Arch Microbiol (1983) 135:58–62

Archives of
Microbiology

A phylogenetic analysis of the myxobacteria *Myxococcus fulvus*, *Stigmatella aurantiaca*, *Cystobacter fuscus*, *Sorangium cellulosum* and *Nannocystis exedens*

Wolfgang Ludwig[1], Karl-Heinz Schleifer[1], Hans Reichenbach[2], and Erko Stackebrandt[1]

[1] Lehrstuhl für Mikrobiologie, Technische Universität München, Arcisstraße 21, D-8000 München 2, FRG
[2] GBF, Gesellschaft für Biotechnologische Forschung, Abt. Mikrobiologie, Mascheroder Weg 1, D-3300 Braunschweig, FRG

Abstract. Five representatives of the order *Myxobacterales* were characterized by oligonucleotide cataloguing of their 16S ribosomal RNA to determine their phylogenetic relationship to one another and to other gliding and non-gliding Gram-negative bacteria. *Myxococcus fulvus*, *Stigmatella aurantiaca* and *Cystobacter fuscus* are highly related, while *Sorangium cellulosum* and *Nannocystis exedens* are clearly separated from each other and from the former organisms. All myxobacteria are members of one line of descent, which is specifically related to the broad groups of non-sulphur and sulphur purple bacteria and their non-phototrophic relatives. Myxobacteria are distantly related to *Cytophaga johnsonae*, which stands completely isolated at present.

Key words: *Myxobacterales* – *Myxococcus fulvus* – *Stigmatella aurantiaca* – *Cystobacter fuscus* – *Sorangium cellulosum* – *Nannocystis exedens* – *Cytophaga johnsonae* – Phylogeny – 16S rRNA cataloguing

During the last 5 years the information about the natural relationships among the Gram-negative eubacteria has steadily increased. The breakthrough was achieved by DNA-DNA and DNA-rRNA hybridization or by comparative analysis of oligonucleotides of the 16S rRNA. While the DNA-DNA reassociation technique is used to detect closest relationships, DNA-rRNA hybridization studies are valuable to determine relationships at the intra-family level while sequence analysis allows detection of even the most distant phylogenetic relationships (Woese and Fox 1977; Fox et al. 1980; Stackebrandt and Woese 1981a). It is therefore not surprising that especially the results of the latter method provided valuable information about the phylogenetic relatedness of Gram-negative bacteria, e.g. the existence of several independent lines of descent (Fox et al. 1980; Gibson et al. 1979; Stackebrandt and Woese 1981a; Woese et al. 1982), the finding, that the photosynthetic phenotype is an ancient one, and that non-photosynthetic species have evolved from photosynthetic ancestors independently and many times in parallel (Gibson et al. 1979; Seewaldt et al. 1982; Woese et al. 1982). Furthermore, the phylogenetic heterogeneity of the morphologically defined genera *Spirillum* (Woese et al. 1982), *Rhodopseudomonas* and *Rhodospirillum* (Gibson et al. 1979), as well as of the physiologically defined groups like the chemolithoautotrophic bacteria (Gibson et al. 1979; Seewaldt et al. 1982; Stackebrandt, unpublished) could be demonstrated.

One of the major morphologically defined groups of Gram-negative bacteria, the non-phototrophic gliding bacteria, has rarely been included in phylogentic studies. Comparative nucleic acid analysis, including DNA-DNA homology studies on cytophagas (Callies and Mannheim 1980; Behrens 1978), DNA-rRNA cistron similarity studies on *Myxococcus xanthus*, *M. fulvus* and *Sorangium cellulosum* (Moore and McCarthy 1967) and on *Cytophaga johnsonae* (Bauwens 1980), and sequencing analysis of the 16S rRNA from *Lysobacter enzymogenes* (Stackebrandt and Woese 1981a) do not allow any conclusion about the phylogeny of the gliding bacteria, because of the very limited number of organisms investigated.

Reichenbach (1974, 1981) and Reichenbach and Dworkin (1981) divide the non-phototrophic gliding bacteria into two clusters, one containing the apochlorotic relatives of the cyanobacteria, mainly filamentous organisms, the other containing the unicellular gliding bacteria. The latter are united in a class, *Flexibacteriae*, which is divided into two orders, the *Myxobacterales* and the *Cytophagales*. While the myxobacteria are likely to form a natural group, because all of them go through a unique and complex life cycle, and the G+C content of their DNA falls into the narrow range of 68 to 72%, the members of the order *Cytophagales* are genetically much more divers as seen from the wide G+C range of their DNA (28 to 68 mol%). To answer the question whether or not members of the *Myxobacterales* form a phylogenetically coherent group we analyzed the 16S rRNA of 5 species from 5 genera of this order and compared the RNase T1 resistant oligonucleotides to those of two members of the *Cytophagales*, *Cytophaga johnsonae* and *Lysobacter enzymogenes*, and of a variety of non-gliding Gram-negative eubacteria.

Materials and methods

Organisms and culture conditions. *Myxococcus fulvus* strain Mx f2 (= HR 1; = DSM 434) was isolated in 1967 from deer dung collected in Finland Forest, Minnesota, USA; *Cytobacter fuscus* strain Cb f2 (= HR 1) in 1977 from rabbit dung collected on Teneriffe, Spain; *Stigmatella aurantiaca* strain Sg a1 (= HR 2) in 1966 from bark of a rotting willow trunk in Minneapolis, Minnesota; *Sorangium cellulosum* ssp. *fulvum* strain So ce14 is strain ATCC 25532 (= J. E. Peterson SMP 78) and is the producer of the antibiotic ambruticin (Ringel et al. 1977); *Nannocystis exedens* strain Na e1 (= HR 1; = DSM 71) is the type strain (Reichenbach 1970).

Offprint requests to: E. Stackebrandt

Table 1. Oligonucleotide catalogues of myxobacteria. The sequences listed are found in the organisms as numbered: *1, Myxococcus fulvus; 2, Stigmatella aurantiaca; 3, Cystobacter fuscus; 4, Sorangium cellulosum; 5, Nannocystis exedens*

Sequence	Organisms
6-mers	
CCCACG	1
CCCAAG	1–3
CACAAG	1–5
CAAACG	4
CCUCAG	1, 3
CUCCAG	1, 2, 4, 5
UCCACG	1–5
CUAACG	1–5
CAACUG	1
AACCUG	1, 4, 5
AACUCG	4
CAAUAG	5
UCAAAG	4
UAAACG	1–5
AUAACG	5
AACUAG	1–3
AAUACG	1–5
AAACUG	1–3
AAAAUG	4
UUCCCG	1–5
CCUUCG	4, 5
CCUCUG	1–3
UCUCAG	1, 2, 5
UCACUG	3
AUCCUG	1–5
CAAUUG	2
UAACUG	1–4
UAAUCG	1–3, 5
AUAUCG	4, 5
AACUUG	4
UAAUAG	5
UCUUCG	2, 5
CAUUUG	4
7-mers	
CCCCCAG	4
CACCCCG	4
ACCCCCG	1–3
CCAACCG	2
AACACCG	1–3
CAAACAG	1–5
CCCUCAG	1, 2
CCACCUG	1, 3
CACUCCG	5
CAUCCCG	5
CAACUCG	1–5
UAACACG	1–5
AACAUCG	4
UACAAAG	5
CCCUUCG	5
CUACCUG	2
UCCUCAG	4
ACUCCUG	4
CUAAUCG	1–3
CAUUACG	1–3
AACUCUG	5
AAUCUCG	5
CAUUAAG	4
UAAUACG	5
AAAUUCG	1–5
CCUUCUG	4
7-mers	
CCUUUCG	1
UUCUCCG	3
CCUUUAG	1–3
UCAAUUG	2
UAAUCUG	2, 4
AAUCUUG	4
AAUAUUG	5
AAUUUUG	1–3
8-mers	
CCCCCAAG	4
CCAACCCG	1, 2, 4
CCCAUCAG	1–5
CCACACUG	1–4
CCAACUCG	3
CCAAUCCG	4
UACAAACG	4
AUAACCAG	1, 2
AAUACCAG	5
CUCACAUG	1, 2
CACUCUAG	4
AUACCCUG	1–5
UCACACUG	5
AAUUCCCG	5
ACUCCAUG	1–3
CUAAUACG	4
CUACAAUG	1–5
UUAAACCG	1, 3
UAAUACCG	2
UAUACAAG	2, 3
UAAUACAG	1–3
CCCUUAUG	4, 5
CACUUUCG	1–3
UCCUCAUG	1–5
AUCUCUAG	2, 3
AAUUCUCG	4
AUAAUCUG	3
AAUCAUUG	5
AAUUACUG	4
CCUUUAUG	1–3
ACUCUUUG	4
AAUUAUUG	1–3
UUUCUUCG	1
9-mers	
CCCACCAAG	1–3
AAAAAACCG	4
CAACCCUCG	1–3
CCUACCAAG	4
CUCACCAAG	5
CUACACACG	1–5
UACACACCG	1–5
AAACUCACG	4
CCACCAUUG	5
CUAACUCCG	5
CAAUCCUCG	2, 3
ACCCCUUAG	5
ACUCCUACG	1–5
ACAUCCUCG	1–3
CUAAUACCG	5
UCUAAACCG	5

Table 1. Continue

Sequence	Organisms
9-mers	
AUUACACAG	4
CUAACUCUG	4
UAAUCCCUG	4
UUUAAUUCG	5
10-mers	
CCCUACCAAG	5
AAAACCCCUG	3
CAUAAAACCG	1–3
CUCAACCCUG	5
CAACCCUUAG	1
CUAAUACCAG	2
AAUCCUUAAG	2
CCUCUUCAUG	4
11-mers	
AACCUCAACCG	5
CCUAACACAUG	1–3, 5
AAUUCCCCAAG	1–3
AACCUUACCUG	1–5
CUUAACACAUG	4
UACCCCUUUAG	4
UAUCUCCUUAG	5
12-mers	
CAACCCCUAUCG	4, 5
CUAACAUCCACG	4
CUAAUACUCCAG	3
UUAAAUCCACUG	5
AUAUUUAACUCG	4
13-mers	
CUAUCACAACCAG	1
UCACUUCACCAAG	1
CUAUCACAUCCAG	3
CUAUCACUUCCAG	2
14-mers	
UAAUCAACCCCUCG	5
ACUAAAACUCAAAG	1–5
18-mers	
AAAACCCCCAACCUA(AC)G[a]	2
CAAAUCUCAAAAAACCAG	5
Modified oligonucleotides	
$\overset{*}{U}$AACAAG[b]	1–5
UCA$\overset{*}{C}$ACCAUG[b]	1–5
CUAACUCU$\underset{*}{\overline{UU}}$G[b]	1–3
3′terminus	
AUCACCUCCUUUCU$_{OH}$	1–5

[a] Order uncertain
[b] Modified nucleotide

All organisms were cultivated in shake flasks at 160 r.p.m. and 30° C, using 1 l Erlenmeyer flasks with 300 ml of medium. Mx f2, Cb f2 and Sg a1 were grown in cas l.m. (Casitone, Difco 1%; $MgSO_4 \cdot 7\ H_2O$ 0.15%; pH 7.2); So ce14 in Amb l.m. (soluble starch 0.5%; Casitone, Difco 0.25%;

Table 2. Binary comparisons among the 16S rRNA cataologues of myxobacteria and various sulphur- and non-sulphur purple bacteria and their relatives and other referece organisms

	Myxococcus fulvus	*Stigmatella aurantiaca*	*Cystobacter fuscus*	*Sorangium cellulosum*	*Nannocystis exedens*
Myxobacteria					
Myxococcus fulvus	1.0	0.80	0.80	0.42	0.43
Stigmatella aurantiaca	0.80	1.0	0.78	0.41	0.41
Cystobacter fuscus	0.80	0.78	1.0	0.39	0.40
Sorangium cellulosum	0.42	0.41	0.39	1.0	0.44
Nannocystis exedens	0.43	0.41	0.40	0.44	1.0
Non-sulphur purple bacteria and relatives I					
Rhodopseudomonas sphaeroides (1)	0.33	0.33	0.32	0.30	0.37
Rhodopseudomonas capsulata (1)	0.31	0.31	0.32	0.25	0.34
Rhodopseudomonas palustris (1)	0.27	0.26	0.26	0.26	0.34
Rhodopseudomonas viridis (1)	0.35	0.34	0.33	0.30	0.36
Rhodomicrobium vannielii (1)	0.28	0.27	0.27	0.27	0.31
Rhodospirillum rubrum (1)	0.34	0.32	0.35	0.31	0.36
Nitrobacter winogradskyi (2)	0.26	0.25	0.25	0.27	0.32
Aquaspirillum itersonii (3)	0.34	0.33	0.33	0.32	0.40
Azospirillum brasiliense (3)	0.40	0.36	0.37	0.36	0.42
Non-sulphur purple bacteria and relatives II					
Rhodopseudomonas tenue (1)	0.30	0.29	0.29	0.32	0.31
Rhodopseudomonas gelatinosa (1)	0.30	0.28	0.28	0.34	0.30
Aquaspirillum serpens (3)	0.28	0.27	0.28	0.28	0.32
Aquaspirillum gracile (3)	0.32	0.31	0.31	0.29	0.29
Spirillum volutans (3)	0.23	0.23	0.22	0.28	0.28
Nitrosolobus spec	0.27	0.26	0.26	0.25	0.27
Sulphur purple bacteria and relatives					
Chromatium vinosum (1)	0.29	0.28	0.30	0.28	0.37
Ectothiorhodospira halochloris	0.32	0.31	0.34	0.31	0.35
Escherichia coli (4)	0.29	0.29	0.30	0.26	0.34
Oceanospirillum maris (3)	0.27	0.25	0.27	0.36	0.36
Oceanospirillum minutulum (3)	0.25	0.25	0.26	0.26	0.31
Serpens flexibilis (3)	0.27	0.29	0.27	0.28	0.38
Cellulomonas flavigena	0.24	0.22	0.24	0.25	0.22
Streptococcus mutans	0.25	0.24	0.27	0.22	0.27
Nostoc strain MAC (5)	0.21	0.21	0.21	0.23	0.25
Synechococcus 6301 (5)	0.20	0.20	0.21	0.21	0.18
Deinococcus radiodurans (6)	0.18	0.19	0.19	0.21	0.27
Cytophaga johnsonae	0.17	0.17	0.18	0.18	0.23

The oligonucleotide catalogues of the reference organisms have been published: (1) = Gibson et al. (1979); (2) = Seewaldt et al. (1982); (3) = Woese et al. (1982); (4) = Woese et al. (1974); (5) = Bonen et al. (1979); (6) = Brooks et al. (1980).

$MgSO_4 \cdot 7\,H_2O$ 0.05%; K_2HPO_4 0.025%; from Ringel et al. 1977); and Na e1 in PL l.m. (Probion LS 600, single cell preparation from Hoechst 1%; $MgSO_4 \cdot 7H_2O$ 0.1%; $CaCl_2 \cdot 2\,H_2O$ 0.1%; pH 7.0). The cells were harvested in middle to upper log phase by centrifugation and immediately frozen at 80°C until needed for the experiments.

Isolation of 16S rRNAs, digestion of RNAs with RNase T_1 (Calbiochem-Behring, La Jolla, CA, USA) labelling of the 5′ ends with γ-^{32}P-ATP [New England Nuclear, Dreieich, FRG (NEN), 1000–3000 Ci mmol^{-1}], fingerprinting of the oligonucleotides and the sequence determination followed described methods (Stackebrandt et al. 1981, 1982) with the modifications that the phosphatase-containing polynucleotide T_4-kinase used in previous studies was replaced by a phosphatase-free polynucleotide T_4-kinase (NEN, EC 2.7.1.78). The calculation of the binary coefficients, S_{AB} values, has been described by Gibson et al. 1979.

Results and discussion

The oligonucleotide catalogues for each of the five representatives of Myxobacterales are shown in Table 1. Table 2 contains the respective binary association values (S_{AB} values) together with those, found between myxobacteria and a variety of Gram-negative eubacteria and representatives of other major lines of descent. Figure 1 is a dendrogram, derived from the S_{AB} values.

All myxobacteria investigated are members of one evolutionary line of descent in which *Myxococcus fulvus*, *Stigmatella aurantiaca* and *Cystobacter fuscus* are closely

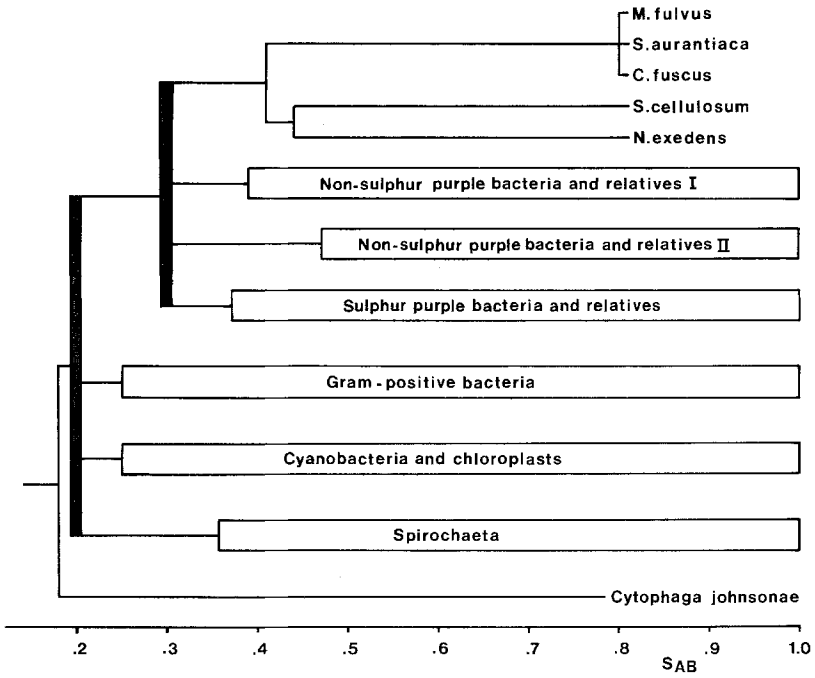

Fig. 1
Dendrogram showing the relationship of myxobacteria among each other and to *Cytophaga johnsonae* and various groups of eubacteria

related (S_{AB} values above 0.78), while *Nannocystis exedens* and *Sorangium cellulosum* are clearly separated from each other and from the *Myxococcus-Stigmatella-Cystobacter* group by S_{AB} values of 0.44 and 0.41, respectively.

At a low level of relationship the phylogenetic structure of the myxobacteria is in accord with their present classification (Reichenbach 1974, 1981), in which representatives of the suborder Cystobacterineae (*Myxococcus*, *Stigmatella* and *Cystobacter*) are separated from those of the second suborder Sorangineae (*Sorangium*, *Nannocystis*). This classification is based on pronounced differences in the shape of vegetative cells and myxospores and in the morphology of the swarm colony, and is also supported by chemosystematic differences, e.g. the staining behavior of the slime (McCurdy 1969) and the fatty acid pattern (Fautz et al. 1981). However, *Sorangium cellulosum* and *Nannocystis exedens*, members of one family, Sorangiaceae, are phylogenetically far less related among each other than members of Cystobacterineae, classified in two families, Myxococcaceae and Cystobacteraceae. The high degree of relationship we found among members of the latter two families brings their present classification into question. The phylogenetic analysis does not relate members of the Cystobacteraceae, *S. aurantiaca* and *C. fuscus* to the exclusion of *Myxococcus fulvus*. S_{AB} values of ≥ 0.78 found for these three species have also frequently been found among species of various coryneform and actinomycete genera (Stackebrandt et al. 1980; Stackebrandt and Woese 1981b), *Bacillus* (Fox et al. 1980), *Staphylococcus* (Ludwig et al. 1981) and *Legionella* (Ludwig and Stackebrandt 1983).

Our results point towards a classification of members of the Cystobacterineae within one taxon, which, from the 16S RNA data could be considered a genus in spite of considerable differences in fruiting body and cell morphology. To get more insight into the situation, DNA-DNA hybridization should be applied.

Myxobacteria are specifically related to members of the broad group of purple bacteria and their non-phototrophic relatives (Gibson et al. 1979; Woese et al. 1982; Fox et al. 1980; Stackebrandt and Woese 1981a). S_{AB} values found for myxobacteria and organisms defining the three subgroups of the purple bacteria (Gibson et al. 1979) range between 0.25 and 0.42 for non-sulphur purple bacteria of group I (*Rhodopseudomonas sphaeroides* and relatives), 0.23–0.34 for non-sulphur purple bacteria of group II (*Rhodospirillum tenue* and relatives) and 0.35–0.38 for sulphur purple bacteria (*Chromatium vinosum* and relatives). Values in this range have also been found to separate members of the three subgroups of this major phylogenetic grouping (Gibson et al. 1979; Woese et al. 1982).

As also seen for the major lines of descent (Fox et al. 1980; Stackebrandt and Woese 1981a), the three subgroups of purple bacteria and the myxobacteria-subgroup diverged from each other over a relatively short period of time, making the exact order of branching points difficult to determine. These regions of the phylogenetic tree are therefore indicated as solid bars. The independence of the myxobacteria group as a fourth subgroup of the purple bacteria and their relatives is also demonstrated by the lack of those oligonucleotides in the catalogues of myxobacteria, which are characteristic for members of the three individual subgroups of the purple bacteria (Gibson et al. 1979). Surprisingly high S_{AB} values were found between certain myxobacteria and several members of the purple bacteria subgroup I, especially with *Aquaspirillum itersonii*, *Azospirillum brasiliense* and *Rhodospirillum rubrum* Cluster Ic, according to Gibson et al. 1979). Values up to 0.42 were found for *Nannocystis exedens* and *A. brasiliense*, which is as high as those separating *N. exedens* from the other myxobacteria. However, we have reasons to assume that these values do not reflect a specific relationship of these organisms. Firstly, as indicated above, the oligonucleotide catalogue of *N. exedens* does not contain the oligonucleotide 'signature' for members of cluster Ic, and, secondly, *Nannocystis exedens* and the two spirilla show high S_{AB} values not only among each other but each of them shows unexpectedly high S_{AB} values to organisms which belong to the different subgroups of purple bacteria and their relatives

(Table 2, Woese et al. 1982) and even to organisms belonging to different main lines of descent, as seen in Table 2 for *N. exedens* and *Deinococcus radiodurans* and *Cytophaga johnsonae*. We think this is caused by an evolutionary rate (the rate at which mutations become fixed in the 16S rRNA), that is slower than in other bacteria. This results in the presence of more regions which are conserved (carried over from a common ancestor) in the primary structure of the 16S rRNA and consequently in a higher number of common RNase T_1 resistant oligonucleotides. Organisms with a 'slow clock' have artificially increased S_{AB} values with unrelated organisms, compared to those organisms which are isochronic, which is by and large true for most of the eubacteria (Stackebrandt and Woese, 1981 a). So far, a few organisms with a 'fast clock' (Woese et al. 1980; Stackebrandt and Woese 1981 a) have been encountered. These organisms, detectable by the absence of conserved and/or universal oligonucleotides, present in the catalogues of organisms which appear isochronic, show branching points that are deeper than their true branchings, as seen with the mycoplasmas (Woese et al. 1980). With more organisms investigated the S_{AB} values have to be examined carefully to avoid misinterpretation of relationships.

Myxobacteria are phylogenetically not specifically related to any other group of gliding bacteria investigated so far. Myxobacteria are clearly not related to *Cytophaga johnsonae*, *Saprospira grandis*, *Flexibacter* (unpublished results) and *Lysobacter enzymogenes*, which are also unrelated among each other, and myxobacteria are not related to *Herpethosiphon giganteus*, which is remotely related to *Chloroflexus* (Woese, Ludwig, Stackebrandt, unpublished). Except for *Lysobacter enzymogenes*, a specific relative of the xanthomonads and *Pseudomonas maltophila* (subgroup of sulphur purple bacteria) (Stackebrandt and Woese 1981 a), gliding bacteria so far are not found to be closely related with non-gliding organisms. Our data indicate that gliding motility is an ancient feature of eubacteria, since gliding bacteria show deep branching points among each other and they are members of different major lines of descent in the phylogenetic tree of the 16S rRNA of eubacteria.

Acknowledgement. This work was financed by the Gesellschaft für Biotechnologische Forschung through a research grant of the German Collection of Microorganisms.

References

Bauwens M (1980) Intrageneric and intergeneric similarities of ribosomal ribonucleic acid cistrons of *Flavobacterium*. Antonie van Leeuwenhoek J Microbiol Serol 46:95

Behrens H (1978) Charakterisierung der DNA gleitender Bakterien der Ordnung Cytophagales. PhD Thesis, Technical University Braunschweig, FRG

Bonen L, Doolittle WF, Fox GE (1979) Cyanobacterial evolution: results of 16S ribosomal ribonucleic acid sequence analysis. Can J Biochem 57:879–888

Brooks BW, Murray RGE, Johnson JL, Stackebrandt E, Woese CR, Fox GE (1980) Red pigmented micrococci: a basis for taxonomy. Int J Syst Bacteriol 30:627–646

Callies E, Mannheim W (1980) Deoxyribonucleic acid relatedness of some menaquinone-producing *Flavobacterium* and *Cytophaga* strains. Antonie van Leeuwenhoek J Microbiol Serol 46:41–49

Fautz E, Grotjahn L, Reichenbach H (1981) 2- and 3-hydroxy fatty acids as valuable chemosystematic markers in gliding bacteria. In: Reichenbach H, Weeks OB (eds) The *Flacobacterium-Cytophaga* group. Verlag Chemie, Weinheim, pp 127–133

Fox GE, Stackebrandt E, Hespell RB, Gibson J, Maniloff I, Dyer TA, Wolfe RS, Balch WE, Tanner RS, Magrum LJ, Zablen LB, Blackemore R, Gupta R, Bonen L, Lewis BJ, Stahl DA, Luehrsen KR, Chen KN, Woese CR (1980) The phylogeny of prokaryotes. Science 209:457–463

Gibson J, Stackebrandt E, Zablen LB, Gupta R, Woese CR (1979) A phylogenetic analysis of the purple photosynthetic bacteria. Curr Microbiol 3:59–64

Ludwig W, Stackebrandt E (1983) A phylogenetic analysis of *Legionella*. Arch Microbiol 135:45–50

Ludwig W, Schleifer KH, Fox GE, Seewaldt E, Stackebrandt E (1981) A phylogenetic analysis of staphylococci, *Peptococcus saccharolyticus* and *Micrococcus mucilaginosus*. J Gen Microbiol 125:357–366

McCurdy HD (1969) Studies on the taxonomy of the Myxobacterales. I. Record of Canadian isolates and survey of methods. Can J Microbiol 5:1453–1461

Moore RL, McCarthy BJ (1967) Comparative study of ribosomal ribonucleic acid cistrons in Enterobacteria and Myxobacteria. J Bacteriol 94:1066–1074

Reichenbach H (1970) *Nannocystis exedens* gen. nov., spec. nov., a new myxobacterium of the family Sorangiaceae. Arch Mikrobiol 70:119–138

Reichenbach H (1974) Die Biologie der Myxobakterien. Biol Uns Zeit 4:33–45

Reichenbach H (1981) Taxonomy of the gliding bacteria. In: Starr MP, Ingraham JL, Balows A (eds) Annual review of microbiology 35. Annual Review Inc, Palo Alto, pp 339–364

Reichenbach H, Dworkin M (1981) The order Myxobacterales. In: Starr MP, Stolp H, Trüper HG, Balows A, Schlegel HG (eds) The prokaryotes. Springer, Berlin Heidelberg New York, pp 328–355

Ringel SM, Greenough RC, Roemer S, Connor D, von Strandtmann M (1977) Ambruticin (W 7783), a new antifungal antibiotic. J Antibiotics 30:371–375

Seewaldt E, Schleifer KH, Bock E, Stackebrandt E (1982) The close phylogenetic relationship of *Nitrobacter* and *Rhodopseudomonas palustris*. Arch Microbiol 131:287–290

Stackebrandt E, Woese CR (1981 a) The evolution of prokaryotes. In: Carlile MI, Collins IF, Moseley BEB (eds) Molecular and cellular aspects of microbial evolution. Cambridge University Press, Cambridge, pp 1–32

Stackebrandt E, Woese CR (1981 b) Towards a phylogeny of actinomycetes and related organisms. Curr Microbiol 5:131–136

Stackebrandt E, Lewis BJ, Woese CR (1980) The phylogenetic structure of the coryneform group of bacteria. Zbl Bakt Hyg I Abt Orig C2:137–149

Stackebrandt E, Ludwig W, Schleifer KH, Gross HJ (1981) Rapid cataloging of ribonuclease T_1 resistant oligonucleotides from ribosomal RNAs for phylogenetic studies. J Mol Evol 17:227–236

Stackebrandt E, Seewaldt E, Ludwig W, Schleifer KH, Huser BA (1982) The phylogenetic position of *Methanothrix soehngenii*. Elucidated by a modified technique of sequencing oligonucleotides from 16S rRNA. Zbl Bakt Hyg Abt I Orig C3:90–100

Woese CR, Sogin ML, Sutton LAC (1974) Procaryote phylogeny. I. Concerning the relatedness of *Aerobacter aerogenes* to *Escherichia coli*. J Mol Evol 3:293–299

Woese CR, Fox GE (1977) Phylogenetic structure of the prokaryotic domain: The primary kingdoms. Proc Natl Acad Sci USA 74:5088–5090

Woese CR, Maniloff J, Zablen LB (1980) Phylogenetic analysis of the mycoplasmas. Proc Natl Acad Sci USA 77:494–498

Woese CR, Blanz P, Hespell RB, Hahn M (1982) Phylogenetic relationships among various helical bacteria. Curr Microbiol 7:119–124

Received April 10, 1983/Accepted May 4, 1983