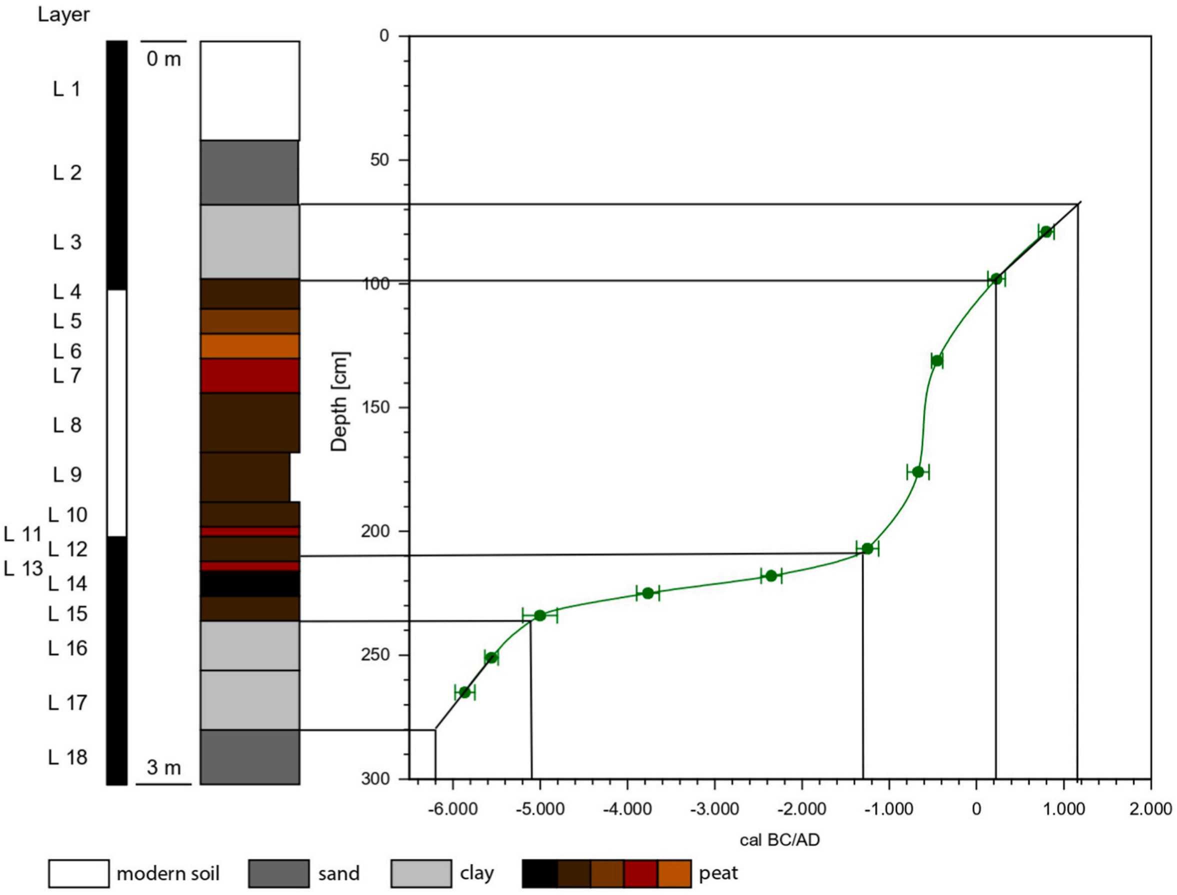

Fig. 2. Sedimentary sequence of Tsovinar-1 with age model showing severe changes in sedimentation rates during peat formation. The interpolation of ages is based on acima spline. Extrapolation beyond ^{14}C dates is linear. For details of the sediment description of layers see Table 1. Grey colors refer to clayish sediments, brownish colors to peat. The variation of peat from black to brown to red is due to differences in iron and carbon content. Results of AMS ^{14}C dating is given in Table 2.

Layers with a thickness less than 15 cm were sampled separately, while thicker layers were split in two levels. The samples were named in alphabetical order from A (top) to T (bottom). One additional sample was taken later on top of sample A, and named –A (Table 3). Due to some inconsistency between field observation and lithological description in the laboratory, one sample (sample R) covers the boundary between Layers 16 and 17. In total, the profile part from L3 to L17 provided 21 carpological samples which cover sediment thicknesses between 5 and 14 cm (average 9.8 cm).

All samples were stored in plastic bags with some drops of phenol (C_6H_6O) added for avoiding fungal contamination and kept in a cold environment until processing.

3.2. Palynological analysis

Palynological material was processed in the Laboratory of the Georgian National Museum in Tbilisi. First, a portion of about 20 g of sediment were weighted and boiled in 10% potassium hydroxide solution (KOH). After boiling, the samples were washed with distilled water and passed through a 100 μm sieve and left for 24 h. With the next step the samples were washed 3 times and dehydrated. Then, the residue was centrifuged in heavy liquid (KJ and CdJ_2) to separate organic remnants from minerals (Grichuk, 1948). The samples were washed and dehydrated again before acetolysis after Erdtman (1966) was performed by putting the samples in a $+80$ °C water bath for 3−4 min, adding a solution made of 6 parts of acetic anhydride ($(CH_3CO)_2O$) and 1 part of concentrated sulfuric acid (H_2SO_4). After dehydrating and washing again, 2−3 drops of glycerin-water (80% glycerol, 20% water) have been added to each sample for final storage in test tubes. During this process one tablet of *Lycopodium clavatum* marker spores was added to each sample to later enable the calculation of pollen concentrations.

For each sample, one full slide was counted under an Olympus SC50 microscope. To identify pollen grains and plant spores, atlases of modern pollen and spores were used (Reille, 1992, 1998; Beug, 2004; Kupriyanova and Alyoshina, 1972, 1978), as well as modern reference collections of pollen and spores at Senckenberg Research Station of Quaternary Paleontology, Weimar, Germany, and Georgian National Museum, Tbilisi. NPP remains of *Ceratophyllum* sp. (NPP taxon HdV-137) were determined after Pals et al. (1980).

3.3. Paleocarpological analysis

Two methods were used for paleocarpological analysis. The method of Nikitin (1969) is primarily employed for small amounts of sediment and enables the detection of all organic residues present in the sediment, especially in densely decomposed peat. The method of Martinetto (2001), on the other hand, is ideal for processing large volumes of samples and has a shorter processing time. To gain a maximum of information from the material, the two complementary methods of processing were applied here.

Following Nikitin (1969), 330 g portions were taken from the samples and were soaked in 10% sodium bicarbonate solution for disaggregation for a day. Portions were boiled with the same solution for 40 min and wet sieved. Wet sieving was carried out with a water jet and four different mesh sizes of 125 μm, 250 μm, 1 mm, and 2 mm, arranged in a sequence on top of one another. The fractionated sediments were left at room temperature for drying.

In parallel, following Martinetto (2001), dried samples of 1–2 kg were divided by hand into small particles and placed in a bucket. A 3% hydrogen peroxide (H_2O_2) solution slowly was added to the bucket until it covered the whole sample and left until the reaction stopped. Then, an additional portion of water was added and mixed. Seeds and fruits that were floating on the surface of the water were collected with a fabric sieve of 0.3 mm mesh size. The remaining material was sieved with a fabric sieve of 1.5 mm mesh size. Finally, the fabric sieves were folded with the washed remnants inside and left to dry at room temperature.

All the different fractions of dry residues of each sample were examined under an Olympus SZX16 stereomicroscope for the collection of plant macro remains. Carpological identifications are based on Flora of Armenia (Avetisyan and Shishikyan, 1956) and paleocarpological atlases such as Katz et al. (1965) and Velichkevich and Zastawniak (2008). Comparative material was available in the modern seed collection at A. Takhtajan Institute of Botany, National Academy of Sciences of the Republic of Armenia, Yerevan, and Nikitin's paleocarpological collection at Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg. In the frame of this study, from the paleocarpological analysis only data on aquatic vascular plants of the genus *Ceratophyllum* is considered.

3.4. Diagram

Palynological and carpological data sets were visualized with the Tilia program, version 1.7.16 (Grimm, 2011). The pollen diagram is based on percentage values relative to the number of pollen and plant spores counted to represent the full spectrum of past vegetation. After applying a cluster analysis (CONNIS) to the data (Grimm, 2011), the resulting clusters were used to define pollen zones, however slightly adjusted with a focus on water plants according to our aim to reconstruct lake level history.

The diagram of the fossil representation of *Ceratophyllum* fruits and spines, aquatic and wetland plants of the palynological assemblages shows concentrations of fossils per sediment weight. Concentrations of micro remains per gram sediment were calculated based on the number of counted *Lycopodium clavatum* spores. Similarly, the concentration of macro remains has been calculated by dividing the number of *Ceratophyllum* fruits in one assemblage by the weight (in kg) of the corresponding sample.

4. Results

4.1. Dating and age model

The results of AMS ^{14}C dating (Table 2) show no reversions and indicate an overall reliability. Based on those dates an age model was calculated using Akima-spline interpolation with the software Xact 8. This interpolation was considered for the sedimentary succession between samples A2 and A6. In the upper and lower part of the profile, beyond sample A2 and A6, respectively, the age model is based on linear extrapolation. All ages, times or time spans given in this study refer to the proposed age model and are given as dates AD/BC with an estimated mean error of about ±100 years. An additional error may be caused by reservoir effects due to intermixture of lake sediments including older carbon or the uptake of dissolved inorganic carbon from the lake water by aquatic plants or, on the other hand, contamination by roots introducing young carbon into the sample. However, those opposing effects cannot be quantified. Lithology and age model are represented in Fig. 2, showing significant changes in sedimentation rates. Especially during the phase of peat formation, sedimentation rates vary considerably, reaching from as high as 5 mm/a (2 a/cm) in L8 to a minimum of 0.05 mm/a (200 a/cm) in L14. In the sandy parts of the succession, which were subjected to linear interpolation to estimate ages, sedimentation rates result in medium values from 0.5 mm/a (20 a/cm in L17) to 0.33

Table 2

Results of AMS ^{14}C dating provided by Leibniz Laboratory for Radiometric Dating and Stable Isotope Research at Christian-Albrechts-University, Kiel, Germany. Dates (95.4% range) calibrated with OxCal v4.4.4 (Ramsey, 2009) and IntCal20 (Reimer et al., 2020).

Sample	Sampling point	Depth (cm)	Layer	Lab. no.	Sediment	Radiocarbon Age (BP)	Calibrated date BC/AD	
							from	to
A1	16 cm above L3/L4 boundary	79	L3	KIA-52219	Mud, soil, sediment/Alkali Residue	1206 ± 23	710	888
A2	3 cm below L3/L4 boundary	98	L4	KIA-52220	Peat/Alkali Residue	1814 ± 27	131	330
A3	4 cm below L6/L7 boundary	131	L7	KIA-52221	Mud, soil, sediment/Alkali Residue	2357 ± 28	−517	−386
A4	10 cm below L8/L9 boundary	176	L9	KIA-52222	Peat/Alkali Residue	2534 ± 29	795	−546
A5	3.5 cm above L12/L13 boundary	207	L12	KIA-52223	Peat/Alkali Residue	2993 ± 29	−1376	−1123
P141	resampled from pollen sample	218	L14	KIA-52716	Mud, soil, sediment/Alkali Residue	3900 ± 35 BP	−2471	−2236
P150	resampled from pollen sample	225	L14	KIA-52717	Mud, soil, sediment/Alkali Residue	4935 ± 45	−3895	−3637
P159	resampled from pollen sample	234	L15	KIA-52718	Mud, soil, sediment/Alkali Residue	6045 ± 40	−5198	−4805
A6	5 cm above L16/L17 boundary	251	L16	KIA-52224	Mud, soil, sediment/Alkali Residue	6655 ± 35	−5636	−5483
A7	9 cm below L16/L17 boundary	265	L17	KIA-52225	Mud, soil, sediment/Alkali Residue	6975 ± 35	−5977	−5751

Table 3

Occurrences of *Ceratophyllum* fruits in succession of Tsovinar-1 with ages of the upper and lower boundaries for each sample according to the age model (Fig. 2).

Sample	Layer	*Ceratophyllum demersum*	*Ceratatophyllum submersum*	*C. demersum* var. *platyacanthum*	*Ceratophyllum* ssp.	date of upper boundary (cal BC/AD)	date of lower boundary (cal BC/AD)
-A	L3	1				918.7	619.5
A	L3	4				619.5	320.3
B	L4	115				320.3	−17.9
C	L5	5	2			−17.9	−211.5
D	L6				3	−211.5	−390.9
E	L7		2	1		−390.9	−553.5
F	L8	2	12	8	2	−553.5	−602.6
G	L8		83	9		−602.6	−624.6
H	L9	1	9		1	−624.6	−670.5
I	L9		28			−670.5	−782.8
J	L10	74				−782.8	−948.3
K	L11	31				−948.3	−1063.5
L	L12	89				−1063.5	−1482.0
M	L13	22	4			−1482.0	−2055.5
N	L14	3	8			−2055.5	−3937.9
O	L15	1	2			−3937.9	−5093.1
P	L16					−5093.1	−5379.9
Q	L16				1	−5379.9	−5581.3
R	L16/ L17		2		2	−5581.3	−5777.0
S	L17					−5777.0	−5994.5
T	L17					−5994.5	−6212.0

mm/a (30 a/cm in L3). Those sedimentation rates are partly higher but overall, very similar to the ones calculated by Leroyer et al. (2016) for a nearby Middle Holocene peat section.

4.2. Palynological results

Pollen analysis so far revealed 91 taxa of higher vascular plants. From those taxa, ten have been determined to species level, and 55 to genera (Fig. 3). The others have been identified at family level. From 91 taxa 25 are trees and shrubs, 54 are herbaceous plants, 10 are aquatic (Fig. 4) and sedge plants, and two taxa are ferns. A total of 128 thousand pollen grains and plant spores were counted with an average sum of 646 grains per sample (between 26 and 3672 grains). Out of 198 samples 14 provided less than 100 grains. Seven main pollen zones (PZ) were distinguished.

Pollen zone 1. This zone corresponds to the time from ca. 6000–5000 BC (235−269 cm profile depth). Arboreal taxa in this zone are quite rich. *Betula* sp. and *Quercus* sp. are dominant woody taxa, but *Pinus* sp., *Carpinus* sp., *Fagus orientalis*, *Juniperus* sp., *Juglans regia* also occur. Poaceae, Cyperaceae, Chenopodiaceae, Asteraceae dominate the herbaceous group. There is also pollen from Polygonaceae, Apiaceae, Caryophyllaceae and domesticated cereals. Pollen of aquatic plants is rare in this zone. However, pollen of hygrophilous taxa *Sparganium* sp. and *Typha* sp. is noticed. In general, in PZ 1, 20% of the pollen counts represent arboreal taxa, 70% are herbs and 10% are plant spores (Fig. 3).

Pollen zone 2. The second pollen zone (235−227 cm profile depth, ca. 5000−4000 BC) is characterized by low numbers of pollen, but high taxonomic diversity. Almost all arboreal taxa represented in the whole succession are present here, as well as all taxa of herbs and aquatic plants. Among arboreal taxa, dominant species are *Pinus* sp., *Carpinus* sp., *Betula* sp., *Quercus* sp., and *Tilia* sp. Poaceae, Cyperaceae, Chenopodiaceae, Polygonaceae, Apiaceae, Asteraceae, *Persicaria amphibia*, and *Plantago* sp. constitute the major part of herbs. Pollen of *Sparganium* sp., *Typha* sp., and *Myriophyllum* sp. is more abundant than pollen from other aquatic plants (Fig. 3).

Pollen zone 3. This zone (227−219 cm profile depth, ca. 4000−2600 BC) demonstrates a significant decrease of pollen. It is distinguished by the lowest number of taxa. From woody plants, pollen of *Pinus* sp. dominates the assemblage. *Juniperus* sp., *Quercus* sp., and *Tilia* sp. are observed in small quantities. The herbaceous group is dominated by Poaceae, Chenopodiaceae, Apiaceae. Chenopodiaceae, Apiaceae, Polygonaceae, and *Plantago* sp. are at their peak in the spectrum. Cyperaceae are found in small numbers. Aquatic plants are even less common than in other layers. *Potamogeton* sp. is almost absent from this layer (Fig. 3).

Pollen zone 4. This zone (219−213 cm profile depth, ca. 2600−1700 BC) is similar to PZ 3 and characterized by a rather rich composition of pollen of herbaceous plants. The total abundance of pollen of woody plants is 5–10%. There is a small amount of *Pinus* sp., *Juniperus* sp., and *Quercus* sp. Herbaceous vegetation is dominated by wild cereals (Poaceae) and sedges (Cyperaceae). The number of Apiaceae sharply decreases in this zone, instead the number of *Artemisia* sp. increases. The abundance of aquatic taxa increases compared to PZ 3. Dominant species are *Sparganium* sp., *Typha* sp., and *Myriophyllum* sp. (Fig. 3).

Pollen zone 5. Almost all plants listed above are reflected in the pollen spectrum of PZ 5 (213−193 cm profile depth, ca. 1700−900 BC). In this zone, the number of woody taxa increases sharply to about 10–15% and is dominated by *Carpinus* sp., *Quercus* sp., and *Pinus* sp. Herbaceous taxa are Poaceae, Asteraceae, Chenopodiaceae, *Artemisia* sp. In this zone, *Myriophyllum* sp. and Cyperaceae reaches the peak in abundance (Fig. 3).

Pollen zone 6. The zone of 193−112 cm profile depth (ca. 900−100 BC) shows a dominance of *Pinus* sp., *Carpinus* sp., *Quercus* sp., and significant amounts of pollen of *Juniperus* sp., *Betula* sp., and *Ulmus* sp. from woody plants. Abundances of pollen from Cyperaceae, *Sparganium* sp., and *Typha* sp. increase in comparison to PZ 5. In this zone, plant spores (Pteridophytes), pollen of sedges (Cyperaceae) and of shallow water plants (*Menyanthes trifoliata*, *Sparganium* sp., and *Typha* sp.) reach their peak in abundance, which is for Pteridophytes up to 40%. Furthermore, the amount of pollen of *Myriophyllum* sp. decreases sharply. The composition and abundances of herbaceous plants are almost the same as in PZ 5 and PZ 7 (Fig. 3).

Pollen zone 7. This pollen zone (112−77 cm profile depth, ca. 100 BC to 900 AD) is distinguished by a rich composition of pollen. *Pinus* sp. dominates the arboreal taxa. Pollen of *Carpinus* sp., *Quercus* sp., and *Fagus* sp. is quite common. Also, *Vitis vinifera* subsp. *sylvestris* is frequent. Among the pollen of herbaceous vegetation, pollen of the families Poaceae, Cyperaceae, Chenopodiaceae, and Asteraceae dominate. From higher aquatic plants, pollen of *Typha* sp., *Sparganium* sp., *Potamogeton* sp., and *Myriophyllum* sp. occur (Fig. 3).

Besides pollen and plant spore analysis, the palynological samples were additionally scanned with a focus on NPP remains of *Ceratophyllum* sp. This led to a total count of 4140 spines of *Ceratophyllum* sp. Most of them (620 spines) come from layer L8 (142−166 cm profile depth, ca.

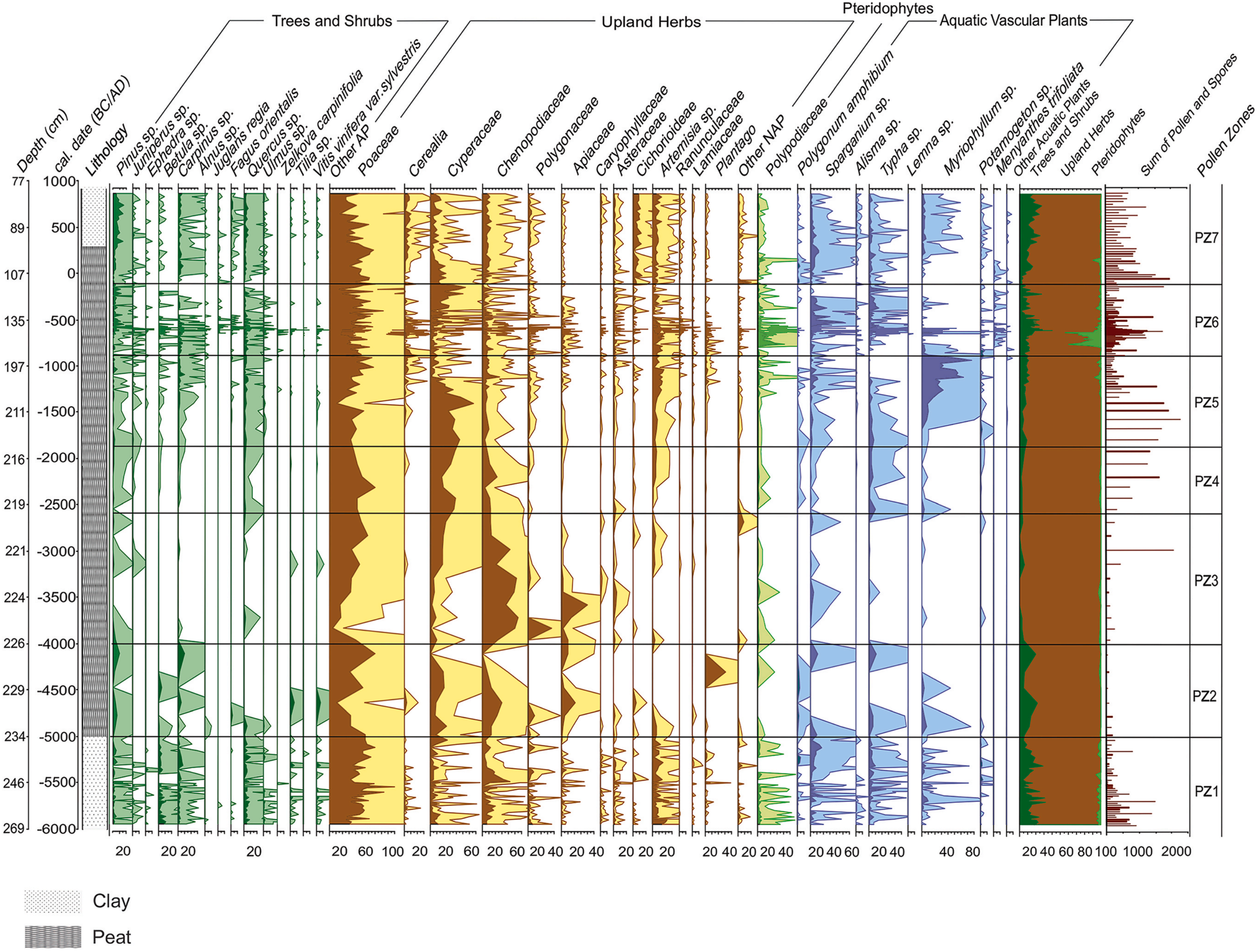

Fig. 3. Pollen diagram of Tsovinar-1 with abundances (%) relative to the total sum of pollen and plant spores. Data are plotted versus age. Profile depths are given as additional information but are not to scale due to the highly variable sedimentation rates. Lithology is simplified. Data are presented as original and with 5x exaggeration, except for 'Other AP' (15x) and 'Other AQVP' (10x). 'Other AP' includes *Abies* sp., *Picea* sp., *Hippophae* sp., *Salix* sp., Rhamnaceae, *Corylus* sp., *Hedera helix*, 'Other NAP' includes *Carduus* sp., *Pimpinella* sp., *Turgenia* sp., *Eryngium* sp., *Astrantia* sp., *Apium* sp., *Achillea* sp., *Centaurea* sp., *Xanthium* sp., *Serratula* sp., *Tanacetum* sp., *Taraxacum* sp., Brassicaceae, *Armeria* sp., Onagraceae, Saxifragaceae, Fabaceae, *Helianthemum* sp., Dipsacaceae, *Scabiosa* sp., *Knautia* sp., *Cephalaria* sp., *Geranium* sp., *Convolvulus* sp., *Valeriana* sp., Lamiaceae, Boraginaceae, *Campanula* sp., *Euphorbia* sp., *Rumex* sp., *Polygonum persicaria*, Rosaceae, Liliales, *Sanguisorba minor*, 'Other AQVP' includes *Nymphaea alba* and *Utricularia* sp.

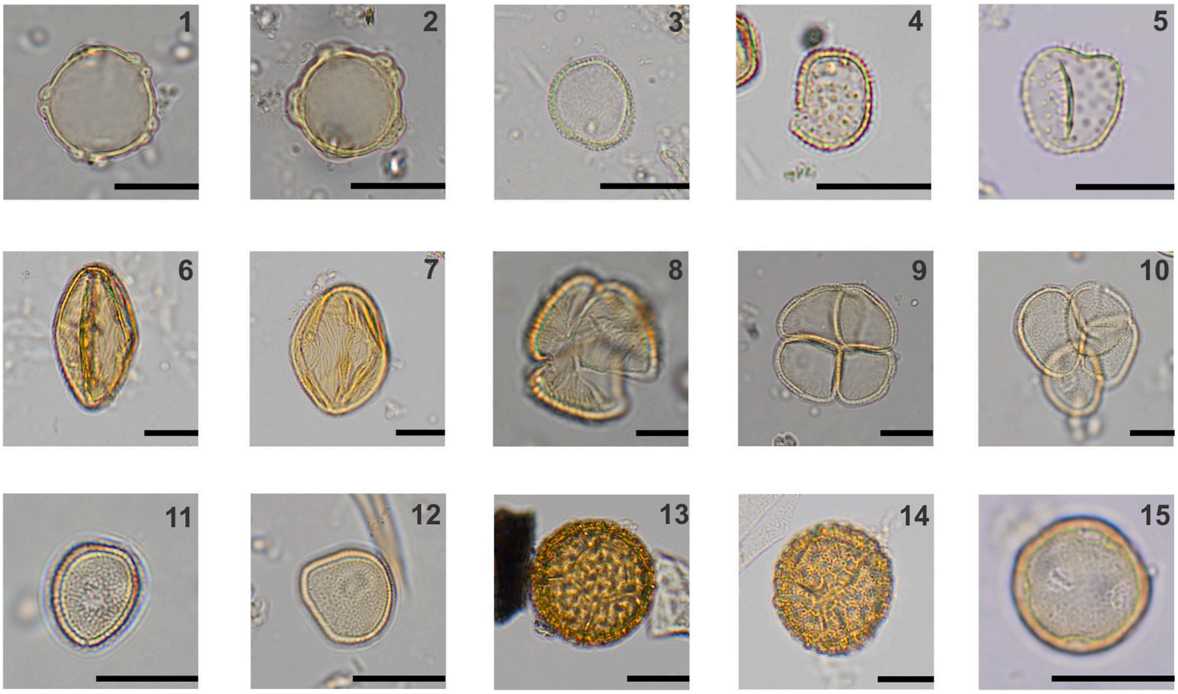

Fig. 4. Pollen of aquatic vascular plants from Tsovinar-1: 1–2 *Myriophyllum* sp., 3- *Potamogeton* sp., 4–5 *Lemna* sp., 6–8 *Menyanthes trifoliata*, 9–10 *Typha* sp., 11–12 *Sparganium* sp., 13–14 Persicaria *amphibi*a, 15- *Alisma* sp. Scale bar is 20 μm.

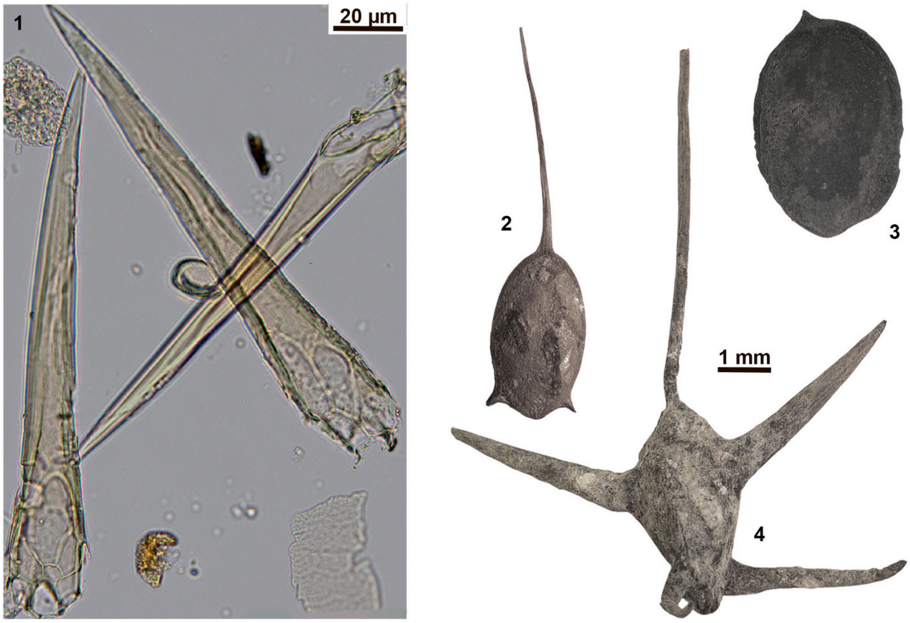

Fig. 5. *Ceratophyllum* remains (fruits and NPP) from Tsovinar-1: 1- spines of *Ceratophyllum* sp. in the NPP record, 2- *Ceratophyllum demersum*, 3- *Ceratophyllum submersum*, 4- *Ceratophyllum demersum* var. *platyacanthum*.

600–500 BC) (Figs. 5 and 6). The part of the profile from ca. 5941 to 2750 BC (236–220 cm profile depth) contains very few palynological remains of *Ceratophyllum* sp. From ca. 2750 to 600 BC, (220–164 cm profile depth) the number of spines gradually increases and reaches its maximum at ca. 600–550 BC (151–164 cm profile depth). The profile section from ca. 550 BC to 905 AD (106–77 cm profile depth) is again marked by somewhat lower, but still rather high abundances of spines of *Ceratophyllum* sp. (Fig. 6).

4.3. *Paleocarpological results*

Generally, 545 fruits of *Ceratophyllum* were recorded. Three taxa could be distinguished, such as *Ceratophyllum demersum*, *C. submersum*, and *C. platyacanthum* var. *pentacanthum*, which all are described below. The presence and abundances of fruits of the different species of *Ceratophyllum* vary throughout the succession (Fig. 5). The dominant species is *C. demersum* that is present nearly in all layers. Especially abundant is this species in sample B (layer L4, 95–108 cm profile depth, ca. 18 BC to 320 AD), but it is also common in the sediments of layers L10 to L13 (ca.

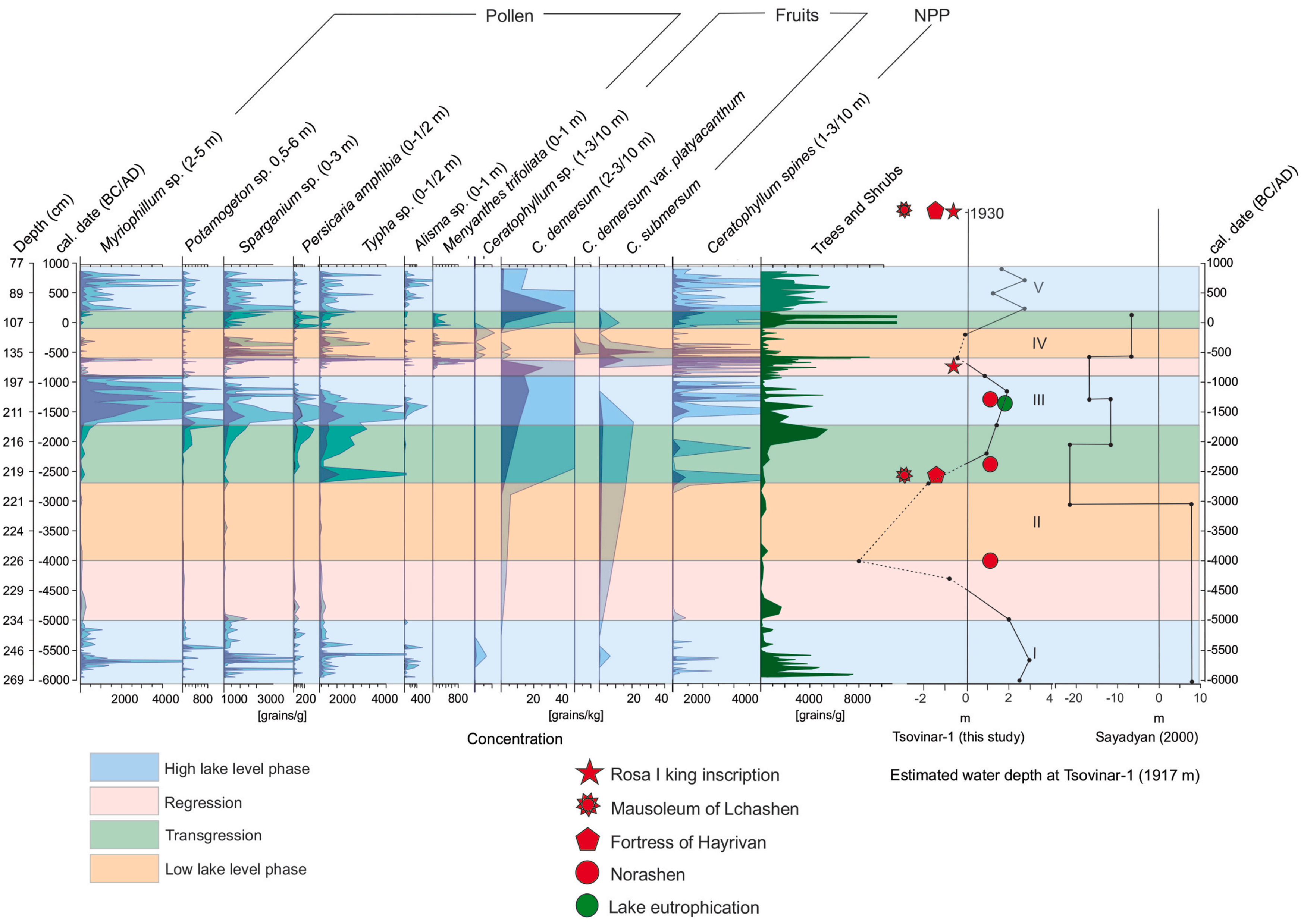

Fig. 6. Lake level phases of Lake Sevan indicated with Latin numbers as defined based on concentrations of palynomorphs of aquatic and wetland taxa and fruits of *Ceratophyllum* sp. in the fossil assemblages of Tsovinar-1. Concentrations given as fossils per sediment weight. The sum of relative abundances of trees and shrubs indicates forest expansion as a proxy for humidity. Water depth at the site of Tsovinar-1 is estimated according to the ecological requirements of the dominating aquatic plants. During the high lake level phase ca. 1700–900 BC eutrophication (green circle) is observed. The position of archaeological sites (red circles) mentioned in the text plot relative to the elevation of Tsovinar-1 (1917 m a.s.l.). If an archaeological site plots left of the water depth curve, this indicates that the respective site was covered by water at that time. Published data on lake terraces (Sayadyan, 2000) are adjusted in relation to the elevation at Tsovinar-1 (1917 m). While relative lake level changes roughly correspond, absolute changes seem to be overestimated by Sayadyan (2000). The ages may vary due to older dating techniques.

2055−783 BC). *C. submersum* occurs in highest amounts in sample G (154–166 cm profile depth, ca. 624−603 BC). This sample also shows a peak of occurrence of *C. demersum* var. *platyacanthum*, however in lower numbers. The lower part of the section is characterized by very low quantities of *Ceratophyllum* fruits, and the fossils were mostly not well preserved. On the other hand, the assemblages of samples B (95–108 cm profile depth) and G (154–166 cm profile depth) stand out with very high abundances of fruits of *Ceratophyllum* (Fig. 6). The assemblage of sample F (141–154 cm profile depth) stands out from other assemblages with its high diversity of *Ceratophyllum* species.

4.3.1. Ceratophyllum demersum L

Fruit size is 2.9–4.8 × 1.2–2.6 mm without spine; the shape is biconvex and elliptical. Fruit surface is smooth; the color is brown to completely black. The walls are thick and woody. Fossil fruit has spines; the apical spine is longer than two basal spines. Apical spine at base is stronger and more flattened; it is longer than the length of the fruit. If the apical spine is completely preserved at the tip, it has a spiral twisting and size is 5–8.4 mm. Basal spines are located on both sides of the base; sometimes those create a flattened area. Basal spines are shorter and thinner compared with the apical one, however sometimes basal and apical spines can be almost equal (Fig. 5).

This species is widespread, more or less cosmopolitan. It is distributed all over Europe, the Mediterranean area, Caucasus, Middle East and Siberia (Velichkevich and Zastawniak, 2008). *C. demersum* is a perennial submerged plant. It exists without roots; it grows near to the bottom of streams, lakes and ponds, attached to the sediment with modified leaves. This species can be an important component in eutrophic lakes and reservoirs (Ejankowski and Solis, 2015). *C. demersum* sometimes can reach up to 10 m water depth (Gaillard and Birks, 2007). It can be found in steep or deep parts of the littoral zone. However, the species has its optimal habitat in 2–3 m of water depth (Nagengast and Gabka, 2016).

4.3.2. Ceratatophyllum submersum L

The size varies between 3.0–6.1 × 1.8–3.7 mm, and the fruit is biconvex and elliptical, near the base sometimes a little enlarged and flattened. The fruit is without basal spines, color varies between dark brown to black. The walls are robust, woody. Fruit has an apical short spine; apex is asymmetrically rounded, deformed in one way. The surface is smooth with wrinkles or covered with small spikes (Fig. 5).

The distribution area of *C. submersum* includes Europe, North Africa and parts of central Africa, Caucasus, Turkmenistan, Uzbekistan, Kazakhstan, western Siberia (Takhtajan, 1954; Lansdown, 2017). It is a floating submerged, non-rooted plant, which forms rhizomes. This species is distributed in shallow ponds and deep lakes, but it has a high abundance especially in shallow waters of less than 0.5 m (Nagengast and Gabka, 2016).

4.3.3. Ceratophyllum demersum var. platyacanthum (Haynald) P.Fourn

Fruit has 2.9–4.0 × 2.0–2.8 mm size, is biconvex, elongated and elliptical, margins subacute. The color is light or dark brown and matt. Basal spine is two times longer than fruit and size is 6.5–7.0 mm; apical spines are much shorter, 2.5–3.0 mm long, and have the same thickness. On both sides of the fruit robust and thick facial spines are located that are 3.0–4.0 mm long. Fruit surface is lined and celled; cells are smaller near to the base.

This species is distributed in Europe, the Far East of Russia, Japan, Korea, and China. *Ceratophyllum demersum* var. *platyacanthum* has very local communities. It grows in ponds and streams (Dezhi and Les, 2001; Velichkevich and Zastawniak, 2008), mainly in shallow (≤0.5 m) waters (Csiky et al., 2010). The species is not reported in the Flora of Armenia (Takhtajan, 1954), but its fossils have been found in samples E, F, and G (ca. 624− 390 BC) of the Tsovinar-1 peat section (Fig. 5).

5. Discussion

The macro and micro plant remains from Tsovinar-1 section provide rich information on the past environment in the Sevan basin, on vegetation and climate, but also on lake level changes which is the main focus of this study. On one hand, mesophytic plant taxa documented in the fossil record of Tsovinar-1 tell about vegetation cover of the landscape. In the Sevan basin, woody vegetation generally is related to more humid, milder climatic conditions, while open and steppe vegetation develop under more arid and colder climates (Joannin et al., 2014; Gorbatov et al., 2019).

On the other hand, the ecological requirements of aquatic taxa occurring in the Tsovinar-1 succession reveal details on the lake itself. The main factors to influence the structure and composition of aquatic vegetation in the lake are depth (Hannon and Gaillard, 1997) and temperature of the water (Gaillard and Birks, 2007), but also water chemistry and nutrients (Scheffer et al., 1993). Characteristic taxa pointing to deeper water at Tsovinar-1 are *Ceratophyllum demersum*, *Myriophyllum* sp., and *Potamogeton* sp. *Myriophyllum* sp. can grow at water depths of up to 5 m, *Potamogeton* sp. up to 6 m, and *C. demersum* even up to 10 m (Gaillard and Birks, 2007; Hannon and Gaillard, 1997). However, the preferred habitats for both, *C. demersum* and *Myriophyllum* sp., is at 2−3 m water depth (Keast, 2011; Aiken et al., 1979; Nagengast and Gabka, 2016) (Fig. 4). Plants that indicate shallow but permanent water are *Sparganium* sp. (0–3 m), *Nymphaea alba* (0–3 m, optimum at 1−1.5 m), and *Utricularia* sp. (0–1 m) (Gaillard and Birks, 2007). Also, *Persicaria amphibia* grows in stagnant or slowly flowing waters up to 2 m with an optimum at 0−1 m (Avetisyan, 1956; Gaillard and Birks, 2007; Kurbatova et al., 2013) (Fig. 4).

Some plants can grow in fluctuating shallow water also at places where the water temporarily recedes which makes these species a good proxy for the location of the shoreline. From the fossil record of Tsovinar-1 such taxa are *Alisma* sp. (0−1 m) which grows in stagnant waters, wet and swampy places (Gabrielyan, 2001), *Typha* sp. (0−1 m) occupying in damp marshy habitats and lakes (Khanjyan, 2001), and *Lemna* sp. (0−1.5 m) which can also grow on wet organic rich soils (Van den Berg et al., 2015). *Menyanthes trifoliata* (0−1 m) prefers peatland environments and is a good indicator of rich fens. It can quickly colonize newly open land at lake margins and therefore can be a good indicator for regression (Thompson et al., 1998; Smith et al., 2007). Also, *Ceratophyllum submersum* grows at shallow or fluctuating water levels. It is more thermophilous than C. *demersum* and prefers water rich in nutrients (Nagengast and Gabka, 2016) (Figs. 4 and 5).

However, shallow water plants generally are not perfect indicators of the changes lake level because they grow at the coast line and their pollen can easily accumulate by wind and water in the lake sediments also during high lake level phases. Especially *Typha* produces large amounts of pollen grains (Ahee et al., 2015). On the other hand, according to Barseghyan (1990), *Ceratophyllum* occurs in Lake Sevan in areas with specific micro-conditions of low wave activity, such as bays and gulfs. This suggests only minor transport distances and similarly calm conditions if fruit abundance of *Ceratophyllum* is high. Still, in combination the ecological requirements of the aquatic plants determined from the Tsovinar-1 succession give a consistent picture of lake level fluctuations (Fig. 6).

For establishing temporal changes of the lake level, not only the ecology of aquatic plants and climatic implications from the fossil flora, but also archaeological evidence and geological data from lake deposits can act as trustworthy sources of information. Combining those data allows for estimating water depths and distinguishing five phases of lake level.

5.1. High Lake level phase I and subsequent regression (ca. 6000−4000 BC)

According to our data, between about 6000 and 5000 BC, the diverse arboreal pollen assemblages from Tsovinar-1 were dominated by mesotherm oaks (*Quercus* sp.) combined with a large amount of other deciduous (*Carpinus* sp., *Ulmus* sp.) and conifer (*Pinus* sp., *Juniperus* sp., *Ephedra* sp.) woody plants. Nevertheless, the abundance of herbaceous taxa (such as Poaceae, Chenopodiaceae, and Asteraceae) is high as well. This suggests that the landscape surrounding Lake Sevan was covered by a fair amount of trees in a relatively open environment. Poaceae seem to be part of this mosaic vegetation rather than part of the wetland during this time. From ca. 5000 BC onwards, the extent of forests started to decrease demonstrating a reduction of humidity (Fig. 3).

Locally, the site of Tsovinar-1 was covered by water. A peak of pollen of *Myriophyllum* sp. at ca. 5700 BC implies a considerably high-water level. At the same time high abundances of *Sparganium* sp. confine the water depth to a maximum of 3 m. From ca. 5000 BC the abundances of *Myriophyllum* sp., *Potamogeton* sp., and *Ceratophylllum* sp. decrease and indicate a regression, which lasted at least until ca. 4000 BC (Fig. 6).

This lake level phase (ca. 6000−4000 BC) falls into the Northgrippian (Walker et al., 2012) climatic optimum (6286−2300 BC, 8236−4250 BC), which is characterized by warm and humid climate (Gorbatov et al., 2019; Sayadyan, 2000; Shatilova et al., 2011). According to palynological data of Tumanyan (1971), the natural forests in the Sevan basin have started to spread since the end of the early Holocene (about 6000 BC) due to increased humidity and reached their maximum extent during the Middle Holocene (Northgrippian). These forests were dominated by broad-leaved trees, in particular oak (*Quercus* sp.). Also pollen data of Leroyer et al. (2016) confirmed increased annual precipitation after ca. 5750 BC (7700 cal. BP) in the Sevan basin. This increase in precipitation is recorded all over the South Caucasus in the rapid spread of forests at that time (Connor and Kvavadze, 2008, 2004; Kvavadze et al., 2007). Also, the occurrence of thermophilous species increased significantly in the region as a result of warmer climate (Shatilova et al., 2011; Kvavadze and Rukhadze, 1989). Therefore, not only higher precipitation, but also the melting of glaciers severely contributed to the rising level of Lake Sevan which lasted until the beginning of the Early Bronze Age (4000−2200 BC) (Balyan, 1984). This is in accordance with our interpretation that the locality Tsovinar-1 (today at 1917 m a.s.l.) was covered by ca. 3 m water depth at ca. 5700 BC. However, lake terraces between the city of Martuni and Tsovinar village seem to indicate that the shoreline of Lake Sevan rose to even 1925 m a.s.l. during the Northgrippian climatic optimum (Sayadyan, 2000; Kazakova, 1958) which may be a sign of an even higher lake level earlier in time. This high stand may not be covered by our fossil record but could be reflected in the layer of grey sand with coarse gravel (L18) below the sampled part of the profile. According to Blair (1999) such a sandy gravel facies can be the result of a depositional environment at the lake beach face and upper-shoreface zone, extending to the lower-shoreface between the normal wave base and the storm wave base, in water depths of about 2–8 m. Indeed, the gravel layer L18 may correspond better to the high the lake level at 1925 m a.s.l. reported by Sayadyan (2000). It is possible that the discrepancy in age could be attributed to limitations of the older dating methods (Fig. 6).

5.2. Low Lake level phase II and transgression (ca. 4000−1700 BC)

After ca. 4000 BC, forest cover was sparse but still some insignificant areas of arid woodlands with *Juniperus* sp., *Pinus* sp., and *Quercus* sp. remained. While the fossils of *Juniperus* sp. certainly originated from the lake surroundings, *Pinus* sp. may indicate longer distance transport from the northern part of Armenia, where it grows today under more humid conditions. Open steppe vegetation dominated the landscape. The abundances of herbaceous pollen taxa such as Chenopodiaceae, Asteraceae, Polygonaceae and Apiaceae are highest from ca. 3800−3000 BC. The number of sedges decreases during this period. After ca. 3000 BC the climate seems to become slightly more humid with higher abundances of Cyperaceae and *Quercus* sp. (Fig. 3).

During the period from ca. 4000 to 2600 BC, the site Tsovinar-1 (1917 m a.s.l.) was not occupied by aquatic vegetation. Aquatic vascular plants, *Myriophyllum* sp., *Potamogeton* sp., and *Ceratophyllum* sp. became absent (Fig. 6). Wetland plants like *Sparganium* sp. and *Typha* sp. occur in extremely low numbers. The absence of aquatic and wetland taxa during this time places the site of Tsovinar-1 on dry land. However, peat formation still continues although on a very low rate, which points to humid conditions of the soil probably due to high groundwater levels. From ca. 2600 to 1700 BC transgression is indicated by increased numbers of *Typha* sp., *Sparganium* sp., and *Persicaria amphibia*. From ca. 2200 BC the occurrence of *Potamogeton* sp. points to already some water covering the Tsovinar-1 site.

Accordingly, arid climate was recorded peat sequence in the Sevan basin by Leroyer et al. (2016). There, a pollen-based climate reconstruction shows a decrease of precipitation between ca. 3750−3150 BC (ca. 5700 and 5100 cal. BP) correlated by the authors to Sayadyan's low lake level phase. This drop of lake level is corresponding with appearance of new land spaces for human use, what is reflecting at settlements increase at the early Bronze Age (3rd millennium BC). That time the large settlements of Lchashen, Norashen, and Ayrivank arose and existed on the regressive sediments until the middle of the 2nd millennium BC (Sayadyan, 1983, 1999; Sayadyan et al., 1977). In Norashen and Lchashen a large number of bone remains of domestic animals and agricultural tools dated to ca. 2500 BC indicates the presence of intensive human activities, mostly cattle breeding (Gorbatov et al., 2019; Hakobyan et al., 1988).

These settlements listed above seem to be an expression of increased population density on higher elevations in the Armenian Highlands during the Early Bronze Age. Due to the general aridification of the climate during this low lake level phase, human populations began to move their activities from the lowlands into the mountains as evidenced also in other regions of Armenia. During this time there was an unprecedented increase in settlements in the Armenian Highlands (Simonyan, 2019). Caused by the expansion of the Kura-Araxes culture into the Sevan basin (from 3600−3500 BC to 2600−2500 BC) population density rose considerably (Hovsepyan, 2015). Also, archaeobotanical investigations from Tsaghkasar-1 settlement (at the western flank of Mt. Aragats) and the pollen record from Zarishat fen (north-western Armenia, at 2116 m a.s.l.) suggest that the Early Bronze Age population settled and practiced agriculture in high mountain zones (Hovsepyan, 2011; Joannin et al., 2014). Agricultural activities are represented also in carpological remains of cultivated plants (mostly wheat (*Triticum* sp.) and barley- (*Hordeum* sp.)) from Early Bronze Age (ca. 3500−2500 BC) at Sotk-2 (southwestern slopes of Sevan Mountain Range) (Hovsepyan, 2013).

According to Sayadyan (2000), lake terraces situated at elevations of 1894–1896 m a.s.l. are believed to represent the shoreline of the lake during the period of around ca. 3000 to 2000 BC (Fig. 6). Similar observations are suggested by our data, which imply dry soil and steppe vegetation in the surroundings of Tsovinar-1. This suggests that during this time, the shoreline was located at a considerably lower level than the site. During the time period of ca. 4000 to 2600 BC, the lake level was likely at least 3 m lower than Tsovinar-1 site. The dry conditions of this period resulted in very low sedimentation rates, with only 11 cm of peat forming over the course of 1400 years. However, the actual presence of peat at Tsovinar-1 points to locally humid soils and a probably high groundwater table. From ca. 2600 to 1700 BC, a transgression was observed, raising the lake level, and water returned to the level of Tsovinar-1 again at around 2200 BC.

5.3. High Lake level phase III and subsequent regression (ca. 1700−600 BC)

Pollen data show that forests started to expand from ca. 1700 BC onwards. A more diverse assemblage of trees developed, and from ca. 600 BC *Quercus* sp., *Carpinus* sp., and *Pinus* sp. became prevalent in the region. Especially, the occurrences of thermophilus species such as *Tilia* sp., *Zelkova* sp., and *Fagus orientalis* also increased significantly, implying warmer and more humid climatic conditions. Also, *Vitis vinifera* var. *sylvestris* occurred in area of Tsovinar-1 after ca. 900 BC for the first time (Fig. 3). Pollen spectra from transgressive sediments from the Norashen section at the west shore of Lake Sevan also indicate an increase in humidity in the region in the middle of the 2nd millennium BC (Sayadyan et al., 1977; Sayadyan, 2000).

Data document high lake level during ca. 1700 to 900 BC by the high number of aquatic vascular plants. *Myriophyllum* sp. and *Potamogeton* sp. microremains reach their maximum abundances here (peak ca. 1200 BC). Based on the preferred habitats of aquatic plants a water depth of not more than 2 m at the Tsovinar-1 locality could be inferred. Also, the Norashen section gives evidence for an elevated lake level during this phase. Lake sediments with mollusk shells point to the beginning of a transgression in the middle of the 2nd millennium BC, which subsequently drowned the Norashen settlement completely (Sayadyan et al., 1977; Sayadyan, 2000). This date roughly corresponds to the beginning of lake level phase III at 1700 BC as defined here (Fig. 6).

From ca. 900 to 600 BC the water level in Lake Sevan retreated again. The abundances of *Ceratophyllum demersum* and *Myriophyllum* sp. sharply decrease. Instead, *Ceratophyllum submersum, Menyanthes trifoliata*, and also *Nymphaea alba, Utricularia* sp., and *Lemna* sp. appear (ca. 600-650 BC), along with emergent Cyperaceae, *Typha* sp., and *Sparganium* sp. The succession of fossil fruits shows a distinct replacement of *Ceratophyllum demersum* which favors deeper water by *C. submersum* preferring more shallow environments. Here, the number of fruits of *C. submersum* is the highest of the whole fossil record (Fig. 6).

Together with the forest extent, from ca. 750 to 600 BC also the number of monolete Pteridophytes spores is on its peak. However, those do not need to originate necessarily from the forests. Despite current mean annual precipitation below 500 mm, some species of monolete Pteridophytes (*Athyrium filix-femina*, *Cystopteris fragilis*, *Polypodium vulgare*, etc.) grow in the Sevan basin today at locally more humid microclimatic conditions.

During the 8th century BC, the Teysheba fortress, which is located not far from the Tsovinar-1 locality and at roughly the same altitude, was built by the Urartian king Rusa 1 (765-714 BC) (Hakobyan et al., 1988; Mikaelyan, 1968). In 1930 (when the level of Lake Sevan was at 1916 m a.s.l.) the cuneiform inscription written by Rusa 1 was situated at the level of wave erosion (Sanamyan, 2002). This proves that during the 8th century BC the water level of the lake was already lower than 1916 m a.s.l. Also, Sayadyan (2009) reports a lake terrace of the 1st millennium BC that reflects this regressive phase of the lake (Fig. 6).

From ca. 900 to 600 BC a large amount of *Myriophyllum* sp. and *Ceratophyllum demersum* can also be associated with an eutrophication of the lake, inasmuch as especially *Myriophyllum* flourishes in eutrophic lakes or other water bodies enriched with nutrients (Aiken et al., 1979; Gaillard and Birks, 2007). The presence of these plants may indicate a natural eutrophication in Lake Sevan. The decay of the macrophyte belt due to rising water levels contributed to the accelerated entry of biogenic elements into the water mass (Hovhannisyan, 1994).

The number of Cerealia grains started to increase at around 1500 BC, which might be associated with increased local farming. Also, the record of pollen of *Vitis vinifera* var. *sylvestris* in Tsovinar-1 (after ca. 900 BC) is most likely a sign of cultivation of grapes in the area. Indeed, pollen diagrams from Southwest Turkey confirm the development of regional farming, and indicate regional forest clearance and the creation of cultural landscape from ca. 3000 BP (1050 BC) onwards (Roberts et al., 2004).

The inhabitants of Sevan basin, along with agriculture, were also engaged in cattle breeding as evidenced by cuneiform inscriptions of the Assyrian king Ashur-Nazirapal (884–860 BC), and the Urartian king Sardur II (755–730 BC). The latter indicates that he took 37800 prisoners, and stole 3500 horses, 40380 cows, and 214700 sheep (Abrahamyan, 1949). Probably Sardur exaggerated; but even if he had doubled the numbers, this still indicates that the Sevan basin was anthropogenically overloaded at that time, which could have directly affected the ecological conditions of the lake. It is quite likely that in Lake Sevan natural eutrophication processes were intensified by human activity.

5.4. *Low Lake level phase IV and subsequent transgression (ca. 600 BC–200 AD)*

At ca. 600 BC the extent of forest vegetation reaches its maximum and after that stepwise became less diverse as a sign for slightly less humid conditions. First at ca. 600 BC, *Zelkova* sp. disappears completely from the pollen record and the number of monolete Pteridophytes spores decreases considerably. From ca. 450 BC *Carpinus* sp. decreased, followed by *Quercus* sp. at ca. 250 BC. After a short more arid phase, at around ca. 100 BC *Quercus* sp. and *Carpinus* sp. spread again (Fig. 3).

During the whole period the lake level was quite low. *Menyanthes trifoliata*, *Persicaria amphibia*, *Alisma* sp., along with emergent Cyperaceae, *Typha* sp., and *Sparganium* sp. formed extensive wetland habitats in the area of Tsovinar-1 (Fig. 6).

Variations in abundances of aquatic (*C. submersum*, *Potamogeton* sp., *Myriophyllum* sp.) and semi-aquatic (*Sparganium* sp. and *Typha* sp.) plants between ca. 600 and 100 BC document lake level fluctuations around the altitude of Tsovinar-1. At the same time the amount of Cyperaceae increased from ca. 500 BC onwards showing a peak at ca. 100 BC.

Only from ca. 100 BC to 200 AD, the replacement of *Ceratophyllum submersum* with high numbers *C. demersum* expresses the next transgressional phase, in a similar but reverse way compared to the regression between ca. 900 and 600 BC.

This phase of regression, fluctuating low lake level and following transgression from ca. 900 BC until 200 AD created an extensive swampy environment at the shallow southern and south-eastern shore of Lake Sevan covered by peatland vegetation. During this period, at Tsovinar-1 sedimentation rates were very high, highest from ca. 600 to 550 BC (4 a/cm). In total, 94 cm of peat formed between 900 BC and 200 AD, which is exploited until modern times in the area (Hayrapetyan et al., 2020).

5.5. *High Lake level phase V (ca. 200–900 AD)*

In the basin of Lake Sevan, forest vegetation developed again during the 1st millennium AD (Fig. 3). The number and diversity of tree taxa in the Tsovinar-1 pollen assemblages of this phase are the richest of the whole sequence. These forests consisted mainly of hornbeam (*Carpinus* sp.) and oak (*Quercus* sp.), with an admixture of linden, maple, and elm. Dry slopes might have been covered with thickets of juniper, while broad-leaved thermophilous taxa grew in the plains. These diverse forests indicate warm and humid climate conditions during this phase.

The sharp increase of abundances of deeper water aquatic plants like *Potamogeton* sp. and *Ceratophyllum demersum* at ca. 300 AD imply a higher lake level at this time. On the other hand, the high amount pollen grains of *Myriophyllum* sp. were observed at ca. 600–700 AD (Fig. 6). In parallel, pollen of shallow water plants remains high except for *Menyanthes trifoliata* and *Ceratophyllum submersum*, which disappear from the record. In combination this points to ca. 2–3 m water depth at Tsovinar-1.

As mentioned by Armenian historian Leo, during the 7th and 8th century AD, on the southern bank of Lake Sevan in the cities of Tsar (meaning 'tree' in Armenian) and Takhtak (meaning 'wood board' in Armenian) handicraft wood production was well-developed. Although these towns do not exist anymore and their exact historical location is unknown, this still proves a considerable forest cover in the Sevan basin at that time (Moreno-Sanchez and Sayadyan, 2005). Also, in the period from the 8th to 10th century thick trees were cut and exploited in large quantities by Arabs in Armenia (Mirimanyan, 1953). In the 10th century, Mount Ararat was covered with dense forests and was declared the Armenian royal hunting grounds (Varpetyan, 1988). Such historic data support the observed pollen signal from Tsovinar-1 indicating that from the 1st to the 10th century AD average temperatures and humidity were increased compared to ca. 600 BC−200 AD.

According to pollen data from Georgia, the climate was cooler during the 3rd and 4th century AD than during the 7th to 11th centuries (Kvavadze et al., 2007). This increase in temperature corresponds to an increase in human population density and agricultural activities, including viticulture, in high mountains. The global trend of relatively mild climate is also considered a driving factor in the North Atlantic region for the Viking expansion (ca. 800−1100 AD), and thus for the Norse settlement of Iceland (ca. 870 AD) and Greenland (ca. 985 AD) (Ogilvie et al., 2000).

In Lake Sevan, the lake level transgression during the 1st millennium AD is indicated not only by the associations of aquatic plants in Tsovinar-1 and observed humid climatic conditions, but also by geological evidence. In the Norashen section the accumulation of sand-shell deposits points to a considerable rise of lake level (Sayadyan et al., 1977; Gorbatov et al., 2019). A similar change in sedimentation occurs at ca. 300 AD in the Tsovinar-1 section with the deposition of sandy clays of layer L3 which are a clear sign of the presence of water in the area, probably formed in a back-barrier pond (Blair, 1999).

6. Conclusion

The Tsovinar-1 section at 1917 m a.s.l. at the southern shore of Lake Sevan in the Caucasus Armenian Highlands reveals a well-dated and diverse pollen and carpo-flora covering a time span from ca. 6000 BC to 900 AD. The abundances of pollen of forest taxa in relation to steppe vegetation indicate climatic changes through time. In parallel, the presence and number of fossils of aquatic and wetland plants, both in micro and macro floras, provide information about the presence of water and allows estimating changes of water depth. Although tectonic influences cannot be ruled out, these data altogether point to a strong correlation of lake level changes with climate.

The period from ca. 6000 to 5000 BC is characterized by warm and humid climate, with expanded broad-leaved forests in the basin. Lake level was high and water covered the site of Tsovinar-1 with ca. 3 m water depth. However, after a peak at ca. 5700 BC (peak of *Myriophyllum* sp.), from ca. 5000 BC water level retreated in the area and aquatic taxa from deeper waters became less abundant.

From ca. 4000 BC climatic conditions started to change and the climate became drier and warmer, indicated by an increase of steppe taxa, which reached its from ca. 3800 to 3000 BC. Also, the amount of pollen here was at its lowest in the whole section, which was most likely due to dry conditions and a very low rate of accumulation of pollen. The virtual absence of aquatic and wetland taxa indicates that the surroundings of the Tsovinar-1 site were dry land between ca. 4000−2600 BC, while continuous, though very slow, peat formation points to locally humid soils.

From ca. 2600 BC the climate became more humid again. Subsequently, the lake level started to rise from and reached its peak at around ca. 1200 BC with not more than 2 m of water covering the Tsovinar-1 locality. Then, the water retreated slightly, leaving wetlands and shallow ponds in the Tsovinar-1 area until at ca. 600 BC.

From ca. 600 to 200 BC climate was slightly more arid and the lake level remained generally low but fluctuating at about the altitude of Tsovinar-1 (1917 m a.s.l.), with two peaks of slightly higher water levels at ca. 500 and 200 BC. From the whole succession *Menyanthes trifoliata* is recorded only from ca. 900 BC until ca. 170 AD. Peat formation culminated with the production of more than 90 cm of peat during this period.

From ca. 200 AD precipitation increased again, and the diversity of forests was at it maximum. The Tsovinar-1 site appears to be covered by water of ca. 2–3 m depth. The lake level reached its highest point in ca. 300 AD and ca. 600−700 AD, but remained high at least until ca. 900 AD.

During the low lake level phase between ca. 4000 BC and ca. 1700 BC, when the Tsovinar-1 area was fully dry, obviously no conclusions can be drawn about the absolute elevation of Lake Sevan or the level of eutrophication. For high lake level phases, the fossil assemblages indicate eutrophication of the lake, which can be explained by natural processes but partly also by human impact due to growing population density in combination with increased farming and cattle breeding.

Author contributions

Narine Hayrapetyan: Conceptualization, Laboratory research, Palynological analysis, Data interpretation, Writing – original draft, Writing – review and editing, Visualization. **Elen Hakobyan:** Laboratory research, Carpological analysis, Data interpretation, Writing – original draft, Writing – review and editing. **Eliso Kvavadze:** Laboratory research, Data interpretation, Writing – original draft, Writing – review and editing. **Edoardo Martinetto:** Carpological analysis, Data interpretation, Writing – review and editing. **Ivan Gabrielyan:** Conceptualization, Data interpretation, Writing – review and editing. **Angela A. Bruch:** Conceptualization, Formal analysis, Data interpretation, Writing – original draft, Writing – review and editing, Visualization.

Data availability

Carpological and C14 data as used for the manuscript are presented in the manuscript tables. Pollen data are not yet available as they are part of the PhD thesis of the main author. Those will be contributed to the Neotoma database after finalizing all analyses.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

First of all, we are particularly grateful to Dr. Hovik Sayadyan (Yerevan) for the scientific advices of literature and Lake Sevan geography. We also wish to acknowledge the assistance provided by Dr. George Fayvush (Yerevan) about wetland plants and their distribution. And we greatly appreciate the help of the laboratory technicians of the Georgian National Museum in Tbilisi with palynological processing.

The authors thank the German Federal Ministry of Education and Research (BMBF) for financial support of the project ‘Plant Biodiversity in Time and Space – Changes of vegetation and plant resources in the Southern Caucasus (PlantBITES). We also thank the “PlantBITES” team for their support during field work. Narine Hayrapetyan expresses her gratitude to the Young Scientists’ Support Program for supporting the development of this article within the framework of the ‘Young Scientists’ Internship Program’ (22-YSIP-009). We also thank Edyta Zawisza and an anonymous reviewers for valuable suggestions on an earlier version of the manuscript.

References

Abrahamyan, A., 1949. Forestedness of the Sevan basin in the past. Bull. Botan. Garden Acad. Sci. Armen. SSR 7, 7–15 (in Russian).

Afrikyan, K.G., 1987. The Current State of the Vegetation Cover of the Lake Sevan Basin, Ways of its Improvement and Rational Use. Institute of Botany of NAS RA final thesis 250.

Ahee, J.E., Van Drunen, W.E., Dorken, M.E., 2015. Analysis of pollination neighbourhood size using spatial analysis of pollen and seed production in broadleaf cattail (*Typha latifolia*). Botany 93 (2), 91–100. https://doi.org/10.1139/cjb-2014-0169.

Aiken, S.G., Newroth, P.R., Wile, I., 1979. The biology of Canadian weeds. 34. *Myriophyllum spicatum* L. Canand. J. Plant Sci. 59, 201–215.

Avagyan, R..Z., 2003. Legal Protection of Lake Sevan. "Science. Publishing House of NAS RA, Yerevan, p. 777 (in Armenian).

Avetisyan, E.M., 1956. Polygonaceae. In: Takhtajan, A.L. (Ed.), Flora of Armenia, Portulacaceae –Pumbaginaceae, vol. 2. Publishing House of Academy of sciences Armenian USSR, Yerevan, pp. 393–450 (in Russian).

Avetisyan, B.E., 1973. Flora of Armenia. Ericaceae-Elaeagnaceae, vol. 6. Publishing house of Academy of sciences Armenia USSR, Yerevan, p. 484.

Avetisyan, E.M., Shishikyan, B.K., 1956. Flora of Armenia, vol. 2. Portulacaceae-Polygonaceae. Publishing house of Academy of sciences Armenia USSR, Yerevan, p. 520 (in Russian).

Babayan, A., Hakobyan, S., Jenderedjyan, K., Muradyan, S., Voskanov, M., 2003. Experience and lessons learned briefly concerning Lake Sevan. Yerevan 1–32.

Balyan, S.P., 1984. Recent History of Sevan and Van Lakes. geographic series 2. Scientific communications of Yerevan State University, pp. 60–67 (in Russian).

Barseghyan, A.M., 1990. Aquatic Flora of Armenia. Armenia National Academy of Sciences. Publishing House of the USSR Academy of Sciences, Yerevan, pp. 1–354 (in Russian).

Berg, L.S., 1950. Natural Regions of the. U.S.S.R. Macmillan, New York.

Beug, H., 2004. Guide to pollen determination for Central Europe and neighboring (Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete). Verlag Dr. Friedrich Pfeil, München, p. 542 (in German).

Blair, T.C., 1999. Sedimentology of gravelly lake lahontan highstand shoreline deposits, churchill butte, Nevada, USA. Sediment. Geol. 123, 199–218.

Climate Handbook of the, U.S.S.R., 1966. Air Temperature, vol. 15. Hydrometeorological publishing house, p. 268 (in Russian).

Climate Handbook of the, U.S.S.R., 1968. Solar Radiation, Radiation Balance and Sunshine, vol. 1. Hydrometeorological publishing house, p. 55 (in Russian).

Climate Handbook of the, U.S.S.R., 1969. Air humidity, precipitation and snow cover. Hydrometeorological publishing house 16 (4), 195 (in Russian).

Connor, S.E., Kvavadze, E.V., 2008. Modeling late Quaternary changes in plant distribution, vegetation and climate using pollen data from Georgia. Caucasus J. Biogeogr. 36 (3), 529–545.

Connor, S.E., Thomas, I., Kvavadze, E.V., Arabuli, G.J., Avakov, G., Sagona, A., 2004. A survey of modern pollen and vegetation along an altitudinal transect in southern Georgia, Caucasus region. Rev. Palaeobot. Palynol. 129, 229–250.

Csiky, J., Mesterházy, A., Szalontai, B., Pótóné Oláh, E., 2010. A morphological study of *Ceratophyllum tanaiticum*, a species new to the flora of Hungary. Preslia 82, 247–259.

Deheryan, S., 2005. Rising Interests, vol. 160. Welcomed increase in water level recorded at Lake Sevan, Yerevan.

Dezhi, F., Les, D.H., 2001. Flora of China. Ceratophyllaceae, 6 21–122. http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=10178.

Ejankowski, W., Solis, M., 2015. Response of hornwort (*Ceratophyllum demersum* L.) to water level drawdown in a turbid water reservoir. Ecol. Environ. Res. 13 (1), 219–228.

Erdtman, G., 1966. Pollen Morphology and Plant Taxonomy: Angiosperms, vol. 2. Hafner publishing Company, p. 553.

Fayvush, G.M., Aleksanyan, A.S., 2016. Habitats of Armenia, vol. 358. Institute of Botany of NAS RA, Yerevan.

Gabrielyan, G.K., 1978. Pearl Sevan. Publishing house "Mysl, Moscow, p. 107 (in Russian).

Gabrielyan, E.T., 2001. Alismataceae. In: Takhtajan, A.L. (Ed.), Flora of Armenia. Monocotyledons 10, (Except of Poaceae). A.R.G. Gantner Verlag KG, pp. 534–540. Ruggell/Liechtenstein, Königstein.

Gaillard, M.J., Birks, H.H., 2007. Plant macrofossil methods and studies, paleolimnological application. Encyclop. Quatern. Sci. 2337–2356.

Garibyan, M., 2007. Lake Sevan Water Levels. T. K. Agyemang. Sevan, Armenia. Hydrometeorological Agency, Ministry of Nature Protection.

Gorbatov, E.S., Vardanyan, A.A., Korzhenkov, A.M., Razumniy, S.D., 2019. Lake Sevan (Armenia) deposits as indicators of paleoclimate and neotectonic processes. Izvestiya Atmos. Ocean. Phys. 55 (8), 860–869.

Grichuk, V.P., 1948. A New Method for Processing Sedimentary Rocks for Pollen and Spores and its Application in Paleogeography. State publishing house of geographical literature (Geografgiz), Moscow, p. 202 (in Russian).

Grimm, E.C., 2011. Tilia 2.1.1. Illinois State Museum, Research and Collections Center, Springfield, USA.

Hakobyan, T.K., Melik-Bakhshyan, S.T., Barsegyan, H.K., 1988. Dictionary of Toponymy of Armenia and Adjacent Territories, vol. 2. Yerevan State University, Yerevan, p. 991 (in Armenian).

Hannon, G.E., Gaillard, M.J., 1997. The plant-macrofossil record of past lake-level changes. J. Paleolimnol. 18, 15–28.

Hayrapetyan, N., Kvavdze, E., Shatilova, I., Gabrielyan, I., Bruch, A.A., 2020. Subfossil palynological spectra from the surroundings of the village Tsovinar (Lake Sevan, Armenia). Biol. J. Armen. Yerevan 3 (72), 52–58.

Hovhannisyan, O.R., 1994. Lake Sevan, Yesterday, Today, vol. 478. Institute of Hydroecology and Ichthyology of NAS RA, Yerevan.

Hovsepyan, R., 2011. Palaeoethnobotanical data from the high mountainous early Bronze age settlement of tsaghkasar-1 (Mt. Aragats, Armenia). Ethnobiol. Lett. 2, 58–62.

Hovsepyan, R., 2013. First archaeobotanical data from the basin of Lake Sevan. Veröffentlichungen des Landesamtes für Denkmalpflege und Archäologie Sachsen-Anhalt. Bandwagon 67, 93–107.

Hovsepyan, R., 2015. On the agriculture and vegetal food economy of Kura-Araxes culture in the South Caucasus. Paléorient, CNRS ÉDITIONS 41 (1), 69–82.

Joannin, S., Ali, A.A., Ollivier, V., Roiron, P., Peyron, O., Chevaux, S., Nahapetyan, S., Tozalakyan, P., Karakhanyan, A., Chataigner, C., 2014. Vegetation, fire and climate history of the Lesser Caucasus: a new Holocene record from Zarishat fen (Armenia). J. Quat. Sci. 29, 70–82.

Karakhanyan, A., Badalyan, R., Harutyunian, A., Avagyan, A., Philip, H., Davtyan, V., Alaverdyan, G., Makaryan, K., Martirosyan, M., 2016. Archaeoseismological studies at the Pambak-Sevan-Syunik fault system, Armenia. Tectonic evolution, collision, and seismicity of southwest Asia. In: Honor of Manuel Berberian's Forty Years of Research Contributions, vol. 21. Geological Society of America.

Katz, N.J., Katz, S.V., Kipiani, M.G., 1965. Atlas and Keys of Fruits and Seeds Occurring in the Quaternary Deposits of the USSR. Academy of Sciences of the USSR. Commission for Investigations of the Quaternary Period. Publishing House "NAUKA", Moscow, p. 367 (in Russian).

Kazakova, N.M., 1958. Geomorphological zoning of the Lake Sevan basin. Issues of geomorphology of Azerbaijan and Armenia. Acad. Sci. USSR 74, 43–75.

Keast, A., 2011. The introduced aquatic *Myriophyllum spicatum* as habitat fish and their invertebrate prey. Can. J. Zool. 52 (7), 1289–1303.

Khanjyan, N.S., 2001. Typaceae. In: Takhtajan, A.L. (Ed.), Flora of Armenia. Monocotyledons, 10 (Except of Poaceae). A.R.G. Gantner Verlag KG, pp. 581–585. Ruggell/Liechtenstein, Königstein.

Krijgsman, W., Tesakov, A., Yanina, T., Lazarev, S., Danukalova, G., Van Baak, C.G.C., Agustí, J., Alçiçek, M.C., Aliyeva, E., Bista, D., Bruch, A., Büyükmeriç, Y., Bukhsianidze, M., Flecker, R., Frolov, P., Hoyle, T.M., Jorissen, E.L., Kirscher, U., Koriche, S.A., Kroonenberg, S.B., Lordkipanidze, D., Oms, O., Rausch, L., Singarayer, J., Stoica, M., van de Velde, S., Titov, V.V., Wesselingh, F.P., 2019. Quaternary time scales for the Pontocaspian domain: interbasinal connectivity and faunal evolution. Earth Sci. Rev. 188, 1–40.

Kupriyanova, L.A., Alyoshina, L.A., 1972. Pollen and Spores of Plant of Flora Eurasian Part SSSR, vol. 1. Publishing house Nauka, Leningrad, p. 438 (in Russian).

Kupriyanova, L.A., Alyoshina, L.A., 1978. Pollen of Dicotyledonous Plants of the Flora of the European Part of USSR, vol. 1. Publishing house Nauka, Leningrad, p. 184 (in Russian).

Kurbatova, N..V., Ametov, A..A., Mukhitdinov, N..M., Abidkulova, K..T., 2013. Botanical research of the medicinal plant Polygonum amphibium L. In: the vicinity of Almaty City. BIOLOGIJA, 59, pp. 279–286.

Kvavadze, E.V., Rukhadze, L.P., 1989. Vegetation and Climate of Holocene Abkhazia. Mecniereba, Tbilisi (in Russian).

Kvavadze, E.V., Connor, S.V., Narimanishvili, G.K., 2007. Late Pleistocene and Holocene history of landscapes of the Tsalka Plateau (Southern Georgia) based on palynological analysis of lake and soil formations. In: Problems of Paleobiology, Georgian National Museum, Tbilisi, 2, pp. 12–23 (in Russian).

Lansdown, R.V., 2017. *Ceratophyllum Submersum*. The IUCN Red List of Threatened Speciese. https://doi.org/10.2305/IUCN.UK.2017-1.RLTS.T167833A96188202.en. T167833A96188202.

Leira, M., Cantonati, M., 2008. Effects of water-level fluctuations on lakes: an annotated bibliography. Water-level fluctuations. Hydrobiologia 613, 171–184.

Leroyer, C., Joannin, S., Aoustin, D., Ali, A.A., Peyron, O., Ollivier, V., Tozalakyan, P., Karakhanyan, A., Jude, F., 2016. Mid Holocene vegetation reconstruction from Vanevan peat (south-eastern shore of Lake Sevan, Armenia). Quat. Int. 395, 5–18.

Martinetto, E., 2001. How to collect and store fruits (fossils). In: Paleo Italy, Newsletter of the Italian Paleontological Society, 3, pp. 4–10.

Mikaelyan, A..C., 1968. The Cyclopean Castles of the Sevan Basin. Academy of Sciences of the Armenian SSR, Institute of Archeology and Ethnography, Yerevan, p. 57 (in Armenian).

Mirimanyan, K.P., 1953. The problem of forest and steppe in the conditions of Armenia. Soil Sci. 9, 62–68 (in Russian).

Moreno-Sanchez, R., Sayadyan, H.Y., 2005. Evolution of the forest cover in Armenia. Int. For. Rev. 7 (2), 113–127.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Nagengast, B., Gabka, M., 2016. Niche partitioning of two congeneric submerged macrophytes in small water bodies: the case of *Ceratophyllum demersum* L. and *C. submersum* L. Aquat. Bot. 137, 1–8.

Nikitin, V.P., 1969. Paleocarpological Methods, vol. 79. Publishing house of Tomsk University, Tomsk.

Ogilvie, A.E.J., Barlow, L.A.K.E., Jennings, A.E., 2000. North Atlantic Climate C. AD 1000: Millennia 1 Reflections on the Viking Discoveries of Iceland, vol. 55. Greenland and North America, Weather, pp. 34–45.

Pals, J.P., van Geel, B., Delfos, A., 1980. Palaeoecological studies in the Klokkeweel bog near Hoogkarspel (prov of Noord-Holland). Rev. Palaeobot. Palynol. 30, 371–418.

Partridge, J.W., 2001. *Persicaria amphibia* (L.) gray (*Polygonum amphibium* L.). J. Ecol. 89, 487–501.

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Koppen-Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644.

Ramsey, C.B., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51 (1), 337–360.

Reille, M., 1992. Pollen and spores from Europe and North Africa. Historical botany and palynology laboratory. (Pollen et spores d'Europe et d'Afrique du nord. Laboratoire de botanique historique et palynology), Marseille, p. 520 (in French).

Reille, M., 1998. Pollen and spores from Europe and North Africa. Historical botany and palynology laboratory. (Pollen et spores d'Europe et d'Afrique du nord, vol. 2. Laboratoire de botanique historique et palynology) Marseille, p. 523 (in French).

Reimer, P., Austin, W., Bard, E., Bayliss, A., Blackwell, P., Ramsey, C.R., Butzin, M., Cheng, H., Edwards, R., Friedrich, M., Grootes, P., Guilderson, T., Hajdas, I., Heaton, T., Hogg, A., Hughen, K., Kromer, B., Manning, S., Muscheler, R., Palmer, J., Pearson, C., van der Plicht, J., Reimer, R., Richards, D., Scott, E., Southon, J., Turney, C., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon 62.

Roberts, N., Stevenson, T., Davis, B., Cheddadi, R., Brewster, S., Rosen, A., 2004. Holocene climate, environment and cultural change in the circum-Mediterranean region. In: Battarbee, R.W., Gasse, F., Stickley, C.E. (Eds.), Past Climate Variability through European Africa. Springer, pp. 343–362.

Sanamyan, H., 2002. The fortress of tsovinar (odzaberd) "the city of [god] teisheba". In: Biscione, R., Hmayakyan, S., Parmegiani, N. (Eds.), The North-Eastern Frontier Urartians and Non-urartians in the Sevan Lake Basin, vol. 7, pp. 319–325. Roma.

Sayadyan, Y.V., 1983. Human and environment in late glacial time in the basin of lake Sevan and adjacent regions (Moscow 1982), Yerevan. In: Academy of Sciences of the Armenian SSR. Geology issues of the Quaternary period of Armenia by the XI Congress INQUA, pp. 67–74 (in Russian).

Sayadyan, Y.V., 1999. Natural environment and people in the Lake Sevan basin in the middle and late Holocene. St. Petersburg News Russian Geogr. Soc. publishing house Nauka 131 (4), 55–66 (in Russian).

Sayadyan, Y.V., 2000. Fluctuations of the shoreline of Lake Sevan in the Holocene (Armenia). St. Petersburg News Russian Geogr. Soc. Publishing house Nauka 132 (3), 37–47 (in Russian).

Sayadyan, Y.V., 2009. Newest Geological History of Armenia, National Academy of Sciences of the Republic of Armenia. Institute of Geological Sciences, publishing house Gitutyun, p. 356 (in Russian).

Sayadyan, Y.V., Aleshinskaya, Z.V., Khanzadyan, E.V., 1977. Late glacial deposits and archaeology of the Sevan coast. In: Geology of Academy of Sciences of the Armenian SSR The Quaternary Period (Pleistocene), Yerevan, pp. 91–109 (in Russian).

Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. TREE 8, 275–279.

Shatilova, I., Mchedlishvili, N., Rukhadze, L., Kvavadze, E., 2011. The History of the Flora and Vegetation of Georgia (South Caucasus). Georgian national museum, institute of paleobiology, Tbilisi, p. 200.

Simonyan, H., 2019. The Ancient Art of the Armenian Highlands. Art Institute author's abstract, Yerevan 38.

Smith, K.B., Smith, C.E., Forest, S.F., Richard, A.J., 2007. A Field Guide to the Wetlands of the Boreal Plains Ecozone of Canada. Ducks Unlimited Canada. Western Boreal Office, Edmonton, Alberta.

Statistical Committee of the Republic of Armenia, 2019. Water Balance of Lake Sevan (2018 Annual and 2019 June Monthly). https://www.armstat.am/am/?module=news&mid=3&id=684.

Takhtajan, A.L., 1954. Flora of Armenia. Lycopodiaceae, Fumarioideae, vol. 1. Publishing house of Academy of Sciences Armenian USSR, Yerevan, p. 119.

Tamanyan, K.G., Fayvush, G.M., 2009. On the issue of floristic zoning in Armenia. Flora. Veget. Plant Resour. Armen. 17, 73–78.

Thompson, F.L., Hermanutz, L.A., Innes, D.J., 1998. The reproductive ecology of island populations of distylous *Menyanthes trifoliata* (Menyanthaceae). Can. J. Bot. 76, 818–828.

Tumanyan, M.R., 1971. The history of vegetation in the Lake Sevan basin in the Holocene. Biol. J. Armen. Acad. Sci. Armen. 24 (11), 57–61.

Van den Berg, H., Van Lidth de Jeude, E., Hak, A., Mooren, C., Leen den Uijl, R., Giomi, T., Kraaijeveld, S., 2015. Duckweed, a Tiny Aquatic Plant with Growing Potential, vol. 63. KWR Watercycle Research Institute, The Netherlands.

Vardanyan, M., 2007. National atlas of Armenia. Yerevan 190 (in Armenian).

Varpetyan, A.A., 1988. After All, Who Were the Aryans? publishing house Eutyun, Yerevan, p. 208 (in Armenian).

Velichkevich, F.Y., Zastawniak, E., 2008. Atlas of the Pleistocene Vascular Plant Macrofossils of Central and Eastern Europe, vol. 2. Herbaceous dicotyledons. W. Szafer Institute of Botany, Polish Academy of Sciences, Krakow, p. 379.

Walker, M.J.C., Berkelhammer, M., Björck, S., Cwynar, L.C., Fisherd, A., Long, A.J., Lowe, J.J., Newnham, R.M., Rasmussen, S.O., Weiss, H., 2012. Formal subdivision of the Holocene series/epoch: a discussion paper by a working group of INTIMATE (integration of ice-core, marine and terrestrial records) and the subcommission on quaternary stratigraphy (international commission on stratigraphy). J. Quat. Sci. 27 (7), 649–659.

Wilkinson, I.P., 2020. Lake Sevan: evolution, biotic variability and ecological degradation. In: Mischke, S. (Ed.), Large Asian Lakes in a Changing World: Natural State and Human Impact. Springer International Publishing, Cham, pp. 35–63.