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Biology and global distribution of myxobacteria in soils

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Abstract

This review presents an overview of the present status of the biology of the myxobacteria, including the molecular biology of the systems that control and regulate myxobacterial gliding movement and morphogenesis. The present status of myxobacterial taxonomy and phylogeny is described. The evolutionary biology of the myxobacteria is emphasized with respect to their social behavior and the molecular basis of their signal chains. Most important within the metabolic physiology are the biologically active secondary metabolites of myxobacteria and their molecular mechanisms of action. The global distribution of myxobacteria in soils is described on the basis of data given in the literature as well as of comprehensive analyses of 1398 soil samples from 64 countries of all continents. The results are analyzed with respect to the spectrum and number of species depending on ecological and habitat-specific factors. The myxobacterial floras of different climate zones are compared. Included are myxobacterial species adapted to extreme biotopes. The efficiency of different methods used presently for isolation of myxobacteria is compared. © 2000 Federation of European Microbiological Societies. Published by Elsevier Science B.V. All rights reserved.

Keywords: Myxobacteria; Soil microflora; Global distribution; Species spectrum; Extremophile; Isolation method; Secondary metabolite

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1. Introduction

Only since about 20 years the myxobacteria have become one of the most fascinating objects of microbiological research. At present they are treated as a taxonomic order, the Myxococcales.

Myxobacteria are Gram-negative unicellular rod shaped bacteria that occur everywhere in soils. They are characterized by an unusual way of life, as they move by gliding or creeping on surfaces. Using exoenzymes they lyse different biological macromolecules as well as whole microorganisms such as bacteria and yeasts. Upon exhaust of nutrients they form myxospores and fruiting bodies. Within the prokaryotes myxobacteria show a unique cooperative social behavior, based on a communication system of cell-to-cell interaction. Myxobacteria synthesize a large number of biologically active secondary metabolites.

2. Biology of myxobacteria

2.1. Discovery and research

Myxobacteria form fruiting bodies, that display bright colors and therefore are often identified with the naked eye. The first myxobacterium, *Polyangium vitellinum*, was discovered and named by the German botanist H.F. Link in 1809 [1] who considered the fruiting body a gastromycete. In 1857, the British biologist M.J. Berkeley [2] discovered and named two more genera and species, *Stigmatella aurantiaca* and *Chondromyces crocatus* which he classified as hyphomycetes. The American botanist Roland Thaxter, in 1892, was the first to identify these species as myxo*bacteria* and describe their life cycles [3].

Several studies on myxobacteria followed since the beginning of the 20th century [4–11]. Most important were those of Baur [4], Jahn [7,8], Krzemieniewska and Krzemieniewski [9], Imshenetzki and Solntzeva [10]. After a period of general studies on cultivation, i.e. enrichment and pure cultures, new focusses of research on myxobacteria were introduced such as developmental biology by Dworkin and Gibson [12] and molecular genetics by Kaiser and coworkers [13,14]. *Myxococcus xanthus* became the central and meanwhile best studied object of myxobacterial research. A further new field was opened up by the discovery of biologically active secondary metabolites by Reichenbach and coworkers [15–17].

At present the main emphasis in myxobacterial research is on molecular biology [18], developmental biology [19–21], taxonomy [22,23] and especially biotechnology [24,25].

In this article the following abbreviations for myxobacterial genera are used: *An. Angiococcus*, *Ar. Archangium*, *Cb. Cystobacter*, *Cc. Corallococcus*, *Cm. Chondromyces*, *H. Haploangium*, *M. Melittangium*, *Mx. Myxococcus*, *Na. Nannocystis*, *Pl. Polyangium*, *Sg. Stigmatella*, *So. Sorangium* [79].

2.2. Distribution and ecology

The genuine habitat of myxobacteria is the soil, as long as the pH is slightly acid to slightly alkaline, i.e. between 5 and 8. Frequently myxobacteria are found on the dung of herbivorous animals, on decaying plant material and on the bark of trees [26]; occasionally they have also been found on the surface of plant leaves [27].

In soils – according to their frequency of occurrence – the following species are most typical: *Na. exedens*, *Cc. coralloides*, *So. cellulosum*, different *Polyangium* species, *Mx. fulvus*, different *Cystobacter* species, and *Mx. stipitatus* [35] (cf. Plates I and II). Although myxobacteria generally prefer soils with an almost neutral pH they have also been reported from acid (pH 3.7) and alkaline (pH 8.0–9.2) soils [28–31]. There is still little information about the population density of myxobacteria in soils. In 1.0 g of different soils between 2000 and 76 000 [32], 80 000 [33] and even 450 000 myxobacterial cells [34] have been counted. With such variating results one has to take into consideration that habitat-depending factors as well as the non-myxobacterial microfloras are highly variable, and that a singly occurring fruiting body of a myxobacterial species in soil may house 10^3 to 10^6 myxospores.

The typical species living on the bark of trees and on rotting wood are *Sg. aurantiaca*, *Cm. apiculatus*, *Cc. coralloides*, *Mx. fulvus*, *Cm. pediculatus*, and different *Haploangium* species [35]. Rotting wood is preferred by *Chondromyces* and *Stigmatella* species [8,36–40].

Dung pellets of herbivores are preferentially colonized by *Mx. fulvus*, *Cc. coralloides*, *Cb. fuscus*, *Cb. ferrugineus*, *Ar. serpens*, *Sg. erecta*, *Mx. virescens*, *Mx. xanthus*, and *Cb. velatus* [35].

→

Plate I. Myxobacterial fruiting bodies. 1: *Mx. fulvus*, on soil crumbs on coli-spot agar, China (CH 11), SM (bar = 600 μm). 2: *Mx. stipitatus*, on wood particles of a soil sample, Haiti (HA 8), SM (bar = 500 μm). 3: *Mx. virescens*, on rabbit dung as bait, Illinois (IL 16), SM (bar = 500 μm). 4: *Mx. xanthus*, on peat particles, Belgium (KTM 3), SM (bar = 600 μm). 5: *Cc. coralloides*, on coli-spot agar, Malawi (MI 2) LM (bar = 250 μm). 6: *Cc. exiguus*, on coli-spot agar, France (F 19), LM (bar = 250 μm). 7: *An. disciformis*, on vy/2 agar, Zaire (ZA 12), LM (bar = 250 μm). 8: *Ar. gephyra*, on rabbit dung as bait, Cyprus (CY 7), SM (bar = 500 μm). 9: *Ar. serpens*, on coli-spot agar, Crete (KR 16) LM (bar = 500 μm). 10: *Cb. fuscus*, on coli-spot agar, China (CH 20), SM (bar = 140 μm). 11: *Cb. ferrugineus*, on vy/2 agar, Israel (I 11), SM (bar = 175 μm). 12: *Cb. minus*, on vy/2 agar, Philippines (PH 5), LM (bar = 500 μm). 13: *Cb. violaceus*, on coli-spot agar, Senegal (SE 15), SM (bar = 350 μm). 14: *Cystobacter* spec., on coli-spot agar, South Africa (SAF 1), LM (bar = 250 μm). 15: *Pl. aureum*, on rabbit dung as bait, Lesotho (LE 24), SM (bar = 500 μm). 16: *Pl. compositum*, on coli-spot agar, Brazil (B 4), LM (bar = 240 μm). Abbreviations: LM, light microscope (transmitted and incident light); SM, stereo microscope (transmitted and incident light).

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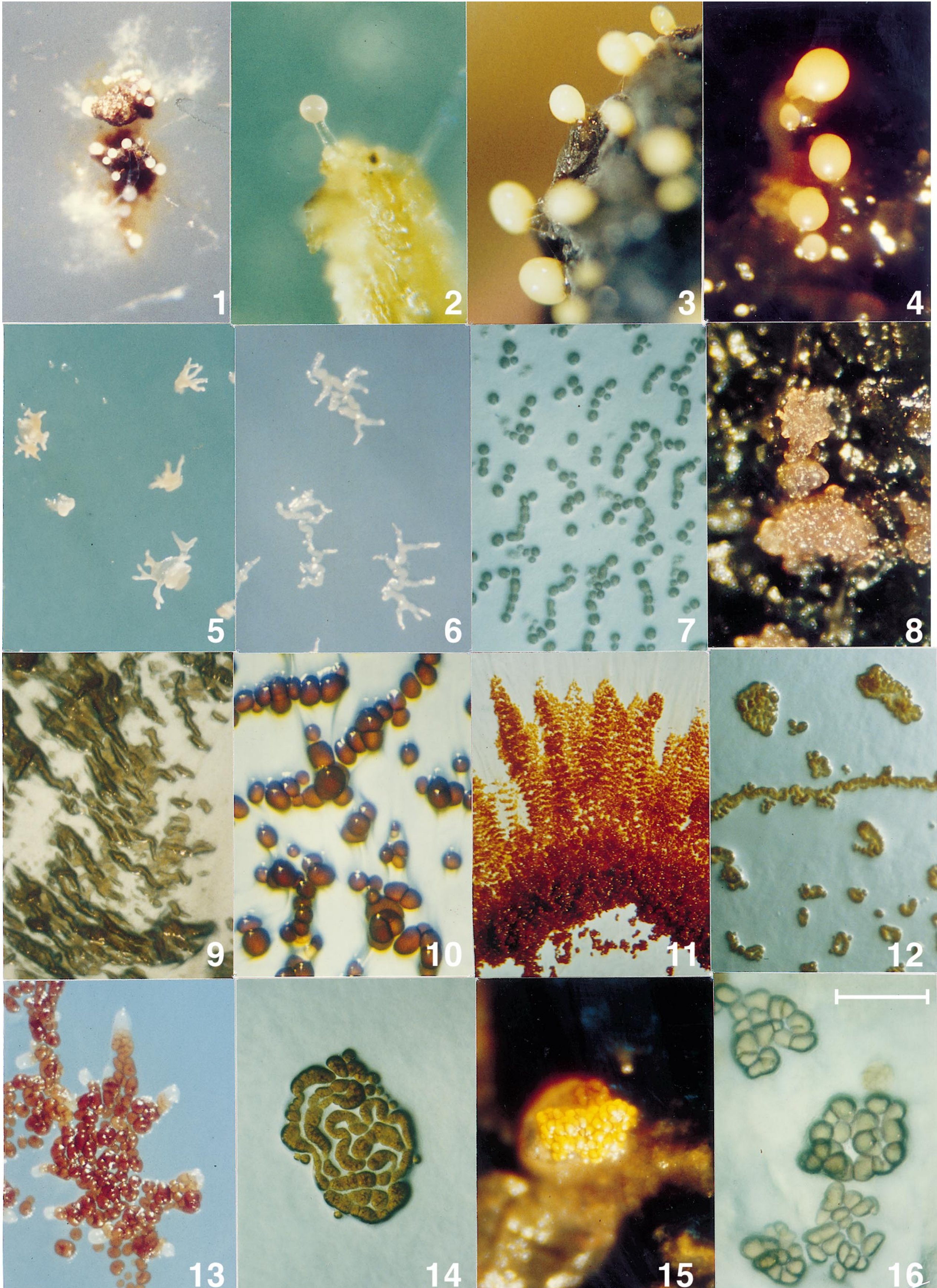

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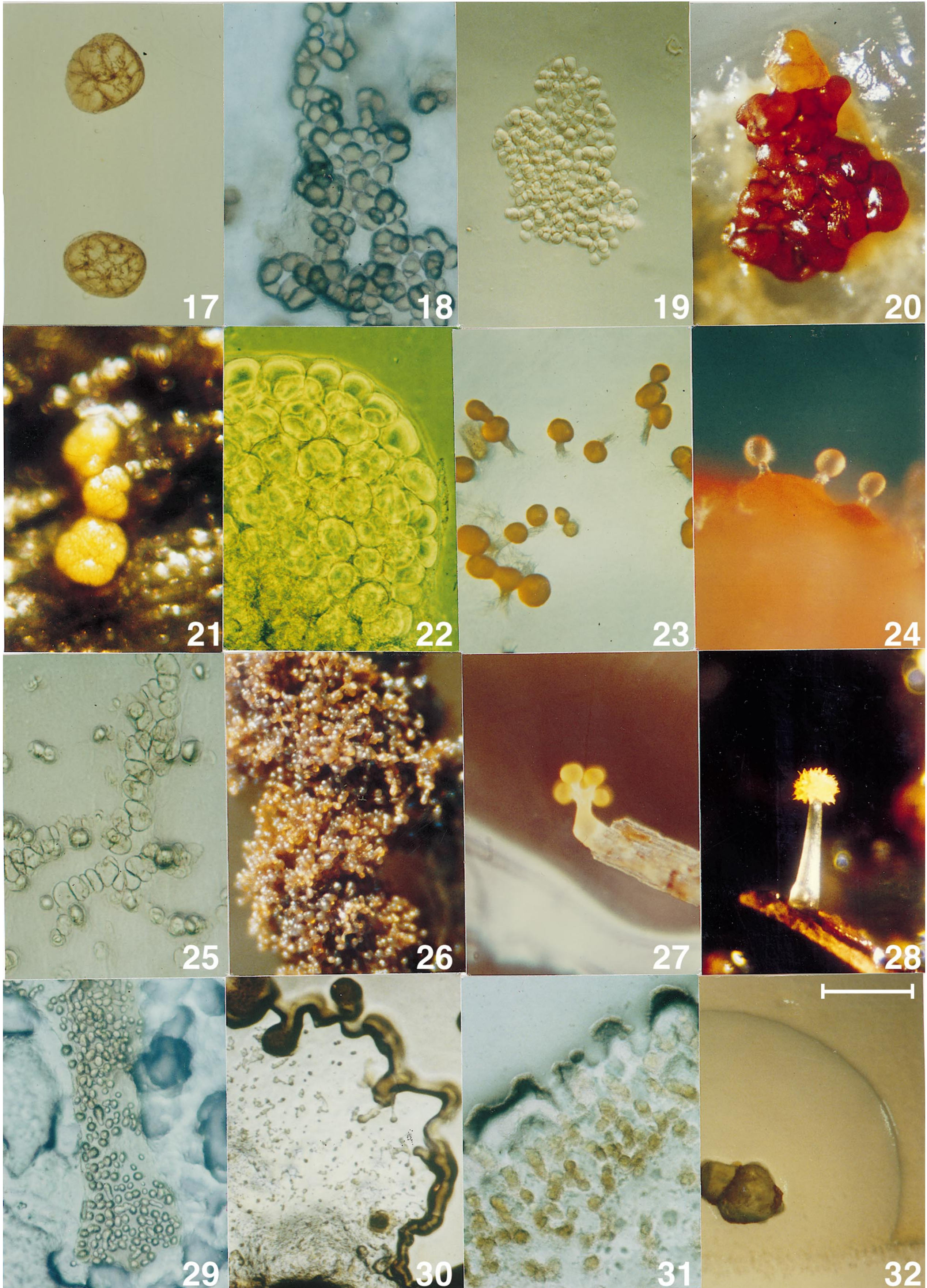

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Plate II. Myxobacterial fruiting bodies. 17: *Pl. fumosum*, on coli-spot agar, Chile (CHI 2), LM (bar = 220 μm). 18: *Pl. sorediatum*, on coli-spot agar, Sri Lanka (CE 21), LM (bar = 150 μm). 19: *Pl. spumosum*, on vy/2 agar, Iran (PE 12), LM (bar = 200 μm). 20: *Pl. thaxteri*, on rabbit dung as bait, Utah (FC 15), SM (bar = 250 μm). 21: *Polyangium* spec., on peat soil, Belgium (WV 8) SM (bar = 100 μm). 22: *Polyangium* spec., sporangioles, Belgium (WV 8 19), LM (bar = 45 μm). 23: *M. boletus*, on coli-spot agar, Tansania (TA 13), LM (bar = 330 μm). 24: *M. lichenicola*, on rabbit feces as bait, Germany (S 80), LM (bar = 120 μm). 25: *So. cellulosum*, on STAN-6 agar, China (CH 56) LM (bar = 100 μm). 26: *Sg. erecta*, on coli-spot agar, Dominican Republic (DR 6), LM (bar = 500 μm). 27: *Sg. aurantiaca*, on wood particles, Germany (S 16), LM (bar = 600 μm). 28: *Cm. apiculatus*, on rabbit dung as bait, Mexico (M 17), LM (bar = 250 μm). 29: *Na. exedens*, on coli-spot agar, Florida (FL 20), LM (bar = 100 μm). 30: Psychrophilic myxobacteria, P type, swarm on coli-spot agar, Antarctica (AA 19/10), 4 months, 4°C, LM (bar = 140 μm). 31: Psychrophilic myxobacteria, N type, swarm and sporangioles on coli-spot agar, Antarctica (AA 19/2), 4 months, 4°C, LM (bar = 120 μm). 32: Psychrophilic myxobacteria, R type, on coli-spot agar, Antarctica (AA 19/4), 6 months, 4°C, SM (bar = 300 μm). Abbreviations: LM, light microscope (transmitted and incident light); SM, stereo microscope (transmitted and incident light).
←

Myxobacteria are generally considered as mesophilic soil microbes with a temperature optimum of 30°C. In antarctic soil samples, however, psychrophilic species of the genera *Polyangium* and *Nannocystis* were found that only grow in the temperature range of 4–9°C [41].

Myxobacteria have also proven to occur in aquatic habitats [23,42–44], although so far never in marine environments [45]. Further aspects on myxobacterial distribution ecology may be found in references [23,27,45–47].

2.3. Cells and structures

The cells of myxobacteria are average sized rods, depending on the species they are 0.6–0.9 μm wide and 3–8 μm long. Vegetative cells occur in two different types:

Cell type I: slender, usually tipped flexible rods up to 1 μm in diameter and up to 20 μm in length (suborder: Cystobacterinae).

Cell type II: cylindrical rigid rods with rounded ends up to 1 μm wide and up to 10 μm long (suborder Sorangineae).

The shape of vegetative cells as well as that of myxospores is used for determination (cf. Fig. 3), thus usually allowing a first systematic identification. Table 1 gives a taxonomic overview of the order Myxococcales.

The cells are enveloped in a cell wall of several layers including a thin peptidoglycan (murein) layer. The murein sacculus appears to be organized in patches [46]. The outer membrane consists of proteins, phospholipids and lipopolysaccharides [48]. The lipopolysaccharide constitution of many myxobacteria is similar to that of most eubacteria. Besides mannose they contain galactose, glucosamine and other sugars. Ketodeoxyoctanoic acid is always present, whereas heptoses do not occur [49].

Table 1
A taxonomic overview of the myxobacteria [79]

Order:	Myxococcales (= the myxobacteria)	
Suborder:	Cystobacterineae	
Families:	Myxococcaceae	Cystobacteraceae
Genera (number of species):	*Myxococcus* (4)	*Archangium*
	Corallococcus (3)	*Cystobacter* (5)
	Angiococcus (1)	*Melittangium* (3)
		Stigmatella (2)
Suborder:	Sorangineae	
Families:	Polyangiaceae	Nannocystaceae
Genera (number of species):	*Polyangium* (7)	*Nannocystis* (2)
	Haploangium (2)	
	Chondromyces (5)	
	Sorangium (3)	

In the cells mesosomes and mesosome-like membrane bodies have been found [50], and further different intracellular granules and inclusion bodies (polyphosphates, polysaccharides). Burchard [51] detected bundles of microtubules and fibrils in the cytoplasm. This system of contractile fibrils has hence been considered as responsible for the gliding movement of vegetative cells.

Lünsdorf and Reichenbach [52] detected a strictly ordered chain-like structure beneath the outer cell membrane. This structure – consisting of rings and elongate components – by contraction causes propagating waves that seem to act on the cell surface, thus propelling the gliding cell (cf. Section 2.5). The slime excreted during movement is visible as a slime track and has been described as a protein–polysaccharide–lipid complex [53]. It is involved in the proteolytic activities of myxobacteria by denaturing native proteins of lysed prey cells and thus supplying the proteolytic exoenzymes of myxobacteria with appropriate substrates.

On the cell surface of *Mx. xanthus* pili and fimbriae were detected that are involved in cell to cell interactions. The pili appear polarly while fimbriae are peritrichously arranged. The latter play an important role in intercellular cohesion and in social behavior [21], cf. Section 2.5.

2.4. Genome and phylogeny

The genome of myxobacteria is a typical bacterial ring chromosome, and with 9450 kbp it has about twice the size of that of *Escherichia coli* and about the size of that of the genus *Streptomyces*.

Myxobacterial DNA has a GC content between 64 and 72 mol%, in *Mx. xanthus* it is 65.5 mol%; in the suborder Sorangineae the GC content (70–72 mol%) is somewhat higher than in the Cystobacterineae (64–70 mol%). Between different DNA segments the GC content varies considerably, e.g. in *Mx. xanthus* between 36 and values over 80 mol% [55].

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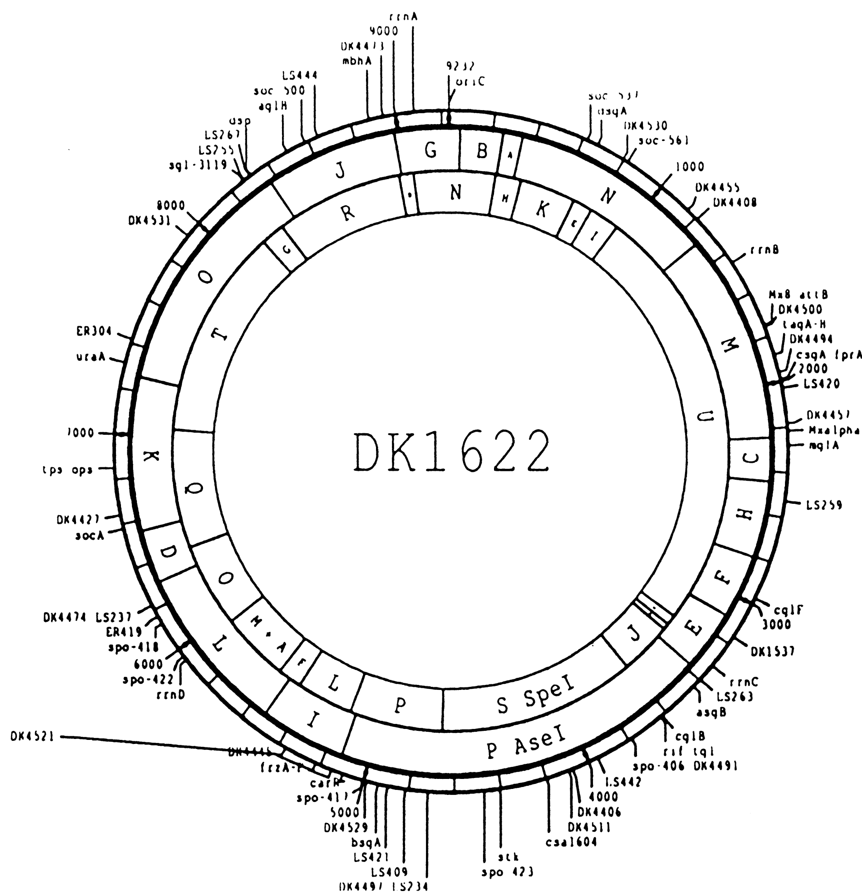

Fig. 1. Physical and genetic map of the *Mx. xanthus* (strain DK 1612) chromosome [54].

The genome structure of *Mx. xanthus* has been revealed by hybridization using 16 *Ase*I restriction fragments with a genomic library prepared in yeast artificial chromosomes and *Spe*I-digested genomic DNA [54]. Fig. 1 shows the complete gene map of the genome of *Mx. xanthus* (type) strain DK 1622.

The myxobacterial species *Mx. xanthus* and *Sg. aurantiaca* were the first prokaryotes in which a new class of retroelements, called retrons, have been found. Retrons encode reverse transcriptases similar to those occurring in retroviruses. They also code for an unusual satellite DNA produced as multicopy single-stranded DNA (msDNA) by reverse transcription.

Extrachromosomal DNA containing resistance factors transferred by conjugation was found in resistant strains of *Mx. xanthus*. By using phages of *E. coli* it was possible to transfer extraneous plasmids into myxobacteria [56]. These plasmids survived in cells of myxobacteria, appear to become integrated into the genome and are expressed.

All myxobacterial phages known so far (Mx 8, Mx alpha, etc.) are DNA phages with a GC content of 56 mol%. These phages as well as such plasmids as RP 4 are important tools for gene mapping [26,54].

Sequence analyses of 16S rRNA genes [54,57] resulted in the dendrogram shown in Fig. 2.

From their common occurrence together with sulfate- and sulfur-reducing bacteria and with bdellovibrios in the delta branch of the Proteobacteria one may speculate whether the myxobacteria represent aerobic descendants of sulfate- or sulfur-reducing bacteria. The sequence differences in the 5S and 16S rRNA molecules suggest that the delta branch may have originated 750 to 1100 million years ago [54].

2.5. Motility and swarming behavior

Myxobacteria display social behavior expressed by collective food uptake, cooperative motility and social development [21,58]. On solid surfaces but also at the water–air interface they show gliding movement. This movement is accompanied by bending of cells and by secretion of slime. The gliding speed is 10–60 μm/min. Extracellular motility organelles such as flagella are lacking [52,59]. Several models have been proposed to explain the gliding mechanism. Burchard proposed that it is based upon bundles of filaments and tubules that are arranged longitudinally as well as diagonally beneath the cell membrane [51] (see also above Section 2.3). Waves of contraction are supposed to propel the cells [60]. Another model claims that conformation changes of chain-like structures produce pro-

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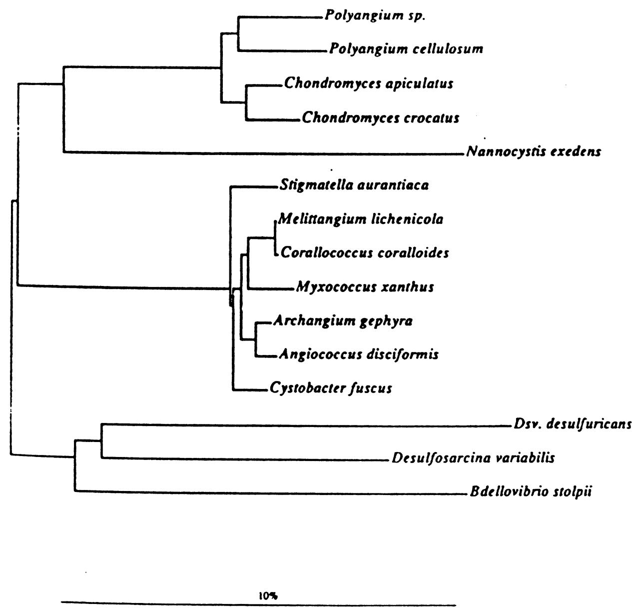

Fig. 2. Phylogenetic tree of the myxobacteria. The tree has been derived from evolutionary distances of the 16S rRNA molecules. Abbreviation: Dsv., *Desulfovibrio* [57].

gressing waves on the cell surface and subsequently the gliding motility [52]. The patchy structured nature of the peptidoglycan layer could serve as a morphological argument for cell contractions [61]. Final proof for any model has not been produced so far [21,61,62].

Organization and control of the gliding behavior is governed by three (so far as known) independent multigene systems: The A system consists of about 22 gene loci and controls the movement of single cells [63]. The S system consists of about 10 gene loci and controls the movement of groups of cells [64]. The third, so-called Frizzy system controls the direction reversal behavior of the cells [65].

The cooperative motility behavior must be based on intra- and extracellular interactions. This is shown by studies on surface structures and extracellular appendages. Disturbances in lipopolysaccharide biosynthesis lead to defects in the movement of single cells [66]. Extracellular appendages are usually found at one pole of the cell, whereas Behmlander and Dworkin [67] reported them from both poles of *Mx. xanthus*. Such pili and fimbria have been considered essential for keeping a swarm of cells together by cell–cell interaction [21]. Part of the extracellular matrix is formed by fibrils at the outer membrane. Their formation differs for single cells versus groups of jointly moving cells: High cell density with close intercellular contacts increases fibril formation as compared with a low cellular density [21,68].

A characteristical trait of myxobacterial colonies is their swarming behavior, a multicellular spreading of the myxobacteria into an unoccupied area. This spreading is called swarming, the colony is called swarm [69]. The spreading of the swarm is seen by the increase of the colony diameter and is mainly due to the motility of single cells, to a lesser extent to cell multiplication. The spreading rate is a measure for the gliding activity of the cells. The motility of myxobacteria is determined by the temperature, nutrient concentrations and the original cell density [70].

Swarming colonies of the Sorangineae on agar plates show a compact bulging rim and in the inner swarm deep tracks and grooves (cf. Plate II, 31). On the other hand, swarms of Cystobacterineae are flat and thin layered. Often they may be picked up with a needle from the agar surface like wall paper. The rim of their swarm shows toung- and finger-like peninsulae of cells. Tracks left behind by 'pioneer' cells serve as preferred gliding ways for other cells of the same species.

The structure of swarms is used as a generic property during determination of isolated myxobacteria (cf. Section 3.4.3).

Another phenomenon of cooperative motility are pulsating wave tracks that produce rippling patterns [71]. These are accumulations of oriented cells that move forward synchronously and pulsating with a maximum velocity of 2 μm/min. This behavior may be induced by the addition of peptidoglycan or its subunits [72]; about tactical behavior, signals and their transduction – also during cooperative morphogenesis – cf. Dworkin [21].

2.6. Formation of fruiting bodies and myxospores

The capability to form fruiting bodies is the most conspicuous and most interesting property of the myxobacteria. In their simplest appearance, e.g. in *Myxococcus*, the fruiting bodies are globular and of soft mucous consistency (cf. Plate I, 1–4). Other genera (*Corallococcus*, *Archangium*) form rather bizarre shapes of hardened slime (Plate I, 5, 6, 8). Most species enclose the myxospores in sporangioles that are surrounded by a defined wall.

Sporangioles may occur singly or in groups. They are either embedded in the substrate (*Angiococcus*, *Polyangium*, *Cystobacter*, *Sorangium*; Plate I, 7, 10, 16; Plate II, 17–19, 25, 29) or they sit on hardened slime stems as one (*Melittangium*, *Stigmatella*; Plate II, 23, 24, 26) or more sporangioles (*Stigmatella*, *Chondromyces*; Plate II, 27, 28). The color of fruiting bodies may be white, brown or bright yellow, orange, red or lilac. Their size varies between 10 and 100 μm.

Shape and size, color and arrangement of sporangioles and fruiting bodies are used as traits for specific determination (cf. Section 3.4.3).

The formation of fruiting bodies is induced by nutritional deficiency and is controlled by nutrient concentrations, pH, cations and temperature [21]. It is a cooperative morphogenesis by the vegetative swarming cells. The process is a sequence of the following steps: (1) A large number (10^5–10^7) of swarming cells loose their physical individuality during morphogenesis. (2) Vegetative growth of the rods ceases. (3) In certain positions of the swarm the

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cells assemble to form aggregates. (4) Molecules formed on the cell surface cause that cells stick together. (5) The consequence is an unstructured agglutination of masses of cells that autolyse to about 65–90%. (6) The formation of special structural elements (stem, base plate, sporangiole wall) starts. (7) The characteristic (specific) shape of the fruiting body is formed. (8) During the maturation phase the vegetative rod cells are transformed into myxospores by cellular morphogenesis [26,21,73] (cf. Fig. 3, (5), Fig. 4).

The complete process of fruiting body formation takes 12–14 h under optimal conditions. Little detail is known so far about the regulatory processes involved.

Sg. aurantiaca is considered as a model for photomorphogenesis in fruiting body forming myxobacteria: The structure of the fruiting bodies and the light dependent developmental cycle have been studied most intensively. Besides environmental factors extracellular signal molecules, pheromones, determine the developmental cycle. These are low molecular weight lipophilic compounds that are excreted by *Sg. aurantiaca* upon nutrient deficiency. Their formation is considerably enhanced by light. The pheromone possesses fruiting body inducing activities. Its molecular structure has been determined as 8-hydroxy-2,5,8-trimethyl-4-nonanone [74].

The formation of myxospores occurs inside the maturing sporangioles and fruiting bodies (Figs. 3 and 4). The vegetative rod cells undergo a cellular morphogenesis (Fig. 4) by becoming shorter and rounder. The whole vegetative cell turns into a myxospore. The change in shape is conspicuous: Myxospores are much shorter and thicker than vegetative cells, they appear rounded, strongly light-refringent and surrounded by a thin capsule. As survival cells myxospores differ from eubacterial endospores (e.g. in the genus *Bacillus*) by structure, physiological properties and way of formation [35].

Myxospores are dehydrated, resistant against dryness, heat, ultrasonification and ultraviolet radiation. Due to their dry resistance myxospores, harvested from agar plate cultures on sterile filter paper strips, and dried in a desiccator, will survive for 10–25 years (W. Dawid, unpublished).

Inside the cells myxospores contain granules of polyphosphates and polysaccharides, surrounded by an envelope of ribosome-like particles, and lipid inclusions. The contents in myxospores of other biomolecules shows strong differences to that in vegetative cells [62]. The DNA content (17×10^{-9} μg) is higher than in vegetative cells and amounts to that of 3–4 chromosomes [77].

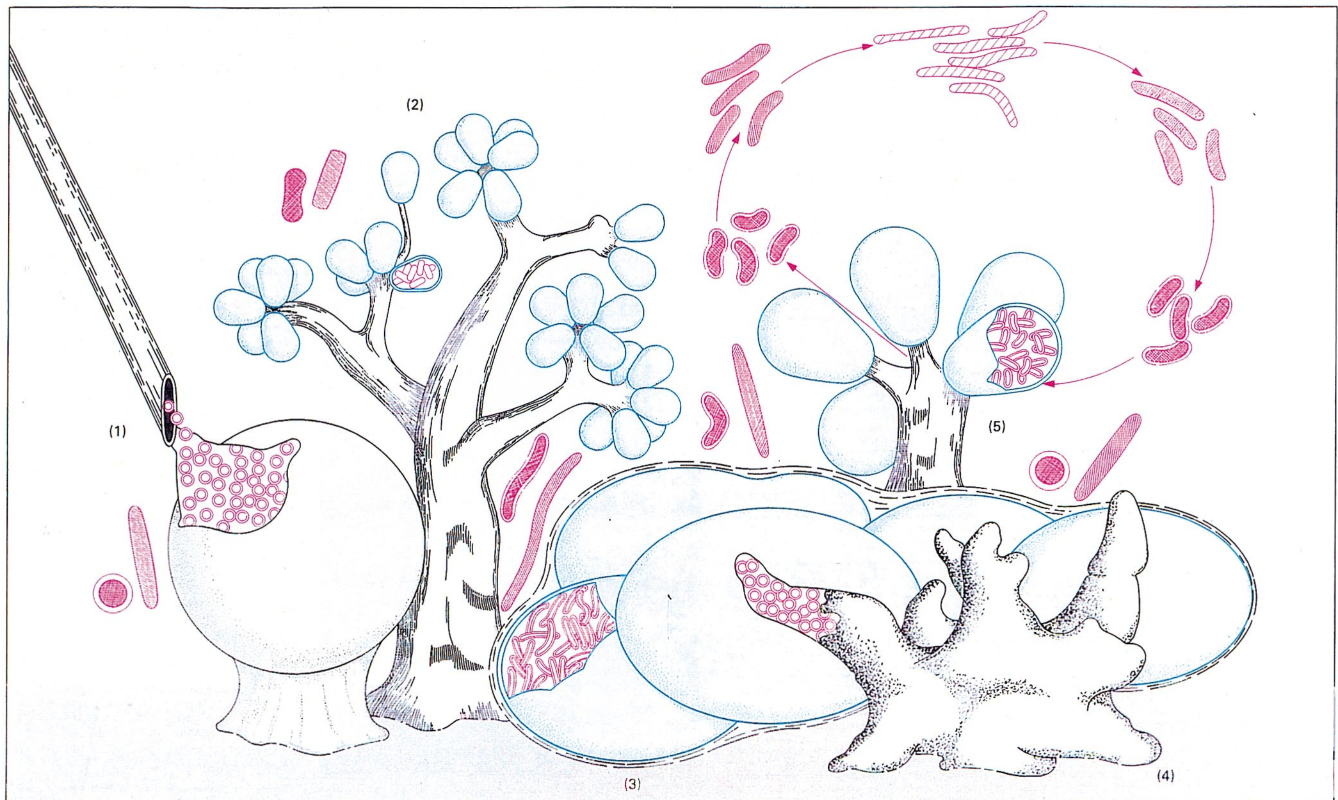

Fig. 3. Fruiting bodies of myxobacteria, partly broken open to show the myxospores inside (red). Sporangioles with tough shells are given in blue, slimy material in black. On the immediate left of each fruiting body the vegetative cell is shown, further left a myxospore typical of that genus. (1) *Myxococcus*: soft and slimy, so that material may be removed easily with the needle of a syringe. (2) *Cm. crocatus*. (3) *Cystobacter*. (4) *Corallococcus*: hard, cartilaginous slime. (5) *Sg. aurantiaca*: shown above the fruiting body in the cycle of cellular morphogenesis from myxospore to the vegetative cell and back to the myxospore. The figures are not drawn to scale [22].

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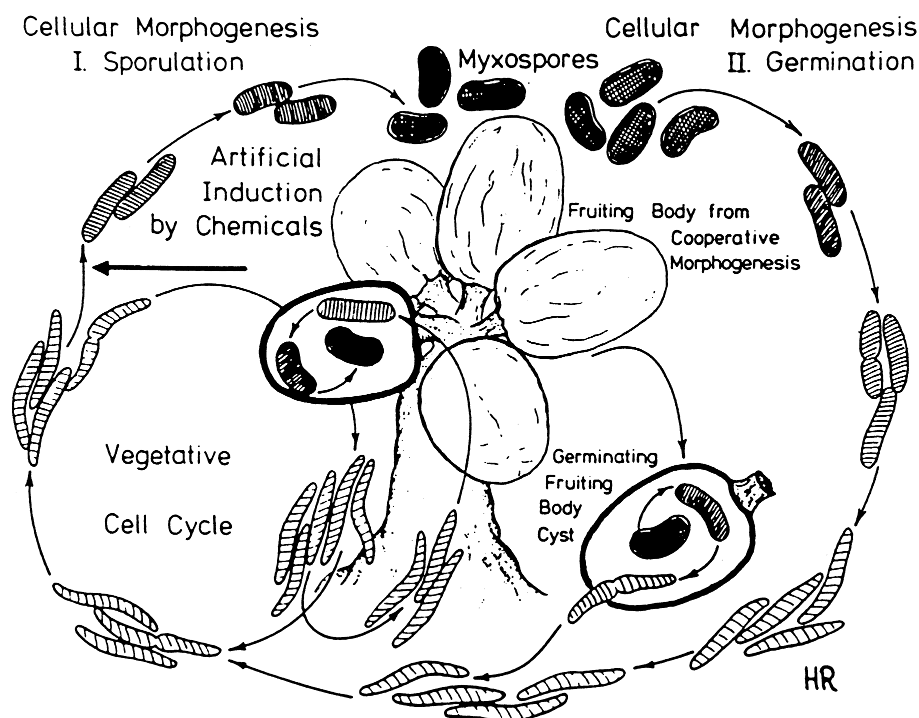

Fig. 4. Cellular morphogenesis of myxobacteria, shown by the example of *Sg. aurantiaca* [76].

For the research into the developmental biology of myxobacteria model systems for *Mx. xanthus* and *Sg. aurantiaca* have been designed [54,75].

Very little is known so far about the processes involved in germination of myxospores. Suspendes in phosphate buffer myxospores may be brought to germinate, not so fruiting bodies [73].

The purpose of myxospores is the survival of myxobacteria during periods of unfavorable living conditions such as cold and heat periods, dryness, acid pH or anoxic conditions. The purpose of the fruiting bodies is to start a new life cycle with a large population, to hydrolyze extracellular biopolymers together in a swarm using common exoenzymes, and thus utilize such nutritional sources with maximal efficiency.

2.7. Physiology and biologically active secondary metabolites

Myxobacteria are strictly aerobic organotrophic and mesophilic organisms. They propagate at 9–38°C. Their generation time lies between 4 and 12 h [4]. All myxobacteria are characterized by their ability to degrade biological macromolecules. With respect to cellulose utilization they form two groups depending on their ability to utilize inorganic nitrogen compounds. Group I (cellulose degraders, suborder Sorangineae) is capable of utilizing inorganic nitrogen compounds while growing on cellulose and glucose. The formation of cellulase is suppressed by higher sugar contents [26,77]. Group II represents the majority of the myxobacterial species, which are unable to make use of cellulose. With respect to nitrogen they depend upon amino acid containing growth substrates (peptones), that are supplied by enzymatic degradation of proteins as oligopeptides or single amino acids. Under natural conditions in the environment these myxobacteria feed on other organisms such as eubacteria or yeasts by bacteriolysis or cellular lysis: excreted exoenzymes (proteases, nucleases, lipases, glucanases) destroy intact living cells, further exoenzymes hydrolyze starch, xylan and chitin. The nutrient lysate formed this way is the nutritional basis of these myxobacteria, that therefore have been called micropredators [26,32,47]. The bacteriolytic capability of myxobacteria is made use of during enrichment and isolation from soil and from dung pellets of plant-eating animals (cf. Sections 3.3 and 3.8). As aerobic microbes myxobacteria possess respiratory enzymes (Cytochromes), NADH oxidase and a complete tricarboxylic acid cycle. For further information on their intermediary metabolism, cf. [78,26].

In spite of their cellulolytic and bacteriolytic activities myxobacteria are susceptible to antibiotics in being sensitive to erythromycin, neomycin, kanamycin, streptomycin, and tetracycline [34,26]. Rather unusual for Gram-negative bacteria, almost all myxobacteria are sensitive against actinomycin. After Dworkin [80] this is due to the strongly lipophilic cell surface.

About 80% of all biologically active secondary metabolites are synthesized by prokaryotes (e.g. *Streptomyces*, *Bacillus*, *Pseudomonas* species), about 20% by eukaryotes (predominantly fungi). At present some 10 000 bioactive compounds of microbial origin are known. The myxobac-

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teria produce a large number of such bioactive molecules with antifungal, antibiotic, and antitumor activities. More than 80 basic structures with nearly 350 structural variants have been identified so far, of which some may have chances for medical application (for details cf. [79]). Of 2150 bacteriolytical myxobacteria strains studied, 55% turned out to be producers of bioactive substances, of 720 cellulose decomposing isolates even 95% [81].

The biosynthetic potential of the myxobacteria is rather promising: 50–100% of all myxobacteria produce compounds with biological activities, belonging to different molecular classes such as polyketides from acetate and propionate, linear and cyclic peptides, hetrocyclic compounds, etc. [81].

Twenty years ago the first chemical structure of a myxobacterial antibiotic – ambrucitin (Fig. 5) – became known [82], that of myxothiazol formed by *Mx. fulvus* followed [83]. More than 20 structural variants of myxovirescin formed by *Mx. virescens* and more than 50 structural variants of soraphen formed by *So. cellulosum* were identified [84].

Most bioactive substances originate in the metabolism of acetate or amino acids. The synthetic ability is strain-specific, not species-specific. This is of practical importance: As so far only about 40 species of myxobacteria have been found, but a large number of strains has been isolated, this means that the same compounds occur in strains of different species, genera and even families of myxobacteria.

In some cases 30 structural variants of myxothiazol and soraphen were isolated from a single strain. A strain of *Sg. aurantiaca* produced three substances of entirely different structures, stigmatellin, aurachin and myxalamide [81,26] (cf. Fig. 5).

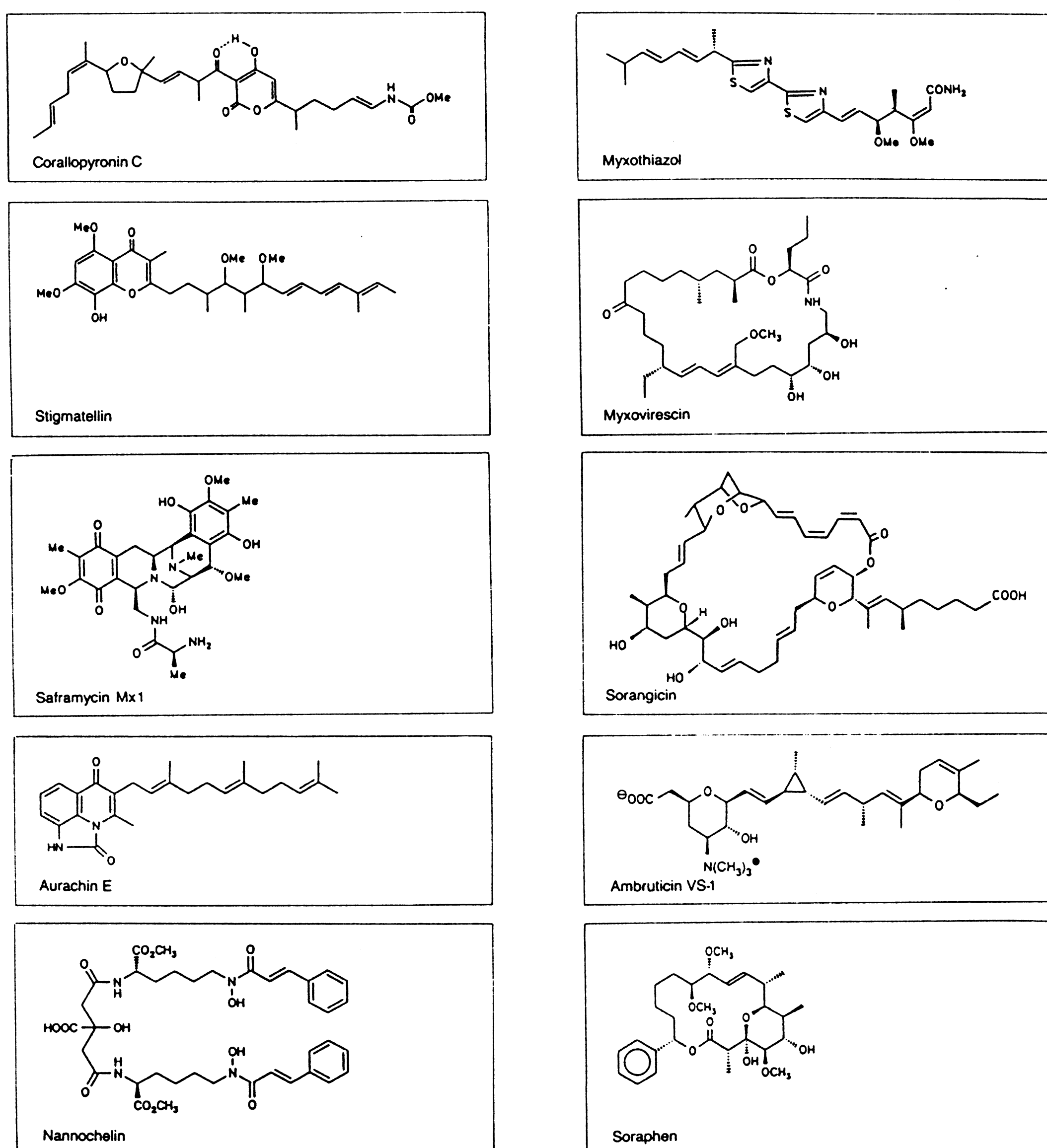

Fig. 5. Chemical structures of some bioactive secondary metabolites of myxobacteria [81].

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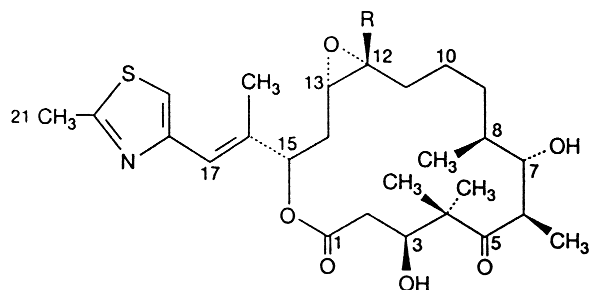

Fig. 6. Chemical structure of epothilon [17].

A few examples for activities of bioactive substances from myxobacteria are the following:

1. Three chemically different new substances and a structural variant have been isolated that block RNA polymerases: Myxosporin, isolated in 1983 from a strain of *Mx. fulvus* and from *Cc. coralloides*, corallopyronin (1985) rather frequently formed by strains of *Cc. coralloides*. Both act upon Gram-positive bacteria and don't seem to penetrate into Gram-negative cells. Sorangicin, produced by *So. cellulosum* strains (1985), acts well against Gram-positive, in higher doses also upon Gram-negative bacteria.
2. Of three myxobacterial antibiotics that block protein synthesis in eukaryotes, myxovalargin is the best studied one. It was found in a strain of *Mx. fulvus*, but also in strains of *Cc. coralloides* and in *Ar. gephyra*. It inactivates yeasts and other fungi and has antibiotic activity against Gram-positive and Gram-negative bacteria as well.
3. Eleven different electron transport inhibitors were isolated from myxobacteria so far. Myxothiazol (1980) from a strain of *Mx. fulvus* blocks the cytochrome complex in the respiration chain, whereas the NADH ubiquinone oxidoreductase is blocked by myxalamide (1983) from *Mx. xanthus* and by aurachine (1987) from *Sg. aurantiaca*. These substances have antifungal activities. So does soraphene, in 1993 isolated from *So. cellulosum*: It blocks the acetyl–CoA carboxylase, acts upon phytopathogenic fungi, not, however, on chloroplast enzymes. Summarizing overviews are provided in [85,79].
4. In 1987 a promising substance was isolated from *So. cellulosum*: epothilon [7] (Fig. 6). It acts upon the cytoskeleton of eukaryotic cells, blocks cell division and leads to cell death (apoptosis). Its action spectrum is narrow: bacteria are not affected and rarely are fungi. Epothilon acts upon cancer cells. It stops growth of numerous human cancer cell lines, such as breast, intestinal and ovarian cancers. There is a good chance that epothilon will become important for cancer treatment in clinical applications [17].

An unusual myxobacterial substance is geosmin, better known as a product of streptomycetes, responsible for the typical odor of soil. It is produced by *Nannocystis exedens*. Finally it has to be mentioned that also the pigments of myxobacteria (orange, red, purple, and brown) that are especially accumulated in fruiting bodies, are secondary metabolites. They are fatty acid esters of carotenoids.

3. Global distribution of myxobacteria in soils

3.1. Studies published so far on soil myxobacteria in different regions

Up to now more than hundred publications have appeared that deal with the occurrence of myxobacteria in soils. The following summary of that work contains non-standardized data about soil samples of varying origins, low sample numbers, insufficient information about biotopes and unexact mapping [4–6,85–91]. Although the comparability of these data is limited – in addition due to varying sample numbers, isolation techniques and incubation times – the results give information and hints about occurrence and distribution of myxobacteria. Table 2 gives an overview on the myxobacteria reported.

3.1.1. Tropical rain forests

In soils of rain forests in India, Singh and Singh [39] could not detect regularities in the occurrence of myxobacteria; they found *Ar. gephyra* and species of *Stigmatella*. In Queensland, Australia, McNeil and Skerman [92] found – besides the three most common *Myxococcus* species – *Sg. erecta*, *Cm. apiculatus* and *Cm. crocatus*. In the Brazilian rain forest, Drozdowicz [93] isolated *Mx. virescens*, *Mx. fulvus*, *Ar. gephyra* and *So. cellulosum*. Dawid [30] reported the occurrence of 10 myxobacteria species in Brazilian soils: *Mx. fulvus*, *Mx. virescens*, *Cc. coralloides*, *Ar. gephyra*, *Pl. sorediatum*, *Cb. fuscus*, *Sg. aurantiaca*, *Sg. erecta*, *M. lichenicola*, and *Mx. stipitatus*. In rain forest soils of Columbia and Peru, Rückert [96] found *M. boletus*, *Cm. apiculatus*, *Cm. crocatus*, and *Cm. pediculatus*.

Table 2
Overview of myxobacteria found in soils

Myxococcus	*fulvus*, *stipitatus*, *virescens*, *xanthus*
Corallococcus	*coralloides*, *exiguus*
Angiococcus	*disciformis*
Archangium	*gephyra*, *serpens*
Cystobacter	*ferrugineus*, *fuscus*, *minus*, *velatus*, *violaceus*
Melittangium	*alboraceum*, *boletus*, *lichenicola*
Stigmatella	*aurantiaca*, *erecta*
Sorangium	*cellulosum*
Polyangium	*aureum*, *compositum*, *fumosum*, *rugiseptum*, *sorediatum*, *spumosum*, *thaxteri*, *vitellinum*
Haploangium	spp.
Chondromyces	*apiculatus*, *catenulatus*, *crocatus*, *lanuginosus*, *pediculatus*
Nannocystis	*exedens*

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The average number of species in tropical rain forest soils was 4.5.

3.1.2. Central European forests

Soils of deciduous and mixed forests in south western Germany were studied by Rückert [94–96], who found nine species of myxobacteria: *Ar. gephyra* was always present, frequent were *Mx. fulvus*, *Mx. virescens*, *Cc. coralloides* and *Cb. fuscus*, whereas *Mx. stipitatus*, *M. lichenicola*, *Pl. sorediatum* and *Sg. aurantiaca* were rare in occurrence. In a limited area, the Siebengebirge ('Seven Mountains') near Bonn, Dawid [40,97] isolated and determined about 28 000 strains representing 17 different myxobacterial species from deciduous and mixed forest soils: Most common were *Mx. fulvus*, *Mx. virescens*, *Mx. xanthus*, *Cc. coralloides*, *Ar. gephyra*, and *Polyangium* species; rare were *Mx. xanthus*, *Pl. vitellinum*, *M. lichenicola*, and *Sg. erecta*. In the thin dry dusty soil layers on bare rock he found 14 species, most frequently *Cc. coralloides*, *Mx. fulvus*, and *Ar. gephyra*, rarely, however, *Mx. xanthus*, *Pl. vitellinum*, *M. lichenicola* and *Sg. erecta*.

3.1.3. Mediterranean regions

As early as 1927 Lievre (cited in [30]) studied soils of the Mediterranean region in France and Algeria and reported six species: *Mx. fulvus*, *Mx. virescens*, *Cc. coralloides*, *Cb. fuscus*, *Sg. erecta* and *M. lichenicola*. In Yugoslavian soils, Sabados-Saric [33] found five species: *Mx. fulvus*, *Mx. stipitatus*, *Mx. virescens* and *Cc. coralloides*. Soils bearing anthropogenous vegetations in central Italy, Yugoslavia and Greece were studied by Rückert [96], who regularly found *Mx. fulvus*, *Mx. virescens*, *Ar. gephyra*, *Cb. fuscus* and *Pl. sorediatum*, rarely, however *M. boletus*, *Sg. erecta* and *Cm. pediculatus*; the average species number per sample was 3.8.

3.1.4. Extreme biotopes

Extreme biotopes for myxobacteria are characterized by climate and ecological factors as extremely hot and dry, extremely cold and poor in nutrients, extreme in soil acidity or extreme due to their exposed altitude and several environmental parameters.

3.1.4.1. Peat bogs. Peat bogs or mosses and moors are usually biotopes with rather low pH values and deficiency of nutrients. Such undisturbed, intact acid (pH 3.7) high moors in Belgium (Haute Fagne) were studied by Dawid [28,98–100], who found that only three species lived in this environment: *Mx. fulvus*, *Mx. xanthus* (rarely) and a *Polyangium* species. A comparable study on high peat mosses in Germany (Rotes Moor, Schwarzes Moor in the Rhön area, and Zwillbrocker Venn) yielded *Mx. fulvus*, *Mx. virescens* and *Cc. coralloides* [98]. In contrast, a study on an alkaline peat bog near Vestaburg (MI, USA) resulted in 10 myxobacterial species from the open water and five species from the mud, the latter all myxococci: *Mx. fulvus*, *Mx. virescens*, *Mx. xanthus*, *Cc. coralloides*, and *An. disciformis* [31].

3.1.4.2. Cold biotopes. In antarctic soils on King George Island with a pH of 5.7–6.9, Rückert [101] found *Mx. virescens* and *Mx. stipitatus* in two out of four samples. These isolates did not grow under laboratory conditions for psychrophilic bacteria, but at 30°C. It remains possible that these strains were 'carried in' and not autochtonous psychrophilic myxobacteria. Enrichment cultures under controlled cold conditions and long-time observation may result in more reliable autochtonous psychrophilic myxobacteria [99]. Dawid [41] studied 24 soil samples from McMurdo Valley (South Victoria Land, Antarctica) for myxobacteria. Only one sample turned out to be positive; in this sample four different myxobacterial types (perhaps species) were found after an observation time of 8 and more months at an incubation temperature of 4°C. The isolates grew neither at 30°C nor at room temperature, they were bacteriolytic, agarolytic and psychrophilic. This was the first proof for the existence of genuine psychrophilic myxobacteria [41].

In sediments of caves in the Bavarian Alps, visited for the first time by humans, Rückert and Menne [102,103] applying incubation temperatures of 6–8°C, regularly found *Mx. fulvus* and *Cc. coralloides*, rarely however, *Mx. virescens* and *Na. exedens*. These isolates formed fruiting bodies after 6–8 weeks, at 30°C already after 1–2 weeks. In arctic tundra soils from northern Sweden, Noren [104,105] found only 17 positive cases out of 50 samples, and was able to isolate only four species: *Mx. fulvus*, *Mx. virescens*, *Cc. coralloides* and *Ar. gephyra*. A study on Alaskan and north Canadian soils by Brockman and Boyd [29] had similar results: Only four out of 17 samples were positive and only *Mx. fulvus* and *Pl. sorediatum* were isolated. North Norwegian and Icelandic soils were found to contain only *Mx. fulvus*, *Mx. virescens*, *Cc. coralloides* and *Ar. gephyra* [107,108], cf. [106]. Summarizing the occurrence of myxobacteria in subarctic soils, Rückert [96] stated that frequent species are *Mx. fulvus*, *Mx. virescens* and *Cc. coralloides*, rare ones are *Ar. gephyra*, *Cb. fuscus* and *Sg. erecta* (= *Podangium erectum*). Hot and acid Icelandic soils turned out to be free of myxobacteria.

3.1.4.3. Hot biotopes. In desert soils of Arizona (USA), Elbein [109], besides several *Myxococcus* species, found even *Sg. aurantiaca*, *M. lichenicola*, *Cm. apiculatus* and *Cm. pediculatus*, not however, *Ar. gephyra* and *Cb. fuscus*. Reichenbach isolated *Na. exedens* from Arizona soil [110], Larkin and Dunigan reported *Myxococcus*, *Cystobacter* and *Polyangium* species from desert soils [112]. Arid Mexican soils yielded *So. cellulosum* (= *Pl. cellulosum*) [88,89], *Mx. fulvus*, *Mx. virescens*, *Mx. stipitatus*, *Cc. coralloides*, *Cm. apiculatus* and *Cm. crocatus* [111,112]. Soils of the Sahara rim were found to contain

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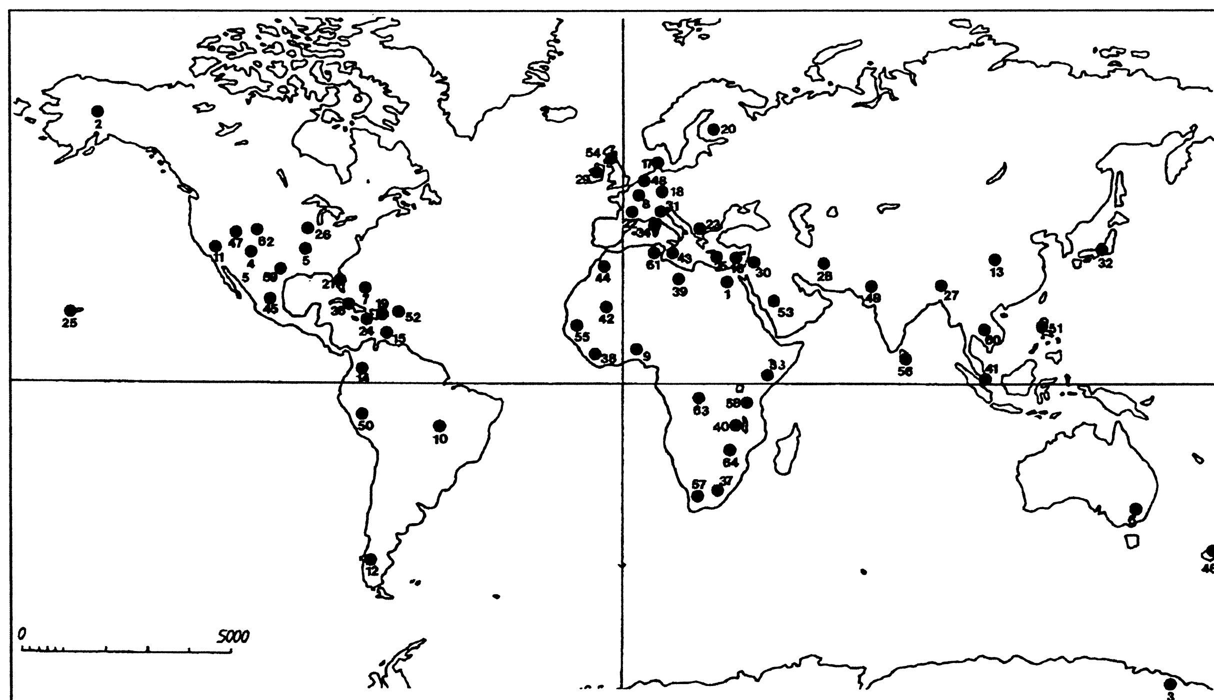

Fig. 7. Global distribution of sampling sites of soils studied with respect to the occurrence of myxobacteria.

Mx. fulvus, *Mx. virescens*, *Cc. coralloides*, *Ar. gephyra* and *Cb. fuscus* [113], whereas soils from the coastal desert contained *Mx. virescens*, *Cb. fuscus* and *Ar. gephyra*, rarely *Mx. fulvus*, *Cc. coralloides* or *Pl. sorediatum*.

3.1.4.4. High altitude biotopes. In alpine soils of the east Carpathians, Krzemieniewska and Krzemieniewski found *Mx. fulvus*, *Cc. coralloides*, *Cb. fuscus* and *Pl. sorediatum*, and came to the conclusion that mountain soils would always be poorer in myxobacteria than soils of less elevated territories [9,115,116]. In Japanese mountain soils almost only *Mx. fulvus* has been reported [117]. Studies in the European Alps in Austria, Germany, Switzerland, and Italy showed a predominance of *Mx. fulvus*, *Mx. virescens*, *Cc. coralloides* and *Ar. gephyra*, whereas *Cb. fuscus* was rarely found, and the 'higher' species of the genera *Melittangium*, *Stigmatella* and *Chondromyces* were completely missing [118]. Mountain soils from very high altitudes such as the tropical Andes and the Himalayan Mount Everest area contained *Mx. fulvus*, *Mx. virescens*, *Cc. coralloides*, *Ar. gephyra*, but rarely *Cb. fuscus* [114,119].

3.1.4.5. Saline biotopes. In coastal samples from South Carolina *Cc. coralloides* occurred as the sole myxobacterial species [120], while samples from splash water zones and dunes in North Carolina contained *Mx. fulvus*, *Mx. xanthus*, *Cc. coralloides*, *Ar. gephyra* and *Cb. fuscus* [121]. Brockman [122] stated that dune soils are almost always myxobacteria-positive and richer in species than samples from coastal areas of the USA, the Bahamas and Brazil. Indeed, samples from Brazilian sand beaches yielded four species: *Mx. fulvus*, *Mx. virescens*, *Mx. stipitatus* and *Cc. coralloides* [30]. Iizuka and coworkers reported 'marine' myxobacteria from wet sands at rocky coasts of Japan [123]: From 90 samples of the coastal region of Hachijo-Jima and the Miura peninsula they isolated two myxobacterial species that formed fruiting bodies and on the basis of morphological traits and a phylogenetical analysis belong into the genus *Nannocystis*. It remains open, however, whether these are genuine marine species, because already Rückert [96] reported about salt tolerance and enhancement of fruiting body formation by NaCl in *Mx. virescens*. In highly saline soils (almost 34% NaCl) of the Tüz Gölü area near Ankara, Turkey, Rückert [96] found *Mx. virescens* and *Ar. gephyra*, but very seldom *Mx. fulvus* and *Cb. fuscus*.

The reasons for the strong quantitative and qualitative variations seen in these results are to be sought in very different sample numbers studied, strongly differing isolation and culture techniques as well as in the difficulties of species identification. The different individual experience of the authors in species knowledge, the lack of reference cultures, the preference for fruiting bodies and the underestimation of cytological and biochemical traits add up to such differences. It is therefore rather difficult to draw a comparison between such older results and newly added information. In spite of this tendencies may be recognized: Myxobacteria obviously occur always there where sufficient nutrients are available; further limiting factors are soil acidity, temperature and water content.

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3.2. Objectives of a comprehensive study

The basis of a study by Dawid (unpublished) were 1398 samples collected from soils in 64 countries or states of all continents. Standardized methods for enrichments, isolations and determination of myxobacterial species were used throughout. The following data were collected: The species spectrum of the sum of all samples, of single sample series and of single samples, the average number of species in sample series, the frequency of species worldwide.

Simultaneously it was studied how far occurrence and distribution of myxobacterial species depend on the climate zone and on the type of biotope and its parameters. Fig. 7 and Table 4 present an overview of the countries of origin and the sample numbers.

3.3. Critical evaluation of the methods used

The soil samples were taken as mixed samples following a standardized scheme: Depth 1–5 cm below the soil surface; biotopes not within human walking areas; amounts 50–150 g, collected in pre-sterilized plastic bags or vials.

Table 3
Climates of the Earth [125]

I	Polar and subpolar zones	
	1	High-polar ice-cap climates
	2–4	Polar climates–subpolar climates
II	Cold temperate boreal zone	
	1	Oceanic boreal climates
	2	Continental boreal climates
	3	Highly continental boreal climates
III	Cold temperate zones	
	1	Woodland climates, highly oceanic climates
	2	Oceanic climates
	3	Suboceanic climates
	4	Subcontinental climates
	5	Continental climates
	6	Highly continental climates
	7	Humid and warm summer climates
	8	Permanently humid, warm summer climates
	9	Steppe climates with cold winters
	10	Dry steppe climates with cold winters
	11	Humid summer steppe climates with cold winters
	12	Semi-desert and desert climates with cold winters
IV	Warm temperate subtropical zones	
	1	Dry summer, Mediterranean climates with humid summer
	2	Dry summer steppe climates with humid winters
	3	Steppe climates with short summer humidity
	4	Dry winter climates with long summer humidity
	5	Semi-desert and desert climates
	6	Permanently humid grassland climates
	7	Permanently humid climates with hot summer
V	Tropical zones	
	1	Tropical rainy climates
	2	Tropical humid summer climates with humid winters
	3	Wet and dry tropical climates
	4	Tropical dry climates with humid winters
	5	Tropical semi-desert and desert climates

Location and properties of the habitat were recorded. The soil samples were taken at random and were not representative for a certain biotope or region. The classification of countries or biotopes into geographically termed climate zones was done by use of the climate map of Troll and Paffen [124] and is shown in Tables 3 and 4.

Altogether, 1398 soil samples from 64 countries were collected. After collecting, the samples were brought or air mailed to the laboratory and processed in a standardized scheme: air drying if they were not air dry at arrival; visual inspection and description of sample (color, grain size, content); determination of acidity; inoculation of enrichment plates; set-up of humidity chambers with sterile dung pellets from wild rabbits; classification of samples in climate zones.

During the whole study three methods for the enrichment of myxobacteria were applied [28,30,40,97,98]:

Method 1: 'Dung bait plates' after Krzemieniewska and Krzemieniewski [125] and Reichenbach and Dworkin [26]: Sterile glass Petri dishes were supplied with three round filters that were then wetted with sterile water supplemented with cycloheximide (0.08 mg/ml) to curb possible growth of fungi. The soil sample was then brought in at about 1 cm height. As bait, per Petri dish 20 small autoclaved dung pellets (collected in a uniform territory) were deposited on the soil sample. Two dung bait plates were prepared for every soil sample.

Method 2: 'Coli-spot plates' after Singh [32], and Reichenbach and Dworkin [26], modified by Dawid [30]: Sterile water agar plates (so-called wcx plates, containing water, 0.1% $CaCl_2 \cdot 2H_2O$, and 1.5% agar) were prepared by standard methods. After cooling down but just before pouring, the agar was supplemented with 2.5% heximide. The agar surfaces were inoculated with five separate drops of a heavy living cell suspension of *E. coli*. (For this purpose, *E. coli* strain K12 was grown on nutrient agar plates, scraped off with a sterile spatula, suspended in sterile water to a cell density of about 10^{10} to 10^{14} cells/ml.) The plates were dried in an oven before the coli-spots were inoculated with crumbs of the soil samples in their respective centers. Ten coli-spot plates were inoculated from every soil sample.

Method 3: 'STAN-6 plates' after Reichenbach and Dworkin [26]: wcx agar (cf. method 2) was supplemented with 0.4% cellulose powder, autoclaved and poured into Petri dishes. From every soil sample a STAN-6 plate with 25 partial samples was prepared.

Altogether, 2796 dung bait plates, 13 980 coli-spot plates and 1398 STAN-6 plates were prepared from the 1398 soil samples. They were incubated in the dark at 30°C, regularly over a period of 6 weeks. Exception: Antarctic samples were incubated in three series: at 4°C and 30°C in the dark for 6 weeks or up to 12 months [41].

The enrichments were monitored every 5–7 days by inspection with a stereo microscope (magnification: 4–60×), Antarctic samples at first weekly, later monthly. More de-

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tails about enrichment culture techniques are given by Reichenbach and Dworkin [26].

For isolation and pure cultures the following media were used: Coli-spot plates, cy plates [126], dung pellet agar plates and STAN-6 medium [126]. Isolation was obtained by transfers of cell material from swarms or fruiting bodies to fresh vy/2 plates.

Isolation, pure culture and identification of the myxobacteria from enrichment plates was carried out on vy/2 plates (water, 1.5% agar, 0.5% fresh baker's yeast; after autoclaving and cooling, but short before pouring, the agar was supplemented with sterile filtered cyanocobalamine to a final concentration of 0.5 mg/ml).

For the identification of pure and enrichment cultures the determination keys of McCurdy [23,127] and of Reichenbach and Dworkin [26,126] were applied. The myxobacteria listed by Reichenbach and Dworkin [26] are considered as 'confirmed species' (cf. Table 2). As 'unconfirmed species', those species are considered that displayed a variability in the morphology of fruiting bodies and therefore may be varieties of a species or subspecies, and that have been called '*species incertae sedis*' [126]. In difficult cases reference cultures (kindly provided by Hans Reichenbach, Braunschweig, Germany) were used to facilitate identifications, cf. also [137]. Some of the isolated strains were generously determined by Hans Reichenbach himself. The species found were recorded by photographs.

Soil acidity was determined after Steubing [128] using a pH meter.

Stock cultures were prepared as myxospore preparations [126]. Own experience has shown that such preparations stay viable for more than 20 years.

A critical comparison of enrichments of myxobacteria with respect to efficiency and reliability was first performed by McCurdy [34]. Later, Rückert [96] stated that every method would be a compromise, as different myxobacterial species would grow well on one medium, others would grow less well, show little tendency to form fruiting bodies, and would be identified differently. The different enrichment methods complement each other during the registration of a wide spectrum of species. With respect to quality and quantity of feed organisms it was shown that autoclaved cells of bacteria (*E. coli*, *Micrococcus luteus*, *Serratia marcescens*) and yeasts (*Saccharomyces cerevisiae*, *Candida utilis*) are lysed by myxobacteria from soil particles and utilized slower than living cells. The formation of swarms and fruiting bodies is retarded. The development of contaminants such as amoebae, mycelial fungi and other microbes is favored. It also became clear that yeasts are lysed slower than feed bacteria. From the work of authors who used living baker's yeast as feed organisms it becomes clear that they found smaller spectra of species [96]. The importance of the quantity and the form of offered feed organisms is shown by the methodological comparison in Section 3.8.

3.4. Global spectrum of species

For quality judgement of the obtained results, it has to be stated here that in contrast to many of the publications cited above (Section 3.1), in this study identical standardized methods from sampling to identification were used during the whole investigation period of 18 years.

3.4.1. Overview over species found worldwide in soils

In the soil samples studied from worldwide origins altogether 30 'confirmed' myxobacterial species were found:

Myxococcaceae: *Mx. fulvus*, *Mx. stipitatus*, *Mx. virescens*, *Mx. xanthus*, *Cc. coralloides*, *Cc. exiguus*, *An. disciformis*. *Archangiaceae*: *Ar. gephyra*, *Ar. serpens*. *Cystobacteraceae*: *Cb. fuscus*, *Cb. ferrugineus*, *Cb. minor*, *Cb. velatus*, *M. boletus*, *M. lichenicola*, *Sg. aurantiaca*, *Sg. erecta*. *Sorangiaceae*: *So. cellulosum*, *Pl. aureum*, *Pl. compositum*, *Pl. fumosum*, *Pl. rugiseptum*, *Pl. spumosum*, *Pl. thaxteri*, *Na. exedens*, *Cm. apiculatus*, *Cm. lanuginosus*, *Cm. pediculatus*.

Of the 12 presently known genera of myxobacteria 11 were thus found in soils. Species of the genus *Haploangium* as well as the species *Cc. macrosporus*, *M. alboraceum*, *Pl. luteum*, *Cm. crocatus* were not found.

Besides these 'confirmed species' other strains were isolated that probably are to be considered as new species. Taxonomic names and descriptions of these 10 'new species' have not yet been published. The psychrophilic myxobacteria isolated from Antarctic soils seem to belong into the genera *Nannocystis* (N type) or *Polyangium* (P type), a third type (R type) could not yet be assigned to an existing genus [41].

3.4.2. Species spectrum in sample series

Table 4 presents the number of species found in the sample series of the countries (states) of origin.

Sample series free of myxobacteria: In between the 64 sample series none were found in which all samples were free of myxobacteria. In 31 countries (states) samples occurred in which no myxobacteria were detected. These countries belonged to different climate zones. About 9% of all samples turned out to be free of myxobacteria. The high proportion of negative samples from peat bogs and Antarctic soils is conspicuous and seems to be due to high soil acidity or very low soil temperatures, respectively.

3.4.2.1. Narrow spectrum of species (1–6 species per sample series: 14% of all countries). The nine countries of origin with low species spectra are predominantly located in polar, cold temperate and cool temperate zones and in transition climates. The majority of such samples originates from peat areas, others from New Zealand and Antarctica. The low soil temperatures in the polar and boreal climate zones as well as soil acidity seem to be the species limiting factor again.

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Table 4
Overview of countries of origin of the sample series, their total and average species numbers

No.	Country	Number of samples	Species			Average species number	Climatic zone
			Certain	Uncertain	Total		
1	Egypt	18	15	3	18	4.0	IV/2+5
2	Alaska	16	5	1	6	1.8	II/2+3
3	Antarctica	35	0	0	3	2.4[a]	I/1
4	Arizona	36	17	4	21	4.6	IV/2
5	Arkansas	6	8	3	11	7.0	IV/3
6	Australia	24	12	3	15	4.9	IV/7
7	Bahamas	8	11	1	12	4.1	V/1
8	Belgium	40	3	1	4	0.3	II/3
9	Benin	4	17	2	19	11.3	V/2
10	Brasil	56	21	4	25	5.7	V/2
11	California	10	8	3	11	2.1	IV/2
12	Chile	13	9	2	11	2.1	III/1
13	China	50	23	3	26	5.2	IV/7
14	Columbia	9	14	3	17	5.4	V/1
15	Curacao	6	10	2	12	5.5	V/4
16	Cyprus	7	15	4	19	8.9	IV/1
17	Denmark	5	6	1	7	2.6	III/3
18	Germany	442	16	3	19	3.0 (1.8)[b]	III/3
19	Dominican Rep.	12	18	3	21	6.3	V/1
20	Finland	11	4	1	5	1.0	II/2+3
21	Florida	44	23	7	30	5.7	IV/7
22	France	21	12	1	13	3.7	III/1
23	Greece	24	15	2	17	3.5	IV/1
24	Haiti	6	13	2	15	7.7	V/2
25	Hawaii	7	13	2	15	5.6	V/1
26	Illinois	24	15	2	17	6.3	III/7
27	India/Burma/Nepal	9	14	2	16	4.2	V/1+2
28	Iran	12	14	3	17	7.4	IV/2
29	Ireland	14	7	1	8	1.4	III/2
30	Israel	15	12	3	15	3.9	IV/1
31	Italy	25	6	1	7	1.4	III/3
32	Japan	9	7	2	9	2.3	IV/7
33	Kenia	4	5	3	8	3.5	V/3
34	Corsica	16	13	5	18	5.7	IV/1
35	Crete	19	16	5	21	6.8	IV/1
36	Cuba	1	6	1	7	(7.0)	V/2
37	Lesotho	33	16	2	18	4.8	IV/4
38	Liberia	3	10	1	11	5.7	V/2
39	Libya	1	3	1	4	(4.0)	IV/2
40	Malawi	2	6	0	6	(5.0)	V/3
41	Malaysia	7	9	2	11	4.0	V/1
42	Mali	11	20	3	23	9.8	V/5
43	Malta	14	14	3	17	6.4	IV/2
44	Marocco	5	8	1	9	5.8	IV/2
45	Mexico	24	13	3	16	3.4	V/4
46	New Zealand	11	5	1	6	1.8	III/1
47	Nevada	3	5	2	7	3.7	IV/5
48	Netherlands	10	8	1	9	3.2	III/3
49	Pakistan	4	10	3	13	9.0	IV/5
50	Peru	13	10	2	12	4.1	V/1
51	Philippines	27	19	6	25	7.0	V/1
52	Puerto Rico	7	11	3	14	6.0	V/1
53	Saudi Arabia	11	9	4	13	3.5	IV/5
54	Scotland	6	4	1	5	0.8	III/2
55	Senegal	15	19	3	22	6.9	V/4
56	Sri Lanka	22	19	3	22	5.1	V/4
57	South Africa	7	5	2	7	3.0	IV/2
58	Tansania	17	19	4	23	6.8	V/3
59	Texas	2	10	3	13	(10.0)	IV/7
60	Thailand	29	17	5	22	4.9	V/1
61	Tunesia	14	14	4	20	4.9	IV/2

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Table 4 (*continued*)

No.	Country	Number of samples	Species			Average species number	Climatic zone
			Certain	Uncertain	Total		
62	Utah	11	13	4	17	3.9	III/10
63	Zaire	28	16	4	20	3.2	V/2
64	Zimbabwe	3	4	2	6	4.3	V/3

[a]New species [41].

[b]The value refers to 54 peat bog samples.

3.4.2.2. Medium species spectrum (7–21 species per sample series: 73% of all countries). These series originated from almost all countries and climate zones as well as from widely differing biotopes with a wide variety in pH values. Conclusions about limiting factors in these cases are not possible.

3.4.2.3. Wide species spectrum (22–30 species: 12.5% of all countries). It is obvious that such countries are situated in the warm to temperate subtropical and tropical zones. Comparisons showed that here the number of species did not depend on the number of samples studied. All 30 myxobacterial species found worldwide were present in a single sample series from soils of Florida.

3.4.3. Species spectrum in single samples

In a total of 1398 soil samples investigated some were found not to contain myxobacteria. They originated from countries of all five climate zones. More frequent in this respect than others were samples from countries of the climate zones I (ice deserts) and III (cool moderate forest climates) (Table 5). The biotopes of these samples were peat bogs (Alaska, Belgium, Germany and Finland), scree fields of rock debris and glaciers (Antarctica, New Zealand), but also steppes, deserts as well as deciduous and coniferous forests (Chile, Egypt, Florida, Mexico). One of the reasons for lack of myxobacteria is soil acidity. Almost half of the negative samples had a pH value between 3 and 4, two thirds were below pH 6. An other important factor is low temperature in polar and boreal climates (Table 5).

3.4.3.1. Narrow spectrum of species (1–3 species per sample). About one third (34%) of the samples showed a rather narrow spectrum of species: *Mx. fulvus* (284 times), *Cc. coralloides* (211 times), *Ar. gephyra* (197 times) and *Pl.* spp. (156 times). In combination with these species, *Pl. sorediatum* (95 times), *Na. exedens* (42 times), *Mx. virescens* (42 times) and *An. disciformis* (27 times) were detected; rarely, *Cm. apiculatus* (7 times), *M. lichenicola* (5 times), *Sg. erecta* (twice) and *Sg. aurantiaca* (once) occurred. In polar ice climates three species of psychrophilic myxobacteria were detected, however, with very low frequency. Most soil samples with low species variety originated from countries of the cool moderate forest climates (Table 5), and almost that many were from tropic zones. They originated from Alaska (peat mosses, taiga), Belgium (high peat moss), China (wasteland, desert), Greece and Italy (thin soil layers on rocks), Central Africa (wasteland, jungle). One third of the samples showed a pH value of 4–7. This allows the conclusion that number and variety of species increase with increasing pH of soils, especially with respect to myxococci, corallococci and archangia.

3.4.3.2. Medium spectrum of species (4–9 species per sample). In more than half of the samples (58%) a medium spectrum of species was found. The soils of these samples originated from countries of all climate zones and regions, except from polar zones. The types of habitats were rather diverse and their solid acidity showed a wide distribution (pH 3–9). In this group of samples 29 myxobacterial species were found to occur. The most com-

Table 5
Species spectrum: arrangement of soil samples by climate zones

Number of myxobacterial species per soil sample		Distribution of soil samples over climate zones					Total number of samples
		I	II	III	IV	V	
0	(a)	23	7	64	19	11	124
	(b)	18.5	5.6	51.6	15.3	8.9	
1–3	(a)	3	16	259	63	72	413
	(b)	0.7	3.9	62.7	15.3	17.4	
4–9	(a)	18	45	621	92	36	812
	(b)	2.2	5.5	76.4	11.3	4.4	
10–16	(a)	0	0	12	12	25	49
	(b)	0	0	24.5	24.5	51.0	

(a) Absolute number of samples from the respective climate zone.
(b) Percentage of the number of samples.

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Table 6
Species spectrum: distribution of soil samples with respect to soil pH

Number of myxobacterial species per soil sample	Total number of samples		Soil pH of the samples						
			pH 3	pH 4	pH 5	pH 6	pH 7	pH 8	pH 9
0	124	(a)	21	42	19	16	17	7	2
		(b)	17.0	33.1	15.3	12.9	13.7	5.6	1.6
1–3	413	(a)	15	93	124	57	98	19	7
		(b)	3.6	22.5	30.0	13.8	23.7	4.6	1.7
10–16	49	(a)	0	1	7	15	14	11	1
		(b)	0	2.0	14.3	30.6	28.6	22.4	2.0

(a) Absolute number of samples with respective pH values.
(b) Percentage of the number of samples.

mon ones were: *Cc. coralloides* (623 times), *Na. exedens* (412 times), *Ar. gephyra* (372 times), *Mx. fulvus* (294 times). Rarely seen were *Sg. erecta* (14 times), *Sg. aurantiaca* (6 times), *Cm. lanuginosus* (3 times) and *Pl. aureum* (twice).

3.4.3.3. Wide spectrum of species (10–16 species per sample). A wide spectrum in this sense was present only in 3.5% of the 1398 soil samples. It was found in soils of the climate zone V, i.e. tropical territories, humid savannahs and savannahs subjected to humidity changes, where more than half of the samples contained 10 to 13 species, rarely 16 species. About one quarter of each of the samples originated from warm temperate subtropic and from cool temperate climates. In this group altogether 26 different myxobacterial species were found, with the highest species number in a soil sample from Mali (west Africa). In this group the following species were found: *Mx. fulvus*, *Mx. virescens*, *Cc. coralloides*, *Cb. fuscus*, *Cb. ferrugineus*, *Cb. minor*, *Cb. velatus*, *Cb. violaceus*, *Sg. erecta*, *Pl. fumosum*, *Pl. rugiseptum*, *Pl. sorediatum*, *Pl. thaxteri*, *Cm. apiculatus*, *Cm. lanuginosus*, *Na. exedens*. In a sample from Crete (climate zone IV/1, wasteland, pH 8), 14 species were detected with the following predominance: *Na. exedens* (48 times), *Pl. fumosum* (42 times), *Ar. gephyra* (36 times), *Mx. virescens* (33 times), *Cc. coralloides* (33 times) and *Cb. fuscus* (33 times). Together with these, but less frequent were *An. disciformis* (15 times), *M. lichenicola* (18 times), *Sg. erecta* (18 times), *Cm. apiculatus* (16 times). Comparatively seldom in this wide spectrum occurred *Pl. thaxteri* (9 times), *Cb. violaceus* (7 times), *Cm.* species (4 times) and *M. boletus* (twice). Considering the countries and biotopes of the samples with the wide spectrum of species it becomes clear that within the sample series of most countries of origin single samples with a high number of different species may occur. Such biotopes reach from deciduous and mixed forests via mangroves, wastelands, pastures, savannahs and deserts to coastal rims and high mountains. It may be concluded that soils with an acidity of pH 6 to 8 allow a high number of species to grow and to be found (Table 6).

3.4.4. Average numbers of species

The average number of species in a single sample of a country of origin was calculated using the following equation:

$$\text{average number of species} = \frac{\text{sum of species numbers of all samples of a series}}{\text{sum of all samples of that series}}$$

In this formula the 'safe' and 'unsafe' species, the myxobacteria-positive as well the myxobacteria-negative samples were included.

An exceptionally high average species number was thus determined for soils from the countries Benin, Mali, Pakistan, Cyprus, Haiti, Iran, that belong to the winter rain climates of the Mediterranean type (IV/1), the permanent wet rain forest climates (V/1) and the tropical semi-desert climates (V/5).

A low average species number was found in the soils of the countries Belgium, Scotland, Finland, Italy, Alaska, Germany (peat). These countries belong to the cold temperate coniferous forest climates (II/1+2) and the cool temperate intermediate climates (III/2+3) with peat mosses and coniferous forests. The samples from Italy in this group originated from mountain climates (Ötztal Alps) with alpine peat formation.

A medium average species number was found in the soil samples of the 52 countries left.

Myxobacterial populations poor in species (group I: 1–3 species/sample) are common in soils from Alaska (63%), Antarctica (31%), Belgium (70%), Germany (69%), Italy (92%), New Zealand (91%) and Zaire (64%). These countries belong to the continental boreal climates, oceanic climates, mountain climates and permanent wet rain forest climates. Poverty of species therefore occurs in soils of peat mosses, coniferous forests and mountains. In general, the values – also those from Antarctica – correlate with the data on species varieties described above.

None of the sample series studied revealed a population predominantly rich in species (group III: 10–16 species) in all samples. A tendency may though be seen in samples of

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the following countries: Benin (100% with four samples), Cyprus (57% with seven samples), Mali (55% with 11 samples), Pakistan (75% with four samples). It seems that not alone the strongly varying pH (5.6–8.3) is responsible for this high species variety. These countries of origin belong to the climate zones V/2 (humid savannah: Benin), IV/1 (winter rain climate: Cyprus), V/3 (humidity varying dry savannah: Mali) and IV/5 (subtropical half deserts and deserts: Pakistan).

An average distribution (group II: 4–9 species per sample) was found in two thirds of all samples and in one quarter of all countries of origin (16 out of 64 countries). In this group the percentage varies between 52% (Mexico) and 94% (Germany).

The average distribution was determined in the soils of Arizona (55%), Brazil (75%), China (64%), Crete (79%), Egypt (61%), Florida (64%), Germany (94%), Illinois (91%), Israel (66%), Lesotho (76%), Malta (86%), Senegal (73%), Sri Lanka (81%), and Tanzania (59%). These countries lie in cool temperate zones (III), but also in warm temperate subtropic zones (IV) and tropic zones (V), but not in polar and subpolar zones (I) or cold temperate zones (II). This finding supports the assumption that the parameter temperature is strongly involved in determining the spectrum of species as well as the average species number and the distribution density.

3.4.4.1. Average number of species with respect to climate zone. When the average number of species is correlated with the respective climate zones, the result is the following:

Polar and subpolar zones	(I)	0.5
Cold temperate zones	(II)	1.4
Cool temperate zones	(III)	2.5
Warm temperate subtropic	(IV)	5.3
Tropic zones	(V)	7.7

All sample series with low average species numbers (0.3–1.8), altogether nine, originated from climate zones I–III. Sample series with high average species numbers (7.4–11.3), altogether six, only occurred in countries of climate zones IV and V. In the latter zones not a single sample series had a low average species number. Thus a clear tendency may be seen in the dependence of the average species number upon parameters of the climate zones. From the poles to the equator, climate zone I to climate zone V, the average number of species increases clearly (from 0.3 to 11.3).

3.5. Global species frequency

Table 7 shows the frequency in which the myxobacterial species found occur in the soils studied worldwide.

The globally most frequently occurring soil myxobacteria are the myxococci with the absolutely most frequent species *Cc. coralloides* with 61.1% frequency of detection. In second position is *Ar. gephyra* (43.2%), in third *Mx. fulvus* (43.1%), followed by *Polyangium* species (42.1).

The globally rare species (under 1%) were *Pl. thaxteri*, *Sg. aurantiaca*, *Cm. pediculatus*, *M. boletus*, *Pl. aureum* and *Cc. exiguus*. The 'middle field' is represented by species of all genera with frequencies between 2 and 30%.

These results (Dawid, unpublished) differ from those summarized in the literature [96,126]. The species so far seen as ubiquitous, *Na. exedens*, was only found with a

Table 7
Global incidence of myxobacteria in soils

No.	Species	Absolute	%	No.	Species	Absolute	%
1	*Cc.c.*	854	61.1	21	*Cb.viol.*	43	3.0
2	*Ar.g.*	605	43.2	22	*Ar.s.*	42	3.0
3	*Mx.f.*	602	43.1	23	*Mx.sp.*	35	2.5
4	*Pl.sp.*	588	42.1	24	*Cb.vel.*	34	2.4
5	*Na.e.*	469	33.5	25	*Sg.e.*	34	2.4
6	*Pl.fum.*	284	20.3	26	*Cm.sp.*	34	2.4
7	*Mx.v.*	275	19.6	27	*Cb.min.*	31	2.2
8	*An.d.*	195	13.9	28	*Pl.comp.*	27	1.9
9	*Cb.f.*	188	13.4	29	*Pl.th.*	13	0.9
10	*Cb.sp.*	157	11.2	30	*Sg.a.*	7	0.5
11	*Pl.rug.*	133	9.5	31	*Cm.p.*	6	0.4
12	*Pl.spum.*	113	8.0	32	*Cc.ex.*	6	0.4
13	*Mx.st.*	111	7.9	33	*M.b.*	4	0.3
14	*Mx.x.*	90	6.4	34	*Cm.l.*	4	0.3
15	*M.l.*	79	5.6	35	*M.sp.*	2	0.1
16	*Pl.sor.*	78	5.6	36	*Pl.aur.*	2	0.1
17	*So.cel.*	73	5.2	37	R type	2	0.1
18	*Cb.fer.*	70	5.0	38	P type	1	0.07
19	*Ar.sp.*	62	4.4	39	N type	1	0.07
20	*Cm.a.*	52	3.7				

For abbreviations see cf. text and compare Table 2.

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Table 8
Comparison of climate zones with respect to soil floras of myxobacteria

Country of origin	Number of samples	Number of species	Variation species/sample	Average number of species	Average pH value	Variation of pH
Climate zone IV/2: humid warm						
Egypt	8	15	0–6	4.7	6.7	5.4–8.4
Arizona	2	6	3–6	4.5	6.0	5.0–6.0
California	10	11	0–5	3.5	6.4	3.8–8.8
Libya	1	4	0	0	6.4	0
Tunesia	3	13	5–9	7.0	7.0	6.7–7.3
Iran	12	17	4–13	7.4	6.4	4.2–8.2
Climate zone IV/5: dry warm						
Egypt	10	14	1–7	5.0	5.8	4.2–7.4
Pakistan	4	13	7–11	9.0	7.2	6.8–7.4
Saudi Arabia	11	12	1–7	3.5	5.8	4.1–7.3

frequency of 33.5%, the 'moderately frequent' species *So. cellulosum* occurred with the low frequency of 5.2%, and the likewise *Polyangium* species with the higher frequency of 43.1%. With respect to the species *Cc. coralloides*, *Ar. gephyra*, *Mx. stipitatus* and the *Cystobacter* group these results are in good agreement with those of Reichenbach and Dworkin [126].

3.6. Comparison of the myxofloras of two climate zones

The aim of this comparison was to elucidate the influence of climate factors (dryness/humidity) upon species number, species frequency and species spectrum within warm climates (IV). Two climates of the warm moderate subtropic zone were chosen: Climate zone IV/a: humid and warm; winter humid and summer dry steppe climate; grass and shrub steppe; countries: Arizona, California, Egypt, Iran, Libya, Tunesia; number of samples: 36; myxobacteria-negative: five samples. Climate zone IV/5: dry and warm; tropical half-desert and desert climate; number of samples: 25; myxobacteria-negative: two samples.

The most important data are summarized in Table 8. It is evident that in both climate zones the number of species found is relatively large and almost equal, the average species number in the dry warm climate is slightly higher. In the humid warm climate the species spectrum is more diverse than in the dry warm climate.

Table 9 shows a specification of the myxobacteria found. It becomes clear that *Cc. coralloides*, *Ar. gephyra* and *Na. exedens* were most frequently encountered, less though in the dry warm climate. The least frequent species were *Cb. fuscus*, *An. disciformis* and *Mx. virescens* with rather varying frequencies and a slightly higher tendency in soils of the dry warm climate.

The difference between the two myxobacterial floras is not really remarkable with respect to species contents. This could be explained by the regular annual hot dry period in the humid warm climate belt, besides the fact that myxobacteria can survive long periods of dryness and thus reduce the difference between the two climate zones.

Table 9
Abundance of species in the climate zones IV/2 and IV/5

Species	Climate zone IV/2		Climate zone IV/5	
	Absolute	%[a]	Absolute	%[b]
Mx.f.	14	45	8	35
Mx.v.	5	16	2	9
Mx.x.	1	3	1	4
Mx.s.	9	29	2	9
Mx.sp.	3	10	0	0
Cc.c.	22	71	11	48
An.d.	6	19	6	26
Ar.g.	22	71	15	65
Ar.s.	1	3	0	0
Cb.f.	6	19	8	35
Cb.fer.	1	3	0	0
Cb.min.	2	7	0	0
Cb.vel.	3	10	3	12
Cb.viol.	2	7	0	0
Cb.sp.	5	16	10	44
M.l.	2	7	0	0
Sg.e.	0	0	1	4
Pl.fum.	7	23	8	35
Pl.spum.	8	26	4	17
Pl.rug.	0	0	3	12
Pl.sor.	8	26	4	17
Pl.comp.	5	16	0	0
Pl.sp.	17	55	6	26
So.cel.	7	23	1	4
Na.e.	18	58	14	60
Cm.a.	3	10	0	0
Cm.sp.	1	3	4	17
Most common species	*Cc.c.* 22× = 71%		*Ar.g.* 15× = 65%	
	Ar.g. 22× = 71%		*Na.e.* 14× = 60%	
	Na.e. 18× = 58%		*Cc.c.* 11× = 48%	
Least common species	*Cb.f.* 6× = 19%		*Cb.f.* 8× = 35%	
	An.d. 6× = 19%		*An.d.* 6× = 26%	
	Mx.v. 5× = 16%		*Mx.v.* 2× = 9%	
Certain species	19		16	
Total	25		19	

For abbreviations see cf. text and compare Table 2.
[a]Referring to 31 myxobacteria-positive soil samples.
[b]Referring to 23 myxobacteria-positive soil samples.

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3.7. Special observations and results

3.7.1. Acidophilic myxobacteria

It was surprising that in extremely acid environments like peat bogs (pH 3.2–3.3) myxobacteria occurred at all. In samples from undisturbed peat bogs in Belgium (Haute Fagne) *Myxococcus* and *Polyangium* species were found [28]. Based on experimental data it had been generally assumed that myxobacteria occur only in soils of neutral to slightly alkaline pH values [23,126,127], although Rückert [96] had pointed out that especially *Myxococcus* species may be found also in soils with a pH below 5. The occurrence of myxobacteria in extremely acid soils, however, does not prove whether they occur as physiologically active cells or just survive as myxospores. One cannot exclude that within the peat soil, microenvironments with locally higher pH (6–7) exist, that allow growth of myxobacteria. These should, perhaps, be called acid tolerant; genuine acidophilic myxobacteria have yet to be found.

3.7.2. Alkaliphilic myxobacteria

In soil samples from the shore of Lake Nakuru (Kenia) two *Myxococcus* species with an average frequency of 15% were isolated on coli-spot plates: *Mx. fulvus* and *Mx. xanthus*. It was conspicuous that the fruiting bodies of these strains only occurred upon or very close to the soil particles on the agar surface. The lysis of the feed bacteria was limited to a very narrow zone around the soil particles, although a wide zone of 10–15 mm of the coli-spot was present.

When fruiting bodies were transferred from soil particles to vy/2 plates, swarm and fruiting body formation no longer occurred. On vy/2 plates with a pH of 9.5, however, swarms as well as fruiting bodies were formed. Transfers of fruiting bodies and swarm material from vy/2 plates of pH 9.4 to such with pH 7.2 did never succeed in growth.

Obviously in these biotopes both *Myxococcus* species had adapted to extremely alkaline pH values and are to be considered as genuine alkaliphilic myxobacteria.

3.7.3. Psychrophilic myxobacteria

Studies of antarctic soil samples [41,100] have shown that myxobacteria exist at extremely low temperatures, i.e. have adapted to such extreme conditions. The isolated strains appear to belong to the genera *Polyangium* and *Nannocystis*. Growth was observed only under cold conditions (4°C) after 7–9 months of incubation. 'Normal conditions' (18 or 30°C) did not allow growth (cf. Section 3.1.4) [41]. So far myxobacteria had been considered as mesophilic bacteria growing within a temperature range between 6 and 38°C, with a temperature optimum at 34°C [45]. The reported results prove for the first time that genuine psychrophilic myxobacteria exist.

3.7.4. Myxobacteria producing antibiotic substances

During own long-term studies of soils a large number of myxobacterial strains were isolated and part of these were screened for the production of unusual substances by the Department of Microbiology of the Gesellschaft für Biotechnologische Forschung, Braunschweig-Stöckheim, Germany. During these studies it was found that a considerable number of the strains were able to produce several so far completely unknown antibiotics and other biologically active secondary metabolites. Strain 'S Cbfer 3 Dawid' of *Cb. ferrugineus*, found on a wood particle in the Siebengebirge (Seven Mountains) near Bonn produces pyrrolnitrin [129]. A strain of *Ar. gephyra* (BA Ag 2 Dawid), isolated in 1977 from a Bahama soil sample produces myxovalargin [130]. Myxalamid is produced by *Myxococcus* species (e.g. strain 'S Mv 9 Dawid'), isolated from soil samples of the Siebengebirge near Bonn [131]. Stigmatellin [132] is produced by strain 'S Sga 16 Dawid' of *Sg. aurantiaca*, isolated from wood in the Siebengebirge, in 1986; this strain further produces the antibiotic aurachin [133,134].

In the mean time many other antibiotics that are formed by myxobacteria have been found and isolated by other authors. E.g., a strain of the cellulose degrading myxobacterium *So. cellulosum* (So cel 90), isolated from the shore of the river Sambesi in South Africa was found to produce antifungal and antitumor substances. The cytostatic substance epothilon A inhibits the growth of multiresistant

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Table 10
Results of a comparison of methods for enrichment of myxobacteria from soils with *E. coli* as feed organism

Soil samples from Marocco	'Coli-cross method' after Reichenbach	'Coli-spot method' after Dawid	Number of species found Reichenbach/Dawid
No. 887	*Ar. gephyra*, *Na. exedens*, *Polyangium* sp., *Chondromyces* sp.	*An. disciformis*, *Cc. coralloides*, *Ar. gephyra*, *Na. exedens*	4/4
No. 888	*Ar. gephyra*, *Cc. coralloides*, *Na. exedens*	*An. disciformis*, *Mx. fulvus*, *Cc. coralloides*, *Ar. gephyra*, *Polyangium* sp., *Na. exedens*	3/6
No. 889	*Na. exedens*	*An. disciformis*, *Mx. fulvus*, *Mx. virescens*, *Cc. coralloides*, *Ar. gephyra*, *Polyangium* sp., *Na. exedens*	1/7
No. 890	*Na. exedens*	*An. disciformis*, *Cc. coralloides*, *Ar. gephyra*, *Ar. serpens*, *Cystobacter* sp., *Polyangium* sp., *Na. exedens*	1/7
No. 891	*Na. exedens*, *Cc. coralloides*	*An. disciformis*, *Cc. coralloides*, *Ar. gephyra*, *Ar. serpens*, *Cystobacter* sp., *Na. exedens*	2/6

For abbreviations see cf. text. The arrangement of the species corresponds with their frequency of occurrence.

tumor cells (lines of breast and colon cancer) in cell cultures [17,135]. Several summarizing articles bring more details about these new antibiotics and the possibilities of their biotechnological utilization [16,24,85,136].

3.8. Critical comparison of methods used in enrichment of myxobacteria from soil samples

The quantitative assessment of the myxobacterial flora in a soil sample depends upon the amount of feed organisms as well as on the way of offering them on agar plates for enrichment. This became obvious from a comparison of methods performed by Reichenbach and Dawid 1984/85 (unpublished):

Material to be studied: five soil samples from Marocco, collected by Reichenbach (April 1984).

Incubation: 30°C in the dark, 6 weeks.

Parallels: two plates per sample (Reichenbach) and five plates per sample (Dawid).

'Coli-cross method' (Reichenbach): Living cells of *E. coli* directly from the culture plates were streaked out on wcx plates in form of a cross (cf. Section 3.3). The center of the cross was inoculated with a lentil size soil particle.

'Coli-spot method' (Dawid): As described above (cf. Section 3.3). The size of the coli-spots was about 2–3 cm in diameter. The spots were inoculated with about 3 mm^3 of the soil sample.

The results of this comparison are given in Table 10 and show that – even with the reservation of the relatively small number of samples studied – the coli-spot method may result in the assessment of two to seven times more myxobacteria species. Obviously myxococci, especially *An. disciformis* have better chances to develop in coli-spots than in the coli-cross method. It seems as if the coli-spot method provides better prevention against mutual inhibitions between microorganisms. Also the larger number of partial samples is depicted by the results. Further, the numerous soil amoebae in the Marocco samples might have encountered better chances for development in the cell paste of the coli-cross. Hans Reichenbach (personal communication, 1985) confirmed that the coli-spot method in general will yield higher numbers of isolates. The methodological comparison above has shown that for the assessment of a wide species spectrum of myxobacteria the coli-spot method should be the method of choice.

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