Preslia, Praha, 56 : 125—152, 1984

Bryophyte communities of sandstone rocks in Bohemia

Společenstva mechorostů na pískovcových skalách v Čechách

† Jaroslava Zittová - Kurková

Zittová - Kurková J. (1984): Bryophyte communities of sandstone rocks in Bohemia. — Preslia, Praha, 56 : 125—152.

Bryophyte communities of sandstone rocks in Northern and North-Eastern Bohemia are described; the discussion of their observational ecology and successional relationships is also given. Temperature and evaporation regime are shown to be the major factors determining species distribution in the deep and narrow gorges of sandstone rocks complexes. Bryophyte succession is described: Initial stages are species-rich communities with high evenness. Competitive interactions in later stages of succession eliminate most of the component species and species-poor communities develop. This succession is usually a cyclic process on steep rocks, due to mechanical disturbances; in favourable places, succession may continue further and even reach the stage of coniferous forest.

Botanical Institute, Czechoslovak Academy of Sciences, 252 43 Průhonice, Czechoslovakia [Reprint requests: T. Herben, the same address]

INTRODUCTION

Bryophytic communities on sandstone are formed by a very specific vegetation type which includes almost no plants belonging to other taxonomic groups. Their description is thus independent of the description of any other taxocoenosis, which makes them a source of readily available information on the environment.

Because Bohemian sandstone with rectangular jointing is a relatively homogeneous substrate both chemically and physically (Řezáč 1955); the decisive factor determining community composition and range is the microclimate and, in some cases, the hydrological regime.

These communities also form an ideal model for the study of problems of succession.

This paper deals with the sociology of bryophytic communities, which is a necessary first step before further studies can be undertaken. An explanation of the relationships of the communities to principal environmental factors and some elucidation of successional relationships is also attempted, although primarily at an observational level. The results of microclimatic measurements in one gorge, where a catena of bryophytic communities was found, is presented to illustrate microclimate differences in sandstone rock-cities.

Many studies dealing with sandstone bryophytic communities in Central Europe have already been published, although the names included in many of these are not valid according to the Code of Phytosociological Nomenclature (Barkman et al. 1977). Schade (1923, 1934) was the first to describe communities from sandstones in Saxony and carried out a detailed ecological

study of light, temperature and humidity conditions. DUDA (1951) published the results of a bryosociological study on sandstone in the Beskydy (N — Moravia) Mountains, which includes relevé material. He used the system of HADAČ and ŠMARDA (1944) and extended it to include the names of some communities published previously (e.g. SCHADE 1934). Another classification was

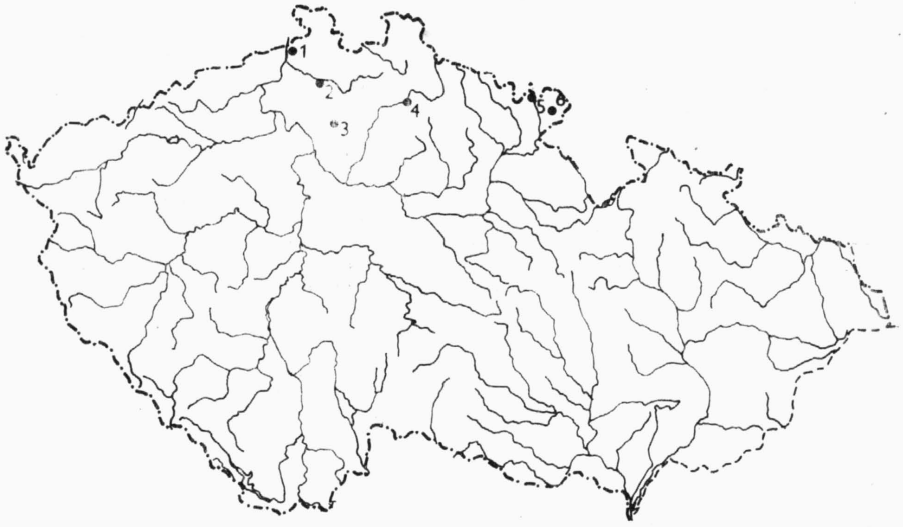


Fig. 1. Sandstone areas under study: 1. Děčínské mezihoří-rocks; 2. valley of the Robečský potok-stream; 3. Kokořínský důl-valley; 4. Hrubá Skála area; 5. Adršpašské skály-rocks and Teplické skály-rocks; 6. Broumovské stěny-rocks.

suggested by DUNK (1972) in his paper dealing with sandstones in Mittel- and Oberfranken. A survey of the bryophyte communities of Northern Bohemia was published by the present author (KURKOVÁ 1978). It contains descriptions of some new associations together with the synoptic table, based on the original relevé material from the author's Ph.D. thesis (KURKOVÁ 1977).

PHYTOSOCIOLOGICAL METHODS

The description and classification of commu nities is based on the Braun Blanquet approach. Compared with floweringplants, however, cryptogamic-communities pose some special problems.

The choice of suitable sample plot size is complicated by the mosaic-like structure of bryophytic vegetation. The vegetation mosaic has several hierarchical levels, resulting from individual plant competition and microhabitat diversity. If the mosaic of microhabitats is comparable in size to individual moss plants, a microhabitat boundary may easily pass through the area of one sample plot, and species ecologically very different from each other may be recorded (YARRANTON 1966). In the communities studied, however, ecological conditions change with distances of the order of tens or

hundreds of centimeters, while the individual moss plant cover is much smaller. Therefore, the risk of recording two microhabitats is minimal provided that a suitable sample plot size is chosen.

The sample plot area used in this study was 0.07 to 2 m^2. It was chosen on the basis of observation and after assessment of minimal area according to MORAVEC (1973) in a homogeneous community of *Lophozio guttulatae-Cephalozietum bicuspidatae*. In this community, mean homogeneity levels off at an area of 625 cm^2 (KURKOVÁ 1977).

For semi-quantitative estimations of cover in sample plots, Braun-Blanquet's scale was employed. This scale has been used by a number of Czechoslovak bryologists (ŠMARDA 1947, PECIAR 1967, PILOUS 1961, STUCHLÝ 1976).

Another problem is whether to describe and classify the cryptogamic component separately, or rather as a part of the vegetation as a whole. There have been many different opinions on this question, expressed for example by different choices of units describing moss vegetation (synusia, associations, sociations). A discussion of these problems may be found in the works of BARKMAN (1958) and PILOUS (1961), among others. The solution to this problem depends to a large extent on the type of vegetation studied. For example HÜBSCHMANN (1967) describes pure bryophyte communities as associations, the rest are considered parts of communities of higher plants without syntaxonomic distinction. NEUMAYR (1971), nevertheless, distinguishes associations formed exclusively by mosses, and he describes communities which are a part of higher plant communities as synusia of corresponding associations or higher syntaxonomic units. Similarly, STUCHLÝ (1976) uses the syntaxonomic unit of union for synusia and places them among phanerogamic communities.

Because almost no other plants except bryophytes occur on sandstone rocks, I chose association as the basic unit. An association is characterized by a diagnostic species group, which includes species whose joint occurrence and quantitative relationship is typical of the community considered. Communities that are documented by a small number of relevés are not given any specific rank.

AREA UNDER STUDY

Geography and geology

Bryophyte communities were studied in Northern and North-Eastern Bohemia (Fig. 1.). These areas are part of the system of Krušné hory, of the Bohemian Cretaceous platform and of the Sudeten system.

The regions studied are formed by rectangularly jointed sandstone of the Lower to Upper Turonian period, in some places of the Adršpašsko-Teplické skály rocks probably also of the younger Coniacian (SVOBODA et al. 1964). In the North Bohemian Cretaceous platform (the sandstones of Děčínské mezihoří, Ralská and Jičínská pahorkatina uplands) the majority of the strata are in the sandstone and clay-sandstone facies (Cenomanian, Upper and Middle Turonian and part of the Upper Turonian — Lower Senonian series) of SOUKUP (1963). Broumovské stěny rocks are formed by Middle Turonian sandstone, the Adršpašsko-Teplická tabule plateau probably belongs to the upper part of Middle Turonian (DEMEK 1965). The geological structure of all the areas mentioned is described in detail by SOUKUP (1963).

A system of gorges characterizes today's sandstone area. Gradual weathering has transformed the gully walls into chimneys, rock arches, groups of towers and, finally, into sand or boulder scree.

ŘEZÁČ (1955) divides the sandstone plateau into three zones according to its degree of weathering: The external zone (the most denuded one), the central zone (with deepening gullies) and the

internal zone (denudation not manifest). For a diagram of this division see Fig. 2. Micro-relief formations in the shapes of small ledges, joints following the direction of sedimentation, pitting, niches and opening or "hour-glasses" are often found on the surfaces of boulders, rocks and on the walls of the edges of the internal zone. These formations are due to a different degree of solubility of the cement, but they are not dependent on the size of the siliceous grains.

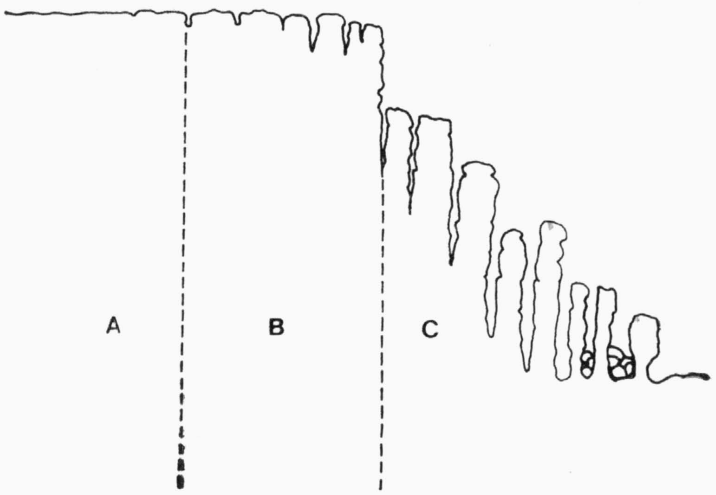


Fig. 2. Schematic representation of the denudation of a sandstone plateau: A — inner denudation zone; B — central denudation zone; C — external denudation zone.

From the bryological viewpoint, the most interesting parts of sandstone areas are those whose degree of disintegration places them in the central and external denudation zones. On these steep rock walls, towers and boulders, bryophytes are the principal vegetation component, in the cases of dryer habitats they are joined by lichens.

Walls of sandstone rock cities are shaded by neighbouring rock massifs. This influences light and temperature conditions of bryophyte communities.

Character of substrate

The ecological peculiarities of sandstone are caused mainly by its water regime and by its lack of nutrients.

Sandstone is water permeable; further, water not only soaks downwards through it but may also rise by absorption from the bases of rock which are in contact with running water. The rock surface dries slowly because it is saturated by water from the interior of the rock massifs.

Flow of water through the rock causes the washing out of the cementing components and the formation of pores between siliceous grains. These pores enable moss rhizoids to take hold in the rock and bryophytes may thus be found even on vertical walls. The develcpment of bryophyte communities is made easier by the microrelief structures.

Macroclimate

Macroclimatic data give only a rough estimate of the real situation in sandstone rock cities, where relief is the most important factor.

Besides, there are no marked differences in macroclimate between the individual sandstone regions. They may be divided roughly into two groups (Fig. 3.): The first one contains areas situated in a mildly warm, very humid region of highland character. Summer days are fewer in number, frosty days begin earlier, and there is a longer-lasting and thicker snow-cover (Broumovské stěny rocks, Adršpašsko-Teplické skály rocks, Ostaš and Hejda). The second group includes the remaining areas. They are situated in upland which is mildly warm, mildly humid

and with a mild winter. Kokořínský důl has a tendency to mild dryness. The Hrubá Skála region has the features of a hilly and lowland region of humid character.

Microclimatic measurements

In addition to phytosociological research, microclimate measurements were carried out in Adršpašsko-Teplické skály rocks. The climatic conditions of a sandstone rock city are documented by a gorge belonging to the central denudation zone. The model gorge is located approximately in the centre of Adršpašsko-Teplické skály rocks. It is accessible from Vlčí rokle (a valley which intersects the area approximately in a north-western to south-eastern direction). In the place where microclimatic measurements were made the gorge was about 50 m deep, with a width of 10 to 15 m at the bottom and widening upwards. The gorge has a south western to

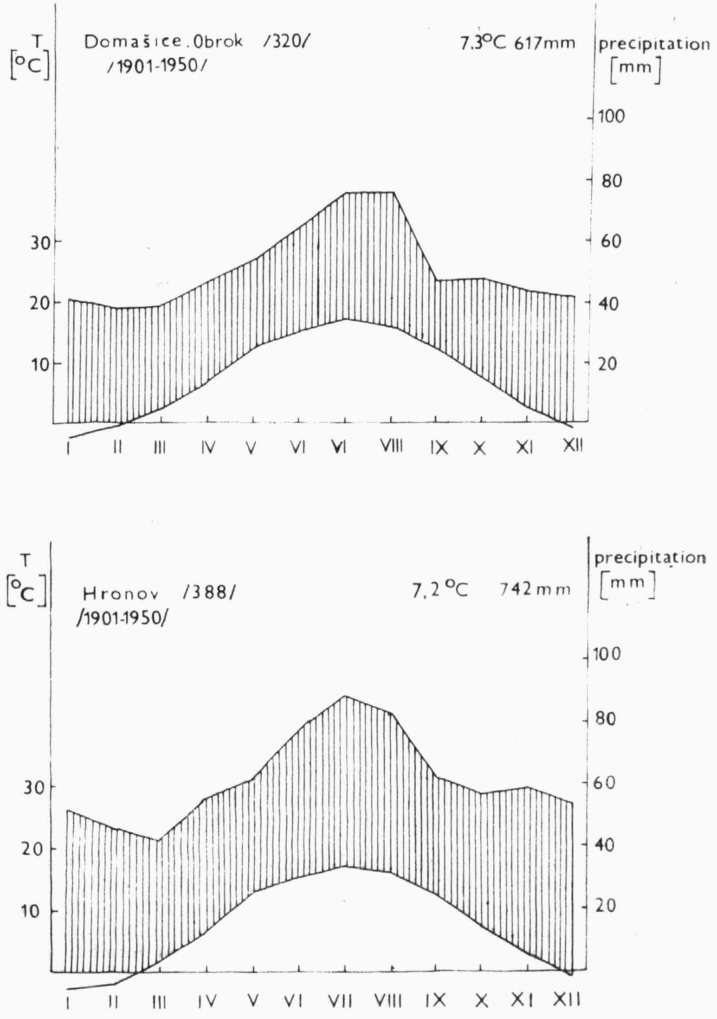


Fig. 3. Climatic diagrams representing two climatic regimes of sandstone areas (based on data in Vesecký et al. 1958).

north eastern direction, and the bottom slopes to the North-East, where a brook flows from the gorge through a cleft between blocks of rock.

The opposite (southwest) end is piled with boulders, some of which reach a height of 5 meters.

The north-west border of the gorge is formed by an almost perpendicular rock wall (inclination of 85°), with a smaller rock block with an inclination of 60°. The southeastern wall is broken up by step-like terraces covered with sand and fine scree.

Measurements were carried out on the 29th and 30th of May in 1975. Changes of temperature and evaporation above the surface of moss vegetation were observed. Mercury thermometers and Piche's evaporimeters (diameter of paper discs was 4 cm) were placed directly above the moss layer (Fig. 4.). Thermometer sensors were shaded by covers made of aluminium foil. Two or three thermometers and one or two pairs of evaporimeters were placed above each other on

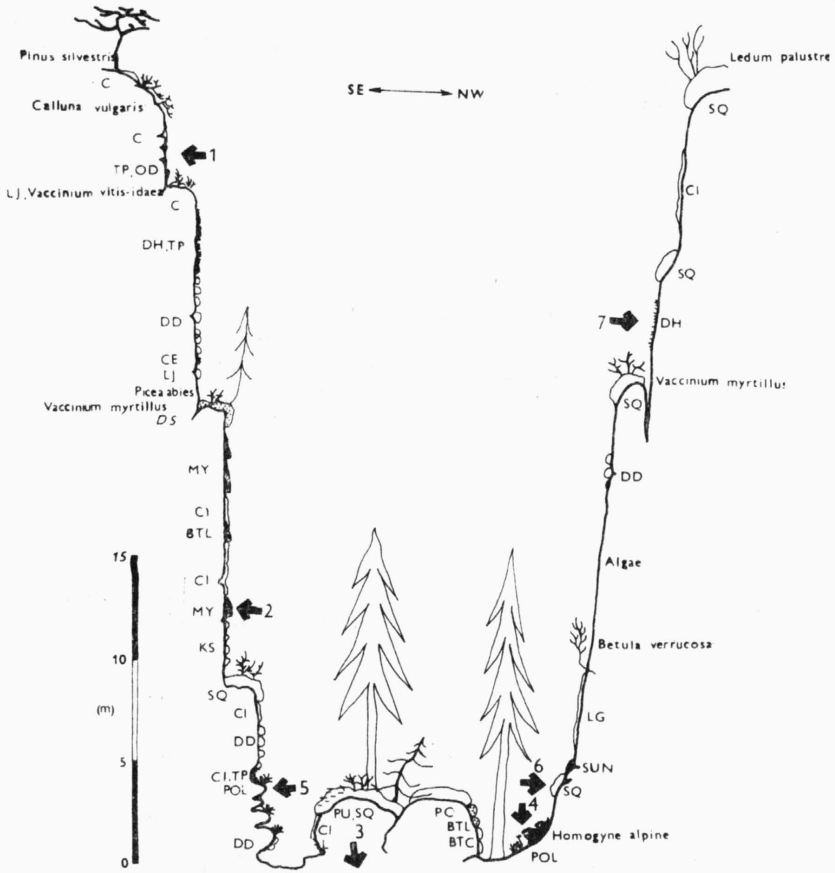


Fig. 4. Transect across the model gorge. Arrows denote the sites, where the microclimatic measurements were carried out. Distribution of individual species is marked in the following way: AO — *Anastrepta orcadensis*, BG — *Barbilophozia attenuata*, BTC — *Bazzania tricrenata*, BTL — *Bazzania trilobata*, CI — *Calypogeia integristipula*, CE — *Cephalozia* sp. div., C — *Cladonia* sp. div., DH — *Dicranella heteromalla*. DD — *Dicranodontium denudatum*, DS — *Dicranum scoparium*, DA — *Diplophyllum albicans*, KS — *Kurzia sylvatica*, LJ — *Leucobryum juniperoideum*, LG — *Lophozia guttulata*, MY — *Mylia taylorii*, OD — *Odontoschisma denudatum*, PL — *Plagiothecium laetum*, PU — *Plagiothecium undulatum*, PON — *Pohlia nutans*, PC — *Polytrichum commune*, PF — *Polytrichum formosum*, POL — *Polytrichum longisetum*, SUN — *Scapania undulata*, SP — *Schistostega pennata*, SQ — *Sphagnum quinquefarium*, SM — *Sphenolobus minutus*, TP — *Tetraphis pellucida*.

Tab. 1. — Vertical distance of thermometer sensors

Thermometers	site 1	site 2	site 3	site 5	site 7
1—2	32	42	65	25	60
2—3	30	65	87	—	—

chosen measuring sites. The vertical distance between evaporation surfaces of evaporimeters in site no. 3 was 115 cm. For distances between thermometer sensors on each station see tab. 1.

On the days when measuring took place the weather was as follows: On the 29th May 1975, the sky was clear from 7.00 to 10.15 a.m. Cumulus clouds began forming at 10.15, and they remained for the rest of the day. Cloudiness increased in the early hours of 30th May, at 5.00 a.m. two thirds of the sky were cloudy, and at 7.00 a.m. the whole sky was overcast. A mild wind blew during the entire period of measurement.

These measurements document the situation of moss vegetation on practically vertical walls which are not colonized by other plants, and whose microclimatic conditions are dependent on terrain configurations and to a lesser degree on the tree cover on plateaus (including the plateaus of individual rock towers), terraces, and gorge bottoms.

Measuring sites were chosen to give a picture of the principal temperature and evaporation situations in the gorge: Sunny parts of rugged wals (site no. 1), both shaded (site no. 7) and sunny (site no. 2) positions in the central parts of these walls, sunny (site no. 5) and shaded (site no. 3) places at the bases of rook blocks, and the flat, mildly sloping bottoms of gorges (site nos. 4 and 6).

Measurements were compared graphically (Fig. 5).

Places exposed to sunshine for at least part of the day, and therefore with a higher average temperature (nos. 1, 2, 5, 6) showed greater variations of values measured than shaded ones with lower average temperatures (nos. 3, 4, 7).

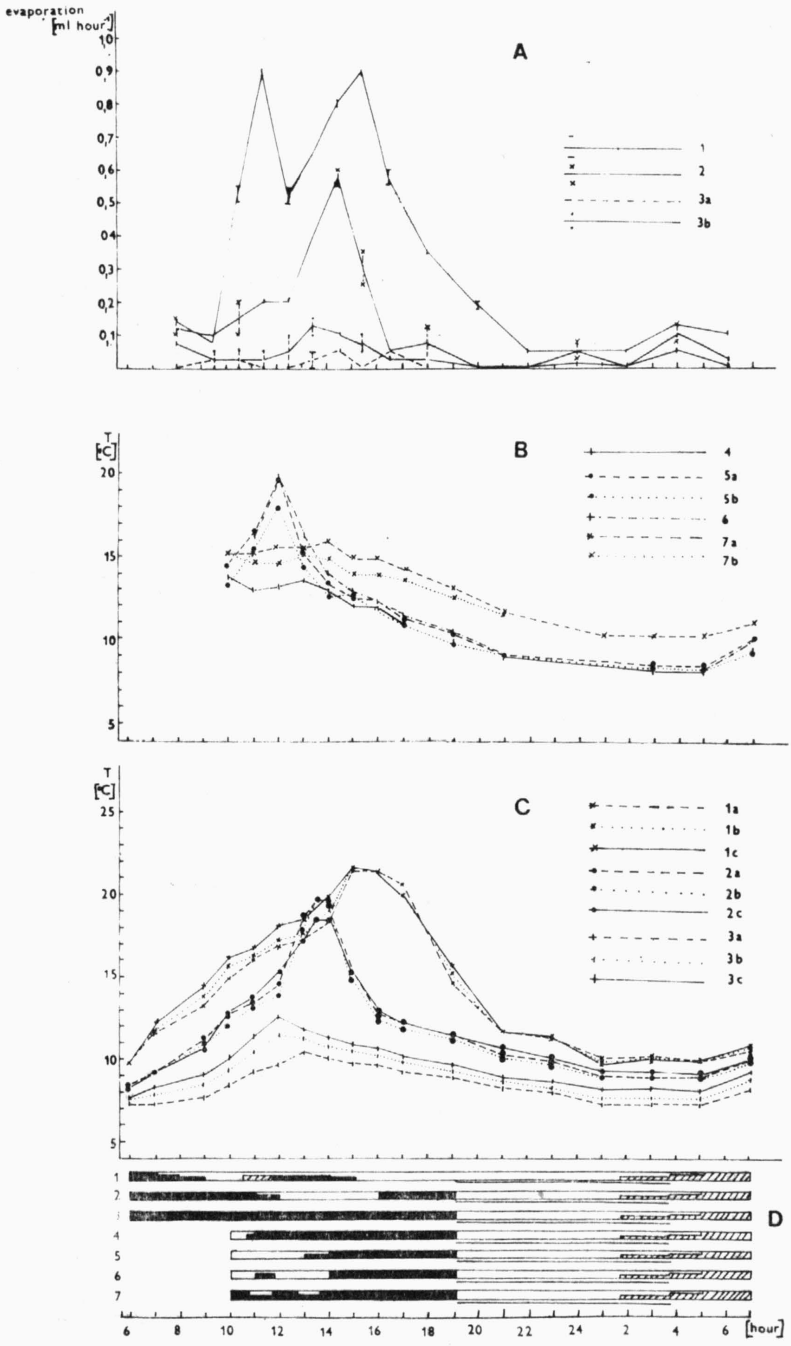
The results made possible a rough comparison of the temperature and humidity conditions of communities in which measurements were made: site 1 — *Tetraphidetum pellucidae dicranelletosum heteromallae*, site 2 — *Mylietum taylorii*, site 3 — *Lophozio guttulatae—Cephalozietum bicuspidatae* var. with *Lophozia guttulata*, site 6 — *Plagiothecio undulatae—Sphagnetum quinquefarii* var. with *Polytrichum longisetum*, site 7 — *Tetraphidetum pellucidae calypogeietosum integristipulae*.

The association *Lophozio guttulatae-Cephalozietum* had the most uniform temperature and humidity course of the strictly epilithic communities studied. The daily temperature span was about 3 °C. Greater variations were observed in the associations *Mylietum taylori* (10 °C) and *Tetraphidetum pellucidae* (10°—12°), which also differ substantially in their evaporation regime.

Localities of phytosociological relevés

The following list contains all the localities, where phytosociological observations were carried out. The individual localities are numbered as follows:

1. Teplické skály — rocks, Teplice rock city; 2. Teplické skály — rocks, Vlčí rokle — gorge; 3. Teplické skály — rocks, parallel gorge W of Černý příkop, S of Vlčí rokle — gorge; 4. Teplické skály — rocks, valley between Ozvěna and Teplice rock city; 5. Teplické skály — rocks, Černý příkop S of Vlčí rokle — gorge; 6. Teplické skály — rocks, Střmen — area; 7. Teplické skály — rocks, Sedm schodů — area; 8. Teplické skály — rocks, Bludiště — area; 9. Teplické skály — rocks, area above Bludiště; 10. Teplické skály — rocks, gorge near rock formation "Smetana u klavíru"; 11. Adršpašské skály — rocks, gorges between Řeřichová and Vlčí rokle — gorge; 12. Adršpašské skály — rocks, Řeřichová rokle — gorge; 13. Adršpašské skály — rocks, Ptačí příkop — gorge; 14. Adršpašské skály — rocks, Velký vodopád — area; 15. Ostaš — hill; 16. Hejda — hill; 17. Broumovské stěny — rocks, slope of Loučná hora; 18. Broumovské stěny — rocks, Kovářova rokle — gorge; 19. Broumovské stěny — rocks, Koruna — hill; 20. Broumovské stěny — rocks, slopes NE of Slavný village; 21. Broumovské stěny — rocks, Hvězda — hill; 22. Broumovské stěny — rocks, area 1 km NW of Koruna — hill; 23. Broumovské stěny — rocks, SW slope between Koruna and Loučná hora — hills; 24. Broumovské stěny — rocks, SW slope above Suchý důl — valley; 25. Broumovské stěny — rocks, SE slope of Koruna — hill; 26. Dě-


evaporation
[ml hour⁻¹]
A
1
2
3a
3b
T
[°C]
B
4
5a
5b
6
7a
7b
C
1a
1b
1c
2a
2b
2c
3a
3b
3c
D
[hour]

čínské stěny — rocks, Ve strži — gorge; 27. Děčínské stěny — rocks, Tichá soutěska — gorge; 28. Děčínské stěny — rocks, Divoká soutěska — gorge; 29. Děčínské mezihoří — rocks, valley of Chřibská Kamenice; 30. Děčínské mezihoří — rocks, valley of Bělá — creek 500 m from its mouth; 31. Kokořínský důl — valley, Močidla — area; 32. Kokořínský důl — valley, Jestřebické pokličky — area; 33. Kokořínský důl — valley, valley between Kokořínský důl and Sedlec; 34. Peklo u České Lípy — valley, valley of Robečský potok — creek; 35. Hrubá skála — rocks, Bukovina; 36. Děčínské mezihoří — rocks, valley of Srbská Kamenice.

DESCRIPTION OF COMMUNITIES

Classification of communities

alliance: *Tetraphidion pellucidae* MAURER 1961
association: *Tetraphidetum pellucidae* MAURER 1961
association: *Mylietum taylorii* PHILIPPI 1956
association: *Lophozio guttulatae-Cephalozietum bicuspidatae* KURKOVÁ 1978
Sphenolobus minutus — community
alliance: *Diplophyllion albicantis* PHILIPPI 1956 em. HERTEL 1974
association: *Diplophylletum albicantis* HERTEL 1974
Scapania nemorea — community
alliance: *Hylocomion* NEUMAYR 1971
association: *Polytricho longiseti-Dicranetum scoparii* KURKOVÁ 1978
association: *Plagiothecio undulati-Sphagnetum quinquefarii* KURKOVÁ 1978
alliance: *Dicranellion heteromallae* PHILIPPI 1963
Pellia epiphylla — community

Tetraphidetum pellucidae MAURER 1961

Table 2a, b.

Nomenclatural type: MAURER 1961 : 16, tab. 6, rel. 137 (lectotypus hoc loco).
Diagnostic species: *Tetraphis pellucida*, *Lepidozia reptans*, *Dicranodontium denudatum*, *Calypogeia integristipula*, *Dicranella cerviculata*.

It is a one-layer community, rich in species number but with low species evenness. It is dominated by the species *Tetraphis pellucida*, *Calypogeia integristipula*, *Dicranodontium denudatum*, *Dicranella cerviculata*. The community most often occupies sheer smooth sandstone rocks (inclination 60° to 90°) with microrelief sometimes broken up by small ledges, crevices and depressions (usually several centimeters in depth and width). Temperature fluctuates during the day, but it is always higher than on habitats of the

Fig. 5. Daily course of evaporation (A) and temperature (B, C) above the moss surface and the weather conditions (D). A — evaporation: 1 — site no. 1., 2 — site no. 2, 3a — site no. 3 (lower evaporimeter), 3b — site no. 3 (upper evaporimeter); B — temperature: 4 — site no. 4, 5a — site no. 5 (lower thermometer), 5b — site no. 5 (upper thermometer), 6 — site no. 6, 7a — site no. 7 (lower thermometer), 7b — site no. 7 (upper thermometer); C — temperature: 1a — site no. 1 (lower thermometer), 1b — site no. 1 (central thermometer), 1c — site no. 1 (upper thermometer), 2a — site no. 2 (lower thermometer) 2b — site no. 2 (central thermometer), 2c — site no. 2 (upper thermometer), 3a — site no. 3 (lower thermometer), 3b — site no. 3 (central thermometer), 3c — site no. 3 (upper thermometer); D — weather conditions: open rectangle — irradiated site, closed rectangle — shaded site, hatched rectangle — cloudy weather; the solid line — night.

Tab. 2a. — *Tetraphidetum pellucidae calypogietosum integristipulae* var. *typicum*

Subassociation													*calypogeietosum*
Variant													*typicum*
Relevé No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Exposure	SE	NW	SE	N	E	SSE	N	W	N	N	NE	NW	NNE
Inclination [°]	85	87	80	75	80	45	90	40	85	85	80	45	90
Relevé area [m²]	1	0.6	0.5	0.4	0.75	0.9	1	1.2	1	4	0.25	0.1	0.3
Date: month	8	7	8	5	5	7	7	11	8	5	8	7	11
year	75	75	75	75	75	75	73	75	75	75	75	75	75
Locality	4	18	16	13	1	3	18	6	34	11	31	19	6
E_0: cover [%]	100	95	95	55	90	100	100	40	100	85	100	90	90
number of species	8	8	7	7	5	9	7	8	7	4	5	5	6
Tetraphis pellucida HEDW.	4	1	1	2	+	1	1	1	5	4	3	3	3
Lepidozia reptans (L.) DUM.	1	1	5	1	+	+	1	1	+	2	3	1	1
Calypogeia integristipula STEPH.	1	2	+	1	1	+	1	1	+	1	2—3	1	1
Dicranodontium denudatum (BRID.) BRITT.	1	3	+	+	5	3	5	1	1	.	.	.	.
Kurzia sylvatica (EVANS) GROLLE	.	.	.	.	.	.	.	.	.	.	.	.	.
Pohlia nutans (HEDW.) LINDB.	.	2	.	.	.	+	1	.	.	.	.	.	.
Mnium hornum HEDW.	.	.	.	.	.	.	.	.	+	.	.	.	.
Cladonia sp. div.	2	3	+	2	.	.	1	1	.	.	.	.	1
Cephalozia bicuspidata (L.) DUM.	.	.	.	.	+	.	.	.	.	.	.	2	.
Cephalozia catenulata (HÜB.) LINDB.	.	.	.	3	.	.	.	.	.	.	.	.	.
Cephalozia lunulifolia (DUM.) DUM.	.	.	+	.	.	.	.	.	.	.	.	.	2
Odontoschisma denudatum (NEES in MART.) DUM.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mylia taylorii (HOOK.) GRAY	1	.	.	.	.	.	.	.	.	.	.	.	.
Bazzania trilobata (L.) S. GRAY	1	1	+	+	.	+	.	.	.	.	+	.	.
Sphenolobus minutus (SCHREB.) BERGGR.	1	.	.	.	.	.	.	.	.	.	.	.	.
Leucobryum juniperoideum (BRID.) C.M.	.	1	.	.	.	.	+	.	+	.	.	.	.
Lophozia ventricosa (DICK.) DUM.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicranum scoparium HEDW.	.	.	.	.	.	+	.	+	.	.	.	.	.
Orthodontium lineare SCHWAEGR.	.	.	.	.	.	.	.	1	.	.	.	.	3
Plagiothecium laetum B. S. G.	.	.	.	.	.	.	.	.	+	1	.	.	.
Plagiothecium denticulatum (HEDW.) B. S. G.	.	.	.	.	.	.	.	1	.	.	1	.	.
Barbilophozia attenuata (MART.) LOESKE	.	.	.	.	.	2	.	.	.	.	.	.	.

14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
W	S	SSW	SSW	SSW	E	S	S	S	N	NE	NNW	SE	NE	NNE	E	W	E	E
65	85	85	80	85	75	85	70	85	85	85	80	70	80	65	80	75	85	85
1	4	0.1	1	0.1	1	1	2	1	0.3	0.5	1	1	2	0.5	0.5	1	2	0.75
5	8	6	7	6	8	1	8	1	1	10	5	8	7	8	10	7	1	1
75	75	73	73	73	73	75	75	75	75	75	75	75	75	75	75	75	75	75
13	30	3	28	3	3	18	34	18	7	4	11	29	18	31	1	20	7	7
80	90	90	95	50	55	90	75	90	85	90	85	100	90	80	100	100	100	70
7	9	7	10	6	11	6	7	4	4	5	5	2	5	3	3	3	3	3
2	2	2	+	1	+	1	2	1	2	2	.	.	.	.	.	.	.	.
1	2	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
1	2	+	2	1	1	3	+	1	3	4	2	5	1	2	3	+	3	4
.	.	.	.	.	3	3	2	4	2	1	4	1	5	3—4	3	5	2	3
.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	+	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
2—3	2	3	2	2	1	1	3	3	1	.	.	.	+	.	.	.	.	.
3	1	.	1	+	1	1	.	.	.	2	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
.	2	3	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2	1	.	1	.	1	.	.	.	.	.	2	.	.	.	1	.	.	.
.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	1	2	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	+	.	.
.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	2	.	.	.	.	.	+	.	.	.	.	.	.	.

Tab. 2a. — Continued

Barbilophozia barbata (Schmid. ex Schreb.) Loeske	
Sphagnum quinquefarium (Lindb.) Warnst.	
E_1 cover [%]	
Dryopteris austriaca (Jacq.) Woynar	

community *Lophozio guttulatae-Cephalozietum*. A thin layer of humus (1 mm) is preserved on smooth walls by a liverwort cover. If the liverworts die away, the humus layer falls off or is washed off immediately by rainwater. Exceptions are of less steep boulder sides (inclination 30° to 50°), where a humus layer reaching a thickness of 2 cm may form.

The communities belonging to this association fall into two subassociations:

T. p. subass. *dicranelletosum heteromallae* Philippi 1965

Nomenclatural type: Tab. 2a, relevé 8 (neotypus hoc loco)
Differential species: *Dicranella heteromalla*, *D. cerviculata*, *Diplophyllum albicans*, *Isopterygium elegans*, *Cladonia sp.* div. with two variants (*Dicranella heteromalla* and *D. cerviculata*).

T.p. subass. *calypogeietosum integristipulae* Kurková 1978

Nomenclatural type: Table 2a, relevé 21 (holotypus hoc loco)
Differential species: *Dicranodontium denudatum*, *D. asperulum*, *Calypogeia integristipula*, *Mnium hornum*, *Kurzia sylvatica*, with four variants (*typicum*, *Mnium hornum*, *Kurzia sylvatica*, *Dicranodontium asperulum*).

On dryer and shadier habitats, *Tetraphis pellucida* and *Dicranella heteromalla* prevail, together with species of the genus *Cladonia* (subassociation *dicranelletosum heteromallae*). Their respective quantities depend on the humidity of the substrate. On mildly humid, partly shaded habitats the community develops into the variant *Dicranella cerviculata*, with various hepatics (*Lepidozia reptans*, *Lophozia* sp. div.). Dry habitats are occupied by *Dicranella heteromalla*, lichens (*Cladonia* sp. div.), *Tetraphis pellucida* and *Leucobryum juniperoideum* (var. *Dicranella heteromalla*). Lichens (*Cladonia* sp. div.) have higher competitive ability here and their vegetation is more compact. *Odontoschisma denudatum* appears in greater quantity on partly shaded habitats after long dry spells.

Damp and sunny habitats are covered by compact tufts of the subassociation *calypogeietosum integristipulae* with diverse species composition. Because of its wide ecological amplitude, it has many variants with different demands on habitat conditions. The typical variant occupies partly and fully shaded habitats, where the course of temperature and humidity fluctuates noticeably; it is characterized by a well-developed covering of *Calypogeia integristipula* and turfs of *Dicranodontium denudatum*. The variant *Dicranodontium asperulum* is found on sunny boulders and rock blocks. The variant *Kurzia sylvatica* usually occupies shaded damp rock walls in mildly warm or cool parts of gorges. Stands of the variant *Mnium hornum* are found on

+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	
.	1	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	1	.	.		
.	r	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.		

Only in one relevé:

E_0: *Dicranella heteromalla* (Hedw.) Schimp. 2 (15), *Kurzia sylvatica* (Evans) Grolle + (19), *Diplophyllum albicans* (L.) Dum. 1 (33), *Lophozia ventricosa* (Dicks.) Dum. + (24), *Lophozia guttulata* (Lindb.) Evans + (6), *Polytrichum formosum* Hedw. 1 (34), *Dicranella crispa* (Hedw.) Schimp. 2 (12), *Bazzania tricrenata* (Wahlenb.) Lindb. + (17).
E_1: *Vaccinium myrtillus* L. r (7), *Oxalis acetosella* L. r (30).

very damp, slightly sloping boulder sides with a layer of soil of up to 2 cm. Species common in the moss level of spruce forests (*Plagiothecium laetum, P. denticulatum, Pohlia nutans*) are often found in this variant.

The studies of Philippi (1965, 1972), Neumayr (1971), Dunk (1972), and Hertel (1974) include phytosociological material documenting the association *Tetraphidetum pellucidae* Maurer 1961. Maurer's (1961) assignment of this association to the alliance of bryophyte communities on rooting wood *Tetraphidion pellucidae* (Herzog 1943) Krusentsjerna 1945, was widely accepted.

Mylietum taylori Philippi 1956

Table 3.
Nomenclatural type: Philippi 1956: 115, tab. 21, rel. 3 (lectotypus hoc loco)
Diagnostic species: *Mylia taylori, Dicranodontium denudatum, Polytrichum pallidisetum*

This is a one- or two-layer community, with almost 100 % cover. The prevailing species that determines its morphology is *Mylia taylorii*. The community grows on completely shaded and partly shaded, humid and partly humid rocks, with surface inclination of 45° to 90° and rock walls that are almost smooth or broken up by small ledges and depressions. It is developed best on midly damp, warm, sunny walls with inclination of 60° to 80°.

A division into two subassociations is suggested here:

M.t. subass. ***polytrichetosum formosi*** subass. nova

Nomenclatural type: relevé 12 (holotypus hoc loco).
Differential species: *Polytrichum formosum, Dicranum scoparium.*

M.t. subass. ***dicranodontietosum denudatae*** subass. nova

Nomenclatural type: relevé 5 (holotypus hoc loco).
Differential species: *Dicranodontium denudatum, Calypogeia integristipula.*

Tab. 2b. — *Tetraphidetum pellucidae* (excl. subass. *calypogeietosum integristipulae* var. *typicum*)

								dicranelletosum heteromallae		
	Dicranella cerviculata							*Dicranella*		
Relevé No.	1	2	3	4	5	6	7	8	9	10
Exposure	W	S	S	SSW	SSW	W	WSW	SW	SW	SW
Inclination [°]	75	87	80	87	80	90	75	45	90	85
Relevé area [m²]	0.5	0.3	0.5	0.5	0.6	1	1	0.3	0.6	0.4
Date: month	8	5	8	5	5	8	5	4	8	7
year	75	75	75	75	75	75	75	73	73	73
Locality	1	11	15	11	12	26	13	2	3	27
E_0: cover [%]	40	80	95	98	85	100	90	90	95	90
number of species	4	3	7	6	6	6	7	8	7	10
Tetraphis pellucida HEDW.	+	.	.	3	3	2–3	2	2	3–4	1
Lepidozia reptans (L.) DUM.	.	.	.	2	1	2	+	+	.	.
Calypogeia integristipula STEPH.	.	.	1	.	3	2	2	2	+	2
Dicranella cerviculata (HEDW.) SCHIMP.	2	4	3	3	2	3	1	.	.	.
Dicranella heteromalla (HEDW.) SCHIMP.	.	.	.	.	.	.	.	2–3	2	2
Cladonia digitata (L.) HOFFM.	.	.	.	+	.	.	2	.	.	.
Cladonia subsquamosa (NYL.) KREMPELH	.	.	.	.	1	.	.	.	.	.
Cladonia sp.	.	1	+	.	+	.	.	3	1	+
Dicranodontium asperulum (MITT.) BROTH.	.	.	.	.	.	.	.	.	.	.
Kurzia sylvatica (EVANS) GROLLE	.	.	.	.	.	.	.	.	.	1–2
Mnium hornum HEDW.	.	.	.	.	.	.	.	.	.	.
Dicranodontium denudatum (BRID.) BRITT.	.	.	.	+	.	.	.	.	+	.
Cephalozia bicuspidata (L.) DUM.	2	1	+	.	.	2	2	.	.	1
Mylia taylorii (HOOK.) S. GRAY	.	.	.	.	+	.	1	1	.	2
Pohlia nutans (HEDW.) LINDB.	.	.	.	.	.	1	.	.	1	.
Leucobryum juniperoideum (BRID.) C.M.	.	.	.	.	.	.	.	+	.	.
Bazzania trilobata (L.) S. GRAY	.	.	.	.	.	.	.	.	.	.
Sphenolobus minutus (SCHREB.) BERGGR.	.	.	1	.	.	.	.	.	.	.
Diplophyllum albicans (L.) DUM.	.	.	+	.	.	.	.	.	.	2
Lophozia guttulata (LINDB. et H. ARN.) EVANS	2	.	.	.	.	.	.	.	.	1
Plagiothecium laetum B.S.G.	.	.	.	.	.	.	.	.	.	.
Lophozia ventricosa (DICK.) DUM.	.	.	3	.	.	.	.	.	.	.
Hypnum cupressiforme HEDW.	.	.	.	.	.	.	.	1	+	.
E_1 cover [%]	.	.	.	.	.	.	.	.	.	.
Vaccinium myrtillus L.	.	.	.	.	.	.	.	.	.	.
Dryopteris austriaca (JACQ.) WOYNAR	.	.	.	.	.	.	.	.	.	.
Oxalis acetosella L.	.	.	.	.	.	.	.	.	.	.

Only in one relevé:

Polytrichum longisetum BRID. 1 (12), *Mylia anomala* (HOOK.) S. GRAY 2 (11), *Scapania umbrosa* (SCHRAD.) DUM. + (9), *Polytrichum formosum* HEDW. 1 (23), *Cephalozia lunulifolia* (DUM.) DUM. 1 (25).

The colonization by *Mylia taylorii* begins on small ledges and in crevices. Later it spreads to smooth rock walls, where other bryophytes also occur. It spreads especially rapidly on more broken-up walls, where it displaces turf-forming mosses. Later its competitive ability in comparison with other

								calypogeietosum integristipulae								
				Dicranodontium				*Kurzia*								
heteromalla				*asperulum*				*sylvatica*			*Mnium hornum*					
11	12	13	14	15	16	17	18	19	20	21	22	23	23	23	26	27
SE	S	N	W	S	E	W	E	NW	NNW	W	SEE	NW	N	NWW	S	W
85	70	80	80	87	90	80	90	90	87	85	60	60	85	75	50	90
0.1	0.5	1	0.3	1	0.5	0.2	0.6	0.3	1	0.5	0.6	0.5	2	0.6	0.7	2
8	8	7	8	10	8	8	4	8	8	5	8	7	8	8	7	8
75	75	75	75	73	73	73	73	75	73	75	75	75	75	75	75	75
29	31	17	26	4	2	5	2	26	2	11	4	21	34	29	19	31
100	100	90	95	100	100	100	85	90	100	90	90	100	100	100	60	100
6	8	5	5	4	8	7	8	4	10	7	6	6	7	7	7	8
2	3	3	3	.	2	2	2	2	2	2	2	2	1	3	1	3
.	.	.	1	1	2	+	2	.	+	2	.	.	1	1	.	1
3	.	2	2	2	4	3	2	3–4	2	3	3	3	2	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
1	3	2	2–3	.	.	.	+	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	+	.	.	.	.	.	1	.	.	.	1	.	.	.	+	1
.	.	.	.	5	1	2	2	2	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	2–3	3	1–2	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	2	2	2	2	2
.	.	.	.	.	.	.	.	2	2	3	2	3–4	4	3	3	3
1	.	2	1	+	+	2	.	.	2	2	1	.	1	.	.	.
.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
.	1	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1
.	+	+	.	.	.	.	.	.	.	.	.	.	.	1	1	.
.	+	.	.	.	1	+	.	.	2	1	.	.	.	.	.	.
.	.	.	.	.	1	.	+	.	+	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1
.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	1	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	1
.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
.	.	.	.	.	.	.	.	.	.	.	.	r	1	+	.	+
.	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.

liverworts is enhanced by an increase in the thickness if its felt. Finally the whole wall (which may have a surface of several square meters) is overgrown with a carpet of *M. taylorii* of varying thickness. It forms a suitable environment for tree seedlings, which are not able to reach maturity in the community, however, and are broken off together with the old moss layer, fall to the rock base and may continue their growth on detritus-enriched sand.

Table 3. — *Myletum taylorii*

Subassociation	*dicranodontietosum denudatae*										*polytrichetosum formosi*			
Variant	*typicum*						*Calypogeia integristipula*							
Relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Exposure	NE	NW	S	SE	SW	NNW	N	SE	N	N	NW	N	NE	NNW
Inclination [°]	75	75	65	70	70	85	60	85	60	70	45	60	40	70
Relevé area [m²]	1	0.75	0.75	0.5	0.6	1	1	0.6	0.85	0.7	1	3	1	1
Date: month	8	1	5	8	5	5	5	7	5	8	10	5	10	8
year	1975	1975	1975	1975	1975	1973	1975	1973	1975	1975	1975	1975	1975	1975
Locality	26	22	12	26	13	4	11	4	11	8	9	13	8	4
E_0: cover[%]	95	100	98	90	90	90	100	100	100	100	100	100	99	95
number of species	4	3	5	4	7	7	9	7	6	6	5	3	4	2
Mylia taylorii (Hook.) S. Gray	4	4	3	4	3—4	3—4	4	4	4	4	5	4	5	5
Dicranodontium denudatum (Brid.) Britt.	2—3	3	3	2	3—4	3	1	.	.	.	.	.	.	.
Calypogeia integristipula Steph.	.	.	.	.	+	1	1	2	2	2	.	.	.	.
Bazzania trilobata (L.) S. Gray	.	.	.	.	.	+	2	.	1	2	1	.	.	.
Dicranum scoparium Hedw.	.	.	.	.	.	.	+	.	.	+	1	2	+	.
Lepidozia reptans (L.) Dum.	.	1	.	.	.	1	+	1—2	+	.	.	.	.	.
Tetraphis pellucida Hedw.	.	.	.	.	+	.	.	2	+	.	.	.	.	.
Cephalozia bicuspidata (L.) Dum.	.	.	.	.	+	.	.	.	2	+	.	.	.	.
Cephalozia lunulifolia (Dum.) Dum.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Polytrichum formosum Hedw.	.	.	.	.	.	.	.	.	.	.	.	2	1	.
Sphagnum quinquefarium (Braithw.) Warnst.	.	.	.	.	.	.	.	.	.	+	.	.	+	.
Pohlia nutans (Hedw.) Lindb.	.	.	.	.	+	.	1	.	.	.	.	.	.	.
Leucobryum juniperoideum (Brid.) C. Müll.	.	.	.	.	.	.	1	1	.	.	.	.	.	.
Anastrepta orcadensis (Hook.) Schiffn.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Sphenolobus minutus (Schreb.) Berggr.	.	.	.	.	.	1	.	+	.	.	.	.	.	.
Cladonia sp.	.	.	.	.	.	+	+	.	.	.	.	.	.	.
E_1: cover [%]	.	.	.	1	.	.	5	.	1	.	1	20	.	5
Vaccinium myrtillus L.	.	.	.	.	.	.	1	.	+	.	r	1	.	.
Vaccinium vitis-idaea L.	.	.	.	.	.	.	.	.	.	.	.	+	.	1
Picea excelsa (Lamk.) Lk. juv.	.	.	.	r	.	.	.	.	.	.	1	2	.	.

Only in one relevé:
Cephalozia leucantha Spruce 2 (3), *Dicranella heteromalla* (Hedw.) Schimp. 1 (1), *Dicranodontium asperulum* (Mitt.) Broth. 2 (8), *Kurzia sylvatica* (Evans) Grolle 1 (1), *Lophozia guttulata* (Lindb.) Evans + (5), *Mnium hornum* Hedw. 2 (3), *Scapania umbrosa* (Schrad.) Dum. 1 (3).

Lophozio guttulatae-Cephalozietum bicuspidatae KURKOVÁ 1978

Tab. 4.
Nomenclatural type: tab. 4., rel. 12 (holotypus hoc loco)
Diagnostic species: *Lophozia guttulata, L. ventricosa, Cephalozia bicuspidata, C. lunulifolia*

The community is formed by a partial to complete liverwort cover and a sparse short moss turf. It grows on almost vertical (70° to 80°), damp to very damp, shaded, cool rock and boulder sides. The habitats of this community are characterized by a low level of direct illumination, low temperature with small daily fluctuations, and high atmospheric and substrate humidity. These conditions give an advantage to small liverworts, which form dense patches, over larger mosses and liverworts. The humus layer is very thin (not more than 3 mm) and it is continually washed out by rainwater that runs along the surface or soaks into the sandstone. Such conditions are found in narrow passages formed by rock blocks, which often reach heights of 40 m and in pits and holes between boulders piled at the bottoms of valleys. The community is found on the lower parts of rock walls that are in contact with the permanent or periodical streams draining the gorges.

The early stages of development of the community are characterized by separately growing liverwort patches, especially *Lophozia* sp. div. and *Cephalozia* sp. div. Later, the plant cover gradually increases and, depending on light and humidity conditions, certain species prevail and form different subassociations or variants.

These communities are divided here into two subassociations:

L.g.-C.b. subass. ***lophozietosum guttulatae*** subass. nova

Nomenclatural type: relevé 12 (holotypus hoc loco)
Differential species: *Lophozia guttulata, L. ventricosa, Cephalozia bicuspidata* with two variants (*Lophozia guttulata* and *Cephalozia bicuspidata*)

L.g.-C.b. subass. ***cephalozietosum lunulifoliae*** subass. nova

Nomenclatural type: relevé 22 (holotypus hoc loco)
Differential species: *Cephalozia lunulifolia*

Rocks with low illumination are dominated by *Cephalozia bicuspidata*, accompanied by hygrophytic species such as *Scapania umbrosa* and *Diplophyllum albicans*, together with individual stems of the *Mylia taylorii* (subass. *lophozietosum* var. *Cephalozia bicuspidata*). Habitats with higher illumination by diffused light are occupied by *Lophozia guttulata* or in some cases by *L. ventricosa*. Their dense covers are interwoven by *Lepidozia reptans*, or small liverworts of the genus *Cephalozia*, together with patches of the liverworts *Calypogeia integristipula*, *Bazzania tricrenata*, and *Mylia taylorii*. These species, however, do not form a many-layered cover in this case, but only a one-layer felt firmly attached to the sandstone substrate (subass. *lophozietosum* var. *Lophozia guttulata*). Habitats with higher substrate humidity and similar light and temperature conditions permit faster development of liverworts of the species *Cephalozia lunulifolia*, *Calypogeia integristipula*, and *Mylia taylorii* and of short sparse turfs of *Tetraphis pellucida* (subass. *cephalozietosum lunulifoliae*).

Table 4. — *Lophozio guttulatae-Cephalozietum bicuspidatae*

Subassociation	*lophozietosum guttulatae*							
Variant	*Cephalozia bicuspidata*							
Relevé No.	1	2	3	4	5	6	7	8
Exposure	NE	N	NE	WSW	N	E	W	NNW
Inclination [°]	75	80	90	60	60	65	90	70
Relevé area [m²]	1	0.3	1	0.25	0.5	0.3	0.25	0.6
Date: month	5	8	8	10	8	8	8	10
year	1975	1975	1975	1975	1975	1975	1975	1975
Locality	11	1	26	4	4	10	1	9
E_0: cover [%]	85	90	60	100	80	80	80	80
number of species	5	3	4	5	5	9	3	4
Lophozia ventricosa (Dicks.) Dum.	.	.	.	.	.	.	.	.
Lophozia guttulata (Lindb.) Evans	.	.	.	1	.	+	3	4
Cephalozia bicuspidata (L.) Dum.	3—4	5	3—4	4—5	3—4	5	1	.
Cephalozia lunulifolia (Dum.) Dum.	.	.	.	.	.	.	.	.
Cephalozia catenulata (Hüb.) Lindb.	.	.	.	.	.	.	.	.
Cephalozia leucantha Spruce	.	.	.	.	.	.	.	.
Mylia taylorii (Hook.) S. Gray	2	.	.	+	+	+	3	1
Calypogeia integristipula Steph.	.	.	+	.	.	.	.	.
Tetraphis pellucida Hedw.	2—3	.	.	.	.	+	.	.
Lepidozia reptans (L.) Dum.	.	.	.	.	.	.	.	.
Bazzania tricrenata (Wahlenb.) Lindb.	.	.	.	.	.	.	.	.
Scapania umbrosa (Schrad.) Dum.	.	.	.	1	2	1	.	.
Diplophyllum albicans (L.) Dum.	.	.	1	1	.	.	.	.
Dicranella heteromalla (Hedw.) Schimp.	.	.	1	.	.	.	.	+
Dicranodontium asperulum (Mitt.) Broth.	.	.	.	.	.	.	.	.
Dicranodontium denudatum (Brid.) Britt.	1	+	.	.	.	+	.	.
Cladonia digitata (L.) Hoffm.	.	.	.	.	.	.	.	.
Cladonia sp.	.	.	.	.	.	.	.	.
Bazzania trilobata (L.) S. Gray	2	.	.	.	.	.	.	.
Pohlia nutans (Hedw.) Lindb.	.	+	.	.	+	+	.	.
Plagiothecium laetum B. S. G.	.	.	.	.	.	.	.	.
Leucobryum juniperoideum (Brid.) C. Müll.	.	.	.	.	.	.	.	.
Cynodontium sp. div.	.	.	.	.	.	.	.	.

Only in one relevé:

E_0: *Anastrophyllum michauxii* (F. Web.) Buch ex Evans 1 (11), *Dicranella crispa* (Hedw.) Schimp. 1 (12), *Barbilophozia attenuata* (Mart.) Loeske 2 (24), *Cephalozia lammersiana* (Hüb.) Carring. 2 (16), *Cladonia squamosa* (Scop.) Hoffm. 1 (15), *Plagiothecium denticulatum* (Hedw.) B. S. G. + (6), *Pellia epiphylla* (L.) Corda + (14). *Polytrichum formosum* Hedw. + (5), *P. longisetum* Brid. + (6), *Sphenolobus minutus* (Schreb.) Berggr. + (8).

E_1: *Dryopteris austriaca* (Jacq.) Woynar 1 (16).

Sphenolobus minutus — community

Table 5.

On dry, half-shaded to sunny places the community with *Sphenolobus minutus* (tab. 5) may be found. The physiognomy of the community which occupies sheer rock and boulder sides in the higher and drier parts of gorge slopes, is strongly influenced by other dominants: *Cladonia* sp. div. and *Hypogymnia physodes*, together with the liverwort, *Barbilophozia attenuata*. The community described shows a strong resemblance to the community *Tetraphidetum pellucidae* Maurer 1961. Assigning it to this association, (under the name of subassociation *sphenolobetosum minuti* Philippi 1965) would, how-

			Lophozia guttulata									*cephalozietosum lunulifoliae*					
9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
S	SW	N	E	SSW	N	WSW	NW	ESE	N	E	N	NE	W	S	NW	N
85	80	88	80	80	88	90	80	80	90	80	80	30	60	85	75	75
0.7	0.4	0.3	0.5	0.5	1	0.12	0.1	0.3	1	0.2	0.3	0.5	0.7	4	0.3	0.25
6	8	8	5	7	5	7	7	5	8	—	8	8	5	8	8	8
1973	1975	1973	1975	1975	1973	1975	1975	1975	1973	—	1975	1975	1975	1975	1975	1975
2	15	2	11	28	4	23	24	24	18	3	36	16	13	23	4	4
85	90	75	65	100	100	75	100	75	95	80	100	90	100	95	90	90
12	6	8	9	8	9	6	7	5	7	7	4	6	6	5	8	6
.	3	.	.	.	.	.	3	2	.	.	.	.	.	.	.	.
3	.	3	3	2—3	4	2	.	.	3	3	.	.	.	.	.	.
1	.	+	1	2	+	+	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	2—3	3—4	3	3	2	3
.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.
2	3	.	1	2	.	3	2—3	2	+	2—3	1	.	3	3	1	2
1	+	+	2	2	.	.	2	.	.	.	.	3	3	1	2	+
+	.	.	+	.	.	.	.	+	.	2	3	.	+	3	1	1
2	+	+	+	+	+	.	1	.	.	.	.	.	.	.	1	.
+	.	.	.	.	+	.	.	2	3	.	.	.	.	.	.	.
.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.
.	.	1	.	.	.	.	.	.	+	.	.	.	.	.	.	.
+	.	.	.	3	+	.	.	.	.	.	.	.	.	1	.	.
.	.	3	.	.	2	.	.	.	.	.	.	.	.	.	.	.
1	3	.	+	.	.	+	.	1	2	1	2	2	1	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.
.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	1	.
.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.
.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.
.	.	.	+	.	1	.	.	.	.	+	.	.	.	.	.	.
.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.
.	.	+	.	.	2	.	.	.	.	.	.	.	.	.	.	.

ever, require an unacceptable widening of the concept of this unit. I have therefore classified this unit only as a part of the alliance *Tetraphidion pellucidae*.

Diplophylletum albicantis Hertel 1974

Table 6.

Nomenclatural type: Hertel 1974, tab. 23, rel. 9 (lectotypus hoc loco)
Diagnostic species: *Diplophyllum albicans*, *Dicranella heteromalla*, *Tetrodontium brownianum*

The community colonizes very damp, unbroken walls characterized by extremely low temperature and illumination. Development of the community on slightly shaded habitats requires high humidity of the sandstone and low temperature. In these places the snow cover remains at the foot of the rocks throught part of the vegetation season. *Tetrodontium brownianum* is the only species requiring these specific conditions in total, whereas other component species grow in other communities as well. The community colonizes extreme habitats, where the competition of other bryophytes is

Table 5. — *Sphenolobus minutus* — community

Relevé No.	1	2	3	4
Exposure	NEE	NE	E	SE
Inclination [°]	80	70	90	80
Relevé area [m²]	0.5	0.3	1	0.8
Date: month	8	8	8	10
year	1975	1975	1975	1975
Locality	15	15	32	4
E_0: cover [%]	90	90	40	95
number of species	5	6	4	9
Sphenolobus minutus (SCHREB.) BERGGR.	2	3	3	3
Cladonia sp.	.	1	+	1
Hypogymnia physodes (L.) NYL.	1	1	.	.
Dicranella heteromalla (HEDW.) SCHIMP.	2	1	.	.
Calypogeia integristipula STEPH.	3	3	.	+
Cephalozia bicuspidata (L.) DUM.	2	.	+	.

Only in one relevé:
Cephalozia leucantha SPRUCE 1 (4), *Dicranum scoparium* HEDW. + (4), *Bazzania trilobata* (L.) S. GRAY 1 (2), *Lophozia guttulata* (LINDB.) EVANS + (3) and 2 (4), *Mylia taylorii* (HOOK.) S. GRAY 1 (4), *Lepidozia reptans* (L.) DUM. + (4), *Tetraphis pellucida* HEDW. 2 (4).

reduced. The community closest to it is *Lophozio guttulatae-Cephalozietum bicuspidatae lophozietosum guttulatae* var. *Lophozia guttulata*, which, however, demands more light and higher temperature.

HERTEL (1974) gives a thorough literature review. In connection with the area studied the works of ŠMARDA (1947) and DUDA (1951) from Czechoslovakia are important, as well as contemporary studies of sandstones in Germany (NEUMAYR 1971, DUNK 1972), which contain a wealth of relevé material.

Scapania nemorea — community

Table 7.

The community with *Scapania nemorea* (Tab. 7) grows on partly shaded, damp rocks with a slope of 30° to 50°. Its syntaxonomy has not yet been satisfactorily resolved. ŠMARDA (1947) classifies it as a subsociation of the sociation *Diplophyllum albicans-Scapania nemorosa*. MAURER (1961) places similar communities into *Cephalozia bicuspidata-Scapania nemorosa* Verein HAYBACH 1956 and points out their similarity to the community of the association *Calypogeietum fissae cephalozietosum bicuspidatae* PHILIPPI 1956. In more recent studies, HERTEL (1974) deals with the syntaxonomy of this community, but I do not consider his classification of the community as a part of the association *Diplophylletum albicantis* (SCHADE 1923) HERTEL 1974 to be an appropriate solution, because it does not take into account the differences in ecological conditions between the two communities. Until further studies are undertaken, I would therefore classify this community as a part of the alliance *Diplophyllion albicantis*.

Table 6. — *Diplophylletum albicantis*

Relevé No.	1	2	3	4
Exposure	NNW	W	NE	WNW
Inclination [°]	80	85	90	85
Relevé area [m²]	1	1	1	0.5
Date: month	10	10	8	11
year	1975	1975	1975	1975
Locality	8	9	1	14
E_0: cover [%]	90	95	60	60
number of species	4	2	2	4
Diplophyllum albicans (L.) DUM.	4	5	3	1
Dicranella heteromalla (HEDW.) SCHIMP.	1	1	.	1
Tetrodontium brownianum (DICKS.) SCHWAEGR. s.l.	.	.	1	2
Mylia taylorii (HOOK.) S. GRAY	1	.	.	.
Lophozia guttulata (LINDB.) EVANS	1	.	.	.
Cephalozia bicuspidata (L.) DUM.	.	.	.	1

Pellia epiphylla — community

Table 8.

A community with *Pellia epiphylla* as the dominant and with several liverwort species commonly found on sandstone (*Calypogeia integristipula*, *Cephalozia bicuspidata* etc.) grows on the lower parts of sandstone walls and at their foot. For the time being, I shall consider this community, already described by SCHADE (1923), as a part of the association *Pellietum epiphyllae* NEUMAYR 1971. However, its author understood the association to be a community of mineral soils. Its substantial part is formed by the species *Atrichum undulatum* and *Thuidium tamariscinum*, which do not grow on sandstone.

Polytricho longiseti-Dicranetum scoparii KURKOVÁ 1978

Table 9.
Nomenclatural type: tab. 9, relevé 7; (Holotypus hoc loco)
Diagnostic species: *Dicranum scoparium*, *Bazzania trilobata*, *Polytrichum longisetum*, *P. pallidisetum*

These are communities with several layers: The cover of the herb layer (with V. *myrtillus*, *V. vitis-idaea*, and seedlings of *Picea excelsa*) may reach 50 %. The most important bryophytes are large tufts of the genera *Dicranum* and *Polytrichum*. The community develops on the edges of the summit plateau and on rocks and boulders on the sunny, gradually sloping sides of valleys. It colonizes mildly damp to dry habitats with protoranker soil 1 to 5 cm deep. The habitats, partly shaded by forest trees, are the gradually sloping surfaces (inclination 20° to 60°) of small rocks and boulders. They constitute the ecological optimum of the community. The community may also be found in crevices and on ledges, especially its variant with *Cephalozia bicuspidata*.

The community descends from gradually sloping habitats with deeper soil (3 to 5 cm) by way of earth-filled crevices between boulders and rock blocks, to sheer sandstone walls (inclination up to 80°). *Bazzania trilobata*, *Calypogeia integristipula*, *Mylia taylorii* and other liverworts colonize the

Table 7. — *Scapania nemorea* — community

Relevé No.	1	2	3
Exposure	SE	NE	NEN
Inclination [°]	30	40	50
Relevé area [m²]	0.1	0.3	1
Date: month	8	8	8
year	1975	1975	1975
Locality	29	33	31
E_0: cover [%]	80	80	100
number of species	5	8	10
Scapania nemorea (L.) GROLLE	2	3	3
Dicranella heteromalla (HEDW.) SCHIMP.	2	1	1
Cephalozia bicuspidata (L.) DUM.	2	2	1
Mnium hornum HEDW.	.	2	2
Lepidozia reptans (L.) DUM.	.	+	+
Pohlia nutans (HEDW.) LINDB.	1	.	1
Dicranum scoparium HEDW.	1	+	.
E_1: cover [%]	.	5	5
Vaccinium myrtillus L.	.	r	r

Only in one relevé:
E_0: *Lophozia guttulata* (LINDB.) EVANS + (2), *Leucobryum juniperoideum* (BRID.) C. MÜLL. + (2), *Diplophyllum albicans* (L.) DUM. + (3), *Scapania umbrosa* (SCHRAD.) DUM. + (3), *Polytrichum longisetum* BRID. 1 (3), *Sphagnum girgensohnii* RUSS. + (3).
E_1: *Dryopteris* sp. juv. r (3).

surrounding smooth walls, while *Dicranum scoparium* and species of the genus *Polytrichum* are found only in the crevices. On the edges of summit plateaus with decreasing humidity and increasing soil depth, individual species (*Dicranum scoparium*, *Pohlia nutans*) gradually become parts of the bryophyte synusia of forest communities.

The species composition of the community described is similar to that of the communities of the alliance *Hylocomion* NEUMAYR 1971. However, bryophyte synusia of artificially grown spruce forests are placed into this alliance by its author.

Plagiothecio undulati-Sphagnetum quinquefarii KURKOVÁ 1978

Table 10.
Nomenclatural type: tab. 10, relevé 9 (Holotypus hoc loco)
Diagnostic species: *Sphagnum quinquefarium*, *Plagiothecium undulatum*, *Polytrichum longisetum*

This community is related to the previous one in structure, but it requires higher humidity conditions. The communities are found typically on the upper surfaces of boulders and on wide ledges shaded by other rocks and well-soaked with water. The community tolerates low temperature and wide daily temperature fluctuations. Its dense cushions adhere to surfaces with an inclination of up to 40°. However, they usually get torn off from steeper walls (inclination 30—40°), and afterwards may continue their development on partly disintegrated sandstone or on sand covered valley floors. At the bottoms of the wider gorges the community offers suitable conditions for the growth of tree-seedlings. In cases where the surface of the boulders is large enough, the seedlings may reach maturity. The variant *Calypogeia inte-*

Table 8. — *Pellia epiphylla* — community

Relevé No.	1	2	3	4
Exposure	N	S	NNW	NE
Inclination [°]	80	60	110	80
Relevé area [m²]	0.9	1	0.1	0.8
Date: month	7	8	7	5
year	1975	1975	1973	1975
Locality	4	36	36	35
E_0: cover [%]	70	70	40	95
number of species	7	3	3	5
Pellia epiphylla (L.) CORDA	3	1	2	3
Dicranella heteromalla (HEDW.) SCHIMP.	3	3	2	2
Calypogeia integristipula STEPH.	1–2	.	1	1
Rhizomnium punctatum (HEDW.) T. KOP.	2	.	.	1
E_1: cover [%]	.	5	.	1
Dryopteris sp. juv.	.	r	.	+

Only in one relevé:
E_0: *Cephalozia bicuspidata* (L.) DUM. 2 (2), *Diplophyllum albicans* (L.) DUM. 1 (1), *Plagiothecium succulentum* (WILS.) LINDB. 1 (1), *Lophozia ventricosa* (DICK.) DUM. 1 (1), *Pohlia nutans* (HEDW.) LINDB. 1 (4).
E_1: *Vaccinium myrtillus* L. r (2), *Festuca gigantea* (L.) VILL. r (2).

gristipula forms on mildly humid, well illuminated habitats. It is characterized by the species *Dicranum scoparium* and *Bazzania trilobata*, by a decline in the occurrence of *Plagiothecium undulatum* and by frequent occurrence of *Vaccinium vitis-idaea* in the herb layer. Species composition of the variant *Polytrichum longisetum* is more uniform. It occurs on valley bottoms which are well illuminated or lack a tree level owing to former drainage operations, and on large, very damp cones.

As in the case of *Polytricho longiseti-Dicranetum scoparii*, this community is close to the communities described by NEUMAYR (1971) as forest synusiae and classified by him as part of the alliance *Hylocomion* NEUMAYR 1971.

DISCUSSION

The initial stages of development of bryophyte communities are characterized by high evenness and by a large number of species. Some of these species (e.g. *Lophozia* sp. div., *Cephalozia* sp. div.) have a low competitive ability, and are found only in these initial stages. At the same time species of larger liverworts appear (*Mylia taylorii*, *Calypogeia integristipula*). These have strong competitive abilities in relation to all other species, and they may overgrow the small liverworts. Mosses (*Dicranella*, *Dicranum*, *Dicranodontium*) are less expansive than the large liverworts. Their turfs either spread and gradually displace the liverworts, or else the liverworts overgrow them from the edges invards. Small moss turfs are often completely overgrown. The formation of a complete bryophyte cover thus reduces the species number in communities. Species which had not been present in the initial stage, or at least in the immediate vicinity of the colonized area, seldom become part of a bryophyte coenosis. The gradual "maturation" of communities eliminates species with lower competitive abilities. There appears

Table 9. — *Polytricho longiseti - Dicranetum scoparii*

Relevé No.	1	2	3	4	5	6	7	8	9	10
Exposure	NW	E	N	SE	NNE	S	N	E	N	E
Inclination [°]	40	30	25	55	30	60	60	20	60	60
Relevé area [m²]	0.5	0.16	1	1	0.4	0.9	1	2	1.5	1
Date: month	7	7	4	8	8	7	8	7	5	7
year	1975	1975	1973	1975	1973	1973	1975	1975	1975	1975
Locality	17	20	2	4	2	4	4	20	13	25
E_0: cover [%]	50	95	90	90	80	90	95	100	80	70
number of species	5	7	9	11	11	10	7	7	4	4
Cephalozia bicuspidata (L.) Dum.	1	1	.	+	.	.	.	.	.	.
Calypogeia integristipula Steph.	.	.	+	1–2	1	+	1	.	.	+
Lepidozia reptans (L.) Dum.	.	.	.	1–2	1	1	+	.	.	1
Mylia taylorii (Hook.) S. Gray	2	3	2	3	+	.	.	+	1	.
Bazzania trilobata (L.) S. Gray	2	2	2	+	3	2	2	2	2–3	4
Dicranum scoparium Hedw.	.	3	2	3	2	4	5	3–4	2–3	.
Polytrichum longisetum Brid.	2–3	.	2	.	.	+	+	.	3	1
Polytrichum pallidisetum Funck	.	2	.	.	+	.	.	2–3	.	.
Polytrichum formosum Hedw.	.	.	.	2	.	.	.	.	.	.
Sphagnum quinquefarium (Braithw.) Warnst.	.	.	.	+	.	.	+	1	.	.
Pleurozium schreberi (Brid.) Mitt.	.	2	+	.	.	+	.	.	.	.
Hylocomium splendens (Hedw.) B.S.G.	.	.	1	.	.	.	.	+	.	.
Lophozia ventricosa (Dicks.) Dum.	.	1	.	.	+	+	.	.	.	.
Mnium hornum Hedw.	.	.	1	.	2	.	.	.	.	.
E_1: cover [%]	5	15	.	1	.	.	10	12	10	.
Vaccinium myrtillus L.	+	2	.	r	.	.	1	2	1	.
Dryopteris austriaca (Jacq.) Woynar juv.	.	r	.	.	.	.	.	.	.	.
Picea excelsa (Lamk.) Lk. juv.	.	.	.	.	.	.	+	+	1	.
Vaccinium vitis-idaea L.	.	.	.	.	.	.	+	+	.	.

Only in one relevé:
Anastrepta orcadensis (Hook.) Schiffn. 1 (3), *Cephalozia lunulifolia* (Dum.) Dum. + (4), *Lophozia guttulata* (Lindb.) Evans 1 (4), *Pohlia nutans* (Hedw.) Lindb. 1 (6), *Plagiothecium denticulatum* (Hedw.) B. S. G + (4, 7), *P. laetum* B. S. G. + (6), *Dicranella heteromalla* (Hedw.) Schimp. + (1), *Dicranodontium denudatum* (Brid.) Britt. 1 (5), *Leucobryum juniperoideum* (Brid.) C. Müll. + (6), *Barbilophozia barbata* (Schmid. ex Schreb.) Loeske + (9), *Sphenolobus minutus* (Schreb.) Berggr. + (5), *Cladonia* sp. + (5).

to be a tendency to forming monocoenoses, or communities with one dominant species which is permeated by other species, usually of different growth forms.

Bryocenoses which do not include plants of other groups colonize only extremely exposed parts of the terrain, where other plants influence them only indirectly. In this case the inner balance of the plant community is maintained only by bryophytes and liverworts. As succession progresses, the thickness of the humus layer and the amount of silica grains under the bryophyte cover increase. Finally, the whole community is torn off the rock by force of mechanical factors (especially in winter), leaving the rock exposed as it had been before. This phenomenon is especially characteristic of the association *Mylietum taylorii*. Only single-layer liverwort communities, which are found, as a rule, on extremely shaded habitats, do not accumulate humus and silica grains and therefore are not subject to such processes.

Table 10. — *Plagiothecio undulati - Sphagnetum quinquefarii*

Relevé No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Exposure	NW	NNW	W	NE	N	N	S	SW	NW	W			N
Inclination [°]	50	40	35	20	10	15	40	35	40	15	0	0	15
Relevé area [m²]	4	1	0.5	0.8	1	1	0.7	0.25	0.6	1	1	1	0.7
Date: month	10	5	8	10	7	5	8	10	8	7	5	7	5
year	1975	1975	1975	1975	1973	1973	1973	1975	1975	1975	1975	1973	1975
Locality	8	13	4	2	4	4	2	4	4	17	13	2	13
E_0: cover [%]	85	100	100	100	100	100	100	100	100	100	100	100	100
number of species	7	6	4	4	8	6	7	4	3	3	2	2	2
Calypogeia integristipula STEPH.	1	+	2	.	.	.	1	.	.	.	.	.	.
Polytrichum formosum HEDW.	.	.	3	.	.	.	.	.	3	.	.	.	.
Polytrichum longisetum BRID.	.	3	.	.	2	3	3	3	.	3	3	3	2
Sphagnum quinquefarium (BRAITHW.) WARNST.	3	2	3	2	1	3	3	3	1	3	3	4	5
Plagiothecium undulatum (HEDW.) B.S.G.	.	.	.	4	3	3	2	3	3	.	.	.	.
Pleurozium schreberi (BRID.) MITT.	.	.	.	.	2	1	+	.	.	.	.	.	.
Bazzania trilobata (L.) S. GRAY	1	1	2	2	.	.	1	r	.	1	.	.	.
Dicranium scoparium HEDW.	2	+	.	2	+	+	.	.	.	.	.	.	.
Mylia taylorii (HOOK.) S. GRAY	2	.	.	.	.	+	.	.	.	.	.	.	.
E_1: cover [%]	75	30	5	1	.	.	.	.	50	10	5	.	.
Vaccinium myrtillus L.	1	+	.	.	.	.	.	.	.	1	1	.	.
Oxalis acetosella L.	+	+	+	.	.	.	.	.	.	.	.	.	.
Dryopteris austriaca (JACQ.) WOYNAR juv.	2	2	.	.	.	.	.	.	r	.	.	.	.
Picea excelsa (LAMK.) LK. juv.	r	+	r	r	.	.	.	.	.	.	.	.	.

Only in one relevé:

E_0: *Cephalozia lunulifolia* (DUM.) DUM. 1 (1), *Cladonia* sp. 1 (1), *Hylocomium splendens* (HEDW.) B. S. G. 2 (5), *Kurzia sylvatica* (EVANS) GROLLE + (5), ***Mnium hornum*** HEDW. 1 (2), *Plagiothecium laetum* B. S. G. + (5).

E_1: *Betula pubescens* EHRH. juv. r (10), *Empetrum* sp. 4 (1), *Vaccinium vidis-idaea* L. 1 (1).

More favourable places are later colonized by species of flowering plants. As the soil depth increases, the influence of sandstone is less manifest and the communities become closer to terrestrial ones, mostly as synusiae of coniferous forests.

Different species take part in the general succession changes described, depending on conditions of illumination and humidity. Therefore, the individual associations may be arranged along few axes, representing humidity and illumination conditions, and succession time (Fig. 6). In all cases we observe a general trend from initial stages rich in species to communities with a marked dominant and relatively few accompanying species.

Bare rock surfaces with varied temperature, light and humidity conditions are colonized by a species-rich procoenosis which gradually develops

towards a community reflecting the ecology of the habitat. The first member of the succession series is *Tetraphidetum pellucidae*. Its subassociation *dicranelletosum heteromallae* grows on mildly damp to dry, partly shaded places. On dry habitats it is overgrown by species of the genus *Cladonia*, forming a xerophytic community which probably belongs to the association

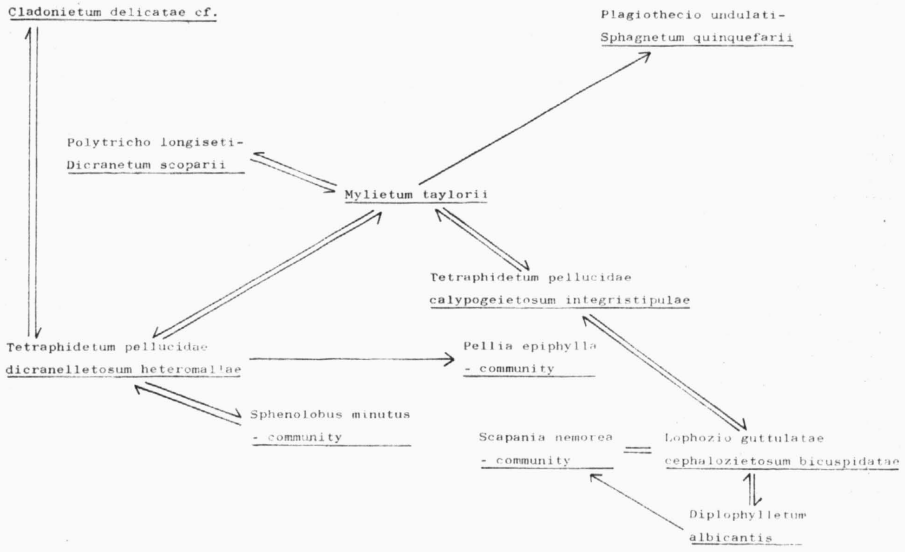


Fig. 6. Bryophyte succession on sandstone: Substrate humidity increases from left to right; illumination decreases from the top down.

Cladonietum delicatae POELT 1951. On mildly damp to dry habitats growths of *Tetraphidetum pellucidae dicranelletosum heteromallae* may develop into communities with *Sphenolobus minutus*. Under favorable light and temperature conditions on rock walls, *Tetraphidetum pellucidae dicranelletosum heteromallae* changes into the association *Mylietum taylorii*, which eventually becomes *Polytricho longiseti-Dicranetum scoparii* on mildly damp to dry, gradually sloping rocks.

The community *Tetraphidetum pellucidae calypogeietosum integristipulae* is the most species-rich link in the chain of succession on damp rocks. Two directions of succession are possible here: In case of low temperature and light we find the community of very damp, cold, dark walls — the association *Diplophylletum albicantis*. The association *Lophozio guttulatae-Cephalozietum bicuspidatae*, which colonizes very damp, mildly warm and shaded habitats, stands between the two communities mentioned above in the succession series. Rock walls with milder temperature conditions are colonized by the community with *Scapania nemorea*, which is closely related to the two communities mentioned above. The community with *Pellia epiphylla* succeeds the association *Tetraphidetum pellucidae* on damp habitats with low illumination. Better light and temperature conditions enable the development of the community *Mylietum taylorii*, the culmination

of the actual succession on sandstone walls. It colonizes mildly damp, sunny to partly shaded, mildly warm habitats. The association *Plagiothecio undulati-Sphagnetum quinquefarii* replaces it on milder slopes with higher humidity.

ACKNOWLEDGEMENT

I am indebted to the staff of the Geobotanical Department of the Botanical Institute (Czechoslovak Academy of Sciences, Průhonice) and the staff of Division of Geobotany of the Botany Department (Charles University, Prague), who discussed problems of plant ecology with me. Special thanks is due to my Ph.D. supervisor Dr. J. Moravec, CSc. Special appreciation is given to doc. Dr. J. Váňa, CSc. for his advice in bryophyte determination and supervision of my M.Sc. thesis. The assistance of prof. Dr. Zd. Černohorský, DrSc. and Dr. I. Pišút, CSc. with lichen determination is gratefully acknowledged.

Editorial comment

The author died on 12 January 1982. This paper is a condensed version of her Ph.D. thesis, submitted at the Faculty of Natural Sciences of Charles University (KURKOVÁ 1977). Preliminary information on sandstone bryocenoses has already been published by the author (KURKOVÁ 1978). This article was prepared for print by T. Herben and F. Krahulec, N. Johanisová translated the text and E. Jirousová drew the figures. We are indebted to Dr. J. Liška, Dr. J. Marek, and doc. Dr. J. Váňa, CSc. for their help in preparing this text.

SOUHRN

Jsou popisována společenstva mechorostů na pískovcových skalách severních a severochodních Čech a je diskutována jejich ekologie a sukcesní vztahy. Teplota a vlhkostní režim jsou hlavní faktory určující rozšíření druhů mechorostů v úzkých a hlubokých roklích pískovcových skalních měst. Prvotními stadii sukcese mechorostů jsou zde na druhy bohatá, vyvážená společenstva; kompetitivní interakce v pozdějších fázích sukcese způsobují vývin druhově ochuzených společenstev. Na strmých skalách jde obvykle o cyklický proces, závislý na mechanickém narušování; na příhodných místech však sukcese může pokračovat a dosáhnout až stadia jehličnatého lesa.

Na mírně suchých, dosti výslunných skalách se vyskytuje společenstvo *Tetraphidetum pellucidae* MAURER 1961 *dicranelletosum heteromallae* PHILIPPI 1965 a společenstvo se *Sphenolobus minutus*. *Tetraphidetum pellucidae calypogeietosum integristipulae* KURKOVÁ 1978 a *Mylietum taylorii* PHILIPPI 1965 se vyvíjí na středně vlhkých a zastíněných středních částech skalních stěn. Při extrémně stinných a silně vlhkých úpatích skal se vyskytují následující společenstva: *Lophozio guttulatae-Cephalozietum bicuspidatae* KURKOVÁ 1978; *Diplophylletum albicantis* HERTEL 1974, společenstvo se *Scapania nemorea* a společenstvo s *Pellia epiphylla*. Na mírnějších svazích, kde není vliv substrátu tak výrazný, se nacházejí společenstva *Polytricho longiseti-Dicranetum scoparii* KURKOVÁ 1978 a *Plagiothecio undulati-Sphagnetum quinquefarii* KURKOVÁ 1978.

LITERATURE

BARKMAN J. J. (1958): Phytosociology and ecology of cryptogamic epiphytes. — Van Gorcum, Assen [628 pp.].

— (1968): Das synsystematische Problem der Mikrogesellschaften innerhalb der Biozönosen. — In: TÜXEN R. [red.]: Pflanzensoziologische Systematik. — Den Haag.

— MORAVEC J. et RAUSCHERT S. (1977): Code of phytosociological nomenclature. — Vegetatio, Den Haag, 32 : 131—185.

DEMEK J. (1965): Geomorfologie Českých zemí. — Praha.

DUDA J. (1951): Společenstva bryophyt na pískovcových skalách v Beskydách. — Přírod. Sborn. Ostrav. Kraje, Opava, 12 : 323—334.

DUNK K. von der (1972): Moosgesellschaften im Bereich des Sandsteinkeupers in Mittel- und Ober- Franken. — Ber. Naturwiss. Ges. Bayreuth, 14 : 8—100.

HADAČ E. et ŠMARDA J. (1944): Příspěvek k výzkumu společenstev našich rezervací. — Krása Našeho Domova, Praha, 36 : 120—122.

HERTEL E. (1974): Epilitische Moose und Moosgesellschaften im nordöstlichen Bayern. — Beih. Ber. Naturwiss. Ges. Bayreuth, 1 : 1—489.

Hübschmann A. von (1967): Über die Moosgesellschaften und das Vorkommen der Moose in den übrigen Pflanzengesellschaften des Moseltales. — Schriftenr. Vegetk., Bad Godesberg, 2 : 63—121.
Kurková J. (1977): Společenstva mechorostů na pískovcích v Čechách. — Ms. [depon. in Kat. Bot. PřF UK, Praha].
Kurková J. (1978): The survey of bryophyte communities on sandstones in Bohemia. — Proc. Cryptogamol. Symp. Slovak Acad. Sci., Smolenice, p. 251—257.
Maurer W. (1961): Die Moosvegetation des Serpentingebietes bei Kirchdorf in Steinmark. — Mitt. Abt. Zool. Bot. Landesmus. „Joanneum" Graz, 13 : 1—29.
Moravec J. (1973): The determination of the minimal area of phytocenoses. — Folia Geobot. Phytotax., Praha, 8 : 23—47.
Neumayr L. (1971): Moosgesellschaften des Südöstlichen Frankenalb und des Vorderen Bayerischen Waldes. — Hoppea, Regensburg, 29 : 1—364.
Peciar V. (1967): Moose (Bryophyta) des südlichen Teils der ostslowakischen Tiefebene. — Acta Fac. Rer. Natur. Univ. Comenianae — Bot., Bratislava, 14 : 25—82.
Philippi G. (1965): Moosgesellschaften des morschen Holzes und des Rohhumus im Schwarzwald, in der Rhön, im Weserbergland und im Harz. — Nova Hedwigia, Weinheim, 9 : 185 bis 232.
— (1972): Die Moosvegetation der Wälder in der Rheinau zwischen Basel und Mannheim. — Beitr. Naturk. Forsch. Südwestdeutschl., Karlsruhe, 31 : 5—64.
Pilous Z. (1961): Mechová vegetace Demänovské doliny v Nízkých Tatrách. — Rozpravy Čs. Akad. Věd, Praha, 71/2 : 1—99.
Řezáč B. (1955): Terasy řeky Metuje a tabulová plošina Adršpašsko-Teplická. — Rozpravy Čs. Akad. Věd, Praha, 65/7 : 1—75.
Schade A. (1923): Die kryptogamischen Pflanzengesellschaften an den Felswänden der Sächsischen Schweiz. — Ber. Deutsch. Bot. Ges., Berlin, 41 : 49—66.
Schade A. (1934): Die kryptogamische Pflanzenwelt an den Felswänden des Elbsandsteingebirges und ihre Lebensbedingungen. — Feddes Repert., Beih., Berlin, 76 : 12—32.
Soukup J. (1963): Křídový útvar. — In: Kopecký L. [red.]: Vysvětlivky k přehledné geologické mapě ČSSR 1 : 200 000, M-33-IX, Děčín — Praha, p. 43—74.
Stuchlý J. (1976): Společenstva mechorostů Císařské rokle u Berouna. — Studie Čs. Akad. Věd, Praha, (1976)/2 : 1—93.
Svoboda J. et al. (1964): Regionální geologie ČSSR. 1. — Praha.
Šmarda J. (1947): Mechová a lišejníková společenstva ČSR. — Čas. Morav. Mus. v Brně, Vědy Přír., Brno, 31 : 39—88.
Vesecký A. [red.] et al. (1958): Atlas podnebí československé republiky. — Praha.
Yarranton G. A. (1966): A plotless method of sampling vegetation. — Journ. Ecol., Oxford, 54 : 229—237.

Received 13 April, 1983