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Ecological distribution of cellular slime molds in forest soils of Germany

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Abstract

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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: *Acytostelium leptosomum*, *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-nutrient 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, sporae 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.

Niedersachsen (Lower Saxony)

LH **Site:** Lüneburger Heide
Date: 7.29.93
Region: Lüneburger Heide (Luneberg Heath)
Forest type: Mixed coniferous-deciduous
Dominant trees: Beech (*Fagus*), Oak (*Quercus*), Birch (*Betula*), Pine (*Pinus*), Spruce (*Picea*)
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

Nordrhein-Westfalen (North Rhine Westphalia)

KV **Site:** Kottenforstville in Brühl
Date: 7.23.93
Region: Rhine Valley, northern Rheinisches Schilefergebirge
Forest type: Deciduous
Dominant trees: Basswood (*Tilia*), Maple (*Acer*), 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
Geologic features: Mountain, basalt cliffs
Elevation: 200–500 m
Humus type: mull
Soil pH: 4.7

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

Rheinland-Pfalz (Rhineland Palatinate)

KM **Site:** Kobern/Mosel
Date: 7.23.93
Region: Eifel, Mosel Valley
Forest type: Deciduous
Dominant trees: Hornbeam (*Ostrya*)
Geologic features: elevated terrain along Mosel river
Elevation: 150–250 m
Humus type: mull
Soil pH: 4.2

ME **Site:** Mäuseberg/Eifel
Date: 7.21.93
Region: Eifel
Forest type: Deciduous
Dominant trees: Beech, Hawthorn (*Crataegus*)
Geologic features: north facing slope of lake basin
Elevation: 450–550 m
Humus type: mull
Soil pH: 5.7

Hessen (Hesse)

RG **Site:** Rheingau
Date: 7.20.93
Region: Rheingaugebirge, Taunus
Forest type: Deciduous
Dominant trees: Chestnut (*Castanea*), Oak, Cherry (*Prunus*), 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 **Site:** Taunus summit
Date: 7.20.93
Region: Taunus
Forest type: Deciduous
Dominant trees: Alder (*Alnus*) Birch, Beech, Larch (*Larix*), Oak
Geologic features: mountainous gorge
Elevation: 500 m
Humus type: mull
Soil pH: 4.5

SO **Site:** Starkenberg/Odenwald
Date: 8.9.93
Region: Odenwald
Forest type: Deciduous
Dominant trees: Walnut (*Juglans*), Maple, Beech, Sycamore (*Platanus*), Oak, Chestnut, Basswood, Ash (*Fraxinus*)
Geologic features: limestone parent material
Elevation: 500 m
Humus type: mull
Soil pH: 7.0

Baden-Württemberg

RO **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

EB **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

EK **Site:** Eriskirch/Bodensee
Date: 8.7.93
Region: Lake Constance, below Schwäbische Alb
Dominant trees: Beech
Geologic features: lake shore
Elevation: 400 m
Humus type: moder
Soil pH: 4.4

KS **Site:** Kaiserstuhl
Date: 8.9.93
Region: Schwarzwald (Black Forest)
Forest type: Coniferous
Dominant trees: Hazel Nut (*Corylus*), Maple, Beech, Ash, Locust (*Robinia*), Poplar (*Populus*)
Geologic features: loess deposits
Elevation: <450 m
Humus type: mull
Soil pH: 7.6

Bayern (Bavaria)

WO **Site:** Wonsee/Fränkische Schweiz
Date: 8.2.93
Region: Fränkische Schweiz
Forest type: Mixed coniferous-deciduous
Dominant trees: Oak, Alder, Beech, Ironwood (*Carpinus*), Basswood, Hornbeam, Spruce, Birch
Geologic features: limestone outcrops
Elevation: 400–450 m
Humus type: mull
Soil pH: 7.0

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

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

Table 1. Collection sites (continued).

SV **Site:** Spitzing-See/Voralpen
Date: 8.6.93
Region: Bayerische Alpen (Bavarian Alps)
Forest type: Coniferous
Dominant trees: Spruce, Fir (*Abies*)
Geologic features: steep mountain slope, limestone parent material
Elevation: 1200–1500 m
Humus type: mull
Soil pH: 7.3
Comments: forest die-back evident

Thüringen (Thuringia)

BH **Site:** Barbarossahöhle
Date: 7.30.93
Region: Thüringer Becken, Hainleite
Forest type: Deciduous
Dominant trees: Maple, Oak
Geologic features: limestone, Karst topography
Elevation: 200–250 m
Humus type: mull
Soil pH: 7.3

SH **Site:** Sondershausen
Date: 7.30.93
Region: Thüringer Becken, Hainleite
Forest type: Deciduous
Dominant trees: Oak
Geologic features:
Elevation: 200–250 m
Humus type: mull
Soil pH: 4.7

FT **Site:** Friedrichroda/Thüringer Wald
Date: 7.31.93
Region: Thüringer Wald
Forest type: Mixed coniferous-deciduous
Dominant trees: Spruce, Birch, Beech, Maple, Hazel Nut, Alder
Geologic features: bordering an upland swamp
Elevation: 600–800 m
Humus type: moder
Soil pH: 3.5

Freistaat Sachsen (Free State of Saxony)

HE **Site:** Homersdorf/Erzgebirge
Date: 8.2.93
Region: Sächsisches Bergland just above the Erzgebirge
Forest type: Coniferous
Dominant trees: Spruce
Geologic features: mountainous
Elevation: 550 m
Humus type: mor
Soil pH: 3.5

FB **Site:** Fichtelberg/Czech border
Date: 8.2.93
Region: Erzgebirge
Forest type: Coniferous
Dominant trees: Spruce
Geologic features: mountainous
Elevation: 1200 m
Humus type: mor
Soil pH: 3.7
Comments: serious forest die-back

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

Collection site	LH		TH		EW		FT		HE		FB		HS		SV		RS	
pH	3.6		3.8		4.8		3.5		3.5		3.7		4.6		4.9		4.8	
Species	rd	f	rd	f	rd	f	rd	f	rd	f	rd	f	rd	f	rd	f	rd	f
Acytostelium leptosomum																		
Dictyostelium aureo-stipes																		
Dictyostelium aureo-stipes var. *helvetium*			44	40			3	20	7	20	38	20	13	40	1	20		
Dictyostelium fasciculatum																	2	20
Dictyostelium giganteum											32	40			1	20		
Dictyostelium implicatum	4	20					1	20					4	20				
Dictyostelium minutum	18	40											4	20			48	40
Dictyostelium mucoroides S type			6	20	88	60	8	20			24	60	8	20	94	80	47	60
Dictyostelium mucoroides L type																		
Dictyostelium polycarpum																		
Dictyostelium septentrionalis	4	20	6	20	6	20	9	40			3	20	17	20	1	20	1	20
Dictyostelium sphaerocephalum							11	60			3	20			3	20		
Dictyostelium microsporum			6	20	6	20			10	20								
Dictyostelium capitatum			38	40														
Dictyostelium germanicum																		
Polysphondylium candidum																		
Polysphondylium filamentosum																	1	40
Polysphondylium pallidum	13	60					5	20	40	20			25	20			1	40
Polysphondylium violaceum	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																	
average clones/g for this group	238																	
average pH for this group	4.1																	

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

Collection site	SO		RO		KV		EB		KS		WO		DF		BH	
pH	7.0		7.7		7.0		6.9		7.6		7.0		7.3		7.3	
Species	rd	f	rd	f	rd	f	rd	f	rd	f	rd	f	rd	f	rd	f
Acytostelium leptosomum																
Dictyostelium aureo-stipes			<1	20					4	20	<1	20				
Dictyostelium aureo-stipes var. *helvetium*																
Dictyostelium fasciculatum	17	40	12	40			9	80	33	100						
Dictyostelium giganteum					5	40			1	20			1	20		
Dictyostelium implicatum							7	80								
Dictyostelium minutum	4	20	16	40	1	20										
Dictyostelium mucoroides S type	75	100	63	100	70	100	62	100	52	100	63	100	79	100	100	100
Dictyostelium mucoroides L type					18	60										
Dictyostelium polycarpum	1	20	<1	20					<1	20						
Dictyostelium septentrionalis			1	40					<1	20						
Dictyostelium sphaerocephalum																
Dictyostelium microsporum	1	20							<1	20			20	100		
Dictyostelium capitatum																
Dictyostelium germanicum																
Polysphondylium candidum			3	20	2	60	<1	20	<1	20			2	40		
Polysphondylium filamentosum	2	20	<1	20			<1	20					<1	20		
Polysphondylium pallidum					<1	20	3	20								
Polysphondylium violaceum			4	60	3	60	18	80	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. Dictyostelids recovered from acid soils in deciduous forests of Germany

Collection site	DR		KM		ME		RG		TN		EK		SH	
pH	4.7		4.2		5.7		4.5		4.5		4.4		4.7	
Species	rd	f	rd	f	rd	f	rd	f	rd	f	rd	f	rd	f
Acytostelium leptosomum	<1	20												
Dictyostelium aureo-stipes														
Dictyostelium aureo-stipes var. *helvetium*														
Dictyostelium fasciculatum	1	40												
Dictyostelium giganteum					1	20								
Dictyostelium implicatum					1	20							<1	20
Dictyostelium minutum	25	60	1	20			23	60			57	100	39	60
Dictyostelium mucoroides S type	69	100	80	100	68	100	66	100	94	100	18	100	29	100
Dictyostelium mucoroides L type							<1	20						
Dictyostelium polycarpum														
Dictyostelium septentrionalis											1	20		
Dictyostelium sphaerocephalum											8	20	<1	40
Dictyostelium microsporum														
Dictyostelium capitatum														
Dictyostelium germanicum					5	80								
Polysphondylium candidum	2	40			5	60								
Polysphondylium filamentosum	<1	20			1	40								
Polysphondylium pallidum											4	20	<1	20
Polysphondylium violaceum	2	20	19	80	19	100	10	40	6	40	12	100	30	80
clones/g	583		233		650		650		563		854		593	
average clones/g for all collection sites	462													
average clones/g for this group	589													
average pH for this group	4.7													

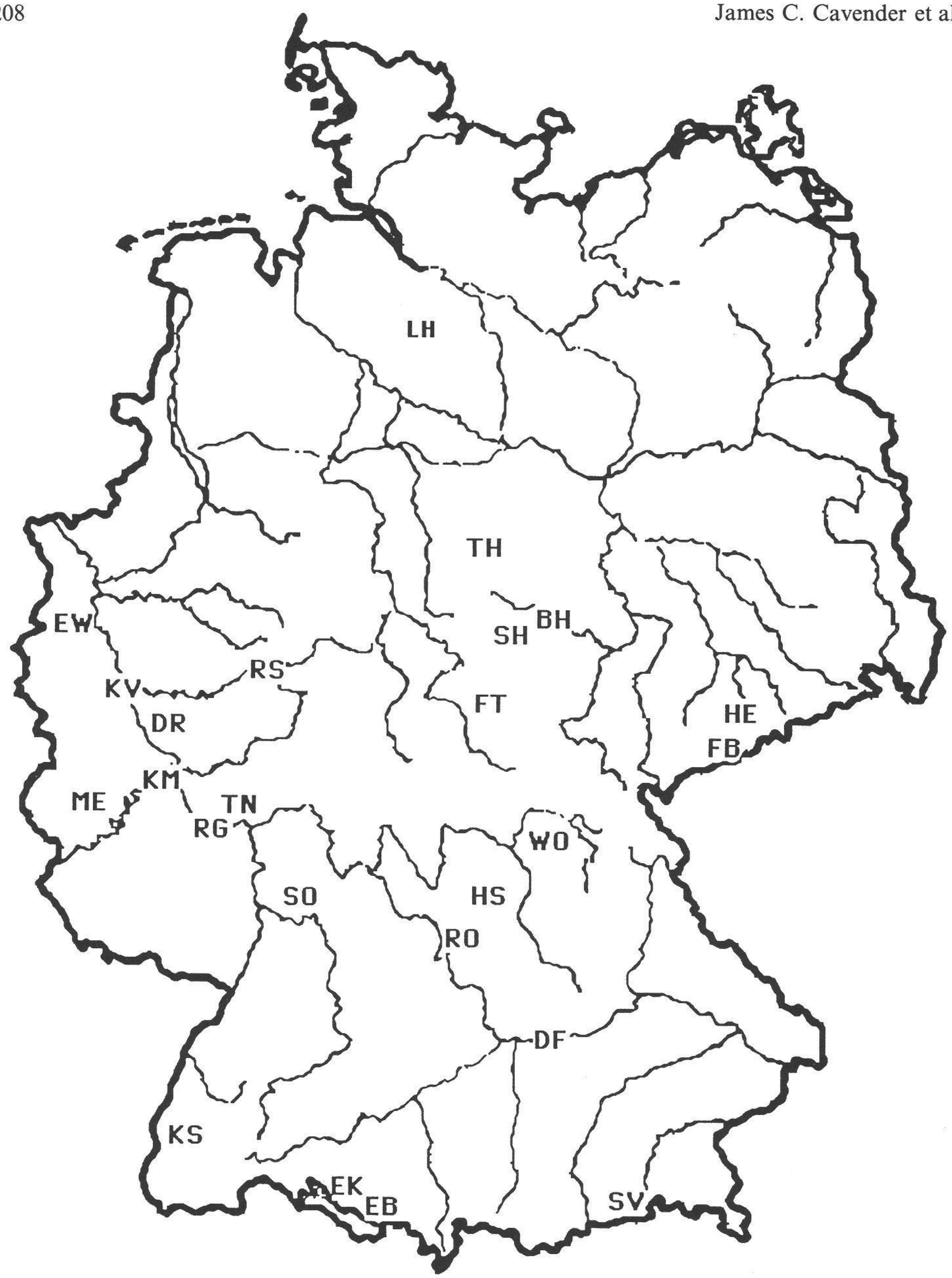
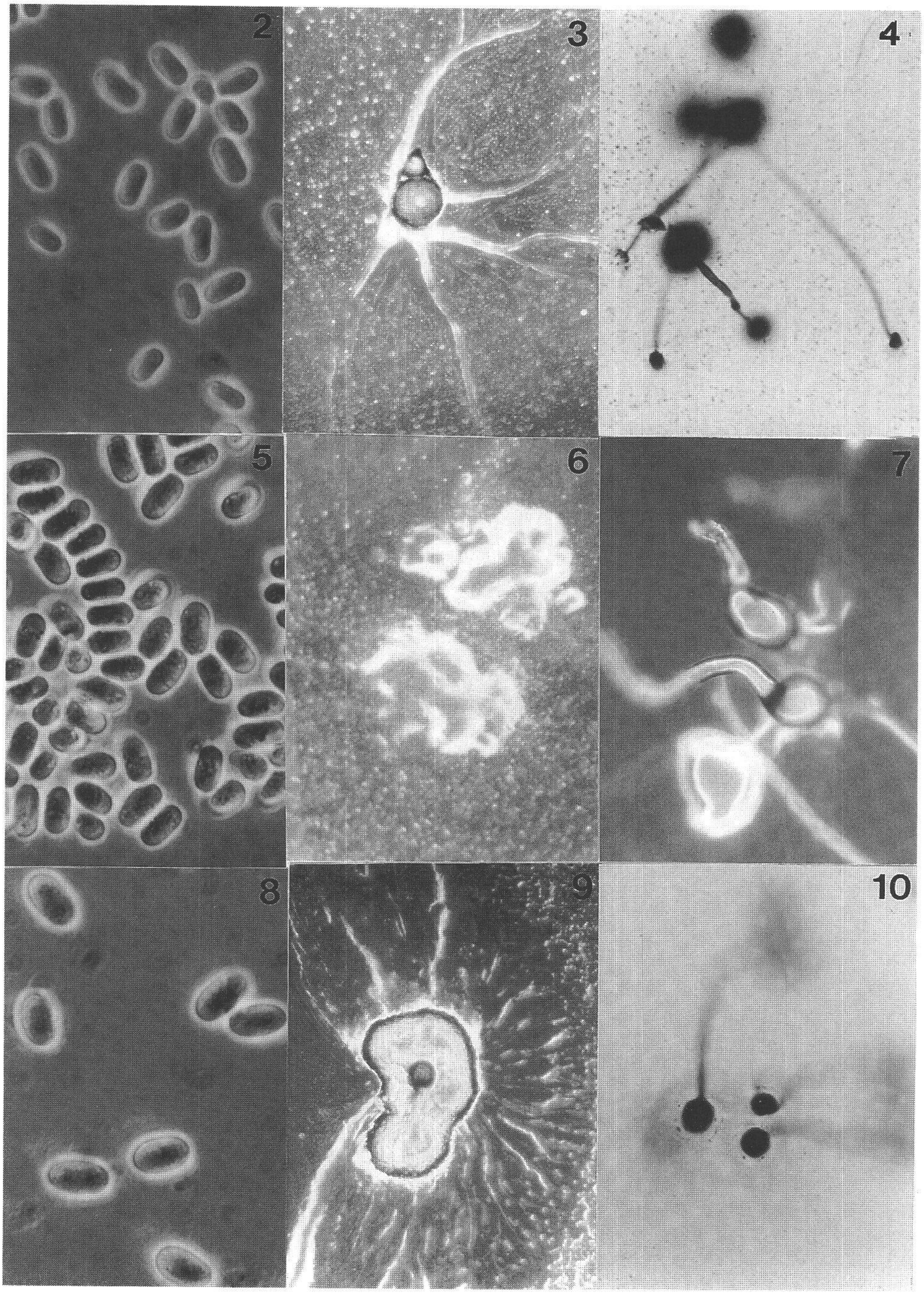
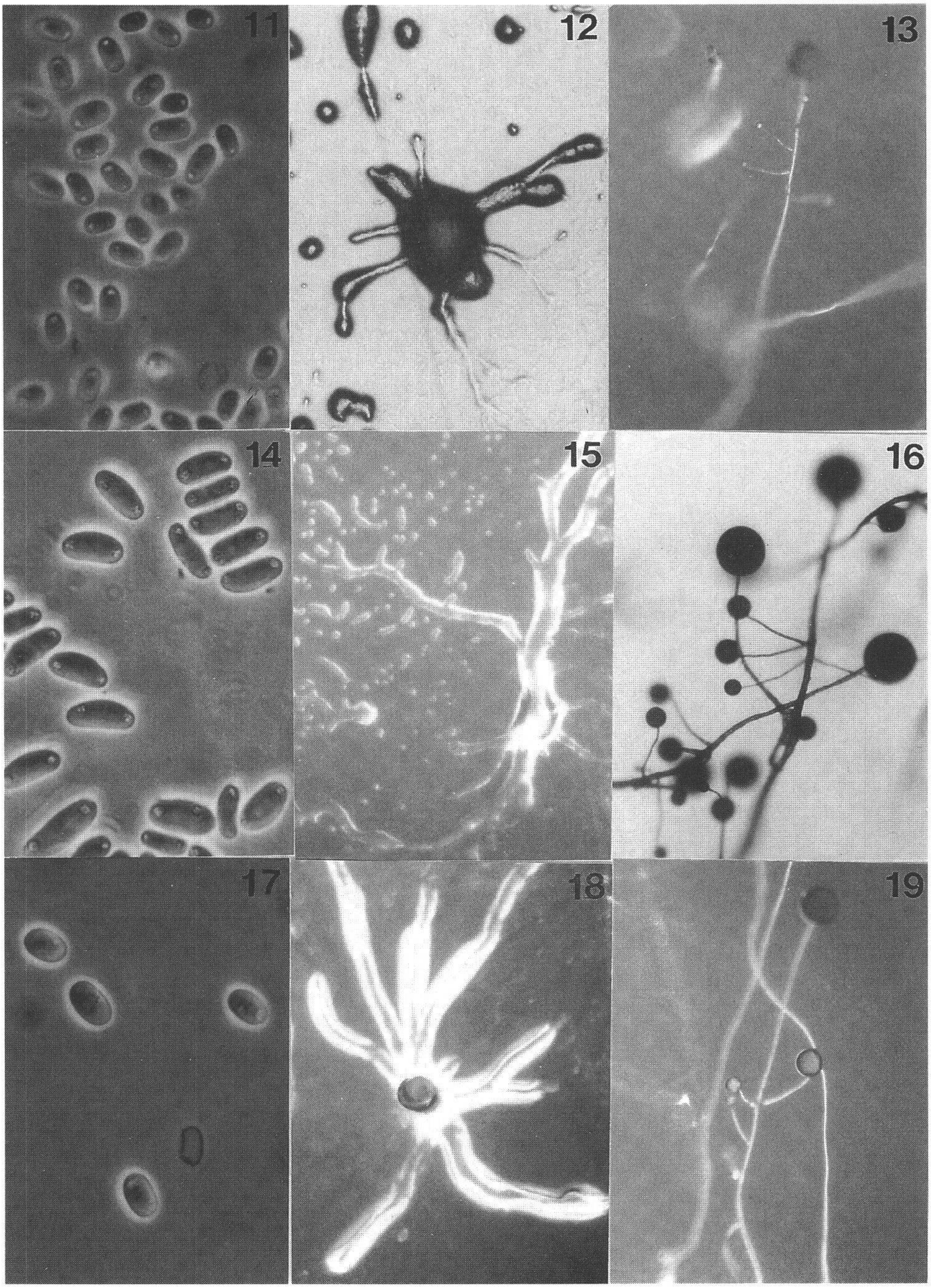


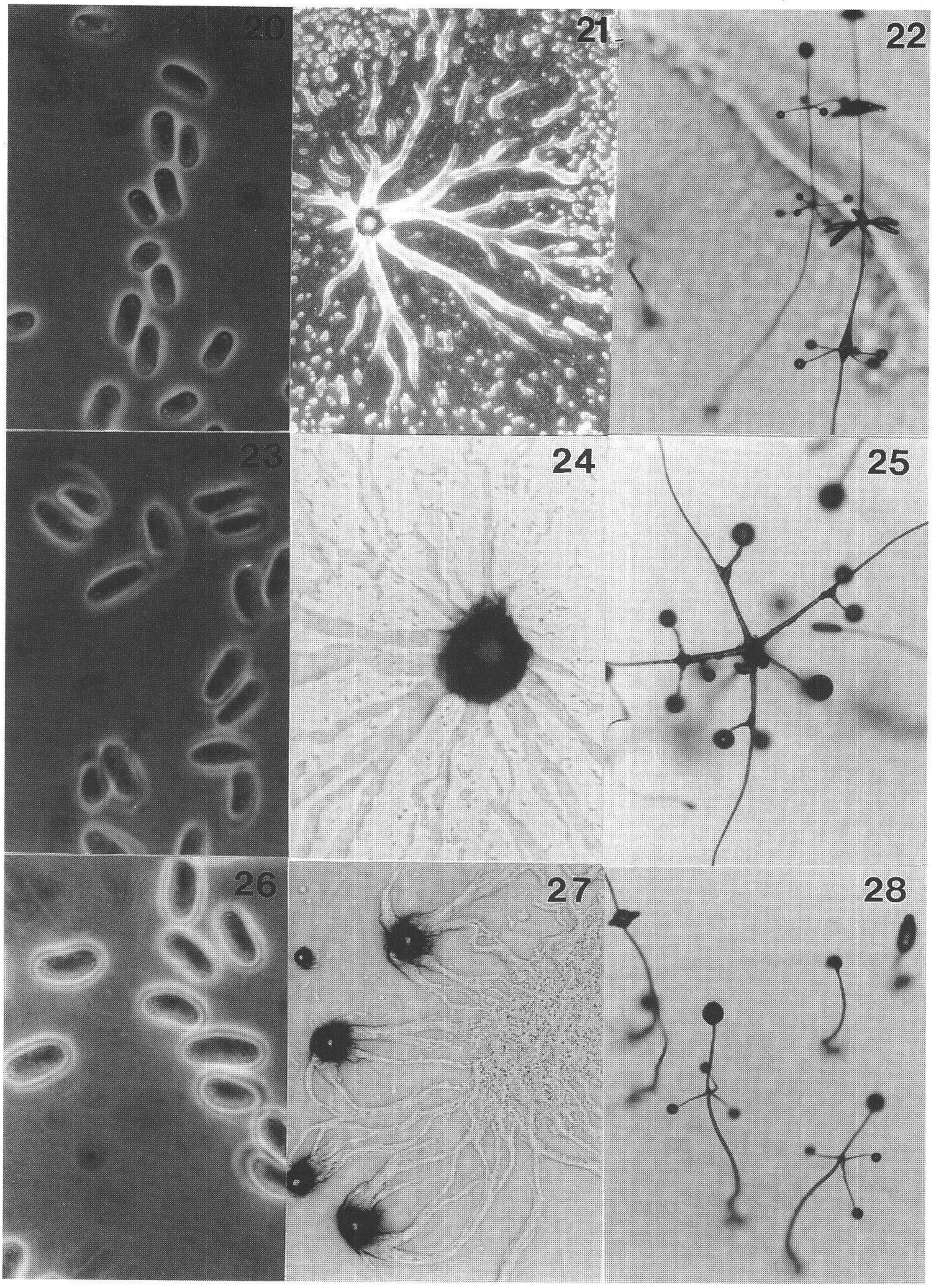
Fig. 1. Map of Germany showing the locations of the twenty-four collection sites. LH – Lüneburger Heide, TH – Torfhaus/Harz, KV – Kottenforstville in Brühl, EW – Elmpter Wald/Netherlands border, DR – Drachenfels/Rhein, RS – Rothaargebirge/Siegen, KM – Kobern/Mosel, ME – Mäuseberg/Eifel, RG – Rheingau, 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.



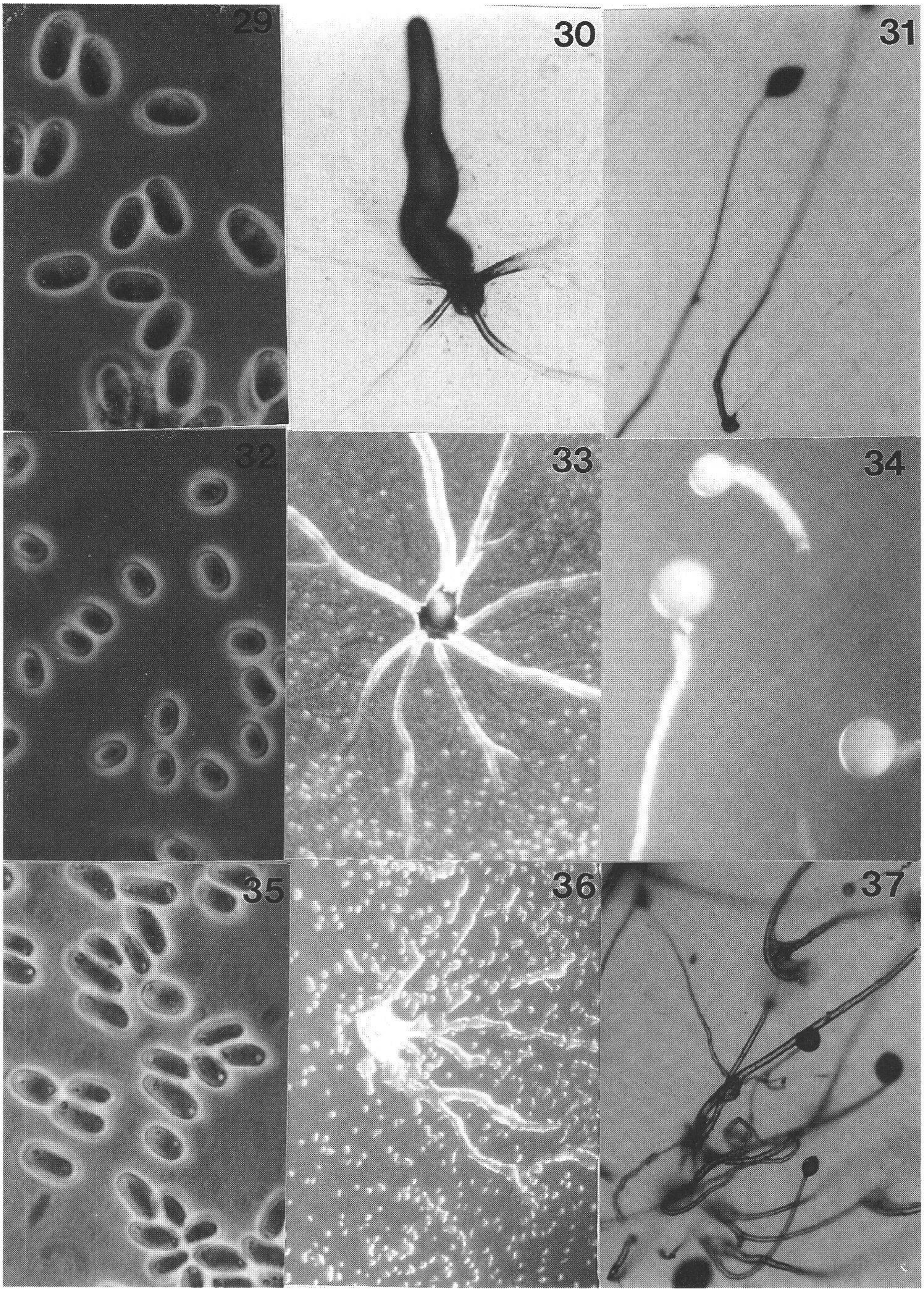
Figs. 2–10. Photomicrographs of *Dictyostelium mucoroides* S-type, *D. mucoroides*, L-type, and *D. implicatum*. 2–4. *D. mucoroides*, S-type. 2. Spores, ×750. 3. Aggregation, ×40. 4. Sorocarps, ×40. 5–7. *D. mucoroides*, L-type. 5. Spores, ×750. 6. Aggregation, ×40. 7. Sorogens, ×40. 8–10. *D. implicatum*.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



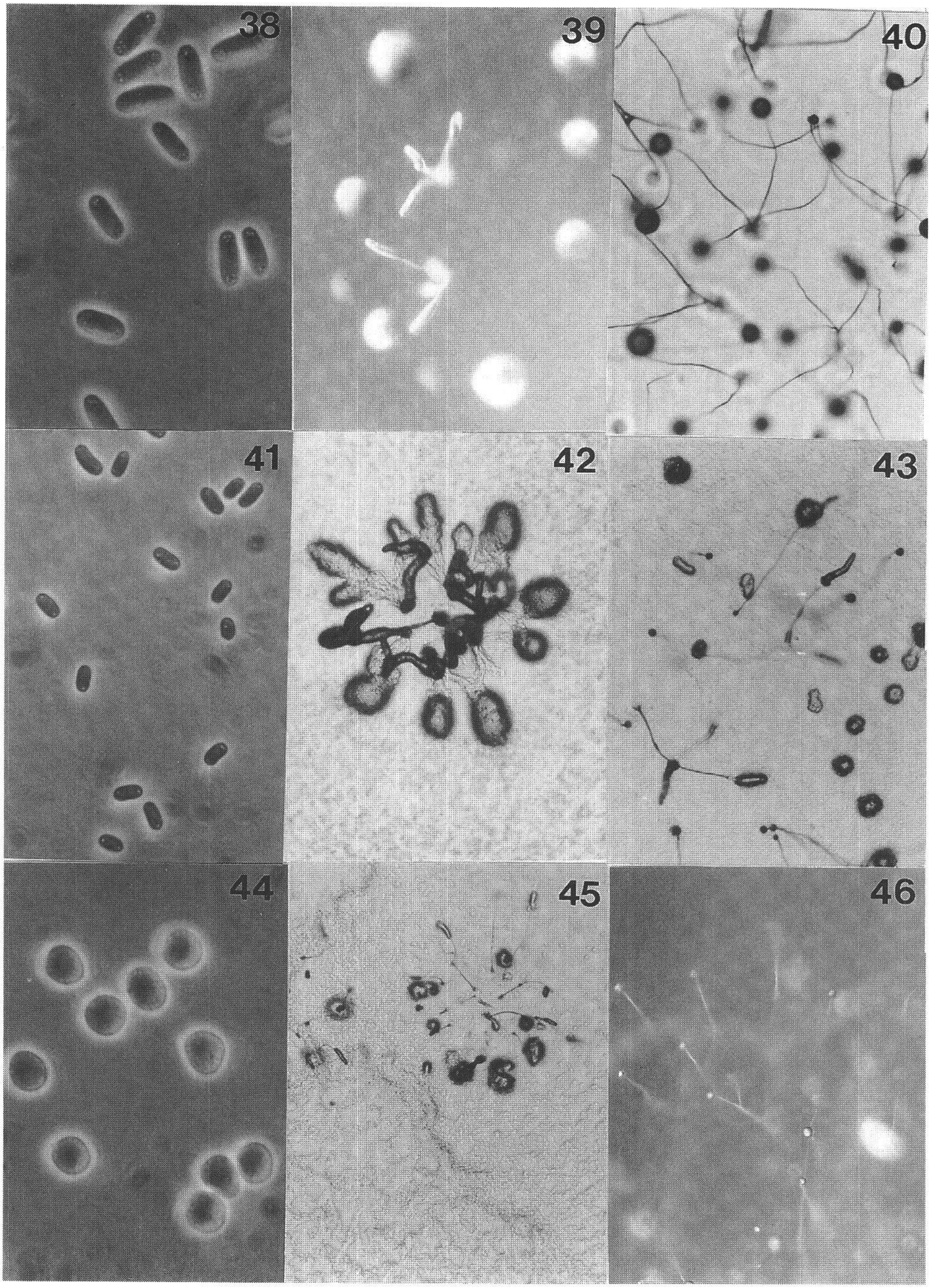
Figs. 11–19. Photomicrographs of *Dictyostelium aureo-stipes* var. *aureo-stipes*, *D. aureo-stipes* var. *helvetium* and *Polysphondylium violaceum*. 11–13. *D. aureo-stipes* var. *aureo-stipes*. 11. Spores, ×750. 12. Aggregation, ×40. 13. Sorocarps, ×40. 14–16. *D. aureo-stipes* var. *helvetium*. 14.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



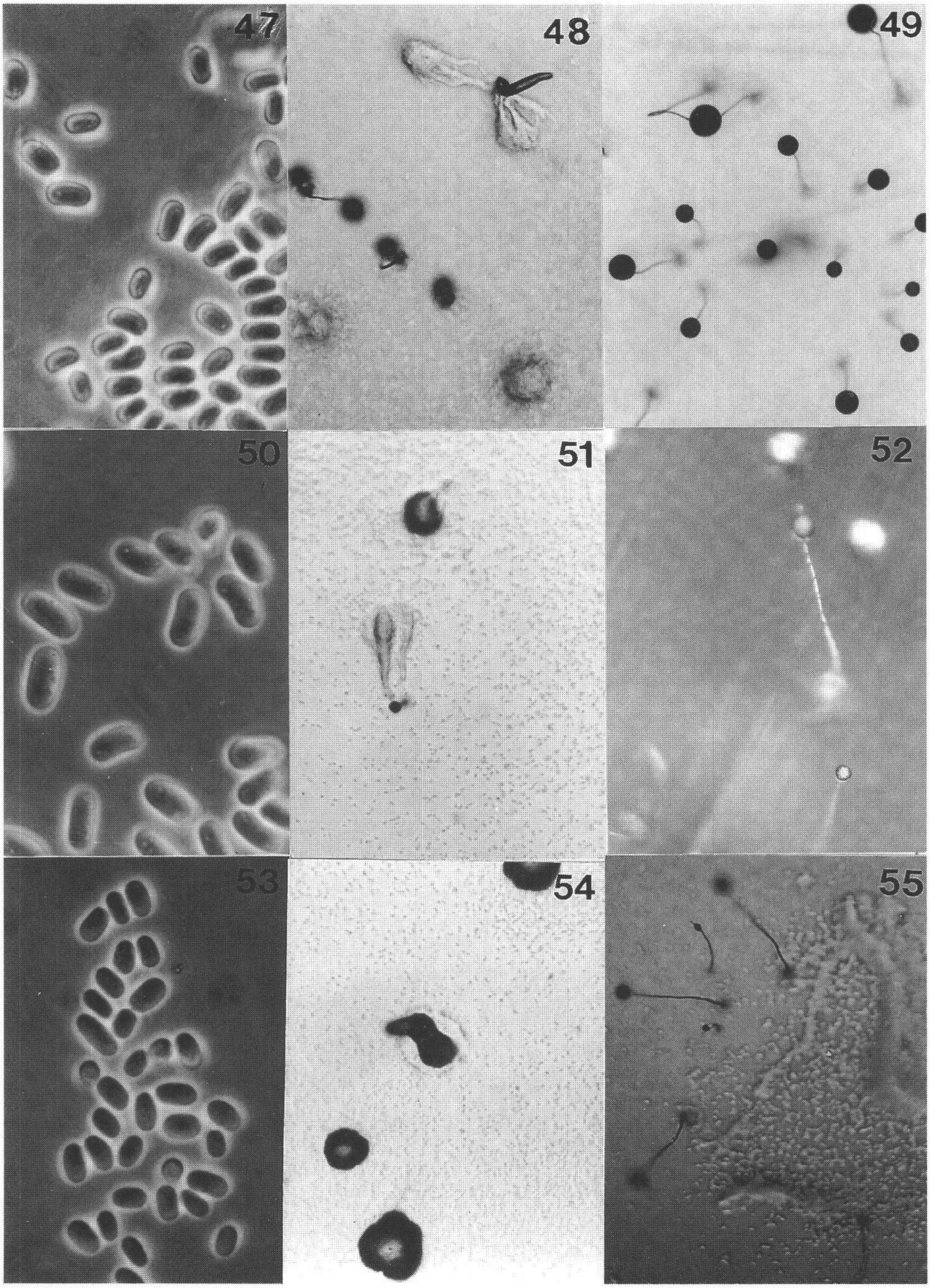
Figs. 20–28. Photomicrographs of *Polysphondylium pallidum*, *P. filamentosum* and *P. candidum*. 20–22. *P. pallidum*. 20. Spores, ×750. 21. Aggregation, ×40. 22. Sorocarps, ×40. 23–25. *P. filamentosum*. 23. Spores, ×750. 24. Aggregation, ×40. 25. Sorocarps, ×40. 26–28. *P. candidum*. 26. Spores, ×750.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



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



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



Figs. 47–55. Photomicrographs of *Dictyostelium minutum*, *D. germanicum*, and *D. capitatum*. 47–49. *D. minutum*. 47. Spores, ×750. 48. Aggregation, ×40. 49. Sorocarps, ×40. 50–52. *D. germanicum*. 50. Spores, ×750. 51. Aggregation, ×40. 52. Sorocarps, ×40. 53–55. *D. capitatum*. 53. Spores, ×750. 54. Aggregation, ×40. 55. Sorocarps, ×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. *Dictyostelium 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 capitate 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 leptosomum* (Figs. 44–46)
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)
3. Sorocarps unpigmented 4
4. Whorls numerous . . . . *Polysphondylium pallidum* (Figs. 20–22)
4. Whorls few 5
5. Lateral branch tips elongated, tips of main axis also elongated . . . . *Polysphondylium filamentosum* (Figs. 23–25)
5. Lateral branches not elongated, main axis tips may be elongated . . . . *Polysphondylium candidum* (Figs. 26–28)
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. *helvetium* (Figs. 14–16)
7. Sorophores prone or flexuous, branched; spores with conspicuous polar granules;
   deciduous forest . . . . *Dictyostelium aureo-stipes* var. *aureo-stipes* (Figs. 11–13)
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. 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. Sorocarps erect, 5–10 mm high, or commonly greatly elongated by migration, up to several cm
    in length . . . . *Dictyostelium giganteum* (not illustrated)
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)
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. 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 × 6–8 µm with numerous conspicuous unconsolidated polar granules . . . . *Dictyostelium germanicum* (Figs. 50–52)
16. Spores smaller mostly 2–3 × 4–6 µm 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 bistate 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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