

Ecology of sandstone ravine myxomycetes from Saxonian Switzerland (Germany)

by

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Abstract: We describe the ecology of a highly specialized community of ravine myxomycetes from sandstone gorges of the Saxonian Switzerland region (near Dresden, Germany). Five taxa, *Colloderma robustum*, *Diderma ochraceum*, *Lamproderma columbinum*, *L. puncticulatum* agg. and *Lepidoderma tigrinum*, account for 87% of all records. *Colloderma robustum* and *Diderma lucidum* are new records for Germany; *Diderma ochraceum* was known from a few collections only. A total of 127 small-scale vegetation relevés showed that the community occurs only in deep and narrow ravines (mean horizon openness 4.9%) on nearly vertical rocks (mean inclination 79°), and preferentially in northern exposition (42% of all relevés). Substrate pH is very acidic (mean 3.35). At the fructification time of the myxomycetes (beginning of October) the microclimate is very constant with temperatures around 10°C and nearly 100% relative humidity around the day. Beside green algae (associated with 100% of all myxomycete records, most common was *Coccomyxa confluens* (Kütz.) Fott s.l.) the bryophytes *Mylia taylorii* (64%), *Dicranodontium denudatum* (59%), *Tetraphis pellucida* (50%) and *Diplophyllum albicans* (40%) were of high indicator value for this community. Low values for niche width of the five more common myxomycete species reflect the high degree of specialization for the community as a whole, whereas niche overlap between species is high. Low values for the Cole index of association can be interpreted as competition between species or, more likely, reflect the relative rarity of fruiting colonies.

Key words: ecology, microhabitat, plasmodial slime molds, taxonomy.

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Introduction

Most mycologists traditionally expect myxomycetes (plasmodial slime molds) to be rather ubiquitous inhabitants of decaying wood in moist forests. However, during the last decades it became increasingly obvious that many if not most species are not ubiquitous in distribution and habitat preferences (Stephenson et al. 2007). A number of microhabitats with specialized taxa have been described during the last decade, like succulent desert plants (Lado et al. 1999, Mosquera et al. 2000), inflorescences of large Neotropical herbs (Schnittler & Stephenson 2002); bark of desert shrubs (Novozhilov et al. 2005); decaying fronds of palms (Stephenson 2003); epiphyllous bryophyte communities in the understorey of tropical forests (Schnittler 2001a); lianas (Wrigley de Basanta et al. 2008), or bark and decaying twigs in the forest canopy (Snell & Keller 2003, Schnittler et al. 2006).

The so-called bryophilous myxomycetes (Stephenson & Studlar 1985) are long known as inhabitants of bryophyte covers on logs, less common on rocks. Already Hoffmann (1795) described *Diderma ochraceum* originally as occurring "on mosses". Without giving detailed ecological data, Ing (1983) described a community of "ravine myxomycetes" with a preference for bryophyte covers on rocks from numerous localities throughout the most Atlantic parts of the British Isles, occurring either in ravines or Atlantic woodlands (the latter vegetation type not present in Central Europe). As key species he lists *Craterium muscorum*, *Diderma lucidum*, *D. ochraceum*, *Lamproderma columbinum* and *Lepidoderma tigrinum*. In his treatment of myxomycete communities (Ing 1994), he recognized ravine myxomycetes as a distinct community. However, no attempt has been made so far to quantify the ecological niches for the species using vegetation relevés (estimating abundances of all organisms in a pre-determined area) and measurements of abiotic factors, a technique successfully used to describe niches for ravine bryophyte communities (Holz 1997).

The cretaceous sandstone layers of Saxonian Switzerland and the larger adjacent Bohemian massive are furrowed by deep and narrow ravines, since even small rivulets can carve out the porous and moist sandstone over time. The ravines are characterized by an inverse zonation of vegetation, with montane plants inhabiting their bottom, and species of dry and warm habitats the exposed reefs. The region is long known for its relative paucity in vascular plants, but high diversity in cryptogamic plants, which spurred a number of systematic studies especially on mosses and liverworts (Schaade 1912, 1934). The ravines have isolated outposts of several Atlantic ferns, like the now extinct *Hymenophyllum thunbrigiense* (Wilpert 1937), or the Killarney fern (*Trichomanes speciosum*, present with gametophytes only, Vogel et al. 1993). The main reason is the constantly humid microclimate in the up to 80 m deep and often at their bottom only 3–5 m wide gorges (Beer 2002). During cold fronts, the bottom of a gorge is warmer than the surrounding plateau and reefs; during warm fronts, the pattern reverses.

The ravines of Saxonian Switzerland should be diverse in various groups of cryptogams as well as in myxomycetes, although so far not targeted by a study dedicated to this group of organisms. However, with *Lamproderma granulosum* H. Neubert, Nowotny & Schnittler a new species of this diverse myxomycete genus was described from

the rock walls in a ravine (Uttewalder Grund, near Stadt Wehlen), and is so far known only from this and the adjacent ravines (Neubert et al. 1990).

This study analyses the ecology of a highly specialized community of ravine myxomycetes, presents taxonomic descriptions for the species involved and circumscribes their ecological niches. Although it is limited to the sandstone rocks of the ravines, we also regularly checked litter and decaying wood to look to which degree the rock-inhabiting species are specialized.

Materials and methods

STUDY AREA: Between September 26 and October 4, 2007, several ravines of the region were systematically checked for the presence of myxomycetes on bryophyte-covered or bare sandstone rocks. All larger boulders (exceeding 1.50 m height) at the valley bottom and the surrounding rock walls up to 2.50 m height were systematically surveyed for the presence of fruit bodies or plasmodia. At this time, most myxomycete colonies consisted at least partially of plasmodia, and the light-colored plasmodia are very easy to spot on the dark-green bryophyte turfs. All areas with bare stone (not buried by soil but naked or covered by bryophyte turfs) were surveyed, often using LED headlights in very dark places. With a group of ten students we surveyed an estimated total of 8.7 km ravine bottom, including 200–500 rocks and 500–900 larger boulders. The work was carried out in the following ravines (numbers 1–127 in brackets refer to the respective vegetation relevés, additionally the length of the ravine section surveyed for myxomycetes is given):

Germany, Saxony, Saxonian Switzerland near Wehlen (Vordere Sächsische Schweiz):

Uttewalder Grund

1. Lower "Zscherregrund", 25–150 m from branching of the "Uttewalder Grund"; 1.3 km NNE Stadt Wehlen; 50°58'07"N, 14°02'33"E ± 75 m, 185 ± 10 m a.s.l. [relevés 1–8 and 68–71, length 150 m]
2. "Uttewalder Grund" between branching to "Zscherregrund" and restaurant "Waldidyll"; 1.5 km N Stadt Wehlen; 50°58'18"N, 14°02'07"E ± 300 m, 190 ± 10 m a.s.l. [9–15, 127, length 575 m]
3. "Uttewalder Grund" between restaurant "Waldidyll" and "Felsentor"; 1.8 km N Stadt Wehlen; 50°58'30"N, 14°02'10"E ± 250 m, 192 ± 10 m a.s.l. [16–22, length 450 m]
4. "Uttewalder Grund" between "Felsentor" and branch to "Bruno-Barthel-Weg"; 1.9 km N Stadt Wehlen; 50°58'38"N, 14°02'20"E ± 150 m, 195 ± 10 m a.s.l. [23–35 and 49–63, length 250 m]
5. "Kohlgrund", upper part between branch to "Bruno-Barthel-Weg" and side valley "Holzengrund"; 1.7 km NNE Stadt Wehlen; 50°58'31"N, 14°02'45"E ± 150 m, 200 ± 25 m a.s.l. [64–67, length 300 m]

Amselgrund

6. "Amselgrund" between "Amselsee" and restaurant "Amselallbaude"; 1.3 km NNW Niederrathe; 50°58'30"N, 14°04'40"E ± 350 m, 140 ± 25 m a.s.l. [37–44, length 750 m]
7. "Raaber Kessel", a side valley of the "Amselgrund" W of the "Amselsee"; 900 m NW Niederrathe; 50°58'02"N, 14°04'38"E ± 150 m, 155 ± 25 m a.s.l. [45–48, length 200 m]

Polenztal

8. "Polenztal", E-exp. valley slope to "Hockstein", 35 m above valley bottom; 500 m W Hohnstein; 50°58'87"N, 14°06'08"E ± 70 m, 200 ± 20 m a.s.l. [36, length 50 m]
9. "Polenztal", western valley bottom from "Annenloch" to "Waltersdorfer Mühle"; 1.5 km SSW Hohnstein; 50°58'15"N, 14°06'12"E ± 900 m, 165 ± 10 m a.s.l. [95–100, length 2000 m]
10. "Polenztal", western valley bottom from branch to "Schindergraben" to "Annenloch"; 750 m SW Hohnstein; 50°58'42"N, 14°06'10"E ± 350 m, 170 ± 10 m a.s.l. [84–89, length 750 m]

Germany, Saxony, Saxonian Switzerland near Bad Schandau (Hintere Sächsische Schweiz):

Schießgrund (Schrammsteine)

11. "Schießgrund", lower part from "Zahnsgrund" to its dichotomous branching; 1.3 km ESE Ostrau; 50°55'07"N, 14°11'40"E ± 250 m, 215 ± 25 m a.s.l. [90–94, length 500 m]

Großer Zschand

12. Lower part of "Großer Zschand", from "Neumannsmühle" to branch to "Winterstein"; 2.5 km S Ottendorf; 50°55'15"N, 14°17'20"E ± 600 m, 215 ± 25 m a.s.l. [72–76 and 101–110, length 1300 m]

13. "Richterschlüchte", a NE-exp side valley of "Großer Zschand", mouth half way to "Richters Grotte"; 5 km S Ottendorf; 50°54'05"N, 14°17'45"E ± 300 m, 265 ± 15 m a.s.l. [77–83, length 750 m]

14. "Weberschlüchte", a NE-exp side valley of "Großer Zschand", mouth to "Jortanshorn"; 5.3 km S Ottendorf; 50°53'56"N, 14°17'45"E ± 300 m, 265 ± 25 m a.s.l. [111–126, length 700 m]

VEGETATION RELEVÉS: To estimate abundances of all larger organisms forming ravine community, at all places where a colony of rock-inhabiting myxomycetes was discovered, we carried out a vegetation relevé covering an area of 20 cm x 20 cm which was chosen in a way to include the majority of the myxomycete plasmodia or fructifications encountered. Myxomycete colonies were only considered if still within reach; not higher than 2.5 m for vertical walls. First, ten environmental parameters were recorded: (1) height of the myxomycete colony above ground (where soil starts, precision 10 cm, possible range 0–80 m); (2) height of the locality above valley bottom (with the rivulet taken as baseline, precision 0.5 m, range 0–80 m); (3) height of the rocks above the colony (all rocks not covered by soil, precision 0.5 m, range 0–80 m); (4) per cent horizon opening, as seen with a fisheye lens (precision 1%, range 1–100%); (5) exposition of the rock surface (in degrees from North = 0 degrees, precision 5°, range 0–360°); (6) inclination of the rock surface (using a ruler and a compass with inclination scale, precision 2°, range 0–180°); (7) pH (measured three times on three samples of bryophytes covered by myxomycetes using an Orion 610 pH meter with a touch down probe, precision 0.05 units, range 2.5–4.5 units). In the relevé areas (20 cm x 20 cm), we recorded per cent coverage of (8) bryophyte covered rock surface, (9) algae-covered rock and (10) naked rock. To complete the relevé, we counted the number of myxomycete fruiting bodies (including all developing fruiting bodies as soon as the plasmodia segregated); estimated the total number of myxomycete fruiting bodies on the surface of the rock or boulder; and finally assessed species and per cent coverage of mosses, liverworts and vascular plants (if any) according to the following scale: + = 1%, 1 > 1–6%, 2 > 6–12.5%, 3 > 12.5–25%, 4 > 25–50%, 5 > 50% coverage. For data evaluation, we used as additional environmental factors (11–14) the coverage of the four most abundant bryophyte species (*Mylia taylorii*, *Dicranodontium denudatum*, *Tetraxis pellucida*, and *Diplophyllum albicans*; all precision 5%, range 0–100%).

For each relevé, three samples of bryophytes and/or algae, and one for myxomycetes, each covering about 2 cm x 2 cm, were taken and used to determine substrate pH at the evening after collecting using an Orion 635 device (Thermo Orion Inc.) with a solid state electrode. To record horizon opening, we used a digital camera Nikon Coolpix 8400 with a Fisheye objective FC-E9 (angle 183°) which was mounted on an adapter with a compass and a spirit level. This allows to adjust the camera horizontally and take the picture in a way that the upper side is always facing North. Images were analyzed with the software WinSCANOPY (Regent Instruments, Canada) to calculate the proportion of open sky.

MICROCLIMATIC DATA: Air temperature and humidity were recorded at several places with a total of 16 data loggers Hobo Pro H08-032-08 with the following specifications: temperature, precision 0.1°C; relative humidity, precision 0.1%. Four pairs of loggers were placed at the first four localities ("Uttewalder Grund"), covering the regions of the relevés 1–63 and 68–71 in a way that for each pair of loggers one was placed at a vertical rock in a myxomycete colony (maximum height above valley bottom: 5m), the second on the ground beneath the rock. Of the remaining eight loggers, two were placed at half height of a rock wall at the "Uttewalder Grund", two in a side gorge of the "Uttewalder Grund" half way between plateau and valley bottom, three on exposed reefs in plateau height, and the last at a shaded wall of Hohnstein castle, the highest and most exposed point in the whole region. The

height above the nearest valley bottom was measured or estimated from a topographic map. All loggers were sheltered from direct sunlight. Data were recorded for 24 hours from midnight to midnight in intervals of 5 min within a period of cloudless sky (01.10.2007). For the four localities in the ravine "Uttewalder Grund", these measurements were repeated one year later prior to the appearance of myxomycete plasmodia (26.08.2008).

SAMPLING AND SPECIES DETERMINATION: Bryophytes were determined in the field wherever possible, carefully surveying the 20 cm × 20 cm rectangle of a vegetation relevé with LED headlights and hand lenses. In addition, the three bryophyte samples per relevé were checked with a dissecting microscope to reveal minute species, and air dried in paper bags for laboratory investigation of critical taxa. Herbarium specimens of all taxa are deposited in JE, duplicates of most samples are included in the private collection of the third author. Bryophytes were determined according to standard literature, and localities were cross-checked with the distribution atlas of Saxony (Müller 2004). For myxomycetes, one sample for each species in a relevé was made, taking away a piece of moss 2 cm × 2 cm in size. It was assumed that sporocarps that shared the same substratum and were separated by a distance that could be overcome by a migrating plasmodium had developed from the same plasmodium; these sporocarps were considered as one record. Sporocarps with the underlying bryophyte or algae substrate were air-dried and mounted in small boxes. In addition, permanent slides of individual sporocarps were prepared for study using polyvinyl lactophenol. If not stated otherwise, all collections were made by the first author and deposited at the Botanical State Collection, Munich (M). Scanning electron micrographs of some specimens were prepared at St. Petersburg, using a Jeol 35 c scanning electron microscope (SEM).

DATA ANALYSIS: To estimate the completeness of the survey, a species accumulation curve was constructed according to the rarefaction formula with the programme EstimateS (Version 7, Colwell 2004), which computes a number of estimators of species richness as well. A hyperbolic regression according to the formula $y = ax/(b+x)$, resulting in a curve shape coming very close to a broken-stick model (Magurran 2004, compare Unterseher et al. 2008) was applied to the data, with the parameter a giving an estimate for the maximum number of species to be expected at this kind of substrate.

Using the fourteen environmental parameters described above, niche width according to Levins (1968) was calculated for the more common myxomycete species (represented by more than 20 records) according to the formula $B = 1 / \sum p_i^2$, with p_i as the proportion of individuals in resource state i . This value was standardized to a 0–1 range as $BS = (B-1)/(n-1)$ with n as the number of resource states (eight for each environmental parameter, reaching from its minimum to maximum possible value, see figures in section Vegetation Relevés). Niche overlap between the common myxomycete species was calculated with the symmetrical measure proposed by Pianka (1973) as $NB = \sum p_{ij} p_{ik} / \sqrt{(\sum p_{ij}^2 \sum p_{ik}^2)}$, with p_{ij} as the proportion of individuals of species j and k in resource state i . The interspecific index of association after Cole (1949) with corrections of Ratliff (1982) was calculated and tested for significance, using a Chi square test with $P = 0.05$ as the critical threshold.

To resolve the taxonomy of 43 collections of *Lamproderma* spp., especially those allocated to the *L. granulosum-puncticulatum* complex, 14 morphological characters were recorded and subjected to a detrended correspondence analysis (DCA, see Table 1). Characters were either measured (m) or estimated according to a scale (s); and observed on three well developed sporocarps of average size (+) or by looking over the whole collection (++). Characters included in the analysis were (1) Sporotheca shape (s++; 1 = depressed, 2 = slightly depressed, 3 = round, 4 = ovate, 5 = ellipsoid); (2) sporotheca width (m+) and (3) height (m+); (4) minimum and (5) maximum capillitium diameter, measured on first-order threads between origin and first branching (m+); (6) capillitium shape (s++; 1 = thread-like, 2 = slightly flattened, 3 = clearly band-like flattened) and (7) color under transmitted light (s+; 1 = nearly colorless, 2 = pale brown, 3 = brown); (8) capillitium origin (s+; 1 = on top of columella only, 2 = somewhat decurrent, 3 = from the whole length of columella); (9) peridium color (s++; 1 = iridescent blue, 2 = mixed, 3 = dull silvery); (10) ratio stalk length to sporotheca height (s++); (11) stalk length (m+); (12) spore diameter (m+; 15–25 spores per sporocarp); (13) length of spore ornaments (spinulae, m+; 5–10 spores per sporocarp) and (14) density of spore ornaments (m+; spinulae per 9 μm^2 spore surface, 3 spores per sporocarp). One trait (presence of capillitium granula) was excluded from the analysis since only three collections were observed with a granulated capillitium. The program PC-Ord V. 5 for Windows (McCune & Mefford 1999) was used with default settings (rescaling threshold = 0, number of segments = 26). To evaluate the importance of

Table 1. Morphological traits used for the detrended correspondence analysis of 45 samples of *Lamproderma*. Given is the relevé number (first column) and the species assignment (second column, *col* = *L. columbinum*, *pun* = *L. puncticulatum* agg.). Numbers of traits are in parentheses, see text for details. The two last rows give the correlation values between the respective trait and the ordination axes.

RV	Trait	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
	Det	sporotheca	width	height	capillitium	max	features	flat	ori	col	stalk	spore	diam	spine	spine
		shape			width				peridium		to spc	len		height	density
					min						ratio				
1	<i>pun</i>	2	840	740	3.2	7.2	3	2	1	3	1.0-1.5	1133	15.4	0.9	4.2
2	<i>col</i>	5	530	753	2.1	3.6	1	3	3	1	2.0-2.5	1850	14.2	0.7	13.5
3	<i>pun</i>	3	717	810	3.6	6	3	2	1	1	1.0-1.6	1347	14.2	1.0	6.3
4	<i>pun</i>	3	810	763	3.2	6.5	2	3	1	3	0.7-1.2	883	16.5	0.8	9.0
6	<i>pun</i>	3	700	807	2.9	6.3	3	2	1	3	1.0-1.5	603	16.6	0.8	6.8
7	<i>pun</i>	3	710	707	1.5	4.6	2	2	1	2	1.0-2.0	763	16.1	0.9	7.3
8	<i>pun</i>	3	700	760	2.6	4.9	3	2	1	3	1.1-2.0	1317	16.9	0.8	6.8
14	<i>col</i>	5	650	810	1.1	1.5	1	2	2	1	3.0-3.5	1750	10.4	0.7	14.3
30	<i>pun</i>	3	850	787	1.4	3.1	2	2	1	3	1.0-1.3	1317	16.3	0.6	4.3
32	<i>col</i>	5	637	703	1.6	1.8	1	2	3	2	2.0-2.3	2200	11.9	0.8	11.5
33	<i>pun</i>	3	707	727	2.3	7.7	3	2	1	2	1.0-1.4	783	15.0	1.0	10.6
36	<i>col</i>	5	650	920	1.3	1.5	1	2	3	1	1.7-2.6	2000	11.7	0.8	9.8
50	<i>pun</i>	1	800	687	2.7	9.5	3	2	1	3	1.0-1.4	1383	14.4	1.3	3.7
54	<i>col</i>	3	610	670	1.6	3.7	2	2	2	1	1.5-2.5	1890	12.9	0.5	13.7
55	<i>pun</i>	3	690	817	2.4	8.5	3	2	1	2	0.8-1.3	733	14.5	0.9	13.3
57	<i>pun</i>	2	813	853	1.6	5.3	2	2	1	1	1.1-1.6	633	14.0	0.4	13.3
58	<i>pun</i>	3	780	797	4.1	9.1	3	2	1	1	1.5-1.9	1300	14.7	0.7	7.0
63	<i>pun</i>	3	707	733	3.5	6.8	3	3	1	1	1.3-1.5	983	14.9	0.7	9.3
64	<i>col</i>	5	590	737	1.3	1.8	1	2	3	1	2.3-3.1	2300	11.8	0.6	13.0
65	<i>pun</i>	3	527	617	4.8	7.1	3	2	1	3	1.0-1.3	683	15.5	1.0	7.5
67	<i>pun</i>	2	693	733	3.2	4.9	3	2	1	2	0.5-0.7	533	16.2	1.0	7.8
73	<i>pun</i>	3	630	760	3	4.8	3	2	1	2	1.7-1.9	1017	14.5	1.0	7.8
76	<i>col</i>	5	647	780	0.8	1.4	1	3	3	1	2.9-3.3	1783	15.4	0.8	12.8
77	<i>pun</i>	3	803	830	2.9	5.3	3	2	1	1	1.3-1.7	1250	14.9	1.2	3.8
80	<i>pun</i>	3	770	827	2.2	5.7	3	2	1	3	1.0-1.5	1000	14.3	0.9	8.5
86	<i>col</i>	5	690	857	2	3	1	2	2	1	2.5-3.5	1933	11.4	0.4	12.7
90	<i>col</i>	4	590	850	1.8	2	1	3	2	2	2.3-2.9	2250	11.8	0.5	9.6
91	<i>pun</i>	1	810	757	3.2	8.2	3	2	1	3	1.0-1.2	583	16.1	1.1	3.7

RV	Trait	(1) sporothecca shape	(2) width	(3) height	(4) capillitium width min	(5) max	(6) features flat	(7) col	(8) periidium ori	(9) col	(10) stalk to spc ratio	(11) spore len	(12) diam	(13) spine height	(14) spine density
92	<i>pun</i>	2	760	760	3	4.5	2	1	2	2	1.3-1.9	717	14.7	0.9	3.4
93	<i>pun</i>	3	650	737	4.4	7.4	3	1	3	2	0.3-0.8	360	17.3	0.7	3.7
94	<i>pun</i>	3	747	780	2.9	3.6	2	1	1	2	1.3-1.7	1333	14.2	0.5	10.4
95	<i>col</i>	5	677	873	2.4	3.1	1	2	1	2	2.1-2.4	1800	10.9	0.4	14.6
96	<i>col</i>	5	637	770	2.6	3.7	1	3	2	3	2.0-2.9	2000	10.4	0.6	13.0
97	<i>col</i>	5	633	890	1.7	2.1	1	3	1	2	2.8-3.2	1617	14.9	0.6	12.8
101	<i>col</i>	5	667	967	2.6	2.9	1	3	1	1	2.1-2.6	1950	14.1	0.6	12.3
102	<i>pun</i>	4	750	820	3.8	5.5	3	2	3	1	1.0-1.5	1067	15.3	0.6	6.8
103	<i>col</i>	5	633	890	1.9	2.6	1	2	1	2	2.7-3.3	1383	14.2	0.6	11.7
104	<i>pun</i>	3	797	810	3.2	5	3	2	1	2	1.6-2.4	1343	14.3	0.9	4.0
106	<i>col</i>	5	627	790	2.4	4.3	2	3	1	3	2.3-2.8	1600	11.3	0.3	10.2
110	<i>col</i>	5	577	723	2.5	3.4	1	3	1	3	2.0-2.4	2100	12.6	0.5	11.0
114	<i>col</i>	4	630	863	2.7	3.8	1	2	2	2	2.5-2.8	1850	13.3	0.7	9.3
118	<i>col</i>	4	697	773	1.5	2.9	1	3	2	2	2.0-2.3	2300	11.9	0.5	12.0
123	<i>pun</i>	3	703	893	2.7	7.2	3	1	3	2	1.3-1.8	833	15.7	0.7	4.0
30a	<i>pun</i>	5	883	807	3.1	6.0	3	1	3	3	1.5-1.8	1200	14.2	1.7	8.4
64a	<i>pun</i>	4	617	737	4.0	6.2	3	1	2	2	0.8-1.3	827	13.6	2.7	6.8
R1	-0.75	0.58	-0.15	0.54	0.72	0.76	-0.41	-0.81	0.52	-0.81	-0.99	0.75	0.43	0.32	-0.38
R2	0.26	-0.09	-0.15	-0.25	-0.18	-0.38	0.37	0.41	-0.22	0.24	0.54	-0.41	-0.19	-0.50	0.09

individual characters for the distribution of samples in ordination space, correlation coefficients of the characters for the two most important axes were analyzed.

A second multivariate analysis was performed to evaluate the environmental data from the 127 relevés. Here, the sample-species matrix (main matrix in PC-Ord) included 143 records from nine taxa. To reduce noise from infrequent species we decided to omit the single doubtful record of *Trichia botrytis* and the four records of *Physarum album*, since a preliminary ordination showed the position of the four relevés of this species so far from all other of the data set that the positions of the latter could not be resolved. This resulted in a final data set of 122 records from 7 myxomycete species. Multivariate analysis was performed as a DCA with default settings in PC-Ord, using values of the fourteen environmental parameters explained above. In case of significant effects, the parameters were superimposed as radiating vectors on the resulting ordination (cutoff r^2 value = 0.01, vector scaling = 700%). Their relative strength and direction from the centroid indicated the correlation with the ordination. To increase the interpretability of the results, the ordination was rotated continuously to bring the most important parameter parallel to the most important axis. Then, the percentage of explained variation was calculated for the two most important axes. Despite the large number of zeros (absence) in the species-samples matrix, the transformation of the data with the Beals smoothing function of PC-Ord (McCune 1994, Ewald 2002, Schnittler et al. 2006) did not increase the explanation values of the ordination. Therefore this tool was not considered further.

Results

SPECIES DIVERSITY: Within a total of 143 records from 127 rocks and boulders (each represented by a vegetation relevé), nine species of myxomycetes were identified. Nomenclature of species' names in the annotated list follows Lado (2001) in the online version of Hernández-Crespo & Lado (2005). The abbreviation 'cf.' after the relevé number indicates that it could not be assigned to this name without remaining doubts, whereas '?' denotes a collection represented by scanty, immature or moldy sporocarps. In brackets follows the number of all relevés with the respective species and a five-digit number in parentheses (collection number of the first author), if a voucher specimen was collected.

Colloderma robustum Meyl. - 23 records [Relevés 16, 18 (21792), 19, 20 (21793), 21, 32, 34, 53 (21819), 55, 56, 58 (21827), 63, 70 (21840), 71 (21841), 79 (21849), 82, 83 (21853), 85 (21855), 100 (21870), 117 (21885), 120 (21888), 122 (21889), 126 (21892)]

This species is associated with *Mylia taylorii* (96% of all records). This liverwort has a northern-alpine distribution, but an isolated outpost in the region (Müller 2004) and is well known to be restricted to the deepest parts of the ravines with the most uniform microclimate. *M. taylorii* forms turfs typically 2–5 cm thick, where the plasmodium of *C. robustum* lives. If these turfs grow too large and the rock is too steep, they fall down in regular intervals of time, leaving bare rocks which will be overgrown anew. Probably due to this reason, the rocks inhabited by *C. robustum* have the lowest mean inclination (72°) of all myxomycete habitats. *C. robustum* forms often large colonies with 500–1000 plasmodiocarps on a single turf of *Mylia* 10–20 cm in diameter.

Plasmodia are first cream-white and hidden in *Mylia* turfs with a high proportion of green algae in deeper layers. About 2–3 weeks prior to fructification, the plasmodia

emerge, having an appearance like a phaneroplasmodium (which is peculiar, as this character is considered exclusive to Physarales, but *Colloderma robustum* is regarded as a member of the Stemonitales). Later they turn sulfur-yellow in color and start to form distinct plasmodiocarps at the tip of the *Mylia* shoots, secreting a solid translucent slime sheath. Within another week, the dark color of the fructification develops. Sometimes the slime sheath ruptures during maturation; in this case the plasmodiocarps show the blue-iridescent false color of the peridium. More often peridium and the dried, horny slime sheath remain together, resulting in a dull grey color. Fructifications develop as plasmodiocarps of irregular shape, 1–3 mm in diameter on plasmodial remains forming an irregular hypothallus. Capillitium arising from a large, flat columella (Fig. 1), connected to the translucent peridium (Fig. 2), consisting of long, slender threads (Fig. 3) that appear nearly translucent under a compound microscope. Spores are dark brown in mass, 11.5–13.7(–16.3) $\mu\text{m} \times$ 10.0–12.0(–13.5) μm , of irregular ovoid shape (Fig. 4) and covered with blunt baculae (Fig. 5), appearing violet brown in transmitted light. The much larger plasmodiocarps developing from a sulfur-yellow plasmodium, a well-developed columella and the more persistent slime layer distinguish this species from *Colloderma oculatum* (C.Lippert) G.Lister, the most common species of the genus.

This species is regarded as very rare; we report the first collections from Germany. In the studied region it was fairly common in ravines with rocks or boulders carrying *Mylia taylorii*, sometimes forming multiple colonies with thousands of plasmodiocarps on a single boulder. It was described by Meylan (1933) from the Swiss Jura, who gives a range of 13–17 μm for spore size. Most probably not knowing Meylan's work, Krziemiewska (1934) described *C. dubium* from wet wood covered with mosses and liverworts of the Zaroœlak forest (eastern Carpathians). All characters given by her coincide well with our specimens; spore size is given as 10–13 $\mu\text{m} \times$ 10–12 μm . We assume this taxon to be conspecific with *C. robustum*. A recent report of *C. robustum* comes from mossy bark in high elevation pine forests of the Mexican state of Tlaxcala (McHugh, pers. comm.).

Diderma lucidum Berk & Broome - 3 records [Relevés 22 (21794), 46 (21812), 64 (21835)]

A new record for Germany but rare in the study area; two of the three collections were associated with *Tetraphis pellucida*. During development, the bright orange phaneroplasmodium and developing fructifications are easy to confuse with those of *Lepidoderma tigrinum*, especially if the latter species does not form conspicuous lime scales. However, if a boxed specimen dries out, the peridium opens quickly, rolling back in large flakes which give the sporocarps the appearance of a flower (Fig. 6). Prominent microscopic characters are the flattened capillitium with expanded edges (Fig. 7) and the dense spore ornamentation (Figs. 8, 9).

The species is so far known only from the most Atlantic parts of the British Isles (Ing 1983) and Japan (Yamamoto 1998: 296, Ing 1999: 307).

Diderma ochraceum Hoffm. - 24 records [Relevés 104, 105 (21875), 18 (21791), 25 (21797), 26 (21798), 27 (21799), 31 (21801), 37 (21806), 38, 39 (21807), 40

(21808), 41 (21809), 49, 51 (21817), 53 (21821), 59 (21829), 62 (21832), 68 (21838), 69 (21839), 70, 72 (21842), 84 (21854), 87 (21857), 88 (21858), 104, 105 (21875)]

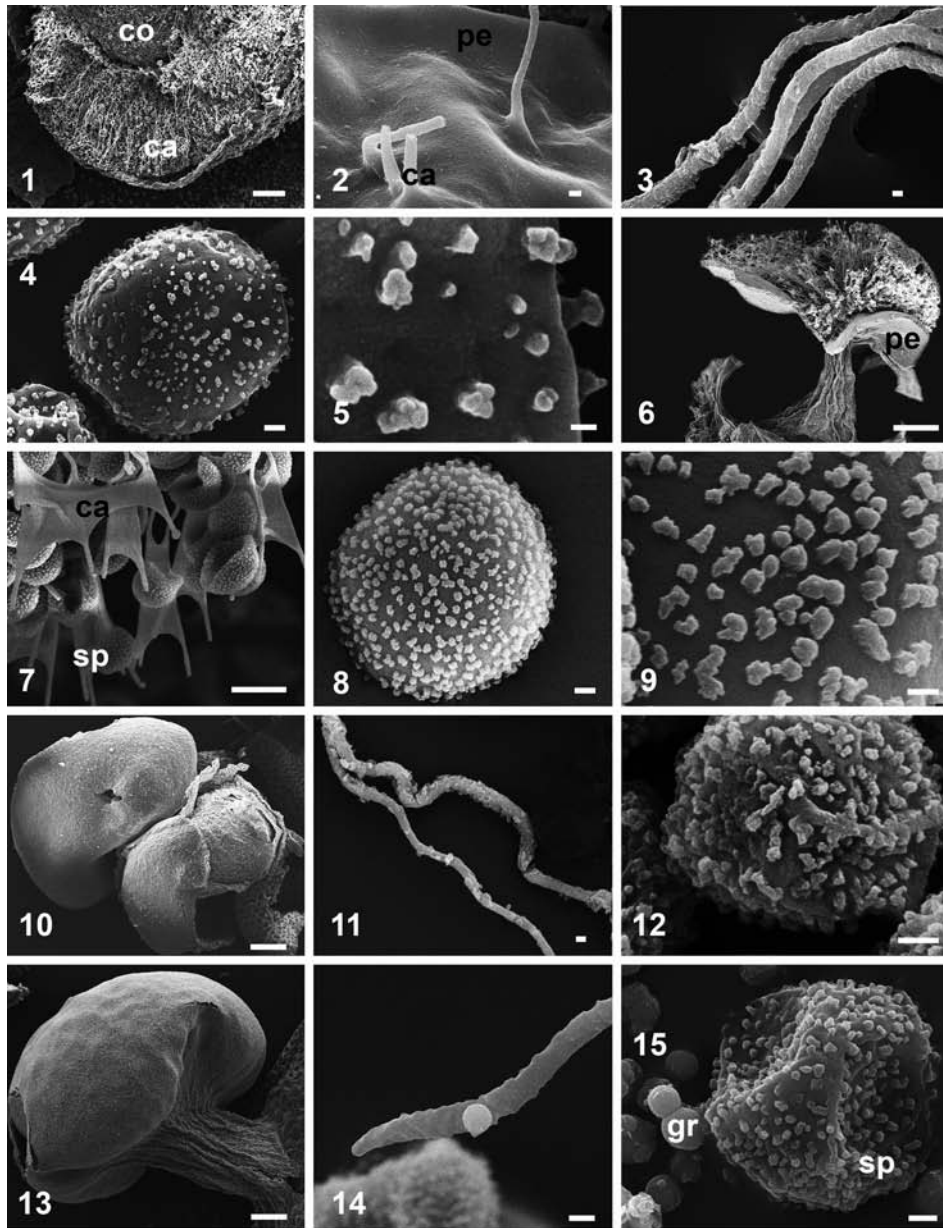
A species described from Germany (Hoffmann 1795). Usually regarded as very rare, it is one of the most common species in the ravines and was recognized as a stable member of this community by Ing (1983). In the Saxonian Switzerland region it is most often associated with *Mylia taylorii* and *Dicranodontium denudatum*. Actively moving plasmodia were bright yellow and very conspicuous at the time of the study. They segregate and form distinct plasmodiocarps on the tip of bryophyte shoots (Fig. 10), often assuming a doughnut-like shape around the narrow lanceolate leaves of *Dicranodontium*. Maturation takes a long time, perhaps several weeks; during which the plasmodia turn brownish and a brittle calcareous peridium develops. From this reason, many of the collections made by us do not appear as fully mature (Figs 11, 12). Like the two previous species never found before in a lignicolous situation.

Diderma umbilicatum Pers. - 10 records [Relevés 82 (21852), 107 (21877), 109 (21879), 111 (21881), 112 (21882), 113 (21883), 116, 119 (21887), 124 (21891), 125]

A species found most often not on bryophytes but on thin mats of green algae covering otherwise naked rocks and boulders. However, both *Dicranodontium denudatum* and *Mylia taylorii* grew often in close vicinity to the colonies (70% of all records). The species was most common in the very moist and more elevated ravine "Richterschlüchte". The plasmodium is first white, turning rose during maturation, forming stalked fructifications with a large columella (Figs 13–15). Apparently a rare species which is usually found lignicolous in cool and damp situations; most often in the mountains (Neubert et al. 1995:93).

Lamproderma columbinum (Oers.) - Rostaf. 22 records [Relevés 2 (21775), 14 (21788), 15 (? , 21789), 32 (21802), 36 (21805), 44 (? , 21810), 54 (21822), 64 (21834), 66, 76 (21846), 86 (21856), 90 (21860), 95 (21865), 96 (21866), 97 (21867), 101 (21871), 103 (21873), 106 (21876), 110 (21880), 114 (21884), 115, 118 (21886)]

A species common on well sheltered, nearly vertical rocks, more rarely on boulders, preferring thin turfs of bryophytes (especially *Tetraphis pellucida*, 73% of all records) that are sprinkled with green algae. The spores of our collections are very different in size, ranging from 10.4–15.4 µm in diameter (means of 20 measurements per specimen, 18 specimens investigated). Beside the significantly thinner and darker capillitial threads (compare Table 1), the capillitium arising from most of the columella length, the more ovoid sporotheca and the longer stalk are useful characters to distinguish this species from the forms of the *L. puncticulatum* group. The milky-white plasmodium appears on the substratum only a few days prior to fructification and is very conspicuous for a short time. The two species of *Lamproderma* are the only myxomycetes of the community that develop within days. *L. columbinum* was found on wood as well: one colony was observed on a still solid, decorticated log of *Picea* covered with a mat of *Coccomyxa* algae.



Figs 1–15. Scanning electron micrographs of myxomycetes from sandstone gorges of the Saxonian Switzerland region. Figs 1–5. *Colloderma robustum*, specimen 21855. 1. Opened sporocarps (co: columella, ca: capillitium and spores). 2. Capillitium threads (ca) attached to the inner peridium surface (pe). 3. Capillitium. 4. Spore. 5. Spore ornamentation. Figs 6–9. *Diderma lucidum*, specimen 21812. 6. Opened sporocarp (pe-peridium). 7. Capillitium (ca) and spores (sp). 8. Spore. 9. Spore ornamentation. Figs 10–12. *Diderma ochraceum*, specimen 21809. 10. Sporocarps. 11. Capillitium. 12. Spore. Figs 13–15. *Diderma umbilicatum*, specimen 21891. 13. Sporocarp. 14. Capillitium. 15. Spore (sp) and granules (gr) of crystalline lime. Bars: 1, 13 = 100 μm , 2–5, 8, 9, 11, 12, 14, 15 = 1 μm , 6, 10 = 200 μm , 7 = 10 μm .

Lamproderma puncticulatum agg. (*L. puncticulatum-granulosum* complex) - 25 records [Relevés 1 (21774), 3 (21776), 4 (21777), 6 (21779), 7 (21780), 8 (21781), 30 (21800), 33 (21802, 21803), 50 (21816), 55 (21824), 57 (21826), 58 (21828), 63 (21833), 65 (21836), 67 (21837), 73 (21843), 77 (21847), 80 (21850), 91 (21861), 92 (21862), 93 (21863), 94 (21864), 102 (21872), 104 (21874), 123 (21890), 30a (AFMD268), 64a (AFMD269)]

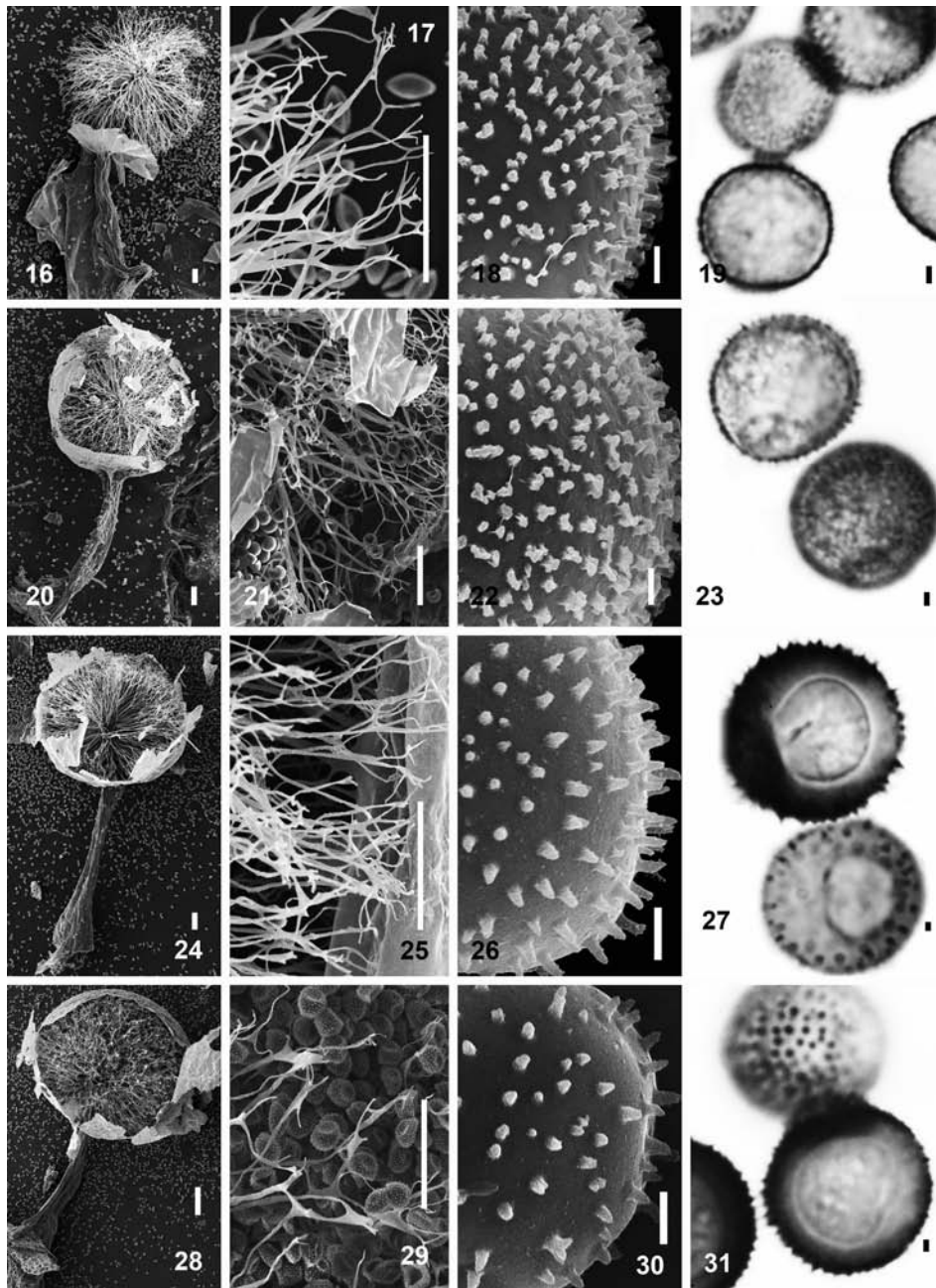
In contrast to *L. columbinum* with a tendency to inhabit thicker bryophyte tufts (64% of all records associated with *Mylia taylorii*, 56% with *Tetraphis pellucida*). Several times large colonies developed directly on pure, 0.3–1 cm thick mats of green *Coccomyxa* algae. Useful characters to separate it from *L. columbinum* are first the belt-like, flattened capillitial threads, the stalk reaching only 1–1.5 times sporocarp length, and the globose to slightly depressed sporotheca. In addition, spores are often larger than those of typical *L. columbinum*, ranging from 11.0–17.3 µm in diameter (means of 20 measurements, 25 specimens investigated).

Differences in spore size and ornamentation (compare Table 1) suggest the presence of at least two forms. One (Figs 16–23) possesses smaller spores (11.0–15.0 µm in diameter) ornamented with minute and dense spinulae (10.4–13.7 per 9 µm spore surface); the other (Figs 24–31) deviates by rather large spores (14.0–17.3 µm in diameter) with a coarse ornamentation of large and distant spines (3.7–7.0 per 9 µm spore surface). Only three specimens (relevés 65, 67, and 77) possessed few to many conspicuous granula (1.5–3.0 µm in diameter) at the capillitium as described for *L. granulosum* (Neubert et al. 1990), the others lacked these granula but had often a patchy capillitium color. As already stated in Neubert et al. (2000: 174), we currently cannot rule out that *L. granulosum* is conspecific with *L. puncticulatum* Härkönen and the granula are connected with a malformed capillitium. Molecular investigations are under way to elucidate the taxonomy of this species complex, which we here tentatively name *L. puncticulatum* agg. after the form described first as a species.

Lepidoderma tigrinum (Schrad.) Rostaf. - 31 records [Relevés 5 (21778), 9 (21782), 10 (21783), 11 (21784), 12 (21785), 13 (21787), 23 (21795), 24 (21796), 28, 29, 35 (21804), 42, 43, 49 (21815), 52 (21818), 53 (21820), 54 (21823), 56 (21825), 61 (21831), 70, 74 (21844), 75 (21845), 78 (21848), 79, 81 (21851), 89 (21859), 98 (21868), 99 (21869), 108 (21878), 121, 127 (21786)]

Perhaps due to the low pH values of the substrate, the sporocarps often develop only few or no lime scales. Especially if nearly limeless, the in moist condition nearly black sporocarps are difficult to detect. In contrast, the long-living, bright orange plasmodia and developing fructifications are very conspicuous and were repeatedly seen on almost bare rock with thin layers of algae between the sandstone grains. From the time the plasmodia segregate, fructifications need at least one, but more

Figs 16–31. Light microscope (LM) and scanning electron micrographs (SEM) of *Lamproderma puncticulatum* agg., from the Saxonian Switzerland region. Figs 16–19: specimen 21802. 16. Sporocarp. 17. Capillitium. 18. Spore ornamentation (SEM). 19. Spores by LM. 20. Figs 20–23: specimen 21833. 20. Sporocarp. 21. Capillitium. 22. Spore ornamentation (SEM). 23. Spores by LM.



Figs 24–27: specimen 21800. 24. Sporocarp. 25. Capillitium. 26. Spore ornamentation (SEM). 27. Spores by LM. Figs 28–31: specimen 21779. 28. Sporocarp. 29. Capillitium. 30. Spore ornamentation (SEM). 31. Spores by LM. Bars: 16, 17, 21, 25 = 50 μ m, 18, 19, 22, 23, 26, 27, 30, 31 = 1 μ m, 20, 24, 28, 29 = 100 μ m.

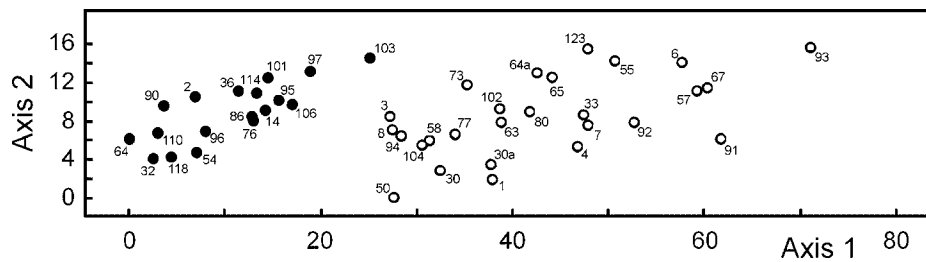


Fig. 32. DCA ordination of 45 *Lamproderma* collections in character space. Collections determined as *L. columbinum* are indicated by black, these determined as *L. puncticulatum* agg. by open circles. Numbers correspond with the relevé numbers given in the annotated species list. Axis 1 accounts for 98.3%, Axis 2 for 1.2 % of the variation in character space.

probably two weeks to develop. The species is most often associated with *Dicranodontium denudatum* (74% of all records) and *Myliia taylorii* (65%) but was also seen several times on *Sphagnum* tufts at the foot of large rocks.

Physarum album (Bull.) Chevall. - 4 records [Relevés 17 (21790), 45 (21811), 47 (21813), 48 (21814)]

The four records of this species were found in dryer and more open conditions at the «Raaber Kessel», three were associated with *Tetraphis pellucida*, one with *Dicranodontium denudatum*. This species, well known from decaying wood, was also recorded several times on this substrate. In Lado 2001 for priority reasons cited as *Physarum album* (Bull.) Chevall., better known under the name *P. nutans* Pers.

Trichia botrytis (J.F.Gmel.) Pers. 1 record [Relevé 60 (? , 21830)]

One scanty record of three immature sporocarps in a large patch of *Tetraphis pellucida*; determination remains doubtful.

MULTIVARIATE ANALYSIS OF LAMPRODERMA CHARACTERS: The DCA ordination in character space (Fig. 32) separates the collections of *Lamproderma* into two groups. The collections are preferentially oriented alongside axis 1, which explains 98 per cent of the observed variation. The 16 collections determined as *L. columbinum* cluster together in the left part of the ordination; remarkably separated from the remaining 27 collections assigned to *L. puncticulatum* agg. which form a more variable group. However, collections 97 and 103 (determined as *L. columbinum*) possessed large spores (14.9 and 14.2 μm) and comparatively short sporocarps, giving them an intermediate position between the two groups. Nevertheless we placed them into the *L. columbinum* group because of their overall appearance (shape of sporotheca, peridium color, stalk length and capillitium origin and shape).

VEGETATION RELEVÉS: The analysis of the species accumulation curve constructed from 127 samples resulted in 9.00 ± 0.47 species to expect for the Chao2 estimator;

Table 2. Mean number of records and mean coverage of all plant species recorded more than 10 times in 127 relevés of rock-inhabiting myxomycetes. Mean coverage was calculated as the average of cover values according to the following scale: 0.5 = 1%, 1 > 1–6%, 2 > 6–12.5%, 3 > 12.5–25%, 4 > 25–50%, 5 > 50% coverage.

Species	Records	Coverage
<i>Coccomyxa confluens</i> (Kütz) Fott. s.l. (algae)	127	2.05
<i>Mylia taylorii</i> (Hook.) Gray	77	3.53
<i>Dicranodontium denudatum</i> (Brid.) E.Britton	74	2.64
<i>Tetraphis pellucida</i> Hedw.	64	1.98
<i>Diplophyllum albicans</i> (L.) Dumort.	51	2.62
<i>Bazzania trilobata</i> (L.) Gray	24	1.48
<i>Calypogeia integristipula</i> Stephani	24	2.17
<i>Lepidozia reptans</i> (L.) Dumort.	24	1.33
<i>Dicranella heteromalla</i> (Hedw.) Schimp./ (<i>Dicranella cerviculata</i> (Hedw.) Schimp.)*	23	1.83
<i>Mnium hornum</i> Hedw.	21	1.12
<i>Dryopteris</i> spp. (mostly prothallia)	17	1.06
dust lichens (div. sterile lichens)	16	1.09
<i>Scapania umbrosa</i> (Schrad.) Dumort.	15	1.53
<i>Odontoschisma denudatum</i> (Nees) Dumort.	10	1.10

* these species were not distinguished in the field

the hyperbolic regression according to the formula $y = ax/(b+x)$ gave $a = 9.33 \pm 1.88$ ($R^2 = 0.994$) for the number of species to be expected. Although we surveyed at least 700 rocks and boulders (all together 8.7 km of valley bottoms), less than 120 of these were inhabited by myxomycetes, plus about 20 occurrences out of reach (higher than 2 m), and about 25 with young plasmodia or extremely moldy fructifications not allowing a safe determination.

Within the vegetation relevés we recorded at least eight moss species and eight species of liverworts. Most often observed were *Mylia taylorii* (77 relevés); *Dicranodontium denudatum* (74), *Tetraphis pellucida* (64) and *Diplophyllum albicans* (L.) Dumort. (51, Table 2). During sampling we noticed that myxomycetes occurred very often in closed turfs of both *Mylia taylorii* and *Dicranodontium denudatum* but avoided the commonly occurring pure short turfs of *Tetraphis pellucida*, which is indicated by the lower average coverage of this species (Table 2). Beside prothallia and very young plants of *Dryopteris* spp. (18 records), vascular plants occurred only exceptionally in the relevés, mostly as very small plants of *Oxalis acetosella*, *Vaccinium myrtillus* and *Calluna vulgaris* in rock fissures. In several cases the basidiomycete *Rickenella fibula* (A.H.Smith) Gulden was seen with scattered basidiomata. In all relevés we found green algae of the genus *Coccomyxa*, often forming slimy green mats up to 1 cm thickness. Most common in these mats was *Coccomyxa confluens* (Kütz) Fott s.l. Pure mats of green algae reached a mean coverage of $13.6 \pm 15.1\%$ in all relevés, $77.7 \pm 21.7\%$ of the rectangular areas were covered by bryophytes, $7.8 \pm 13.1\%$ are nearly naked rock (although with a lens in almost all cases algae were visible between sandstone grains).

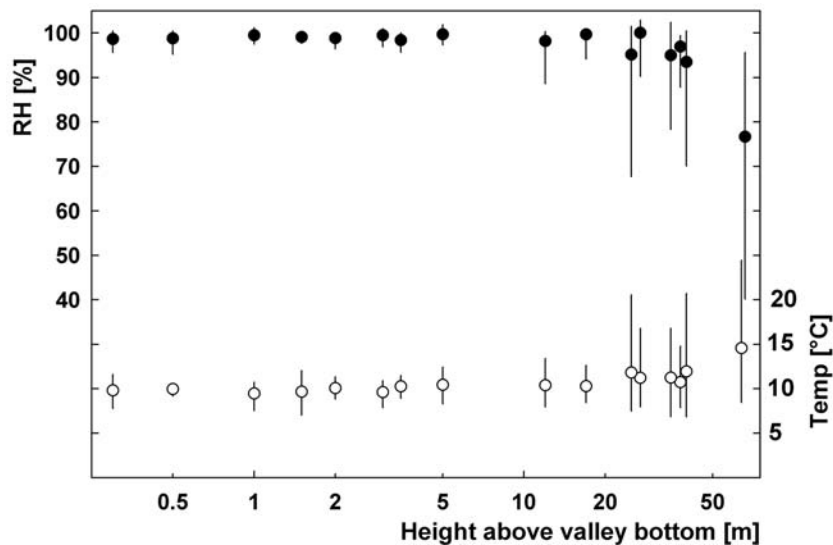


Fig. 33. Minimum and maximum values (end of bars) and mean (circles) for relative humidity (filled circles) and temperature (open circles) measured at different positions in the ravines during a 24 hr interval (midnight to midnight Oct. 1, 2007) with 16 data loggers. All measurements below 10 m height above valley bottom were taken at places inhabited by ravine myxomycetes.

ABIOTIC CONDITIONS: The data logger at the most exposed point of the region (castle Hohnstein, above the ravine "Polenztal") recorded the highest fluctuations in temperature, relative humidity (Fig. 33) and dew point (not shown). During Oct. 1, 2007, a day with clear sky, air temperature in shade reached 24.5°C around 15:00, and relative humidity dropped to 40.2%. The minimum temperature during this time was 8.5°C after midnight. In contrast, the microclimatic conditions at myxomycete localities (all points below 10 m height above valley bottom in Fig. 33, ravine "Uttewalder Grund") were remarkably stable. For these eight data loggers, temperature fluctuated only between 9.2 and 12.5°C (mean 10.4°C), and relative humidity dropped never below 95% throughout the 24 h period (mean 99.7%). Similar values were recorded for the dew point: 8.4–12.6°C, mean 10.4°C (not shown in Fig. 33). A repeated logging at August 26, 2008 (slightly cloudy, no rain) at the same localities in the ravine resulted in temperature fluctuations between 12.1 and 12.4°C (mean 12.2°C) and relative humidity was always higher than 99%.

Table 3 gives mean figures for abiotic parameters recorded in the relevés. Most of the myxomycete colonies occurred at breast height. Although the bright-colored plasmodia of many species are well visible, only about 20 colonies were seen above 2.5 m height where no relevé could be made. Usually the deepest parts of the valleys are inhabited by myxomycetes; only exceptionally we found colonies on rocks half way up the valleys. Figures for horizon openness as seen with a fisheye lens (where trees and rocks appeared dark) are very low throughout (mean $4.9 \pm 2.0\%$ open horizon, range 0.8–14.1%). Although the exposition of the inhabited rocks varies

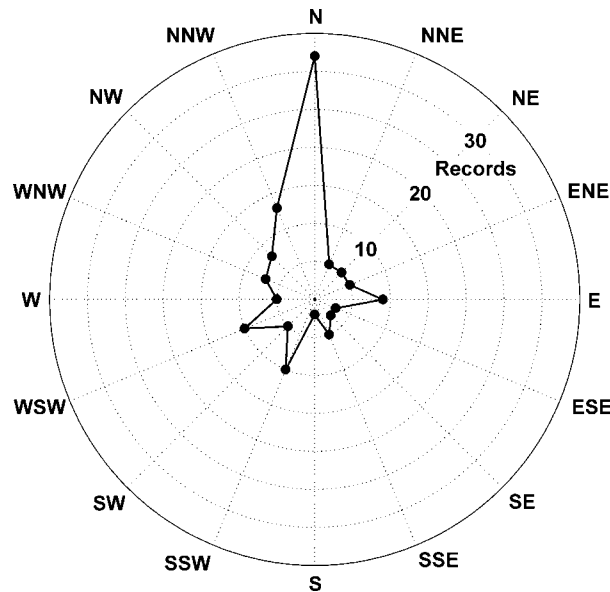


Fig. 34. Exposition of rocks and large boulders inhabited by ravine myxomycetes. Exposition data of 143 records are divided into 16 classes according to the directions indicated.

greatly (mean $136 \pm 113^\circ$), 39.3 % of all rocks were NNW, N, or NNE-exposed (Fig. 34). With many rock surfaces in the valleys being less steep, the high value for inclination ($79 \pm 11^\circ$) of the rocks carrying myxomycetes is most astonishing. Only three of the 127 relevés had an inclination below 60° ; but overhanging rocks were mostly avoided as well (19 relevés exceeding 90° , with six of those exceeding 100°). Throughout all relevés, the pH of the bryophyte/algae layers forming the substrate is very acidic (mean 3.35 ± 0.33 units, range 2.71–4.32).

The ordination of myxomycetes in sample space (Fig. 35) explains 44% (axis 1) and 10% (axis 2) of the variation in the environmental parameters recorded. It reflects the association of different myxomycete species with the bryophytes *Mylia taylorii* and *Tetraphis pellucida*, which can serve as indicators for the community as a whole. The two taxa of *Lamproderma* are clearly separated from each other. However, parameters characterizing the community as a whole, like horizon opening, inclination or pH do not explain its internal structure.

Niche width, calculated as the mean of fourteen environmental parameters, was very low for all of the five more common myxomycete species (mean values for the fourteen environmental parameters ranging from 0.15 to 0.20 on a 0–1 scale (Table 4). In contrast, the resulting values for niche overlap between species are extremely high, ranging from 0.89 to 0.98 for the ten combinations of the five most common species (Table 5). The Cole index of association is always negative, indicating rather avoidance than association of species, with all combinations of *Lamproderma* spp. and any other of the more common species except for *Colloderma* being significant

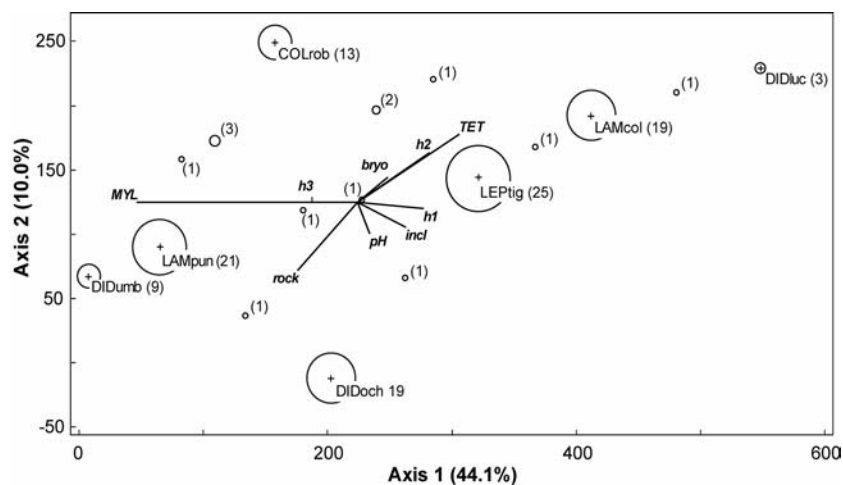


Fig. 35. Biplot of a DCA ordination of bryophilous myxomycetes (indicated by the abbreviations for species names listed in Tab. 5) in sample space with environmental variables overlaid. The lines radiating from the centroid indicate the relative direction and strength of correlation of variables with the ordination. Cross marks indicate the position of myxomycetes, circles indicate the position of samples. Their diameter corresponds to the number of samples with an identical position in ordination space (figures in parentheses). Environmental parameters (cutoff value 0.01) are h1: height of the sample above the valley bottom, h2: height of the rock above the sample, h3: height above ground, bryo: total coverage of bryophytes, rock: total coverage of naked rock, incl: steepness of the rock wall (< 90° less than vertical, 90° vertical, > 90° overhanging), pH: mean pH value of three substrate samples per relevé, MYL, TET: per cent coverage of *Mylia taylorii* and *Tetraxis pellucida*, respectively.

($P = 0.05$). Most often, only one species of the community was found at one rock, although in several cases two species occurred jointly: *Colloderma robustum* with *Diderma ochraceum* (three times), *Lamproderma puncticulatum* agg. (three times) and *Lepidoderma tigrinum* (four times).

Discussion

Sporadic observations of myxomycetes on bryophyte- and algae-covered rocks are well known, but Ing (1983) was the first to recognize a community of ravine myxomycetes. First observations of such species for Germany are reported in Schnittler (1999) for boulderfields, another microhabitat with a cool and damp microclimate. As confirmed by this study, such communities are formed by only a few but highly specialized species of myxomycetes.

The crucial point for their survival seems to be the long development time: repeated observations of the same plasmodia over about one week revealed that most species (except for those of the genus *Lamproderma*) need about two weeks from the time plasmodia segregate until fully mature fructifications are formed. Thus, maturing

Table 3. Environmental data for all myxomycete records, including number of records and average figures for number of nearly mature or mature sporocarps (spc) in the 20 cm × 20 cm rectangle of a relevé, height above ground, above valley bottom and of rocks above, canopy openness (%), exposition (degrees with North = 0°), inclination (degrees), pH (mean of three measurements per relevé) and per cent coverage of bryophyte layers, algae and naked rock. Given are also per cent proportions of records associated with the four most common bryophytes *Mylia taylorii* (MYLtay), *Dicranodontium denudatum* (DICden), *Tetraphis pellucida* (TETpel), and *Diplophyllum albicans* (DIPalb).

	records	spc	height	above	rocks	Open	Exp.	Incl.	pH	Coverage	algae	rock	MYL	DIC	TET	DIP
		ground	valley						moss	algae	algae	rock	den	pel	alb	Alb
<i>Colloderma robustum</i>	23	181	1.2	2.3	5.3	4.8	105.7	71.6	3.30	81.9	13.8	5.3	96	74	30	52
<i>Diderma lucidum</i>	3	11	1.1	2.6	29.7	6.1	170.7	82.0	3.32	89.0	9.3	2.0	0	0	67	33
<i>Diderma umbilicatum</i>	10	98	1.1	1.7	2.7	4.9	123.8	77.4	3.03	64.7	7.3	27.2	70	70	70	30
<i>Diderma ochraceum</i>	24	89	1.1	4.1	4.9	5.1	116.5	78.9	3.43	79.4	12.9	7.7	79	63	38	58
<i>Lepidoderma tigrinum</i>	31	78	1.2	3.0	4.8	4.7	140.5	78.4	3.47	79.5	12.7	8.4	65	74	42	42
<i>Lamproderma columbinum</i>	22	73	1.4	5.1	7.1	4.8	141.8	84.8	3.21	79.3	16.0	5.0	32	41	73	23
<i>Lamproderma puncticulatum</i> agg.	25	377	2.3	3.5	8.3	4.9	176.0	83.0	3.35	77.5	15.6	4.6	64	48	56	44
<i>Physarum nutans</i>	4	106	1.2	9.2	25.9	4.8	113.5	83.8	3.54	43.3	16.0	13.5	0	25	75	0
<i>Trichia botrytis</i>	1	3	1.7	8.0	2.5	5.0	100.0	84.0	3.87	90.0	10.0	0.0	0	0	100	0
all myxomycetes	143	148	1.4	3.6	6.8	4.9	135.7	79.4	3.35	77.7	13.6	7.8	64	59	50	41

Table 4. Values for niche width for the five most common myxomycete species, calculated according to Levins (1968) and standardized to a 0-1 range. Fourteen environmental parameters were divided in eight resource states each, ranging from its minimum to maximum possible value (see text for explanation).

mean	Niche	width	height	above	rocks	Open	Exp.	Incl.	pH	Coverage	algae	rock	MYL	DIC	TET	DIP
	SD	ground	valley						moss	algae	algae	rock	Den	pel	alb	alb
<i>Colloderma robustum</i>	0.18	0.24	0.00	0.00	0.07	0.00	0.53	0.15	0.24	0.22	0.14	0.01	0.86	0.19	0.04	0.06
<i>Diderma ochraceum</i>	0.17	0.17	0.00	0.03	0.04	0.01	0.44	0.06	0.35	0.37	0.17	0.12	0.47	0.19	0.03	0.13
<i>Lepidoderma tigrinum</i>	0.17	0.18	0.00	0.00	0.03	0.01	0.61	0.10	0.36	0.30	0.17	0.07	0.26	0.36	0.06	0.09
<i>Lamproderma columbinum</i>	0.15	0.16	0.00	0.03	0.07	0.00	0.46	0.17	0.39	0.36	0.25	0.03	0.05	0.11	0.06	0.06
<i>Lamproderma puncticulatum</i> agg.	0.20	0.23	0.02	0.04	0.16	0.00	0.71	0.07	0.46	0.37	0.29	0.02	0.50	0.06	0.04	0.08
all myxomycetes, mean			0.00	0.02	0.07	0.00	0.55	0.11	0.36	0.32	0.20	0.05	0.43	0.18	0.05	0.08

Table 5. Values for niche overlap (upper right) and Cole index of association (lower left) for the ten combinations of the five most common species of myxomycetes. Association values with an asterisk indicate significant avoidance (P = 0.05).

	COD	DID	LEP	LAM	LAM
	rob	och	tig	col	pun
<i>Colloderma robustum</i> (CODrob)	-	0.94	0.94	0.89	0.92
<i>Diderma ochraceum</i> (DIDoch)	-0.31	-	0.98	0.94	0.95
<i>Lepidoderma tigrinum</i> (LEPtig)	-0.29	-0.49	-	0.95	0.94
<i>Lamproderma columbinum</i> (LAMcol)	-0.75	-1.00*	-0.81*	-	0.94
<i>Lamproderma puncticulatum</i> agg. (LAMpun)	-0.34	-0.79*	-1.00*	-1.00*	-

fructifications are exposed at the surface of algal or bryophyte substrates over a relatively long time. Remarkable are the bright colors of the plasmodia (*Lamproderma*: white, *Colloderma robustum*: sulfur yellow, *Diderma ochraceum*: bright yellow, *Diderma lucidum* and *Lepidoderma tigrinum*: bright orange).

As reflected by the low values of niche width for the more common (> 20 records) myxomycete species (calculated from the possible range an environmental parameter can assume), several factors should strictly limit the occurrence of ravine myxomycetes: Most limiting seems to be inclination (range from 0° = even to 180° = hanging rocks). An angle below 60° exposes the fragile plasmodia to rain. An experiment with plasmodia of *Lepidoderma tigrinum* showed that the plasmodia can be destroyed by water drops falling down from 1 m height. At the other hand, overhanging walls do not allow water to seep in; such areas are often covered by dust lichens. Optimum figures for inclination are around 80°; such places are greatly sheltered from rain but water seeping through bryophyte turfs and algal mats provides moisture. To ensure a continuous supply of moisture through the sandstone, the rock above a colony should not be too small. Boulders less than 1 m tall are usually not inhabited, and an average of 6.8 m of rock was recorded above the colonies (range 0.4–65 m, range assumed to calculate niche width: 0–80 m, equaling the deepest ravines in the region). Further limiting factors are direct sunlight or strong wind, both quickly desiccating plasmodia. Only places sheltered the day around from any direct sunlight seem to be inhabited, with an average horizon opening of 4.8% (range 0.8 to 14.1 %) and a mostly north-facing exposition (one fourth of all inhabited rocks directed northwards, compare Fig. 34). Only the deepest ravines with a very constant microclimate are inhabited: all data loggers placed at valley sections where myxomycetes had been found showed less than 5% daily fluctuations in relative humidity (which comes very close to 100%) and temperature (around 10°C). At least in late summer and autumn, these constant conditions seem to prevail over several weeks, as indicated by the repeated measurement a year later. However, the cool microclimate may act as a limitation in itself, causing the unusual long development times for most species. More measurements in the ravines, especially during high pressure situations in summer and winter, are needed to determine the time period allowing myxomycete development. Since they are limiting the occurrence

of the community as a whole, these limiting factors do not show up in the biplot of the detrended correspondence analysis of fourteen environmental factors (Fig. 35) with the chosen cutoff value of 0.01. In contrast to the factors discussed above, the acidic pH may not act as a limiting factor. The sandstone of the region possesses a rather acidic pH throughout (range in our relevés 2.7–4.3). Evidence that this community is not limited to habitats with low pH comes from observations of the community made by Ing (1994) on base-rich rocks from Wales (Snowdonia region).

Small-scale vegetation relevés as carried out in this study are often difficult to analyze. On one hand, the small scale ensures microclimatic conditions and rock structure to be well circumscribed; on the other hand it causes statistical uncertainties in vegetation coverage. Especially large bryophyte colonies, like the turfs of *Mylia taylorii*, are often 10–20 cm wide and 5–8 cm high; a single turf may take half of the 20 cm × 20 cm relevé area. In spite of these ambiguities, the relevés showed a clear co-occurrence of myxomycetes with *M. taylorii* (65% of all records, total coverage as mean of all relevés 24.7%) and *Dicranodontium denudatum* (59% of all records, total coverage 13.2%). Especially turfs of *M. taylorii* grow thicker each year, and finally their weight causes them to slide off the rock, starting the growth cycle again. Thus, a rock exceeding 60 degrees in inclination will only be covered up to 50% by *M. taylorii*, even if this is the dominating bryophyte species at this place. Turfs of *Dicranodontium* are slightly thinner (2–5 cm) and more stable. Less steadily (50% of all relevés) occurred *Tetraphis pellucida*, whose mean coverage was significantly lower (6.9%). This moss forms short turfs (0.5 cm tall) which occur often as pure stands. However, even in suitable inclinations pure *Tetraphis* turfs were rarely seen to be inhabited by myxomycetes, and tended to have less trickling water and algae. Less common and rarely forming big stands is the liverwort *Diplophyllum albicans*, observed in 40% of all relevés (mean coverage 9.5%). In the region, the liverwort *Mylia taylorii* can serve as an indicator organism for ravine myxomycetes; it forms large, easy to recognize tufts on moist non-calcareous rocks like sandstone (or granite, gneiss) in sheltered conditions with high humidity and a cool climate, very rarely it is encountered on decaying wood, humus, or (*Sphagnum*) peat. Generally this liverwort shows a montane-(sub)oceanic distribution in the Northern Hemisphere (e.g. Sauer 2005).

Stephenson & Studlar (1985) listed a number of myxomycete-bryophyte associations. From the five more common species in this study these authors mentioned only *Lepidoderma tigrinum* as associated with *Dicranodontium denudatum*. The only species identified in this paper as steadily associated with bryophytes was *Barbeyella minutissima* Meyl., usually inhabiting decorticated coniferous wood. It is associated with the liverwort *Nowellia curvifolia* (Dicks.) Mitt. which was identified as an indicator organism by Schnittler et al. (2000). In spite of intense search, this boreal-montane myxomycete was never found within this study.

As described by Ing (1983) for Great Britain, only a few species of myxomycetes regularly inhabit ravines. Most of them are only rarely found outside such habitats. Prominent examples are *Colloderma robustum*, recorded as new for Germany, or *Diderma ochraceum*. Others, like *Lamproderma columbinum* and *Lepidoderma tigrinum*, are found in constantly humid conditions on wood as well. The DCA

biplot (Fig. 35) indicates a closer association of the latter two species with the moss *Tetraphis pellucida*, whereas the first two species tended to be more often associated with *Mylia taylorii*. *Lamproderma puncticulatum* agg. and *L. columbinum* differed clearly with respect to ecological traits (Fig. 35). *L. puncticulatum* agg. is located at the left part to which the vector of coverage for *Mylia taylorii* points, but *L. columbinum* is located in opposite position to which the vector of coverage for *Tetraphis pellucida* points. These patterns are explained by the joint occurrence of *L. puncticulatum* agg. with the liverwort *M. taylorii*, whereas *L. columbinum* was found in closer association with the moss *T. pellucida* on rocks with a higher inclination. Similar patterns account for the myxomycetes *Diderma ochraceum* and *Lepidoderma tigrinum*. The habitats of *Diderma umbilicatum* were characterized by larger areas of naked rock and slightly lower pH values, since the two corresponding vectors point to the position of this myxomycete. However, *D. umbilicatum* was found as well in close neighborhood to the bryophytes *Mylia taylorii* and *Dicrano-dontium denudatum*. *Colloderma robustum* inhabited rocks and boulders with a lower mean inclination (72°) than all other myxomycetes of the survey.

Although having many abiotic parameters in common, in most (90%) of the relevés we could find only a single species of myxomycetes, and only 2 relevés had three species. We estimated that only one in ten boulders or rock walls of the surveyed sections of the ravines carried myxomycetes. This relative rarity caused the large number of relevés falling together in sample space of the DCA, since they represented only one species of myxomycetes. Calculated niche width was extremely narrow for the more common myxomycetes, niche overlap was very high, and the species tended to avoid each other, as indicated by the constantly negative values for the Cole index of association. This pattern can be interpreted as a direct competition of the species, as assumed for desert myxomycetes (Schnittler 2001b), or may be the result of a low probability of establishment of the respective myxamoebal populations. Myxamoebae seemed to inhabit a certain rock or boulder over several years, as indicated by a repeated brief survey in 2008, where fructifications of a species were often found again at a boulder surveyed positively in 2007 in the ravine "Uttewalder Grund".

Beside the environmental limitations outlined above, ravine myxomycetes may be limited by its food source. Myxomycetes are known to feed principally on bacteria, also on yeasts and some species on fungi. Although systematic research is needed to establish a food chain, there is some evidence pointing to green or blue-green algae as a possible food source of ravine myxomycetes. First, algae of the genus *Coccomyxa* were found as slimy green layers in all myxomycete relevés. Several times *Lamproderma puncticulatum* agg. developed on pure algal mats, and the very mobile, bright orange plasmodia of *Lepidoderma tigrinum* were sometimes observed on almost bare rock, with only thin algal layers between sandstone grains. Second, myxomycetes can be successfully cultured with algae, as shown already by Lazo (1961). Using ³²P-labelled sodium hydrophosphate, Zabka & Lazo (1962) demonstrated the possibility of nutrient transfer between the green algae *Chlorella xantella* and the myxomycete *Fuligo cinerea*. Although we were unable to detect it regularly in the field during recording vegetation relevés, punctual microscopic examinations of samples revealed that blue-green algae of the genus *Nostoc* seem to be another regular member of the

community. We guess with Ing (1994), that the N-fixating activity of the cyanobacteria is directly or indirectly beneficial to myxomycetes. However, we cannot rule out that bacteria living in algal mats are the true source of food for ravine myxomycetes, and cultures with feeding experiments are needed to prove the hypothesis that ravine myxomycetes are specialized algae predators. If this holds true, the so-called bryophilous myxomycetes (Stephenson & Studlar 1985) would be in fact phycophilous, using the more conspicuous bryophytes only as substrates to elevate the developing fruit bodies.

The soft and porous sandstone rocks are a substrate which allows a community of algae and bryophytes to grow without being out-competed by vascular plants. The porous texture allows water to seep through the stone and helps to ensure the constant humid microclimate needed to avoid desiccation in the delicate phase of sporocarp maturation. However, in a sufficiently damp climate any rock could support the bryophyte/algae community, as proven by observations of myxomycetes growing on bryophyte tufts covering concrete in Japan (Yamamoto 2006). However, the unique structure of the sandstone rocks allows the ravines to be carved out, creating the special microclimate required for the ravine myxomycete community. Although the Saxonian Switzerland region is undoubtedly the best example of a sandstone ravine landscape in Germany, successful long-distance dispersal as documented for the Hymenophyllaceous fern *Trichomanes speciosum* (Vogel et al. 1993, Horn 1998, Rumsey et al. 2002) indicate that similar myxomycete communities can be expected in other sandstone ravines of the temperate zone as well, like the 'Petite Suisse' sandstone area in Luxembourg, where both *Hymenophyllum thunbrigense* and *T. speciosum* occur (Krippel 2002, Muller et al. 2006). We hope that the observations described herein will help to understand the ecological limitations of this unique myxomycete community and find other sites where this community of myxomycetes occurs.

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