SELECTIONS FROM

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A Handbook on Habitats, Isolation, and Identification of Bacteria

Phytopathogenic Bacteria

Edited by
MORTIMER P. STARR

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Preface

A century has elapsed since the appearance of the pioneering reports by Burrill, Wakker, and Savastano on plant diseases caused by prokaryotes. A great deal has been learned in the intervening years about these diseases and their bacterial causal agents. Publication of *The Prokaryotes* at the end of 1981 provided a vehicle for summarizing the centennial status of certain aspects of phytobacteriology, mainly those aspects indicated by the work's subtitle *(A Handbook on Habitats, Isolation, and Identification of Bacteria)*. Although particular plant diseases, per se, are not in the purview of *The Prokaryotes,* the community of phytopathologists seemed to find the chapters on phytopathogenic bacteria sufficiently useful to warrant repeated requests for a work derived from this Handbook consisting solely of material on phytopathogenic bacteria. *Phytopathogenic Bacteria* is the result.

The chapters selected for inclusion in this volume are those dealing exclusively with phytopathogenic bacteria. It was not feasible to include certain highly relevant portions of other chapters, the main contents of which were primarily on nonphytopathogenic bacteria. For example, an excellent treatment on phytopathogenic species of *Streptomyces* can be found in Chapter 156 of *The Prokaryotes*. Unfortunately, it was not possible to include in this volume the entire 68-page chapter on the genus *Streptomyces,* and no inexpensive method could be developed for excising the three or four pages (plus their specific literature citations) relevant to the present volume. Chapter 4 (included in this volume) bears a long table (Table 1, pages 126–128) that cross-refers items such as the aforementioned *Streptomyces* example. The Table of Contents of the entire Handbook, which is found at the end of this volume, should aid in locating the desired information in *The Prokaryotes*.

Several measures were taken to keep the costs as low as possible to permit use of *Phytopathogenic Bacteria* as a textbook. No updating or other textual alteration—which would have necessitated new and costly typesetting—has been undertaken. The original pagination has been retained, a measure which should also reduce bibliographic confusion. Indexes of the same high quality as in the unabridged Handbook have been prepared; naturally, they cover only the material in this volume. It should be noted that one of the indexes covers all authors of the extensive original literature cited in each included chapter, providing thereby a veritable vade mecum for phytobacteriologists. The other index is by subject, including names of microorganisms and practical details such as recipes of culture media.

The Handbook is both didactic and practical. Each chapter provides a text in the indicated area. In addition, most chapters include up-to-date recipes for media and reagents, directions for laboratory and field procedures, and other technical details; these practical items are marked by distinctive marginal grey bars. These bars serve not only to keep the eye of the worker focused upon the procedure when the volume is being used as a "cookbook" on the laboratory bench, but also to aid the reader in skipping over such practical details when the text is being scrutinized.

The scientific enterprise is a dynamic one. By the very nature of the cumbersome technology whereby scientific works are nowadays published by mechanical means (i.e., composed, printed, and bound between covers), there must be a time-gap between the advancing edges of the scientific discipline and the textual material frozen in black-on-white. Experienced teachers know how to bridge such gaps by turning to the well-known primary and secondary periodical literature in both bacteriology and phytopathology (alas! there is not a periodical dealing mainly with plant bacteriology). However, it might be useful to record here the titles of three current or forthcoming books containing material either a bit more recent than this volume or presenting views of phytobacteriology outside the scope of *The Prokaryotes:*

Lozano, J. C. (ed.). 1982. Proceedings of the Fifth International Conference on Plant Pathogenic Bacteria, Cali, Colombia, August, 1981. Cali, Colombia: CIAT. Columbia, Missouri: University of Missouri.

Mount, M. S., Lacy, G. H. (eds.). 1982. Phytopathogenic prokaryotes. New York, London: Academic Press.

Starr, M. P., Klement, Z. (eds.). 1984. Bacterial phytopathogens. Budapest: Akadémiai Kiadó.

Many people are involved in the making of a book. Since this volume derives from the Handbook, the appreciative remarks made by the Editors in the Preface of *The Prokaryotes* are hereby extended to the present enterprise. In addition, I must record my gratitude to the following persons: Phoebe Betty Starr, who once again aided in her meticulous way with manifold details connected with this volume; Jean Marie Schmidt, whose hospitality at Arizona State University, Tempe, provided the necessary ambience while I was on sabbatical leave from the University of California, Davis; and the designers and manufacturers of the components of a word processor consisting of a TeleVideo TS-802 microcomputer, a C. Itoh F-10 printer, and a Perfect Writer program (all of which eased immeasurably my pecking out whatever had to be "typed").

Mortimer P. Starr
December 1982

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Prokaryotes as Plant Pathogens

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Prokaryotes as Plant Pathogens

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The phytopathogenic bacteria are, in the main, rather ordinary bacteria. They are exceptional primarily in their ecological relationships: They live in and around plants in which they cause infectious diseases. Most kinds of plants are subject to one or more such diseases, which range in economic importance from considerable to negligible.

Certain historical and conceptual factors have been decisive in fashioning the notions held about phytopathogenic bacteria and, hence, in determining the methodological approaches used in isolating them from their plant and other habitats and in studying them. For this reason, some of the more important of these historical and conceptual factors will first be discussed, emphasizing those issues which have had significant effects on methods used in isolating and identifying the phytopathogenic bacteria and in gaining an understanding of their relationships to plant and other habitats.

Historical Background

The latter half of the nineteenth century was an exciting period in the history of infectious disease. One after another, microorganisms involved in the major diseases of man and other animals were isolated in axenic culture and rigorously proved to be the actual causal agents of these diseases. Many fungi were also conclusively shown to be the primary causes of infectious diseases of plants. The same approaches were applied to several bacterial diseases of plants, and by the 1880s the bacterial etiology was unmistakably demonstrated in the cases of fireblight disease of pears (Burrill, 1882), yellows disease of hyacinths (Wakker, 1883), and olive knot disease (Savastano, 1886). By the end of the nineteenth century, over a score of such diseases had been shown conclusively to be caused by bacteria, and the first cases of what are now known to be virus-caused diseases of plants were uncovered.

Despite this mounting and unequivocal evidence, curious denials appeared—usually in the form of declarations to the effect that the primary causes of these diseases were fungi and that the bacteria were inconsequential secondary invaders. A particularly strong stand in this direction was taken by the influential German medical microbiologist, Alfred Fischer (1897, 1900):

> With the exception of the root-nodules of the Leguminosae, we know of no single instance where bacteria invade the closed, living cells of plants. . . . The only organisms whose entrance [into plants] is accompanied by any danger are those whose spores contain sufficient reserve nutriment to enable them to germinate in pure water, to grow at first without food, and open the attack on the [plant] cell-wall at their own expense. Such are the spores of the parasitic fungi. . . . Bacteria are totally unable to act in this way, and the uninjured plant is impregnable to their attacks. . . . Notwithstanding these well-known facts, there appear time after time descriptions (generally insufficient enough) of the new "bacterial" diseases in plants. Bacteria, it is true, are often found in diseased plants in enormous numbers, but they are living metatrophically only, living on tissues that have already been disintegrated and decayed by parasitic fungi . . . [and] the first attack on the plant is always made by fungi. . . . All the cases of so-called "bacteriosis" in plants, from the "*gommose bacillaire*" of the vine down to the "*schorf*" of the potato, are primarily diseases of nonbacterial origin in which the bacteria are present merely as accidental invaders.

This opinion was eloquently challenged by Erwin Frink Smith, an eminent American plant pathologist and bacteriologist. Smith had shown—in still unsurpassed, meticulous, and detailed pioneering studies (Smith, 1895, 1896, 1897)—that the bacteria he had studied could indeed cause several important plant diseases. A public polemic ensued (Smith, 1899a,b, 1901; Fischer, 1899) in which Smith's forceful rhetoric and impeccable logic, bolstered by a mountain of experimentally determined fact, demolished forever the prejudiced notions of Fischer.

The early workers with phytopathogenic bacteria were primarily disease-oriented plant pathologists, whose main microbiological expertise pertained to mycology. The often inappropriate methods they used for studying phytopathogenic bacteria consisted of curious mixtures of procedures used by plant pathologists for phytopathogenic fungi plus techniques employed by medical scientists in the emerging science of medical bacteriology. This methodological impropriety led to some early descriptions of phytopathogenic bacteria which—by modern standards—are incomplete, inaccurate, and/or irrelevant. The introduction of more appropriate bacteriological methods into bacterial phytopathology was the work of a few pioneering spirits. The most notable of these is Smith, whose several books (Smith, 1905, 1911, 1914, 1920) and hundreds of research papers and monographs—which can be traced through a biographical memoir (Jones, 1939)—laid a rational foundation for the methodological corpus. Smith, a towering intellect and experimentalist of prodigious productivity—the subject of an excellent biography (Rodgers, 1952)—introduced numerous novel procedures into phytopathogenic bacteriology, many of which are still used today. Other pioneers, whose methodological contributions during the first half of the twentieth century are notable, include Elliott (1930, 1943, 1951), Stapp (1956), Ark (1937), Israilski (1955), Burkholder (1930, 1939, 1948), and Dowson (1949, 1957). All of these individuals were basically plant pathologists with a strong expertise in bacteriology.

An explosive worldwide development of the field, evident during the 1950s and 1960s, continues unabated today (see, for example, Maas Geesteranus, 1972; Station de Pathologie Végétale et Phytobactériologie, 1979). Nowadays, most good university departments and research institutions of plant pathology include one or more expert bacteriologists who are also competent phytopathologists. However, another trend can be perceived in that there are sometimes bacteriologists and biochemists who work with phytopathogenic bacteria without knowledge or appreciation of plant pathology and without adequate liaison in phytopathological matters. One must never lose sight of the fact that the major uniqueness of phytopathogenic bacteria resides in their ability to cause diseases of plants.

Conceptual Issues

Several historically determined conceptual issues of considerable significance need first to be considered for a proper understanding of the present methodological art pertaining to the phytopathogenic bacteria.

Diversity of Phytopathogenic Bacteria

The early polemic between Smith and Fischer has already been noted. Once the ability of certain kinds of bacteria to cause infectious disease of plants was firmly established, no further questions have been publicly raised on this general point. However, from time to time, one sees the effects of the derivative issue inherent in the operative words "certain kinds of bacteria" in the previous sentence. Practically every phytopathologist and bacteriologist now believes that certain kinds of bacteria do indeed cause particular plant diseases and, of course, nobody believes that all kinds of bacteria cause infectious diseases of plants. Nevertheless, the view that only very few bacterial sorts are to be expected as the etiological agents in plant diseases has perhaps stultified the uncovering of new sorts of phytopathogenic bacteria. This factor is exemplified by the long delay before "mycoplasma-like" and "rickettsia-like" organisms were shown to be phytopathogenic (Hopkins, 1977; Maramorosch, 1974; Whitcomb and Tully, 1979; this Handbook, Chapters 163, 167, and 169), even though some of the plant diseases caused by these bacteria had been well-known phytopathological entities for decades. Since few of these plant mycoplasma-like and rickettsia-like creatures have yet been cultivated axenically (apart from the plant), a methodology quite different from standard plant bacteriology is involved. The same might be said for several of the other uncommon sorts of phytopathogenic bacteria listed in Table 1.

The lesson to be gleaned from this note is the necessity for plant bacteriologists to be alert to the possible existence of nonstandard or even novel bacterial phytopathogens and, consequently, eclectic in their methodology. They must also be certain that they are working with the actual etiological agent of the disease under investigation! In connection with this latter caveat, it might be instructive to mention three recent cases. The long-sought etiological agent of Pierce's disease of grapevine has now been shown to be the Gram-negative, "rickettsia-like" (but cultivable) organism isolated by Davis, Purcell, and Thomson (1978), rather than the Gram-positive *Lactobacillus* sp. that was earlier announced as the pathogen (Auger and Shalla, 1975; Auger, Shalla, and Kado, 1974), which is now known to be a nonphytopathogenic inhabitant of the leafhopper vector of the actual Pierce's disease agent (Latorre-Guzman, Kado, and Kunkee, 1977; Purcell et al., 1977). The mycoplasma-like organism thought to be the cause of a pea disease has now been shown to be a contaminant or an artifact, "probably vesicles of host-cell membranes enclosing cytoplasm, ribosomes, and DNA-like strands"; the *Mycoplasma* sp. isolated from the diseased plants probably "orginated from animal rather than plant sources"; the etiology of the "pea disease may have been viral rather than bacterial" (Hampton et al., 1976). The etiological agent of cadang-cadang disease of coconut has been thought, in recent years, to be one of the currently fashionable mycoplasma-like or rickettsia-like entities; however, the latest words on the subject are that "prokaryotes probably have no primary role in the disease [and that] a virus or viroid is the most probable cause of cadang-cadang" (Randles et al., 1977).

Disciplinal and Nomenclatural Insularity

For decades following Burrill's report on the bacterial etiology of fireblight disease of pears, the phytopathogenic bacteria were studied exclusively by plant pathologists—usually in facilities physically quite separate from those devoted to other areas of bacteriology. There was little intellectual contact between bacterial phytopathologists and other bacteriologists: Their papers were published in different periodicals; they attended different scientific meetings; the paths of phytopathologists, animal pathologists, and bacteriologists rarely crossed. Although the barriers have been breached somewhat in recent years, they have by no means disappeared. This disciplinal insularity (Starr, 1979) has had important methodological consequences, such that the phytopathogenic bacteria were usually studied by methods quite different, for example, from those used by the then dominant (medical) bacteriologists. It is not surprising, given these circumstances of disciplinal insularity, that the early bacterial taxonomists practiced a derivative nomenclatural insularity by erecting separate taxa for the phytopathogenic bacteria, segregating them from all other bacteria solely on the basis of plant pathogenicity. For example, the first edition of *Bergey's Manual of Determinative Bacteriology* handled the phytopathogenic bacteria by placing all of them in a tribe Erwinieae, defined simply as "plant pathogens" (Bergey et al., 1923). The effects of this "Erwinieae notion" remain with us today.

The "New Host–New Species" Cliché

From the earliest times until quite recently, there was an unfortunate practice—when reporting a previously undescribed bacterial plant disease—of presenting an inadequate description of the "new" bacterial species. Usually no, or only feeble, attempts were made at direct bacteriological comparison with possibly related species. More deplorable—and much less understandable—are the equally feeble attempts to explore rigorously the range of plants that could be infected by the "new" species. In fact, the usual emphasis lay in "proving" the uniqueness of the "new" species by overweighting the significance of its isolation as the causal agent of a disease in a "new" (i.e., previously unreported) kind of plant. It is, therefore, not particularly surprising to a contemporary microbiologist, when these hundreds of "species" are scrutinized comparatively, to discover a chaos of probable synonymy that no bacterial taxonomist—regardless of his splitter tendencies—could find satisfactory. The variability in bacteriological traits exhibited in a direct side-by-side comparison of individual clones ("isolates") of a particular "species" is frequently as great as that shown among different "species". This has been documented from the earliest days to the present, though many of the writers overlook this obvious interpretation of their own data by their uncritical acceptance of the "new host–new species" cliché.

The firmly entrenched "new host–new species" notion resulted in the publication of many new "specific" names each year during the first half of the twentieth century. The problem was considerably aggravated by an attitude that the "new" bacteria, even when observed to be similar in bacteriological characteristics to named species, somehow deserved designation as distinct species merely because they had been isolated from different host plants. The promotion of truly unique phytopathogenic varieties and special forms to the rank of a sort of "practical" species might be tolerated. Unfortunately, in entirely too many cases the effort made to determine the phytopathogenic specialization (host range) of the "new" bacterial species was as nonexistent or ineffectual as was the bacteriological comparison (this Handbook, Chapter 62). The common errors and omissions included absence of direct comparisons with already named bacteria, failure to control the choice of horticultural varieties used in testing pathogenicity, unconcern over the preparation and condition of the inoculum, indifference to the site and mode of inoculation, inattention to the physiological and environmental situation of the host plant during the infective incubation period, and bias in the reading and evaluation of the pathological response.

Terminological Problems

Infectious diseases of plants constitute a particular kind of organismic association, one between antagonistic bacteria and plants. The terminology now used for describing this sort of organismic association has been borrowed largely from medical pathology and invertebrate zoology. This practice has had unfortunate consequences, because the associations to which the borrowed terms have been applied often are different in format and bases from those for which the terms had originally been used. This terminological confusion pervades all areas of organismic associations, and there have been few serious attempts to rectify the situation (Starr, 1975a,b). A particularly useful effort to clarify the terminology pertaining to plant diseases has been made by Hall (1974).

Table 1. Genera in which phytopathogenic bacteria (and other, possibly harmful, plant-associated bacteria) are placed, and some salient features of each genus.

Genus or trivial name	Part[a]	Gram stain	Flagellation	Morphology	G+C (mol%)	Pigmentation	Remarks	Key references	Chapter(s), this Handbook
Acetobacter	7	–	Peritrichous; none	Rods	55–64	None; pink; brown	"Vinegar" bacteria	Rohrbach and Pfeiffer (1976); Hine (1976)	64
Acetomonas[b]	7	–	Polar	Rods	60–64	None	"Vinegar" bacteria	Rohrbach and Pfeiffer (1975); Hine (1976)	64
Agrobacterium	7	–	Peritrichous	Rods	60–63	None	Some cause plant tumors	Lippincott and Lippincott (1975)	68
Anabaena	—		None			Blue-green	Phototrophic, N_2-fixing, cyanobacterial symbiont of *Azolla*	Newton and Herman (1979)	8, 12
Aplanobacter[c]	?	–	None[c]	Ovoid rods	?[c]	Cream[c]		Bradbury (1970)	—[c]
Arthrobacter	17	+;±	None; polar; lateral	Rods; coccoid elements	68–75	Yellow; orange; pink[d]	Rod ↔ coccus morphogenesis; synonym of *Corynebacterium* and *Curtobacterium* (in part)	Kuhn and Starr (1962)	141, 142, 143
Bacillus	15	+	Peritrichous	Rods; endospores	43–46	None	Aerobic	Volcani (1949); Tenne, Foor, and Sinclair (1977)	135
Clostridium	15	+;?	Peritrichous	Rods; endospores	52–54	None	Strictly anaerobic	Stankewich, Cosenza, and Shigo (1971)	138
Corynebacterium	17	+;±	None; polar	Pleomorphic; V-forms	65–75	None; orange; yellow[d]; blue[e]	Includes *Arthrobacter* *Curtobacterium*, and *Nocardia* spp.	Starr, Mandel, and Murata (1975)	141, 142, 143
Curtobacterium	17	+;±	Lateral	Short rods; coccoid elements	66–71	Yellow; orange; pink	Synonym of *Arthrobacter* and/or *Corynebacterium*	Yamada and Komagata (1972)	141, 142, 143
Enterobacter	8	–	Peritrichous	Rods	50–58	None; yellow[f]	Synonym of *Erwinia* (in part)	Ewing and Fife (1972)	95, 102
Erwinia	8	–	Peritrichous	Rods	50–58	None; yellow[f]; blue[g]; pink[h]	Fermentative	Starr and Chatterjee (1972); Imbs et al. (1977)	95

Escherichia	8	–	Peritrichous	Rods	50–51	None	Fermentative; causes (?) coconut budrot	Johnston (1911)	89
Frankia	17	+;±	None	Mycelial; bacteroids	—	—	Mainly unculti-vable; N_2-fixing in root nodules of non-leguminous plants	Callaham, Torrey, and Del Tredici (1978)	152
Methanobacterium	13	+	None	Rods	?	None	Strictly anaerobic; form methane	Zeikus and Henning (1975)	76
Mycoplasma-like	19	–	None	Pleomorphic; very small; no cell wall	23–40?	None	Uncultivable; intracellular	Maramorosch (1974); Whitcomb and Tully (1979)	167
Nocardia	17	+	None	Rods, tendency toward fila-ments that fragment	63—67	Orange[i]; none	Usually called *Corynebacterium* spp.	Starr, Mandel, and Murata (1975); Goodfellow and Minnikin (1977)	143, 155
Nostoc	—		None				Phototrophic, N_2-fixing, cyano-bacterial com-ponent of some lichens	Sampaio et al. (1979)	8,12
Pectobacterium	8	–	Peritrichous	Rods	50–58	None	Synonym of *Erwinia* (in part)	Waldee (1945)	102
Pierce's disease agent	?		None	Rods	?	None	"Rickettsia-like"; but cultivable	Davis, Purcell, and Thompson (1978)[j]	163
Pseudomonas	7	–	Polar	Rods	58–70	None; green; blue[k]	Oxidative	Palleroni and Doudoroff (1972)	60
Ratoon stunting disease agent	?	+	None	Branching rods	?	?	Uncultivable; coryneform; prominent meso-some	Gillaspie, Flax, and Koika (1976); Weaver, Teakle, and Hayward (1977)	143, 163
Rhizobium	7	–	Peritrichous; subpolar	Rods; "bacteroids"	59–63	None	Causes root nodules of leguminous plants in which N_2 is fixed	Dixon (1960)	67
Rickettsia-like	18	–	None	Tiny rods			Uncultivable; intracellular	Maramorosch (1974); Hopkins (1977)	163
Serratia	8	–	Peritrichous	Rods	53–59	Red; none	Synonym of *Erwinia* (in part)	Grimont et al. (1977); Grimont, Grimont, and Starr (1978)	97, 102

Table 1. Genera in which phytopathogenic bacteria (and other, possibly harmful, plant-associated bacteria) are placed, and some salient features of each genus. *(Continued)*

Genus or trivial name	Part[a]	Gram stain	Flagellation	Morphology	G+C (mol%)	Pigmentation	Remarks	Key references	Chapter(s), this Handbook
Spiroplasma	19	–	None; but motile!	Helical; no cell wall!	26	None	Pathogenic also to vertebrates	Maramorosch (1974); Tully et al. (1977); Whitcomb and Tully (1979)	169
Streptomyces	17	+	None	Mycelial; conidia	69–73	Variable		Waksman (1959); Corbaz (1964); Labruyère (1971)	143, 156
Xanthomonas	7	–	Polar	Rods	63–69	Yellow[l]	Forms copious slime[m]	Murata and Starr (1973)	62

[a] The major subdivisions of the bacteria in the eighth edition of *Bergey's Manual of Determinative Bacteriology* (Buchanan and Gibbons, 1974) are called "Parts". The nature of these taxonomic entities is discussed by Starr (1975c).
[b] Sometimes referred to the genus *Gluconobacter*.
[c] The single phytopathogenic species currently in the genus *Aplanobacter*. *A. populi,* was recently assigned (Ridé and Ridé, 1979) to the genus *Xanthomonas* as *X. populi* on the basis of serological, molecular, and cultural properties. The description of *X. populi* (Ridé and Ridé, 1979) differs substantially from that given here (after Bradbury, 1970) for *A. populi;* e.g., *X. populi* is yellow pigmented (not cream colored), and polarly flagellated (not aflagellated), and its DNA has 62.1–65.6 mol% G+C (not reported for *A. populi*).
[d] Starr and Saperstein (1953); Saperstein, Starr, and Filfus (1954).
[e] Kuhn et al. (1965).
[f] M. P. Starr, A. G. Andrewes, D. G. Gilliland, and others, unpublished data.
[g] Starr, Cosens, and Knackmuss (1966).
[h] Roberts (1974).
[i] Prebble (1968).
[j] The text notes the situation regarding the leafhopper-borne *Corynebacterium* or *Lactobacillus* sp., which had erroneously been thought to be the etiological agent of Pierce's disease of grapevines.
[k] Water-soluble, green-fluorescent pigments and/or phenazine pigments (Palleroni and Doudoroff, 1972).
[l] Noncarotenoid, brominated, aryl-polyene ("xanthomonadin") pigments (Starr et al., 1977).
[m] Thixotropic polysaccharides (Jeanes, 1974).

Genera in Which Phytopathogenic Bacteria Currently Are Placed

The generic assignments of phytopathogenic bacteria have been influenced by the disciplinal and taxonomic insularity alluded to above. Although the earliest assignments were in accordance with the nomenclatural scheme of the medical bacteriologists—see Elliott (1943) and Starr (1959) for historical summaries—the insular system put forth by a committee of the Society of American Bacteriologists (Winslow et al., 1917, 1920) was adopted by the editors of *Bergey's Manual of Determinative Bacteriology* (Bergey et al., 1923) and held sway for a half century. This system involved segregating the phytopathogenic bacteria from other bacteria solely on the basis of phytopathogenicity. Thus, the first edition of *Bergey's Manual* contained in the family Bacteriaceae a tribe Erwinieae, the total description of which was "Plant pathogens" (Bergey et al., 1923). This tribe Erwinieae was, in turn, divided into two genera: *Erwinia* ("Motile rods, possessing peritrichous flagella. The rods are white and a few species form pigment.") and *Phytomonas* ("Rods, yellow and white, motile and non-motile, the motile species possessing either mono- or lophotrichous flagella. May or may not form yellow pigment.").

Decidedly strange taxonomic bedfellows were thrown together by this Erwinieae notion, which gained the remarkable and negative accolade of the following terse acknowledgement (cited by Jones, 1939) from the usually verbose gentleman—Erwin F. Smith—who was thus commemorated: " . . . the species I have mentioned ought not to be put into one genus (Erwinia) simply because they are plant parasites." By 1930, Burkholder (1930), who had set up a comparative study on a grand scale, had sorted out the major groups of bacteria that had previously been lumped into *Phytomonas;* further refinements are seen in his 1939 paper (Burkholder, 1939), which suggested division of the genus *Phytomonas* into several "groups" whose affinities to genera of nonpathogens are specified. With the recognition that the bacterial genus *Phytomonas* was homonymous with a group of protozoan flagellates in apparent conflict with international nomenclatural regulation (Elliott, 1937), new generic names for Burkholder's groups were desirable. These formal generic designations were forthcoming from Dowson (1939, 1942, 1943), Conn and Dimmick (1947), and others, leading to the reassignment of the bacterial phytopathogens to an assortment of genera in the sixth (Breed, Murray, and Hitchens, 1948), seventh (Breed, Murray, and Smith, 1957), and eighth (Buchanan and Gibbons, 1974) editions of *Bergey's Manual.* Table 1 lists these genera, the major taxonomic subdivisions (called "parts" in that edition of the *Manual*) to which each genus belongs, and some salient features of each genus. In some cases, a genus listed in Table 1 may not be treated as a repository for phytopathogenic bacteria in the eighth edition of *Bergey's Manual;* in others, the claimed phytopathogenicity is perhaps dubious. Individual treatments—referenced here in Table 1—regarding each major genus that contains phytopathogenic bacteria appear separately in the appropriate sections of this Handbook.

Habitats of Phytopathogenic Bacteria

In terms of habitats, most phytopathogenic bacteria are known—principally or solely—as antagonistic inhabitants or associants ("parasites" in conventional terminology; Starr, 1975a) of the plants in which they cause infectious diseases. Much of the extensive primary literature on this topic can be traced through monographs and textbooks, most of which are either limited in scope or now somewhat outdated (Dowson, 1949, 1957; Elliott, 1930, 1951; Gorlenko, 1965; Israilski, 1955; Maas Geesteranus, 1972; Rangaswami, 1962; Smith, 1905, 1911, 1914, 1920; Stapp, 1956, 1958; Station de Pathologie Végétale et Phytobactériologie, 1979; U. S. Department of Agriculture, 1960). Abstract journals, such as the *Review of Plant Pathology,* provide another means for entering the literature. Further information about the diseases caused by each major kind of phytopathogenic bacteria will be found in the chapters of this Handbook (referenced here in Table 1) dealing with the individual genera. Some of these plant diseases are known to be mediated by phytotoxins elaborated by the phytopathogenic bacteria; current knowledge in this area is summarized by Strobel (1977).

Phytopathogenic bacteria have been infrequently sought and even more rarely found with certainty in habitats other than the diseased plant or immediately adjacent loci. One major reason for this limitation probably lies in the lack, until quite recently, of adequate selective media and determinative criteria whereby such organisms might be isolated, identified, and enumerated. Another reason is the seeming inability of some phytopathogenic bacteria to persist in nonphytopathological habitats for extended periods (Schuster and Coyne, 1974, summarize the little that is known about this subject). In general, most reports on the persistence (sometimes, overwintering) of phytopathogenic bacteria in nonphytopathological situations deal with their occurrence on dormant plants and in the soil (usually soil adjacent to diseased plants or plant residues). Occasionally, other habitats have been explored; e.g., feces of sheep that had been fed on beans infected with *Pseudomonas phaseolicola* (Starr and Kercher, 1969), packinghouse waters (Segall, 1971), vector and other insects (Carter, 1962; Oldfield et al., 1977), and asymptomatic host or nonhost plants (Goto, 1972; Leben, 1965; Miller and Schroth, 1972). The ''normal'' (i.e., assumedly nonphytopathogenic) bacterial flora of plants has come in for some attention in this connection (Crosse, 1971; Gibbins, 1972; Dickinson and Preece, 1976; Mundt and Hinkle, 1976). Phytopathogenic *Erwinia* and *Xanthomonas* spp. and possibly others are used in industrial fermentations (Grossowicz and Rasooly, 1972; Jeanes, 1974); the fermentation plants thus constitute another, man-made habitat.

Some phytopathogenic bacteria and some epiphytic (usually, but not always certainly, nonphytopathogenic) plant bacteria have emerged recently as important pathogens of man and other animals, usually as opportunistic pathogens of compromised hospital patients (Starr, 1979). Several of the more significant kinds of such nosocomial (hospital-acquired) pathogens of man clearly relate to bacteria that normally live on and/or infect plants: for example, the members of the yellow-pigmented *Erwinia herbicola* group (Schneierson and Bottone, 1973), called *Enterobacter agglomerans* by some medical bacteriologists (Ewing and Fife, 1972); various *Pseudomonas* spp. (Cother, Darbyshire, and Brewer, 1976; Gelbart, Reinhardt, and Greenlee, 1976; Kawamoto and Lorbeer, 1974; von Graevenitz, 1973; Wright, Kominos, and Yee, 1976; but see Knösel and Nimitan, 1976); and *Serratia* (Grimont, Grimont, and Starr, 1978). These plant-associated bacteria and other opportunists that cause nosocomial infections in man (von Graevenitz, 1977) are treated in the appropriate chapters elsewhere in this Handbook.

General Remarks about Isolation of Phytopathogenic Bacteria

Isolation of the more common phytopathogenic bacteria from fresh, diseased plant material is not a particularly difficult task because the populations of the pathogens in the fresh, active lesions are high—both absolutely and relatively to nonphytopathogens. In most such cases, all that is necessary is to dissect material aseptically from a fresh lesion, to macerate it in a drop of sterile water, to check microscopically for the presence of a uniform and abundant bacterial flora of the expected morphology, and to streak the material from the aqueous suspension onto one or another of the selective and nonselective media commonly used for that purpose. As already noted, one must be alert to those less well known phytopathogenic bacteria that require special culture media or other unusual conditions (e.g., anaerobic incubation), and even the existence of phytopathogenic bacteria that cannot be cultivated axenically (Table 1). All too often, the plates are overgrown by the common epiphytic bacteria that abound on plant surfaces (Dickinson and Preece, 1976), and the ''pathogen'' turns out on later scrutiny to be one of these nonphytopathogenic epiphytes.

The situation changes drastically when the plant material is not freshly infected and is possibly overgrown by contaminating microbes (e.g., when it has been in transit or storage for some time). Moreover, it often becomes futile to try to isolate phytopathogenic bacteria from possible habitats other than infected plants (e.g., soil, water, plant residues, healthy plants and animals), because the art has not progressed sufficiently to permit the desired selectivity in resolving such heterogeneous microbial mixtures. In the detailed treatments of individual genera that appear elsewhere in this Handbook, those methods are emphasized that are suitable mainly for the relatively simple function of isolating phytopathogenic bacteria from fresh lesions. Where rational procedures (enrichment and/or selection) are known, which are adequate for the more difficult task of isolating phytopathogenic bacteria from overgrown lesions or from other than plant habitats, such procedures are noted separately.

General Remarks about Identification of Phytopathogenic Bacteria

It is not particularly difficult to determine the generic placement of the more common phytopathogenic bacteria when they have been isolated from diseased plants or from soil and other habitats immediately adjacent to (or otherwise related to) diseased plants. In fact, provided the plant disease is an already known one, it is a relatively simple and quite common practice (but, in logical terms, a circular one) to come to a reasonable identification of the bacterium based mainly on knowledge of the phytopathogenic habitat, demonstration that the disease can be reproduced by experimental inoculation of plants with the axenic bacterial culture, use of a few bacteriological tests (such as those given in Table 1), and reference to a host index of plant diseases (U. S. Department of Agriculture, 1960).

There are at least three general situations in which identification of phytopathogenic bacteria is either difficult or well-nigh impossible: (i) when the bacteria have been isolated from a habitat having no discernible relationship to a known plant disease; (ii) when a ''new'' (i.e., previously unreported) plant disease or symptom is involved; and (iii) when a bacterial pathogen that is unrelated to one of the common genera of phytopathogenic bacteria is the cause of the plant disease under investigation. Ex-