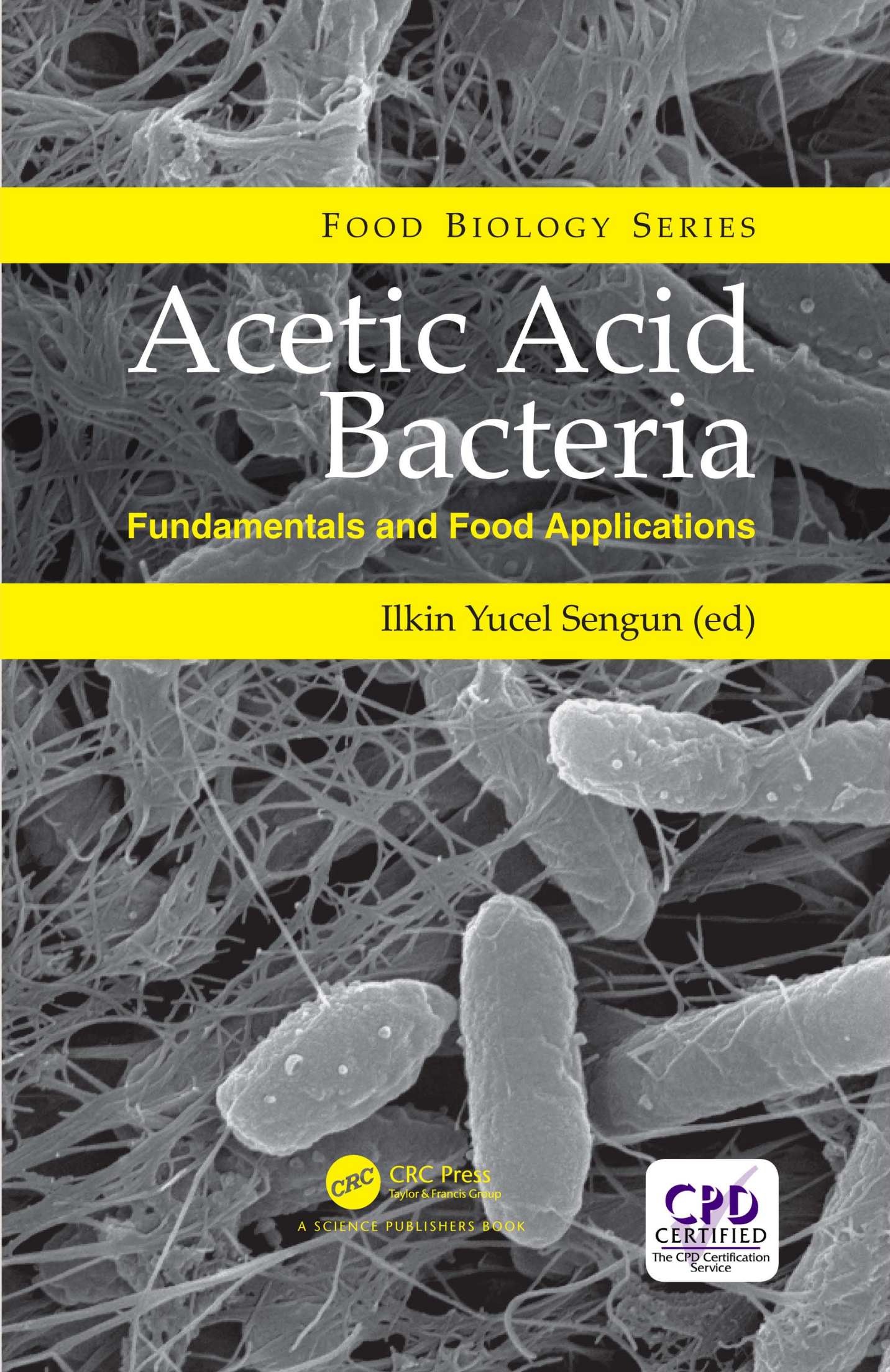
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Food Biology Series

Acetic Acid Bacteria

Fundamentals and Food Applications

Editor

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Preface to the Series

Food is the essential source of nutrients (such as carbohydrates, proteins, fats, vitamins, and minerals) for all living organisms to sustain life. A large part of daily human efforts is concentrated on food production, processing, packaging and marketing, product development, preservation, storage, and ensuring food safety and quality. It is obvious, therefore, our food supply chain can contain microorganisms that interact with the food, thereby interfering in the ecology of food substrates. The microbe-food interaction can be mostly beneficial (as in the case of many fermented foods such as cheese, butter, sausage, etc.) or in some cases, it is detrimental (spoilage of food, mycotoxin, etc.). The Food Biology series aims at bringing all these aspects of microbe-food interactions in form of topical volumes, covering food microbiology, food mycology, biochemistry, microbial ecology, food biotechnology and bio-processing, new food product developments with microbial interventions, food nutrification with nutraceuticals, food authenticity, food origin traceability, and food science and technology. Special emphasis is laid on new molecular techniques relevant to food biology research or to monitoring and assessing food safety and quality, multiple hurdle food preservation techniques, as well as new interventions in biotechnological applications in food processing and development.

The series is broadly broken up into food fermentation, food safety and hygiene, food authenticity and traceability, microbial interventions in food bio-processing and food additive development, sensory science, molecular diagnostic methods in detecting food-borne pathogens and food policy, etc. Leading international authorities with background in academia, research, industry and government have been drawn into the series either as authors or as editors. The series will be a useful reference resource base in food microbiology, biochemistry, biotechnology, food science and technology for researchers, teachers, students and food science and technology practitioners.

Ramesh C. Ray
Series Editor

Preface

Acetic acid bacteria are a group of microorganisms found widespread in Nature. They are characterized by their capability to oxidize sugars, alcohols and sugar alcohols into their corresponding organic acids. They can be involved in a variety of biological processes and are used for the production of fermented foods and beverages, because of their special and unique characteristic called 'oxidative fermentation'. The main well-known application of acetic acid bacteria is the production of acetic acid in the form of vinegar. Although acetic acid bacteria have an important role in producing special types of foods, it is not common to use them as a starter culture in food fermentations because of technological and economical reasons. Acetic acid bacteria were previously regarded as a small taxonomic group, which included only two genera, *Acetobacter* and *Gluconobacter*, but their classification has entirely changed in the last years due to the development of novel molecular detection and identification techniques. Currently, this important and diverse group of bacteria includes eighteen genera. However, there are only few sources dealing with their relevant reclassification.

This book presents a comprehensive and updated information on both fundamentals and food applications of acetic acid bacteria. It contains 13 chapters categorized under two parts. The first part gives detailed information on the general characteristics and current taxonomy of acetic acid bacteria. One chapter of particular interest describes the important findings that have emerged from genome studies of this diverse group of bacteria. The physiology and biochemistry, acetic acid resistance, exopolysaccharide production and thermotolerant properties of acetic acid bacteria are described separately in specific chapters. Two chapters are devoted to the latest identification and preservation techniques of acetic acid bacteria which are the most active fields of research today. Microbial collections of acetic acid bacteria and the available online databases are also given in this part. The second part of the book describes the importance of acetic acid bacteria in the food industry by giving information on the microbiological properties of fermented foods as well as their production procedures. A chapter is devoted to the microbiology of fermented foods, including dairy products, cereal-based products, fruit and vegetable products, meat products, locally produced traditional fermented foods and innovative functional foods. Several foods and beverages performed by acetic acid bacteria are discussed separately. Special attention is given to vinegar and cocoa fermentation, which are the most familiar and extensively used industrial applications of acetic acid bacteria. The chapter titled 'Vinegars' provides information on the types of vinegar, fermentation technologies, mass balance and yields, vinegar microbial community, vinegar spoilage and intended use of different vinegars. It is major concern in food science to provide safe foods and improve the health of consumers. Therefore, two chapters are devoted on detrimental and beneficial effects of acetic acid bacteria in terms of food safety and benefits to human health.

The chapters have been written by leading international authorities in the field with recent scientific data on microbiology, food science and technology and engineering. About thirty scientists from eleven countries have contributed to the preparation of this book. It is hoped that this book covers all the basic and applied aspects of acetic acid bacteria to satisfy the needs of readers, be the scientists, technologists, students or those working in this field. I want to thank the contributors for their kind support and sharing their valuable experiences, as well as to the production team at CRC Press for bringing out this book. I am also pleased to learn the reason why authors/editors always thank their families for the works completed successfully.

Ilkin Yucel Sengun
Editor

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PART I

DESCRIPTION OF ACETIC ACID BACTERIA

1

Systematics of Acetic Acid Bacteria

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Introduction

Acetic acid bacteria are Gram-negative, rod-shaped, and obligate aerobes and commonly known as vinegar-producing microorganisms (Asai 1968, Sievers and Swings 2005, Kersters et al. 2006, Komagata et al. 2014). The acetic acid bacteria in general have an ability to oxidize ethanol to acetic acid and glucose to gluconic acid and are classified in the family *Acetobacteraceae* Gillis and De Ley 1980 (Gillis and De Ley 1980, Sievers and Swings 2005, Kersters et al. 2006, Komagata et al. 2014). The members of the family are separated into two groups, i.e., the acetous and the acidophilic groups (Komagata et al. 2014). The acetic acid bacteria are included in the former group.

The genus *Acetobacter*, the type genus of the family *Acetobacteraceae* was introduced by Beijerinck (1898), with *Acetobacter aceti* (Pasteur 1864) Beijerinck 1898, the type species of the genus. Asai (1935) divided acetic acid bacteria into two genera. One was the genus *Acetobacter* Beijerinck 1898, and the other was the genus *Gluconobacte*r Asai 1935. The former was comprised of the species that oxidized ethanol more intensely than glucose and an ability to oxidize acetic acid to carbon dioxide and water, and the latter was of the species that oxidized glucose more intensely than ethanol and no ability to oxidize acetic acid (Asai 1935). The genus '*Acetomonas*' Leifson 1954 was then proposed for the species that formed polar flagellation and were non acetate-oxidizing (Leifson 1954). On the other hand, the species of the genus *Acetobacter* formed peritrichous flagellation and oxidized

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acetic acid to carbon dioxide and water. The proposal of the two generic names caused confusion in classifying non acetate-oxidizing acetic acid bacteria (Asai and Shoda 1958, Shimwell 1958, Shimwell and Carr 1959, Carr and Shimwell 1960).

De Ley (1961) recognized the priority of *Gluconobacter,* but not of '*Acetomonas*' in the generic name. Since Asai (1935) did not designate the type species of the genus *Gluconobacter*, *Gluconobacter oxydans* (Henneberg 1897) De Ley 1961 was designated as the type species (De Ley 1961, De Ley and Frateur 1970).

Asai et al. (1964) reported two types of intermediate strains, in addition to the strains of the genera *Acetobacter* and *Gluconobacter*. One was composed of the strains that had peritrichous flagellation, and the other was of the strains that had polar flagellation in spite of "being acetate-oxidizing." The two types of the intermediate strains were designated by the ubiquinone system (Yamada et al. 1969a). The two genera were chemotaxonomically distinguished from each other by the presence of the major ubiquinone, i.e., UQ-9 in the genus *Acetobacter* and UQ-10 in the genus *Gluconobacte*r. In the two types of the intermediate strains, however, the peritrichously flagellated intermediate strains that were acetate-oxidizing and once classified as '*Gluconobacter liquefaciens*' (= *Acetobacter liquefaciens*) (Asai 1935, Asai and Shoda 1958, Asai 1968, Gosselé et al. 1983a, Yamada 2016), had UQ-10, as found in the genus *Gluconobacter*, and the polarly flagellated intermediate strains that were "acetate-oxidizing" (Asai et al. 1964, Yamada et al. 1976a) and once classified as '*Acetobacter aurantius*' (Kondo and Ameyama 1958) had UQ-8, which was never found in any other strains of acetic acid bacteria (Yamada et al. 1969a). The polarly flagellated intermediate strains equipped with UQ-8 were later classified as *Frateuria aurantia* (ex Kondo and Ameyama 1958) Swings et al. 1980 (Swings et al. 1980). In addition to the peritrichously flagellated intermediate strains equipped with UQ-10, the strains of *Acetobacter xylinus* were UQ-10-equipped in the genus *Acetobacte*r (Yamada et al. 1969a, b, 1976b, Yamada 1983).

In the Approved Lists of Bacterial Names 1980, the UQ-10-having peritrichously flagellated intermediate strains were classified as *Acetobacter aceti* subsp. *liquefaciens*, and the UQ-10-having *A. xylinus* strains were classified as *Acetobacter aceti* subsp. *xylinus* (Skerman et al. 1980). For the UQ-10-having *Acetobacter* strains mentioned above, the subgenus *Gluconacetobacter* Yamada and Kondo 1984 was proposed within the genus *Acetobacter* (Yamada and Kondo 1984). However, the subgenus was not accepted, together with the name of the genus *Acidomonas* Urakami et al. 1989 (Swings 1992, Sievers et al. 1994). The subgenus was later elevated to the generic level as the genus *Gluconacetobacter* Yamada et al. 1998, along with the recognition of the genus *Acidomonas* (Yamada et al. 1997).

In the genus *Gluconacetobacter*, there were two subclusters or the two subgroups, i.e., the *Gluconacetobacter liquefaciens* group and the *Gluconacetobacter xylinus* group (Franke et al. 1999, Yamada et al. 2000). The two groups were suggested to be distinguished from each other at the generic level based on morphological, physiological, ecological, and phylogenetical aspects (Yamada and Yukphan 2008). For the latter group, the genus *Komagataeibacter* Yamada et al. 2013 was introduced (Yamada et al. 2012a, b). Eighteen genera are recognized at present in the acetous group of the family *Acetobacteraceae*, i.e., *Acetobacter* Beijerinck 1898, *Gluconobacter* Asai 1935, *Acidomonas* Urakami et al. 1989 emend. Yamashita et al. 2004, *Gluconacetobacter* Yamada et al. 1998, *Asaia* Yamada et al. 2000, *Kozakia* Lisdiyanti et al. 2002, *Swaminathania* Loganathan and Nair 2004, *Saccharibacter* Jojima et al. 2004, *Neoasaia* Yukphan et al. 2006, *Granulibacter* Greenberg et al. 2006, *Tanticharoenia* Yukphan et al. 2008, *Ameyamaea* Yukphan et al. 2010, *Neokomagataea* Yukphan et al. 2011, *Komagataeibacter* Yamada et al. 2013, *Endobacter* Ramírez-Bahena et al. 2013, *Nguyenibacter* Vu et al. 2013, *Swingsia* Malimas et al. 2014, and *Bombella* Li et al. 2015 (Fig. 1).

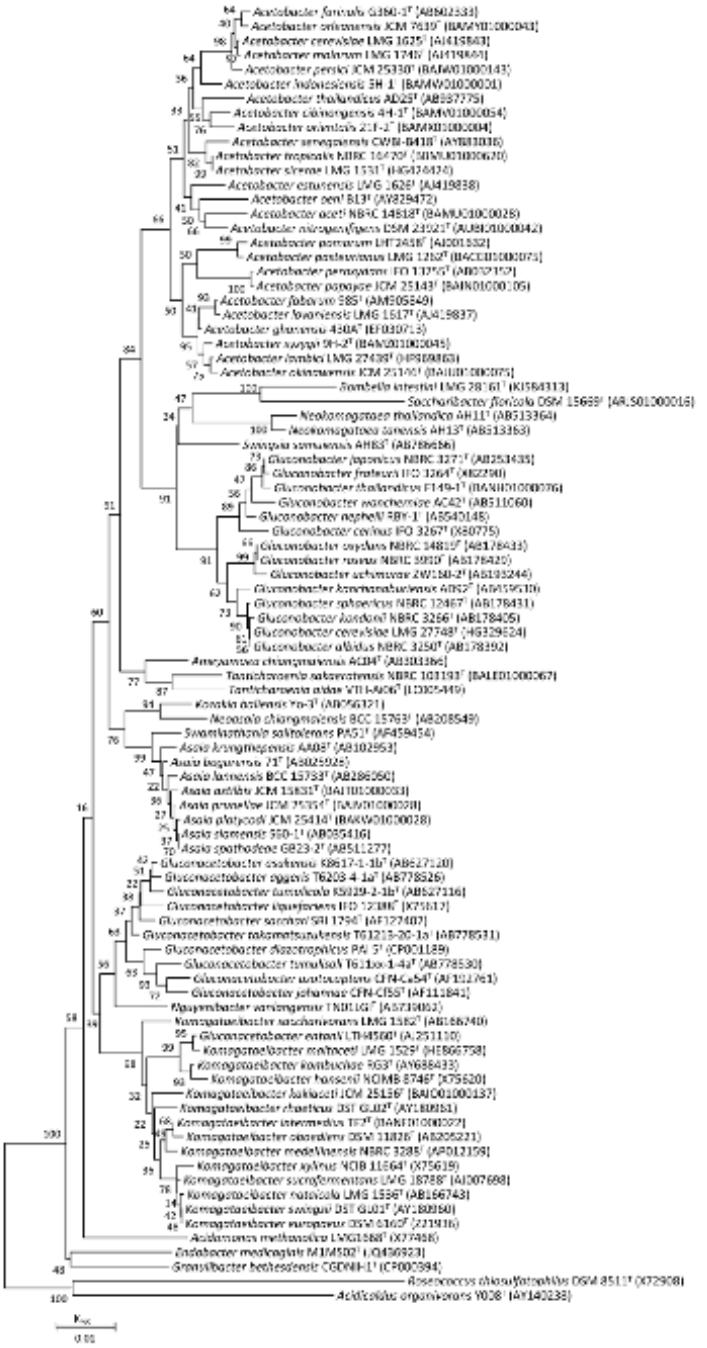

Figure 1: A neighbor-joining tree of acetic acid bacteria. The phylogenetic tree based on 16S rRNA gene sequences of 1213 bases was constructed by using MEGA6 (Tamura et al. 2013). The numerals at the nodes of respective branches indicate bootstrap values (per cent) derived from 1000 replications.

General Characteristics of Acetic Acid Bacteria

The acetic acid bacteria, obligate aerobes are quite unique. The strains assigned to the representative genera *Acetobacter* and *Gluconobacter* have a lack of the Embden/Meyerhof/

Parnas pathway, but the pentose phosphate cycle is functioning instead (Cheldelin 1961, De Ley 1961, Arai et al. 2016, Bringer and Bott 2016). In addition, the strains of the genus *Gluconobacter* lack the TCA cycle, differing from those of the genus *Acetobacter*, and the pentose phosphate cycle acts as a terminal oxidation system. In fact, glucose-6-phosphate dehydrogenase and 6-phospholuconate dehydrogenase reduce NAD except for NADP, and the two dehydrogenases play an important role in the respiratory chain phosphorylation (Cheldelin 1961).

The acetic acid bacteria additionally have the direct oxidation system for alcohols, sugars, and sugar alcohols and accumulate a large amount of the corresponding oxidation products, i.e., acetic acid from ethanol, gluconic acid, 2-ketogluconic acid, 5-ketogluconic acid, and 2,5-diketogluconic acid from glucose, fructose from mannitol, L-sorbose from sorbitol, and 5-ketofructose from fructose or sorbitol (Cheldelin 1961, De Ley 1961, Komagata et al. 2014). Such a partial or incomplete oxidation is traditionally called "oxidative fermentation" and carried out by the membrane-bound dehydrogenases that are linked to the energy-yielding or the non energy-yielding respiratory chain (Matsushita et al. 2004, Komagata et al. 2014, Adachi and Yakushi 2016, Matsushita and Matsutani 2016).

When acetic acid bacteria are grown on alcohols, sugars, or sugar alcohols, the biphasic growth is generally seen. In the 5-ketofructose fermentation of '*Gluconobacter suboxydans*' strain 1, e.g., the first phase of the growth seemed to be due to the oxidation of sorbitol to L-sorbose and then to 5-ketofructose catalyzed respectively by glycerol dehydrogenase [EC 1.1.99.22] and by L-sorbose 5-dehydrogenase [EC 1.1.99.12], which were linked to the energy-yielding respiratory chain (Sato et al. 1969a, Matsushita et al. 2004, Komagata et al. 2014, Adachi and Yakushi 2016, Matsushita and Matsutani 2016). In the second phase of the growth, the resulting 5-ketofructose was reduced to fructose catalyzed by 5-ketofructose reductase [EC 1.1.1.124], and then the resulting fructose flowed into the pentose phosphate cycle, which was coupled with the energy-yielding respiratory chain, probably via fructose-6-phosphate after phosphorylation (Fig. 2).

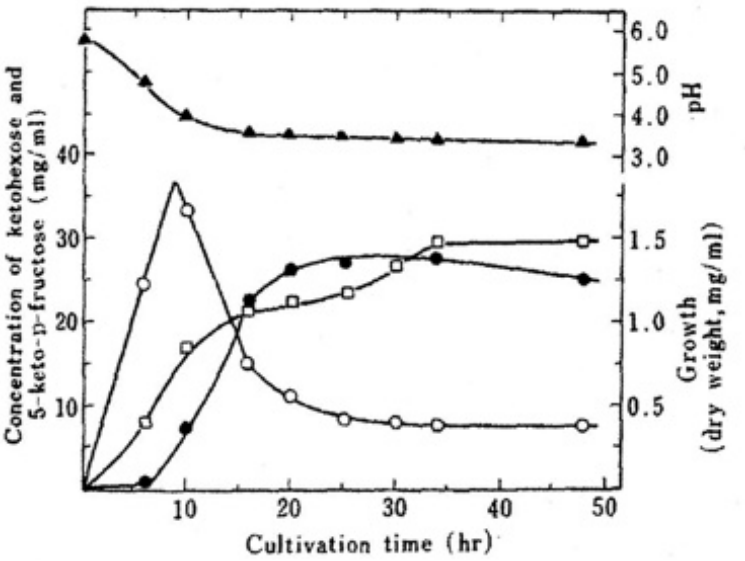

Figure 2: The biphasic growth of '*Gluconobacter suboxydans*' strain 1. The organism was cultured in 500 ml of a medium containing 4.0 per cent sorbitol (w/v) and defatted soybean extract (w/v) in a 5-liter conical flask. The cultivation was done at 30 °C on a rotary shaker at 160 rpm [The figure was cited from Sato et al. (1969b). ○, L-sorbose; ●, 5-ketofructose; □, growth; ▲, pH].

Isolation of Acetic Acid Bacteria

For the isolation of acetic acid bacteria, an enrichment culture approach is effectively used (Komagata et al. 2014). A medium for the enrichment culture procedure and for the isolation of acetic acid bacteria, designated as the pH 3.5 medium (Yamada et al. 1999), is composed, e.g., 1.0 per cent glucose (w/v), 0.5 per cent ethanol (99.8 per cent) (v/v), 0.3 per cent peptone (w/v), 0.2 per cent yeast extract (w/v), and 0.01 per cent cycloheximide (w/v) and adjusted to pH 3.5 with concentrated hydrochloric acid. In the isolation of acetic acid bacteria capable of fixing atmospheric nitrogen, the LGI medium that contains 10.0 per cent sucrose (w/v), 0.06 per cent KH_2PO_4 (w/v), 0.02 per cent K_2HPO_4 (w/v), 0.02 per cent $MgSO_4$ (w/v), 0.002 per cent $CaCl_2$ (w/v), 0.001 per cent $FeCl_3$ (w/v), and 0.0002 per cent Na_2MoO_4 (w/v) is used at pH 6.0 (Cavalcante and Döbereiner 1988). When microbial growth is seen in the LGI medium, the culture is transferred to the pH 3.5 medium mentioned above (Vu et al. 2013). To obtain and purify candidates of acetic acid bacteria, the culture in the pH 3.5 medium is streaked onto agar plates, which are composed of 2.0 per cent glucose (w/v), 0.5 per cent ethanol (99.8 per cent) (v/v), 0.3 per cent peptone (w/v), 0.3 per cent yeast extract (w/v), 0.7 per cent calcium carbonate (precipitated, e.g., by Japanese Pharmacopoeia) (w/v), and 1.5 per cent agar (w/v) (Yamada et al. 1999), and the resulting colonies that dissolve calcium carbonate on the agar plates are picked up and transferred onto agar slants containing the same in composition as the agar plates for temporary preservation. The strains isolated were examined again for growth on the pH 3.5 medium.

When the composition, especially of the carbon sources, of the medium in the enrichment culture procedure is changed, the selective isolation of acetic acid bacteria can be expected. In fact, the strains of *Asaia bogorensis* and *Asaia siamensis* were first isolated using sorbitol or dulcitol instead of glucose (Yamada et al. 2000, Katsura et al. 2001). Several kinds of media employed for the enrichment culture procedure result in the effective isolation of acetic acid bacteria (Lisdiyanti et al. 2003b, Suzuki et al. 2010).

To isolate acetic acid bacteria, sugary and alcoholic materials have widely been utilized as isolation sources. In some cases, the habitats of acetic acid bacteria are to be isolation sources (Sievers and Swings 2005, Kersters et al. 2006, Komagata et al. 2014, Li et al. 2015).

Most acetic acid bacteria can be maintained at 4 °C for one month on agar slants containing an appropriate medium. The long-term preservation of acetic acid bacteria can be achieved by lyophilization or by storage in liquid nitrogen, or by cryoconservation at -80 °C by the use of low-temperature refrigerators and appropriate cryoprotectants (Sievers and Swings 2005, Kersters et al. 2006, Komagata et al. 2014).

Identification of Acetic Acid Bacteria

To make a check whether the strains isolated are acetic acid bacteria or not, the growth test is applied at pH 3.5 (Yamada et al. 1999). The medium to be utilized has the same composition as the pH 3.5 medium mentioned above.

In the genera that are not monotypic, i.e., include more than several species and are therefore restricted only to *Acetobacter*, *Gluconobacte*r, *Gluconacetobacter*, *Asaia*, and *Komagataeibacter*, which are supposed to be taxonomically and ecologically in common but not in rare existence, the generic-level, routine identification for certain strains of acetic acid bacteria can be achieved by the combination of only two conventional phenotypic tests comprised of acetate and lactate oxidation and production of acetic acid from ethanol (Yamada and Yukphan 2008).

In strains to be assigned to the genus *Acetobacter*, a deep blue color appears fast and clearly in the acetate and lactate oxidation tests, and acetic acid is produced in the acetic

acid production test (Asai et al. 1964, Yamada and Yukphan 2008). In acetate and lactate oxidation, strains to be assigned to the genus *Gluconobacter* show a clear yellow color, and the color change to blue is not so vigorous in strains to be assigned to the genera *Gluconacetobacter* and *Komagataeibacter*, in contrast to the genus *Acetobacter*. The latter two genera, *Gluconacetobacter* and *Komagataeibacter* are additionally discriminated from each other by water-soluble brown pigment production and cell motility. Strains to be assigned to the former generally produce a water-soluble brown pigment, being motile, but strains to be assigned to the latter do not, being non motile. Strains to be assigned to the genus *Asaia* show no or little acetic acid production from ethanol, differing from the above-mentioned four genera, and the color change is very slow in acetate and lactate oxidation. The two conventional tests described above are very useful, especially when a large number of isolates are routinely identified or classified at the generic level.

The acetic acid bacteria can be routinely identified at the species level phylogenetically. The so-called partial 16S rRNA gene 800R-regions of the PCR products that are produced by the ordinal method are sequenced using the primer of 800R (5′-TACCAGGGTATCTAATCC-3′, positions 802-785; the numbering of the positions was based on the *Escherichia coli* numbering system, Brosius et al. 1981, accession number V00348), and a phylogenetic tree is constructed based on the sequence data obtained (Vu et al. 2013). On the other hand, the polyphasic taxonomic analysis is applicable to the identification (Cleenwerck and De Vos 2008). When a certain strain of acetic acid bacteria, e.g., a new isolate is precisely identified, DNA-DNA hybridization will be inevitable.

Genera and Species in Acetic Acid Bacteria

The acetic acid bacteria classified in the acetous group constitute the family *Acetobacteraceae*, the class *Alphaproteobacteria* Stackebrandt et al. 1988, along with the acidophilic group (Stackebrandt et al. 1988, Sievers and Swings 2005, Komagata et al. 2014). The type genus of the family is *Acetobacter* Beijerinck 1898. Eighteen genera are presently reported (Table 1).

1. *Acetobacter* Beijerinck 1898

A.ce.to.bac′ter. L. neut. n. *acetum*, vinegar; N. L. masc. n. *bacter*, rod; N. L. masc. n. *Acetobacter*, vinegar rod.

The genus *Acetobacter* is the oldest in the classification of acetic acid bacteria and the type genus of the family *Acetobacteraceae*. In the Approved Lists of Bacterial Names 1980, the three species, *Acetobacter aceti*, *Acetobacter pasteurianus,* and *Acetobacter peroxydans* were listed with their nine subspecies (Skerman et al. 1980). The genus is related phylogenetically to the genera *Gluconobacter*, *Neokomagataea*, *Swingsia*, *Saccharibacter*, and *Bombella*. In the genus *Acetobacter*, there are two phylogenetically different groups, i.e., the *Acetobacter aceti* group and the *Acetobacter pasteurianus* group.

Cells are Gram-negative, ellipsoidal to rod-shaped, measuring 0.4 to 1.0 by 1.2 to 3.0 μm, rarely longer cells. Cells occur singly or short chains and occasionally long chains. Peritrichously flagellated when motile, however, *Acetobacter nitrogenifigens* exceptionally has polar flagella (Dutta and Gachhui 2006). Colonies are generally circular, smooth, entire, convex, cream color to beige, opaque, and butyrous on glucose/ethanol/yeast extract/peptone agar.

Strictly aerobic. Catalase positive, but negative in *Acetobacter peroxydans*. Oxidase negative. Acetic acid is produced from ethanol. Acetate and lactate are oxidized to carbon dioxide and water. Grows very weakly on mannitol agar while does not grow on

Table 1: Characteristics differentiating the genera of acetic acid bacteria

Characteristic	*Acetobacter*	*Gluconobacter*	*Acidomonas*	*Gluconacetobacter*	*Asaia*	*Kozakia*	*Swaminathania*	*Saccharibacter*	*Neoasaia*	*Granulibacter*	*Tanticharoenia*	*Ameyamaea*	*Neokomagataea*	*Komagataeibacter*	*Endobacter*	*Nguyenibacter*	*Swingsia*	*Bombella*
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Flagellation	per[a]	pol[a]	n[c]	per	per	n	per	n	n	n	n	pol	n	n	spol	per	n	n
Oxidation of																		
Acetate	+	-	+	+	w	w	w	-	-	w	-	+	-	+	-	+	-	-
Lactate	+	-	-	+	w	w	w	w	-	+	-	w	-	+	-	-	-	-
Growth on																		
30 per cent Glucose (w/v)	-	-[b]	+	-	+	-	+	+	+	nd	+	-	+	nd	nd	w	+	+
1 per cent Glucose (w/v)	+	+	+	+	+	+	nd	-	+	nd	+	+	+	+	+	+	+	nd
Glutamate agar	-	-	nd	+	+	-	+	-[e]	+	+	w	w	+	+	+	+	+	nd
Mannitol agar	vw	+	nd	+	+	+	+	-[e]	+	w	+	+	+	+	+	+	+	nd
Raffinose	-	-	-	-	+	w	nd	nd	+	nd	-	-	-	nd	nd	+	-	nd
Utilization of methanol	-	-	+	-	-	-	-	-	-	+	-	w	nd	nd	-	nd	nd	nd
Growth in the presence of																		
0.35 per cent acetic acid (w/v)	+	+	+	+	-	+	+	-	+	nd	+	+	-	+	nd	w	-	nd
1 per cent KNO_3 (w/v)	-	-	+	-	-	-	+	nd	-	nd	-	-	-	nd	nd	-	+	nd
Production of acetic acid from ethanol	+	+	+	+	-	+	+	w/-	+	vw	+	+	w	+	+	-	w	-

(*Contd.*)

Table 1: (*Contd.*)

Characteristic	*Acetobacter*	*Gluconobacter*	*Acidomonas*	*Gluconacetobacter*	*Asaia*	*Kozakia*	*Swaminathania*	*Saccharibacter*	*Neoasaia*	*Granulibacter*	*Tanticharoenia*	*Ameyamaea*	*Neokomagataea*	*Komagataeibacter*	*Endobacter*	*Nguyenibacter*	*Swingsia*	*Bombella*
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Water-soluble brown pigment production	-	-[b]	-	+	-	-	+	-	-	nd	+	-	-	-	nd	+	+	-
Production of dihydroxyacetone from glycerol	+	+	-	+	w	+	+	-	w	-	+	w	-	+	+	-	+	nd
Production of levan-like polysaccharide	-	-	-	-	-	+	nd	-	-	nd	-	-	-	-	nd	+	-	nd
Assimilation of ammoniac nitrogen on																		
Glucose	-	+	w	+	+	-	nd	-	-	+	-	vw	-	nd	+	-	-	-
Mannitol	-	+	w	+	+	-	nd	-	w	nd	-	vw	-	+	nd	w	+	-
Ethanol	w	-	w	-	-	-	nd	-	-	nd	-	vw	-	nd	nd	-	-	-
Production of																		
2-Ketogluconate	+	+	-	+	+	+	nd	+	+	nd	+	+	+	+	nd	+	+	+
5-Ketogluconate	+	+	-	+	+	+	nd	+	+	nd	+	+	+	+	nd	-	+	-
2,5-Diketogluconate	-	-[b]	-	+	-	-	nd	-	-	nd	+	-	+	-	nd	+	+	nd
Acid production from																		
Mannitol	-	+	w	-	+	-	-	+	w	-	-	-	-	-	-	-	+	+
Sorbitol	-	+	-	-	+(d)	-	+	-	+(d)	-	-	-	-	-	-	-	-	-

(*Contd.*)

Dulcitol	-	w	-	-	+(d)	-	v	-	w	-	-	-	-	nd	-	-	-	nd
Glycerol	-	+	+	-	+	+	+	-	+	w	+	w	-	nd	+	-	-	-
Raffinose	-	-	-	-	+	+	nd	-	+	nd	w	-	-	nd	nd	w	w	-
Ethanol	+	+	+	+	-	+	+	-	+	+	+	+	-	+	+	-	-	-
Major isoprenoid quinone	UQ-9	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10	UQ-10
DNA G+C (mol per cent)	57.2	60.3	62	64.9	60.2	57.2	57.6-59.9[d]	52.3	63.1	59.1	65.6	66.0	56.8	62.5	60.3	66.8[f]	46.9	54.9

Abbreviations: pol, polar; per, peritrichous; spol, subpolar; n, none; +, positive; -, negative; w, weakly positive; vw, very weakly positive; d, delayed; v, variable; nd, not determined;

1, *Acetobacter aceti* NBRC 14818^T; 2, *Gluconobacter oxydans* NBRC 14819^T; 3, *Acidomonas methanolica* NRIC 0498^T; 4, *Gluconacetobacter liquefaciens* NBRC 12388^T; 5, *Asaia bogorensis* NBRC 16594^T; 6, *Kozakia baliensis* NBRC 16664^T; 7, *Swaminathania salitolerans* PA51^T; 8, *Saccharibacter floricola* S-877^T; 9, *Neoasaia chiangmaiensis* AC28^T; 10, *Granulibacter bethesdensis* CGDNIH1^T; 11, *Tanticharoenia sakaeratensis* AC37^T; 12, *Ameyamaea chiangmaiensis* AC04^T; 13, *Neokomagataea thailandica* AH11^T; 14, *Komagataeibacter xylinus* JCM 7644^T; 15, *Endobacter medicaginis* M1MS02^T; 16, *Nguyenibacter vanlangensis* TN01LGI^T; 17, *Swingsia samuiensis* AH83^T; 18, *Bombella intestini* LMG 28161^T.

[a]Some strains in the genus are non-motile. [b]Some strains in the genus are positive. [c]Some strains of the genus are polarly flagellated. [d]The DNA G+C content of the type strain was not recorded. [e]According to Jojima et al. (2004), growth was shown on 7 per cent glutamate but not on 1 per cent glutamate. [f]Data from N. Tanaka, NODAI, Japan.

glutamate agar. Dihydroxyacetone is not usually produced from glycerol, but produced by a few species. Gluconate is produced from glucose by all the species, 2-ketogluconate is produced by a considerable number of species, and 5-ketogluconate is by a few species. 2,5-Diketogluconate is not generally produced. Acid production depends on the kind of sugars, sugar alcohols, and alcohols as well as on the kinds of species and strains. In the type strain of *Acetobacter aceti*, acid is produced from L-arabinose, xylose, glucose, galactose, mannose, or ethanol. Ammoniac nitrogen is in general hardly utilized.

The optimal growth temperature is around 30 °C. Most of the species are able to grow at 37 °C, but not at 45 °C. Grows at pH 3.5. Most of the species are not able to grow on 30 per cent glucose (w/v). The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is UQ-9. The DNA G+C content ranges from 53.5 to 60.7 mol per cent. For more details of characteristics, see Komagata et al. (2014).

The type species of the genus is *Acetobacter aceti* (Pasteur 1864) Beijerinck 1898. Twenty-six species are reported.

1.1. *Acetobacter aceti* (Pasteur 1864) Beijerinck 1898

For the characteristics of the species, refer to Gosselé et al. (1983b), Sievers and Swings (2005), Kersters et al. (2006), Komagata et al. (2014).

The type strain is ATCC 15973^T (= DSM 3508^T = JCM 7641^T = LMG 1261^T = LMG 1504^T = NBRC 14818^T = NCIMB 8621^T), isolated from beechwood shavings of a vinegar plant. The DNA G+C content of the type strain is 57.2 mol per cent.

1.2. *Acetobacter pasteurianus* (Hansen 1879) Beijerinck and Folpmers 1916

For the characteristics of the species, refer to Beijerinck and Folpmers (1916), Sievers and Swings (2005), Kersters et al. (2006), Komagata et al. (2014).

The type strain is LMG 1262^T (= ATCC 33445^T = DSM 3509^T = JCM 7640^T = LMD 22.1^T = LMG 1262^T), isolated from beer, Netherlands. The DNA G+C content of the type strain is 52.7 mol per cent.

1.3. *Acetobacter peroxydans* Visser't Hooft 1925

For the characteristics of the species, refer to Visser't Hooft (1925), Komagata et al. (2014).

The type strain is NBRC 13755^T (= ATCC 12874^T = JCM 25077^T = LMG 1635^T), isolated from ditch water, Delft, Netherlands. The DNA G+C content of the type strain is 60.3 mol per cent.

1.4. *Acetobacter pomorum* Sokollek, Hertel and Hammes 1998

For the characteristics of the species, refer to Sokollek et al. (1998).

The type strain is LTH 2458^T (= CIP 105762^T = DSM 11825^T = LMG 18848^T), isolated from a submerged cider vinegar fermentation at a factory in the southern part of Germany. The DNA G+C content of the type strain is 50.5 mol per cent.

1.5. *Acetobacter estunensis* (Carr 1958) Lisdiyanti, Kawasaki, Seki, Yamada, Uchimura and Komagata 2001

Basonym: *Acetobacter pasteurianus* subsp. *estunensis* (Carr 1958) De Ley and Frateur 1974.

For the characteristics of the species, refer to Lisdiyanti et al. (2000).

The type strain is NBRC 13751^T (= ATCC 23753^T = DSM 4493^T = JCM 21172^T = LMG 1626^T = NCIMB 8935^T), isolated from cider, Bristol. The DNA G+C content of the type strain is 59.7 mol per cent.

1.6. *Acetobacter lovaniensis* (Frateur 1950) Lisdiyanti, Kawasaki, Seki, Yamada, Uchimura and Komagata 2001

Basonym: *Acetobacter pasteurianus* subsp. *lovaniensis* (Frateur 1950) De Ley and Frateur 1974.

For the characteristics of the species, refer to Lisdiyanti et al. (2000).

The type strain is NBRC 13753^T (= ATCC 12875^T= DSM 4491^T = JCM 17121^T = LMG 1579^T = LMG 1617^T = NCIMB 8620^T), isolated from sewage on soil by J. Frateur in 1929. The DNA G+C content of the type strain is 58.6 mol per cent.

1.7. *Acetobacter orleanensis* (Henneberg 1906) Lisdiyanti, Kawasaki, Seki, Yamada, Uchimura and Komagata 2001

Basonym: *Acetobacter aceti* subsp. *orleanensis* (Henneberg 1906) De Ley and Frateur 1974.

For the characteristics of the species, refer to Lisdiyanti et al. (2000).

The type strain is NBRC 13752^T (= ATCC 12876^T = DSM 4492^T = JCM 7639^T = LMG 1583^T = NCIMB 8622^T), isolated from beer by J. Frateur in 1929. The DNA G+C content of the type strain is 58.6 mol per cent.

1.8. *Acetobacter indonesiensis* Lisdiyanti, Kawasaki, Seki, Yamada, Uchimura and Komagata 2001

For the characteristics of the species, refer to Lisdiyanti et al. (2000).

The type strain is 5H-1^T (= JCM 10948^T = LMG 19824^T = NBRC 16471^T = NRIC 0313^T), isolated from the fruit of zirzak (*Annona muricata*) in Indonesia. The DNA G+C content of the type strain is 53.7 mol per cent.

1.9. *Acetobacter tropicalis* Lisdiyanti, Kawasaki, Seki, Yamada, Uchimura and Komagata 2001

For the characteristics of the species, refer to Lisdiyanti et al. (2000).

The type strain is Ni-6b^T (= JCM 10947^T = LMG 19825^T = NBRC 16470^T = NRIC 0312^T), isolated from coconut (*Coccos nucifera*) in Indonesia. The DNA G+C content of the type strain is 55.9 mol per cent.

1.10. *Acetobacter cerevisiae* Cleenwerck, Vandemeulebroecke, Janssens and Swings 2002

For the characteristics of the species, refer to Cleenwerck et al. (2002).

The type strain is LMG 1625^T (= ATCC 23765^T = DSM 14362^T = JCM 17273^T = NCIMB 8894^T), isolated from beer (ale) in storage at Toronto, Canada. The DNA G+C content of the type strain is 57.6 mol per cent.

1.11. *Acetobacter malorum* Cleenwerck, Vandemeulebroecke, Janssens and Swings 2002

For the characteristics of the species, refer to Cleenwerck et al. (2002).

The type strain is LMG 1746^T (= DSM 14337^T = JCM 17274^T), isolated from a rotten apple in Ghent, Belgium. The DNA G+C content of the type strain is 57.2 mol per cent.

1.12. *Acetobacter cibinongensis* Lisdiyanti, Kawasaki, Seki, Yamada, Uchimura and Komagata 2002

For the characteristics of the species, refer to Lisdiyanti et al. (2001).

The type strain is 4H-1^T (= CIP 107380^T = DSM 15549^T = JCM 11196^T = NBRC 16605^T), isolated from mountain soursop (*Annona montana*) in Indonesia. The DNA G+C content of the type strain is 54.5 mol per cent.

1.13. *Acetobacter orientalis* Lisdiyanti, Kawasaki, Seki, Yamada, Uchimura and Komagata 2002

For the characteristics of the species, refer to Lisdiyanti et al. (2001).

The type strain is 21F-2^T (= CIP 107379^T = DSM 15550^T = JCM 11195^T = NBRC 16606^T = NRIC 0481^T), isolated from canna flower (*Canna hybrida*) in Indonesia. The DNA G+C content of the type strain is 52.3 mol per cent.

1.14. *Acetobacter syzygii* Lisdiyanti, Kawasaki, Seki, Yamada, Uchimura and Komagata 2002

For the characteristics of the species, refer to Lisdiyanti et al. (2001).

The type strain is 9H-2^T (= CIP 107378^T = DSM 15548^T = JCM 11197^T = NBRC 16604^T = NRIC 0483^T), isolated from fruit of Malay rose apple (*Syzygium malaccense*) in Indonesia. The DNA G+C content of the type strain is 55.3 mol per cent.

1.15. *Acetobacter nitrogenifigens* Dutta and Gachhui 2006

For the characteristics of the species, refer to Dutta and Gachhui (2006).

The type strain is RG1^T (= LMG 23498^T = MTCC 6912^T), isolated from Kombucha tea. The DNA G+C content of the type strain is 64.1 mol per cent.

1.16. *Acetobacter oeni* Silva, Cleenwerck, Rivas, Swings, Trujillo, Willems and Velázquez 2006

For the characteristics of the species, refer to Silva et al. (2006).

The type strain is B13^T (= CECT 5830^T = LMG 21952^T), isolated from spoiled red wine of the Dão region, Portugal. The DNA G+C content of the type strain is 58.1 mol per cent.

1.17. *Acetobacter ghanensis* Cleenwerck, Camu, Engelbeen, De Winter, Vandemeulebroecke, De Vos and De Vuyst 2007

For the characteristics of the species, refer to Cleenwerck et al. (2007).

The type strain is R-29337^T (= 430A^T = DSM 18895^T = LMG 23848^T), isolated from a traditional heap fermentation of Ghanaian cocoa beans. The DNA G+C content of the type strain is 57.3.mol per cent.

1.18. *Acetobacter senegalensis* Ndoye, Cleenwerck, Engelbeen, Dubois-Dauphin, Guiro, Van Trappen, Willems and Thonart 2007

For the characteristics of the species, refer to Ndoye et al. (2007).

The type strain is CWBI-B418^T (= DSM 18889^T = LMG 23690^T), isolated from mango fruit in Senegal (sub-Saharan Africa). The DNA G+C content of the type strain is 56.0 mol per cent.

1.19. *Acetobacter fabarum* Cleenwerck, González, Camu, Engelbeen, De Vos and De Vuyst 2008

For the characteristics of the species, refer to Cleenwerck et al. (2008).

The type strain is 985^T (= R-36330^T = DSM 19596^T = LMG 24244^T), isolated from Ghanaian cocoa heap fermentation. The DNA G+C content of the type strain is 57.6 mol per cent.

1.20. *Acetobacter farinalis* Tanasupawat, Kommanee, Yukphan, Muramatsu, Nakagawa and Yamada 2011

For the characteristics of the species, refer to Tanasupawat et al. (2011a).

The type strain is G360-1^T (= BCC 44845^T = NBRC 107750^T = PCU 319^T), isolated from fermented rice flour. The DNA G+C content of the type strain is 56.3 mol per cent.

1.21. *Acetobacter papayae* Iino, Suzuki, Kosako, Ohkuma, Komagata and Uchimura 2013

For the characteristics of the species, refer to Iino et al. (2012a).

The type strain is 1-25^T (= JCM 25143^T = LMG 26456^T = NRIC 0655^T), isolated from a papaya fruit, Okinawa, Japan. The DNA G+C content of the type strain is 60.5 mol per cent.

1.22. *Acetobacter okinawensis* Iino, Suzuki, Kosako, Ohkuma, Komagata and Uchimura 2013

For the characteristics of the species, refer to Iino et al. (2012a).

The type strain is 1-35^T (= JCM 25146^T = LMG 26457^T = NRIC 0658^T), isolated from a piece of the stem of sugarcane, Okinawa, Japan. The DNA G+C content of the type strain is 59.3 mol per cent.

1.23. *Acetobacter persici* corrig. Iino, Suzuki, Kosako, Ohkuma, Komagata and Uchimura 2013

For the characteristics of the species, refer to Iino et al. (2012a).

The type strain is T-120^T (= JCM 25330^T = LMG 26458^T), isolated from a peach fruit, Okinawa, Japan. The DNA G+C content of the type strain is 58.7 mol per cent.

1.24. *Acetobacter lambici* Spitaels, Li, Wieme, Balzarini, Cleenwerck, Van Landschoot, De Vuyst and Vandamme 2014

For the characteristics of the species, refer to Spitaels et al. (2014a).

The type strain is LMG 27439^T (= DSM 27328^T), isolated from fermenting lambic beer. The DNA G+C content of the type strain is 56.2 mol per cent

1.25. *Acetobacter sicerae* Li, Wieme, Spitaels, Balzarini, Nunes, Manaia, Van Landschoot, De Vuyst, Cleenwerck and Vandamme 2014

For the characteristics of the species, refer to Li et al. (2014).

The type strain is LMG 1531^T (= NCIMB 8941^T), isolated from traditionally produced kefir. The DNA G+C content of the type strain is 58.3 mol per cent.

1.26. *Acetobacter thailandicus* Pitiwittayakul, Yukphan, Chaipitakchonlatarn, Yamada and Theeragool 2016

For the characteristics of the species, refer to Pitiwittayakul et al. (2015).

The type strain is AD25^T (= BCC 15839^T = NBRC 103583^T), isolated from a flower of the blue trumpet vine. The DNA G+C content of the type strain is 51.4 mol per cent.

2. *Gluconobacter* Asai 1935

Glu.co.no.bac'ter. N. L. neut. n. *acidum gluconicum*, gluconic acid; N. L. masc. n. *bacter*, rod; N. L. masc. n. *Gluconobacter*, gluconate rod.

The genus *Gluconobacter* was proposed by Asai (1935), who selected a variety of fruits for isolation and found two taxonomic groups in the isolated strains on the oxidation of ethanol and glucose. One had intense ethanol oxidizability rather than glucose and oxidized acetic acid to carbon dioxide and water, and the other had intense glucose oxidizability rather than ethanol and did not oxidize acetic acid. For the latter group, the generic name *Gluconobacter* was given. In the Approved Lists of Bacterial Names 1980, the only species, *Gluconobacter oxydans* was listed with five subspecies (Skerman et al. 1980). However, the range of DNA G+C contents was 8.6 mol per cent from 54.2 to 62.8 mol per cent in the single species (Yamada et al. 1981b, 1984).

Cells are Gram-negative, ellipsoidal to rod-shaped, measuring 0.4 to 1.2 by 1.0 to 3.0 µm, and polarly flagellated when motile. Colonies are smooth, raised to convex, entire, and glistening on ethanol/glucose/yeast extract/calcium carbonate/agar. Some strains produce pink colonies.

Strictly aerobic. Catalase positive and oxidase negative. Acetic acid is produced from ethanol. Acetate and lactate are not oxidized. Grows on mannitol agar, but not on glutamate agar. Dihydroxyacetone is produced from glycerol. Gluconate, 2-ketogluconate, and 5-ketogluconate are produced from glucose, and a few strains produce 2,5-diketogluconate. A water-soluble brown pigment is produced in strains of a few species. Acid is produced from L-arabinose, xylose, glucose, galactose, mannose, fructose, melibiose, mannitol, sorbitol, glycerol, or ethanol. Grows on glucose, fructose, mannitol, sorbitol, and glycerol. Strains of several species require nicotinic acid for growth.

Optimum temperature for growth is between 25 °C and 30 °C. Many species grow at 35 °C, and a few species grow at 37 °C. Optimum pH for growth is around pH 5.5. Most of the species grow at pH 3.5. The major cellular fatty acid is $C_{18:1}\omega7c$. The major ubiquinone is UQ-10. The DNA G+C content ranges from 54.0 to 61.5 mol per cent. Strains of *Gluconobacter* are isolated from fruits, flowers and other sugar-rich materials. For more details of characteristics, see Komagata et al. (2014).

The type species of the genus is *Gluconobacter oxydans* (Henneberg 1897) De Ley 1961. Fourteen species are reported.

2.1. *Gluconobacter oxydans* (Henneberg 1897) De Ley 1961

For the characteristics of the species, refer to Gosselé et al. (1983a), Sievers and Swings (2005), Kersters et al. (2006), Komagata et al. (2014).

The type strain is ATCC 19357^T (= DSM 3503^T = DSM 7145^T = JCM 7642^T = LMG 1408^T = NBRC 14819^T = NCIMB 9013^T), isolated from beer by J. G. Carr. The DNA G+C content of the type strain is 60.3 mol per cent.

2.2. *Gluconobacter cerinus* (ex Asai 1935) Yamada and Akita 1984 emend. Katsura, Yamada, Uchimura and Komagata 2002

Synonym: *Gluconobacter asaii* Mason and Claus 1989.

For the characteristics of the species, refer to Yamada and Akita (1984), Yamada et al. (1984), Tanaka et al. (1999), Katsura et al. (2002).

The type strain is NBRC 3267^T (= ATCC 19441^T = DSM 9533^T = DSM 9534^T = LMG 1368^T = NRRL B-4241^T), isolated from cherry (*Prunus* sp.). The DNA G+C content of the type strain is 55.9 mol per cent.

2.3. *Gluconobacter frateurii* Mason and Claus 1989

For the characteristics of the species, refer to Mason and Claus (1989).

The type strain is Kondo 40^T (= NBRC 3264^T = ATCC 49207^T = DSM 7146^T = LMG 1365^T), isolated from strawberry (*Fragaria ananassa*). The DNA G+C content of the type strain is 55.1 mol per cent.

2.4. *Gluconobacter albidus* (ex Kondo and Ameyama 1958) Yukphan, Takahashi, Potacharoen, Tanasupawat, Nakagawa, Tanticharoen and Yamada 2005

For the characteristics of the species, refer to Yukphan et al. (2004a).

The type strain is NBRC 3250^T (= BCC 14434^T = JCM 20271^T), isolated from a flower of dahlia by Kondo and Ameyama (1958). The DNA G+C content of the type strain is 60.0 mol per cent.

2.5. *Gluconobacter thailandicus* Tanasupawat, Thawai, Yukphan, Moonmangmee, Itoh, Adachi and Yamada 2005

For the characteristics of the species, refer to Tanasupawat et al. (2004).

The type strain is F-149-1^T (= BCC 14116^T = JCM 12310^T = NBRC 100600^T = TISTR 1533^T),

isolated from a flower of Indian cork tree (*Millingtonia hortensis*) in Bangkok, Thailand. The DNA G+C content of the type strain is 55.8 mol per cent.

2.6. *Gluconobacter kondonii* Malimas, Yukphan, Takahashi, Kaneyasu, Potacharoen, Tanasupawat, Nakagawa, Tanticharoen and Yamada 2007

For the characteristics of the species, refer to Malimas et al. (2007).

The type strain is Kondo 75^T (= BCC 14441^T = NBRC 3266^T), isolated from strawberry. The DNA G+C content of the type strain is 59.8 mol per cent.

2.7. *Gluconobacter roseus* (ex Asai 1935) Malimas, Yukphan, Takahashi, Muramatsu, Kaneyasu, Potacharoen, Tanasupawat, Nakagawa, Tanticharoen and Yamada 2008

For the characteristics of the species, refer to Malimas et al. (2008a).

The type strain is Asai G-2^T (= BCC 14456^T = JCM 20293^T = NBRC 3990^T), isolated from a fruit of kaki (persimmon, *Diasporas kaki*). The DNA G+C content of the type strain is 60.5 mol per cent.

2.8. *Gluconobacter sphaericus* (Ameyama 1975) Malimas, Yukphan, Takahashi, Muramatsu, Kaneyasu, Potacharoen, Tanasupawat, Nakagawa, Tanticharoen and Yamada 2008

Basonym: *Gluconobacter oxydans* subsp. *sphaericus* Ameyama 1975.

For the characteristics of the species, refer to Ameyama (1975), Malimas et al. (2008b).

The type strain is NBRC 12467^T (= BCC 14448^T = LMG 1414^T), isolated from fresh grapes by Ameyama (1975). The DNA G+C content of the type strain is 59.5 mol per cent.

2.9. *Gluconobacter kanchanaburiensis* Malimas, Yukphan, Lundaa, Muramatsu, Takahashi, Kaneyasu, Potacharoen, Tanasupawat, Nakagawa, Suzuki, Tanticharoen and Yamada 2009

For the characteristics of the species, refer to Malimas et al. (2009a).

The type strain is AD92^T (= BCC 15889^T = NBRC 103587^T), isolated from a spoiled fruit of jackfruit (*Artocarpus heterophyllus*). The DNA G+C content of the type strain is 59.5 mol per cent.

2.10. *Gluconobacter japonicus* Malimas, Yukphan, Takahashi, Muramatsu, Kaneyasu, Potacharoen, Tanasupawat, Nakagawa, Tanticharoen and Yamada 2009

For the characteristics of the species, refer to Malimas et al. (2009b).

The type strain is Kondo 7^T (= BCC 14458^T = NBRC 3271^T), isolated from a fruit of Chinese bayberry. The DNA G+C content of the type strain is 56.4 mol per cent.

2.11. *Gluconobacter wancherniae* Yukphan, Malimas, Lundaa, Muramatsu, Takahashi, Kaneyasu, Tanasupawat, Nakagawa, Suzuki, Tanticharoen and Yamada 2011

For the characteristics of the species, refer to Yukphan et al. (2010).

The type strain is AC42^T (= BCC 15775^T = NBRC 103581^T), isolated from unknown seed. The DNA G+C content of the type strain is 56.6 mol per cent.

2.12. *Gluconobacter uchimurae* Tanasupawat, Kommanee, Yukphan, Moonmangmee, Muramatsu, Nakagawa and Yamada 2011

For the characteristics of the species, refer to Tanasupawat et al. (2011b).

The type strain is ZW160-2^T (= BCC 14681^T = NBRC 100627^T), isolated from rakam fruit (*Zalacca wallichiana*). The DNA G+C content of the type strain is 60.5 mol per cent.

2.13. *Gluconobacter nephelii* Kommanee, Tanasupawat, Yukphan, Malimas, Muramatsu, Nakagawa and Yamada 2011

For the characteristics of the species, refer to Kommanee et al. (2011).

The type strain is RBY-1^T (= BCC 36733^T = NBRC 106061^T), isolated from rambutan (*Nephelium lappaceum*). The DNA G+C content of the type strain is 57.2 mol per cent.

2.14. *Gluconobacter cerevisiae* Spitaels, Wieme, Balzarini, Cleenwerck, Van Landschoot, De Vuyst and Vandamme 2014

For the characteristics of the species, refer to Spitaels et al. (2014b).

The type strain is LMG 27748^T (= DSM 27644^T), isolated from fermenting lambic beer. The DNA G+C content of the type strain is 58.0 mol per cent.

3. *Acidomonas* Urakami, Tamaoka, Suzuki and Komagata 1989 emend. Yamashita, Uchimura and Komagata 2004

A.ci.do.mo'nas. L. adj. *acidus*, sour or acid; L. fem. n. *monas*, unit or monad; *Acidomonas*, acidophilic monad.

The genus *Acidomonas* was introduced for the facultatively methylotrophic bacterium, *Acetobacter methanolicus* Uhlig et al. 1986 (Urakami et al. 1989). However, the generic name was not accepted for a long time (Swings 1992, Sievers et al. 1994). The phylogenetic relationship between the genus *Acidomonas* and other genera of acetic acid bacteria was remote from each other and enough to establish the new genus (Bulygina et al. 1992, Yamada et al. 1997, Yamashita et al. 2004).

Cells are Gram-negative, short rods, measuring 0.5 to 0.8 by 1.5 to 2.0 µm. Cells occur singly, in pairs or rarely in short chains and are either motile with a single polar flagellum or non-motile. Colonies are shiny, smooth, circular, convex, entire, and beige to pink, and 1–3 mm in diameter on glucose/peptone/yeast extract/malt extract (PYM) agar (pH 4.5) after five days incubation at 30 °C. Pellicles are produced in PYM broth.

Aerobic. Catalase positive and oxidase negative. Acetic acid is produced from ethanol. Acetate is oxidized, but lactate is not or only weakly oxidized. Dihydroxyacetone is not produced from glycerol. Gluconate is produced from glucose. 2-Ketogluconate, 5-ketogluconate, or 2,5-diketogluconate is not produced in culture media. Acid is produced from L-arabinose, xylose, ribose, glucose, galactose, mannose, glycerol, ethanol or methanol. Methanol, ethanol, glucose, mannose, glycerol, or succinic acid is utilized as a sole source of carbon. Pantothenic acid is essentially required for growth.

Grows on 30 per cent glucose (w/v) and 0.35 per cent acetic acid (v/v). Grows at pH 3.0. Grows at 30 °C but not at 45 °C. The major cellular fatty acids are $C_{18:1}\omega7c$, $C_{16:0}$, and $C_{18:1}2OH$. The major quinone is UQ-10. The DNA G+C content is from 62 to 63 mol per cent. Strains of *Acidomonas* were abundantly isolated from activated sludges, except for the type strain, but not from vegetables, fruit, decayed wood and leaves, manure, and paddy soil. For more details of characteristics, see Komagata et al. (2014).

3.1. *Acidomonas methanolica* (Uhlig et al. 1986) Urakami, Tamaoka, Suzuki and Komagata 1989. emend. Yamashita, Uchimura and Komagata 2004

Basonym: *Acetobacter methanolicus* Uhlig, Karbaum and Steudel 1986.

For the characteristics of the species, refer to Uhlig et al. (1986), Urakami et al. (1989), Yamashita et al. (2004).

The type strain is MB 58^T (= DSM 5432^T = JCM 6891^T = LMG 1668^T = NRIC 0498^T), isolated from a non-sterile fermentation process for the production of single cell protein (SCP) from methanol with *Candida* species. The cells of the type strain are non motile, and the DNA G+C content is 62 mol per cent.

4. *Gluconacetobacter* corrig. Yamada, Hoshino and Ishikawa 1998

Glu.con.a.ce.to.bac'ter. N. L. neut. n. *acetum gluconicum*, gluconic acid; L. neut. n. *acetum*, vinegar; N. L. masc. n. *bacter*, rod; N. L. masc. n. *Gluconacetobacter*, gluconate-vinegar rod.

The genus *Gluconacetobacter* was introduced by the elevation of the subgenus *Gluconacetobacter* corrig. (ex Asai 1935) Yamada and Kondo 1984 for the UQ-10-equipped *Acetobacter* species (Yamada et al. 1997). Phylogenetically, the genus *Gluconacetobacter* consisted of two groups. One was the *Gluconacetobacter liquefaciens* group, and the other was the *Gluconacetobacter xylinus* group. For the latter group, the genus *Komagataeibacter* Yamada et al. 2013 was proposed (Yamada et al. 2012a, b).

Cells are Gram-negative rods, measuring 0.6 to 0.9 by 1.2 to 2.0 μm, with peritrichous flagella when motile and occur singly or in pairs. Colonies are generally light brown to brown.

Aerobic. Catalase positive. Oxidase negative. Acid is produced from ethanol. Oxidizes acetate and lactate. Grows on glutamate agar and mannitol agar. A few species produce dihydroxyacetone from glycerol. 2-Ketogluconate is produced from glucose. Most of the species produce 2,5-diketogluconate, and a few species produce 5-ketogluconate. Most of the species produce a water-soluble brown pigment. Acid is produced from L-arabinose, xylose, glucose, mannose, or ethanol. Grows on glucose, fructose, sucrose, mannitol, or ethanol. Ammoniac nitrogen is used as a sole nitrogen source. Strains of the most species have the activity of nitrogen fixation.

Most of the species grow on 30 per cent glucose (w/v). Grows between 15 °C and 30 °C but not at 37 °C. The optimum growth temperature is around 30 °C. Grows at pH 3.0. The optimum growth pH is about 5.5. The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is UQ-10. The DNA G+C content ranges from 58 to 65 mol per cent. For more details of characteristics, see Komagata et al. (2014).

The type species of the genus is *Gluconacetobacter liquefaciens* (Asai 1935) Yamada et al. 1998. Ten species are reported.

4.1. *Gluconacetobacter liquefaciens* (Asai 1935) Yamada, Hoshino and Ishikawa 1998

Basonym: *Acetobacter aceti* subsp. *liquefaciens* (Asai 1935) De Ley and Frateur 1974.

Synonyms: *Acetobacter liquefaciens* (Asai 1935) Gosselé, Swings, Kersters, Pauwels and De Ley 1983; '*Gluconobacter liquefaciens*' Asai 1935.

For the characteristics of the species, refer to Asai et al. (1964), Yamada and Kondo (1984), Yamada et al. (1997), Navarro and Komagata (1999), Sievers and Swings (2005), Kersters et al. (2006), Komagata et al. (2014).

The type strain is Asai G-1^T (= ATCC 14835^T = DSM 5603^T = JCM 17840^T = LMG 1381^T = LMG 1382^T = NBRC 12388^T), isolated from dried persimmon. The DNA G+C content of the type strain is 64.9 mol per cent.

4.2. *Gluconacetobacter diazotrophicus* (Gillis et al. 1989) Yamada, Hoshino and Ishikawa 1998

Basonym: *Acetobacter diazotrophicus* Gillis, Kersters, Hoste, Janssens, Kroppenstadt, Stephan, Teixeira, Döbereiner and De Ley 1989.

For the characteristics of the species, refer to Gillis et al. (1989).

The type strain is LMG 7603^T (= ATCC 49037^T = CCUG 37298^T = CIP 103539^T = DSM 5601^T), isolated from roots and stems of sugarcane in Alagoas, Brazil. The DNA G+C content of the type strain is 61 mol per cent.

4.3. *Gluconacetobacter sacchari* Franke, Fegan, Hayward, Leonard, Stackebrandt and Sly 1999

For the characteristics of the species, refer to Franke et al. (1999).

The type strain is SRI 1794^T (= CIP 106693^T = DSM 12717^T), isolated from the leaf sheath of sugar cane and from the pink sugar-cane mealy bug. The DNA G+C content of the type strain is 65 mol per cent.

4.4. *Gluconacetobacter johannae* Fuentes-Ramírez, Bustillos-Cristales, Tapia-Hernández, Jiménez-Salgado, Wang, Martínez-Romero and Caballero-Mellado 2001

For the characteristics of the species, refer to Fuentes-Ramírez et al. (2001).

The type strain is CFN-Cf55^T (= ATCC 700987^T = CIP 107160^T = DSM 13595^T), isolated from the rhizosphere of coffee plants. The DNA G+C content of the type strain is 57.96 mol per cent.

4.5. *Gluconacetobacter azotocaptans* Fuentes-Ramírez, Bustillos-Cristales, Tapia-Hernández, Jiménez-Salgado, Wang, Martínez-Romero and Caballero-Mellado 2001

For the characteristics of the species, refer to Fuentes-Ramírez et al. (2001).

The type strain is CFN-Ca54^T (= ATCC 700988^T = CIP 107161^T = DSM 13594^T), isolated from the rhizosphere of coffee plants. The DNA G+C content of the type strain is 64.01 mol per cent.

4.6. *Gluconacetobacter tumulicola* Tazato, Nishijima, Handa, Kigawa, Sano and Sugiyama 2012

For the characteristics of the species, refer to Tazato et al. (2012).

The type strain is K5929-2-1b^T (= JCM 17774^T = NCIMB 14760^T), isolated from a black viscous substance in a plaster hole at the center of the ceiling in the stone chamber of the Kitora Tumulus in Asuka village, Nara Prefecture, Japan. The DNA G+C content of the type strain is 64.7 mol per cent.

4.7. *Gluconacetobacter asukensis* Tazato, Nishijima, Handa, Kigawa, Sano and Sugiyama 2012

For the characteristics of the species, refer to Tazato et al. (2012).

The type strain is K8617-1-1b^T (= JCM 17772^T = NCIMB 14759^T), isolated from a brown viscous gel on the north-east area of the ceiling in the stone chamber of the Kitora Tumuli in Asuka village, Nara Prefecture, Japan. The DNA G+C content of the type strain is 65.4 mol per cent.

4.8. *Gluconacetobacter tumulisoli* Nishijima, Tazato, Handa, Tomita, Kigawa, Sano and Sugiyama 2013

For the characteristics of the species, refer to Nishijima et al. (2013).

The type strain is T611xx-1-4a^T (= JCM 19097^T = NCIMB 14861^T), isolated from clay soil taken from near the spider's web and an ant hole at a plugging stone directly under the plugging stone of the upper north side at the space adjacent to Takamatsuzuka Tumulus in Asuka village, Nara Prefecture, Japan. The DNA G+C content of the type strain is 66.5 mol per cent.

4.9. *Gluconacetobacter takamatsuzukensis* Nishijima, Tazato, Handa, Tomita, Kigawa, Sano and Sugiyama 2013

For the characteristics of the species, refer to Nishijima et al. (2013).

The type strain is T61213-20-1a^T (= JCM 19094^T = NCIMB 14859^T), isolated from soil taken from the left side wall of the west side in the stone chamber exterior during dismantling work of Takamatsuzuka Tumulus in Asuka village, Nara Prefecture, Japan. The DNA G+C content of the type strain is 66.6 mol per cent.

4.10. *Gluconacetobacter aggeris* Nishijima, Tazato, Handa, Tomita, Kigawa, Sano and Sugiyama 2013

For the characteristics of the species, refer to Nishijima et al. (2013).

The type strain is T6203-4-1a^T (= JCM 19092^T = NCIMB 14860^T), isolated from soil taken from 5 cm below the surface in a bamboo grove of the burial mound of Takamatsuzuka Tumulus in Asuka village, Nara Prefecture, Japan. The DNA G+C content of the type strain is 65.4 mol per cent.

5. *Asaia* Yamada, Katsura, Kawasaki, Widyastuti, Saono, Seki, Uchimura and Komagata 2000

A.sa'i.a. N. L. fem. n. *Asaia*, Asai, named after Professor Toshinobu Asai, a Japanese bacteriologist who contributed to the systematics of acetic acid bacteria.

The strains of the genus *Asaia* were first found and isolated from flowers collected in Indonesia. In the beginning, the distribution of the *Asaia* strains was supposed to be restricted only to the tropical zone, viz., in Thailand, the Philippines, and Indonesia (Yamada and Yukphan 2008). However, the *Asaia* strains were isolated in the temperate zone, viz., in Japan (Suzuki et al. 2010). The strains of the genus *Asaia* produced no or a very little amount of acetic acid from ethanol and did not grow in the presence of 0.35 per cent acetic acid (w/v).

Cells are Gram-negative, rod-shaped, measuring 0.4 to 1.0 by 1.0 to 2.5 µm, and motile with peritrichous flagella. Colonies are smooth, entire, raised, shiny, and light brown or pink to dark pinkish on glucose/peptone/yeast extract agar.

Aerobic. Catalase positive and oxidase negative. Produces no or a limited amount of acetic acid from ethanol. Oxidizes acetate and lactate to carbon dioxide and water. Grows on glutamate agar and mannitol agar. Dihydroxyacetone is generally produced. Produces 2-ketogluconate and 5-ketogluconate from glucose, but not 2,5-diketogluconate. Acid is produced from glucose, galactose, fructose, or other sugars and sugar alcohols. Grows on glucose, fructose, or mannitol. Ammoniac nitrogen is assimilated on glucose or mannitol.

Grows on 30 per cent glucose (w/v), but not in the presence of 0.35 per cent acetic acid (v/v). Growth generally occurs between 10 and 30 °C, but not at 37 °C. Grows at pH 3.0. The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is UQ-10. The DNA G+C content ranges from 58.6 to 61.0 mol per cent. For more details of characteristics, see Komagata et al. (2014).

The type species of the genus is *Asaia bogorensis* Yamada et al. 2000. Eight species are reported.

5.1. *Asaia bogorensis* Yamada, Katsura, Kawasaki, Widyastuti, Saono, Seki, Uchimura and Komagata 2000

For the characteristics of the species, refer to Yamada et al. (2000).

The type strain is 71^T (= JCM 19569^T = NRIC 0311^T), isolated from a flower of orchid tree (*Bauhinia purpurea*) in Bogor, Indonesia. The DNA G+C content of the type strain is 60.2 mol per cent.

5.2. *Asaia siamensis* Katsura, Kawasaki, Potacharoen, Saono, Seki, Yamada, Uchimura and Komagata 2001

For the characteristics of the species, refer to Katsura et al. (2001).

The type strain is S60-1^T (= JCM 10715^T = NBRC 16457^T = NRIC 0323^T), isolated from a flower of crown flower (*Calotropis gigantea*), in Bangkok, Thailand. The DNA G+C content of the type strain is 59.3 mol per cent.

5.3. *Asaia krungthepensis* Yukphan, Potacharoen, Tanasupawat, Tanticharoen and Yamada 2004

For the characteristics of the species, refer to Yukphan et al. (2004b).

The type strain is AA08^T (= BCC 12978^T = NBRC 100057^T = NRIC 0535^T = TISTR 1524^T), isolated from a heliconia flower (*Heliconia* sp.) in Bangkok, Thailand. The DNA G+C content of the type strain is 60.3 mol per cent.

5.4. *Asaia lannensis* corrig. Malimas, Yukphan, Takahashi, Kaneyasu, Potacharoen, Tanasupawat, Nakagawa, Tanticharoen and Yamada 2008

For the characteristics of the species, refer to Malimas et al. (2008c).

The type strain is AB92^T (= BCC 15733^T = NBRC 102526^T), isolated from a flower of spider lily (*Crynum asiaticum*) in Chiang Mai, Thailand. The DNA G+C content of the type strain is 60.8 mol per cent.

5.5. *Asaia spathodeae* Kommanee, Tanasupawat, Yukphan, Malimas, Muramatsu, Nakagawa and Yamada 2010

For the characteristics of the species, refer to Kommanee et al. (2010).

The type strain is GB23-2^T (= BCC 36458^T = NBRC 105894^T = PCU 307^T), isolated from a flower of the African tulip (*Spathodea campanulata*) in Thailand. The DNA G+C content of the type strain is 59.7 mol per cent.

5.6. *Asaia astilbis* corrig. Suzuki, Zhang, Iino, Kosako, Komagata and Uchimura 2010

For the characteristics of the species, refer to Suzuki et al. (2010).

The type strain is T-6133^T (= DSM 23030^T = JCM 15831^T), isolated from astilbe (*Astilbe thunbergii* var. *congesta*), Yamanashi Prefecture, Japan. The DNA G+C content of the type strain is 58.9 mol per cent.

5.7. *Asaia platycodi* Suzuki, Zhang, Iino, Kosako, Komagata and Uchimura 2010

For the characteristics of the species, refer to Suzuki et al. (2010).

The type strain is T-683^T (= JCM 25414^T = DSM 23029^T), isolated from balloon flower (*Platycodon grandiflorum*) in Akita Prefecture, Japan. The DNA G+C content of the type strain is 60.0 mol per cent.

5.8. *Asaia prunellae* Suzuki, Zhang, Iino, Kosako, Komagata and Uchimura 2010

For the characteristics of the species, refer to Suzuki et al. (2010).

The type strain is T-153^T (= DSM 23028^T = JCM 25354^T), isolated from self-heal (*Prunella vulgaris*) in Akita Prefecture, Japan. The DNA G+C content of the type strain is 58.9 mol per cent.

6. *Kozakia* Lisdiyanti, Kawasaki, Widyastuti, Saono, Seki, Yamada, Uchimura and Komagata 2002

Ko.za'ki.a. N. L. fem. n. *Kozakia*, Kozaki, named after Professor Michio Kozaki, a Japanese bacteriologist who contributed to the study of microorganisms in tropical regions, especially Southeast Asia.

The genus *Kozakia* was phylogenetically related to the genera *Asaia* and *Neoasaia*. However, the genus especially differed from the genus *Asaia* in oxidation of ethanol to acetic acid and in the production of a large amount of levan-like mucous substances from sucrose.

Cells are Gram-negative, rod-shaped, and non-motile, measuring 0.6 to 0.8 by 2.0 to 3.0 μm. Colonies are not pigmented.

Strictly aerobic. Catalase positive and oxidase negative. Acetic acid is produced from ethanol. Acetate and lactate are oxidized to carbon dioxide and water, but the activity is weak. Grows on mannitol agar but not on glutamate agar. Dihydroxyacetone is produced from glycerol. Gluconate, 2-ketogluconate, and 5-ketogluconate are produced from glucose, but 2,5-diketogluconate is not. A water-soluble brown pigment is not produced from glucose. Acid is produced from L-arabinose, xylose, glucose, galactose, mannose, melibiose, raffinose, *meso*-erythritol, glycerol, or ethanol. Methanol is not utilized. Ammoniac nitrogen is not assimilated on glucose, mannitol, or ethanol medium without vitamins. Levan-like mucous substance is produced from sucrose or fructose. γ-Pyrone is produced from fructose but not from glucose.

Growth is not inhibited by 0.35 per cent acetic acid (v/v) at pH 3.5. Does not grow on 30 per cent glucose (w/v). Grows at pH 3.0 and 30 °C. The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is UQ-10. The DNA G+C content ranges from 56.8 to 57.2 mol per cent. For more details of characteristics, see Komagata et al. (2014).

6.1. *Kozakia baliensis* Lisdiyanti, Kawasaki, Widyastuti, Saono, Seki, Yamada, Uchimura and Komagata 2002

For the characteristics of the species, refer to Lisdiyanti et al. (2002).

The type strain is Yo-3^T (= DSM 14400^T = JCM 11301^T = NBRC 16664^T = NRIC 0488^T), isolated from palm brown sugar collected in Bali, Indonesia in 1996. The DNA G+C content of the type strain is 57.2 mol per cent.

7. *Swaminathania* Loganathan and Nair 2004

Swa.mi.na.tha'ni.a. N. L. fem. n. *Swaminathania*, Swaminathan, named after Swaminathan, an Indian biologist, the father of the Green Revolution in India.

The strains of the genus *Swaminathania*, which were isolated using a nitrogen-free semi-solid LGI medium at pH 5.5 from the rhizosphere, roots, and stems of salt-tolerant, mangrove-associated wild rice, was phylogenetically related especially to those of the genus *Asaia*. However, the genus was distinguished phenotypically from the genus *Asaia* by growth in the presence of 0.35 per cent acetic acid (v/v), 3 per cent NaCl (w/v), or 1 per cent KNO_3 (w/v).

Cells are Gram-negative, straight rods with round ends, measuring approximately 0.7 to 0.9 by 1.9 to 3.1 μm, and motile with peritrichous flagella. Colonies are initially yellowish and become dark orange later, smooth, and raised, with entire margin on LGI medium.

Aerobic. Catalase-positive and oxidase negative. Acetic acid is produced from ethanol under neutral and acidic conditions. Acetate and lactate are oxidized to carbon dioxide and water, but the activity was weak. Grows on mannitol agar and glutamate agar. Acid is produced from L-arabinose, glucose, galactose, mannose, sorbitol, glycerol, or ethanol. Methanol is not utilized. A water-soluble brown pigment is produced on glucose/calcium carbonate-containing agar. Strains are able to fix nitrogen. Solubilization of phosphate is shown. Grows intensely in the presence of 0.35 per cent acetic acid (v/v) at pH 3.5 and 3 per cent NaCl using 1 per cent KNO_3 (w/v) as a nitrogen source.

The major cellular fatty acid is $C_{18:1}\omega7c/\omega9t/\omega12t$. The major quinone is UQ-10. The DNA G+C content ranges from 57.6 to 59.9 mol per cent. For more details of characteristics, see Komagata et al. (2014).

7.1. *Swaminathania salitolerans* Loganathan and Nair 2004

For the characteristics of the species, refer to Loganathan and Nair (2004).

The type strain is PA51^T (= LMG 21291^T = MTCC 3852^T), isolated from mangrove-associated wild rice (*Porteresia coarctata*) in Pichavaram, Tamil Nadu, India. The DNA G+C content of the type strain is not reported.