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Ecological distribution of cellular slime molds in forest soils of Germany

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Abstract

Cavender J. C., Cavender-Bares J., and Hohl H. R. 1995. Ecological distribution of cellular slime molds in forest soils of Germany. *Bot. Helv.* 105: 199–219.

Surface soils were collected from deciduous, coniferous and mixed coniferous-deciduous forest of Germany during the latter half of July 1993 and were plated out for cellular slime molds at Ohio University during the first half of August, 1993. Twenty-four sites were sampled from different geographical regions in southern, central and western Germany. Germany has a fairly diverse cellular slime mold flora/fauna similar to that of the cool temperate zone of Japan and to the North American bi-state region of Ohio and West Virginia. Eighteen morphological species were isolated which match those described in the literature. Three entities were isolated only once, hence are considered to be rare: *Acystostelium leptosorum*, *Dictyostelium capitatum*, and a new species, *Dictyostelium germanicum*. Four species originally described from Japan were isolated for the first time from Europe: *Dictyostelium microsporum*, *D. capitatum*, *D. implicatum* and *Polysphondylium candidum*. The most commonly isolated were *Dictyostelium mucoroides*, S-type and *Polysphondylium violaceum*. Cellular slime mold populations of deciduous and coniferous forests have distinct differences. Numbers of clones per gram and species richness were higher in soils of deciduous forests than in coniferous forests.

Key words: Cellular slime mold, dictyostelid, ecological distribution, forest soil.

Introduction

Cellular slime molds were introduced to the world by Oskar Brefeld, a German mycologist, with his report of the discovery of *Dictyostelium mucoroides* in 1869. He also described *Polysphondylium violaceum* (1884), although he did not find these cellular slime molds in forest soils. Oehler (1922), working in Würzburg, reported that *D. mucoroides* could be isolated from forest soil. We have found these two species to be the most common in Central Europe. Hagiwara (1984) has assembled evidence to show that

Brefeld's description of *D. mucoroides* matches most closely another cosmopolitan species which Raper (1984) designated as *D. sphaerocephalum* (Oud.) Sacc. et March. Hagiwara created the name *D. brefeldianum* for the taxon we are naming *D. mucoroides*, S-type. Because there is no holotype designated and preserved from Brefeld's description, we are, for the time being, using Raper's taxonomy.

Cavender (1969) was the first to make an ecologically-based distributional study of Europe. However, only two sites were sampled in Central Europe, one in West Germany and one in Switzerland. Traub (1972) later did a comprehensive survey of cellular slime molds in Switzerland which was augmented by further collections of Cavender and published in 1981 (Traub, Hohl and Cavender 1981 a, 1981 b). Three new species were described: *Dictyostelium fasciculatum*, *D. polycarpum*, and *Polysphondylium filamentosum*. Traub also designated two types of *D. mucoroides* as S and L types. This differentiation of *D. mucoroides* has been continued in this study. They may represent distinct species. Leitner (1987) made some interesting observations of three cellular slime molds with respect to forest soil pH. He found *Dictyostelium mucoroides* and *D. fasciculatum* more prevalent in deciduous forest with neutral or slightly alkaline soils while *D. minutum* was more common in deciduous forest soils which were acidic (ca. pH 5.0).

In this study, *Dictyostelium implicatum* Hagiwara, *D. microsporum* Hagiwara, *D. capitatum* Hagiwara, *D. germanicum* nsp., *D. septentrionalis* Cavender, and *Polysphondylium candidum* Hagiwara are reported for the first time from Europe. *Dictyostelium germanicum* was isolated from a mature beech forest within a Tertiary volcanic cone in the Eifel region of the Rhineland Palatinate. It is unique in having small solitary sorocarps bearing oblong spores with numerous unconsolidated polar granules.

Study Area

Germany, with an area of 357,000 square km, has a great diversity of topography and soils due to a rather complex orogeny. Among the microenvironments present are those influenced by glacial till, including sand and bog environments, limestone, sandstone and basaltic bedrock, as well as considerable loess deposits in certain areas. Most of the country is broken into mountains and valleys by a network of rivers of considerable water volume indicative of an abundant rainfall distributed throughout the year (Ellenberg 1988). Air temperature in summer seldom exceeds 30°C and in winter –20°C. "Such a climate encourages the universal growth of trees" (Ellenberg 1988). Despite considerable agricultural activity, Germany still has over one third of its land in forest. The climate favors beech (*Fagus sylvatica*) and oak (*Quercus robur*) but there are also some deciduous woodlands with an assortment of dominants such as maple (*Acer*) and linden (*Tilia*). Conifers, spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are naturally dominant in the northeast and at higher elevations although much of the deciduous forest of central and western Germany has been replaced by conifer plantations.

Methods

Fifty gram soil samples were collected in Whirl Pac plastic bags during late July and early August 1993 and processed for Dictyostelidae in a way similar to that reported by Cavender and Raper (1965). However, all cultures were shaken by hand rather than by machine. All of the soils were processed during late August 1993 at Ohio University upon return from Germany.

The method of analyzing dictyostelid populations in soil is based on the appearance of clones of cellular slime molds on a dilute hay-infusion agar surface which has been inoculated with an appropriate soil dilution and a pre-grown bacterial food supply. Colonies of the developing organisms are identified and counted in the isolation plates. Unidentifiable colonies are removed to two-membered cultures with *Escherichia coli* B/r for further study. The acrasian populations in each forest are expressed in terms of frequency, relative density, and density (Tables 2–4). Density is the total number of clones per gram of soil while frequency is the number of times a species occurs at a particular site expressed as a percentage, and relative density is the relative number of colonies of each species at a site expressed as a percentage. Isolates of each species were cultivated on non-nutritive agar with 24 hour pre-grown *E. coli* and preserved by lyophilization in the Kenneth B. Raper cellular slime mold collection housed at Ohio University. Soil pH was measured in the lab using a Radiometer ION83 ION METER. Photomicrographs were taken using an Olympus phase contrast microscope.

Forests in foothills, mountainous areas and lowlands were sampled in central, western, and southern Germany (Fig. 1). The lowlands of northern and eastern Germany, however, were excluded due to time constraints except for one site (LH). Characteristics of each site are listed in Table 1. These include location, date of collection, geographical region, forest type, dominant trees, geological features, elevation, humus type and soil pH.

Results

The results of the distributional study are presented in Tables 2–4. Dictyostelids recovered from soils of coniferous or mixed coniferous deciduous forest are presented in Table 2, dictyostelids recovered from neutral or alkaline soils in deciduous forests are presented in Table 3, and dictyostelids recovered from acid soils in deciduous forests are presented in Table 4. Comparisons of the cellular slime mold populations in these three environments within Germany can, therefore, be made more easily.

Eighteen of the nineteen species isolated are illustrated with photomicrographs in Figs. 2–55. Spores, aggregation pattern and sorocarps are reproduced. Descriptions of these species except for Traub's *D. mucoroides* L-type may be found in either Raper's (1984) or Hagiwara's (1989) monographs, therefore our comments are limited to salient features. A description and Latin diagnosis of *D. germanicum* is presented here.

Dictyostelium germanicum Cavender, Cavender-Bares, et Hohl sp. nov. (Figs. 50, 51, 52) Sorocarpia plerumque solitaria, erecta, magnitudine regularissima, normaliter 0.5–1.5 mm longa, ecolorata; sorophoria cellulis uniserialiter dispositis, diametro basali circa 23–26 µm ad 4–6 µm angustata ad apicem; sori globosi 60–120 µm; aggregationes tumuliformes 160–260 µm, interdum margine brevibus radiis striatae, spora ellipticae obtusae, plerumque 3–4 × 6–8 µm granulis polaribus non consolidatis, Stirps typica: ME-1. Sorocarps usually solitary, erect, very uniform in size, usually 0.5–1.5 mm long, unpigmented, sorophores with a single tier of cells taper from about 23–26 µm at the base to 4–6 µm at the tip; sori spherical mostly 60–120 µm in diameter; aggregations mound-like 160–260 µm, sometimes with short streams, spores elliptical with blunt ends, mostly 3–4 × 6–8 µm with numerous unconsolidated polar granules. Type strain ME-1 deposited in Kenneth B. Raper dictyostelid collection at Ohio University.

Habitat: leaf mold of a mature beech forest located within a volcanic cone of the Eifel region in the Rhineland Palatinate.

1. *D. mucoroides*, S-type, RO-1b, Figs. 2–4. Unpigmented, single large sorocarps with basal discs of supporting cells, radiate aggregates, spores without polar granules.

Table 1. Collection sites.

<i>Niedersachsen (Lower Saxony)</i>	
LH	Site: Lüneburger Heide Date: 7.29.93 Region: Lüneburger Heide (Luneberg Heath) Forest type: Mixed coniferous-deciduous Dominant trees: Beech (<i>Fagus</i>), Oak (<i>Quercus</i>), Birch (<i>Betula</i>), Pine (<i>Pinus</i>), Spruce (<i>Picea</i>) Geologic features: glacial moraine Elevation: 50–100 m Humus type: mor Soil pH: 3.6
TH	Site: Torfhaus/Harz Date: 7.30.94 Region: Harz Forest type: Coniferous Dominant trees: Spruce Geologic features: mountainous Elevation: 800 m Humus type: mor Soil pH: 3.8
<i>Nordrhein-Westfalen (North Rhine Westphalia)</i>	
KV	Site: Kottenforstville in Brühl Date: 7.23.93 Region: Rhine Valley, northern Rheinisches Schiefergebirge Forest type: Deciduous Dominant trees: Basswood (<i>Tilia</i>), Maple (<i>Acer</i>), Birch Geologic features: glacial lake basin Elevation: 150 m Humus type: mull Soil pH: 7.0
EW	Site: Elmpter Wald/Dutch Border Date: 7.23.93 Region: Niederländisches Tiefland (Dutch lowland) Forest type: Mixed coniferous-deciduous Dominant trees: Pine, Oak, Birch Geologic features: glacial moraine Elevation: <100 m Humus type: mor Soil pH: 4.8
DR	Site: Drachenfels/Rhein Date: 7.25.93 Region: Siebengebirge Forest type: Deciduous Dominant trees: Beech
<i>Rheinland-Pfalz (Rhineland Palatinate)</i>	
RS	Site: Rothaargebirge/Siegen Date: 7.26.93 Region: Rothaargebirge Forest type: Mixed coniferous-deciduous Dominant trees: Beech, Oak, Spruce Geologic features: mountainous Elevation: 600 m Humus type: mor Soil pH: 4.8
<i>Hessen (Hesse)</i>	
RG	Site: Rheingau Date: 7.20.93 Region: Rheingaugebirge, Taunus Forest type: Deciduous Dominant trees: Chestnut (<i>Castanea</i>), Oak, Cherry (<i>Prunus</i>), Hawthorn, Basswood Geologic features: elevated terrain along Rhine river Elevation: 450–500 m Humus type: mull Soil pH: 4.5

Table 1. Collection sites (continued).

TN	<p>Site: Taunus summit Date: 7.20.93 Region: Taunus Forest type: Deciduous Dominant trees: Alder (<i>Alnus</i>), Birch, Beech, Larch (<i>Larix</i>), Oak Geologic features: mountainous gorge Elevation: 500 m Humus type: mull Soil pH: 4.5</p>	<p>Dominant trees: Beech Geologic features: lake shore Elevation: 400 m Humus type: moder Soil pH: 4.4</p>
SO	<p>Site: Starkenberg/Odenwald Date: 8.9.93 Region: Odenwald Forest type: Deciduous Dominant trees: Walnut (<i>Juglans</i>), Maple, Beech, Sycamore (<i>Platanus</i>), Oak, Chestnut, Basswood, Ash (<i>Fraxinus</i>) Geologic features: limestone parent material Elevation: 500 m Humus type: mull Soil pH: 7.0</p>	<p>KS Site: Kaiserstuhl Date: 8.9.93 Region: Schwarzwald (Black Forest) Forest type: Coniferous Dominant trees: Hazel Nut (<i>Corylus</i>), Maple, Beech, Ash, Locust (<i>Robinia</i>), Poplar (<i>Populus</i>) Geologic features: loess deposits Elevation: <450 m Humus type: mull Soil pH: 7.6</p>
<i>Baden-Württemberg</i>		
RO	<p>Site: Rothenburg ob der Tauber Date: 8.4.93 Region: Schwäbisch-Fränkisches Stufenland Forest type: Deciduous Dominant trees: Walnut, Maple, Birch, Basswood Geologic features: limestone parent material, steep slope Elevation: 450–500 m Humus type: mull Soil pH: 7.7</p>	<p><i>Bayern (Bavaria)</i> WO Site: Wonsee/Fränkische Schweiz Date: 8.2.93 Region: Fränkische Schweiz Forest type: Mixed coniferous-deciduous Dominant trees: Oak, Alder, Beech, Ironwood (<i>Carpinus</i>), Basswood, Hornbeam, Spruce, Birch Geologic features: limestone outcrops Elevation: 400–450 m Humus type: mull Soil pH: 7.0</p>
EB	<p>Site: Eriskirch/Bodensee/ Reid Naturschutzgebiet Date: 8.7.93 Region: Lake Constance, below Schwäbische Alb Forest type: Deciduous Dominant trees: Oak, Birch Geologic features: lake shore Elevation: 400 m Humus type: mull Soil pH: 6.9</p>	<p>HS Site: Haag/Steigerwald Date: 8.3.93 Region: Steigerwald Forest type: Mixed coniferous-deciduous Dominant trees: Beech, Spruce, Oak, Pine, Birch Geologic features: sandstone ravine Elevation: 450 m Humus type: moder Soil pH: 4.6</p>
EK	<p>Site: Eriskirch/Bodensee Date: 8.7.93 Region: Lake Constance, below Schwäbische Alb</p>	<p>DF Site: Danube, west of Ingolstadt Date: 8.5.93 Region: Danube flood plane, Fränkische Alb Forest type: Deciduous Dominant trees: Ash Geologic features: Danube river flood plain Elevation: 380 m Humus type: mull Soil pH: 7.3</p>

Table 1. Collection sites (continued).

SV	<p>Site: Spitzing-See/Voralpen</p> <p>Date: 8.6.93</p> <p>Region: Bayerische Alpen (Bavarian Alps)</p> <p>Forest type: Coniferous</p> <p>Dominant trees: Spruce, Fir (<i>Abies</i>)</p> <p>Geologic features: steep mountain slope, limestone parent material</p> <p>Elevation: 1200–1500 m</p> <p>Humus type: mull</p> <p>Soil pH: 7.3</p> <p>Comments: forest die-back evident</p>	<p>Site: Friedrichroda/Thüringer Wald</p> <p>Date: 7.31.93</p> <p>Region: Thüringer Wald</p> <p>Forest type: Mixed coniferous-deciduous</p> <p>Dominant trees: Spruce, Birch, Beech, Maple, Hazel Nut, Alder</p> <p>Geologic features: bordering an upland swamp</p> <p>Elevation: 600–800 m</p> <p>Humus type: moder</p> <p>Soil pH: 3.5</p>
<i>Thüringen (Thuringia)</i>		
BH	<p>Site: Barbarossahöhle</p> <p>Date: 7.30.93</p> <p>Region: Thüringer Becken, Hainleite</p> <p>Forest type: Deciduous</p> <p>Dominant trees: Maple, Oak</p> <p>Geologic features: limestone, Karst topography</p> <p>Elevation: 200–250 m</p> <p>Humus type: mull</p> <p>Soil pH: 7.3</p>	<p>Site: Homersdorf/Erzgebirge</p> <p>Date: 8.2.93</p> <p>Region: Sächsisches Bergland just above the Erzgebirge</p> <p>Forest type: Coniferous</p> <p>Dominant trees: Spruce</p> <p>Geologic features: mountainous</p> <p>Elevation: 550 m</p> <p>Humus type: mor</p> <p>Soil pH: 3.5</p>
SH	<p>Site: Sondershausen</p> <p>Date: 7.30.93</p> <p>Region: Thüringer Becken, Hainleite</p> <p>Forest type: Deciduous</p> <p>Dominant trees: Oak</p> <p>Geologic features:</p> <p>Elevation: 200–250 m</p> <p>Humus type: mull</p> <p>Soil pH: 4.7</p>	<p>Site: Fichtelberg/Czech border</p> <p>Date: 8.2.93</p> <p>Region: Erzgebirge</p> <p>Forest type: Coniferous</p> <p>Dominant trees: Spruce</p> <p>Geologic features: mountainous</p> <p>Elevation: 1200 m</p> <p>Humus type: mor</p> <p>Soil pH: 3.7</p> <p>Comments: serious forest die-back</p>

2. *D. mucoroides*, L-type, KS-2, Figs. 5–7. Unpigmented, single, large phototrophic sorocarps; sorophores without basal discs, radiate aggregations develop distinctive lumpy centers, sorogens elongated, slightly larger spores than S-type, spores without polar granules.
3. *D. implicatum*, HS-4, Figs. 8–10. Radiate aggregation, robust solitary sorocarps with basal discs become tangled when grown in diffuse light; spores tend to germinate to form secondary sorocarps, spores without polar granules and larger than those of *D. mucoroides* S-type.
4. *D. aureo-stipes* var. *aureo-stipes*, RO-4, Figs. 11–13. Irregularly branched flexuous sorocarps with yellow sorophores when grown in the dark; aggregates break up into smaller centers; spores with conspicuous consolidated polar granules.

Table 2. Dictyostelids recovered from acid soils in coniferous or mixed coniferous-deciduous forests of Germany

Species	Collection site	LH		TH		EW		FT		HE		FB		HS		SV		RS		
		pH	rd f	3.6	rd f	3.8	rd f	4.8	rd f	3.5	rd f	3.5	rd f	3.7	rd f	4.6	rd f	4.9	rd f	4.8
<i>Acystostelium leptosorum</i>																				
<i>Dictyostelium aureo-stipes</i>																				
<i>Dictyostelium aureo-stipes</i> var. <i>helvetica</i>																				
<i>Dictyostelium fasciculatum</i>																				
<i>Dictyostelium giganteum</i>																				
<i>Dictyostelium implicatum</i>				4	20					1	20					4	20			
<i>Dictyostelium minutum</i>				18	40											4	20			
<i>Dictyostelium mucoroides</i> S type						6	20	88	60	8	20				24	60	8	20	94	80
<i>Dictyostelium mucoroides</i> L type																		48	40	
<i>Dictyostelium polycarpum</i>																				
<i>Dictyostelium septentrionalis</i>				4	20	6	20	6	20	9	40				3	20	17	20	1	20
<i>Dictyostelium sphaerocephalum</i>										11	60				3	20		3	20	
<i>Dictyostelium microsporum</i>						6	20	6	20											
<i>Dictyostelium capitatum</i>						38	40													
<i>Dictyostelium germanicum</i>																				
<i>Polysphondylium candidum</i>																				
<i>Polysphondylium filamentosum</i>																				
<i>Polysphondylium pallidum</i>						13	60			5	20	40	20			25	20			
<i>Polysphondylium violaceum</i>						61	60			63	80	43	80			29	40			
clones/g						77	60	53	213	100	123	80	490	947						
average clones/g for all collection sites															462				1	40
average clones/g for this group															238			1	40	
average pH for this group															4.1					

Table 3. Dictyostelids recovered from neutral or alkaline soils in deciduous forests of Germany

Species	Collection site		SO		RO		KV		EB		KS		WO		DF		BH	
	pH	7.0 rd f	7.7 rd f		7.0 rd f		6.9 rd f		7.6 rd f		7.0 rd f		7.0 rd f		7.3 rd f		7.3 rd f	
<i>Acyostelium leptosomum</i>			<1	20							4	20	<1	20				
<i>Dictyostelium aureo-stipes</i>																		
<i>Dictyostelium aureo-stipes</i> var. <i>helvetium</i>	17	40	12	40			5	40	9	80	33	100						1 20
<i>Dictyostelium fasciculatum</i>											1	20						
<i>Dictyostelium giganteum</i>																		
<i>Dictyostelium implicatum</i>																		
<i>Dictyostelium minutum</i>	4	20	16	40	1	20			7	80								
<i>Dictyostelium mucoroides</i> S type	75	100	63	100	70	100	62	100	52	100	63	100	79	100	100	100	100	
<i>Dictyostelium mucoroides</i> L type					18	60												
<i>Dictyostelium polycarpum</i>	1	20	<1	20							<1	20						
<i>Dictyostelium septentrionalis</i>			1	40							<1	20						
<i>Dictyostelium sphaerocephalum</i>																		
<i>Dictyostelium microsporum</i>	1	20									<1	20						20 100
<i>Dictyostelium capitatum</i>																		
<i>Dictyostelium germanicum</i>																		
<i>Polysphondylium candidum</i>																		
<i>Polysphondylium filamentosum</i>	2	20	<1	20							<1	20						2 40
<i>Polysphondylium pallidum</i>											3	20						<1 20
<i>Polysphondylium violaceum</i>											9	60	36	40	2	20		
clones/g	543	717	354	821							800	720	567	303				

average clones/g for all collection sites 462
 average clones/g for this group 603
 average pH for this group 7.2

Table 4. Dictyosteliids recovered from acid soils in deciduous forests of Germany

Species	Collection site	DR	KM		ME		RG		TN		EK		SH	
			pH	4.7 rd f	4.2 rd f		5.7 rd f		4.5 rd f		4.5 rd f		4.4 rd f	
<i>Acystostelium leptosorum</i>		<1	20											
<i>Dictyostelium aureo-stipes</i>														
<i>Dictyostelium aureo-stipes</i> var. <i>helvetica</i>		1	40				1	20						
<i>Dictyostelium fasciculatum</i>							1	20						
<i>Dictyostelium giganteum</i>		25	60	1	20		23	60						
<i>Dictyostelium implicatum</i>		69	100	80	100	68	100	66	100	94	100	57	100	<1
<i>Dictyostelium minutum</i>								<1	20			39	60	
<i>Dictyostelium mucoroides</i> S type												29	100	
<i>Dictyostelium mucoroides</i> L type														
<i>Dictyostelium polycarpum</i>														
<i>Dictyostelium septentrionalis</i>												1	20	
<i>Dictyostelium sphaerocephalum</i>												8	20	<1
<i>Dictyostelium microsporum</i>														40
<i>Dictyostelium capitatum</i>														
<i>Dictyostelium germanicum</i>		2	40				5	80						
<i>Polyphondylium candidum</i>		<1	20				5	60						
<i>Polyphondylium filamentosum</i>							1	40						
<i>Polyphondylium pallidum</i>		2	20	19	80	19	100	10	40	6	40	4	20	<1
<i>Polyphondylium violaceum</i>												30	80	
clones/g		583	233			650		563		563		854		593

average clones/g for all collection sites

average clones/g for this group

average pH for this group

462

589

4.7

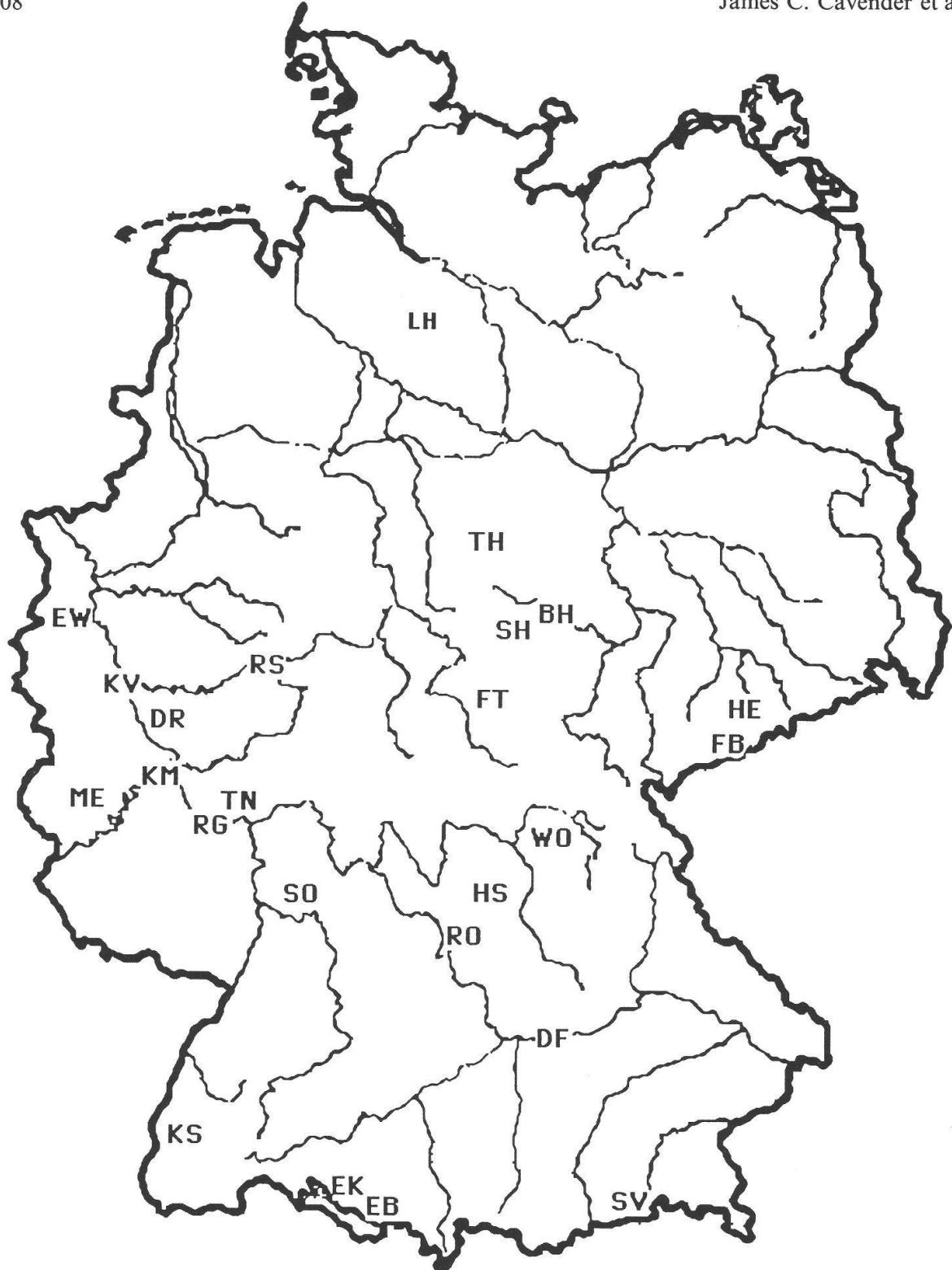
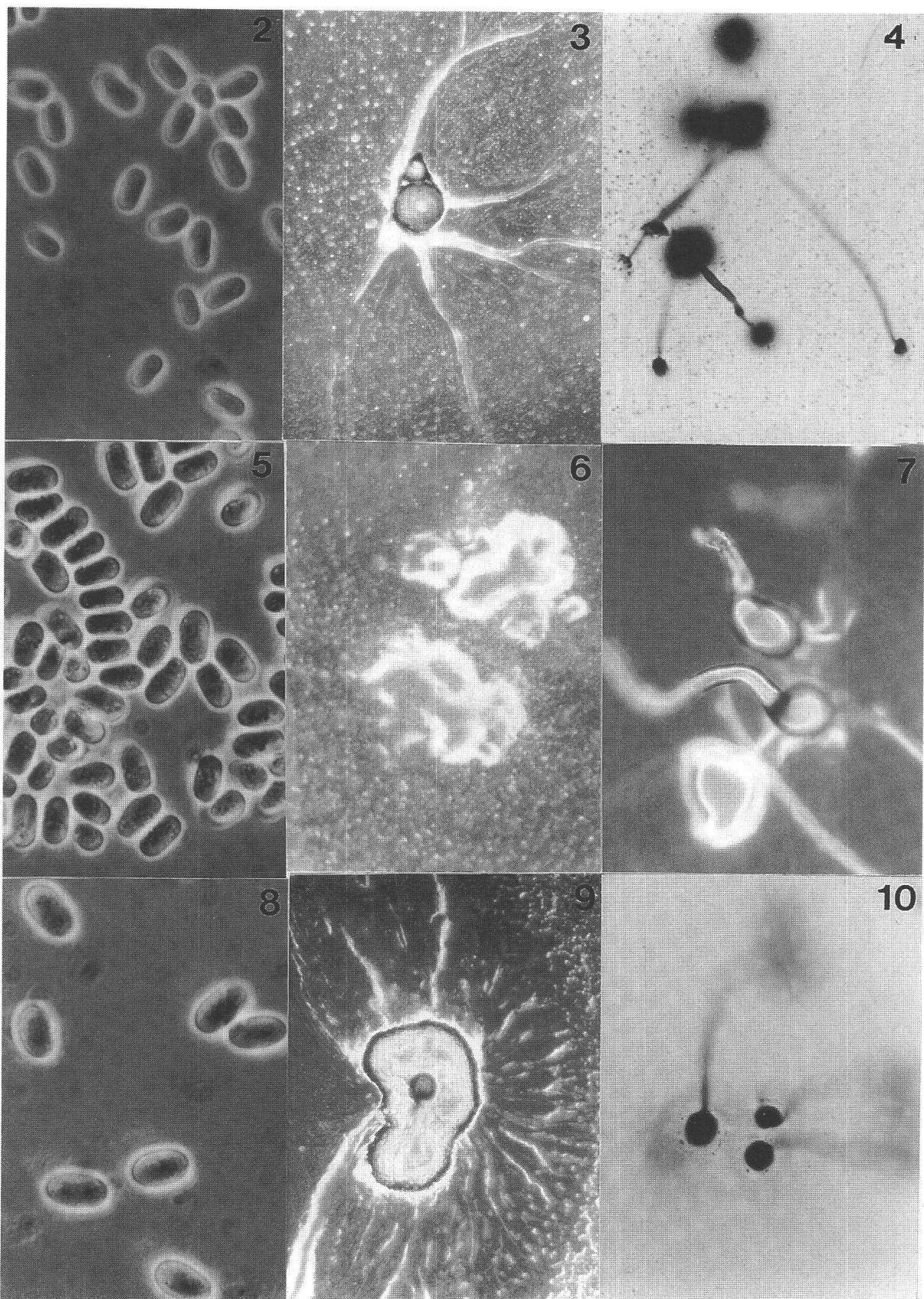
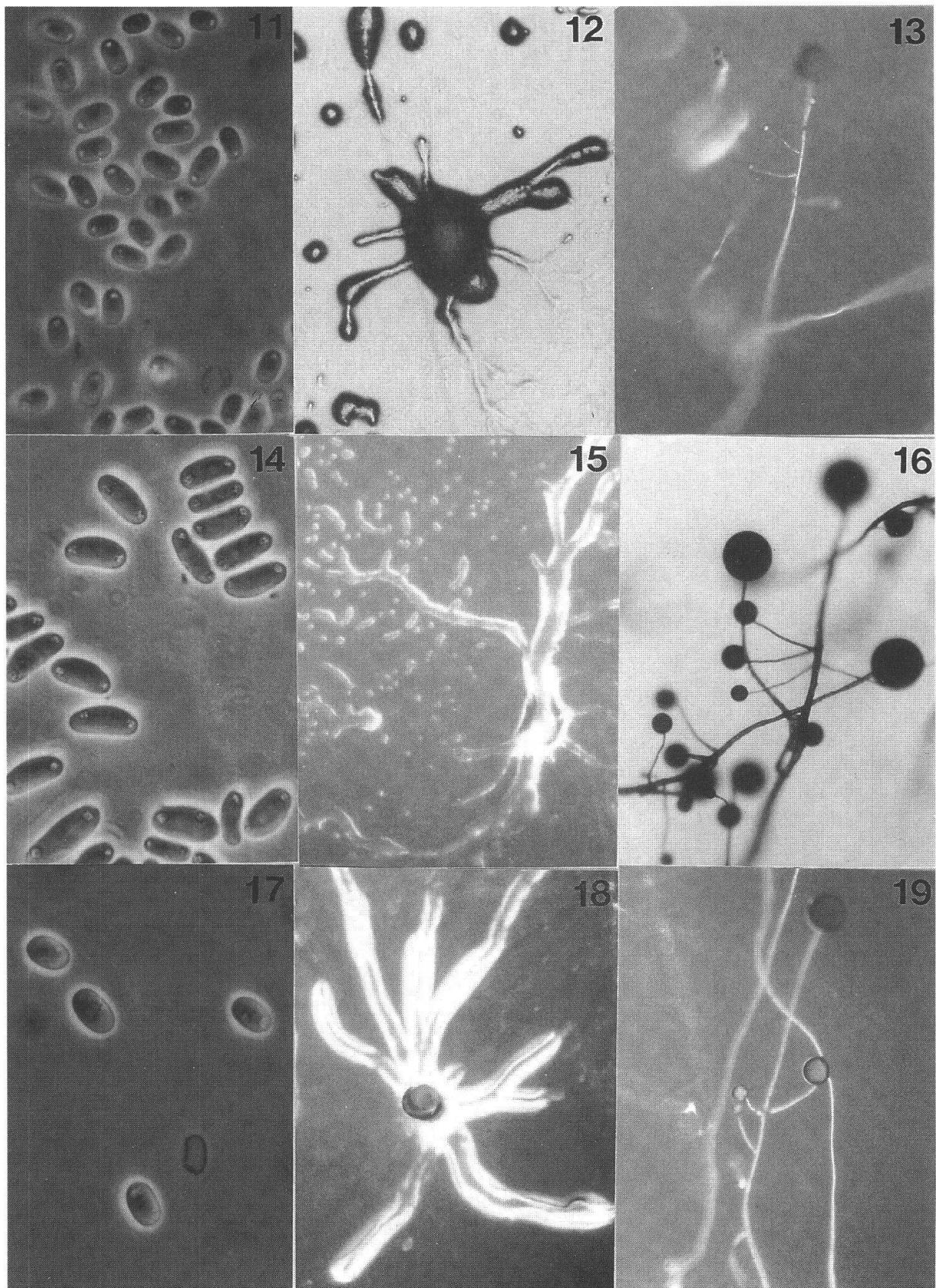


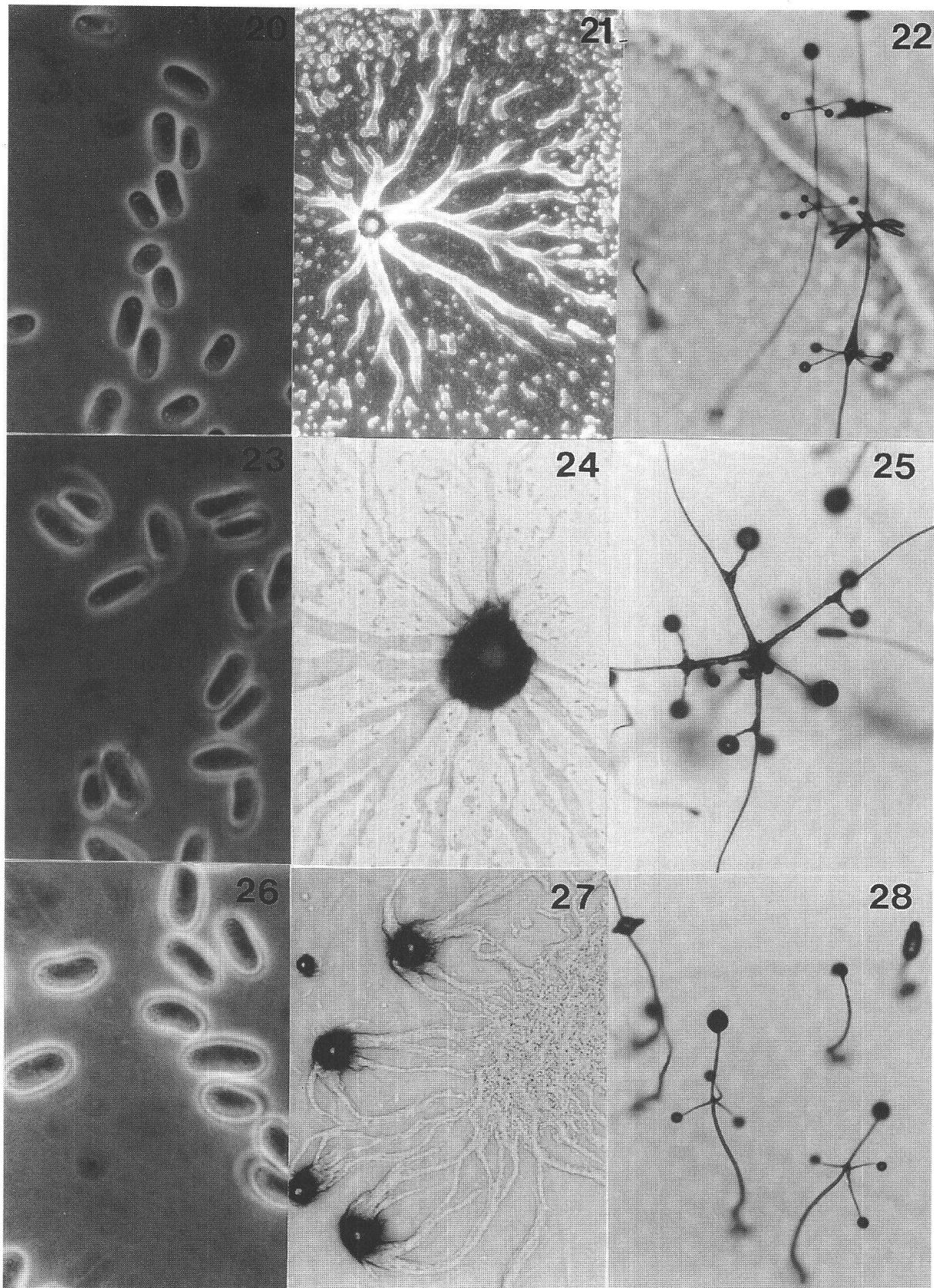
Fig. 1. Map of Germany showing the locations of the twenty-four collection sites. LH – Lüneburger Heide, TH – Torfhaus/Harz, KV – Kottenforstville in Brühl, EW – Elmpter Wald/Netherlands border, DR – Drachenfels/Rhein, RS – Rothaargebirge/Siegen, KM – Kobern/Mosel, ME – Mäuseberg/Eifel, RG – Rheingau, TN – Taunus summit, SO – Starkenberg/Odenwald, RO – Rothenburg ob der Tauber, EB – Eriskirch/Bodensee/Reid Naturschutzgebiet, EK – Eriskirch/Bodensee, KS – Kaiserstuhl, WO – Wonsees/Fränkische Schweiz, HS – Haag/Steigerwald, DF – Danube floodplain, Ingolstadt, SV – Spitzing-See/Voralpen, BH – Barbarossahöhle, SH – Sonderhausen, FT – Friedrichroda/Thüringer Wald, HE – Homersdorf/Erzgebirge, FB – Fichtelberg/Czech border.



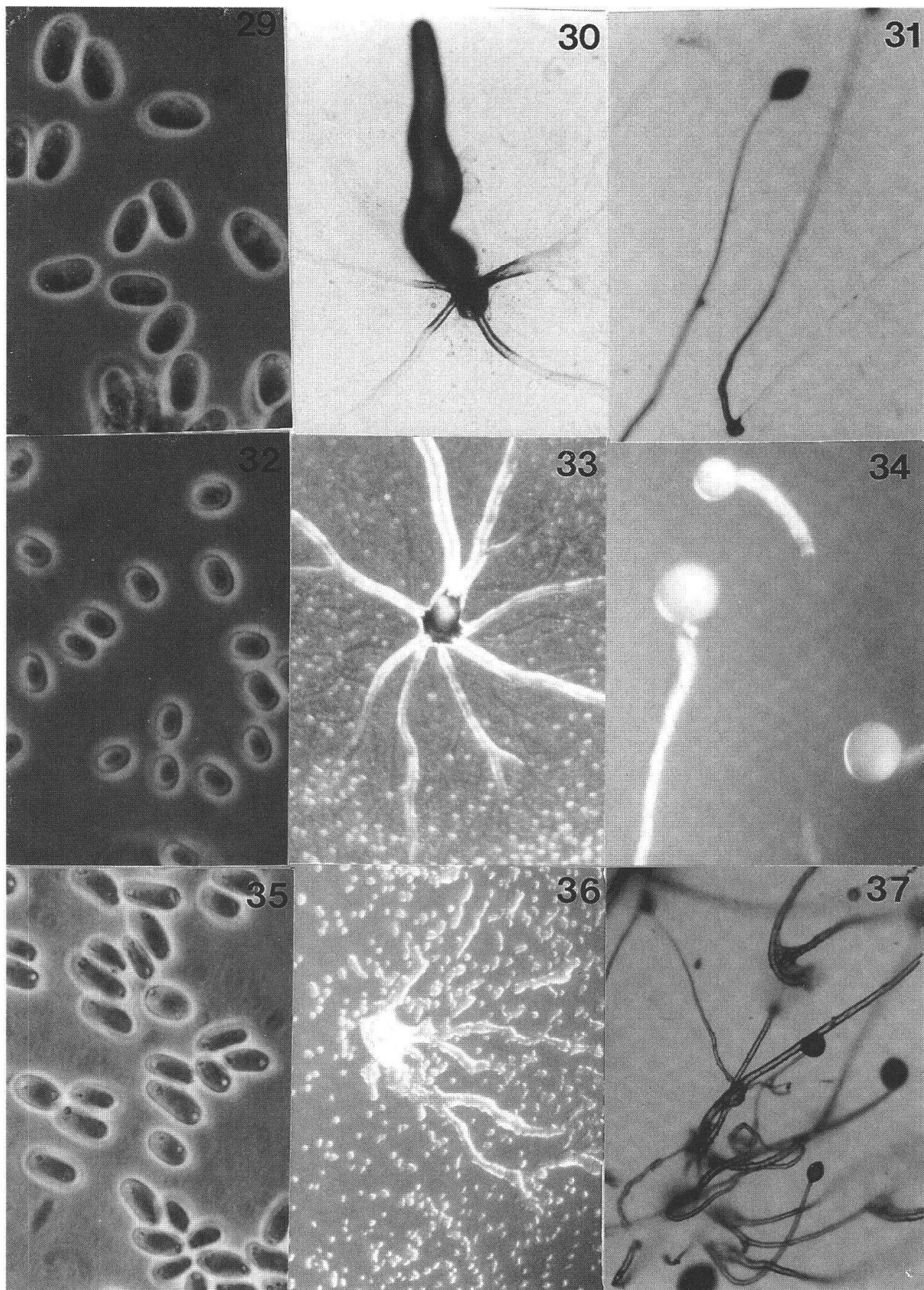
Figs. 2–10. Photomicrographs of *Dictyostelium mucoroides* S-type, *D. mucoroides*, L-type, and *D. implicatum*. 2–4. *D. mucoroides*, S-type. 2. Spores, $\times 750$. 3. Aggregation, $\times 40$. 4. Sorocarps, $\times 40$. 5–7. *D. mucoroides*, L-type. 5. Spores, $\times 750$. 6. Aggregation, $\times 40$. 7. Sorogens, $\times 40$. 8–10. *D. implicatum*. 8. Spores, $\times 750$. 9. Aggregation, $\times 40$. 10. Sorocarps, $\times 40$.



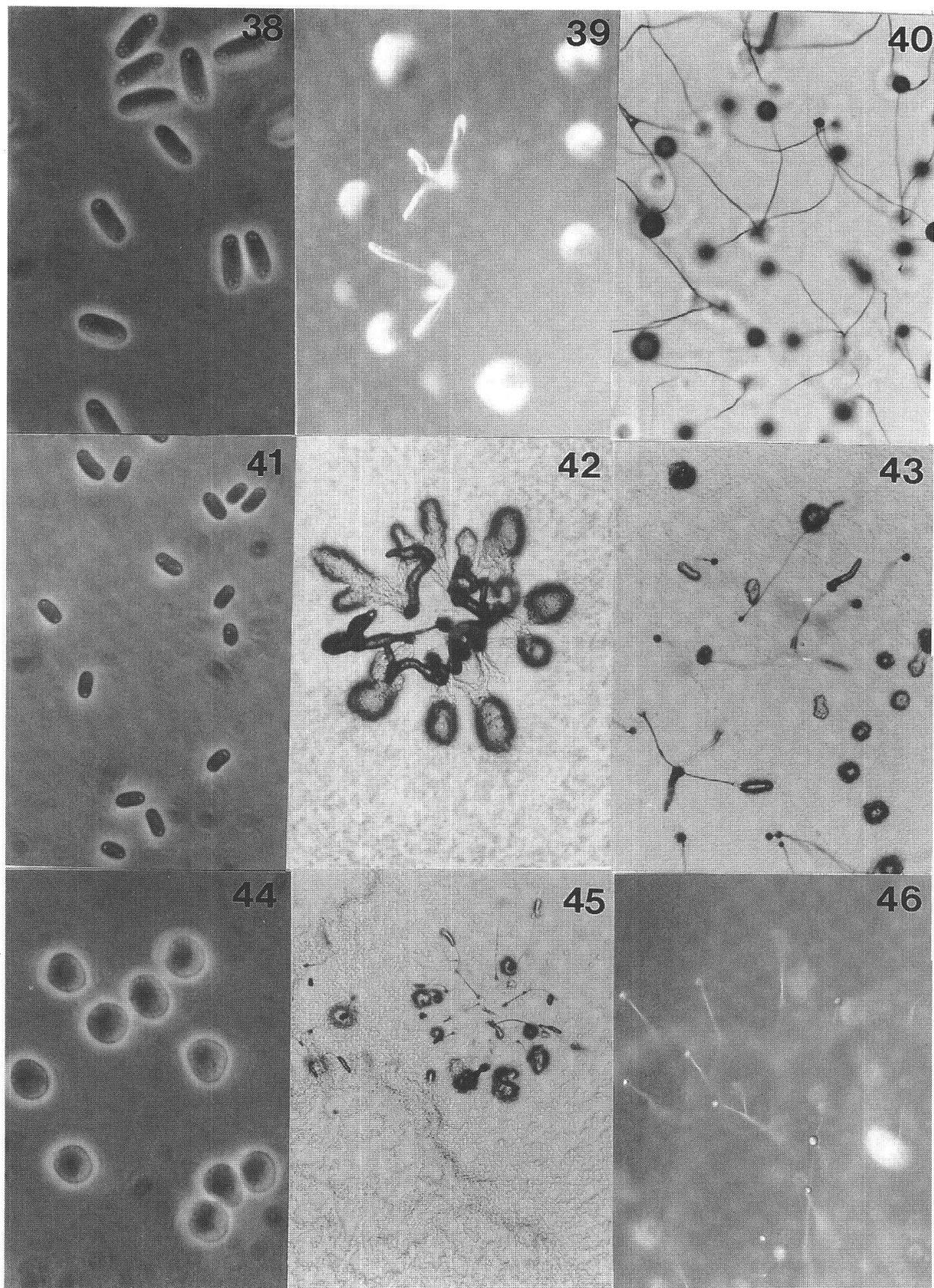
Figs. 11–19. Photomicrographs of *Dictyostelium aureo-stipes* var. *aureo-stipes*, *D. aureo-stipes* var. *helvetium* and *Polysphondylium violaceum*. 11–13. *D. aureo-stipes* var. *aureo-stipes*. 11. Spores, $\times 750$. 12. Aggregation, $\times 40$. 13. Sorocarps, $\times 40$. 14–16. *D. aureo-stipes* var. *helvetium*. 14. Spores, $\times 750$. 15. Aggregation, $\times 40$. 16. Sorocarps, $\times 40$. 17–19. *P. violaceum*. 17. Spores, $\times 750$. 18. Aggregation, $\times 40$. 19. Sorocarps, $\times 40$.



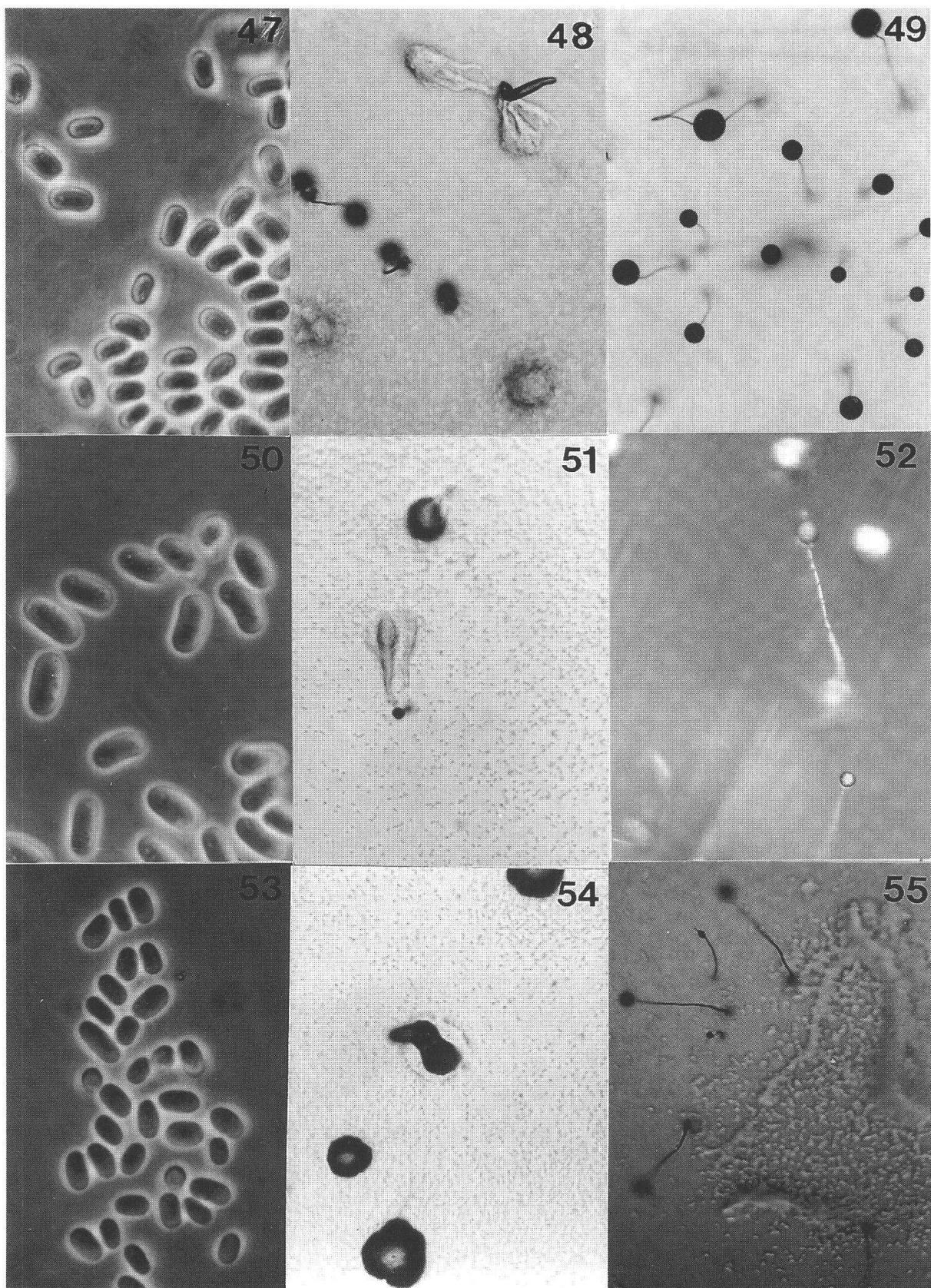
Figs. 20–28. Photomicrographs of *Polysphondylium pallidum*, *P. filamentosum* and *P. candidum*. 20–22. *P. pallidum*. 20. Spores, $\times 750$. 21. Aggregation, $\times 40$. 22. Sorocarps, $\times 40$. 23–25. *P. filamentosum*. 23. Spores, $\times 750$. 24. Aggregation, $\times 40$. 25. Sorocarps, $\times 40$. 26–28. *P. candidum*. 26. Spores, $\times 750$. 27. Aggregation, $\times 40$. 28. Sorocarps, $\times 40$.



Figs. 29–37. Photomicrographs of *Dictyostelium septentrionalis*, *D. sphaerocephalum*, and *D. fasciculatum*. 29–31. *D. septentrionalis*. 29. Spores, $\times 750$. 30. Aggregation, $\times 40$. 31. Sorocarps, $\times 40$. 32–34. *D. sphaerocephalum*. 32. Spores, $\times 750$. 33. Aggregation, $\times 40$. 34. Sorocarps, $\times 40$. 35–37. *D. fasciculatum*. 35. Spores, $\times 750$. 36. Aggregation, $\times 40$. 37. Sorocarps, $\times 40$.



Figs. 38–46. Photomicrographs of *D. polycarpum*, *D. microsporum* and *Acytostelium leptosomum*. 38–40. *D. polycarpum*. 38. Spores, $\times 750$. 39. Aggregation, $\times 40$. 40. Sorocarps, $\times 40$. 41–43. *D. microsporum*. 41. Spores, $\times 750$. 42. Aggregation, $\times 40$. 43. Sorocarps, $\times 40$. 44–46. *Acytostelium leptosomum*. 44. Spores, $\times 750$. 45. Aggregation, $\times 40$. 46. Sorocarps, $\times 40$.



Figs. 47–55. Photomicrographs of *Dictyostelium minutum*, *D. germanicum*, and *D. capitatum*. 47–49. *D. minutum*. 47. Spores, $\times 750$. 48. Aggregation, $\times 40$. 49. Sorocarps, $\times 40$. 50–52. *D. germanicum*. 50. Spores, $\times 750$. 51. Aggregation, $\times 40$. 52. Sorocarps, $\times 40$. 53–55. *D. capitatum*. 53. Spores, $\times 750$. 54. Aggregation, $\times 40$. 55. Sorocarps, $\times 40$.

5. *D. aureo-stipes* var. *helvetium*, FT-1, Figs. 14–16. Irregularly branched sorocarps, robust and erect sorocarps with yellow sorophores when grown in the dark; aggregates break up into smaller units, spores with conspicuous consolidated polar granules.
6. *P. violaceum*, FT-5, Figs. 17–19. Purple to violaceous pigmentation of sorocarps, whorled branches; aggregates break up, spores with consolidated polar granules.
7. *P. pallidum*, LH-4, Figs. 20–22. Unpigmented sorocarps, numerous whorls of branches, radiate aggregation, spores with unconsolidated polar granules.
8. *P. filamentosum*, RS-5, Figs. 23–25. Distinguished by the elongated terminus of the main axis as well as the axes of the whorled branches of the sorocarps, radiate aggregation, unconsolidated polar granules.
9. *P. candidum*, ME-2, Figs. 26–28. Unpigmented sorocarps, terminal segment may be elongated, radiate aggregation, more robust than *P. pallidum* with fewer whorls, large spores with unconsolidated polar granules.
10. *D. septentrionalis*, FB-1, Figs. 29–31. Very robust thick sorocarps often with expanded bases, radiate aggregations, will not grow above 20 °C, large spores without polar granules.
11. *D. sphaerocephalum*, KS-5, Figs. 32–34. Small but stout sorocarps, characterized by thick sorophore tips with slime collars and well developed supporters of prostate sorophores, spores without polar granules.
12. *D. fasciculatum*, RO-1 a, Figs. 35–37. Several sorocarps per aggregate, aggregates break up, conspicuous consolidated polar granules.
13. *D. polycarpum*, KS-4, Figs. 38–40. Small coremiform sorocarps, mound-like aggregates or short streams, relatively long spores with conspicuous unconsolidated polar granules.
14. *D. microsporum*, HE-4, Figs. 41–43. Several delicate sinuous sorocarps develop from an aggregate, aggregates mound-like developing a lobed stream network when older, spores of two sizes with conspicuous consolidated polar granules.
15. *Acytostelium leptosomum*, DR-4, Figs. 44–46. Minute size; mound-like aggregates, sometimes with streams; acellular, very delicate sorocarps; spherical spores.
16. *Dicyostelium minutum*, HS-2, Figs. 47–49. Small size; mound-like aggregation with reverse streaming when older, solitary or more commonly several sorocarps per aggregate, spores with or without inconspicuous polar granules.
17. *D. germanicum*, ME-1, Figs. 50–52. Small size; mound-like aggregates; single sorocarp per aggregate; oblong spores with numerous unconsolidated polar granules.
18. *D. capitatum*, TH-2, Figs. 53–55. Delicate; mound-like aggregates or short, coarse streams; several sorocarps per aggregate; sorophores with capitellate tips; spores with inconspicuous polar granules.
19. *D. giganteum*, FT-2, not illustrated. Very similar to *D. mucoroides* S-type with much longer erector creeping sorophores.

Key to the dictyostelids of Germany

1. Sorophores acellular (*Acytostelium*)
spores spherical, sorocarps very delicate *Acytostelium leptosorum*
(Figs. 44–46) 2
1. Sorophores cellular, spores elliptical 2
2. Sorocarps unbranched or branched but never with whorled branches (*Dictyostelium*) 6
2. Sorocarps typically with whorls of branches (*Polysphondylium*) 3
3. Sorocarps pigmented, sorophores and sori violet to purple *Polysphondylium violaceum*
(Figs. 17–19) 4
3. Sorocarps unpigmented 4
4. Whorls numerous *Polysphondylium pallidum*
(Figs. 20–22) 5
4. Whorls few 5
5. Lateral branch tips elongated, tips of main axis also elongated
· · · · · *Polysphondylium filamentosum*
(Figs. 23–25) 5
5. Lateral branches not elongated, main axis tips may be elongated
· · · · · *Polysphondylium candidum*
(Figs. 26–28) 6
6. Sorocarps unpigmented and without whorled branches 8
6. Sorocarps pigmented, sorophores yellow in reduced light or darkness 7
7. Sorophores erect, branched, spores with conspicuous polar granules,
conifer or mixed coniferous deciduous forests *Dictyostelium aureo-stipes* var. *helvetica*
(Figs. 14–16) 7
7. Sorophores prone or flexuous, branched; spores with conspicuous polar granules;
deciduous forest *Dictyostelium aureo-stipes* var. *aureo-stipes*
(Figs. 11–13) 8
8. Sorocarps small, mostly <2 mm high, sorophores composed of a single tier of cells 15
8. Sorocarps medium, large or very large >2 mm to 1.5 cm, sorophores composed
of more than one cell in cross section 9
9. Aggregation large, radial, do not break up 10
9. Aggregations large, initially radial but break up into numerous smaller aggregations,
sorocarps clustered, spores with conspicuous polar granules, abundant in deciduous forests
with neutral or alkaline humus *Dictyostelium fasciculatum*
(Figs. 35–37) 10
10. Sorocarps very large, reaching 5–15 mm in height 11
10. Sorocarps large but mostly <5 mm unless exposed to one-sided illumination 12
11. Sorocarps erect, robust 1.0–1.5 cm high, very large sori (up to 500 µm), arising from
expanded, conical bases; will not fruit above 20°C *Dictyostelium septentrionalis*
(Figs. 29–31) 11
11. Sorocarps erect, 5–10 mm high, or commonly greatly elongated by migration, up to several cm
in length *Dictyostelium giganteum*
(not illustrated) 12
12. Sorocarps mostly 2–5 mm when erect, sorophores partially prostrate showing little taper,
sori relatively large, 175–350 µm in diameter with cupule-like residues
at bases of sori *Dictyostelium sphaerocephalum*
(Figs. 32–34) 13
12. Sorocarps mostly 2–5 mm when erect unlike the above 13
13. Sorocarps becoming entangled in diffuse light, spores of collapsed sori germinate
to form secondary sorocarps with basal discs *Dictyostelium implicatum*
(Figs. 8–10) 13
13. Sorocarps not becoming entangled in diffuse light 14

14. Sorocarps with slightly expanded conical bases *Dictyostelium mucoroides*, S-type
(Figs. 2–4)

14. Sorocarps without expanded bases, aggregations assume a “lumpy” appearance in late stages,
sorogens elongated, sorophores migrating extensively . . . *Dictyostelium mucoroides*, L-type
(Figs. 5–7)

15. Sorocarps clustered, aggregations usually mound-like 18

15. Sorocarps solitary or weakly clustered, aggregations usually mound-like 16

16. Spores oblong $3-4 \times 6-8 \mu\text{m}$ with numerous conspicuous unconsolidated
polar granules *Dictyostelium germanicum*
(Figs. 50–52)

16. Spores smaller mostly $2-3 \times 4-6 \mu\text{m}$ with inconspicuous polar granules 17

17. Sorophore tips capitate, coniferous or mixed coniferous deciduous forest
· · · · · *Dictyostelium capitatum*
(Figs. 53–55)

17. Sorophore tips not capitate, abundant in deciduous forest with acid humus
· · · · · *Dictyostelium minutum*
(Figs. 47–49)

18. Sorocarps in coremiform clusters, spores long, with numerous conspicuous
unconsolidated polar granules *Dictyostelium polycarpum*
(Figs. 38–40)

18. Sorocarps in irregular clusters, spores small and of two sizes both with conspicuous
consolidated polar granules *Dictyostelium microsporum*
(Figs. 41–43)

Discussion

With 19 species, the region studied in Germany has very similar species richness to both the bimodal region of Ohio and West Virginia and the cool temperate zone of Japan. This could be the result of close similarity in the degree of topographical, geographical and forest variation.

Some species, are plentiful and common on all three continents, such as *Dictyostelium mucoroides* S type, *D. sphaerocephalum*, *D. minutum*, *Polysphondylium pallidum* and *P. violaceum*. Others are absent or very infrequent on one continent while they are prevalent on one or both of the others. The species which are absent or relatively infrequent in Europe but common in North America and Japan include *D. discoideum*, *D. purpureum*, and *D. polycephalum*. Those absent or less frequent in Eastern North America but more common in Europe are *P. candidum*, *P. filamentosum*, *D. polycarpum*, *D. septentrionalis*, and *D. implicatum*. The last two species appear to be more common in the Pacific Northwest than elsewhere in North America (Cavender, unpublished data). *D. fasciculatum* is an endemic to Europe.

Three new species not found in Switzerland or elsewhere in Europe occur in Germany. One of these, *D. capitatum*, was isolated from a mixed coniferous-deciduous forest in the Harz mountains on the former border between East and West Germany, while the second, *D. germanicum*, occurred in a deciduous forest in the Eifel region of Rhineland Palatinate. The most common of the three, *D. microsporum*, was found at three separate coniferous sites. This is a fairly common species in mixed coniferous-deciduous forest in Japan.

Coniferous forests with acid mor humus and deciduous forests with neutral or alkaline mull humus have distinct differences in their dictyostelid populations. Numbers

per gram are higher in deciduous forests, even those with acid soils, probably due to higher bacterial populations.

Dictyostelium aureo-stipes var. *helvetium* is an indicator species for coniferous forest. Other characteristic species are *D. septentrionalis*, and *D. microsporum*. *Dictyostelium fasciculatum*, *D. polycarpum*, *P. candidum* and *D. aureo-stipes* var. *aureo-stipes* are characteristic of deciduous forest with neutral or alkaline mull humus. *Dictyostelium minutum* is characteristic of deciduous forest with acid humus.

Dictyostelium mucoroides S-type is dominant in most forests of Germany regardless of forest or humus type although it appears to be most prevalent in deciduous forest with mull humus and neutral or alkaline pH. *Polysphondylium violaceum* and *Dictyostelium minutum* may also dominate dictyostelid populations, the former in coniferous forest and the latter in deciduous forest with acid humus.

The two sites with greatest species richness, Kaiserstuhl in the Black Forest region and Rothenburg on the Tauber river in central Germany, had mull humus with slightly alkaline pH. Yet two other sites with alkaline soil, Barbarossahöhle south of the Harz mountains in the former East Germany and Wonsee in the Fränkische Schweiz mountains, had low species richness. These sites appeared to have experienced greater anthropogenic disturbances.

The highest numbers per gram were found in the Rothaargebirge near Siegen, a mixed forest with acid humus. This forest had species characteristic of both acid coniferous and alkaline deciduous forest. Because of the high density and diversity of its dictyostelid populations this forest should be investigated further for other species.

The lowest numbers per gram (<100) were in soils of four coniferous forests (spruce or pine) with acid humus. Again, this is most likely due to the lower densities of bacteria in mor humus.

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