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# Distribution of Isoprenoid Quinone Structural Types in Bacteria and Their Taxonomic Implications

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## INTRODUCTION

Chemotaxonomic methods, such as cell wall analyses and deoxyribonucleic acid base ratio and homology determinations, now figure prominently in microbial systematics. To date, the use of lipids as chemical characters has generally received less attention by bacterial taxonomists. However, studies involving fatty acid and polar lipid analyses have yielded encouraging results (146). A class of terpenoid lipids with a similar inherent potential in chemotaxonomy are the isoprenoid or respiratory quinones (34, 39, 48, 227).

Isoprenoid quinones are constituents of bacterial plasma membranes (176) and play important roles in electron transport, oxidative phosphorylation, and, possibly, active transport (19, 65, 184, 211). The results of the early studies of Bishop et al. (17), Crane (53), Lester and Crane (148) and Page et al. (174) indicated that the inherent structural variation exhibited by isoprenoid quinones might be of value in microbial systematics. The majority of subsequent studies on the isoprenoid quinones of bacteria have been performed by biochemists, whose primary interest is in the function of these compounds in bacterial cells and not in their value as taxonomic markers. Over the last decade, however, there have been a number of comparative studies designed to assess the value of these compounds in microbial taxonomy (34, 35, 38-50, 200, 227, 239-248). Thus, there is now a considerable body of material on isoprenoid quinone structural types and their distribution in a large number of bacterial genera. However, a great deal of this information is fragmentary and scattered through the literature in papers not necessarily concerned with taxonomy. Therefore, it seemed opportune to review the literature in this field and, where possible, to attempt to evaluate the data in the context of taxonomic groupings based on other criteria.

## STRUCTURE AND ANALYSIS

### General Structures

Two major structural groups of bacterial isoprenoid quinones can be recognized, the naphthoquinones and benzoquinones. Naphthoquinones can be divided further into two main types on the basis of structural considerations; these are the phylloquinones (Fig. 1, compound I) and the menaquinones (Fig. 1, compound II).

Phylloquinone, or vitamin $K_1$, was first isolated in 1939 from alfalfa and was shown by MacCorquodale et al. (153) in degradation and synthetic studies to be 2-methyl-3-phytyl-1,4-naphthoquinone. Normally, phylloquinone is associated with the green parts of plants and occurs less commonly in bacteria. The first representative of the menaquinone family (formerly designated vitamin $K_2$) was isolated by McKee et al. (160) from putrefied fish meal and was thought to be 2-methyl-3-farnesyl-farnesyl-1,4-naphthoquinone (15, 160). However, it was not until 1958 that the plurality of menaquinones was established, when it was shown that the main compound from fish meal was a menaquinone with seven isoprene units (abbreviated MK-7) and that the related compound MK-6 was present only in minor amounts (109, 110). In 1948, Tishler and Sampson (222) found that a soil bacterium named *Bacillus brevis* contained a menaquinone which, as we now know, had a $C_{35}$ (farnesylgeranylgeranyl) side chain. Another member of the menaquinone series was discovered in 1949 by Francis et al. (74) in *Mycobacterium tuberculosis*. This compound was subsequently shown to have a $C_{45}$ (solanesyl) side chain (171). Today, naturally occurring menaquinones form a rather large class of molecules, and the length of the C-3 isoprenyl side chains in these molecules varies from 1 to 14 isoprene units (200, 218).

Varying degrees of saturation or hydrogenation of the C-3 polyprenyl side chain have also been reported in bacterial menaquinones. The principal menaquinone isolated from *Mycobacterium phlei* was shown to have a $C_{45}$ side chain with one isoprene unit saturated [abbreviated MK-9($H_2$)] (82), whereas the principal menaquinone from *Corynebacterium diphtheriae* was shown to be MK-8($H_2$) (9, 195, 196). Subsequent studies have indicated that such dihydromenaquinones are widespread in corynebacteria and mycobacteria, whereas even more highly saturated menaquinones have been reported in certain actinomycetes (34, 48, 161, 163, 243, 244). A rather unusual modification of the polyprenyl side chain of menaquinones has been observed in chlorobiumquinone (Fig. 1, compound III), which is produced by a green photosynthetic bacterium named "*Chlorobium thiosulphatophilum*" (see below for an explanation of quotation marks around names of organisms) (78, 185). Whereas initially chlorobiumquinone was thought to be a modified MK-7 in which the first methylene of the normal polyisoprenoid side chain was absent (78), subsequent work by Powls et al. (181) has shown that chlorobium-

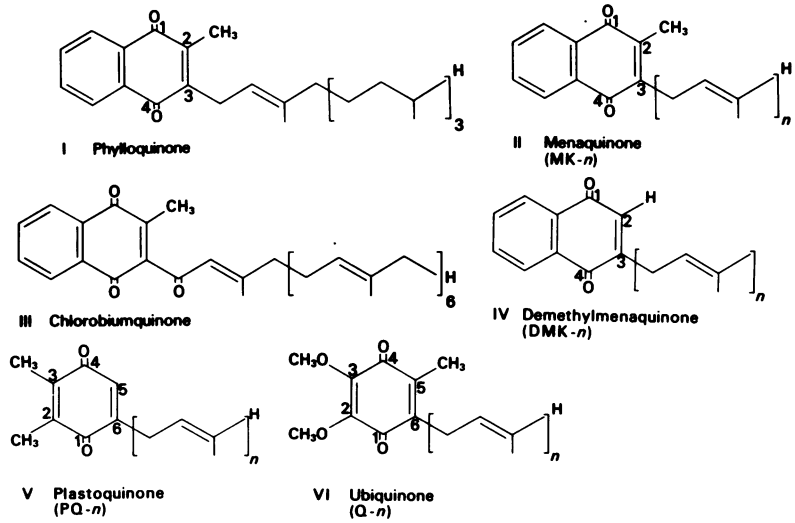



FIG. 1. *Structures of phylloquinone (compound I), menaquinone (compound II), chlorobiumquinone (compound III), demethylmenaquinone (compound IV), plastoquinone (compound V), and ubiquinone (compound VI).*

quinone is in fact 1'-oxomenaquinone with seven isoprene units (1'-oxomenaquinone-7). Chlorobiumquinone is the only example of a bacterial polyisoprenoid quinone containing a side chain carbonyl group. Demethylmenaquinones (Fig. 1, compound IV), which lack the ring methyl substituent (C-2), have also been isolated from bacteria (7, 8, 39, 40, 150). To date, demethylmenaquinones with polyprenyl side chains varying in length from one to nine isoprene units have been described (98). An unusual desmethylmenoquinol derivative has been isolated from green photosynthetic bacteria. This compound was assigned the structure 4-*O*-methyl-2-heptaprenyl naphthoquinol by Powls (180).

The second major class of bacterial isoprenoid quinones are the benzoquinones, of which there are two main types, the plastoquinones (Fig. 1, compound V) and the ubiquinones (Fig. 1, compound VI).

Plastoquinone was isolated originally by Kofler (135) in 1946 from alfalfa but was not identified. This quinone was rediscovered by Crane in 1959 and in subsequent studies was shown to be 2,3-dimethyl-5-solanesyl-1,4-benzoquinone (abbreviated PQ-9) (136, 137). Plastoquinone is found not only in the photosynthetic tissues of higher plants but also in red, brown, and green algae and in blue-green algae (cyanobacteria) (148, 218, 221). However, it appears to be absent from photosynthetic bacteria.

The discovery of ubiquinones (formerly called coenzyme Q) was the result of independent studies by Morton and associates in Liverpool, England, and Crane and colleagues in the United States. Ubiquinones contain a 2,3-dimethoxy-5-methyl-1,4-benzoquinone nucleus with a polyprenyl side chain in position 6 (Fig. 1, compound VI) (52, 72, 111). Like menaquinones, the ubiquinones are distributed widely in nature, and a whole range of isoprenologs (Fig. 1, compound VI; $n = 1$ to 12) are found in bacteria (168, 218, 220, 221). However, in addition to the simple homologs of ubiquinones, other modifications of the side chains, such as hydrogenation (218, 221) and even epoxidation (77), have been discovered. In rhodoquinone, a purple quinone isolated from *Rhodospirillum rubrum* by Glover and Threlfall (87), the methoxyl group in position 3 of ubiquinone is replaced by an amino group (Fig. 2, compound VII) (164, 165, 218).

Recently, a rather novel quinone, designated caldariellaquinone, was isolated from the extremely thermophilic and acidophilic bacterium "*Caldariella acidophila*" (61) and was shown to be 6-(3,7,11,15,19,23-hexamethyltetracosyl)-5-methylthiobenzo-[b]-thiopen-4,7-quinone (Fig. 2, compound IX) (59). Caldariellaquinone is the only sulfur-containing bacterial isoprenoid quinone that has been isolated to date.

## Extraction and Purification

Isoprenoid quinones are susceptible to strong acid or alkaline conditions and are photooxidized quite rapidly in the presence of oxygen and strong light (65, 151). Thus, it is preferable to conduct extraction and subsequent purification procedures as rapidly as possible in dim light, avoiding extremes of pH. Isoprenoid quinones are soluble in the usual lipid solvents; the most popular of these are acetone, diethyl ether, chloroform, ethanol, and petroleum ether (65). Adequate extraction of these components can be achieved with any one of these solvents or a mixture of two. any procedures which are used extensively are direct extraction of bacterial cells with acetone-petroleum ether (18, 65) and direct extraction with a chloroform-methanol (2:1, vol/vol) mixture (48, 65). Both of these extraction procedures yield a complex mixture of lipids plus a small amount of nonlipid material. Isoprenoid quinones can be isolated from this mixture by a variety of chromatographic procedures; the most common of these are adsorption column chromatography and adsorption thin-layer chromatography (65). Preparative chromatography in

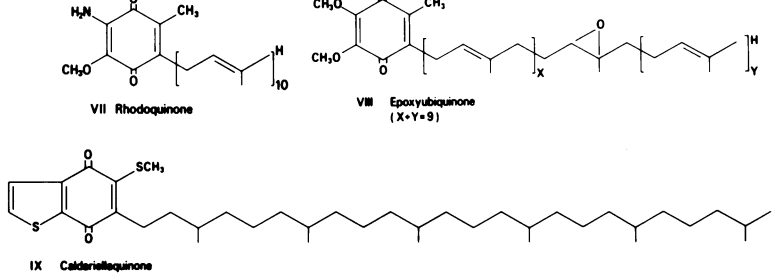



FIG. 2. *Structures of rhodoquinone (compound VII), epoxyubiquinone (compound VIII), and caldariellaquinone (compound IX).*

which layers of Silica Gel HF-254 and solvent mixtures such as petroleum ether (boiling point, 60 to 80°C)-diethyl ether (85:15, vol/vol) are used provides a particularly simple and rapid method for separating menaquinones ($R_f \sim 0.7$) and ubiquinones ($R_f \sim 0.4$) (48). Isoprenoid quinones may be detected easily on the resulting chromatograms by brief irradiation with short-wave ultraviolet light (254 nm) and may be eluted with a variety of solvents, such as acetone or chloroform.

### Chromatographic Analysis

The compositions of purified isoprenoid quinone fractions may be investigated further by using silver ion-impregnated and reverse-phase thin-layer chromatography. The ability of silver ions to form reversible complexes with olefinic bonds is well established. The use of Silica Gel G impregnated with silver nitrate and developing in nonpolar solvent mixtures, such as methanol-benzene (5:95, vol/vol), permit the separation of isoprenoid mixtures according to the number of double bonds that the compounds contain. The incorporation of indicators, such as rhodamine 6G, into the layers permits easy visualization of the separated isoprenologs on developed chromatograms (65). In reverse-phase partition chromatography a stationary, nonvolatile hydrocarbon (such as liquid paraffin or hexadecane) and polar developing mixtures (such as acetone-water or dimethyl formamide-water) are used (54, 65, 67). Reverse-phase chromatography facilitates the separation of isoprenoid quinone components according to their overall physical properties, which depend mainly on their chain lengths and their degrees of unsaturation. Since natural mixtures of isoprenoid quinones often vary both in degree of unsaturation and in polyisoprenoid chain length, both of these chromatographic techniques should be used to define the composition of an unknown mixture of quinones. The value of silver ions and reverse-phase thin-layer chromatography in the analysis of bacterial menaquinone mixtures has been demonstrated in two excellent studies (67, 98).

### Physicochemical Analysis

**Ultraviolet spectrophotometry.** Purified isoprenoid quinones can be analyzed further by using a variety of physicochemical techniques (207). In particular, ultraviolet spectroscopy provides a simple method for investigating the category or class to which an unknown isoprenoid quinone belongs. Details of the ultraviolet absorption characteristics of some of the major types of bacterial quinones are shown in Table 1.

The ultraviolet spectra of the majority of the bacterial naphthoquinones fall into the following two main groups: (i) the 2,3-disubstituted quinones, as exemplified by phylloquinone and the menaquinones; and (ii) the monosubstituted (or demethylated) quinones, such as demethylmenaquinones. Both menaquinones and phylloquinones exhibit qualitatively identical ultraviolet spectra, with five absorption maxima ($\lambda_{max}$) at 242, 248, 260, 269, and 326 nm and one point of inflection at 238 nm (Fig. 3 and Table 1). Absorption bands at 242, 248, and 238 nm (shoulder) are due to benzenoid contributions, whereas bands at 260 and 269 nm are due to quinone absorption (65). However, removal of the methyl group from C-2 of the naphthoquinone nucleus (as in demethylmenaquinones and demethylphylloquinones) causes a shift in the quinone absorption contribution of about 6 nm to shorter wavelengths ($\lambda_{max}$, 254 and 263 nm), whereas the benzenoid contributions ($\lambda_{max}$, 243 and 248 nm and 238 nm [point of inflection]) remain virtually unaltered. Thus, ultraviolet spectrophotometry provides a simple method for distinguishing menaquinones and phylloquinones from their demethylated derivatives (Table 1). Chlorobiumquinone (1'-oxomenaquinone-7) isolated from green photosynthetic bacteria (78, 185) exhibits ultraviolet absorption characteris-

TABLE 1. *Ultraviolet absorption characteristics of menaquinones, ubiquinones, and related compounds*

| Compound | Solvent | $\lambda_{max}$ (nm)[a] | Reference(s) |
|---|---|---|---|
| Phylloquinone | Isooctane | 242, 248, 260, 269, 326, 238 (inf) | 65 |
| Menaquinone | Isooctane | 242, 248, 260, 269, 326, 238 (inf) | 65 |
| Demethylphylloquinone | Isooctane | 243, 248, 254, 263, 326, 238 (inf) | 65 |
| Demethylmenaquinone | Isooctane | 243, 248, 254, 263, 326, 238 (inf) | 65 |
| Chlorobiumquinone | Ethanol | 254, 265 (inf) | 78, 181 |
| Plastoquinone | Isooctane | 254, 262 | 207 |
| Ubiquinone | Ethanol | 275, 405 | 207 |
| Rhodoquinone | Cyclohexane | 251, 280, 320, 500 (inf) | 87 |
| Rhodoquinone | Ethanol | 253, 283, 320, 500 (inf) | 87 |
| Caldariellaquinone | Methanol | 241, 283, 333, 471 | 59 |

[a] Each major peak is underlined. inf, Point of inflection.

tics quite distinct from those of menaquinones and demethylmenaquinones, with $\lambda_{max}$ at 254 nm in ethanol and a point of inflection at 265 nm (181).

The two commonly encountered benzoquinones, plastoquinones and ubiquinones, can be distinguished easily by ultraviolet spectrophotometry. Plastoquinones (Fig. 1, compound V) have $\lambda_{max}$ at 254 and 262 nm (isooctane) (Fig. 4). In contrast, ubiquinones have a $\lambda_{max}$ at about 270 to 275 nm and a second absorption band at 405 to 407 nm (Fig. 5). The replacement of the methoxyl group in position 3 by an amino group, as in rhodoquinone (2-methyl-3-amino-5-methyl-6-nonaprenyl-1,4-benzoquinone) isolated from *R. rubrum*, causes a marked change in the spectrum; in this case, three $\lambda_{max}$ (251 to 253, 280 to 283, and 500 nm) and one point of inflection (320 nm) are produced.

The rather unusual terpenoid benzo-[b]-thiopen-4,7-quinone (designated caldariellaquinone) from "*C. acidophila*" exhibits a very characteristic ultraviolet spectrum ($\lambda_{max}$, 241, 283, 333 and 471 nm), which is quite distinct from the spectrum of any other described bacterial isoprenoid quinone (Table 1).

**Mass spectrometry.** The most precise and sensitive method for determining isoprenoid quinone structure is mass spectrometry. This method provides both accurate molecular weights of the isoprenoid quinones and structural information, such as the nature of the ring system, the length and degree of saturation of the isoprenyl side chain, etc. An excellent review on mass spectral analysis of naphthoquinones and benzoquinones has been published by Sommer and Kofler (207). When subjected to mass spectrometry, both menaquinones and ubiquinones produce characteristic fragmentation patterns (Fig. 6). The base peaks in the mass spectra of menaquinones (including phylloquinone) occur at *m/e* 225 (Fig. 7, compounds X and XI) and are derived from the naphthoquinone nucleus (Fig. 6). Ubiquinones and plastoquinones have corresponding nuclear fragments at *m/e* 235 and 189, respectively (65, 207). Strong peaks in the mass spectra of both menaquinones and ubiquinones corresponding to molecular ions ($M^+$) are observed. The pattern of fragmentation of the isoprenoid substituent at the C-3 position of menaquinones (Fig. 6) is characteristic of the

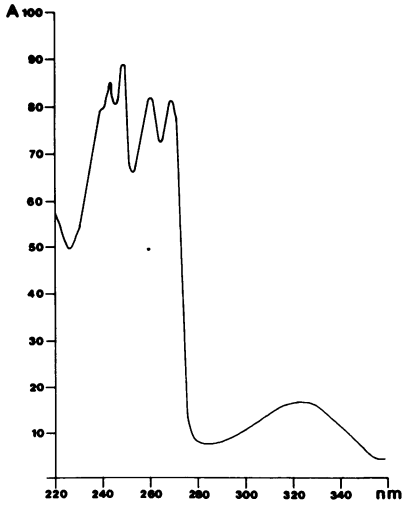



FIG. 3. *Ultraviolet spectrum of MK-6 (solvent, isooctane).*

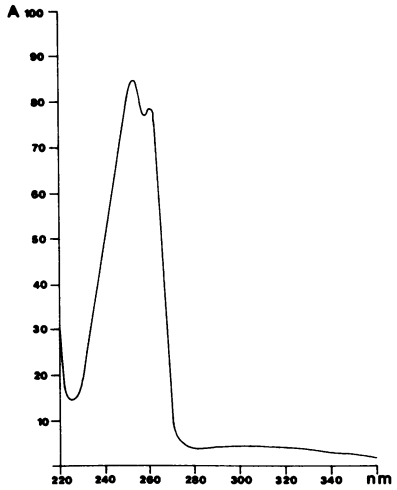



FIG. 4. *Ultraviolet spectrum of PQ-9 (solvent, isooctane).*

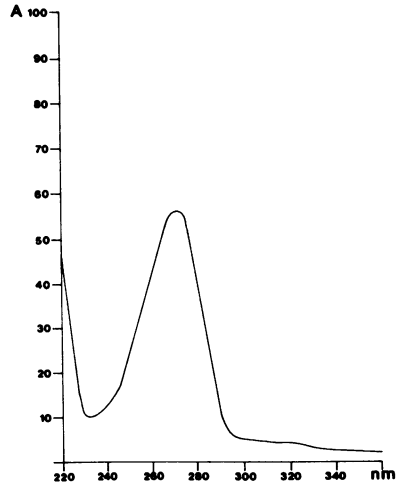



FIG. 5. *Ultraviolet spectrum of Q-10 (solvent, isooctane).*

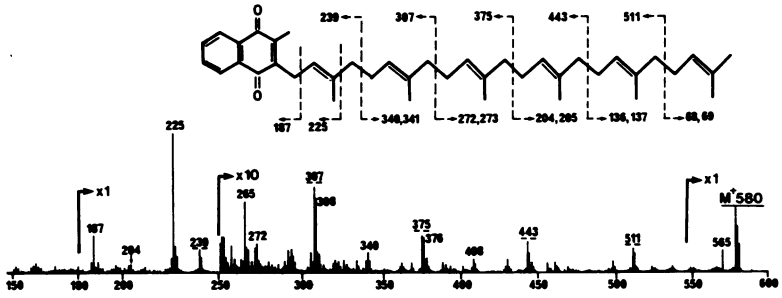


FIG. 6. *Mass spectrum of MK-6 from B. ochraceus.*

cracking pattern exhibited by polyisoprenoid chains in general. Fragmentation of the side chain under electron impact involves solely diallylic bonds, following the rule (M-69) − (68 × *N*), where *N* is the number of isoprene units in the side chain minus one. Thus, using the mass spectrum of MK-6 from *Bacteroides ochraceus* as an illustration (Fig. 6), fragmentation of the side chain involves the loss of a terminal isoprenyl unit $(M-69)^+$, followed by four successive losses of 68 mass units. Saturation of an olefinic bond within the side chain of a menaquinone causes a marked alteration in the cracking pattern and provides information on the position of hydrogenation (5). The fragmentation patterns of the various bacterial isoprenoid quinones (e.g., menaquinones, phylloquinones, plastoquinones, ubiquinones) are all very similar. The simplicity of these patterns and the ease of determining accurate molecular weights provide an unequivocal means for determining isoprenoid quinone structures (207).

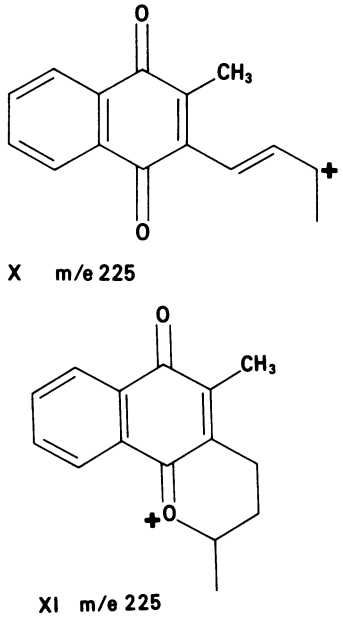


FIG. 7. *Nuclear fragments at m/e 225 (compounds X and XI) derived from the naphthoquinone nuclei of menaquinones.*

## DISTRIBUTION OF ISOPRENOID QUINONES AND TAXONOMIC IMPLICATIONS

Molecular genealogical analyses based upon transfer and ribosomal ribonucleic acid sequence homologies have revealed that bacteria do not constitute a phylogenetically monolithic group (237). The kingdom *Procaryotae* is now considered to contain two phylogenetically distinct groups, the archaebacteria and the eubacteria, including the mycoplasmas and cyanobacteria (73, 237).

Where possible, the names of the bacterial taxa referred to here are names that are included in the Approved Lists of Bacterial Names (206). However, although the Approved Lists now determine the nomenclature of bacteria, it is necessary to refer to strains bearing names not included in the Approved Lists. Where this is done, the names are placed in quotation marks (e.g., "*Actinobacillus actinoides*"). The nomenclature of Rippka et al. (187) is used for the cyanobacteria.

### Archaebacteria

The first organisms recognized as archaebacteria were the methanogens, which are fastidious anaerobes whose metabolism is centered around the reduction of carbon dioxide to methane (237). Detailed studies on the isoprenoid quinone contents of the methanogens have not been performed, although Zeikus and colleagues (249) reported that *Methanobacterium thermoautotrophicum* contains neither menaquinones nor ubiquinones.

Representatives of the extreme halophilic taxa *Halobacterium* and *Halococcus* have also now been identified as archaebacteria (237). Early

studies indicated that unsaturated MK-8 constituted the sole isoprenoid quinones within these extreme halophilic taxa (142, 223). However, a recent systematic study of the genera *Halobacterium* and *Halococcus* has shown that dihydrogenated menaquinones are also present in all species of these genera (49) (Table 2). The extreme thermophilic archaebacterium *Thermoplasma acidophilum* also contains menaquinones as its sole isoprenoid quinones, with MK-7 predominating (143).

An unusual terpenoid, benzo-[b]-thiopen-4,7-quinone (caldariellaquinone), has been isolated from the extreme acidophile "*C. acidophila*" (59). Caldariellaquinone is the only sulfur-containing bacterial isoprenoid quinone known. Although the present isoprenoid quinone data on the archaebacteria are fragmentary, several patterns are evident (Table 2). These suggest that further quinone studies on these taxa could provide information of taxonomic value.

## Eubacteria

For clarity of presentation, the groups of the eubacteria are treated, where possible, as they are in *Bergey's Manual of Determinative Bacteriology*, 8th ed. (21).

**Cyanobacteria.** In *Bergey's Manual of Determinative Bacteriology* (21), the cyanobacteria (blue-green algae) are given little consideration. Subsequent studies by Rippka et al. (187) have indicated that these bacteria can be divided into five major subgroups which contain 22 genera. Systematic studies on the distribution of isoprenoid quinones in the cyanobacteria have not been performed, but preliminary data on the five taxa (Table 3) examined so far suggest that such an investigation may be rewarding.

Cyanobacteria are unusual in that they possess neither ubiquinones nor menaquinones (Table 3). They do contain phylloquinone (vitamin $K_1$) and a plastoquinone (PQ-9), which are indigenous to the plant kingdom but are not normally found in bacteria. Furthermore, members of the genera *Anabaena*, *Chlorogloeopsis*, *Fischerella*, and *Nostoc* have also been reported to contain α-tocopherolquinone (Fig. 8, compound XII), which is normally associated with chloroplasts in higher plants and algae (218). The genus *Synechococcus* apparently lacks α-tocopherolquinone but contains a polar naphthoquinone (probably a monohydroxy derivative of phylloquinone [144]) not reported in the other four species of cyanobacteria that have been examined (Table 3). Sun and co-workers (210) also reported the presence of plastoquinones B and C in a strain of the genus *Anabaena*, al-

TABLE 2. *Distribution of isoprenoid quinones in archaebacteria*

| Taxon | Major isoprenolog(s) | Minor components | Reference(s) |
|---|---|---|---|
| "*Amoebobacter morrhuae*" | MK-8 | | 142 |
| "*Caldariella acidophila*"[a] | Caldariellaquinone | | 60 |
| *Halobacterium cutirubrum* | MK-8 | | 142, 223 |
| *H. cutirubrum* | MK-8 | MK-8($H_2$), MK-7($H_2$), MK-7 | 49 |
| *Halobacterium halobium* | MK-8 | | 142 |
| *H. halobium* NCMB 736, NCMB 764, NCMB 777, and NCMB 2080 | MK-8, MK-8($H_2$) | MK-7($H_2$), MK-7 | 49 |
| *Halobacterium saccharovorum* | MK-8, MK-8($H_2$) | | 49 |
| *Halobacterium salinarium* | MK-8 | | 142 |
| *H. salinarium* | MK-8, MK-8($H_2$) | MK-7($H_2$), MK-7 | 49 |
| "*Halobacterium simoncinii* subsp. *neapolitanium*" | MK-8, MK-8($H_2$) | MK-7($H_2$), MK-7 | 49 |
| *Halobacterium trapanicum* | MK-8, MK-8($H_2$) | MK-7($H_2$), MK-7 | 49 |
| *Halobacterium volcanii* | MK-8 | MK-8($H_2$) | 167 |
| *H. volcanii* | MK-8, MK-8($H_2$) | MK-7($H_2$), MK-7 | 49 |
| *Halobacterium* sp. | MK-8, MK-8($H_2$) | MK-7($H_2$), MK-7 | 49 |
| *Halococcus morrhuae* | MK-8, MK-8($H_2$) | MK-7($H_2$), MK-7 | 49 |
| "*Paracococcus haloxanthus*" | MK-8 | | 142 |
| "*Sarcina morrhuae*"[b] | MK-8, MK-8($H_2$) | MK-7($H_2$), MK-7 | 49 |
| "*Sarcina litoralis*"[b] | MK-8($H_2$) | MK-8, MK-7($H_2$), MK-7 | 49 |
| "*Sarcina sreenivasani*"[b] | MK-8($H_2$) | MK-8, MK-7($H_2$), MK-7 | 49 |
| Alkalophilic halophiles SP1, SP2, and MS3[c] | MK-8, MK-8($H_2$) | MK-7($H_2$), MK-7 | 49 |
| *Thermoplasma acidophilum* | MK-7 | | 106, 143 |

[a] The archaebacterium (59) "*C. acidophila*" was described by De Rosa et al. (61).
[b] "*S. morrhuae*," "*S. litoralis*," and "*S. sreenivasani*" are now classified as *Halococcus morrhuae*.
[c] From alkaline soda lakes.

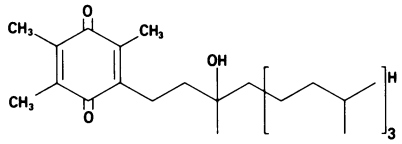
TABLE 3. *Distribution of isoprenoid quinones in the cyanobacteria*

| Taxon | Major quinone types[a] | Reference(s) |
|---|---|---|
| *Anabaena* ("*A. variabilis*") | PQ-*9*, $K_1$, α-TQ | 22, 30, 31 |
| *Anabaena* ("*A. variabilis*") | PQ-*9*, $K_1$, α-TQ, PQ-B, PQ-C | 210 |
| *Synechococcus* ("*Anacystis nidulans*") | PQ-*9*, $K_1$, OH-$K_1$[b] | 3, 144, 234 |
| *Synechococcus* ("*Anacystis nidulans*") | PQ-*9*, $K_1$, polar naphthoquinone? | 31, 177, 210 |
| *Synechococcus* ("*Anacystis nidulans*") | PQ-*9*, OH-$K_1$, polar naphthoquinone? | 99 |
| *Synechococcus* ("*Anacystis nidulans*") | PQ-*9*, $K_1$? | 148 |
| *Chlorogloeopsis* ("*Chlorogloae fritschii*") | PQ-*9*, $K_1$, α-TQ | 22, 30, 31[d] |
| *Fischerella* ("*Mastigocladus laminosus*") | PQ-*9*, $K_1$, α-TQ | 30, 31 |
| *Nostoc* ("*N. muscorum*") | PQ-*9*, $K_1$, α-TQ | 30, 31 |
| *Nostoc* sp. | PQ-*9*, PQ-C, $K_1$, α-TQ | 210 |
| *Nostoc* sp. | PQ-*9*, $K_1$ | 68 |

[a] Abbreviations: $K_1$, phylloquinone; OH-$K_1$, hydroxyphylloquinone; PQ-B, plastoquinone B; PQ-C, plastoquinone C; α-TQ, α-tocopherolquinone.

[b] α-Tocopherolquinone was absent (31, 99, 210). The hydroxyphylloquinone has been shown to be 5-monohydroxyphylloquinone (144).

[c] The presence of phylloquinone was not investigated by Bucke et al. (22).




XII α-Tocopherolquinone (α-TQ)

FIG. 8. *Structure of α-tocopherolquinone (compound XII).*

though this finding awaits confirmation.

**Mycoplasmas.** The distribution of isoprenoid quinones within the mycoplasmas is summarized in Table 4.

Apart from an early report of the absence of isoprenoid quinones in *Mycoplasma gallisepticum* (83), all of the mycoplasmas that have been examined so far contain menaquinones as their sole isoprenoid quinones. Strains of *Acholeplasma axanthum* and *Mycoplasma arthritidis* have been reported to contain MK-*4* as their major isoprenolog (106). To our knowledge, such short-chain menaquinones have not been reported as major components in any other bacteria. However, this report must be treated with some caution, as Hollander et al. (106) used only reverse-phase partition thin-layer chromatography to characterize the quinones. Since natural mixtures of menaquinones often vary both in degree of unsaturation and in polyisoprenoid chain length, reverse-phase thin-layer chromatography by itself is insufficient to define an unknown quinone mixture (see above) (50, 65, 67) and should be used in conjunction with either argentation chromatography or some physiochemical method, such as mass spectrometry. No data are available on the structures of the menaquinones isolated from *Spiroplasma citri*, although two studies on *T. acidophilum*

TABLE 4. *Distribution of isoprenoid quinones in mycoplasmas*[a]

| Taxon | Major isoprenolog | Reference(s) |
|---|---|---|
| *Acholeplasma axanthum* | MK-*4* | 106 |
| *Acholeplasma granularum* | MK-*n* | 106 |
| *Acholeplasma laidlawii* | MK-*n* | 106 |
| *Mycoplasma arthritidis* | MK-*4* | 106 |
| *Mycoplasma gallinarum* | MK-*n*[b] | 106 |
| *Mycoplasma homini* | MK-*n* | 106 |
| *Mycoplasma neurolyticum* | MK-*n* | 106 |
| *Thermoplasma acidophilum*[c] | MK-*7* | 106, 143 |
| *Spiroplasma citri* | MK-*n* | 106 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).

[b] Gale et al. (83) did not detect both menaquinones and ubiquinones in *Mycoplasma gallisepticum*.

[c] *T. acidophilum* may be more appropriately grouped with the archaebacteria (see text).

(see above) indicate that MK-*7* predominates in this species (106, 143). Further structural studies on the isoprenoid quinones of other mycoplasmas will be necessary to determine the value of these compounds in the classification of this group.

**Gram-negative bacteria. (i) Gram-negative facultatively anaerobic rods.** The distribution of isoprenoid quinones in gram-negative facultative anaerobes is shown in Table 5. Several genera within the family *Enterobacteriaceae* (e.g., *Escherichia*, *Klebsiella*, and *Proteus*) and certain species of the genera *Aeromonas* and *Erwinia* are unusual in that they contain mixtures of menaquinones, demethylmenaquinones, and ubiquinones. Structural studies have indicated that the lengths of the side chains of the major components of these

TABLE 5. *Distribution of isoprenoid quinones in gram-negative bacteria: gram-negative facultatively anaerobic rods*[a]

| Taxon | Major isoprenolog(s)[b] | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Enterobacteriaceae* | | | |
| *Edwardsiella tarda* | Q-*n* | | 139 |
| | MK-*n* | | |
| *Enterobacter aerogenes* | Q-8[c] | | 58 |
| *Enterobacter agglomerans* | Q-*n* | | 103 |
| "*Enterbacter liquefaciens*" | Q-8[c] | | 58 |
| *Erwinia amylovora* | Q-*n* | | 103 |
| *Erwinia carotovora* | Q-*n* | | 103 |
| | MK-*n* | | |
| *Erwinia carotovora* | Q-8 | Q-7 | 232[d] |
| | MK-8 | MK-*n* | |
| | DMK-8 | DMK-*n* | |
| "*Escherichia aurescens*" | Q-8 | Q-7, Q-6, Q-5, Q-4 | 232[d] |
| | MK-8 | MK-*n* | |
| | DMK-8 | DMK-*n* | |
| *Escherichia coli* | Q-*n* | | 124 |
| *E. coli* | Q-8[c] | | 58, 174, 183 |
| *E. coli* | Q-8[c] | Q-7, Q-6, Q-5, Q-4, Q-3, Q-2, Q-1 | 56 |
| *E. coli* | Q-8 | | 148 |
| | MK-*n* | | |
| *E. coli* | Q-8 | | 16, 17 |
| | MK-8 | | |
| *E. coli* | MK-8 | MK-9, MK-7, MK-6 | 25 |
| | DMK-8 | DMK-7 | |
| *E. coli* | Q-8 | Q-7, Q-6, Q-5, Q-4 | 232[d] |
| | MK-8 | MK-*n* | |
| | DMK-8 | DMK-*n* | |
| "*Escherichia freundii*" | Q-8 | Q-9, Q-7, Q-6, Q-5, Q-4 | 232[d] |
| | MK-8 | MK-*n* | |
| | DMK-8 | DMK-*n* | |
| "*Klebsiella aerogenes*" | Q-8[c] | | 132, 133 |
| "*K. aerogenes*" | Q-8 | Q-7, Q-6, Q-5, Q-4 | 232[d] |
| | MK-8 | MK-*n* | |
| | DMK-8 | DMK-*n* | |
| *Proteus mirabilis* | Q-8[c] | Q-7, Q-6, Q-5, Q-4 | 230, 231[e] |
| *P. mirabilis* | MK-8 | | 20 |
| | DMK-8 | | |
| *P. mirabilis* | Q-*n* | | 106 |
| | MK-*n* | | |
| | DMK-*n* | | |
| *P. mirabilis* | Q-8 | Q-7, Q-6, Q-5, Q-4 | 232[d] |
| | MK-8 | MK-*n* | |
| | DMK-8 | DMK-*n* | |
| *Proteus vulgaris* | Q-8 | Q-7, Q-6 | 232[d] |
| | MK-8 | MK-*n* | |
| | DMK-8 | DMK-*n* | |
| *P. vulgaris* | MK-*n*[c] | | 113 |
| *P. vulgaris* | Q8 | | 17, 96 |
| | MK-8 | | |
| *P. vulgaris* | Q-9, Q-8, Q-7[c,f] | | 174 |
| *Serratia marcescens* | Q-8[c] | | 58, 174 |
| *S. marcescens* | Q-8 | | 14 |
| | MK-8 | | |
| *Yersinia pseudotuberculosis* NCTC 1101 | Q-8 | | 17 |
| *Vibrionaceae* | | | |
| *Aeromonas hydrophila* NCMB 7810 | Q-8 | Q-7, Q-6, Q-5, Q-4 | 232[d] |
| | MK-8 | MK-*n* | |
| | DMK-8 | DMK-*n* | |

TABLE 5—*Continued*

| Taxon | Major isoprenolog(s)[b] | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Aeromonas punctata* | Q-*8*<br>MK-*8* | Q-*7*, Q-*6*, Q-*5*, Q-*4*<br>MK-*n* | 232[d] |
| *Vibrio alginolyticus* | Q-*n*<br>MK-*n* | | 226 |
| *Vibrio costicola* | MK-*8*<br>Q-*8* | MK-*7*, MK-*6*<br>Q-*7* | 49 |
| *Vibrio succinogenes* | MK-*n* | | 140 |
| *Vibrio* sp. NCIB 8250 | Q-*9* | Q-*10*, Q-*8*, Q-*7*, Q-*6* | 232 |
| *Vibrio* sp. strain 01 | Q-*9*[c] | Q-*10*, Q-*8*, Q-*7*, Q-*6*, Q-*5* | 231[e] |
| *Vibrio* sp. | Q-*8*[c] | | 58 |
| Taxa of uncertain affiliation | | | |
| "*Actinobacillus actinoides*" ATCC 15900 | MK-*n* | | 155 |
| *Actinobacillus actinomycetemcomitans* | DMK-*n* | | 155 |
| *Actinobacillus equuli* NCTC 3365 | DMK-*n* | | 155 |
| *Actinobacillus* spp. NCTC 10801 and ATCC 27073 | DMK-*n* | | 155 |
| *Actinobacillus equuli* NCTC 8529 | Q-*n*<br>DMK-*n* | | 155 |
| *Actinobacillus lignieresii* | Q-*n*<br>DMK-*n* | | 155 |
| "*Actinobacillus seminis*" | Q-*n*<br>DMK-*n* | | 155 |
| "*Aerobacter aerogenes*" | Q-*8* | | 17 |
| *Cardiobacterium hominis* | Q-*n* | | 155 |
| "*Chromobacterium prodigiosum*" NCTC 1337 | Q-*8* | | 17 |
| *Chromobacterium violaceum* | Q-*8* | Q-*9*, Q-*7*, Q-*6* | 232 |
| *Eikenella corrodens* NCTC 10596 | Q-*n* | | 104 |
| *Flavobacterium aquatile* | Q-*n* | | 23 |
| *Flavobacterium acidificum* | Q-*n* | | 23 |
| *Flavobacterium capsulatum* | Q-*n* | | 23 |
| *Flavobacterium devorans* | Q-*n* | | 23 |
| *Flavobacterium halmephilum* | Q-*n* | | 23 |
| *F. halmephilum* | Q-*9* | Q-*8*, Q-*7* | 49 |
| *Flavobacterium* sp. ATCC 13945 | Q-*n* | | 23 |
| *Flavobacterium* spp. (six oxidase-positive strains) | Q-*8*[c] | | 58[g] |
| *Flavobacterium* sp. (one oxidase-positive strain) | Q-*9*[c] | | 58[g] |
| "*Flavobacterium arborescens*" | MK-*n* | | 23 |
| "*Flavobacterium breve*" | MK-*n* | | 23 |
| *Flavobacterium esteraromaticum* | MK-*n* | | 23 |
| "*Flavobacterium flavescens*" | MK-*n* | | 23 |
| *Flavobacterium heparinum* | MK-*n* | | 23 |
| *Flavobacterium meningosepticum* | MK-*n* | | 23 |
| *Flavobacterium odoratum* | MK-*n* | | 23 |
| "*Flavobacterium pectinovorum*" | MK-*n* | | 23 |
| "*Flavobacterium suaveolens*" | MK-*n* | | 23 |
| "*Flavobacterium tirrenicum*" | MK-*n* | | 23 |
| *Flavobacterium uliginosum* | MK-*n* | | 23 |
| *Flavobacterium* spp. NCTC 10795, NCTC 10796, and NCTC 10797 | MK-*n* | | 23 |
| *Flavobacterium/Cytophaga* spp. NCMB 249, NCMB 251, NCMB 275, NCMB 289, NCMB 264, NCMB 244, and NCMB 259 | MK-*n* | | 23 |
| *Flavobacterium* sp. | MK-*6*[c] | MK-*5* | 67 |
| *Haemophilus parasuis* | Q-*n* | | 104 |
| *Haemophilus piscium* | Q-*n* | | 104 |
| *Haemophilus vaginalis* ATCC 14018 | Q-*n* | | 104 |
| *Haemophilus haemoglobinophilus* | Q-*n*<br>DMK-*n* | | 104 |

TABLE 5—*Continued*

| Taxon | Major isoprenolog(s)[b] | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Haemophilus parainfluenzae* NCTC 4101 | Q-*n*<br>DMK-*n* | | 104 |
| *Haemophilus paragallinarum* | Q-*n*<br>DMK-*n* | | 104 |
| *Haemophilus aegyptius* | DMK-*n* | | 104 |
| *Haemophilus influenzae* | DMK-*n* | | 104 |
| *Haemophilus parainfluenzae* HIM 170-1 and HIM 449-8 | DMK-*n* | | 104 |
| *Haemophilus parahaemolyticus* | DMK-*n* | | 104 |
| *Haemophilus paraphrophilus* | DMK-*n* | | 104 |
| *Haemophilus paraphrohaemolyticus* | DMK-*n* | | 104 |
| *Haemophilus parainfluenzae* | DMK-*6* | DMK-*7*, DMK-*5* | 150 |
| *Haemophilus parainfluenzae* | DMK-*6* | DMK-*9*, DMK-*8*, DMK-*7*, DMK-*5*, DMK-*4*, DMK-*3*, DMK-*2*, DMK-*1* | 98 |
| "*Pasteurella gallinacum*" | Q-*n*<br>DMK-*n* | | 155 |
| *Pasteurella haemolytica* | Q-*n*<br>DMK-*n* | | 155 |
| "*Pasteurella mastitidis*" | Q-*n*<br>DMK-*n* | | 155 |
| *Pasteurella multocida* | Q-*n*<br>DMK-*n* | | *155* |
| "*Pasteurella piscicida*" | Q-*n*<br>DMK-*n* | | 155 |
| *Pasteurella ureae* | Q-*n*<br>DMK-*n* | | 155 |
| *Pasteurella* spp. NCTC 10699 and NCTC 11051 | Q-*n*<br>DMK-*n* | | 155 |
| *Pasteurella* spp. NCTC 10547, NCTC 10549, and NCTC 10553 | Q-*n*<br>DMK-*n* | | 155 |
| "*Pasteurella bettii*" | DMK-*n* | | 155 |
| *Pasteurella pneumotropica* | DMK-*n* | | 155 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).
[b] DMK-*8*, Demethylmenaquinone containing eight isoprene units.
[c] The possible presence of other respiratory quinones was not investigated.
[d] Minor analogs of menaquinones and demethylmenaquinones were not specified.
[e] Traces of uncharacterized epoxyubiquinones were also present in *P. mirabilis* and *Vibrio* sp. (231).
[f] The major component was not specified (174).
[g] Ubiquinones were reported to be absent from three oxidase-positive and two oxidase-negative *Flavobacterium* spp. (58).

three quinone structural types are the same (eight isoprene units). However, the relative proportions of menaquinones, demethylmenaquinones, and ubiquinones can be influenced by the degree of aeration. Thus, cultivation of *Escherichia coli* and other facultative organisms at a low oxygen tension increases the level of menaquinones but reduces the amount of ubiquinones produced (179, 233). Numerous taxa (e.g., *Enterobacter agglomerans*, *Erwinia amylovora*, *Yersinia pseudotuberculosis*, and *Vibrio succinogenes*) have been shown to contain only ubiquinones, although further studies will be necessary to confirm the absence of naphthoquinones.

The taxonomic significance of respiratory quinones within the genera *Actinobacillus*, *Cytophaga*, *Flavobacterium*, *Haemophilus*, and *Pasteurella* has been studied extensively by Mannheim and associates (23, 104, 155). Invariably, typical strains of species within the genera *Actinobacillus* and *Pasteurella* contain demethylmenaquinones (155), and some of these organisms are capable of synthesizing ubiquinones in addition to demethylmenaquinones (Table 5). However, *Actinobacillus actinomycetemcomitans*, *Actinobacillus suis*, "*Pasteurella bettii*," and *Pasteurella pneumotropica* strains produce only demethylmenaquinones, whereas "*Actinobacillus actinoides*" ATCC

15900 apparently produces menaquinones as its sole respiratory quinones. This last taxon is gram positive and is probably related to the actinomycetes. Members of the genus *Haemophilus* are heterogeneous on the basis of the types of respiratory quinones produced (Table 5). The type species of *Haemophilus*, *Haemophilus influenzae*, and *Haemophilus aegyptius*, *Haemophilus paraphrophilus*, *Haemophilus parahaemolyticus*, and *Haemophilus paraphrohaemolyticus* produce demethylmenaquines as their sole isoprenoid quinones. *Haemophilus paragallinarum*, *Haemophilus haemoglobinophilus*, and *Haemophilus parasuis* produce ubiquinones in addition to demethylmenaquines. *Haemophilus vaginalis*, which contains ubiquinones as its sole respiratory quinones, has been transferred recently to a new genus, *Gardnerella*, as *Gardnerella vaginalis* (95). Members of the genera *Cytophaga* and *Flavobacterium* can be divided into two broad groups on the basis of their isoprenoid quinones (23). Menaquinones are produced by the majority of the flavobacteria and the typical *Cytophaga* strains, whereas ubiquinones have been shown to be present in *Flavobacterium aquatile*, *Flavobacterium acidificum*, *Flavobacterium capsulatum*, *Flavobacterium devorans*, and *Flavobacterium halmephilium* (Table 5). Mannheim and colleagues did not investigate the detailed structures (e.g., isoprene numbers, possible hydrogenation, etc.) of the various quinone classes (Table 5). However, preliminary structural information on the quinones of members of the genus *Haemophilus* and on the quinones of flavobacteria suggests that such an approach will be rewarding for the purposes of taxonomy.

**(ii) Gram-negative aerobic rods.** The majority of the gram-negative aerobic rods which have been examined contain ubiquinones exclusively (Table 6). Members of the genus *Pseudomonas* generally contain ubiquinones with nine isoprene units (abbreviated Q-*9*) as their major components. However, strains labeled "*Pseudomonas denitrificans*" and some unnamed *Pseudomonas* spp. have been shown to possess major amounts of Q-*10* (Table 6). Recently, a *Pseudomonas* sp. (strain M16) has been described which accumulates significant quantities of Q-*11* in addition to Q-*10* (168). This report is of considerable interest, as ubiquinone isoprenologs with more than 10 isoprene units have been found previously only in trace amounts in certain photosynthetic bacteria (218, 220, 221).

The ubiquinone contents of the acetic acid bacteria have been investigated systematically by Yamada and colleagues (238–240, 245, 246). Members of the genus *Acetobacter* contain Q-*9* as their major component, whereas members of the genus *Gluconobacter* and strains labeled "*Acetobacter xylinum*" possess Q-*10* as their major isoprenolog. A number of so-called acetic acid intermediate strains of uncertain taxonomic position have been shown to contain Q-*8* as their major component (Table 6).

Members of the genus *Azotobacter* contain ubiquinones as their respiratory quinones. The early report by Lester and Crane (148) of an unidentified menaquinone in a strain of *Azotobacter vinelandii* is probably in error.

Studies on the ubiquinone compositions of other gram-negative aerobic rods have indicated that there is relatively little structural variation and that Q-*10* predominates in *Agrobacterium* (182, 232) and *Brucella* (186, 215), Q-*9* predominates in *Alcaligenes* (232), and Q-*8* predominates in "*Achromobacter*" (17), "*Comamonas*" (232), "*Hydrogomonas*" (148, 214), and "*Methylomonas*" (64).

Members of the thermophilic genus *Thermus* are unusual among the aerobic, gram-negative rods in that they contain menaquinones as their sole isoprenoid quinones. *Thermus aquaticus* and "*Thermus thermophilus*" contain MK-*8* as their major component (Table 6). It is worth noting that members of the genus *Thermus* are also unusual in that they possess citrate synthases with the sizes and regulatory properties of the citrate synthases of gram-positive bacteria (229).

**(iii) Aerobic gram-negative cocci and coccobacilli.** Data on the isoprenoid quinone contents of aerobic gram-negative cocci and coccobacilli are rather fragmentary (Table 7). All of the *Acinetobacter*, *Branhamella*, *Moraxella* and *Neisseria* species which have been examined contain Q-*8* or Q-*9* or both as their major components. Jones and Weitzman (122) found that "*Brevibacterium leucinophagum*" was gram negative and proposed the transfer of this organism to the genus *Acinetobacter*. The recovery of major amounts of Q-*9* in "*B. leucinophagum*" supports this assignment (34).

*Paracoccus denitrificans* contains major amounts of Q-*10* and on this basis can be distinguished from all *Acinetobacter*, *Moraxella*, and *Neisseria* species which have been examined. The taxonomic position of "*Paracoccus haloxanthus*" remains equivocal. This taxon is not recognized in *Bergey's Manual of Determinative Bacteriology* (21). "*P. haloxanthus*" lacks ubiquinones and contains menaquinones (142), and this organism may be more appropriately classified alongside the genera *Halobacterium* and *Halococcus* in the archaebacteria.

TABLE 6. *Distribution of isoprenoid quinones in gram-negative bacteria: gram-negative aerobic rods*[a]

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Acetobacter aceti* | Q-9 | Q-10, Q-8 | 239 |
| *A. aceti* | Q-9 | Q-8 | 240 |
| "*Acetobacter acetosus*" | Q-9 | Q-8 | 240 |
| "*Acetobacter albuminosus*" | Q-9 | Q-8 | 240 |
| "*Acetobacter ascendens*" | Q-9 | Q-8 | 240 |
| "*Acetobacter dioxyacetonicus*" | Q-9 | Q-8 | 240 |
| "*Acetobacter kutzingianus*" | Q-9 | Q-8 | 240 |
| *Acetobacter pasteurianus* | Q-9 | Q-8 | 240 |
| "*Acetobacter rancens*" | Q-9 | Q-8 | 240 |
| "*Acetobacter xylinum*" | Q-10 | | 12, 240, 245 |
| "*A. xylinum*" | Q-9 | Q-8 | 240 |
| *Acetobacter* spp. A21 to A23 "Acetic acid intermediate strains" | Q-9 | Q-8 | 240 |
| Peritrichously flagellated strains IAM 1834 and AJ 2881 | Q-10 | Q-9, Q-8 | 239 |
| Polar flagellated strain IFO 3246 | Q-8 | Q-7 | 239 |
| Polar flagellated strains | Q-8 | | 246 |
| "*Achromobacter hartlebii*" | Q-8 | | 17 |
| "*Achromobacter*" sp. marine strain 60-20-A5 | Q-n | | 141 |
| *Agrobacterium tumefaciens* | Q-n | | 124 |
| *A. tumefaciens* | Q-10 | | 182, 183 |
| *A. tumefaciens* | Q-10 | Q-9, Q-8 | 232 |
| "*Alcaligenes viscolactis*" | Q-9 | Q-8, Q-7 | 232 |
| "*Azotobacter agilis*" | Q-n | | 124 |
| *Azotobacter chroococcum* | Q-8 | | 17 |
| *Azotobacter vinelandii* | Q-n | | 156 |
| *A. vinelandii* | Q-8 | | 119, 148, 149, 174, 183[b] |
| *Bordetella pertussis* | Q-8 | | 216 |
| *Brucella abortus* | Q-10 | | 186, 215 |
| *Brucella melitensis* | Q-10 | | 216 |
| "*Comamonas percolans*" ATCC 8461 | Q-8 | Q-7, Q-6, Q-5, Q-4 | 232 |
| "*Gluconobacter albidus*" | Q-10 | | 240 |
| "*Gluconobacter capsulatus*" | Q-10 | | 240 |
| "*Gluconobacter cerinus*" | Q-10 | | 238 |
| "*Gluconobacter dioxyacetonicus*" | Q-10 | | 240 |
| "*Gluconobacter gluconicus*" | Q-10 | | 240 |
| "*Gluconobacter industrius*" | Q-10 | | 240 |
| "*Gluconobacter melanogenus*" | Q-10 | | 240 |
| "*Gluconobacter monoxygluconicus*" | Q-10 | | 240 |
| *Gluconobacter oxydans* | Q-10 | | 240 |
| "*Gluconobacter roseus*" | Q-10 | | 240 |
| "*Gluconobacter rubiginosus*" | Q-10 | | 240 |
| "*Gluconobacter seleroideus*" | Q-10 | | 240 |
| "*Gluconobacter suboxydans*" | Q-10 | Q-9, Q-8 | 239, 240 |
| "*Gluconobacter turbidans*" | Q-9 | | 240 |
| "*Hydrogenomonas eutropha*" | Q-8 | | 239 |
| "*Hydrogenomonas*" sp. | Q-8 | | 148, 214 |
| "*Methylomonas*" sp. 2B36-P11 | Q-8 | | 64 |
| *Pseudomonas aeruginosa* | Q-9 | | 17, 174 |
| *Pseudomonas beijerinkii* | Q-9 | Q-8, Q-7 | 49 |
| "*Pseudomonas denitrificans*" | Q-10 | | 174 |
| "*Pseudomonas desmolytica*" | Q-9 | | 224 |
| *Pseudomonas facilis* | Q-n | | 217 |
| *Pseudomonas fluorescens* | Q-9 | | 148 |
| *P. fluorescens* | Q-9 | Q-8, Q-7, Q-6 | 232 |
| *P. fluorescens* | Q-9, Q-8 | | 174 |
| *Pseudomonas fragi* | Q-9 | | 174 |
| *P. fragi* | Q-9 | Q-8, Q-7, Q-6 | 232 |
| *Pseudomonas geniculata* | Q-9 | | 174 |

TABLE 6—*Continued*

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *"Pseudomonas maltophilia"* | Q-*8* | | 107 |
| *"Pseudomonas mildenbergii"* | Q-*9* | | 174 |
| *"Pseudomonas ovalis"* | Q-*9* | | 108 |
| *"P. ovalis"* | Q-*9* | Q-*8*, Q-*7*, Q-*6* | 230, 232 |
| *"P. ovalis"* | Q-*9* | Q-*8*, Q-*7*, Q-*6*, Q-*5*, Q-*4* | 231 |
| *Pseudomonas putida* | Q-*9* | | 174 |
| *P. putida* | Q-*9* | Q-*8*, Q-*7*, Q-*6* | 232 |
| *Pseudomonas* sp. | Q-*9* | | 183 |
| *Pseudomonas* sp. strain N 842 | Q-*10* | | 169 |
| *Pseudomonas* sp. strain M16 | Q-*10* | Q-*11* | 168 |
| *"Protaminobacter ruber"* | Q-*10* | Q-*9*, Q-*8* | 34 |
| *"P. ruber"* | Q-*10* | | 168 |
| *Rhizobium japonicum* | Q-*10* | | 55 |
| *Thermus aquaticus* | MK-*8* | MK-*7* | 50 |
| *"Thermus thermophilus"* | MK-*8* | MK-*7* | Collins and Jones, unpublished data |
| *Xanthomonas campestris* | Q-*8* | Q-*7*, Q-*6*, Q-*5*, Q-*4* | 232 |
| *X. campestris* | Q-*8* | | 107 |
| *"Xanthomonas citri"* | Q-*8* | | 107 |
| *"Xanthomonas oryzae"* | Q-*8* | | 107 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).
[b] Lester and Crane (148) also detected an uncharacterized menaquinone in a strain of *A. vinelandii*.

TABLE 7. *Distribution of isoprenoid quinones in gram-negative bacteria: gram-negative cocci and coccobacilli*[a]

| Taxon | Major isoprenolog(s) | Reference |
|---|---|---|
| *"Acinetobacter anitratum"* (seven strains) | Q-*9* | 58 |
| *"A. anitratum"* (one strain) | Q-*8* | 58 |
| *"A. anitratum"* (two strains) | Q-*9*, Q-*8*[b] | 58 |
| *Acinetobacter lwoffi* | Q-*9*, Q-*8*[b] | 58 |
| *Acinetobacter* sp. | Q-*9* | 154 |
| *Branhamella catarrhalis* | Q-*n* | 11 |
| *"Moraxella kingii"* | Q-*n* | 155[c] |
| *Moraxella urethralis* | Q-*n* | 106 |
| *Moraxella* sp. NCIB 8250 | Q-*9*[d] | 15 |
| *"Neisseria catarrhalis"* | Q-*n* | 10 |
| *"N. catarrhalis"* | Q-*8* | 17 |
| *Neisseria gonorrhoeae* | Q-*n* | 11 |
| *Paracoccus denitrificans* | Q-*10* | 197 |
| *Paracoccus halodenitrificans* | Q-*9*[e] | 49 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).
[b] Q-*8* and Q-*9* were present in comparable amounts (58).
[c] Unpublished data cited by Mannheim et al. (155).
[d] Minor amounts of Q-*10*, Q-*8*, Q-*7*, and Q-*6* were also present in *Moraxella* sp. NCIB 8250 (15).
[e] Minor amounts of Q-*8* and Q-*7* were also reported (49).

**(iv) Gram-negative obligate anaerobes.** Relatively few studies have been performed on the isoprenoid quinone compositions of gram-negative obligate anaerobes (Table 8). With the exception of *Bacteroides furcosus*, *Bacteroides nodosus*, and *Bacteroides preacutus*, which lack both menaquinones and ubiquinones, members of the genus *Bacteroides* generally possess menaquinones as their sole isoprenoid quinones (159, 189, 190, 200, 201). Reports concerning the menaquinone contents of *"Bacteroides melaninogenicus* subsp. *levii"* are confusing (189, 190, 200). *"B. melaninogenicus* subsp. *levii"* has been shown to have a defect in menaquinone biosynthesis above the level of shikimic acid and is normally grown with phylloquinone (vitamin $K_1$) or menadione (2-methyl-1,4-naphthoquinone). Under these growth conditions, this organism has been reported to produce both MK-*9* and MK-*10* (159, 190). However, Shah and Collins (200) failed to detect menaquinones in two strains of *"B. melaninogenicus* subsp. *levii"* when they were grown in the presence of menadione.

The menaquinone components of *Bacteroides asaccharolyticus* strains can be used to divide these strains into two subgroups, containing MK-*9* and MK-*10*, respectively (200). These data are in accord with the existence of two centers of variation within the taxon *B. asaccharolyticus*, as determined by enzyme patterns, deoxyribonucleic acid base composition, and deoxyribonucleic acid reassociation data (200, 201, 203). *Bacteroides melaninogenicus* subsp. *intermedius* strains contain MK-*11* as their major isoprenolog and on this basis can be distinguished from *Bacteroides melaninogenicus*

TABLE 8. *Distribution of isoprenoid quinones in gram-negative bacteria: gram-negative obligate anaerobes*[a]

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Bacteroides asaccharolyticus* strains W50 and W83 | MK-*9* | MK-*10*, MK-*8*, MK-*7* | 200, 201 |
| *B. asaccharolyticus* strains B536 and B537 | MK-*10* | MK-*11*, MK-*9*, MK-*8*, MK-*7* | 200, 201 |
| *Bacteroides distasonis* | MK-*10* | MK-*11*, MK-*9*, MK-*8*, MK-*7* | 206 |
| *Bacteroides eggerthii* | MK-*11*, MK-*10*[b] | MK-*12*, MK-*9*, MK-*8*, MK-*7* | 201 |
| *Bacteroides fragilis* | MK-*11*, MK-*10*[b] | MK-*12*, MK-*9*, MK-*8*, MK-*7* | 201, 202 |
| *B. fragilis* | MK-*11*, MK-*10*[b] | MK-*9* | 50 |
| *Bacteroides melaninogenicus* strain CR2A1 | MK-*7* | MK-*9*, MK-*8*, MK-*6* | 189 |
| *Bacteroides melaninogenicus* subsp. *levii* | MK-*9* | MK-*10* | 190 |
| *B. melaninogenicus* subsp. *levii*[c] | MK-*9* | MK-*10*, MK-*8* | 159 |
| *Bacteroides melaninogenicus* subsp. *intermedius* | MK-*11* | MK-*12*, MK-*10*, MK-*9*, MK-*8*, MK-*7* | 200, 201 |
| *Bacteroides melaninogenicus* subsp. *melaninogenicus*[d] | MK-*11*, MK-*10*[b] | MK-*12*, MK-*9*, MK-*8*, MK-*7* | 200, 201 |
| *Bacteroides ovatus* | MK-*11*, MK-*10*[b] | MK-*12*, MK-*9*, MK-*8*, MK-*7* | 201 |
| *Bacteroides oralis* strains 5540, G9a-C2, and 7880 | MK-*11*, MK-*10*[b] | MK-*12*, MK-*9*, MK-*8*, MK-*7* | 200, 201 |
| *B. oralis* strains 1210 and 1221 | MK-*12*, MK-*11*[b] | MK-*13*, MK-*10*, MK-*9*, MK-*8* | 200, 201 |
| *B. oralis* strains VP1 8906D and HS4 | MK-*13*, MK-*12*[b] | MK-*14*, MK-*11*, MK-*10*, MK-*9*, MK-*8*, MK-*7* | 200, 201 |
| *Bacteroides ruminicola* | MK-*n* | | 166 |
| *Bacteroides ruminicola* subsp. *brevis* oral strains NP333, 75J1, J1, and WP H61 | MK-*13*, MK-*12*[b] | MK-*14*, MK-*11*, MK-*10*, MK-*9*, MK-*8* | 200, 201 |
| *B. ruminicola* subsp. *brevis* rumen strains B5 and 118B | MK-*12*, MK-*11*[b] | MK-*13*, MK-*10*, MK-*9*, MK-*8* | 200, 201 |
| *Bacteroides ruminicola* subsp. *ruminicola* rumen strain R2 | MK-*12*, MK-*11*[b] | MK-*13*, MK-*10*, MK-*9*, MK-*8* | 200, 201 |
| *Bacteroides splanchnicus* | MK-*9* | MK-*10*, MK-*8*, MK-*7* | 201 |
| *Bacteroides thetaiotaomicron* | MK-*11*, MK-*10*[b] | MK-*12*, MK-*9*, MK-*8*, MK-*7* | 200, 201 |
| *B. thetaiotaomicron* | MK-*11*, MK-*10* | MK-*9* | 50 |
| *Bacteroides vulgatus* | MK-*11*, MK-*10*[b] | MK-*12*, MK-*9*, MK-*8*, MK-*7* | 200, 201 |
| *Capnocytophaga gingivalis*[d] | MK-*6* | MK-*5* | 202 |
| *Capnocytophaga ochracea*[d] | MK-*6* | MK-*5* | 50, 200, 202 |
| *Capnocytophaga sputigena*[d] | MK-*6* | MK-*5* | 202 |
| *Desulfovibrio desulfuricans* | MK-*6* | | 157 |
| *Desulfovibrio gigas* | MK-*6* | | 157, 228 |
| *Desulfovibrio vulgaris* | MK-*6* | | 228 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).
[b] Isoprenologs were present in comparable amounts.
[c] Originally described as *Fusiformis nigrescens* (159).
[d] *Capnocytophaga* as described by Leadbetter et al. (145).

subsp. *melaninogenicus* strains, which contain comparable amounts of both MK-*10* and MK-*11* (200).

Rumen strains of *Bacteroides ruminicola* subsp. *brevis* and *Bacteroides ruminicola* subsp. *ruminicola* have been reported to contain major amounts of unsaturated MK-*11* and MK-*12* (Table 8) (200). However, strains of *B. ruminicola* subsp. *brevis* from oral sources have been shown to contain comparable amounts of unsaturated MK-*12* and MK-*13*.

The menaquinone patterns exhibited by members of the "*Bacteroides fragilis*" group (118) show relatively little structural variation (Table 8). *Bacteroides splanchnicus* possesses MK-*9* as its major component, whereas MK-*10* predominates in *Bacteroides distasonis* (Table 8). However, representative strains of *Bacteroides eg-*

*gerthii*, *B. fragilis*, *Bacteroides ovatus*, *Bacteroides thetaiotaomicron*, and *Bacteroides vulgatus* contain comparable amounts of MK-*10* and MK-*11* (Table 8).

The retention of the species *B. ochraceus* within the genus *Bacteroides* has been questioned by several workers (102, 200). This species can be differentiated clearly from other *Bacteroides* spp. by its microaerophilic properties and by its resistance of metronidazole. Recently, a new genus, *Capnocytophaga* (145), has been proposed to accommodate *B. ochraceus* and related strains. The recovery of unusually short menaquinones (MK-*6*) in *B. ochraceus* supports the recognition of the genus *Capnocytophaga* (200, 201, 202).

Members of the strictly anaerobic genus *Desulfovibrio* also contain menaquinones as their sole isoprenoid quinones. *Desulfovibrio gigas* and *Desulfovibrio vulgaris* possess MK-*6* as their sole menaquinone (157, 228).

**(v) Gliding bacteria.** The distribution of isoprenoid quinones in gram-negative gliding bacteria is summarized in Table 9. The single species of *Beggiatoa* which has been examined contains Q-*8* as its major quinone, together with traces of an unidentified naphthoquinone (30). However, the occurrence of menaquinones as the sole isoprenoid quinones in *Cytophaga*, *Flexibacter*, *Herpetosiphon*, and *Myxococcus* is unusual (23, 130, 131). As a rule, aerobic gram-negative bacteria contain exclusively ubiquinones, although the facultative anaerobic enteric bacteria usually synthesize menaquinones in addition to ubiquinones (Table 5). The limited data available suggest that quinone analyses may be of value in the taxonomy of the gliding bacteria, as *Myxococcus fulvus* contains MK-*8* as its major isoprenolog and "*Herpetosiphon giganteus*" contains MK-*6*, whereas MK-*7* predominates in "*Flexibacter elegans*." The menaquinones from the five *Cytophaga* species that have been examined have not been characterized (23).

**(vi) Phototrophic bacteria.** The available information on the isoprenoid quinone compositions of the phototrophic bacteria is summarized in Table 10. "*Chlorobium thiosulfatophilum*" and "*Chloropseudomonas ethylicum*" lack ubiquinones and contain menaquinones as their sole isoprenoid quinones. Both of these species contain unsaturated MK-*7* as their major isoprenoid quinones, together with minor amounts of chlorobiumquinone (1'-oxomenaquinone-*7*). It will be interesting to see whether other members of the family *Chlorobiaceae* (e.g., *Pelodictyon* and *Prosthecochloris*) possess similar isoprenoid quinone compositions.

TABLE 9. *Distribution of isoprenoid quinones in gram-negative bacteria: the gliding bacteria*[a]

| Taxon | Major isoprenolog | Minor component(s) | Reference |
|---|---|---|---|
| *Myxococcus fulvus* | MK-*8* | MK-*9*, MK-*7* | 131 |
| "*Cytophaga aurantiaca*" | MK-*n* | | 23 |
| *Cytophaga fermentans* | MK-*n* | | 23 |
| *Cytophaga hutchinsonii* | MK-*n* | | 23 |
| *Cytophaga johnsonae* | MK-*n* | | 23 |
| "*Cytophaga marinoflava*" | MK-*n* | | 23 |
| "*Flexibacter elegans*" | MK-*7* | MK-*9*, MK-*8* | 131 |
| "*Herpetosiphon giganteus*" | MK-*6* | MK-*7* | 130 |
| *Beggiatoa* sp.[b] | Q-*8* | | 30 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).

[b] Traces of an unidentified naphthoquinone were detected in *Beggiatoa* sp. (30).

The isoprenoid quinone compositions of representatives of only 2 of the 10 genera currently classified in the family *Chromatiaceae* (21) have been investigated. The halophile "*Amoebobacter morrhuae*" contains MK-*8*, and ubiquinones are absent (142). "*A. morrhuae*" should be reclassified in the genus *Halococcus* (73) (Table 2). Reports on the isoprenoid quinone compositions of members of the genus *Chromatium* do not form a coherent picture (Table 10). Osnitskaya et al. (173) recovered major amounts of Q-*8* from *Chromatium vinosum*, whereas other workers (148, 212) have reported that Q-*7* is the predominant isoprenolog in this organism. Reports on the presence of menaquinones in *C. vinosum* are also confusing. Lester and Crane (148) and Osnitskaya et al. (173) reported the occurrence of minor amounts of menaquinones in *C. vinosum*, whereas Halsey and Parson (97) found no evidence at all for the presence of menaquinones or phylloquinones in this species. Further studies on additional *C. vinosum* strains and other species of the genus *Chromatium* will be necessary to clarify this situation.

Preliminary data suggest that isoprenoid quinone composition may be useful in the classification of members of the family *Rhodospirillaceae*. Ubiquinones represent the major isoprenoid quinones within those representatives of the genera *Rhodomicrobium*, *Rhodopseudomonas*, and *Rhodospirillum* that have been examined so far. However, the length of the polyprenyl side chain varies from species to species (Table 10). Thus, Q-*8* predominates in *Rhodopseudomonas gelatinosa*, Q-*9* predominates in *Rhodopseudomonas viridis*, *Rhodospirillum fulvum*, and *Rhodospirillum molischianum*, and Q-*10* predominates in *Rhodomicrobium vannielii*, *Rhodopseudomonas capsulata*, *Rhodopseudomonas palustris*, *Rhodopseudomonas sphaeroides*, and *Rhodospirillum rubrum*. It is inter-

TABLE 10. *Distribution of isoprenoid quinones in gram-negative bacteria: phototrophic bacteria*[a]

| Taxon | Major isoprenolog | Minor component(s) | Reference(s) |
|---|---|---|---|
| *"Chlorobium thiosulfatophilum"* | MK-7 | 1'-oxo-MK-7[b] | 78, 181, 185 |
| *"Chloropseudomonas ethylicum"*[c] | MK-7 | 1'-oxo-MK-7 | 181, 185 |
| *Chromatium vinosum* strain D | Q-7 | MK-*n* | 148 |
| *C. vinosum* strain D | Q-7 | | 212 |
| *C. vinosum* | Q-8 | MK-8 | 173 |
| *C. vinosum* | Q-*n*[d] | | 97 |
| *Chromatium* sp. 8379 | Q-10 | MK-*n* | 94 |
| *Ectothiorhodospira halophila* | Q-8 | Q-7 | 49 |
| *Rhodomicrobium vannielii* | Q-10 | | 28, 29, 158 |
| *Rhodopseudomonas capsulata* | Q-10 | | 28, 29, 158 |
| *Rhodopseudomonas gelatinosa* | Q-8 | | 29 |
| *R. gelatinosa* | Q-8 | MK-8 | 158 |
| *R. gelatinosa* | Q-9 | | 192 |
| *Rhodopseudomonas palustris* | Q-10 | | 28, 29, 129, 158 |
| *Rhodopseudomonas sphaeroides* | Q-10 | | 13, 28, 29, 158 |
| *Rhodopseudomonas viridis* | Q-9 | MK-9 | 158 |
| *Rhodopseudomonas* sp. FRNY | Q-10 | | 158 |
| *Rhodospirillum fulvum* | Q-9 | MK-9 | 158 |
| *Rhodospirillum molischianum* | Q-9 | MK-9 | 158 |
| *Rhodospirillum rubrum* | Q-9 | | 148 |
| *R. rubrum* | Q-10 | | 28, 29, 101, 172, 219 |
| *R. rubrum* | Q-10 | Q-9, Q-8, Q-7, Q-6, Q-5, Q-4, Q-3, Q-2, Q-1 | 56 |
| *R. rubrum* | Q-10 | RQ-10[e] | 87, 158 |
| *R. rubrum* | Q-10 | Q-*n*, RQ-10, RQ-*n*[f] | 170, 235 |
| *R. rubrum* | Q-10 | Epoxy-Q-10[g] | 77 |
| *Rhodospirillum* sp. 2761 | Q-8 | MK-8 | 158 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).
[b] 1'-oxo-MK-7, Chlorobiumquinone (1'-oxomenaquinone-7).
[c] "*C. ethylicum*" has been shown to be a mixture of two organisms (93).
[d] Halsey and Parson (97) did not detect menaquinone in *C. vinosum*.
[e] RQ-10, Rhodoquinone with 10 isoprene units.
[f] Some unspecified minor analogs of ubiquinone and rhodoquinone were also detected (170, 235).
[g] Five new epoxy derivatives of Q-10 (epoxy-Q-10) were detected in *R. rubrum* (77). The concentrations of the epoxyquinones were about 1 to 2% of the concentration of Q-10 (77).

esting that those species which contain Q-8 and Q-9 also contain menaquinones with side chains of the same length (i.e., MK-8 and MK-9, respectively) (Table 10). On the other hand, species that contain Q-10 appear to lack menaquinones. Minor amounts of rhodoquinone and epoxides of ubiquinones have also been reported to occur in *R. rubrum* (77, 164, 165, 219). The taxonomic relevance of these observations awaits further study.

**Gram-positive bacteria. (i) Endospore-forming rods and cocci.** The distribution of isoprenoid quinones in endospore-forming gram-positive rods and cocci is summarized in Table 11.

As presently constituted, the genus *Bacillus* is heterogeneous (86). However, despite this heterogeneity the vast majority of taxa that have been examined have remarkably uniform menaquinone profiles, with unsaturated MK-7 predominating (Table 11). However, Hess et al. (100) have reported recently the presence of major amounts of MK-9 in *Bacillus lentus* and of MK-8 in *Bacillus pantothenticus*.

Members of the genus *Sporolactobacillus* possess characteristics intermediate between those of the genera *Bacillus* and *Lactobacillus* in that they are gram-positive, rod-shaped, microaerophilic, catalase-negative organisms which form endospores. However, whereas members of the genus *Lactobacillus* generally lack isoprenoid quinones (Table 12) (38, 65), *Sporolactobacillus inulinus* and strains presently called "*Sporolactobacillus laevus*" and "*Sporolactobacillus racemicus*" synthesize unsaturated MK-7 (38). The presence of similar menaquinone patterns in sporolactobacilli and members of the genus *Bacillus* is in accord with the similarities in peptidoglycan structures (123, 194) and fatty acid profiles (225) among these bacteria. However, as Collins and Jones have pointed out (38), it would be premature to suggest reclassification of *S. inulinus* or other sporolactobacilli into the genus *Bacillus* as that

genus is presently constituted. When the taxonomy of the genus *Bacillus* is clarified, it is very probable that one of the new taxa will contain both the sporolactobacilli and certain bacteria presently designated *Bacillus* species (e.g., "*Bacillus laevolacticus*," "*Bacillus racemilacticus*," "*Bacillus myxolactis*," and "*Bacillus dextrolacticus*").

*Sporosarcina ureae* possesses many properties in common with the genera *Micrococcus* and *Planococcus* (194). This species is also similar to members of the genus *Bacillus* in its ability to form endospores. The presence of unsaturated MK-7 in *S. ureae* reinforces its relationship to members of the genus *Bacillus* but clearly distinguishes it from planococci (which contain unsaturated MK-8) and from micrococci (which generally contain partially hydrogenated menaquinones) (242). The distinctness of the genera *Sporosarcina* and *Bacillus* is probably justified considering their differences in peptidoglycan structure, mode of cell division, shape, and ability to utilize urea. However, certain bacilli, such as *Bacillus pasteurii*, will probably be classified with *S. ureae* when the taxonomy of the genus *Bacillus* is clarified (242).

Early studies indicated that members of the genus *Clostridium* lacked respiratory quinones (17, 83, 85, 148). This is in accord with the strictly anaerobic nature of clostridia and with their inability to synthesize heme compounds and cytochromes. However, recently Gottwald et al. (92) demonstrated the presence of cytochromes and an uncharacterized menaquinone in *Clostridium formicoaceticum* and *Clostridium thermoaceticum*. Therefore, although it is generally conceded that quinones are absent from most clostridia, further systematic studies will be necessary before the potential of isoprenoid quinone analyses in the taxonomy of this group can be appreciated.

**(ii) Lactic acid bacteria.** Members of the genus *Lactobacillus* generally lack isoprenoid quinones (38, 65). Hess et al. (100) recently reported low levels of an uncharacterized menaquinone in a single strain of *Lactobacillus brevis*. *Lactobacillus mali* and "*Lactobacillus yamanashiensis*" also contain menaquinones as their sole isoprenoid quinones, with MK-8, MK-9, and MK-10 constituting the major components (33). The presence of closely related menaquinone profiles within these latter taxa supports the hypothesis that *L. mali* and "*L. yamanashiensis*" are the same species (27). Members of the genus *Listeria* also contain menaquinones as their sole isoprenoid quinones. *Listeria monocytogenes* (including the organisms referred to in the literature as "*Listeria innocua*" [199] and *L. monocytogenes* Ivanov serotype 5 [112]), *Listeria grayi*, and *Listeria murrayi* all contain unsaturated MK-7 (Table 12), thereby reinforcing the relatedness among these taxa (33, 46, 121). The presence of unsaturated MK-9 in *Listeria denitrificans* supports the hypothesis that this taxon should be removed from the genus *Listeria* (33, 46, 120, 121, 209). The menaquinone composition of the genus *Brochothrix* is controversial. Collins and associates recovered major amounts of MK-7 from several strains of *Brochothrix thermosphacta* (46, 121). However, Hess and colleagues reported the presence of a MK-9 in a single strain of *B. thermosphacta* (100). The results of Hess et al. (100) must be treated with caution, as only reverse-phase partition thin-layer chromatography was used for the menaquinone characterization. As mentioned above, reverse-phase thin-layer chromatography cannot be used by itself to resolve a menaquinone mixture (see above) (67). However, Collins et al. used mass spectrometry as well as reverse-phase thin-layer chromatography. Molecular ions ($M^+$) were found at *m/e* 648, thereby confirming the presence of MK-7 (46). The latter result also confirms the taxonomic relationship between the genera *Brochothrix* and *Listeria*, as determined by numerical phenetic studies (120, 236).

Most members of the genus *Streptococcus* lack isoprenoid quinones, although menaquinones have been reported in a few streptococci of serological groups D and N (7, 8, 39, 40, 100). *Streptococcus faecalis* contains demethylmenaquinones and on this basis can be distinguished from all other members of the family *Streptococcaceae* (39, 40). *Streptococcus faecium* subsp. *casseliflavus*, *Streptococcus faecium* subsp. *mobilis*, *Streptococcus cremoris*, *Streptococcus cremoris* subsp. *alcatosus*, *Streptococcus lactis*, and *Streptococcus lactis* subsp. *diacetylactis* contain fully substituted menaquinones, with MK-8 and MK-7 predominating in the first two taxa and MK-9 predominating in the latter taxa. The presence of menaquinones in *S. lactis* and *S. lactis* subsp. *diacetylactis* is in accord with the reports of cytochrome-mediated electron transport in strains of these taxa when they are grown in the presence of preformed heme (188). To our knowledge, cytochrome-mediated electron transport in *S. cremoris*, *S. faecium* subsp. *casseliflavus*, and *S. faecium* subsp. *mobilis* has not been described, although the menaquinone data suggest that such an investigation might be rewarding. Representatives of other lactic acid taxa (e.g., *Aerococcus*, *Erysipelothrix*, *Gemella*, *Leuconostoc*, and *Pediococcus*) generally lack isoprenoid quinones (39, 40, 46, 100), thereby

TABLE 11. *Distribution of isoprenoid quinones in gram-positive bacteria: endospore-forming rods and cocci*[a]

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Bacillus alcalophilus* | MK-7 | MK-3 | 100 |
| *Bacillus alvei* | MK-7 | | 100, 227 |
| "*Bacillus aminovorans*" | MK-7 | MK-2 | 100 |
| "*Bacillus amyloliquefaciens*" | MK-7 | MK-2 | 100 |
| "*Bacillus aneurinolyticus*" | MK-7 | | 100 |
| *Bacillus anthracis* | MK-*n* | | 100 |
| *Bacillus badius* | MK-7 | MK-3 | 100 |
| *Bacillus brevis* | MK-7 | | 81, 100, 227 |
| *B. brevis* | MK-*n* | | 206 |
| *Bacillus cereus* | MK-7 | | 100, 113, 237 |
| *Bacillus circulans* | MK-7 | | 100, 227 |
| "*Bacillus cirroflagellosus*" | MK-*n* | | 100 |
| *Bacillus coagulans* | MK-7 | | 227 |
| *B. coagulans* | MK-7 | MK-6, MK-5 | 38 |
| *B. coagulans* | MK-7 | MK-3 | 100 |
| "*Bacillus dextrolacticus*" | MK-7 | MK-6 | 38 |
| "*Bacillus epiphytus*" | MK-7 | MK-3 | 100 |
| "*Bacillus filicolonicus*" | MK-7 | | 100 |
| *Bacillus firmus* | MK-7 | MK-3 | 100 |
| *B. firmus* | MK-7 | | 227 |
| "*Bacillus freudenreichii*" | MK-7 | MK-6, MK-5, MK-4 | 50 |
| "*B. freudenreichii*" | MK-7 | | 100 |
| *Bacillus globisporus* | MK-7 | MK-3 | 100 |
| *Bacillus insolitus* | MK-7 | MK-3 | 100 |
| "*Bacillus laevolacticus*" | MK-7 | MK-6 | 38 |
| "*B. laevolacticus*" | MK-7 | | 100 |
| *Bacillus larvae* | MK-7 | | 100 |
| *Bacillus laterosporus* | MK-7 | MK-3 | 100 |
| *Bacillus lentus* | MK-9 | MK-3 | 100 |
| *B. lentus* | MK-7 | | 227 |
| *Bacillus licheniformis* | MK-7 | | 91, 191 |
| *B. licheniformis* | MK-7 | MK-3 | 100 |
| *Bacillus macerans* | MK-7 | MK-3 | 100 |
| *B. macerans* | MK-7 | | 227 |
| *Bacillus macquariensis* | MK-7 | MK-3 | 100 |
| "*Bacillus maroccanus*" | MK-7 | MK-3 | 100 |
| "*Bacillus macroides*" | MK-7 | MK-6 | 38 |
| "*Bacillus medusa*" | MK-7 | MK-3 | 100 |
| *Bacillus megaterium* | MK-7 | | 17, 20, 100, 137, 191, 227 |
| "*Bacillus mesentericus*" | MK-7 | | 69 |
| "*B. mesentericus*" | MK-*n* | | 148 |
| "*Bacillus myxolactis*" | MK-7 | MK-6 | 38 |
| *Bacillus pantothenticus* | MK-8 | MK-2 | 100 |
| *B. pantothenticus* | MK-7 | | 227 |
| *Bacillus pasteurii* | MK-7 | MK-6, MK-5, MK-4 | 50 |
| *B. pasteurii* | MK-7 | MK-2 | 100 |
| *Bacillus polymyxa* | MK-7 | | 100, 227 |
| *Bacillus popilliae* | MK-7 | | 100 |
| "*Bacillus psychrophilus*" | MK-7 | MK-3 | 100 |
| "*Bacillus psychrosaccharolyticus*" | MK-7 | MK-3 | 100 |
| "*Bacillus pulvifaciens*" | MK-7 | MK-2 | 100 |
| *Bacillus pumilus* | MK-7 | | 100, 227 |
| "*Bacillus racemilacticus*" | MK-7 | MK-6 | 38 |
| "*B. racemilacticus*" | MK-7 | | 100 |
| *Bacillus sphaericus* | MK-7 | MK-6, MK-5 | 38 |
| *B. sphaericus* | MK-7 | MK-3 | 100 |
| *B. sphaericus* | MK-7 | | 84, 227 |
| *Bacillus stearothermophilus* | MK-7 | | 67, 100, 227 |

TABLE 11—*Continued*

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Bacillus subtilis* | MK-7 | | 17, 63, 71, 100, 113, 191, 227 |
| *"Bacillus thiaminolyticus"* | MK-7 | MK-2 | 100 |
| *Bacillus thuringiensis* | MK-8, MK-7 | MK-3 | 100 |
| *Clostridium formicoaceticum*[b] | MK-n | | 92 |
| *Clostridium thermoaceticum* | MK-n | | 92 |
| *Desulfotomaculum nigrificans* | MK-7 | | 221 |
| *Sporolactobacillus inulinus* | MK-7 | MK-6 | 38 |
| *S. inulinus* | MK-7 | | 100 |
| *"Sporolactobacillus laevus"* | MK-7 | MK-6 | 38 |
| *Sporolactobacillus racemicus* | MK-7 | MK-6 | 38 |
| *Sporosarcina ureae* | MK-7 | | 242 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).

[b] Menaquinones and ubiquinones have been reported to be absent in *Clostridium butyricum* (100), *Clostridium chauvoei* (100), *Clostridium histolyticum* (85, 100), *"Clostridium oedematiens"* (100), *Clostridium paraputrificum* (100), *Clostridium perfringens* (148), *Clostridium sporogenes* (17), and *Clostridium sticklandii* (83).

TABLE 12. *Distribution of isoprenoid quinones in gram-positive bacteria: gram-positive, asporogenous rod-shaped bacteria containing menaquinones as their sole isoprenoid quinones*[a]

| Taxon[b] | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Brochothrix thermosphacta* | MK-7 | MK-6, MK-5 | 33, 46, 121 |
| *B. thermosphacta* | MK-9[c] | | 100 |
| *Caryophanon latum* | MK-6 | | 50 |
| *"Caryophanon tenue"* | MK-6 | MK-5 | 46 |
| *Lactobacillus casei* subsp. *rhamnosus* | MK-n | | 100 |
| *Lactobacillus mali* | MK-8, MK-9[d] | MK-10, MK-7 | 33, 50 |
| *"Lactobacillus yamanashiensis"* | MK-8, MK-9 | MK-10, MK-7 | 33 |
| *Listeria denitrificans* | MK-9 | MK-8, MK-7 | 33, 46, 121 |
| *Listeria grayi* | MK-7 | MK-6, MK-5 | 33, 46, 121 |
| *"Listeria innocua"* | MK-7 | MK-6, MK-5 | 33 |
| *Listeria murrayi* | MK-7 | MK-6, MK-5 | 33, 46, 121 |
| *Listeria monocytogenes* (including *"Listeria bulgarica"*) | MK-7 | MK-6, MK-5 | 33, 46, 121 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).

[b] Gram-positive, asporogenous rod-shaped bacteria that lack both menaquinones and ubiquinones include *Erysipelothrix rhusiopathiae* (46), *Lactobacillus acidophilus* (100), *Lactobacillus brevis* (33, 100), *Lactobacillus casei* subsp. *casei* (17, 38), *Lactobacillus casei* subsp. *rhamnosus* (38), *Lactobacillus delbrueckii* (38), *Lactobacillus hilgardii* (38), *"Lactobacillus odontolyticus"* (100), *Lactobacillus plantarum* (38), and *Lactobacillus salivarius* (38).

[c] Hess et al. (100) used only reverse-phase partition thin-layer chromatography for quinone characterizations.

[d] MK-8 and MK-9 were present in comparable amounts in *L. mali* and *"L. yamanashiensis"* (33).

reinforcing their affinity with the majority of the streptococci (Table 13).

**(iii) *Micrococcaceae*.** The distribution of menaquinones within the members of the family *Micrococcaceae* is summarized in Table 13. All members of the genera *Planococcus* and *Staphylococcus* that have been examined possess unsaturated manaquinones as their sole respiratory quinones. *Planococcus citreus* and *Staphylococcus aureus* contain MK-8 as their major component, although MK-7 is also present at substantial levels (114–117, 242). However, the coagulase-negative staphylococci (*Staphylococcus capitis, Staphylococcus cohnii, Staphylococcus epidermidis, Staphylococcus haemolyticus, Staphylococcus hominis, Staphylococcus saprophyticus, Staphylococcus simulans*, and *Staphylococcus warneri*) contain MK-7 as their major isoprenolog (Table 13). *Staphylococcus sciuri* subsp. *sciuri* and *Staphylococcus sciuri* subsp. *lentus* contain MK-6 as their major menaquinone component and on this basis can be differentiated from all of other staphylococci that have been examined (Table 13).

Members of the genus *Micrococcus* are heterogeneous with respect to menaquinone composition. *Micrococcus varians* and *Micrococcus agilis* are characterized by the presence of major

TABLE 13. *Distribution of isoprenoid quinones in gram-positive bacteria: gram-positive cocci containing menaquinones or demethylmenaquinones as their sole isoprenoid quinones*[a]

| Taxon[b] | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Micrococcaceae* | | | |
| *Micrococcus agilis* ATCC 966 | MK-*9*($H_x$)[c] | MK-*8*($H_x$) | 114, 115, 116 |
| *Micrococcus agilis* strains ATCC 966, CCM 2390, CCM 2539, CCM 2687, and CCM 2688 | MK-*9*($H_2$) | | 242 |
| "*Micrococcus cyaneus*" | MK-*9*($H_x$) | MK-*8*($H_x$) | 114, 115 |
| "*Micrococcus eucinetus*" CCM 2387[d] | MK-*8* | MK-*7*, MK-*6* | 115 |
| "*M. eucinetus*" | MK-*8*, MK-*7*[e] | | 115 |
| *Micrococcus halobius* | MK-*8* | MK-*7*, MK-*6* | 49 |
| *Micrococcus luteus* strains CCM 134 and CCM 840 | MK-*8*($H_x$) | MK-*9*($H_x$), MK-*7*($H_x$)[f] | 115 |
| *M. luteus* strains CCM 810 and ATCC 398 | MK-*9*($H_x$) | MK-*8*($H_x$) | 114, 115 |
| *M. luteus* CCM 132 | MK-*7*($H_x$) | MK-*8*($H_x$), MK-*6*($H_x$) | 114, 115 |
| *M. luteus* strains CCM 169 and ATCC 4698 | MK-*8* | MK-*7* | 242 |
| *M. luteus* strains CCM 149 and ATCC 272 | MK-*8*($H_2$) | | 242 |
| *M. luteus* strains CCM 810 and ATCC 398 | MK-*9*($H_2$) | | 242 |
| "*Micrococcus lysodeikticus*"[g] | MK-*4*, MK-*3* | MK-*8*($H_2$), MK-*8*, MK-*5* | 67 |
| "*M. lysodeikticus*"[g] | MK-*8* | | 227 |
| "*M. lysodeikticus*"[g] | MK-*9* | | 16, 79, 152, 191 |
| "*Micrococcus morrhuae*"[h] | MK-*8* | MK-*7*, MK-*6* | 114 |
| "*Micrococcus radiodurans*" | MK-*8* | | 247 |
| "*M. radiodurans*" | MK-*8* | MK-*7*, MK-*6* | Collins[i] |
| "*Micrococcus radiophilus*" | MK-*8* | | 247 |
| "*M. radiophilus*" | MK-*8* | MK-*7*, MK-*6* | Collins[i] |
| "*Micrococcus radioproteolyticus*" | MK-*8* | | 247 |
| "*M. radioproteolyticus*" | MK-*8* | MK-*7*, MK-*6* | Collins[i] |
| *Micrococcus varians* | MK-*7*($H_2$) | | 115 |
| *M. varians* CCM 132 | MK-*7*($H_x$) | MK-*8*($H_x$), MK-*6*($H_x$) | 115 |
| *Planococcus citreus* | MK-*8* | MK-*7* | 242 |
| *Planococcus* spp. strains CCM 1849, CCM 2069, CCM 2104, CCM 2414, CCM 2415, and CCM 2416 | MK-*8* | MK-*7* | 242 |
| *Staphylococcus aureus* HS653 | MK-*7*[j] | MK-*8*, MK-*6*, MK-*5*, MK-*4* | 117 |
| *S. aureus* | MK-*8* | MK-*7* | 242 |
| *S. aureus* | MK-*8* | MK-*9*, MK-*7*[k] | 75, 98, 114, 115, 116 |
| "*Staphylococcus albus*" | MK-*7* | | 17 |
| *Staphylococcus capitis* | MK-*7* | MK-*8*, MK-*6*, MK-*5* | Collins and Goodfellow[l] |
| *Staphylococcus cohnii* | MK-*7* | MK-*8*, MK-*6*, MK-*5* | Collins and Goodfellow[l] |
| *Staphylococcus epidermidis* | MK-*7* | MK-*8*, MK-*6*, MK-*5* | Collins and Goodfellow[l] |
| *Staphylococcus haemolyticus* | MK-*7* | MK-*8*, MK-*6*, MK-*5* | Collins and Goodfellow[l] |
| *Staphylococcus hominis* | MK-*7* | MK-*8*, MK-*6*, MK-*5* | Collins and Goodfellow[l] |
| *Staphylococcus saprophyticus* | MK-*7* | MK-*8*, MK-*6*, MK-*5* | Collins and Goodfellow[l] |
| *S. saprophyticus* | MK-*7* | MK-*8*, MK-*6* | 114 |
| *Staphylococcus simulans* | MK-*7* | MK-*8*, MK-*6*, MK-*5* | Collins[i] |
| *Staphylococcus* spp. acetoin-negative bovine strains | MK-*6* | MK-*8*, MK-*7* | 114, 115 |
| *Staphylococcus warneri* | MK-*7* | MK-*8*, MK-*6*, MK-*5* | Collins[i] |
| *Staphylococcus sciuri* subsp. *lentus* | MK-*6* | | Collins[i] |
| *Staphylococcus sciuri* subsp. *sciuri* | MK-*6* | | 50 |
| *Peptococcaceae* | | | |
| "*Peptostreptococcus magnus*" | MK-*n* | | 85 |
| "*Sarcina flava*" | MK-*n* | | 113 |

TABLE 13—*Continued*

| Taxon[b] | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *"Sarcina lutea"* | MK-*8* | | 17 |
| *"S. lutea"* | MK-*9* | | 85 |
| *Streptococcaceae* | | | |
| *Leuconostoc lactis* | MK-*n* | | 106 |
| *Streptococcus cremoris* | MK-*9* | MK-*8*, MK-*7*, MK-*6* | 39 |
| *Streptococcus cremoris* subsp. *alactosus* | MK-*9* | MK-*8*, MK-*7*, MK-*6* | 39 |
| *Streptococcus faecalis* | DMK-*9*[m] | DMK-*8*, DMK-*7* | 7, 8 |
| *S. faecalis* | DMK-*n* | | 100, 106 |
| *Streptococcus faecalis* subsp. *faecalis* | DMK-*9* | DMK-*8*, DMK-*7*, DMK-*6*[n] | 39, 40 |
| *Streptococcus faecalis* subsp. *liquefaciens* | DMK-*9* | DMK-*8*, DMK-*7*, DMK-*6*[n] | 39, 40 |
| *Streptococcus faecalis* subsp. *zymogenes* | DMK-*9* | DMK-*8*, DMK-*7*, DMK-*6*[n] | 39, 40 |
| *Streptococcus faecium* subsp. *casseliflavus* | MK-*8* | MK-*7*, MK-*6* | 39, 40 |
| *Streptococcus faecium* subsp. *mobilis* | MK-*8* | MK-*7*, MK-*6* | 39, 40 |
| *Streptococcus lactis* | MK-*9* | MK-*8*, MK-*7*, MK-*6* | 39 |
| *Streptococcus lactis* subsp. *diacetylactis* | MK-*9* | MK-*8*, MK-*7*, MK-*6* | 39 |

[a] Major groupings as in *Bergey's Manual of Determinative Bacteriology* (21).

[b] Gram-positive cocci that lack both menaquinones and ubiquinones include the following members of the *Streptococcaceae*: *"Aerococcus catalasicus"* (39), *Aerococcus viridans* (39, 100), *Gemella haemolysans* (39, 40, 100), *Leuconostoc cremoris* (100), *Leuconostoc dextranicum* (39), *Leuconostoc mesenteroides* (39), *Leuconostoc paramesenteroides* (100), *Pediococcus acidilactici* (39), *Pediococcus parvulus* (39), *Pediococcus pentosaceus* (39), *Streptococcus agalactiae* (39, 40), *"Streptococcus avium"* (39, 40), *Streptococcus bovis* (39, 40), *"Streptococcus durans"* (39), *"Streptococcus dysgalactiae"* (39, 40), *Streptococcus equi* (39), *Streptococcus equinus* (39, 40), *"Streptococcus equisimilis"* (39, 40), *Streptococcus faecalis* subsp. *malodoratus* (39), *Streptococcus faecium* (39), *"Streptococcus milleri"* (39), *Streptococcus mitis* (85), *Streptococcus mutans* subsp. *sorbrinus* (39), *Streptococcus pneumoniae* (39), *Streptococcus pyogenes* (39), *Streptococcus raffinolactis* (39), *Streptococcus salivarius* (39), *Streptococcus sanguis* (39, 40), *"Streptococcus suis"* (39, 40), *Streptococcus* sp. group E (39), *Streptococcus* sp. strain 77007/71 (100), and *Streptococcus uberis* (39, 40).

[c] ($H_x$) indicates that the degree of hydrogenation was not determined.

[d] *"M. eucinetus"* is now classified as *Planococcus citreus*.

[e] MK-*8* and MK-*7* were present in comparable amounts.

[f] Traces of hydrogenated MK-*5* and MK-*6* were also found in *M. luteus* CCM 134 (114).

[g] Now classified as *Micrococcus luteus*.

[h] *"M. morrhuae"* is now classified as *Halococcus morrhuae*.

[i] M. D. Collins, unpublished data.

[j] Major amounts of MK-*7* were present in an atypical *S. aureus* strain (117).

[k] Trace amounts of smaller isoprenologs were detected in *Streptococcus aureus* (75, 98).

[l] M. D. Collins and M. Goodfellow, unpublished data.

[m] DMK-*9*, Demethylmenaquinone containing nine isoprene units.

[n] Traces of demethylmenaquinone containing 10 isoprene units were found in *S. faecalis* subsp. *faecalis*, *S. faecalis* subsp. *liquefaciens*, and *S. faecalis* subsp. *zymogenes* (39, 40).

amounts of dihydrogenated MK-*7* [MK-*7*($H_2$)] and MK-*9*($H_2$), respectively (242). Three menaquinone patterns have been reported in strains of *Micrococcus luteus*. Strain ATCC 4698, the neotype of *M. luteus* (134), contains unsaturated MK-*8*. However, *M. luteus* strains AJ 1081 and ATCC 398 possess MK-*8*($H_2$) and MK-*9*($H_2$), respectively (242). The radiation-resistant taxa *"Micrococcus radiodurans,"* *"Micrococcus radiophilus,"* and *"Micrococcus radioproteolyticus"* all possess closely related menaquinone profiles, with MK-*8* predominating (247). These three taxa should be removed from the genus *Micrococcus*.

Little information is available on the isoprenoid quinone contents of the *Peptococcaceae*. Gibbons and Engle (85) detected an uncharacterized menaquinone in *"Peptostreptococcus magnus"* by using a microbiological assay. Data on the menaquinone composition of *"Sarcina*

*lutea*" are confusing. Bishop et al. (17) recovered major amounts of MK-*8* from "*S. lutea*," whereas Salton and Schmitt (191) reported the presence of MK-*9* in the same species.

**(iv) Coryneform bacteria and actinomycetes.** In *Bergey's Manual of Determinative Bacteriology* (21), the coryneform group of bacteria contains the genera *Arthrobacter*, *Cellulomonas*, and *Corynebacterium*, and *Brevibacterium* and *Microbacterium* are described as genera incertae sedis. The genus *Kurthia* is also included as a placement of convenience. The genera *Bacterionema* and *Curtobacterium* should also be added to the coryneform group.

The genus *Arthrobacter* is heterogeneous, and *Arthrobacter globiformis* and related strains can be distinguished readily from *Arthrobacter simplex* (36, 126, 127, 194). The menaquinone data underline this division, since *A. globiformis*, *Arthrobacter atrocyaneus*, *Arthrobacter aurescens*, *Arthrobacter crystallopoietes*, *Arthrobacter pascens*, *Arthrobacter ramosus*, and *Arthrobacter ureafaciens* contain major amounts of MK-*9*($H_2$), whereas *A. simplex* possesses major quantities of MK-*8*($H_4$) (Table 14). *A. simplex* contains a peptidoglycan based on LL-diaminopimelic acid (194) and is probably more closely related to certain actinomycetes. The phytopathogen *Cornebacterium ilicis* possesses many properties in common with true *Arthrobacter* spp., and the presence of MK-*9*($H_2$) within this taxon underlines this relationship. However, the menaquinones cast serious doubt on the retention of *Arthrobacter nicotianae* within the genus *Arthrobacter*. *A. nicotianae* contains unsaturated MK-*8* and MK-*9* (241). Major amounts of MK-*8* and MK-*9* have also been described in strains of "*Brevibacterium fuscum*" and *Brevibacterium protophormiae* (50, 241). All three of these taxa possess peptidoglycans based on lysine (structural variation A4$\alpha$) (194) and may constitute the nucleus of an as-yet-unrecognized taxon (36). The menaquinone data are not in accord with the suggestion of Keddie and Jones (127) that the taxon "*Brevibacterium sulfureum*" be included in the genus *Arthrobacter*. "*B. sulfureum*" contains major amounts of MK-*9*, and further studies should be directed to a comparison of this taxon with *A. nicotianae*, "*B. fuscum*," and *B. protophormiae*.

In *Bergey's Manual of Determinative Bacteriology* (21), the genus *Brevibacterium* is described as a taxon incertae sedis. However, this genus has been redefined recently, with *Brevibacterium linens* as the type species (47). *B. linens* possesses MK-*8*($H_2$) as its major components (34, 47, 241). A similar menaquinone pattern has been found in the gram-negative taxon "*Chromobacterium iodinum*" (Table 14). Other chemotaxonomic and numerical phenetic data have led to the recommendation that this species should be reclassified in the genus *Brevibacterium* as *Brevibacterium iodinum* (47), an observation in accord with the menaquinone data.

Chemical and numerical phenetic data indicate that the genus *Microbacterium* should be retained for the type species *Microbacterium lacticum* (34, 120, 126, 194). *M. lacticum* is characterized by the presence of an unusual peptidoglycan based upon lysine (structural variation B1$\alpha$) (194). Similar cell wall structures based upon lysine have also been reported in *Brevibacterium imperiale* and "*Corynebacterium laevaniformans*" (variations B1$\beta$ and B1$\alpha$, respectively) (194). The presence of unusually long unsaturated MK-*11* and MK-*12* within the taxa *M. lacticum*, *B. imperiale*, and "*C. laevaniformans*" supports this apparent relationship.

In *Bergey's Manual of Determinative Bacteriology* (21), the monospecific genus *Kurthia* is treated with the coryneform group of bacteria, although its members do not have a coryneform morphology. *Kurthia zopfii* possesses major amounts of MK-*7* and on this basis can be differentiated from all coryneform bacteria that have been examined, with the exception of *Brevibacterium acetylicum* ATCC 953 and *Brevibacterium halotolerans* (34, 49). *B. acetylicum* should be compared further with *K. zopfii*, whereas *B. halotolerans* is probably more closely related to *Brochothrix thermosphacta* (Table 12).

The genus *Cellulomonas* is a homogeneous taxon. All of the cellulomonads that have been examined possess tetrahydrogenated MK-*9* [MK-*9*($H_4$)] (34, 241). The nocardioform genus *Oerskovia* shares many biochemical properties with the cellulomonads (34, 48, 120, 162, 163). The recovery of MK-*9*($H_4$) from *Oerskovia* spp. reinforces this relationship (34, 48, 241). Representatives of the taxa *Brevibacterium fermentans*, *Brevibacterium lyticum*, "*Cellulomonas cartalyticum*", "*Corynebacterium manihot*," and *Nocardia cellulans* also possess major amounts of MK-*9*($H_4$) (Table 14). Numerical phenetic and chemical data indicate that these taxa should be reclassified in the genus *Oerskovia* (120, 162).

The genus *Curtobacterium* is heterogeneous with respect to menaquinone composition (Table 14). Collins et al. (35) have suggested that "true curtobacteria" should be restricted to those taxa (e.g., *Curtobacterium albidum*, *Curtobacterium citreum*, *Curtobacterium luteum*, *Corynebacterium betae*, *Corynebacterium oortii*, *Corynebacterium flaccumfaciens*, and *Corynebacterium poinsettiae*) which contain MK-*9* as their major isoprenolog. However, *Curtobac-*

*terium saperdae* and *Curtobacterium testaceum* contain major amounts of MK-*11* and MK-*12* and should be removed from the genus *Curtobacterium* sensu stricto (35, 241). Cell wall data indicate that "*Corynebacterium barkeri*" and "*Microbacterium liquefaciens*" may be related to *C. saperdae* (194). The recovery of MK-*11* and MK-*12* from "*C. barkeri*" and "*M. liquefaciens*" is in accord with this view. *C. saperdae, C. testaceum, "C. barkeri,"* and "*M. liquefaciens*" should be compared further to determine whether they constitute the nucleus of a new genus.

Relatively few coryneform bacteria possess peptidoglycans based upon diaminobutyric acid (194). Most of these bacteria have been placed in the genus *Corynebacterium*, and they include six plant pathogens (*Corynebacterium insidiosum, "Corynebacterium isanicum," Corynebacterium michiganense, Corynebacterium nebraskense, "Corynebacterium tritici,"* and *Corynebacterium sepedonicum*), one insect pathogen ("*Corynebacterium okanaganae*"), and a few saprophytic species ("*Corynebacterium aquaticum,*" "*Corynebacterium mediolanum,*" and "*Flavobacterium dehydrogenans*"). Other than to note that none of these belongs to the genus *Corynebacterium*, little comment can be made on their generic positions. Recent studies have shown the diaminobutyric acid-containing taxa can be divided into four groups on the basis of menaquinone patterns (41). *C. insidiosum, C. michiganense, C. nebraskense,* and *C. sepedonicum* possess MK-*9*; "*C. iranicum*" and "*C. tritici*" possess MK-*10*; "*C. aquaticum*" possesses MK-*10* and MK-*11*; and "*C. mediolanum*" and "*F. dehydrogenans*" possess MK-*11* and MK-*12* (41).

There is now general agreement that the genus *Corynebacterium* sensu stricto (127, 163) should be restricted to those taxa which contain a peptidoglycan based upon *meso*-diaminopimelic acid (variation A1$\gamma$) (194), the wall sugars arabinose and galactose (126, 194), a deoxyribonucleic acid base composition of 51 to 59 mol% guanine plus cytosine (127), and relatively short-chain mycolic acids (approximately 22 to 36 carbon atoms) (37, 163). On the basis of menaquinone patterns, "true corynebacteria" can be divided into two broad groups (Table 15). The majority of animal-associated corynebacteria (e.g., *Corynebacterium diphtheriae, Corynebacterium kutscheri, Corynebacterium pseudotuberculosis, Corynebacterium renale, "Corynebacterium ulcerans"*) possess major amounts of MK-*8*($H_2$), whereas many saprophytic species (e.g., *Corynebacterium glutamicum*) and occasional animal-associated taxa (e.g., *Corynebacterium bovis* and "*Corynebacterium minutissimum*") contain predominantly MK-*9*($H_2$) (34, 48, 241). *Bacterionema matruchotii* also possesses a peptidoglycan based upon *meso*-diaminopimelic acid, a guanine-plus-cytosine content of 55 to 57 mol%, and a relatively short-chain mycolic acid (30 to 36 carbon atoms) (163). The recovery of major amounts of MK-*8*($H_2$) and MK-*9*($H_2$) from *B. matruchotii* (50) reinforces this relationship between *Bacterionema* spp. and *Corynebacterium* spp. and suggests that *B. matruchotii* should be reclassified in the genus *Corynebacterium* sensu stricto.

The distribution of menaquinones within the mycolic acid-coantaining actinomycetes and coryneforms is shown in Table 15. The menaquinone data support the exclusion of strains of the rhodochrous complex from the genus *Nocardia*. Primarily on the basis of chemical and numerical phenetic data, the rhodochrous complex and the genus *Gordona* have been merged to form the genus *Rhodococcus* (88). The rhodococci can be divided into two groups on the basis of their menaquinone patterns (48, 161). *Rhodococcus erythropolis, Rhodococcus coprophilus, Rhodococcus rhodochrous,* and *Rhodococcus ruber* contain MK-*8*($H_2$) as their major isoprenolog, whereas MK-*9*($H_2$) predominates in strains of *Rhodococcus bronchialis* and *Rhodococcus corallinus*. In complete contrast, representatives of *Nocardia* sensu stricto have MK-*8*($H_4$) as their major component. A strain of *Micropolyspora brevicatena* has also been reported to contain MK-*8*($H_4$) (48). *M. brevicatena* also contains mycolic acids similar to those found in strains of *Nocardia* (48). It will be interesting to see whether other studies support this apparently close relationship. Members of the genus *Mycobacterium* and the species *Nocardia amarae* and *Nocardia farcinica* contain major amounts of MK-*9*($H_2$) (Table 15).

Numerical phenetic and chemical studies indicate that strains currently called "*Cordona aurantiaca*" form a distinct taxon worthy of generic rank (90). The presence of major amounts of MK-*9* within "*G. aurantiaca*" supports this view (90). It is worth noting that, with the sole exception of *Corynebacterium paurometabolum*, all of the mycolic acid-containing taxa that have been examined possess partially hydrogenated menaquinones (Table 15).

A variety of menaquinone patterns are found in strains of actinomycetes which lack mycolic acids (Table 16). *Promicromonospora citrea, Propionibacterium acnes, "Propionibacterium arabinosum,"* and "*Propionibacterium shermanii*" contain major amounts of MK-*9*($H_4$) (50, 198, 208). Members of the genera *Actinomadura* and *Streptomyces* are unusual in that they contain very complex mixtures of partially hydro-

TABLE 14. *Distribution of isprenoid quinones in gram-positive bacteria: coryneform bacteria lacking mycolic acids*[a]

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Arthrobacter atrocyaneus* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 36 |
| *Arthrobacter aurescens* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 36 |
| *Arthrobacter citreus* | MK-9($H_2$) | | 241 |
| *A. citreus* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 36 |
| *Arthrobacter crystallopoietes* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$)[b,c] | 34, 36 |
| *Arthrobacter globiformis* | MK-9($H_2$) | | 241 |
| *A. globiformis* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$)[b] | 34, 36 |
| *Arthrobacter nicotianae* | MK-8 | MK-9 | 241 |
| *A. nicotianae* | MK-8 | MK-9, MK-7 | 36 |
| *Arthrobacter oxydans* | MK-9($H_2$) | | 241 |
| *A. oxydans* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 36 |
| *Arthrobacter polychromogenes* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *Arthrobacter ramosus* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 36 |
| *Arthrobacter simplex* | MK-7 | | 2 |
| *A. simplex* | MK-8($H_4$) | | 241 |
| *A. simplex* | MK-*n* | | 1 |
| *A. simplex* | MK-8($H_4$) | MK-8($H_2$), MK-7($H_4$) | 34, 36 |
| *Arthrobacter tumescens* | MK-8($H_4$) | MK-8($H_2$), MK-7($H_4$) | 34, 36 |
| *Arthrobacter ureafaciens* | MK-9($H_2$) | | 241 |
| *A. ureafaciens* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *Arthrobacter* sp. A4 | MK-10 | MK-11, MK-9, MK-8, MK-7 | 41 |
| *Brevibacterium acetylicum* ATCC 953 | MK-7 | MK-6 | Collins, unpublished data |
| *Brevibacterium fermentans* | MK-9($H_4$) | MK-9($H_2$), MK-8($H_4$), MK-7($H_4$) | |
| "*Brevibacterium fuscum*" | MK-9 | MK-8 | 241 |
| *Brevibacterium halotolerans* | MK-7 | MK-6 | 49 |
| "*Brevibacterium helvolum*" ATCC 11822 | MK-9($H_2$) | | 241 |
| *Brevibacterium imperiale* | MK-12, MK-11 | MK-13, MK-10, MK-9, MK-8 | Collins, unpublished data |
| *Brevibacterium iodinum* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 47 |
| *Brevibacterium linens* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34, 47 |
| *B. linens* | MK-8($H_2$) | | 241 |
| "*Brevibacterium lipolyticum*" | MK-8($H_4$) | | 241, 243 |
| "*B. lipolyticum*" | MK-8($H_4$) | MK-8($H_2$), MK-7($H_4$) | 36 |
| *Brevibacterium lyticum* | MK-9($H_4$) | MK-9($H_2$), MK-8($H_4$), MK-7($H_4$) | 44 |
| *Brevibacterium protophormiae* | MK-9, MK-8 | MK-7 | 50 |
| "*Brevibacterium sulfureum*" | MK-9 | MK-10 | 241 |
| "*B. sulfureum*" | MK-9 | MK-10, MK-8, MK-7 | 34 |
| *Cellulomonas biazotea* | MK-9($H_4$) | | 241 |
| *C. biazotea* | MK-9($H_4$) | MK-9($H_2$), MK-8($H_4$), MK-7($H_4$) | 34 |
| "*Cellulomonas cartalyticum*" | MK-9($H_4$) | MK-9($H_2$), MK-8($H_4$), MK-7($H_4$) | 34 |
| *Cellulomonas fimi* | MK-9($H_4$) | | 241 |
| *C. fimi* | MK-9($H_4$) | MK-9($H_2$), MK-8($H_4$), MK-7($H_4$) | 34 |
| *Cellulomonas flavigena* | MK-9($H_4$) | MK-9($H_2$), MK-8($H_4$), MK-7($H_4$) | 34 |
| "*Cellulomonas subalbus*" | M-9($H_4$) | MK-9($H_2$), MK-8($H_4$), MK-7($H_4$) | 34 |
| "*Corynebacterium aquaticum*" | MK-11, MK-10 | | 241 |
| "*C. aquaticum*" | MK-11, MK-10 | MK-12, MK-9, MK-8, MK-7 | 34, 41, 50 |
| "*Corynebacterium barkeri*" | MK-11, MK-12 | MK-13, MK-10, MK-9, MK-8 | Collins, unpublished data |
| *Corynebacterium betae* | MK-9 | MK-8, MK-7[d] | 34, 35 |
| *Corynebacterium flaccumfaciens* | MK-9 | | 241 |
| *C. flaccumfaciens* | MK-9 | MK-8, MK-7 | 34, 35 |
| *Corynebacterium ilicis* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | Collins, unpublished data |
| *Corynebacterium insidiosum* | MK-9 | MK-10, MK-8, MK-7 | 41 |
| "*Corynebacterium iranicum*" | MK-10 | MK-11, MK-9, MK-8, MK-7 | 41 |
| "*Corynebacterium manihot*" | MK-9($H_4$) | MK-9($H_2$), MK-8($H_4$), MK-7($H_4$) | 34 |
| "*Corynebacterium mediolanum*" | MK-12, MK-11 | MK-13, MK-10, MK-9, MK-8, MK-7 | 41, 50 |

TABLE 14—*Continued*

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Corynebacterium michiganense* | MK-*9* | MK-*10*, MK-*8*, MK-*7* | 41, 50 |
| *Corynebacterium nebraskense* | MK-*9* | MK-*10*, MK-*8*, MK-*7* | 34, 35, 41 |
| *Corynebacterium oortii* | MK-*9* | MK-*8* | 35, 50 |
| "*Corynebacterium okanaganae*" | MK-*12*, MK-*11* | MK-*10*, MK-*9*, MK-*8* | 42 |
| *Corynebacterium poinsettiae* | MK-*9* | | 241 |
| *C. poinsettiae* | MK-*9* | MK-*8*, MK-*7* | 34, 35 |
| *Corynebacterium sepedonicum* | MK-*9* | MK-*10*, MK-*8*, MK-*7* | 41 |
| "*Corynebacterium tritici*" | MK-*10* | MK-*11*, MK-*9*, MK-*8*, MK-*7* | 41 |
| *Curtobacterium albidum* | MK-*9* | | 241 |
| *Curtobacterium citreum* | MK-*9* | MK-*8*, MK-*7* | 34, 35 |
| *C. citreum* | MK-*9* | | 241 |
| *Curtobacterium luteum* | MK-*9* | MK-*8*, MK-*7* | 34, 35 |
| *C. luteum* | MK-*9* | | 241 |
| *Curtobacterium saperdae* | MK-*12*, MK-*11*[e] | MK-*13*, MK-*10*, MK-*9*, MK-*8* | 35 |
| *Curtobacterium testaceum* | MK-*12*, MK-*11*[f] | MK-*13*, MK-*10*, MK-*9*, MK-*8* | 35 |
| *C. testaceum* | MK-*11* | | 241 |
| *Microbacterium lacticum* | MK-*12*, MK-*11*[g] | MK-*13*, MK-*10*, MK-*9*, MK-*8* | Collins and Jones, unpublished data |
| "*Microbacterium liquefaciens*" | MK-*12*, MK-*11* | MK-*13*, MK-*10*, MK-*9*, MK-*8* | Collins and Jones, unpublished data |
| *Nocardia cellulans*[h] | MK-*9*($H_4$) | MK-*9*($H_2$), MK-*8*($H_4$), MK-*7*($H_4$) | 35 |
| *Oerskovia turbata* | MK-*9*($H_4$) | | 241, 243, 244 |
| *O. turbata* | MK-*9*($H_4$) | MK-*9*($H_2$), MK-*8*($H_4$) | 48 |
| *Oerskovia xanthineolytica* | MK-*9*($H_4$) | MK-*9*($H_2$), MK-*8*($H_4$), MK-*7*($H_4$) | 35 |
| *O. xanthineolytica* | MK-*9*($H_4$) | | 241 |

[a] Mycolic acids are α-alkyl-β-hydroxy long-chain fatty acids (37, 163).
[b] Traces of MK-*10*($H_2$) were also present (34).
[c] Kostiw et al. (138) reported the presence of ubiquinones in a strain of *A. crystallopoietes*.
[d] Traces of MK-*10* were present in some strains (34).
[e] MK-*12* in excess of MK-*11* (35).
[f] MK-*11* in excess of MK-*12* (35).
[g] In an earlier investigation, MK-*10* and MK-*11* were reported as the major components in *M. lacticum* (35). Recently however, the major components have been shown to be MK-*12* and MK-*11* (Collins and Jones, unpublished data).
[h] *N. cellulans* should be reclassified in the genus *Oerskovia* (162).

genated menaquinones. Thus, *Actinomadura medurae*, *Actinomadura pelletieri*, *Streptomyces olivaceus*, and *Streptomyces somaliensis* contain major amounts of tetra-, hexa-, and octahydrogenated MK-*9* (5, 6, 48, 161, 163, 248). Partially hydrogenated MK-*10* have been reported in *Actinomyces israelii*, *Actinomyces viscosus*, and *Nocardiopsis dassonvillei* (48, 248).

Gram-positive bacteria synthesize either menaquinones or demethylmenaquinones, or they lack isoprenoid quinones. Ubiquinones are not formed. However, Kostiw et al. (138) reported the presence of an uncharacterized ubiquinone in a strain of *Arthrobacter crystallopoietes*. Subsequent studies on the same strain of *A. crystallopoietes* have shown that only menaquinones are present (34, 36). The report of Kostiw et al. (138) of ubiquinones in *A. crystallopoietes* is probably in error. Recently, during a systematic investigation of the isoprenoid quinone contents of certain actinomycetes and coryneform bacteria, ubiquinones were detected in strains labeled "*Brevibacterium leucinophagum*," "*Corynebacterium autotrophicum*," "*Corynebacterium nephridii*," "*Mycobacterium flavum*," and "*Mycoplana rubra*" (Table 17) (34). These taxa are misclassified and should all be reclassified in a variety of gram-negative genera. A cautionary note on the dangers of analyzing the ubiquinone contents of bacteria by mass spectrometry alone is necessary. In the mass spectra of ubiquinones from the above-described taxa, Collins and associates (34) detected peaks attributable to unsaturated and dihydrogenated isoprenologs. In a recent study in which reverse-phase partition chromatography was used, dihydrogenated isoprenologs were shown to be absent (42; Collins, unpublished data). Peaks in the mass spectra attributable to molecular ions of dihydroubiquinones were in fact artifacts due to the formation of $(M + 2)^+$ ions. Furthermore, these $(M + 2)^+$ ions increased in number with time until they were approximately the same intensity as the molecular ions $(M)^+$ (Collins, unpublished data).

## FINAL REMARKS

Although the information on the distribution of isoprenoid quinone structural types in bacteria is still fragmentary, as mentioned above, the information which is available indicates that there is an encouraging correlation between classifications based on other criteria and the type

TABLE 15. *Distribution of isoprenoid quinones in gram-positive bacteria: actinomycetes and coryneform bacteria possessing mycolic acids*[a]

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *"Arthrobacter albidus"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *"Arthrobacter roseoparaffineus"* | MK-8($H_2$) | MK-9($H_2$), MK-8, MK-7($H_2$) | 34 |
| *Arthrobacter variabilis* | MK-9($H_2$) | MK-8($H_2$),[b] MK-8, MK-7($H_2$) | 34 |
| *Bacterionema matruchotii* | MK-9($H_2$) | MK-8($H_2$),[b] MK-7($H_2$) | 50 |
| *Brevibacterium ammoniagenes* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *B. ammoniagenes* | MK-9($H_2$) | | 241 |
| *Brevibacterium divaricatum* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *"Brevibacterium flavum"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *"Brevibacterium immariophilum"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *"Brevibacterium lactofermentum"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *"Brevibacterium paraffinolyticum"* | MK-8($H_2$) | MK-9($H_2$), MK-8, MK-7($H_2$) | 34 |
| *"Brevibacterium roseum"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *"Brevibacterium saccharolyticum"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *Brevibacterium stationis* | MK-9($H_2$), MK-8($H_2$) | MK-9, MK-8, MK-7($H_2$) | 34 |
| *"Brevibacterium sterolicum"* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34 |
| *"Brevibacterium thiogenitalis"* | MK-9($H_2$) | MK-8($H_2$) | 125 |
| *Brevibacterium vitarumen* | MK-8($H_2$) | MK-9($H_2$) | 125 |
| *Caseobacter polymorphus* | MK-9($H_2$) | MK-8($H_2$),[b] MK-7($H_2$) | 50 |
| *"Corynebacterium acetoacidophilum"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *Corynebacterium bovis* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$)[c] | 34, 48 |
| *Corynebacterium callunae* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *Corynebacterium diphtheriae* | MK-9 | | 17 |
| *C. diphtheriae* | MK-8($H_2$) | | 4, 91, 96, 241 |
| *C. diphtheriae* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34, 48 |
| *Corynebacterium equi* | MK-8($H_2$) | | 241 |
| *C. equi* | MK-8($H_2$) | MK-8, MK-7($H_2$)[d] | 34, 48 |
| *Corynebacterium fascians* | MK-8($H_2$) | | 241 |
| *C. fascians* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34, 48 |
| *Corynebacterium flavescens* | MK-8($H_2$), MK-9($H_2$) | | 241 |
| *C. flavescens* | MK-8($H_2$), MK-9($H_2$)[e] | MK-8, MK-7($H_2$) | 34 |
| *Corynebacterium flavidum* | MK-8($H_2$) | MK-9($H_2$), MK-7($H_2$) | 48 |
| *Corynebacterium glutamicum* | MK-9($H_2$) | | 241 |
| *C. glutamicum* | MK-9($H_2$) | MK-9, MK-8($H_2$) | 48 |
| *"Corynebacterium herculis"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *Corynebacterium hoagii* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34 |
| *"Corynebacterium hydrocarboclastus"* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34 |
| *Corynebacterium kutscheri* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34 |
| *Corynebacterium lilium* | MK-9($H_2$) | | 241 |
| *C. lilium* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *"Corynebacterium melassecola"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *"Corynebacterium minutissimum"* | MK-9($H_2$)[f] | MK-9, MK-8($H_2$),[b] MK-8, MK-7($H_2$) | 34 |
| *"Corynebacterium mycetoides"* | MK-9($H_2$), MK-8($H_2$) | MK-9, MK-8, MK-7($H_2$)[c] | 34 |
| *Corynebacterium paurometabolum* | MK-9 | MK-10, MK-8, MK-7 | Collins, unpublished data |
| *Corynebacterium pseudotuberculosis* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 48 |
| *Corynebacterium pseudodiphtheriticum* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34 |
| *Corynebacterium renale* | MK-8($H_2$) | MK-8, MK-7($H_2$)[d] | 34, 48 |
| *"Corynebacterium rubrum"* | MK-8($H_2$) | | 9 |
| *"C. rubrum"* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34 |
| *"Corynebacterium ulcerans"* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 34 |
| *Corynebacterium xerosis* | MK-8($H_2$) | MK-8, MK-7($H_2$)[d] | 34, 48 |
| *C. xerosis* | MK-9($H_2$) | | 241 |
| *"Gordona aurantiaca"* | MK-9 | MK-8, MK-7[g] | 90 |
| *"Microbacterium ammoniaphilum"* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 34 |
| *Micropolyspora brevicatena* | MK-8($H_4$) | MK-8($H_2$), MK-7($H_4$), MK-6($H_4$) | 48 |
| *Mycobacterium avium* | MK-9($H_2$)[h] | | 4, 9 |
| *M. avium* | MK-9($H_2$) | MK-9, MK-8($H_2$) | 48 |
| *Mycobacterium bovis* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-8 | 48 |
| *Mycobacterium farcinogenes* | MK-9($H_2$) | MK-9, MK-8($H_2$) | 48 |
| *Mycobacterium fortuitum* | MK-9($H_2$) | | 9 |
| *Mycobacterium intracellulare* | MK-9($H_2$) | MK-9, MK-8($H_2$) | 48 |
| *"Mycobacterium johnei"* | MK-9($H_2$) | MK-9, MK-8($H_2$) | 48 |

TABLE 15—*Continued*

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Mycobacterium kansasii* | MK-9($H_2$)[i] | | 4 |
| *Mycobacterium phlei* | MK-9($H_2$) | MK-9, MK-8($H_2$)[j] | 48 |
| *M. phlei* | MK-9($H_2$) | | 4, 9, 82, 241 |
| *M. phlei* | MK-9($H_2$) | MK-10($H_2$), MK-8($H_2$) | 24 |
| *M. phlei* | MK-9($H_2$) | MK-8($H_2$) | 67 |
| *Mycobacterium smegmatis* | MK-9($H_2$) | MK-9, MK-8($H_2$)[j] | 48 |
| *Mycobacterium tuberculosis* | MK-9($H_2$) | MK-9, MK-8($H_2$)[j] | 48 |
| *M. tuberculosis* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-8, MK-7($H_2$) | 67 |
| *M. tuberculosis* | MK-9($H_2$) | | 9, 241 |
| *Mycobacterium* spp. | MK-9($H_2$) | MK-9, MK-8($H_2$) | 57 |
| *Nocardia amarae* | MK-9($H_2$) | MK-9, MK-8($H_2$), MK-7($H_2$) | 89 |
| *Nocardia asteroides* | MK-8($H_4$) | MK-8($H_2$), MK-7($H_4$), MK-6($H_4$)[k] | 48 |
| *N. asteroides* | MK-8($H_4$) | | 241, 244 |
| *Nocardia brasiliensis* | MK-8($H_4$) | MK-8($H_2$), MK-7($H_4$), MK-6($H_4$)[k] | 48 |
| *N. brasiliensis* | MK-8($H_4$) | | 241, 244 |
| "*Nocardia caviae*" | MK-8($H_4$) | MK-8($H_2$), MK-7($H_4$), MK-6($H_4$)[k] | 48 |
| *Nocardia farcinica* ATCC 3318 | MK-8($H_4$) | | 244 |
| *Nocardia transvalensis* | MK-8($H_4$) | MK-8($H_4$), MK-7($H_4$), MK-6($H_4$)[k] | 48 |
| *Nocardia vaccinii* | MK-8($H_4$) | MK-8($H_2$), MK-7($H_4$), MK-6($H_4$)[k] | 48 |
| *Rhodococcus bronchialis* | MK-9($H_2$) | MK-9, MK-8($H_2$) | 48 |
| *Rhodococcus coprophilus* | MK-8($H_2$) | MK-8, MK-7($H_2$) | Collins, unpublished data |
| *Rhodococcus corallinus* ("*Gordona*" *rubra*) | MK-9($H_2$) | MK-9, MK-8($H_2$) | 48 |
| *Rhodococcus erythropolis* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 48 |
| *Rhodococcus rhodochrous*[l] | MK-8($H_2$) | MK-8, MK-7($H_2$) | 48 |
| *Rhodococcus rhodnii* | MK-8($H_2$) | MK-8, MK-7($H_2$) | Collins, unpublished data |
| *Rhodococcus ruber* | MK-8($H_2$) | MK-8, MK-7($H_2$) | 48 |
| *Rhodococcus* spp. | | | |
| *Rhodococcus terrae* | MK-9($H_2$) | MK-9, MK-8($H_2$) | Collins, unpublished data |
| "*Nocardia butanica*"[j] | MK-8($H_2$) | | 244 |
| "*Nocardia calcarea*"[j] | MK-8($H_2$) | | 244 |
| "*Nocardia corallina*"[j] | MK-8($H_2$) | | 244 |
| "*Nocardia erythropolis*"[m] | MK-8($H_2$) | | 244 |
| "*Nocardia globerula*"[m] | MK-8($H_2$) | | 244 |
| "*Nocardia lutea*"[m] | MK-8($H_2$) | | 244 |
| "*Nocardia opaca*"[m] | MK-8($H_2$) | | 244 |
| "*Nocardia restricta*"[m] | MK-8($H_2$) | | 2,244 |
| "*Nocardia rubra*"[m] | MK-8($H_2$) | | 2,244 |
| "*Nocardia rubropertincta*"[m] | MK-9($H_2$) | | 2,244 |
| "*Nocardia rugosa*"[m] | MK-8($H_2$) | | 2,244 |

[a] Mycolic acids are α-alkyl-β-hydroxy long-chain fatty acids (38, 163).

[b] Component concentration more than 50% of the major isoprenolog concentration.

[c] Trace amounts of MK-10($H_2$) are also present in some strains (34, 48).

[d] Small amounts of MK-9($H_2$) are also present in some strains (34).

[e] Reverse-phase thin-layer chromatography indicates that MK-9($H_2$) and MK-8($H_2$) are present in comparable amounts in *C. flavescens* (Collins, unpublished data).

[f] Reverse-phase thin-layer chromatography indicates that MK-9($H_2$) is present in greater amounts than MK-8($H_2$) (Collins, unpublished data).

[g] Trace amounts of MK-10 are present in some strains (90).

[h] Beau et al. (9) reported the presence of small amounts of a new benzoquinone (designated mavioquinone) in *M. avium*. Mavioquinone has been shown to be 5-methoxy-2-methyl-3-(9,11,13,15-tetramethylheptadecyl)-1,4-benzoquinone (193).

[i] Unpublished data cited by Azerad and Cyrot-Pelletier (4).

[j] Uncharacterized menaquinones have been reported in *M. phlei* (113), *M. smegmatis* (148), and *M. tuberculosis* (148).

[k] MK-6($H_4$) was reported to be present in substantial amounts (48). Recently, as determined by reverse-phase thin-layer chromatography, this isoprenolog has been shown to be present in only trace amounts (Collins, unpublished data).

[l] Silva and Ioneda (205) reported major amounts of MK-8($H_2$) in *Rhodococcus* (*Nocardia*) *rhodochrous*.

[m] These taxa should be classified in the genus *Rhodococcus* (88).

TABLE 16. *Distribution of isoprenoid quinones in gram-positive bacteria: actinomycetes lacking mycolic acids*[a]

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| *Actinomadura madurae* | MK-*9*($H_8$), MK-*9*($H_6$) | MK-*9*($H_4$), MK-*9*($H_2$), MK-*8*($H_8$), MK-*8*($H_6$), MK-*8*($H_4$) | 48 |
| *A. madurae* | MK-*9*($H_6$) | MK-*9*($H_8$), MK-*9*($H_4$) | 244, 248 |
| *Actinomadura pelletieri* | MK-*9*($H_8$) | MK-*9*($H_{10}$), MK-*9*($H_6$), MK-*9*($H_4$), MK-*9*($H_2$), MK-*8*($H_8$), MK-*8*($H_6$) | 48 |
| *A. pelletieri* | MK-*9*($H_6$) | MK-*9*($H_8$), MK-*9*($H_4$) | 248 |
| *Actinomyces bovis* | MK-*10*[b] | | 100[c] |
| *Actinomyces israelii* | MK-*10*($H_4$) | MK-*10*($H_2$), MK-*9*($H_4$), MK-*9*($H_2$) | 48 |
| *Actinomyces viscosus* | MK-*10*($H_4$) | MK-*10*($H_2$), MK-*9*($H_4$), MK-*9*($H_2$) | 48 |
| *Actinopolyspora halophila* | MK-*9*($H_4$) | MK-*8*($H_4$), MK-*7*($H_4$)[d] | 49 |
| *Dermatophilus congolensis* | MK-*9*[b] | | 100 |
| *Elytrosporangium spirale* | MK-*9*($H_8$), MK-*9*($H_6$) | MK-*9*($H_4$), MK-*9*($H_2$) | 50 |
| *Micropolyspora faeni* | MK-*9*($H_4$)[e] | MK-*9*($H_8$), MK-*9*($H_6$), MK-*9*($H_2$), MK-*8*($H_8$), MK-*8*($H_6$), MK-*8*($H_4$)[f] | 48 |
| "*Nocardia leishmani*" | MK-*9*($H_6$), MK-*9*($H_4$) | | 244 |
| *Nocardiopsis dassonvillei* strains ATCC 3218 and ATCC 3219 | MK-*10*($H_4$), MK-*10*($H_6$), MK-*10*($H_2$)[g] | MK-*10*, MK-*9*($H_6$), MK-*9*($H_4$), MK-*9*($H_2$), MK-*8*($H_6$), MK-*8*($H_4$), MK-*8*($H_2$) | 48 |
| *Nocardiopsis dassonvillei* strains IMRU 575 and N3255 | MK-*10*($H_4$), MK-*10*($H_6$) | MK-*10*($H_8$), MK-*9*($H_6$), MK-*9*($H_4$) | 248 |
| *Nocardiopsis dassonvillei* | MK-*10*($H_2$), MK-*10* | MK-*10*($H_4$)[h] | 248 |
| *Promicromonospora citrea* | MK-*9*($H_4$) | MK-*8*($H_4$) | 50 |
| *Propionibacterium acnes*[i] | MK-*9*($H_4$) | MK-*9*($H_2$), MK-*8*($H_4$), MK-*7*($H_4$) | M. D. Collins and M. Goodfellow, unpublished data |
| "*Propionibacterium arabinosum*" | MK-*9*($H_4$) | | 208 |
| *Proprionibacterium arabinosum* | MK-*9*($H_4$) | MK-*9*($H_2$), MK-*8*($H_4$), MK-*7*($H_4$) | M. D. Collins and M. Goodfellow, unpublished data |
| *Proprionibacterium shermanii* | MK-*9*($H_4$) | | 198 |
| *Streptomyces albus* | MK-*9*($H_8$), MK-*9*($H_6$)[j] | | 26 |
| *Streptomyces gardneri* | MK-*8*($H_4$) | | 244 |
| *Streptomyces griseus* | MK-*n* | | 148 |
| *Streptomyces olivaceus* | MK-*9*($H_8$), MK-*9*($H_6$) | MK-*9*($H_4$), MK-*9*($H_2$), MK-*8*($H_8$), MK-*8*($H_6$), MK-*8*($H_4$), MK-*8*($H_2$) | 5, 6 |
| *Streptomyces platensis* | MK-*9*($H_8$), MK-*9*($H_6$)[k] | MK-*9*($H_4$), MK-*9*($H_2$) | 50 |
| *Streptomyces somaliensis* | MK-*9*($H_8$), MK-*9*($H_6$)[l] | MK-*9*($H_4$), MK-*9*($H_2$), MK-*8*($H_6$), MK-*7*($H_8$), MK-*7*($H_6$), MK-*7*($H_4$) | 48 |
| *Streptomyces* spp. strains S6 and S49 | MK-*9*($H_8$), MK-*9*($H_6$)[l] | MK-*9*($H_4$), MK-*9*($H_2$), MK-*8*($H_6$) | 48 |
| *Streptomyces* sp. strain S1 | MK-*9*($H_8$), MK-*9*($H_{10}$), MK-*9*($H_6$)[m] | MK-*9*($H_4$) | 50 |
| *Streptomyces* spp. | MK-*9*($H_6$) | MK-*9*($H_8$), MK-*9*($H_4$), MK-*9*($H_2$), MK-*9* | 67 |
| *Streptomyces* sp. | MK-*9*($H_6$) | MK-*9*($H_8$), MK-*9*($H_4$), MK-*9*($H_2$), | 178 |

TABLE 16—*Continued*

| Taxon | Major isoprenolog(s) | Minor component(s) | Reference(s) |
|---|---|---|---|
| | | MK-*9*, MK-*8*($H_6$), MK-*8*($H_4$), MK-*8*($H_2$) | |
| *Thermoactinomyces sacchari* | MK-*n* | | 100 |

[a] Mycolic acids are α-alkyl-β-hydroxyl long-chain fatty acids (37, 163).
[b] Possible hydrogenation was not investigated (100).
[c] Hess et al. (100) reported that *Actinomyces odontolyticus* lacks respiratory quinones.
[d] Traces of MK-*9*($H_2$) are also present (49).
[e] MK-*9*($H_4$) is the major isoprenolog, although MK-*9*($H_6$) and MK-*9*($H_8$) are also present in substantial amounts.
[f] Trace amounts of MK-*10*($H_4$) and MK-*10*($H_6$) are also present.
[g] MK-*10*($H_4$) is the major component (48).
[h] Minor amounts of MK-*10*($H_8$) and MK-*10*($H_6$) are present in some strains (248).
[i] De Vries et al. (62) reported the presence of uncharacterized menaquinones in *Propionibacterium freudenreichii* and "*Propionibacterium pentosaceum*."
[j] Ten unspecified minor menaquinone isoprenologs have been reported to be present in *S. albus* (26).
[k] MK-*9*($H_8$) in excess of MK-*9*($H_6$) (50).
[l] MK-*9*($H_6$) in excess of MK-*9*($H_8$) (48).
[m] MK-*9*($H_8$) in excess of MK-*9*($H_{10}$) and MK-*9*($H_6$) (50).

TABLE 17. *Distribution of ubiquinones in actinomycetes and coryneform bacteria of uncertain affiliation*

| Taxon | Major isoprenolog | Minor component(s) | Reference |
|---|---|---|---|
| *Arthrobacter crystallopoietes* | Q-*n*[a] | | 138 |
| "*Brevibacterium leucinophagum*" | Q-*9* | Q-*8* | 34 |
| "*Cellulomonas rossica*" | Q-*9* | Q-*8* | 43 |
| *Corynebacterium beticola* | Q-*8*[b] | Q-*7* | 45 |
| "*Corynebacterium autotrophicum*" | Q-*n* | | 217 |
| "*Corynebacterium autotrophicum*" | Q-*10* | Q-*9*[c] | 34 |
| "*Corynebacterium nephridii*" | Q-*10* | Q-*9*, Q-*8*[c] | 34 |
| "*Mycobacterium flavum*" | Q-*8* | | 70 |
| "*M. flavum*" | Q-*n* | | 105 |
| "*M. flavum*" | Q-*10* | Q-*9*[c] | 34 |
| "*Mycoplana rubra*" | Q-*10* | Q-*9*[c] | 34 |
| "*Protaminobacter ruber*" | Q-*10* | Q-*9*, Q-*8*[c] | 34 |

[a] Collins et al. (34) reported the presence of menaquinones in *A. crystallopoietes*. Ubiquinones were not detected (34).
[b] *C. beticola* also contains menaquinones (MK-*8*) (45).
[c] Dihydrogenated ubiquinones were reported to be present. Subsequent investigations have shown that only unsaturated isoprenologs are present (43; Collins, unpublished data).

of isoprenoid quinones found in bacterial cells.

In the archaebacteria, the presence of a novel sulfur-containing isoprenoid quinone in the extreme acidophilic taxon "*Caldariella*" (61) is very interesting in the context of the physiology and metabolism of these bacteria. It will be interesting to see whether other acidophilic taxa, such as *Sulfolobus*, possess similar respiratory quinones. The apparent absence of isoprenoid quinones in the fastidious, strictly anaerobic species *Methanobacterium thermoautotrophicum* is in keeping with the situation most commonly, but not invariably, encountered in other strictly anaerobic bacteria. The presence of dihydrogenated menaquinones in the halophilic taxa *Halococcus* and *Halobacterium* is also unusual. Partially saturated menaquinones have been described previously only in gram-positive eubacteria.

The presence of phylloquinones and plastoquinones in the cyanobacteria reinforces the similarity between these organisms and the chloroplasts of higher plants and algae and raises interesting evolutionary questions. In addition, preliminary data indicate that the distribution of certain structural types of isoprenoid quinones in the cyanobacteria could yield valuable taxonomic information.

Generally, members of the gram-negative family *Enterobacteriaceae* contain ubiquinones, menaquinones, or demethylmenaquinones or a combination of these compounds, whereas members of the genera *Actinobacillus*, *Haemophilus*, and *Pasteurella* and many taxa in the family *Vibrionaceae* produce ubiquinones or demethylmenaquinones or both. The majority of the strictly aerobic gram-negative chemoorganotrophs synthesize only ubiquinones; exceptions to this are the *Cytophaga* spp. and *Myxobacter* spp., which, like the anaerobic gram-negative bacteria (e.g., *Bacteroides*), appear to produce only menaquinones. Members of gram-positive taxa synthesize either menaquinones or, in certain cases, demethylmenaquinones (e.g., *Streptococcus faecalis*) or lack respiratory quinones. Some misclassified strains contain ubiquinones but should no longer be classified with gram-positive bacteria. Although the isoprenoid quinone contents of many gram-positive taxa have not been investigated systematically, preliminary data on micrococci, staphylococci, coryneform bacteria, and certain actinomycetes suggest

that these compounds will be of considerable value in classification. From the available data on procaryotes in general, it appears that menaquinones have a far greater discriminatory value than ubiquinones. Menaquinones possess not only a greater range of isoprenologs, but additional modifications, such as ring demethylation and partial hydrogenation of the polyprenyl side chain, are found.

All evidence is grist for the taxonomic mill, and there is every indication from the available information that the distribution of the structural types of respiratory quinones can provide extra material for elucidating the taxonomic relationships among many bacterial groups. The wide distribution of isoprenoid quinones in bacteria, their structural variation within different taxonomic groups, and the relative ease with which they can now be isolated and characterized make these compounds ideal chemotaxonomic markers.

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