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BERGEY'S MANUAL® OF

Systematic Bacteriology

Second Edition

Volume Two

The *Proteobacteria*

Part B

The *Gammaproteobacteria*

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The *Gammaproteobacteria*

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TO COME

This volume is dedicated to our colleagues,
David R. Boone, Don J. Brenner,
Richard W. Castenholz, and Noel R. Krieg, who
retired from the Board of Trustees of Bergey's Manual
Trust as this edition was in preparation. We deeply
appreciate their efforts as editors and authors; they
have devoted their time and many years in helping
the Trust meet its objectives.

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Preface to Volume Two of the Second Edition of *Bergey's Manual® of Systematic Bacteriology*

There is a long-standing tradition for the Editors of *Bergey's Manual* to open their respective editions with the observation that the new edition is a departure from the earlier ones. As this volume goes to press, however, we recognize a need to deviate from this practice, by offering a separate preface to each volume within this edition. In part, this departure is necessary because the size and complexity of this edition far exceeded our expectations, as has the amount of time that has elapsed between publication of the first volume of this edition and this volume.

Earlier, we noted that systematic procaryotic biology is a dynamic field, driven by constant theoretical and methodological advances that will ultimately lead to a more perfect and useful classification scheme. Clearly, the pace has been accelerating as evidenced in the super-linear rate at which new taxa are being described. Much of the increase can be attributed to rapid advances in sequencing technology, which has brought about a major shift in how we view the relationships among *Bacteria* and *Archaea*. While the possibility of a universally applicable natural classification was evident as the First Edition was in preparation, it is only recently that the sequence databases became large enough, and the taxonomic coverage broad enough to make such an arrangement feasible. We have relied heavily upon these data in organizing the contents of this edition of *Bergey's Manual of Systematic Bacteriology,* which will follow a phylogenetic framework based on analysis of the nucleotide sequence of the small ribosomal subunit RNA, rather than a phenotypic structure. This departs from the First Edition, as well as the Eighth and Ninth Editions of the *Determinative Manual*. While the rationale for presenting the content of this edition in such a manner should be evident to most readers, they should bear in mind that this edition, as in all preceding ones represents a progress report, rather than a final classification of procaryotes.

The Editors remind the readers that the *Systematics Manual* is a peer-reviewed collection of chapters, contributed by authors who were invited by the Trust to share their knowledge and expertise of specific taxa. Citation should refer to the author, the chapter title, and inclusive pages rather than to the Editors. The Trust is indebted to all of the contributors and reviewers, without whom this work would not be possible. The Editors are grateful for the time and effort that each expended on behalf of the entire scientific community. We also thank the authors for their good grace in accepting comments, criticisms, and editing of their manuscripts. We would also like to thank Drs. Hans Trüper, Brian Tindall, and Jean Euzéby for their assistance on matters of nomenclature and etymology.

We would like to express our thanks to the Department of Microbiology and Molecular Genetics at Michigan State University for housing our headquarters and editorial office and for providing a congenial and supportive environment for microbial systematics. We would also like to thank Connie Williams not only for her expert secretarial assistance, but also for unflagging dedication to the mission of Bergey's Manual Trust and Drs. Julia Bell and Denise Searles for their expert editorial assistance and diligence in verifying countless pieces of critical information and to Dr. Timothy G. Lilburn for constructing many of the phylogenetic trees used in this volume. We also extend our thanks to Alissa Wesche, Matt Chval and Kristen Johnson for their assistance in compilation of the bibliography.

A project such as the *Systematics Manual* also requires the strong and continued support of a dedicated publisher, and we have been most fortunate in this regard. We would also like to express our gratitude to Springer-Verlag for supporting our efforts and for the development of the Bergey's Document Type Definition (DTD). We would especially like to thank our Executive Editor, Dr. William Curtis for his courage, patience, understanding, and support; Catherine Lyons for her expertise in designing and developing our DTD, and Jeri Lambert and Leslie Grossberg of Impressions Book and Journal Services for their efforts during the pre-production and production phases. We would also like to acknowledge the support of ArborText, Inc., for providing us with state-of-the-art SGML development and editing tools at reduced cost. Lastly, I would like to express my personal thanks to my fellow trustees for providing me with the opportunity to participate in this effort, to Drs. Don Brenner, Noel Krieg, and James Staley for their enormous efforts as volume editors and to my wife, Nancy, and daughter, Jane, for their continued patience, tolerance and support.

Comments on this edition are welcomed and should be directed to Bergey's Manual Trust, Department of Microbiology and Molecular Genetics, 6162 Biomedical and Physical Sciences Building, Michigan State University, East Lansing, MI, USA 48824-4320. Email: garrity@msu.edu

George M. Garrity

Preface to the First Edition of *Bergey's Manual*® *of Systematic Bacteriology*

Many microbiologists advised the Trust that a new edition of the *Manual* was urgently needed. Of great concern to us was the steadily increasing time interval between editions; this interval reached a maximum of 17 years between the seventh and eighth editions. To be useful the *Manual* must reflect relatively recent information; a new edition is soon dated or obsolete in parts because of the nearly exponential rate at which new information accumulates. A new approach to publication was needed, and from this conviction came our plan to publish the *Manual* as a sequence of four subvolumes concerned with systematic bacteriology as it applies to taxonomy. The four subvolumes are divided roughly as follows: (a) the Gram-negatives of general, medical or industrial importance; (b) the Gram-positives other than actinomycetes; (c) the archaeobacteria, cyanobacteria and remaining Gram-negatives; and (d) the actinomycetes. The Trust believed that more attention and care could be given to preparation of the various descriptions within each subvolume, and also that each subvolume could be prepared, published, and revised as the area demanded, more rapidly than could be the case if the *Manual* were to remain as a single, comprehensive volume as in the past. Moreover, microbiologists would have the option of purchasing only that particular subvolume containing the organisms in which they were interested.

The Trust also believed that the scope of the *Manual* needed to be expanded to include more information of importance for systematic bacteriology and bring together information dealing with ecology, enrichment and isolation, descriptions of species and their determinative characters, maintenance and preservation, all focused on the illumination of bacterial taxonomy. To reflect this change in scope, the title of the *Manual* was changed and the primary publication becomes *Bergey's Manual of Systematic Bacteriology*. This contains not only determinative material such as diagnostic keys and tables useful for identification, but also all of the detailed descriptive information and taxonomic comments. Upon completion of each subvolume, the purely determinative information will be assembled for eventual incorporation into a much smaller publication which will continue the original name of the *Manual*, *Bergey's Manual of Determinative Bacteriology*, which will be a similar but improved version of the present *Shorter Bergey's Manual*. So, in the end there will be two publications, one systematic and one determinative in character.

An important task of the Trust was to decide which genera should be covered in the first and subsequent subvolumes. We were assisted in this decision by the recommendations of our Advisory Committees, composed of prominent taxonomic authorities to whom we are most grateful. Authors were chosen on the basis of constant surveillance of the literature of bacterial systematics and by recommendations from our Advisory Committees.

The activation of the 1976 Code had introduced some novel problems. We decided to include not only those genera that had been published in the Approved Lists of Bacterial Names in January 1980 or that had been subsequently validly published, but also certain genera whose names had no current standing in nomenclature. We also decided to include descriptions of certain organisms which had no formal taxonomic nomenclature, such as the endosymbionts of insects. Our goal was to omit no important group of cultivated bacteria and also to stimulate taxonomic research on "neglected" groups and on some groups of undoubted bacteria that have not yet been cultivated and subjected to conventional studies.

The invited authors were provided with instructions and exemplary chapters in June 1980 and, although the intended deadline for receipt of manuscripts was March 1981, all contributions were assembled in January 1982 for the final preparations. The *Manual* was forwarded to the publisher in June 1982.

Some readers will note the consistent use of the stem -var instead of -type in words such as biovar, serovar and pathovar. This is in keeping with the recommendations of the Bacteriological Code and was done against the wishes of some of the authors.

We have deleted much of the synonymy of scientific names which was contained in past editions. The adoption of the new starting date of January 1, 1980 and publication of the Approved Lists of Bacterial Names has made mention of past synonymy obsolete. We have included synonyms of a name only if they have been published since the new starting date, or if they were also on the Approved Lists and, in rare cases with certain pathogens, if the mention of an old name would help readers associate the organism with a clinical problem. If the reader is interested in tracing the history of a name we suggest he or she consult past editions of the *Manual* or the *Index Bergeyana* and its *Supplement*. In citations of names we have used the abbreviation AL to denote the inclusion of the name on the Approved Lists of Bacterial Names and VP to show the name has been validly published.

In the matter of citation of the *Manual* in the scientific literature we again stress the fact that the *Manual* is a collection of authored chapters and the citation should refer to the author, the chapter title and its inclusive pages, not the Editor.

To all contributors, the sincere thanks of the Trust is due; the Editor is especially grateful for the good grace with which the authors accepted comments, criticisms and editing of their manuscripts. It is only because of the voluntary and dedicated efforts of these authors that the *Manual* can continue to serve the science of bacteriology on an international basis.

A number of institutions and individuals deserve special acknowledgment from the Trust for their help in bringing about the publication of this volume. We are grateful to the Department of Biology of the Virginia Polytechnic Institute and State University for providing space, facilities and, above all, tolerance for the diverted time taken by the Editor during the preparation of the book. The Department of Microbiology at Iowa State University of Science and Technology continues to provide a welcome home for the main editorial offices and archives of the Trust and we acknowledge their continued support. A grant (LM-03707) from the National Library of Medicine, National Institutes of Health to assist in the preparation of this and the next volume of the *Manual* is gratefully acknowledged.

A number of individuals deserve special mention and thanks for their help. Professor Thomas O. McAdoo of the Department of Foreign Languages and Literatures at the Virginia Polytechnic Institute and State University has given invaluable advice on the etymology and correctness of scientific names. Those assisting the Editor in the Blacksburg office were R. Martin Roop II, Don D. Lee, Eileen C. Falk and Michael W. Friedman and their help is sincerely appreciated. In the Ames office we were ably assisted by Gretchen Colletti and Diane Triggs during the early period of preparation and by Cynthia Pease during the major portion of the editing process. Mrs. Pease has been responsible for the construction of the List of References and her willingness to handle the cumbersome details of text editing on a big computer is gratefully acknowledged.

John G. Holt

Preface to the First Edition of *Bergey's Manual®* of *Determinative Bacteriology*

The elaborate system of classification of the bacteria into families, tribes and genera by a Committee on Characterization and Classification of the Society of American Bacteriologists (1911, 1920) has made it very desirable to be able to place in the hands of students a more detailed key for the identification of species than any that is available at present. The valuable book on "Determinative Bacteriology" by Professor F. D. Chester, published in 1901, is now of very little assistance to the student, and all previous classifications are of still less value, especially as earlier systems of classification were based entirely on morphologic characters.

It is hoped that this manual will serve to stimulate efforts to perfect the classification of bacteria, especially by emphasizing the valuable features as well as the weaker points in the new system which the Committee of the Society of American Bacteriologists has promulgated. The Committee does not regard the classification of species offered here as in any sense final, but merely a progress report leading to more satisfactory classification in the future.

The Committee desires to express its appreciation and thanks to those members of the society who gave valuable aid in the compilation of material and the classification of certain species. . . .

The assistance of all bacteriologists is earnestly solicited in the correction of possible errors in the text; in the collection of descriptions of all bacteria that may have been omitted from the text; in supplying more detailed descriptions of such organisms as are described incompletely; and in furnishing complete descriptions of new organisms that may be discovered, or in directing the attention of the Committee to publications of such newly described bacteria.

David H. Bergey, *Chairman*
Francis C. Harrison
Robert S. Breed
Bernard W. Hammer
Frank M. Huntoon
Committee on Manual.
August, 1923.

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Phylum XIV. Proteobacteria *phyl. nov.*

GEORGE M. GARRITY, JULIA A. BELL AND TIMOTHY LILBURN

Pro.te.o.bac.te′ ri.a. Gr. n. *Proteus* ocean god able to change shape; Gr. n. *bakterion* a small rod; M.L. fem. pl. n. *Proteobacteria* the phylum of bacteria having 16S rRNA gene sequences related to those of the members of the order *Pseudomonadales*.

The phylum *Proteobacteria* was circumscribed for this volume on the basis of phylogenetic analysis of 16S rRNA gene sequences. The phylum contains Gram-negative bacteria in the classes *Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria*, *Deltaproteobacteria*, and *Epsilonproteobacteria*.

Type order: **Pseudomonadales** Orla-Jensen 1921, 270.

Class III. **Gammaproteobacteria** *class. nov.*

GEORGE M. GARRITY, JULIA A. BELL AND TIMOTHY LILBURN

Gam.ma.pro.te.o.bac.te′ ri.a. Gr. n. *gamma* name of third letter of Greek alphabet; Gr. n. *Proteus* ocean god able to change shape; Gr. n. *bakterion* a small rod; M.L. fem. pl. n. *Gammaproteobacteria* class of bacteria having 16S rRNA gene sequences related to those of the members of the order *Pseudomonadales*.

The class *Gammaproteobacteria* was circumscribed for this volume on the basis of phylogenetic analysis of 16S rRNA sequences; the class contains the orders *Acidithiobacillales*, *Aeromonadales*, *Alteromonadales*, *Cardiobacteriales*, *Chromatiales*, *Enterobacteriales*, *Legionellales*, *Methylococcales*, *Oceanospirillales*, *Pasteurellales*, *Pseudomonadales*, *Thiotrichales*, *Vibrionales*, and *Xanthomonadales*.

Type order: **Pseudomonadales** Orla-Jensen 1921, 270.

Order I. **Chromatiales** *ord. nov.*

JOHANNES F. IMHOFF

Chro.ma.ti.a′ les. M.L. neut. n. *Chromatium* type genus of the order; *-ales* ending to denote an order; M.L. fem. pl. n. *Chromatiaceae* the *Chromatium* order.

The order *Chromatiales* consists of unicellular Gram-negative bacteria belonging to the *Gammaproteobacteria*. Cells are spherical, vibrioid, spiral, or rod shaped. Multiply by binary fission, motile by flagella or nonmotile; some contain gas vesicles.

The order *Chromatiales* contains anoxygenic phototrophic bacteria, known as phototrophic purple sulfur bacteria, able to perform photosynthesis under anoxic conditions without oxygen production. In addition, the order contains nonphototrophic, purely chemotrophic relatives. Color of cell suspensions of the phototrophic species ranges from purple-violet to purple-red, red, orange-brown, yellowish brown, brownish red, brown, and green. Common to all phototrophic species is the **presence of bacteriochlorophyll *a* or *b*** (see Table BXII.γ.1), and various carotenoids of the spirilloxanthin, okenone, or rhodopinal groups (Table BXII.γ.2). **Photosynthetic pigments are located in the cytoplasmic membrane, and in internal membrane systems** of different fine structure which originate from, and are continuous with, the cytoplasmic membrane.

Phototrophic species are able to grow by a photolithoautotrophic or photoorganoheterotrophic metabolism under anoxic conditions. The photosynthetic metabolism differs from that of the cyanobacteria, algae, and green plants in that water cannot serve as electron donor substrate. Photosynthetic CO_2 assimilation depends on the utilization of external electron donors such

TABLE BXII.γ.1. Bacteriochlorophylls of phototrophic purple bacteria

Pigment	Absorption maxima (nm) in living cells
Bacteriochlorophyll *a*	375–378, 590, 796–805, 820–898
Bacteriochlorophyll *b*	400, 605, 835–850, 980–1030

TABLE BXII.γ.2. Carotenoid groups of phototrophic purple bacteria[a]

Carotenoid group	Major components
Normal spirilloxanthin group	spirilloxanthin, lycopene, rhodopin
Alternative spirilloxanthin group	spheroidene, spheroidenone, chloroxanthin, (spirilloxanthin)
Okenone group	okenone
Rhodopinal group	rhodopinal, rhodopin, lycopenal, lycopene, lycopenol, spirilloxanthin

[a]Data from Schmidt (1978).

as reduced sulfur compounds, reduced iron, molecular hydrogen, or organic compounds. In the presence of sulfide and light, cells of phototrophic members of the *Chromatiales* (purple sulfur bacteria) form highly refractile globules of elemental sulfur either inside or outside their cells. CO_2 is photoassimilated through the reductive pentose phosphate cycle. Fixation of N_2 has been demonstrated in many species. All species contain cytochromes, quinones, and non-heme iron proteins of the ferredoxin type. In addition to their phototrophic capabilities, many species of this order can grow chemotrophically under microoxic to oxic conditions in the dark, but some species, such as *Arhodomonas aquaeolei* (see family *Ectothiorhodospiraceae*), may be purely chemotrophic and unable to grow phototrophically.

Type genus: **Chromatium** Perty 1852, 174 emend. Imhoff, Süling and Petri 1998b, 1138.

Further descriptive information

The available 16S rDNA sequence information for *Ectothiorhodospiraceae* (Imhoff and Süling, 1996) and *Chromatiaceae* species (DeWeerd et al., 1990; Wahlund et al., 1991; Caumette et al., 1997; Guyoneaud et al., 1997, 1998b; Imhoff et al., 1998b) supports the classification of these bacteria in two different families (Imhoff, 1984b). At the same time, it indicates the existence of different genera within the family *Ectothiorhodospiraceae* (Imhoff and Süling, 1996), and the inconsistency of the previous taxonomic classification of the family *Chromatiaceae* (see Pfennig and Trüper, 1989) with its phylogeny (Imhoff et al., 1998b). In addition, the phylogenetic relatedness of both families and their distance to other bacteria of the *Gammaproteobacteria* support their treatment within one order, for which the name *Chromatiales* is proposed. The order *Chromatiales* includes the phototrophic purple sulfur bacteria of the *Ectothiorhodospiraceae* and *Chromatiaceae* (Imhoff, 1984b, 1989; Pfennig and Trüper, 1989) and their purely chemotrophic relatives (see Figs. BXII.γ.3 and BXII.γ.4 of the chapter describing the family *Chromatiaceae*.). The purely chemotrophic bacteria known so far are specifically related to *Ectothiorhodospiraceae*. The 16S rDNA sequence of *Arhodomonas aquaeolei* (Adkins et al., 1993; Imhoff and Süling, 1996) is similar to those of *Halorhodospira* species, but clearly distinct at the genus level. In addition, sequences of *Nitrococcus mobilis* (Teske et al., 1994) and *Nitrosococcus oceani* (Head et al., 1993) place these bacteria in phylogenetic proximity to the *Ectothiorhodospiraceae*, though on a more distant level than the genus *Arhodomonas*.

***Differentiation of* Chromatiaceae *and* Ectothiorhodospiraceae**

Traditionally, the most important and easily recognized distinguishing property within the phototrophic members of the order *Chromatiales* is the deposition of S^0 during growth on sulfide. Sulfur globules appear exclusively inside the cells (*Chromatiaceae*) or outside the cells (*Ectothiorhodospiraceae*). A clear distinction between the two families is also possible based on differences in quinone, lipid, and fatty acid composition (Imhoff and Bias-Imhoff, 1995). Several glucolipids are present in *Chromatiaceae* species, but absent from members of *Ectothiorhodospiraceae* (Imhoff et al., 1982a). In addition, the lipopolysaccharides show significant differences between members of the two families (Weckesser et al., 1979, 1995). The lipid A of all investigated *Chromatiaceae* species (*Allochromatium vinosum*, *Thermochromatium tepidum*, *Thiocystis violacea*, *Thiocapsa roseopersicina*, *Thiococcus pfennigii*) is characterized by a phosphate-free backbone with D-glucosamine as the only amino sugar, having terminally attached D-mannose and amide-bound $C_{14:0\ 3OH}$. In the lipid A of all tested *Ectothiorhodospiraceae* species (*Ectothiorhodospira vacuolata*, *E. shaposhnikovii*, *E. haloalkaliphila*, and *Halorhodospira halophila*), phosphate is present, 2,3-diamino-2,3-dideoxy-D-glucose is the major amino sugar (D-glucosamine is also present), D-mannose is lacking (D-galacturonic acid, and D-glucuronic acid are present instead) and, quite remarkably, $C_{10:0\ 3OH}$ is present as an amide-bound fatty acid (Zahr et al., 1992; Weckesser et al., 1995; Imhoff and Süling, 1996). These distinctive properties of the lipid A appear to be characteristic features of the two families. In addition, sequences of 16S rDNA are significantly different in representatives of the two families, as demonstrated by a number of characteristic signatures (Table BXII.γ.3) and by their overall dissimilarity (Figs. BXII.γ.3 and BXII.γ.4 of the chapter describing the family *Chromatiaceae*).

Key to the phototrophic members of the families of the Chromatiales

I. *Gammaproteobacteria* that contain bacteriochlorophyll *a* or *b* and different carotenoid pigments, have internal photosynthetic membrane structures and are able to grow phototrophically under anoxic conditions in the light.

A. In the presence of both sulfide and light, globules of S^0 are formed inside the cells and further oxidized to sulfate.

Chromatiaceae

B. In the presence of both sulfide and light, globules of S^0 are formed outside the cells (only exceptionally also in the peripheral part of the cell) and may be further oxidized to sulfate. Growth is dependent on saline and alkaline growth conditions.

Ectothiorhodospiraceae

TABLE BXII.γ.3. Differential characteristics of the phototrophic members of the families *Chromatiaceae* and *Ectothiorhodospiraceae*

Characteristic	*Chromatiaceae*	*Ectothiorhodospiraceae*
Sulfur deposition	inside cells	outside cells
Characteristics of polar lipids[a]	several glycolipids	glycolipids absent
Major fatty quinones[a]	Q8/MK8	Q7 or Q8/MK7 or MK8
Major fatty acids[a]:		
$C_{16:0}$	20–35%	11–25%
$C_{16:1}$	25–37%	<10%
$C_{18:1}$	38–45%	50–75%
Properties of lipopolysaccharides [b]:		
Major aminosugar	glucosamine	diamino-dideoxy-glucose
Phosphate	present	absent
D-Mannose	+	−
D-Galacturonic acid	−	+
D-Glucuronic acid	−	+
Amide-bound fatty acid	$C_{14:0\ 3OH}$	$C_{12:0\ 3OH}$
Signature 16S rDNA sequence [c]:		
Position 217	T	G/A[d]
Position 234–235	CA	TG/CG[d]
Position 821–822	TC	AG
Position 876–877	GA	CT
Position 985	A	T/G[d]

[a]Data from Imhoff and Bias-Imhoff (1995).

[b]Data from Weckesser et al. (1995).

[c]Numbering based on *E. coli* 16S rDNA sequence.

[d]Bases above the line are found in the genera *Ectothiorhodospira* and *Thiorhodospira*; bases below the line are found in the genera *Arhodomonas* and *Halorhodospira*.

Family I. **Chromatiaceae** Bavendamm 1924, 125[AL] emend. Imhoff 1984b, 339

JOHANNES F. IMHOFF

Chro.ma.ti.a'ce.ae. M.L. neut. n. *Chromatium* type genus of the family; *-aceae* ending to denote a family; M.L. fem. pl. n. *Chromatiaceae* the *Chromatium* family.

Cells are spherical, ovoid, vibrioid, spiral, or rod shaped, multiply by binary fission, may contain gas vesicles, may be motile by flagella or nonmotile. Motile forms have either monotrichous or multitrichous polar flagella. **Gram negative, belong to the *Gammaproteobacteria*, and contain internal photosynthetic membranes**, which are continuous with the cytoplasmic membrane and of vesicular type in most species (Fig. BXII.γ.1), though some species have tubular internal membranes (Fig. BXII.γ.2) or lamellae. **As photosynthetic pigments, bacteriochlorophyll *a* or *b* and carotenoids of the spirilloxanthin, okenone, or rhodopinal groups are present** in most species, but other carotenoids such as tetrahydrospirilloxanthin, may occur. In general, the color of cultures of strains with carotenoids of the spirilloxanthin group is orange-brown to brownish red or pink, of those with okenone, purple-red, and of those with carotenoids of the rhodopinal group, purple-violet.

Under anoxic conditions in the light, all species are capable of photolithoautotrophic growth with sulfide or S^0 as electron donor. S^0 globules accumulate as an intermediate oxidation product inside the cells. Many species are able to use H_2 as an electron donor under reducing culture conditions, and some use reduced iron ions. All species are potentially mixotrophic and photoassimilate a number of simple organic compounds, of which acetate and pyruvate are the most widely used. Some species are able to photoassimilate organic substances in the absence of sulfide or sulfur, or grow photoorganoheterotrophically. Many species are strictly anaerobic and obligately phototrophic, while others are capable of chemolithoautotrophic or chemoorganoheterotrophic growth under microoxic to oxic conditions in the dark.

The pathway of autotrophic CO_2 assimilation was shown to be the reductive pentose phosphate cycle in all species tested so far. The fixation of dinitrogen has been demonstrated in several species. Storage materials are polysaccharides, poly-β-hydroxybutyrate, elemental sulfur, and polyphosphate. Vitamin B_{12} is required by several species.

In nature, members of the *Chromatiaceae* occur in the illuminated, anoxic, and sulfide-containing parts of a large variety of aquatic environments and sediments from moist and muddy soils, ditches, ponds, lakes, rivers, sulfur springs, estuaries, marine habitats, and even salt and soda lakes.

The mol% G + C of the DNA is: 45.5–70.4.

Type genus: **Chromatium** Perty 1852, 174 emend. Imhoff, Süling and Petri 1998b, 1138.

TAXONOMIC COMMENTS

In the eighth edition of the *Determinative Manual*, the family *Chromatiaceae* was described to include the genus *Ectothiorhodospira*, purple sulfur bacteria that form sulfur globules outside the cells (Pfennig and Trüper, 1974). With the establishment of the new family *Ectothiorhodospiraceae* and an emended description of the family *Chromatiaceae* Bavendamm 1924 (Imhoff, 1984b), the family *Chromatiaceae* exclusively comprises phototrophic sulfur bacteria capable of depositing globules of S^0 inside the cells. This description agrees with Molisch's (1907) definition of the *"Thiorhodaceae"* and is in line with their phylogenetic separation from

FIGURE BXII.γ.1. Ultrathin section of a cell of *Thiocystis gelatinosa* DSM 215 showing internal photosynthetic membranes as numerous small vesicles, which are evenly distributed throughout the cell. Bar = 1 μm (Courtesy of H.G. Trüper and J.B. Waterbury.)

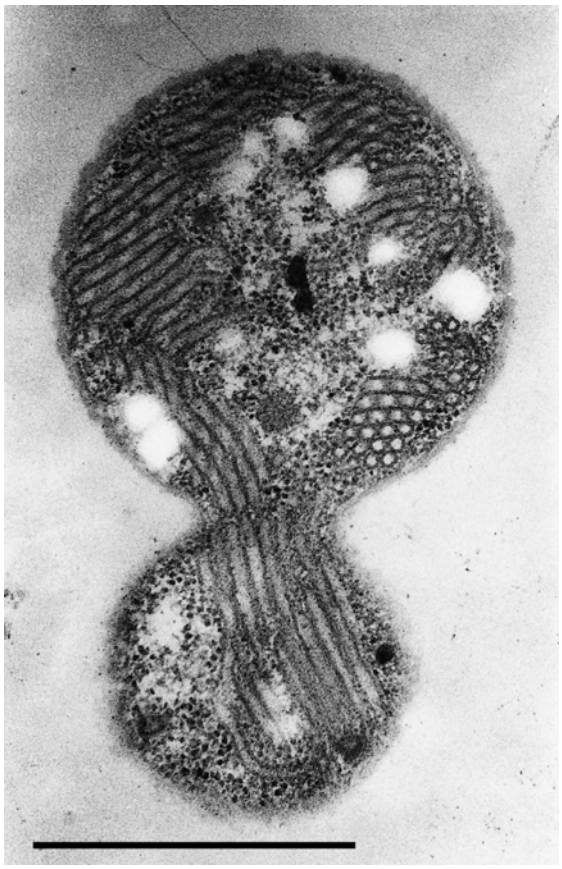

FIGURE BXII.γ.2. Ultrathin section of a cell of *Thiococcus pfennigii* strain 9111 showing tubular internal photosynthetic membranes in longitudinal and cross section. Bar = 0.5 μm (Courtesy of H.G. Trüper and J.B. Waterbury.)

other phototrophic purple sulfur bacteria (Fowler et al., 1984; Imhoff and Süling, 1996; Imhoff et al., 1998b).

In the past, the taxonomy of the phototrophic purple bacteria, including the family *Chromatiaceae*, was entirely based on simple phenotypic characteristics (see the previous editions of this *Manual*, Pfennig and Trüper, 1974, 1989). Until recently, little molecular and sequence-based information, such as rRNA oligonucleotide data for selected species (Fowler et al., 1984) and a few 16S rDNA sequences (DeWeerd et al., 1990; Wahlund et al., 1991), was available for *Chromatiaceae* species. During the past few years, complete 16S rDNA sequences for most of the *Chromatiaceae* species have been determined (see Caumette et al., 1997; Guyoneaud et al., 1998b; Imhoff et al., 1998b). At the time of writing, 16S rDNA sequences of quite a few type strains of purple sulfur bacteria have not yet been determined or are not available: *Chromatium weissei*, *Thiospirillum jenense*, *Thiodictyon elegans*, *Thiodictyon bacillosum*, *Lamprobacter modestohalophilus*, and *Thiopedia rosea*.

The results of 16S rDNA sequence analysis, shown in Figs. BXII.γ.3 and BXII.γ.4, revealed that separate major phylogenetic branches of the family *Chromatiaceae* contain i) truly marine and halophilic species; ii) species that are motile by polar flagella, do not contain gas vesicles, and are primarily freshwater species; and iii) species with ovoid to spherical cells that are primarily freshwater species (some also occur in brackish and marine habitats), the majority of which are nonmotile (except *Lamprocystis roseopersicina*), and most of which contain gas vesicles. Because the phylogenetic relationships were not in congruence with traditional classification, a reclassification based on 16S rDNA sequence similarity, supported by selected phenotypic properties, was proposed (Guyoneaud et al., 1998b; Imhoff et al., 1998b). Positive correlation between 16S rDNA sequence similarity values and particular phenotypic properties of the species were taken as an indication of the importance of these properties in achieving a phylogenetically oriented taxonomy that includes both genetic and phenotypic information (Imhoff et al., 1998b).

Ecological source and adaptation to specific environmental conditions are of importance for phylogeny and taxonomy. Evolution occurs in particular natural environments, and separate phylogenetic lineages are expected to result from bacterial evolution in distinct habitats that, due to their particular properties (e.g., extremes of temperature, salinity, and pH), allow only the development of specifically adapted bacteria. In principle, major phylogenetic branches of the family *Chromatiaceae* can be distinguished on the basis of their salt requirement, which implies a separate evolutionary development in the marine and in the freshwater environment. This suggests that the salt response is an important taxonomic criterion in a phylogenetically oriented taxonomic system of these bacteria. The salt requirement has been considered in the taxonomy of purple nonsulfur bacteria and *Ectothiorhodospiraceae*. It proved to be of relevance for distinguishing the genera *Halorhodospira* and *Ectothiorhodospira* (Imhoff and Süling, 1996), *Rhodovulum*, *Rhodobacter* (Hiraishi and Ueda, 1994), and genera of the spiral, purple nonsulfur *Alphaproteobacteria*, the former *Rhodospirillum* species (Imhoff et al., 1998b).

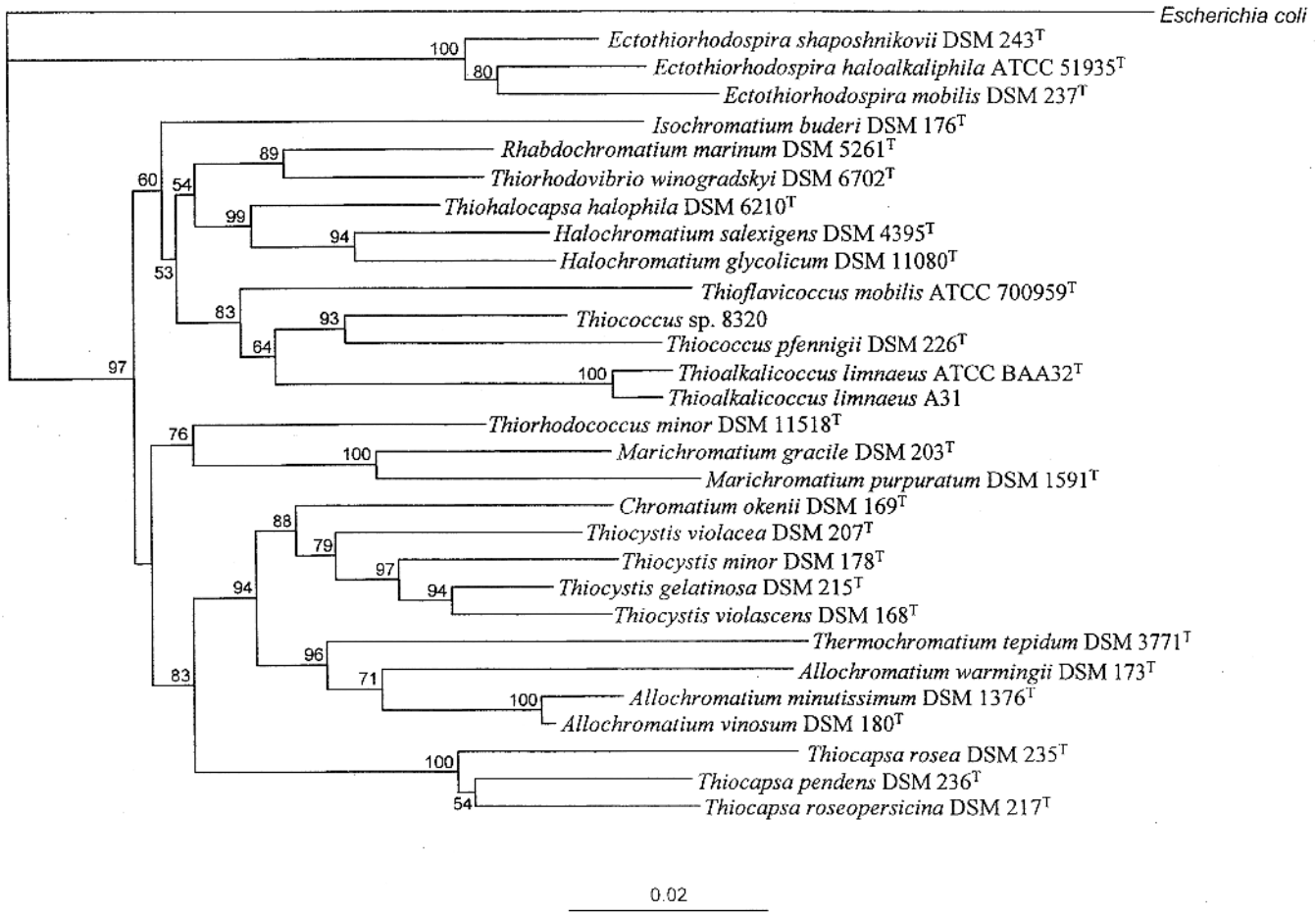

FIGURE BXII.γ.3. 16S rDNA-derived phylogenetic tree of the family *Chromatiaceae* including species of *Chromatium*, *Thiocystis*, *Allochromatium*, *Thermochromatium*, and the halophilic species *Isochromatium*, *Rhabdochromatium*, *Thiorhodovibrio*, *Thiohalocapsa*, *Thiococcus*, *Halochromatium*, *Thiorhodococcus* and *Marichromatium*. Representatives of *Thiocapsa* and *Thiolamprovum* and *Ectothiorhodospira* were included to complete the view on purple sulfur bacteria. The phylogeny of these genera is shown in more detail in Fig. BXII.γ.4 and in Fig. BXII.γ.19 in the chapter on *Ectothiorhodospiraceae*. Sequence data used were published previously (Imhoff et al., 1998b). Sequence alignments, calculation of distance data and tree construction were performed as described earlier (Petri and Imhoff 2000).

Within the family *Chromatiaceae*, both the phylogenetic relationship and the salt responses enable us to distinguish the halophilic *Halochromatium* species from the marine *Marichromatium* and the freshwater *Allochromatium* species, all of which were previously known as species of the genus *Chromatium* (Imhoff et al., 1998b). A differentiation of groups of species is also possible based on compatible solute production. Different compatible solutes are accumulated as osmotica by *Chromatiaceae* species compared to *Ectothiorhodospiraceae* species (Severin et al., 1992; Imhoff, 1993; Welsh and Herbert, 1993). Ectoine, trehalose, and glycine betaine are common among *Ectothiorhodospira* and *Halorhodospira* species, but not found in *Chromatiaceae*. Instead of trehalose, the less compatible sugar sucrose was found as the major component in freshwater species including *Allochromatium vinosum*, *Thiocystis violacea*, *Thiocystis minor*, *Thiocapsa roseopersicina*, and *Thiocapsa rosea* (Welsh and Herbert, 1993). Among the halophilic and marine species (*Halochromatium salexigens*, *Thiohalocapsa halophila*, and *Marichromatium purpuratum*), glycine betaine appears to occur as the major component, along with sucrose and *N*-acetyl-glutaminylglutamine amide (Severin et al., 1992; Imhoff, 1993).

Although morphological properties of the cells appear to be of lower phylogenetic significance, it is apparent that one group of freshwater *Chromatiaceae* species contains motile single cells without gas vesicles (e.g., *Chromatium* and *Allochromatium* species, see Fig. BXII.γ.3), and the possession of gas vesicles is restricted to a second group with predominantly spherical to ovoid cells that are nonmotile (e.g., *Thiocapsa* and *Thiolamprovum* species, with the exception of *Lamprocystis roseopersicina*, see Fig. BXII.γ.4).

The DNA base ratio within the family *Chromatiaceae*, expressed as the mol% G + C content, has been found to span a large scale. Thus, in the previous edition of the *Manual* the genus *Chromatium* (Pfennig, 1989b) had values ranging from 48.0 to 70.4. Because the mol% G + C content is crudely indicative of the genetic relatedness of bacteria, these values already suggested excessive diversity within the genus *Chromatium*. A phylogenetic system would be expected to group bacteria that have much less variation in their mol% G + C content together. Indeed, after rearrangement of the species of the family *Chromatiaceae* according to their genetic relatedness on the basis of 16S rDNA sequence analysis (Guyoneaud et al., 1998b; Imhoff et al., 1998b), a quite narrow range of mol% G + C content is found within most of the newly established genera. The ranges are ~63–66 in the cluster including species of *Thiocapsa*, *Lamprocystis*, and *Thiolamprovum*, 69–70 in *Marichromatium* species, 64–66 in *Halochromatium* species, and 48–50 in the true *Chromatium* species. This correlation appears of such significance, that any case of high

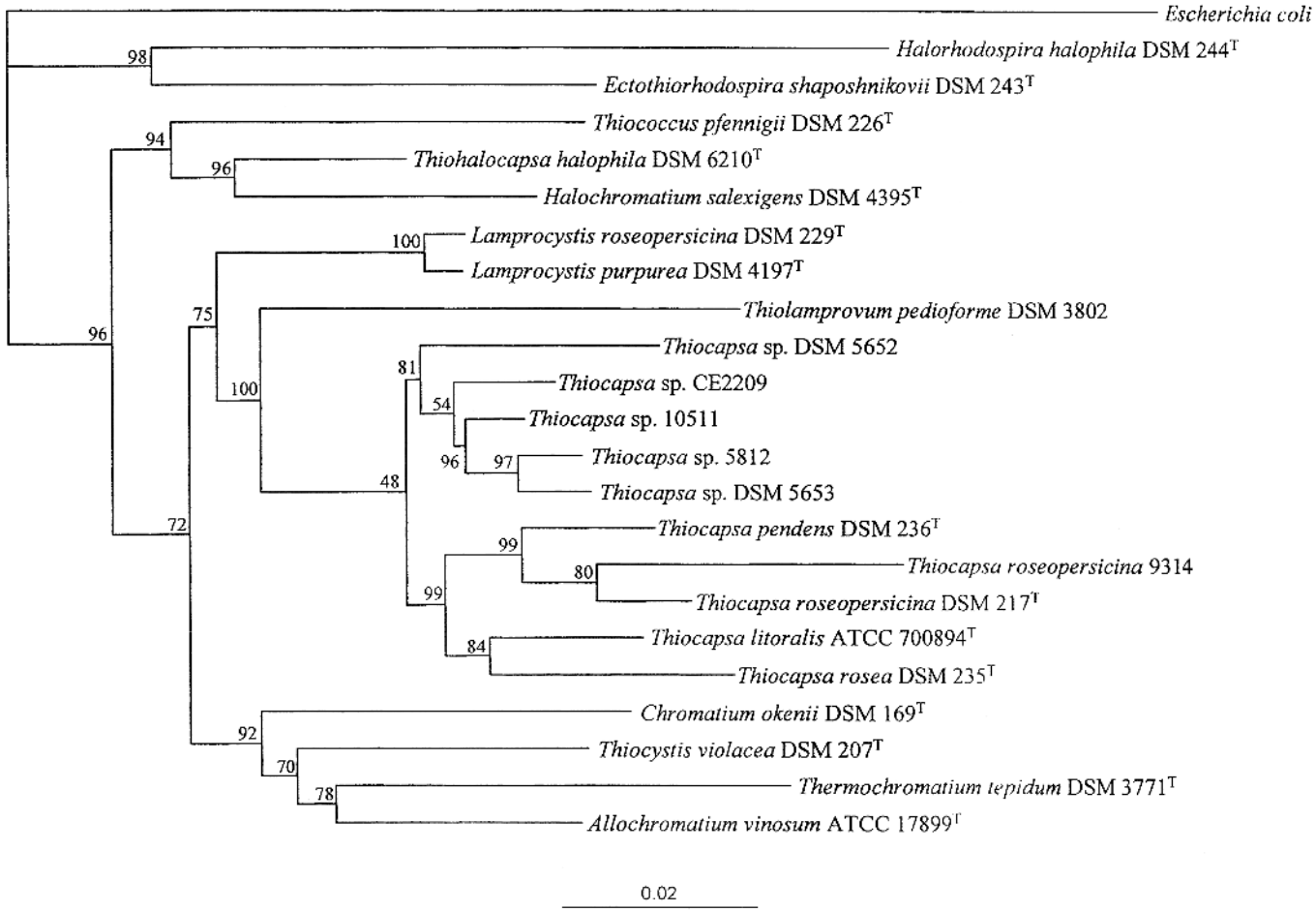

FIGURE BXIIγ.4. 16S rDNA-derived phylogenetic tree of the family *Chromatiaceae* including species of *Thiocapsa*, *Lamprocystis* and *Thiolamprovum*. Representatives of *Ectothiorhodospiraceae* and other *Chromatiaceae* genera were included to complete the view on purple sulfur bacteria. The phylogeny of these genera is shown in more detail in Fig. BXII.γ.3 and in Figure BXII.γ.19 in the chapter on *Ectothiorhodospiraceae*. Sequence data used were published previously (Guyoneaud et al., 1998b; Imhoff et al., 1998b). Sequence alignments, calculation of distance data and tree construction were performed as described earlier (Petri and Imhoff 2000).

intrageneric and intraspecies variation of the mol% G + C content necessitates experimental examination. For example, the high intraspecies variation that has been noted for *Allochromatium vinosum* (61.3–66.3), *Allochromatium warmingii* (55.1–60.2), and *Thiocystis violacea* (62.8–67.9) suggests misclassification of some strains. Further studies are needed to clarify these problems.

Although fatty acid and quinone composition is of great significance for classification of purple nonsulfur bacteria of the *Alphaproteobacteria* and *Betaproteobacteria*, and these compounds are well-accepted tools for taxonomic differentiation of phototrophic bacteria (Imhoff, 1991, 1984a; Imhoff and Bias-Imhoff, 1995; Thiemann and Imhoff, 1996), both show only minor variation and therefore are of minor significance for differentiation within the family *Chromatiaceae* (Imhoff and Bias-Imhoff, 1995). Polar lipids have been analyzed so far in only a limited number of *Chromatiaceae* species. First results, obtained with several freshwater species, showed significant correlations with the new classification, i.e., identical polar lipid composition was found i) in *Allochromatium vinosum* and *Allochromatium warmingii*, ii) in all four *Thiocystis* species, and iii) in the two *Chromatium* species (Imhoff, unpublished results). Thus, polar lipid composition may well turn out to be a relevant property for distinguishing between genera or groups of genera of the family *Chromatiaceae*. This implies that the polar lipid composition reflects phylogenetic relationships and is a rather stable property in evolutionary terms. More analytical data on members of the family *Chromatiaceae* are required to support this concept.

Further Comments Physiological properties have always been important characteristics in taxonomy, although their taxonomic significance is ambiguous. On the one hand, members of the family *Chromatiaceae* are quite conservative in their use of sulfur sources and their restricted use of organic carbon sources: all species are able to grow photolithoautotrophically under anoxic conditions in the light using sulfide or S^0 as an electron donor. On the other hand, we can distinguish two major physiological groups, versatile and specialized species. (i) The specialized species depend on strictly anoxic conditions and are obligately phototrophic. Sulfide is required; thiosulfate and hydrogen are not used as electron donors. Only acetate and pyruvate (or propionate) are photoassimilated in the presence of sulfide and CO_2. These bacteria do not grow with organic electron donors, chemotrophic growth is not possible, and sulfate is not assimilated as a sulfur source. Among these species are *Chromatium okenii*, *Chromatium weissei*, *Allochromatium warmingii*, *Isochromatium buderi*, *Thiospirillum jenense*, and *Thiococcus pfennigii*. (ii) The versatile species photoassimilate a larger variety of organic substrates. Most of them are able to grow in the absence of reduced sulfur sources with organic substrates as electron donors for photosynthesis, and to assimilate sulfate as the sole sulfur