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Subrecent phytolith assemblages of alpine communities in the Teberda Nature Reserve, the north-western Caucasus, Russia

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Abstract. Phytolith analysis uses tiny silica particles of specific shapes, which are produced by certain plant taxa and get deposited in soil, to reconstruct plant community history. Along with better known pollen analysis, phytolith analysis allows studying the history of establishment of ecosystems, improves our understanding of vegetation dynamics, provides insights into the possible future of ecosystem development. Phytolith analysis becomes a new and powerful tool in paleoecology, providing additional data about qualitatuive and quantitative composition of the plant communities in the past.
Key words: phytolith analysis, alpine communities, northwestern Caucasus, paleoecology

Introduction

A few articles discuss the phytolith compositon of the alpine plants in the Caucasus (Kiseleva 1992, Blinnikov 1994). Successful application of phytoliths in the paleoecological research of vegetation in the area is, however, impossible without sufficent knowledge of the composition and diversity of phytolith assemblages in the modern soils. This is due to the fact that not all the plant taxa produce recognizable phytoliths, and also phytoliths of similar shapes can occur in unrelated plant species (Twiss,Suess and Smith 1969, Kiseleva and Knyazev 1984, Piperno 1988, Kiseleva 1989).

The goal of our work was to explore recent phytolith assemblages of the nine types of alpine and subalpine plant communities in the Northwestern Caucasus, and to compare these data with the composition of the contemporary plant communties on this territory. Such assemblages can later be used as a baseline for future reconstructions of the historical dynamics of the alpine vegetation in the area.

Material and methods

The samples were collected in August of 1991, 1992, and 1993 at the alpine ecological research station Malaya Khatipara in the Teberda Nature Reserve. They were gathered from under the communities of 9 types: alpine lichen heaths, *Festuca varia*-dominated alpine grasslands, *Geranium gymnocaulon- Hedysarum caucasicum* dominated alpine meadows, snow bed communities, alpine bogs, forb-dominated subalpine meadows, ruderal tallgrass subalpine meadows, *Bromus variegata-Calamagrostis arundinacea* dominated subalpine grasslands, *Juniperus* and *Rhododendron* shrub communities, and pine forests with *Calamagrostis* near the timberline. Most of these communities were characterized in the earlier papers (Onipchenko *et al.* 1987, Pavlova and Onipchenko 1992, Onipchenko 1994). Table 1 contains data on occurences and frequency of the most common species on the plots we obtained our phytolith samples from. Scientific names of plants are given according to Vorobyeva and Kononov (1991) and Onipchenko (1994).

Our classification of phytolith forms was based primarily on the earlier classification developed for this area (Blinnikov 1994). For the purpose of our work, we distinguished the following principal phytolith shapes (Fig. 1):

1) plates, rectangular or oval from above, trapezoid-like from the side, with more or less straight edges;
2) wavy-edged plates, typically with lobes or waves along the edge, otherwise very similar to 1);
3) conic phytoliths of sedges (*Carex* spp.);
4) so called "hats" (Smithson 1958), coming from short cells in the epidermis of grasses of Festucoid type;
5) forms from long epidermis cells of grasses;
6) hairs and prickles;
7) branched rods of *Nardus stricta* (Smithson 1958);
8) "maces" and "needles" of *Pinus silvestris* L., and
9) phytoliths of "bog group", including spiked forms, large epidermal phytoliths of *Cirsium* spp. and special type of phytoliths from *Carex nigra* L.

The soil samples were collected from the upper topsoil and litter (0-1 sm). Overall, the samples were taken from 61 sample plots from all 9 types of communities mentioned above. Vegetation on each sample plot was described on the area of 1 to 20 square meters.

To obtain phytoliths, we generally followed the common method (Piperno 1988) with some modifications, since we dealt both with plant remains and soil particles in one sample. Samples were thoroughly crushed in porcelain mortar. Large pieces of plant material were cut into smaller pieces (0.3-0.5 mm) with scissors. The sample than was sieved through a sieve with 1000 mkm mesh size to get rid of the large soil aggregates. Sample of 2 to 4 g was boiled for 2.5-3 hours in concentrated nitric acid with potassium chlorate to destroy the organic matter. The remaining suspension was gravitationaly sedimented and treated with 10% solution of hydrochloric acid to

	ALH		FVG		GHM		SBC		BOG		SUB		PIN		JP
	o	c	o	c	o	c	o	c	o	c	o	c	o	c	o
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Aconitum nasutum											6	+			3
Aconitum orientale											13	5			
Agrostis vinealis	11	+	60	2	30	+	33	+	50	1	19	+			
Alchemilla caucasica	33	1	20	+	20	+					25	+			
Alchemilla vulgaris									33	3	19	2			1
Anemone speciosa	78	2									6	+			
Antennaria dioica	67	3													
Anthemis cretica	44	+	20	1	20	+	33	+							+
Anthemis macroglossa											31	1			
Anthemis marshalliana	44	1			10	+					19	+			1
Anthoxanthum odoratum	11	+	40	1	100	2	56	1	100	2	13	+			
Anthriscus sylvestris											25	8			
Arenaria lychnidea	56	1					11	+			13	+			
Astrantia maxima					10	+					44	1			
Betonica macrantha					20	+					56	3			
Briza marcowiczii									67	5					
Bromopsis variegata	11	2	100	5							25	4			
Bupleurum falcatum					20	+					50	3			
Calamagrostis arundinacea											44	10	100	23	3
Campanula tridentata	100	6			30	+	33	11	17	1	13	+			
Campanula collina	22	+	60	1	40	+					50	1	60	1	2
Carex atrata					80	1	56	1			13	+			1
Carex nigra									83	9					
Carex pyrenaica							67	3							
Carex sempervirens	44	1					11	+	33	1					
Carex umbrosa	100	6	80	5					33	1	25	+			1
Carum caucasicum	100	2					33	2	100	3	6	+			+
Carum meifolium					70	1	33	1	17	+	13	+			
Catabrosella variegata					10	+	100	4							
Centaurea cheiranthifolia	11	+	40		1						13	+			
Cephalaria gigantea											50	5			
Cerastium cerastoides							11	+	50	1					
Cirsium munitum					30		+				6	1			
Cirsium simplex									83	20					
Corydalis conorhiza							67	1							
Crepis glabra									50	3					
Cruciata laevipes											31	+			
Deschampsia caespitosa									33	1					
Deschampsia flexuosa	11	+			70	3	11	+			6	+	20	3	+
Erigeron uniflorus	44	+			10	+					6	+			
Eriophorum vaginatum									33	3					
Eritrichium caucasicum	44		+								6	+			
Euphrasia ossica	44	+	20	+			11	+	83	+	19	+			
Festuca brunnescens					90	2	11	+	17	+	19	+			
Festuca ovina	100	8	20	1	30	1	44	+	33	1	13	+			1
Festuca varia			80	35	50	2					44	4			1
Galium verum			80	2							6	+			
Gentiana pyrenaica	78	2	20	+			11	+	67	+	6	+			
Gentiana verna	33	+									19	+			
Gentiana septemfida	33	+			10	+					19	+			3
Geranium gymnocaulon					90	29	11	+	17	+	6	1			
Geranium sylvaticum											44	2			
Gnaphalium supinum							78	3							
Hedysarum caucasicum			40	1	100	16			17	+	38	2			
Helictotrichon versicolor	78	3							17	+	25	2	20	1	1
Hieracium macrolepis					30	+					6	+	20	1	+

Table 1 continued

Table 1 continued

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Hieracium umbellatum													60	1	
Hyalopoa pontica							56	2							
Hypericum linarioides			40	1											
Juniperus communis											6	+	20	1	80
Leontodon hispidus			20	4	90	5					19	+	20	+	
Luzula multiflora					30	+	33	1	100	1	6	+			
Luzula spicata	67	+					11	+			13	+			
Matricaria caucasica					70	1	33	+	17	+					
Millium effusum											25	7			
Minuartia aizoides					60	1	44	4							
Minuartia circassica	67	1			10	+					13	+	20	1	+
Nardus stricta					80	6	78	3	100	11	13	+			
Orchis salina									50	+					
Oxalis acetosella													40	3	
Oxytropis kubanensis	33	4									6	1			
Pedicularis caucasica	33	+													
Pedicularis comosa	44	+									19	+			
Pedicularis condensata					50	+			33	+	13	+			
Pedicularis nordmanniana			40	+			100	2	67	1					
Phleum alpinum					70	2	44	+	50	3	6	+			
Pinguicula vulgaris									33	+					
Pinus silvestris														100	54
Plantago atrata	11	+	40	3	10	+					13	+	20	+	
Poa longifolia					30	+					38	2			
Poa nemoralis													40	1	2
Polygonum bistorta	22	+									44	1			1
Polygonum viviparum									33	1					
Potentilla crantzii							33	1			6	+			
Potentilla gelida	44	+													
Potentilla erecta									33	3					
Primula algida	33	+									6	+			
Primula auriculata									67	2					
Pulsatilla aurea					40	4					6	+	20	2	
Ranunculus caucasicus											25	1			
Ranunculus oreophilus	22	+	60	+	50	4			50	1	31	+	20	1	+
Rumex alpestris					50	3					25	+			
Rumex alpinus											31	6			
Scabiosa caucasica	11	+									31	2	20	+	
Scorzonera cana	11	+			60	1					6	+			
Sedum tenellum	11	+			40	+	44	1			6	+			
Sempervivum caucasicum					30	+					6	+			
Senecio kolenatianus					40	+					13	+			
Seseli alpinum											13	+	100	1	2
Sibbaldia procumbens					40	1	100	21	50	4					
Swertia iberica									33	1					
Taraxacum stevenii	22	+					100	11	50	1	19	+	20	+	
Trifolium ambiguum											50	2			
Trifolium polyphyllum	56	6									6	+			
Vaccinium vitis-idaea	67	3									6	+			3
Veratrum album					10	+			50	+	19	1			
Veronica gentianoides	78	+	20	+	50	1					25	+			
Vicia cracca											25	1	40	1	

Table 1. Occurence and average vascular plant coverage of the alpine and subalpine communities; o - occurence on the plots, %; c - average coverage, %; + - less than 1%; ALH - alpine lichen heaths; FVG - *Festuca varia* grasslands; GHM - *Geranium-Hedysarum* meadows; SBC - snow bed communities; BOG - alpine bogs; SUB - subalpine meadows and grasslands; PIN - pine forests; JP - *Juniper* shrub community. The table contains all the species having occurence over 25% and/or average coverage over 2%.

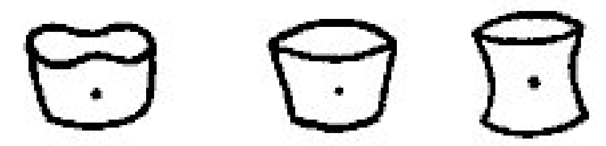
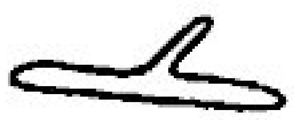
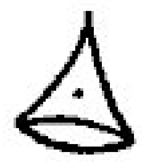
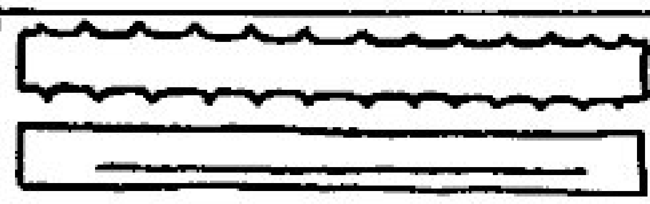
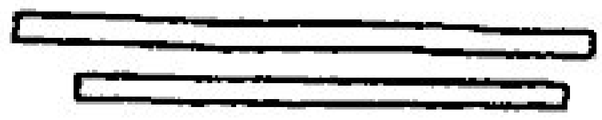
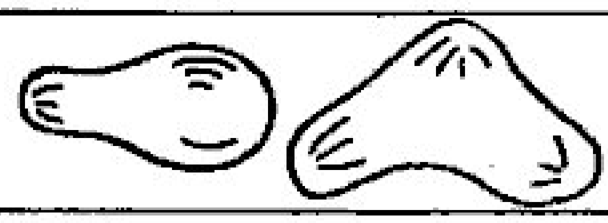
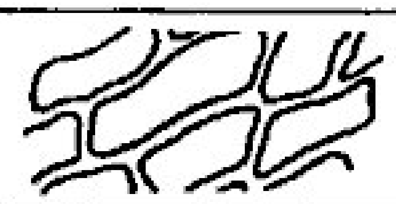
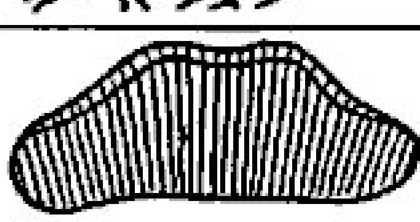
Phytolith Type	Shape	Comments
1. Hats		with keel without keel
2. Straight-edge plates		rectangular,oval, parallelogram, etc.
3. Wavy-edge plates		
4. Branched rods		*Nardus stricta L.*
5. Conical		*Carex spp.*
6. Long cells		
7. Hairs		including prickles, microhairs, etc.
8. Needles		width<<length
9. Maces		large amorphous forms
10. Spiked		
11. Phytoliths of *Cirsium spp.*		epidermal silicified cells
12. Phytoliths of *Carex nigra L.*		species-specific

Fig. 1. Main phytolith types found in the subrecent phytolith assemblages of alpine and subalpine communities.

remove carbonates and other salts. Finally, the residue was washed three times with distilled water.

The phytoliths were examined on temporary slides in glycerine under a regular optical microscope MBI-1. In order to obtain reliable data, we counted at least 250 to 300 phytoliths in each slide, which is usually considered the number sufficient for reliable analysis (Piperno 1988).

Results and discussion

Phytolith assemblages under alpine lichen heaths (ALH) typically contain considerable percentage of short cell "hat" phytoliths, of festucoid grasses (44% of all forms). Other typical festucoid forms are less frequent: straight-edge plates (23%), wavy-edged plates are even more rare (14%). There is also small percentage of other forms in the assemblage, i.e. conical phytoliths of *Carex* spp. (6%), hairs of grasses and some forbs (7%), and long-cell phytoliths of grasses (6%). Branched rods of *Nardus stricta*, "maces" and "needles" of pine, and all the "bog group" phytoliths (spiked forms, highly specific phytoliths of *Carex nigra*, and phytoliths of *Cirsium)* are completely absent from the assemblage.

Hats with profound keel are most likely produced by *Festuca ovina* L., whereas hats lacking such can be

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Subrecent phytolith assemblages of alpine communities

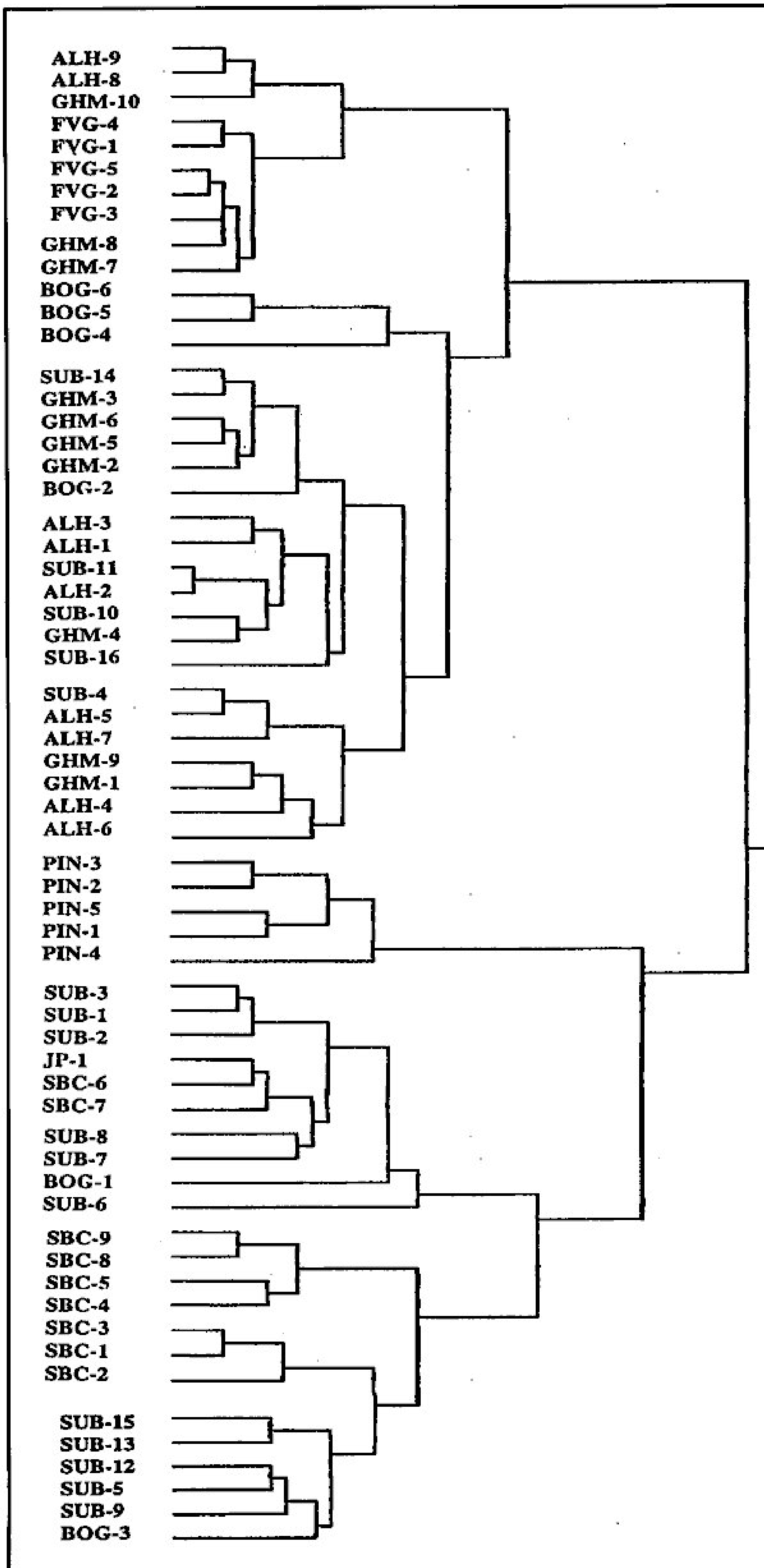

Fig. 2. Results of the cluster analysis of subrecent phytolith assemblages using MULVA-4: ALH - alpine lichen heaths; FVG - *Festuca varia* grasslands; GHM - *Geranium-Hedysarum* meadows; SBC - snow bed communities; BOG - alpine bogs; SUB - subalpine meadows and grasslands; PIN - pine forests; JP - *Juniper* shrub community

	ALH n=9	FVG n=5	GHM n=10	SBC n=9	BOG n=6	PIN n=5	JP n=1	SUB n=16
Hats	44±4	57±1	43±4	9±1	30±5	0	10	22±2
Straight-edge	23±2	30±1	31±2	40±3	24±5	28±2	52	39±3
Wavy-edge	14±1	5±0,3	11±2	29±2	18±4	27±2	23	22±2
Branched	0	0	1±0,2	5±2	2±0,5	0	1	0
Conical	6±1	4±0,3	6±0,8	3±0,8	2±0,5	0	2	3±1
Long cell	6±1	1±0,6	5±0,7	6±0,4	2±0,3	2±0,7	6	5±0,9
Hairs	7±1	2±0,4	3±0,7	8±0,9	5±0,7	4±0,6	5	9±1
Needles	0	0	0	0	0	32±3	0	0
Maces	0	0	0	0	0	7±2	0	0
Spiked	0	0	0	0	3±0,5	0	2	0
ph. of *Cirsium*	0	0	0	0	5±1	0	0	0
ph. *Carex nigra*	0	0	0	0	9±2	0	0	0

Table 2. Composition of phytolith assemblages of the communities studied, %; n - number of relevees. For all communities, except juniper shrub communtiy we provided average values ± standard error.

produced both by *Helictotrichon versicolor* (Vill.) Pillger and *Nardus stricta* L. Straight-edge plates are probably produced by F.ovina and *Bromopsis variegata* (Bieb.)Holub. Wavy-edge forms can belong to *H.versicolor*. Hair-type phytoliths are produced by *Festuca varia* Haenke, *H. versicolor* and *Campanula tridentata* Schreb.(few in the latter). Phytolith composition of all the samples is nearly identical. Both typical and accidental phytolith forms are present in all samples.

Phytolith assemblages under *Festuca varia* dominated grasslands (FVG) are characterized by high percentage (over 50%) of large hats with conspicious keel. Such forms probably belong to *F.varia*. Other hats, lacking keel are not as common, and probably belong to *Nardus stricta*. Straight-edge plates derive from *Bromopsis variegata*. Wavy-edge plates, most likely, are coming from *Agrostis vinealis* Schreb., a species occuring on the plots where the samples were taken from. A small number of conical phytoliths can be attributed to *Carex umbrosa* Host, the only widespread sedge species in this community. These assemblages also contain very few branched phytoliths of *N.stricta*, and a few long-cell phytoliths possibly from *A.vinealis*, and *B.variegata*, and hairs of *B.variegata* and *F.varia*.

The assemblages under Geranium-Hedysarum domiated meadow contain: large amount of hats (43%), straight-edge plates (31%), fewer wavy (11%), conical (6%), and long cell forms (5%). The branched phytoliths of *Nardus* are always present, which permits to distinguish this type of communities from ALH.

Hats with keel again belong to *Festuca varia*, and also *Festuca brunnescens* (Tzvel.) Galushko, whereas lacking keel forms probaly belong to *N.stricta* and *Phleum alpinum* L. Characteristically, this assemblage has relatively large percentage of straight-edge plates, coming probably from *Anthoxantum odoratum* L. and *Deschampsia flexuosa* (L.)Trin. The assumption that these forms are indeed produced by these species is supported by the fact that as the percentage of the species on the plot decines, so does the percentage of the straight-edge phytoliths in the sample. There are few sedge phytoliths in the samples, and most likely all of them belong to *Carex atrata* L.

The assemblage of snow bed communities (SBC) contain all the first 7 classes of phytoliths (Fig.1). Most numerous are the straigt-edge plates (40%), less numerous are wavy phytoliths (29%), and relatively many branched phytoliths of Nardus (5%). This relatively high frequency of *Nardus* phytoliths can be considered a diagnostic feature of this assemblage.

The straight-edge plates probably belong to *Catabrosella variegata* (Boiss.)Tzvel. and *Anthoxantum odoratum*, wavy-edge forms - to *Ph. alpinum*, *Hyalopoa pontica* (Bal.) Tzvel. and *A.odoratum*. Hats withought keel may belong to *N.stricta*, *C.variegata*, *H.pontica*, *Ph.alpinum*. A small number of silicified hairs were noted, probably belonging to *A.odoratum* and *Ph.alpinum*.

There were also present long-cell phytoliths, probably from *C.variegata*, *A.odoratum* and *Ph.alpinum*., and conical forms of *Carex from C.pyrenaica* Wahl., *C.atrata* and *C.oreophila* C.A.Mey.

The assemblages from pine forests with *Calamagrostis arundinacea* (L.)Roth contain specific phytoliths, not present in any other assemblage. These are elongated forms, which we referred to as "needles", and also "maces" (oval-shaped somewhat elongated phytoliths with small rounded pores (see Table 2, and also Golyeva et al. 1987)). The hats, branched phytoliths of *Nardus* and conical phytoliths of sedges are absent, which also helps to distinguish this community type from all others. Besides "needles" and "maces" the assemblage contains considerable number of wavy and straight-edge plates, belonging mostly to *Calamagrostis arundinacea*. Some of the staright-edge forms may also belong to *Poa nemoralis*. Long cell forms and hairs also found here probably belong to the same two species of grasses.

The assemblages from subalpine meadows are represented by straight-edge plates (39%), equal percentage of wavy forms and hats (22 % each), hairs (9%), long-cell forms (5%) and conical *Carex* phytoliths (3%). As mentioned above, we have studied 4 types of subalpine meadows: forb-dominated meadows, ruderal tall-grass meadows, *Bromus variegata* dominated grasslands and grasslands dominated by *Calamagrostis arundinacea*. All these communities produce very similar phytolith assemblages. Only ruderal tall-grass meadows produce slightly different (percentagewise) assemblages with absolute dominance of straight edge plates over hats and wavy-edge forms (14% and 11% respectively). There are very few phytolith producers in ruderal meadows, so the phytolith composition is determined by one-two species (mostly *Millium effusum* L.).

Hats in forb-dominated subalpine meadows are produced by *F.varia*, straight-edge plates - by *Poa longifolia* Trin. In the assemblage of *Bromus* dominated grasslands hats, probably, belong to *F.ovina* and *H.versicolor*, straight-edge and wavy-edge plates to *B.variegata* and *H.versicolor*. In the assemblage of *Calamagrostis* dominated grasslands hats are produced by *F.varia*, whereas plates by *Calamagrostis arundinacea*.

The high-elevation bogs and alpine riparian communities produce 3 distinct types of phytoliths, not occurying in any other assemblage. These are elongated froms with protuberances, or "spikes", peculiar, non-conical phytoliths of *Carex nigra*, and epidermal phytoliths, apparently belonging to *Cirsium* spp.(see Fig.1). We were unable to determine which species produce the first of these three froms, due to lack of studies of the phytoliths in bog plants in our area. Bog assemblages also contain phytoliths of all 7 classes described earlier. Among them hats are the most common (30%)(Table 2), followed by straight-edge (24%) and wavy edge (18%) forms. Hats can be produced by *F.brunnescens*, *F.ovina*, *D.flexuosa*, *N.stricta*, straight-edge plates by *A.odoratum*, *D.flexuosa*, *F.ovina* and *N.stricta*, and wavy-edge forms - by *Agrostis vinealis and A.odoratum*. Conical shapes may belong to *C.nigra and C.umbrosa*.

The assemblages of juniper shrub community are characterized by high percentage of straight-edge plates (51%), with lower percentage of wavy forms (23%) and hats (10%). A few spiked forms, similar to those in bogs, were found here. Since *Juniperus communis* L. does not produce distinguishable forms of phytoliths, the assemblage contains the phytoliths produced by other members of this community. Straight-edge plates may belong to *C.arundinacea*, *D.flexuosa*, and *F.ovina*, wavy forms - to *C.arundinacea* and *H.versicolor*, hats - to *F.varia* and *F.ovina*.

The *Rhododendron*-dominated shrub communities produce too few phytoliths to enable analysis. *Rhododendron caucasisum* Pall., the principal dominant, does not produce recognizable phytoliths. Other components of this community either lack phytoliths themselves, or produce them in unsignificant quantities.

In order to better compare the phytolith assemblages we undertook analysis of clasters using MULVA-4 program. The results are presented on Fig.2. The resulting dendrogramm demonstrates that pine forests are most easily distinguishable from all other communities, since they and they alone contain "needles" and "maces", belonging to *Pinus silvestris* and *Dicranum scoparium*. *Festuca varia* dominated alpine grasslands are also easily distinguishable, since they have over 50% of hats *(F.varia, F.ovina, F.brunnescens)* in the phytolith complex.

Snow bed communities can be easily distinguished from all others, since they produce a lot of plates, but very little hats, and also considerable amount of branched phytoliths of *Nardus*. Bogs can be also eailsy recognized, since their assemblages contain phytoliths of the "bog group", i.e. spiked forms, and special phytoliths of *Carex nigra* and *Cirsium* spp.

Phytoliths produced by alpine lichen heaths and *Geranium-Hedysarum* dominated alpine meadows are very similar to each other, but as a group can be easily distinguished from all other communities. The only good distinction between these two assemblages is the presence of branched phytoliths of *Nardus* in the meadow assemblage. The branched phytoliths were completely absent from the ALH assemblage.

Among subalpine communities ruderal forb-dominated meadow has the most distinct assemblage, with the greatest percentage of straight-edge plates and very low content of hats and wavy plates. As had been expected, the *Calamagrostis*-dominated grasslands produce maximum amount of *Calamagrostis* phytoliths among all the communities studied. *Bromus*-dominated grasslands have a considerable percentage of conical phytoliths of *Carex* in their assemblages. It is apparent that using phytolith analysis types of subalpine communities are easily distinguishable from the alpine communities and from each other.

We compiled the key to provide a quick way for identification of the communities in the alpine and subalpine zone of Teberda Nature Reserve using phytoliths:

1. Phytolith assemblage contain substantial percentage of "needles" and "maces" .... *pine forest with Calamagrostis*

-"Needles" and "maces" are completely absent.........2

2. All, or almost all types of phytoliths from "bog group" are present (i.e., spiked forms, specific non-conical forms of *Carex nigra*, epidermal phytoliths of *Cirsium)*... .... *alpine bogs*

- "Bog group" phytoliths are absent..............................3

3. Large hats with keel make up over 50% of the assemblage............*Festuca varia dominated alpine grasslands*

- Hats make up less than 50% of the assemblage 4

4. Hats occur unfrequently (less than 10%), there are many branched phytoliths of *Nardus*.......................... .... *snow bed communities*

- Hats make up 20 to 40% of the assemblage 5

5. Hats make up not more than 30%, there are many straight-edge plates,but few wavy-edge plates.......... .... *subalpine meadows*

- Hats make up more than 30%.................................... 6

6. Hats comprise 30 to 45 % of the assemblage, straight-edge plates make up 15 to 20%, wavy-edge forms are even less common. There are also conical phytoliths of *Carex*, long-cell phytoliths and silicified hairs present. Branched phytoliths are completely absent................ .... *alpine lichen heaths*

- The assemblage looks very similar, branched phytoliths are always present. ....*Geranium-Hedysarum dominated alpine meadows*

We hope that the subrecent phytolith assemblages described in this article will allow to interpret the paleoassemblages of phytoliths from the alpine soils, which would present new opportunities to reconstruct the history of vegetation in the Caucasus.

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