

Zeitschrift: Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule, Stiftung Rübel, in Zürich

Herausgeber: Geobotanisches Institut, Stiftung Rübel (Zürich)

Band: 115 (1994)

Artikel: Experimental investigation of alpine plant communities in the Northwestern Caucasus

Autor: Onipchenko, Vladimir G. / Blinnikov, Mikhail S. / Senov, Andrej V.

Kapitel: 2: Phytolith analysis and holocene dynamics of alpine vegetation

DOI: <https://doi.org/10.5169/seals-308979>

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 28.03.2026

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

2. Phytolith analysis and holocene dynamics of alpine vegetation

Mikhail S. BLINNIKOV

2.1. INTRODUCTION

Development of industry and agriculture in the Northwestern Caucasus has considerably effected vulnerable mountain ecosystems during the last decades. Constantly increasing public demand for land is threatening yet untouched landscapes and unique wildlife. The necessity of wilderness protection in the Caucasus requires sufficient knowledge of the history of regional ecosystems. In the present paper the attempt has been made to investigate the history of alpine communities using the paleoecological method of phytolith analysis (PIPERNO 1988).

The method yielded interesting results in numerous research works on plant community history throughout the world (CARBONE 1977). Many papers regard the history of wetlands, prairies, boreal and tropical forests and other ecosystems from the viewpoint of the phytolith analysis (BAKER 1959, WITTY and KNOX 1964, WILDING and DREES 1971, PALMER 1976, KISELEVA 1982, ANDREJKO and COHEN 1984, PIPERNO 1991).

Still, the works in which this method is applied to the histories of alpine communities are very rare. In this context, the possibility of using phytolith analysis in the study of alpine ecosystem history is investigated in this paper.

As expressed by ROVNER (1971), phytoliths exhibit three important features, enabling their use in paleoecology: they withstand decomposition, exhibit considerable morphological diversity and occur in the soil in sufficient quantities to reflect the nature of the entire parent community. Phytoliths composed of silicon dioxide or silica are one of the most durable plant fossils (PIPERNO 1991). They are very diverse in size, shape and colour, and therefore can reflect the diversity of parent plant species (e.g. METCALFE 1960, TWISS et al. 1969, BROWN 1984).

PIPERNO (1988) reports important data on phytolith occurrence in different plant taxa, including many tropical families. Despite certain limitations,

restricting wide-spread application of this method, it was quite workable under very diverse conditions. The first limitation is that not all plants are significantly, if at all, represented by adequate amounts of recognizable phytoliths. In the temperate zone, most articles chiefly concern grasses, sedges, composites and a few other families as principal phytolith producers. In many papers grasses are considered the main source of silica phytoliths in temperate communities (SMITHSON 1958, BLACKMAN 1971, KISELEVA 1982, BROWN 1984, DINESMAN et al. 1989).

Second, a single species of some taxa, e.g. grasses, can produce over a dozen different forms, complicating analysis. Therefore, it is crucially important to conduct research on a site-to-site basis, carefully examining local peculiarities of silica bodies distribution in plants (PIPERNO 1988). Keeping in mind these restrictions, reliable data on plant community history can be expected.

An impressive body of results on historical changes in the mountain environment and distribution of vegetation in the Holocene has been collected in the Caucasus in many recent research projects (MAKHOVA and PATYK-KARA 1961, TUSHINSKY 1962, SEREBRANY et al. 1980, SOKOLOVA 1982, MARGALITADZE and KIMERIDZE 1985, SAVINETSKY 1992). Most works deal mainly with broad scale transitions in climate and general changes in distribution of major vegetation types. Only a few articles discussed local historical changes in composition of particular plant communities (KHAPAEV 1976, PAVLOVA and ONIPCHENKO 1992). Probably, this gap is because the most widely used paleoecological method of pollen analysis usually provides data on a more broad than local level. Transition of pollen and spores by wind and alien pollen input from neighbouring communities can significantly distort local pollen spectra.

If applied in the study of open mineral soils instead of buried soils, pollen analysis is also seriously effected by the intensive processes of zoogenic and cryogenic disturbances and the high rate of destruction by soil reducers. It seems that phytolith analysis, being very effective specifically on a local scale, could be successfully applied to the investigation of a particular community history. Alpine conditions of the Northwestern Caucasus are probably favourable for phytolith preservation in soils because of the cold humid climate, acidic soils with high humus content and moderately low microbiological activity (MAKAROV 1985).

In the present work the attempt is made to apply phytolith analysis in the study of the history of four types of alpine communities. The task was: first, to find out, if phytoliths occur in alpine soils in quantities sufficient for analysis, second, to explore their distribution in soil profiles under four types of

communities and to draw phytolith diagrams, third, to interpret Holocene dynamics of different alpine communities from the viewpoint of phytolith analysis and fourth, to compare these results with data obtained earlier in the same place by means of pollen analysis (PAVLOVA and ONIPCHENKO 1992). We also tried to attribute phytolith forms, found in soils, to specific taxa of alpine plants (BLINNIKOV 1992).

Acknowledgement

We express our sincere gratitude to all members of the Moscow State University expedition in Teberda State Reserve for their help in gathering field materials. The author especially thanks N. Kiseleva and all staff members of the Laboratory of Historical Ecology of the Institute of Evolutionary Morphology and Ecology of Animals for providing laboratory techniques and consultations. Thanks also are due to I. Hammamenyuk for provided laboratory materials and the faculty members of the Dept. of Soil Sci. of MSU N. Dronova, T. Ulyanova, V. Ivanov and A. Smagin for guidance in the use of laboratory equipment. In particular, we thank A. Bobrov for his valuable assistance in taking SEM photographs and A. Golyeva for the useful comments on our Diploma thesis. The work was carried out under the the supervision of V. Onipchenko, whose kind assistance was constant and encouraging.

2.2. METHODS

Samples of plants and soils were gathered in the study area of Moscow State University on Mt. Malaja Hatipara, described in detail in Chapter 1 of this volume, in the following communities:

1. Alpine lichen heaths (ALH)
2. *Festuca varia* dominated grasslands (FVG)
3. *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows (GHM)
4. Snow bed communities (SBC).

We analyzed soil samples, taken from four soil profiles under four sample areas, namely ALH(U), FVG(U), GHM(L) and SBC(L) (see Chapter 1.4). A sample of about 100 g was taken from each soil layer in the following way: one sample per each 2 cm of soil profile from 0-2 to 8-10 cm, and one sample per each 5 cm from 10-15 cm to the lower limit of horizon B (25-40 cm dependent on community type).

Soils were treated according to the slightly modified method suggested by PIPERNO (1988). Thirty grams of sample soil were stirred in 15 ml of 4% solution of sodium pyrophosphate to loosen phytoliths from soil aggregates. The obtained suspension was sieved through a 250 µm sieve to remove coarse

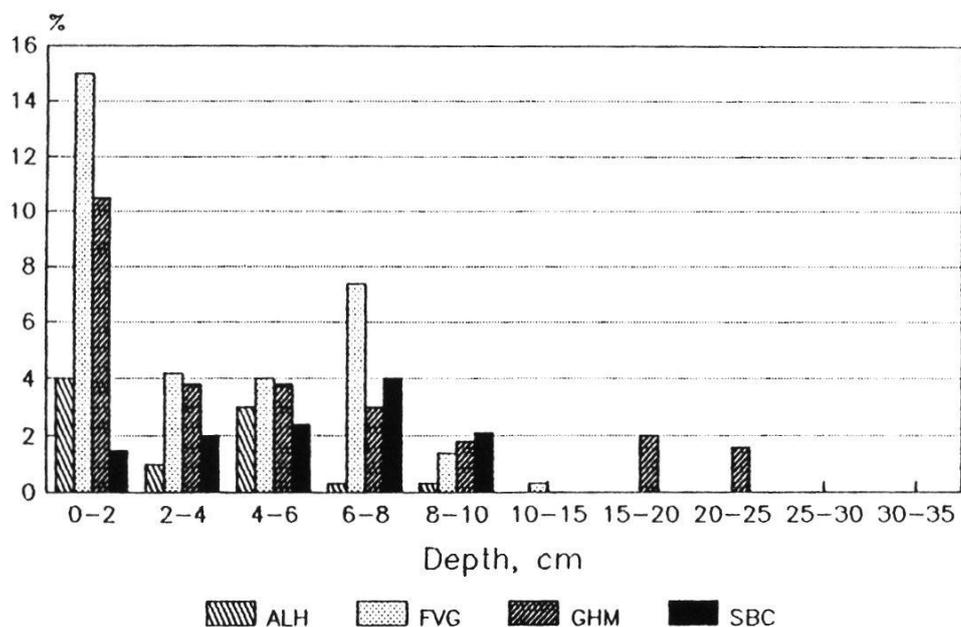


Fig. 2.1. Frequency of opal phytoliths in the silt fraction (10 -50 μm) of alpine soils in 4 communities (percentage of total number of grains in the fraction).

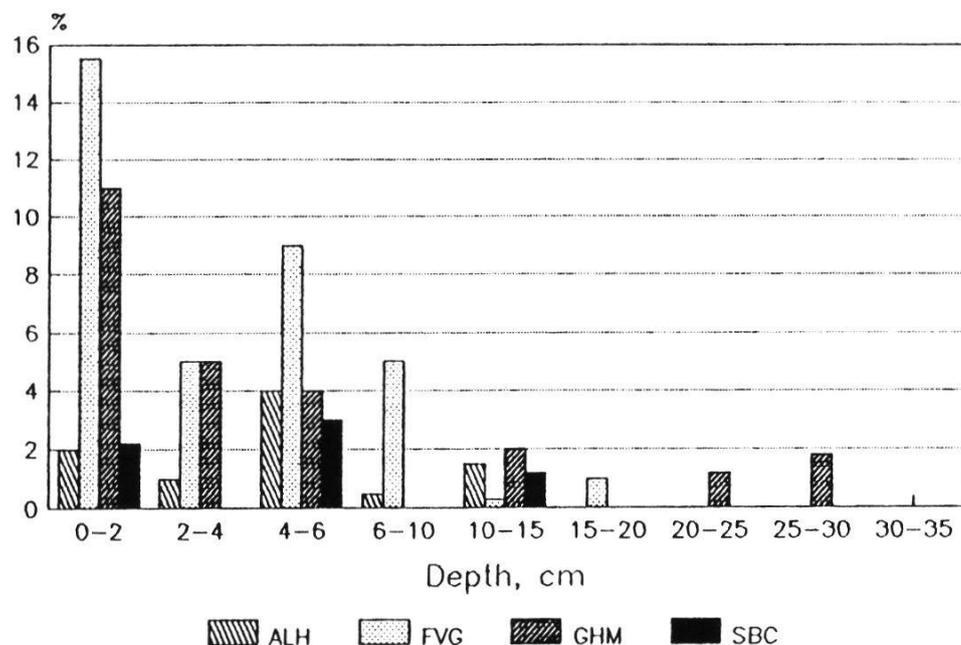


Fig. 2.2. Frequency of opal phytoliths in the fine sand fraction (50 -250 μm) of alpine soils in 4 communities (percentage of total number of grains in the fraction).
 ALH = alpine lichen heaths, FVG= *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

Table 2.1. Percentage of major groups of phytoliths in alpine grasses, % of the total number of phytoliths in a species.

Species	hats	plates	wavy	long cells	hairs	bran. rods	scuti-form	sum of phytol.
<i>Agrostis vinealis</i>	12.5	9.5	21.0	32.0	6.5	-	-	266
<i>Alopecurus ponticus</i>	12.5	76.5	-	3.0	3.5	-	-	253
<i>Anthoxanthum odoratum</i>	2.5	60.0	15.5	7.0	15.0	-	-	74
<i>Briza marcowiczii</i>	5.0	5.0	81.0	5.0	-	-	-	238
<i>Bromopsis variegata</i>	<1.0	41.0	10.0	10.0	7.0	-	29.0	230
<i>Calamagrostis arundinacea</i>	-	32.0	23.5	35.5	7.0	-	-	127
<i>Catabrosella variegata</i>	59.0	36.0	-	4.0	-	-	-	122
<i>Deschampsia flexuosa</i>	65.0	22.0	-	3.0	2.5	-	-	145
<i>Festuca brunnescens</i>	90.5	6.0	-	2.0	-	-	-	162
<i>Festuca ovina</i>	80.0	15.0	-	3.0	<1.0	-	-	396
<i>Festuca varia</i>	88.0	1.0	-	9.5	<1.0	-	-	211
<i>Helictotrichon versicolor</i>	61.5	8.0	29.0	-	<1.0	-	-	231
<i>Nardus stricta</i>	89.5	1.0	-	6.0	-	3.0	-	412
<i>Phleum alpinum</i>	38.5	4.0	14.0	18.5	-	-	14.5	167
<i>Poa alpina</i>	53.0	44.0	7.0	13.0	9.0	-	-	161
<i>Trisetum flavescens</i>	18.0	56.0	3.5	16.5	<1.0	-	-	239

sand and plant tissues. Using the "dropper" method (VADYUNINA and KORCHAGINA 1986) and gravily sedimentation, clays were removed and fine sand (50-250 μm) and silt (10-50 μm) fractions were separated. The latter two fractions were washed with a 10% solution of hydrochloric acid to remove carbonates and other salts. Next samples were centrifuged at 2000 rpm for five minutes and washed then three times with distilled water. Organic matter was removed by adding concentrated nitric acid and potassium chlorate with subsequent boiling in sand a bath for one hour.

A heavy liquid solution of potassium and cadmium iodides, first used by CARBONE (1977), were used to extract phytolith from the samples. Specific gravity of the solution was about 2.1. Floating phytoliths were transferred to a polyethylene microfilter with pores of 1 μm diameter, then washed with distilled water and dried. Finally, phytoliths were examined in glycerine under petrographic and regular optical microscopes at 70 x to 600 x. In each sample, at least 200 phytoliths were counted, the amount considered sufficient by many authors (PIPERNO 1988). The percentage of phytoliths in the total number of soil grains in a sample (Fig. 2.1 and Fig. 2.2) and the percentage of different phytolith forms were determined (Fig. 2.3 and Table 2.2). The individual phytolith shapes were identified in reference to the table of phytolith content in different grasses of the alpine zone (Table 2.1), based on previous research (BLINNIKOV 1992).

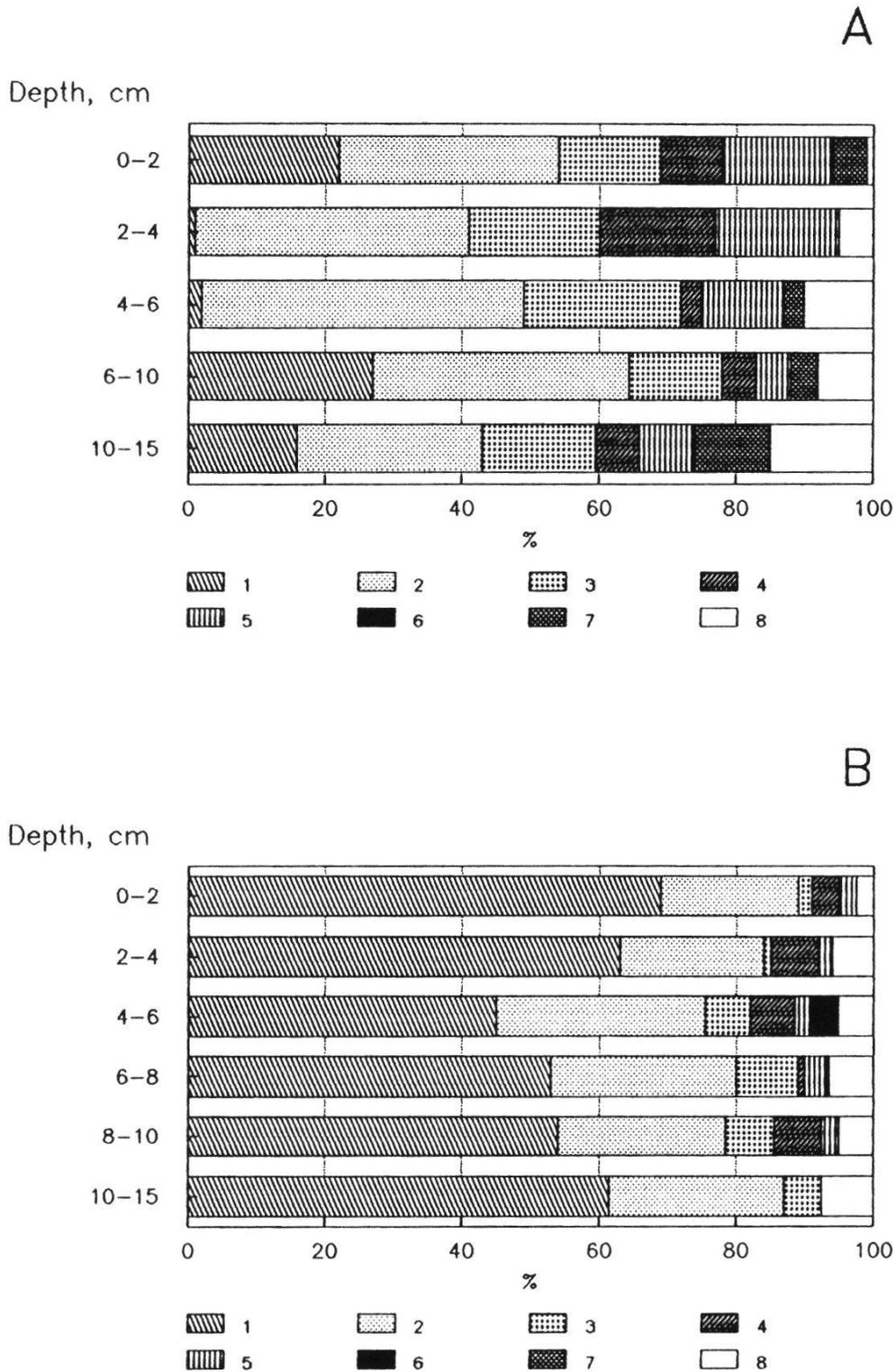
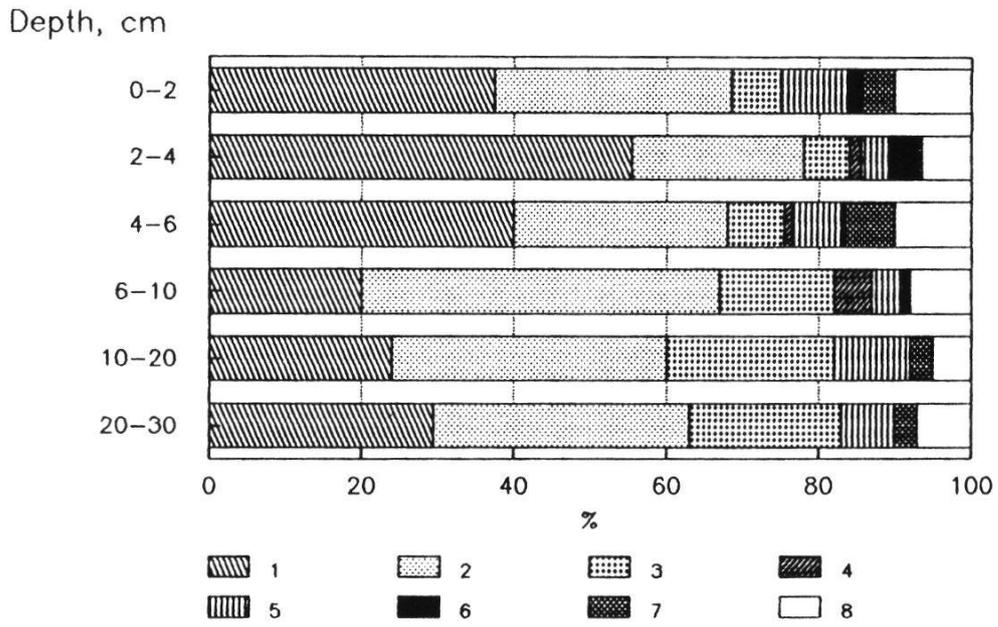


Fig. 2.3. Frequency of 8 major phytolith groups in alpine soil profiles under 4 communities: A = ALH, B = FVG, C = GHM, D = SBC; 1 = hats, 2 = straight-edge plates, 3 = wavy-edge plates, 4 = long cells, 5 = trichomes, 6 = branched rods, 7 = cone-shaped, 8 = other forms.

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

C



D

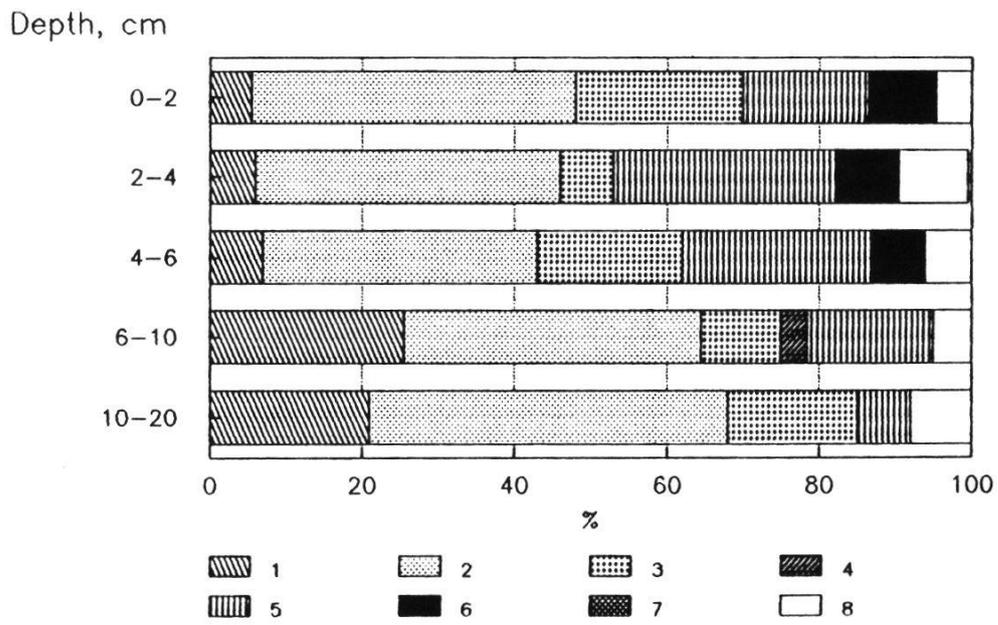


Fig. 2.3. (continued)

Table 2.2. Distribution of principal phytolith forms in 4 soil profiles under 4 types of alpine communities, % of total number of phytoliths in a horizon.

ALH = alpine lichen heaths, FVG = *Festuca varia* dominated grasslands, GHM = *Geranium gymnocaulon* - *Hedysarum caucasicum* dominated meadows, SBC = snow bed communities.

Phytolith principal forms (see fig. 2.5)	Profiles										
	ALH (Upper)					FVG (Upper)					
	0-2	2-4	4-6	6-10	10-15	0-2	2-4	4-6	6-8	8-10	10-15
1	19	1	2	10.0	8.0	67	59	41.5	46.5	40.0	60.5
2	3	-	-	17.0	8.0	<1	4.0	3.5	5.5	12.0	-
3	-	-	-	-	-	<1	-	-	1.0	-	-
4	-	-	-	-	-	<1	-	-	<1.0	2.0	1.0
5	12	31	29	21.0	11.5	8	4.0	13.0	17.0	14.0	15.5
6	3	-	1	2.0	-	4	2.0	8.0	2.0	<1.0	-
7	-	1	-	-	2.0	<1	1.5	-	-	2.5	-
8	3	-	-	2.0	<1.0	-	<1.0	2.0	-	-	1.0
9	11	5	15	8.5	13.5	-	3.0	-	-	-	-
10	-	3	-	-	-	-	-	-	-	<1.0	-
11	-	-	-	-	<1.0	1	1.5	-	<1.0	<1.0	1.0
12	3	-	2	4.0	<1.0	5	9.0	7.5	8.0	7.0	8.0
13	13	14	12	11.0	14.5	<1	-	3.0	5.0	-	5.5
14	2	-	-	-	-	1	<1.0	2.5	3.0	3.5	-
15	-	-	-	-	-	<1	<1.0	<1.0	<1.0	-	-
16	-	5	11	2.5	2.0	-	-	<1.0	<1.0	3.5	-
17	9	10	3	5.0	6.5	-	7.0	6.5	<1.0	4.5	-
18	-	7	-	-	-	4	-	-	<1.0	<1.0	-
19	-	-	-	-	-	-	-	4.0	<1.0	-	-
20	-	-	-	-	-	-	<1.0	<1.0	<1.0	-	-
21	4	-	-	3.5	-	2	1.0	1.5	-	-	-
22	10	7	7	1.5	5.5	<1	<1.0	-	2.0	<1.0	-
23	2	11	5	-	2.5	-	<1.0	1.0	1.0	2.0	-
24	-	-	-	<1.0	-	-	-	-	-	-	-
25	-	-	-	-	-	-	-	-	-	-	-
26	-	-	3	-	-	-	-	-	-	-	-
27	5	-	3	4.0	11.0	-	-	-	-	-	-
28 others	1	5	7	8.0	14.0	3	5.0	5.0	4.5	5.0	-
Total number of phytoliths	103	100	100	117	111	355	310	310	271	114	102

Table 2.2. (continued)

Phytolith principal forms (see fig. 2.5)	Profiles						SBC (Lower)				
	GHM (Lower)						0-2	2-4	4-6	6-10	10-20
	0-2	2-4	4-6	6-10	10-20	20-30	0-2	2-4	4-6	6-10	10-20
1	2.0	5.5	3.5	2	-	7.0	-	-	-	8.5	-
2	35.0	49.5	36.5	17	24.0	21.5	5.5	3.5	7.0	17.0	19
3	-	-	-	-	-	1.0	-	2.5	-	-	1
4	<1.0	<1.0	-	1	-	-	-	-	-	-	1
5	7.5	8.5	15.0	23	11.5	20.5	25.5	23.0	20.0	20.5	21
6	1.5	1.5	-	1	11.5	-	10.0	8.0	10.0	7.0	4
7	4.0	1.0	-	1	1.5	1.0	-	4.5	1.0	1.0	8
8	1.5	<1.0	2.0	2	2.0	1.0	2.0	2.5	2.0	2.5	-
9	5.0	2.5	1.5	6	-	2.0	-	2.0	-	3.5	2
10	-	-	2.0	5	2.0	-	-	-	-	-	-
11	<1.0	-	-	1	-	2.0	-	-	-	3.5	9
12	6.0	7.5	6.0	6	4.0	5.0	5.0	-	1.0	-	-
13	4.5	2.0	5.5	4	7.5	8.0	<1.0	2.0	6.0	9.5	7
14	2.0	3.0	<1.0	10	6.5	5.0	21.5	4.5	8.0	-	6
15	-	-	<1.0	-	5.0	1.0	-	-	5.0	1.0	4
16	-	1.0	1.5	1	3.0	6.0	-	<1.0	-	-	-
17	<1.0	1.5	1.0	5	-	-	-	-	-	3.5	-
18	-	-	-	-	-	-	-	<1.0	-	-	-
19	1.5	3.5	<1.0	1	-	-	9.0	8.0	7.0	-	-
20	4.5	1.0	4.5	4	2.0	2.0	-	2.0	1.0	2.5	2
21	4.0	<1.0	5.5	2	5.0	5.0	4.5	6.0	3.5	3.5	2
22	2.0	2.0	1.0	<1	3.0	2.0	12.0	19.0	21.5	13.0	5
23	3.0	2.0	<1.0	2	2.0	-	-	4.5	-	-	-
24	-	-	-	-	-	-	-	-	-	-	-
25	-	-	1.0	-	-	-	-	-	-	-	-
26	-	-	<1.0	<1	-	-	-	-	-	-	-
27	4.5	<1.0	6.5	-	3.0	3.0	-	-	-	-	-
28 others	10.0	5.0	5.5	5	6.5	7.0	4.5	7.0	7.0	3.5	9
Total number of phytoliths	230	336	200	101	109	102	112	112	84	83	100

2.3. RESULTS

2.3.1. Principal phytolith forms found in alpine plants and soils

We found phytoliths in all 17 grasses and five sedges growing in the study area in the alpine zone (Table 2.1, also BLINNIKOV 1992). Besides that, a much fewer number of silica bodies was found in 15 out of 25 studied species of

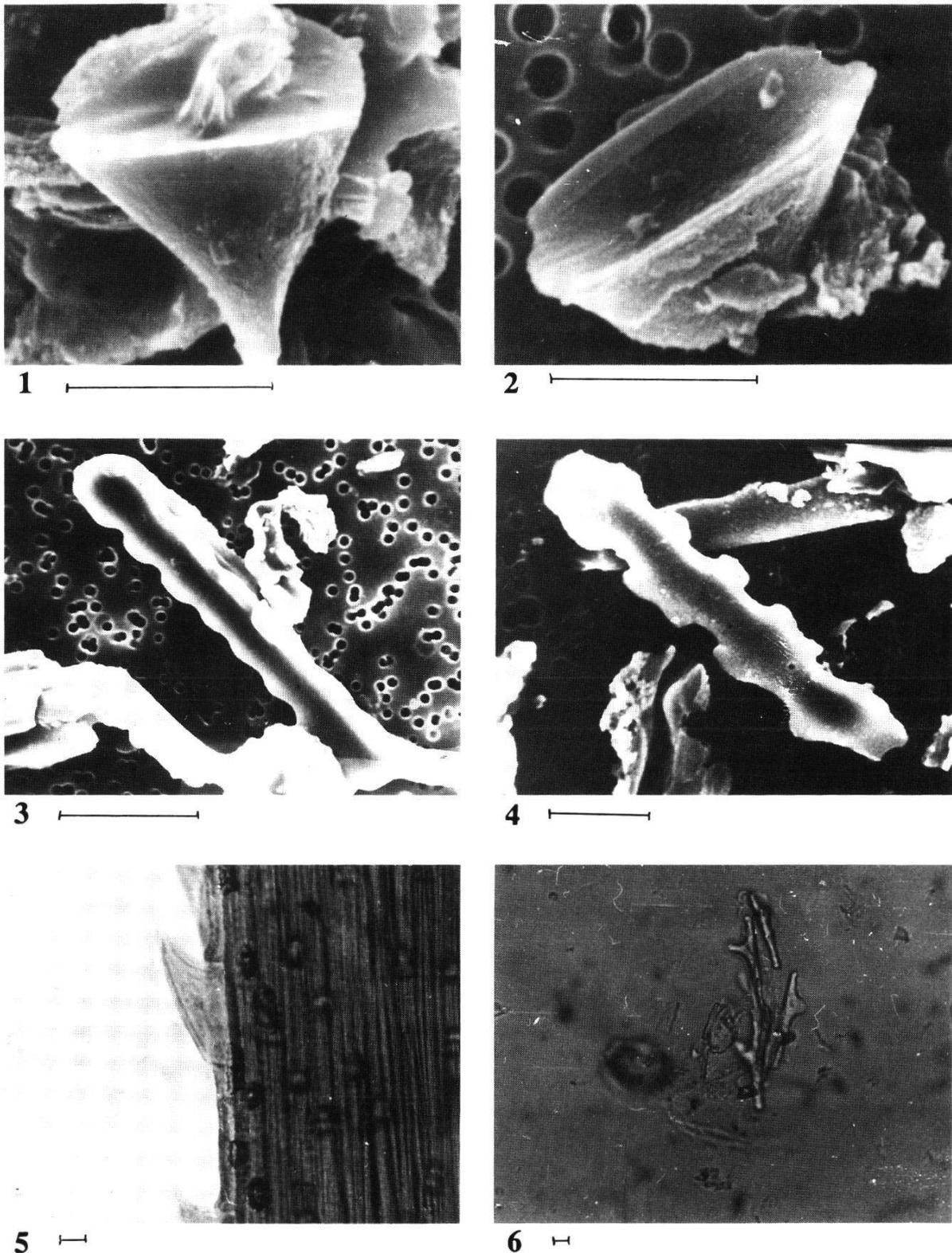


Fig. 2.4. Scanning electron microphotographs of phytoliths from alpine grasses. 1 = keel hat phytolith of *Festuca varia* (group of hats), 2 = simple hat phytolith of *Festuca ovina* (group of hats), 3 = wavy-edge phytolith of *Calamagrostis arundinacea* (group of wavy plates), 4 = lobed phytolith of *Calamagrostis arundinacea* (group of wavy plates), 5 = trichomes on the margin of the leaf of *Helictotrichon versicolor* (trichome group), 6 = branched rods of *Nardus stricta* (branched rod group). The scale is 10 μm .

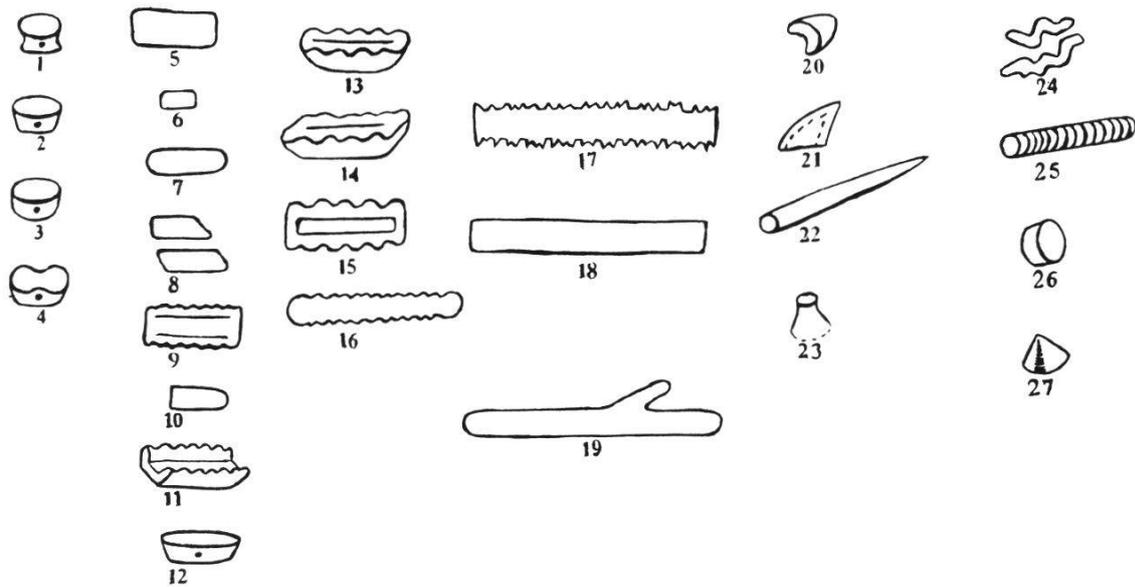


Fig. 2.5. Principal phytolith forms from alpine soils.

1-4 (group of hats): 1 = keel , 2 = simple, 3 = barrellike, 4 = pseudodumbbell; 5-12 (group of straight-edge plates): 5 = rectangular, 6 = small rectangular or round end, 7 = round end, 8 = slanting end, 9 = saw edge, 10 = one round end, 11 = trough, 12 = "boat" phytolith; 13-16 (group of wavy-edge plates): 13 = short with round ends, 14 = short with rectangular ends, 15 = lobed, 16 = long with round ends; 17-18 (long cell group): 17 = saw edge, 18 = straight edge, 19 = branched rods (*Nardus stricta*), 20 = spearheads; 21-23 (trichomes group): 21 = trichomes, 22 = hairs, 23 = hairbases, 24 = "hyphs", 25 = vessels, 26 = round plate, 27 = cone-shaped (*Carex* sp.).

other alpine vascular plants and in the two, most abundant lichens in the study area. Yet only grasses, sedges and, to a lesser extent, some haired dicotyledons, like composites, contributed noteworthy amounts of phytoliths into soil assemblages. In total, about 50 different forms were found in plant material.

However, several important dominants, like *Geranium gymnocaulon* and *Hedysarum caucasicum*, do not accumulate silica at all. Some other species bring certain phytoliths, but at a very insignificant level.

As already mentioned, phytoliths are very diverse in shape and form. Although several more or less fruitful attempts were undertaken (SMITHSON 1958, TWISS et al. 1969, BROWN 1984), there is no well-developed and widely adopted classification (either morphological or genetic) of grass phytoliths. The present work follows, in general, the morphological classification of KISELEVA (1992), which is close to the classification of BROWN (1984). About 30 different phytolith forms (Table 2.2) found in soils were combined into 8 distinct major groups (Fig. 2.4 and Fig. 2.5).

1. Hats (short trapezoids [BROWN 1984]). Phytoliths from short cells of grass epidermis, usually round if seen from above, but hat-like or triangular if

seen from the side (Fig. 2.4). The base of the hat is on the outer epidermal surface, and the apex is directed toward the inside of the leaf (BLACKMAN 1971).

2. Plates with straight edges (usually called rods by many authors [SMITHSON 1958, BLACKMAN 1971]). Forms usually appearing in the coastal regions of grass leaves. It seems feasible to distinguish this group from wavy and lobed plates (the following group).
3. Plates with wavy and lobed edges. Phytoliths called sinuous trapezoids by BROWN (1984). The latter two groups are very diverse, and there are phytoliths, with only slight "waves," which fall between.
4. Elongate phytoliths, usually having protrusions along their sides, from long cells of grasses (TWISS et al. 1969, BROWN 1984) and, possibly, from *Luzula* species.
5. Trichomes. In this group, both grass trichomes and hairs with hairs are combined and hair bases of dicotyledon species (chiefly *Compositae*, *Sibbaldia* and *Campanula*). This is to simplify the counting procedure, as it is sometimes difficult to distinguish the taxonomic origin of a hair found in soil. However, in Fig. 2.5 "trichomes" stands entirely for grass originated hairs, while "hairs," "hair bases" and some other forms represent phytoliths of uncertain origin.
6. Branched rods were first described by SMITHSON (1958) from British soils and found later by BAKER (1959) in Australia. They are clearly attributed to *Nardus stricta*, a species from the monotypic tribes *Nardeae*.
7. Conical phytoliths originating from sedges (MEHRA and SHARMA 1965, PIPERNO 1988).
8. Others. Mixed group of unrecognizable phytoliths.

2.3.2. Subrecent phytolith assemblages and present vegetation

Phytolith assemblages from the upper soil layer (0-2 cm) appeared to be quite different under all four community types. At the same time, phytolith frequencies in two fractions (fine sand and silt) were very similar (Fig. 2.1 and 2.2). ALH and SBC upper soil layer assemblages are poor in phytoliths (2-4% of the total number of grains in both fractions). GHM assemblage is richer (10-11 %), and that of FVG is the richest (15%).

It can be noted that these data closely resemble the distribution of above-ground phytomass of grasses and sedges in the four studied communities (ONIPCHENKO 1985, 1990). If all studied species produce phytoliths in direct

proportion to their aboveground phytomass, we can predict that, for example, under the community with the lowest grass and sedge phytomass (SBC 18 g/m²), the percentage of phytoliths must be the lowest among the four communities. ALH, therefore, must be about 2.7 times richer in phytoliths (81 g/m²), whereas GHM 4.5 times (132 g/m²) and FVG must be the richest community (13.6 times, or 245 g/m²). Results of direct counting of phytolith percentages in both studied soil fractions correspond well to the predicted ratio (Fig. 2.1 and Fig. 2.2).

Phytolith assemblage from the upper soil layer (0-2 cm) of the ALH(U) soil profile is characterized by almost equal content of hats, abundantly produced by *Festuca ovina*, and wavy rods, typical for *Helictotrichon versicolor* (Fig. 2.3a). The role of sedge phytoliths in this assemblage is less significant, but still about 5% of all phytoliths are conical sedge forms and 15% of the assemblage constitute trichomes (including also hairs, hair bases and prickles of various shapes). This points at the considerable number of haired species in the community (e.g. *Antennaria dioica*, *Campanula biebersteiniana*, *Erigeron uniflorus*).

The FVG(U) assemblage is especially rich in hats, for the most part having a distinctive keel (68% of all forms, Fig. 2.3b). Such phytoliths were found in abundance in the dominant species of this community (*Festuca varia*). The role of wavy phytoliths is negligible here (only 3%).

The GHM(L) profile in its upper layer (0-2 cm) also contains many hats, but for the most part lacking keels (35%). They originate from *Nardus stricta* or *Phleum alpinum* (Table 2.1), a species typical for this community type (see Chapter 1.4.3). Because it is so easy to confuse this form with keel hats, they were simply combined for the phytolith diagrams. Wavy forms and trichomes are also very common here. Their origin is probably *Agrostis vinealis* and *Phleum alpinum*.

The SBC(L) contribute lots of plates (42%) and wavy phytoliths (15%). Branched rods of *Nardus* (9%) were also found here. This plant is the most abundant grass species in this community (ONIPCHENKO 1990). A significant number of composites and other hairy species (*Gnaphalium supinum*, *Sibbaldia procumbens*) is stressed by the considerable amount of hairs and trichomes in the upper soil layer. In general, GHM recent assemblages are most diverse (seven major phytolith groups). FVG assemblage resembles the latter, but has only six groups with absolute prevalence of hats. ALH and SBC communities, being very different in their composition and habitat requirements (cf. Chapter 1.4), produce controversially similar assemblages with a

significant percent of trichomes, straight and wavy plates. Probably, certain difficulties will arise in distinguishing these two communities by phytolith analysis. Yet there is an important difference between them. ALH recent assemblage lacks branched rods, whereas that of SBC lacks conical phytoliths of sedges.

2.3.3. Phytolith frequencies in soil profiles under four alpine communities

Analysis of silica phytoliths has shown a considerable difference in their distribution in soil profiles under four communities. Diagrams were drawn based on analysis of the silt fraction, which contains most identifiable forms. However, distribution of phytolith frequencies is very similar in both studied fractions (fine sand, 50-250 μm , and silt, 10-50 μm). Ratio of phytoliths to the total number of grains in a fraction rapidly decreases with depth (Fig. 2.1 and 2.2). Phytoliths were found in countable numbers as deep as 15 cm under ALH, 20 cm under FVG and SBC and 30 cm under GHM. Below this level silica bodies become very infrequent and reliable data on the frequency of different groups becomes unattainable. Thus, phytoliths are common till the border between the A1 and B horizons or somewhat deeper.

These soil horizons were dated using the radiocarbon method (GRISHINA et al. 1987). The average estimated age was 2160 ± 80 years for ALH (10-25 cm), 3610 ± 80 for FVG (25-35 cm), 2950 ± 80 for GHM (19-30 cm) and 3630 ± 60 for SBC (16-25 cm). The real ages of the soils must be higher because of various exchange processes occurring in non-buried alpine soils (PAVLOVA and ONIPCHENKO 1992). The authors report that pollen and spores can be found in the same profiles even at 40 cm below the soil surface.

The deepest penetration of phytoliths under GHM can be at least partly explained as caused by the high rate of burrowing activity of voles and other digging animals, especially active in this community (Chapter 1). The number of damaged, broken or partially dissolved phytoliths increases with depth. While phytolith frequency under GHM decreases almost constantly with depth, ALH and FVG have a "peak" of phytolith content at 4-8 cm (Fig. 2.1). Phytolith frequency under the poorest phytolith producer, i.e. SBC community, shows a strong tendency to grow from 0-2 to 6-8 cm with subsequent decrease at 10-15 cm. The observed peaks correspond to those noted by PAVLOVA and ONIPCHENKO (1992) for grass pollen content in the same soil layers of the same profiles. Probably, at that time, the role of grasses in pre-SBC, FVG and ALH communities was higher than today.

2.3.4. Distribution of different forms of silica phytoliths in four soil profiles

Although alpine plants in the study area bring at least 50 different forms of phytoliths (BLINNIKOV 1992), we found only about 30 different forms of silica bodies in the soil (Table 2.2 and Fig. 2.5). This is possibly due to the instability of some phytoliths in the soil. In the lower soil layers (20 to 35 cm dependent on community type), no essentially new forms were found, compared to the upper layers. According to these investigations, the lower soil layers lacked forms originating from both deciduous trees and conifers (GEIS 1973, KLEIN and GEIS 1978). It confirms data obtained for the same territory with pollen analysis (PAVLOVA and ONIPCHENKO 1992), that herbaceous vegetation has existed in the study area for at least four thousand years.

In the profile under ALH(U) (Fig. 2.3), phytolith assemblage from the 0-2 cm (subrecent) layer greatly resembles that of 10-15 cm. The latter, radiocarbon dated as being 2160 ± 80 years old (CHERKINSKY unpubl. data), however, contains more conical phytoliths of sedges and fewer hats and trichomes. It can be assumed that this community has existed for at least two thousand years. At that time, it looked much like the present community. Nevertheless, in more recent times certain changes in its floristic composition have occurred. Hats are almost absent at 2-4 and 4-6 cm, while the percentage of trichomes remains constant, indicating perhaps, a colder and more humid climate (higher share of composites and lower of *F. ovina*), and can be set in to the XIII-XV centuries, i.e. the vernau glaciation stage (TUSHINSKY 1962). Wavy plates and trichomes are common through all profiles. This proves that *Helictotrichon versicolor*, which produces wavy forms, and haired species, like *Campanula biebersteiniana* and some composites, have played a significant role throughout the community history.

In the FVG(U) reliable data on phytolith relative frequencies below 15 cm could not be obtained, although the soil layer in this community is thicker than in the previous one. Obtained results (Fig. 2.3b) proved that the FVG had been existing for a long time (about 2000 years) with only slight changes in their composition. Keel hats of *Festuca varia* and other short phytoliths absolutely prevail in the upper layer. They become less frequent at 4-6 and 6-8 cm. At this depth, well recognizable branched rods of *Nardus stricta* were found along with a considerable quantity of wavy phytoliths, typical for many broad-leaf grasses (e.g. *Anthoxanthum odoratum*, *Calamagrostis arundinacea* and *Phleum alpinum*). The increasing role of mesophytic grasses can be

connected with a general increase in humidity in the Northwestern Caucasus 500 to 800 years ago in the vernau glaciation stage (TUSHINSKY 1962).

Therefore, the composition of pre-FVG communities was close to that of mesophytic alpine meadows like the present GHM (but possibly with dominants other than *Hedysarum* and *Geranium*): An increase of *Nardus stricta* must have been caused by intensive grazing, typical in the Northwestern Caucasus in that time (SAVINETSKY 1992). This species is usually avoided by sheep and serves as an indicator of grazing (SMITHSON 1958). Again, as in the previous case, the deepest assemblage (10-15 cm) is similar to the uppermost one. It seemingly represents vegetation of the so called "second xerothermic period" with dry conditions, occurred about 2000 years ago (TUSHINSKY 1962).

Thus, it is very probable that FVG developed through a herbaceo-grass stage, resembling the present *Geranium*-dominated meadows, although the role of *Festuca varia* always played a leading role, as there are more than 50% hat phytoliths in each horizon.

In the GHM(L) profile, assemblage (Fig. 2.3c) from the 2-4 cm layer falls somewhere between GHM and FVG recent assemblages. A few percent of the branched phytoliths of *Nardus stricta* indicate an important role played by this species in the nearest past of the community. Again it can be connected with severe grazing in the last two or three centuries (see above). Presence of more than 50% hats and lack of conical sedge phytoliths in this layer lead to the conclusion that very recently GHM were occupied by more xeric FVG-like communities. This corresponds to the data given in PAVLOVA and ONIPCHENKO (1992).

Deep layers are characterized by equal percentages of three major groups, namely hats, straight plates and wavy plates, with a smaller portion of sedge phytoliths and trichomes. Such assemblages lay between ALH and GHM. It is suggested that they represent hypothetical "parent" communities, having developed later into both GHM and ALH. Supposedly they included grasses, sedges and herbs, mixed in a certain proportion without strong dominants.

It is noted that GHM assemblages are least reliable among the four studied profiles as their composition has probably been seriously influenced by the burrowing activity of animals (see Chapter 1.4.3).

The 16-25 cm horizon of the SBC(L) profile, dated 3630 ± 60 (GRISHINA et al. 1987), significantly differs from the upper portion of the profile (Fig. 2.3d) in phytolith forms. The lower assemblage is dominated by plates (50%). Hats and wavy phytoliths are less abundant (20 and 17%, respectively), while

trichomes are rare. In general, this assemblage takes after assemblages from the lower part of the GHM profile, attributed to a hypothetical "parent" community (see above). Such a community could have occupied the territory of the present SBC in the dry period of the second xerothermic stage (TUSHINSKY 1962) two or two and a half millennia ago.

The assemblages at 2-4 and 4-6 cm possess a great deal of trichomes, which suggests the presence of some composites and other haired species in the vernau glaciation stage. Branched rods of *Nardus* are absent in the deep layers and emerge for the first time at 4-6 cm. This also indicates intensive grazing during the last few centuries. SAVINETSKY (1992) provides data that nomadic tribes had occupied the Northwestern Caucasus about 2000 years ago, resulting in a sharp increase in sheep grazing on mountain grasslands and meadows. No *Nardus* phytoliths were observed in the deep layers dated at more than 3000 years.

Thus, on the basis of these results, the following scheme of historical changes in the four alpine communities are suggested:

ALH: ALH → more humid ALH → ALH

FVG: FVG → mesophytic meadows with *Nardus stricta* → FVG

GHM: "parent" herbaceo-grassland → xeric meadows, close to present FVG → GHM

SBC: "parent" herbaceo-grassland communities → SBC

In general, the results of the phytolith analysis confirm and add to the independent results of the pollen analysis (PAVLOVA and ONIPCHENKO 1992). Phytoliths may provide interesting paleoecological data on the local history of the alpine ecosystems.

SUMMARY

The history of four types of alpine communities in the Northwestern Caucasus was studied, using the method of phytolith analysis. All 4 communities produce silica phytoliths, chiefly of grass and sedge origin, in quantities sufficient for the analysis. The phytolith content in the subrecent assemblages (0-2 cm) can range from 1.8% of the total number of grains in silt and fine sand fractions under snow-bed communities to 15.5% under grasslands. The data obtained on phytolith frequencies in the subrecent assemblages closely correspond to the above-ground phytomass distribution of grasses and sedges among four communities.

Subrecent phytolith assemblages of four communities significantly differ. The alpine lichen heath (ALH) assemblage has approximately equal percentages of *Festuca ovina* hats and straight and wavy plates of *Helictotrichon versicolor*. There is also a significant percentage of trichomes, ostensibly produced by *Antennaria dioica*, *Campanula biebersteiniana* and other dicotyledon species. The grassland (FVG) assemblage is characterized by the overwhelming prevalence of keel hats of *Festuca varia* (68%). The shares of

trichomes and wavy plates are negligible. The alpine meadow (GHM) assemblage is the most diverse. It contains approximately equal percentages of hats and plates (about 35% each) as well as a considerable percentage of wavy plates, conical forms and trichomes. There is also a low percentage of branched rod phytoliths of *Nardus*. The assemblage of the snow bed communities (SBC) contains few hats and many wavy and straight edge plates, in addition to a lot of trichomes (of *Sibbaldia* for the most part). There are 10% branched rods in the assemblage, because *Nardus* is the most widespread grass in the SBC.

Phytoliths are not equally distributed in soils. In general their frequency decreases with depth. At a certain point their quantity becomes insufficient for reliable analysis, yet we can trace the history of the alpine communities for at least the last three thousand years. The composition of the lower assemblages differs from subrecent ones. However, no new forms were found, essentially dissimilar with those found in the subrecent assemblages. No traces of any arboreal phytoliths were detected. Apparently, the study area has not been occupied by forest vegetation during the last half of the Holocene and the alpine communities have been quite stable. A scheme of historical changes in the four studied communities is presented.

Under FVG, GHM and SBC *Nardus stricta* phytoliths were found in large quantities, indicating a severe grazing period in the recent history of the communities (several hundred years ago).