Kazunobu Matsushita · Hirohide Toyama
Naoto Tonouchi · Akiko Okamoto-Kainuma *Editors*

Acetic Acid Bacteria

Ecology and Physiology

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Preface

Research for acetic acid bacteria (AAB) has a long history since the discovery of AAB by Louis Pasteur and its identification by Martinus Beijerinck in the nineteenth century. In the twentieth century, basic research on the taxonomic study of AAB and on biochemical study for the unique oxidative reactions of AAB progressed as did the industrial applications of AAB not only in vinegar fermentation but also in the bioconversion process for useful chemical or pharmaceutical products. Entering the twenty-first century, AAB research has continued to expand and is expected to show further progress in all aspects of AAB: classification and ecology, physiology and biochemistry, genetics, and biotechnology of vinegar fermentation and other oxidative fermentations. The research on AAB has developed significantly in the last decade, which makes these bacteria more valuable for various industrial uses. Readers can obtain useful, comprehensive information which is exciting with regard to basic science and provides suggestions for better application of these bacteria to a variety of practical production processes as well.

In order to view the future targets or directions of AAB research, we would like to summarize the distinctive physiological properties of AAB and the recent progress on AAB study, especially in the following areas.

(1) Molecular phylogeny and genome study of AAB; (2) Ecological features of AAB: interaction with plants, natural fermentation systems, and insects; (3) Physiological features and living strategies of AAB: rapid oxidation ability, acid resistance, biofilm formation, and genetic instability, and others; (4) Molecular mechanisms of several oxidative fermentations: acetate fermentation, sorbose fermentation, ketogluconate fermentation, and others; (5) Recent biotechnological aspects of AAB: biocatalysts, biosensors, biofuel cells, biocellulose, other useful polysaccharides, and so on.

Yamaguchi, Japan — Kazunobu Matsushita

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Chapter 1
Systematics of Acetic Acid Bacteria

Yuzo Yamada

Abstract Acetic acid bacteria are currently accommodated in the acetous group, the family *Acetobacteraceae*, the class *Alphaproteobacteria*, based on phylogeny, physiology, and ecology. The acetic acid bacteria are classified at present in 17 genera, of which many species have been reported in the genera *Acetobacter*, *Gluconobacter*, *Gluconacetobacter*, *Asaia*, and *Komagataeibacter*. Of the remaining 12 genera, *Acidomonas*, *Kozakia*, *Swaminathania*, *Saccharibacter*, *Neoasaia*, *Granulibacter*, *Tanticharoenia*, *Ameyamaea*, *Endobacter*, *Nguyenibacter*, and *Swingsia* are monotypic; the genus *Neokomagataea* contains two species. In the class *Gammaproteobacteria*, the genus *Frateuria* has been mentioned taxonomically as pseudacetic acid bacteria. In addition, isolation and identification of acetic acid bacteria are described.

Keywords Acetic acid bacteria • *Acetobacteraceae* • *Alphaproteobacteria* • The acetous group • *Acetobacter* • *Acetobacter aceti* • *Gluconobacter* • *Gluconobacter oxydans* • Pseudacetic acid bacteria • *Gammaproteobacteria* • *Frateuria*

1.1 Introduction

The generic name *Acetobacter*, the oldest name for acetic acid bacteria, was introduced by Beijerinck (1898). However, there is no record of the formal proposal of the generic name as a genus (Komagata et al. 2014; Buchanan et al. 1966; Kluyver 1983). Skerman et al. (1980) cited, 'as it occurs today' in the *Approved Lists of Bacterial Names 1980*, the generic name *Acetobacter* as *Acetobacter* Beijerinck 1898, in which the type species was designated as *Acetobacter aceti* (Pasteur 1864) Beijerinck 1898.

Asai (1935) divided the acetic acid bacteria into two genera: one genus included the species that oxidized ethanol more intensely than D-glucose and had the

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capability of oxidizing acetic acid to carbon dioxide and water, and the other contained the species that are especially isolated from fruit, oxidized D-glucose more intensely than ethanol, and had no capability of oxidizing acetic acid. For the latter genus, the name *Gluconobacter* Asai 1935 was proposed.

Almost 20 years later, the genus '*Acetomonas*' Leifson 1954 was introduced for species that had polar flagellation and were non acetate oxidizing (Leifson 1954). In contrast, the strains of the genus *Acetobacter* had peritrichous flagellation and the capability of oxidizing acetic acid to carbon dioxide and water. The proposals of the two generic names were, of course, the result of confusion in the systematics of acetic acid bacteria (Shimwell 1958; Asai and Shoda 1958; Shimwell and Carr 1959).

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

In acetic acid bacteria, Asai et al. (1964) reported two types of intermediate strains in addition to strains of the genera *Acetobacter* and *Gluconobacter*. One type of the strains had peritrichous flagellation, and the other had polar flagellation despite being acetate oxidizing. The genera *Acetobacter* and *Gluconobacter* were distinguished chemotaxonomically from each other by the presence of the major ubiquinone homologues, that is, Q-9 for the former and Q-10 for the latter (Yamada et al. 1969a). The peritrichously flagellated intermediate strains, which were formerly classified as '*Gluconobacter liquefaciens*' (Asai 1935; Asai and Shoda 1958; Asai 1968) and later regarded as pigment-producing strains of *Acetobacter aceti* (Carr and Shimwell 1960; Kimmit and Williams 1963), had Q-10, which was quite different from the type strain of *Acetobacter aceti* (Q-9), the type species of the genus *Acetobacter*, but similar to strains of the genus *Gluconobacter*. On the contrary, the polarly flagellated intermediate strains, which were once classified as '*Acetobacter aurantium*' (sic) (Kondo and Ameyama 1958), had Q-8, which was never found in any other strains of acetic acid bacteria, and these strains were later classified as *Frateuria aurantia* (ex Kondo and Ameyama 1958) Swings et al. 1980 (Swings et al. 1980).

In the *Approved Lists of Bacterial Names 1980*, the Q-10-equipped peritrichously flagellated intermediate strains were listed as *Acetobacter aceti* subsp. *liquefaciens* (Asai 1935) De Ley and Frateur 1974 (Skerman et al. 1980). The Q-10-equipped strains, which were classified as *Acetobacter liquefaciens* (Asai 1935) Gosselé et al. 1983 (= *A. aceti* subsp. *liquefaciens*) and as *Acetobacter xylinus* (Brown 1886) Yamada 1984 [= *A. aceti* subsp. *xylinus* corrig. (Brown 1886) De Ley and Frateur 1974], were distinguished from the Q-9-equipped strains within the genus *Acetobacter* at the subgeneric level, and the subgenus *Gluconacetobacter* corrig. Yamada and Kondo 1984 was proposed (Yamada and Kondo 1984). However, the subgenus was not accepted in the classification of acetic acid bacteria, along with the genus *Acidomonas* Urakami et al. 1989 for the methanol-assimilating acetic acid bacterium, *Acetobacter methanolicus* Uhlig et al. 1986 (Swings 1992; Sievers et al. 1994).

The subgenus *Gluconacetobacter* was phylogenetically discussed on the basis of the partial 16S rRNA sequences, along with the genus *Acidomonas*, and elevated at the generic level as the genus *Gluconacetobacter* Yamada et al. 1998 with a concomitant existence of the genus *Acidomonas* (Yamada et al. 1997). The type species was designated as *Gluconacetobacter liquefaciens* (Asai 1935) Yamada et al. 1998.

In the genus *Gluconacetobacter*, there were two subclusters in the phylogenetic trees based on 16S rRNA gene sequences (Franke et al. 1999; Yamada et al. 2000). Later, the existence of two phylogenetic groups, that is, the *Gluconacetobacter liquefaciens* group and the *Gluconacetobacter xylinus* group, was suggested to be distinguished at the generic level on the basis of morphological, physiological, chemotaxonomic, and ecological characteristics (Yamada and Yukphan 2008). For the latter group, the genus *Komagataeibacter* Yamada et al. 2013 was introduced with the type species, *Komagataeibacter xylinus* (Brown 1886) Yamada et al. 2013 (Yamada et al. 2012a, b).

At the present time, 17 genera are recognized in acetic acid bacteria or the acetous group of the family *Acetobacteraceae* Gillis and De Ley 1980, the class *Alphaproteobacteria* Stackebrandt et al. 1988, viz., *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, and *Swingsia* Malimas et al. 2014 (Fig. 1.1). Of the 17 genera, the 5 genera *Acetobacter*, *Gluconobacter*, *Gluconacetobacter*, *Asaia*, and *Komagataeibacter* each include a large number of species. However, the remaining 12 genera are monotypic, that is, contain only 1 species, except for the genus *Neokomagataea*, which consists of 2 species.

1.2 Isolation of Acetic Acid Bacteria

The isolation of acetic acid bacteria is in general carried out by an enrichment culture approach (Komagata et al. 2014; Sievers and Swings 2005a). A medium for the enrichment procedure and the isolation of acetic acid bacteria, designated as the pH 3.5 medium (Yamada et al. 1999), is composed, for example, of 1.0 % D-glucose (w/v), 0.5 % ethanol (99.8 %) (v/v), 0.3 % peptone (w/v), 0.2 % yeast extract (w/v), and 0.01 % cycloheximide (w/v), and adjusted at pH 3.5 with hydrochloric acid. In the isolation of acetic acid bacteria capable of fixing atmospheric nitrogen, the LGI medium that contains 10.0 % sucrose (w/v), 0.06 % KH_2PO_4 (w/v), 0.02 % K_2HPO_4 (w/v), 0.02 % $MgSO_4$ (w/v), 0.002 % $CaCl_2$ (w/v), 0.001 % $FeCl_3$ (w/v), and 0.0002 % Na_2MoO_4 (w/v) is used at pH 6.0 (Cavalcante and Döbereiner 1988).

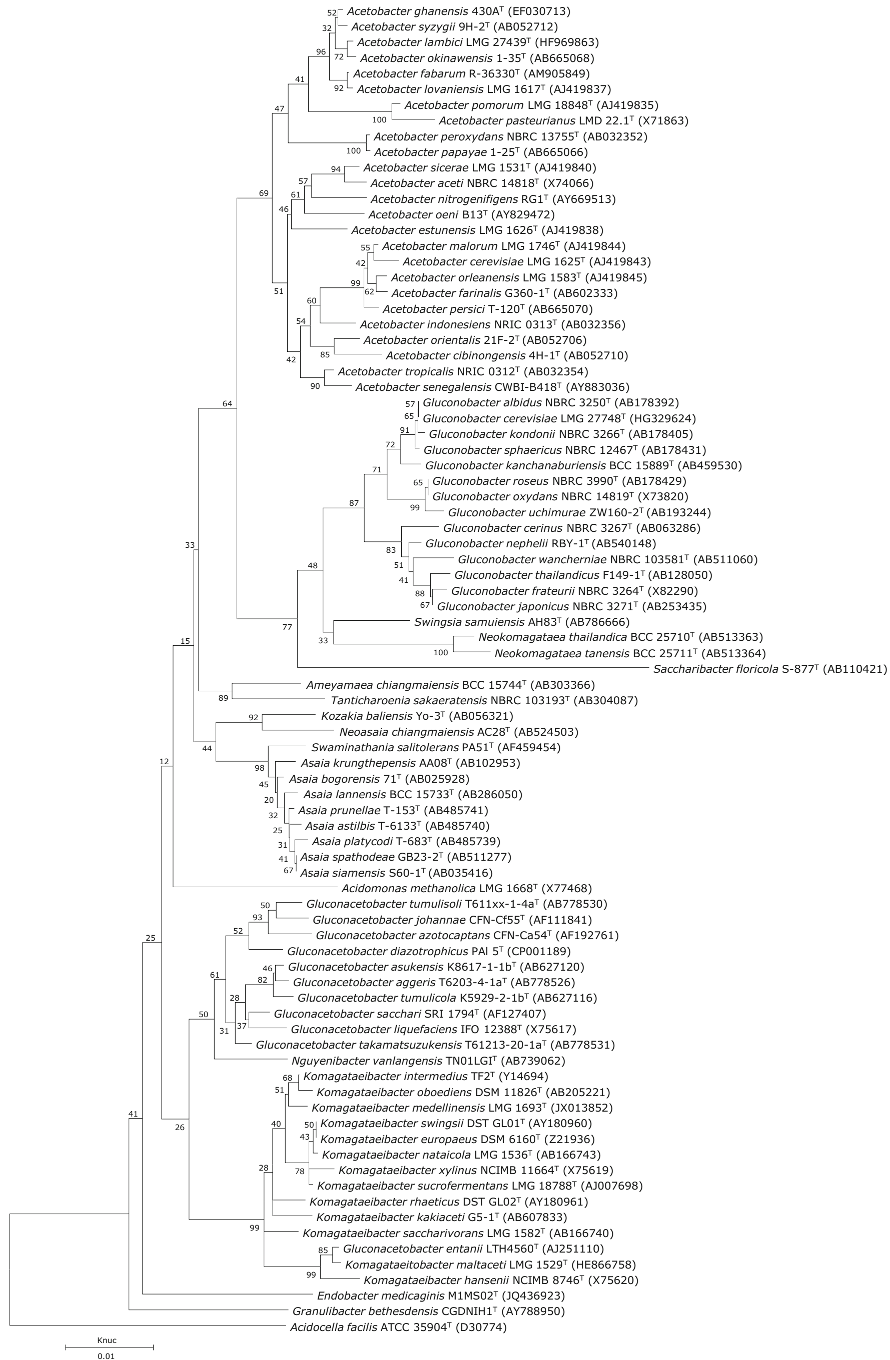

Fig. 1.1 A neighbor-joining phylogenetic tree of acetic acid bacteria. The phylogenetic tree based on 16S rRNA gene sequences of 1213 bases was constructed by using MEGA 5.05 (Tamura et al. 2011). *Numerals* at the nodes of respective branches indicate bootstrap values (%) derived from 1000 replications

When microbial growth is seen in the LGI medium, the culture is transferred to the pH 3.5 medium mentioned previously (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 % D-glucose (w/v), 0.5 % ethanol (99.8 %) (v/v), 0.3 % peptone (w/v), 0.3 % yeast extract (w/v), 0.7 % calcium carbonate (e.g., precipitated by Japanese Pharmacopoeia) (w/v), and 1.5 % agar (w/v) (Yamada et al. 1999), and the resulting colonies that dissolve calcium carbonate on the agar plates are picked up, inoculated, and incubated on agar slants with the same 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 the carbon sources, of the medium in the enrichment procedure is changed, the selective isolation of acetic acid bacteria can be expected. In fact, strains of *Asaia bogorensis* and *Asaia siamensis* were first isolated by the use of D-sorbitol or dulcitol instead of D-glucose (Yamada et al. 2000; Katsura et al. 2001). Several kinds of media employed for the enrichment procedure result in the effective isolation of acetic acid bacteria (Lisdiyanti et al. 2003b; Suzuki et al. 2010). Instead of the pH 3.5 medium, the pH 4.5 medium containing 0.03 % acetic acid (v/v) can be used (Yamada et al. 1976).

In the genera that are not monotypic, including more than several species and therefore restricted to *Acetobacter*, *Gluconobacter*, *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 done by the combination of only two conventional phenotypic tests composed of acetate and lactate oxidation and the production of acetic acid from ethanol (Yamada and Yukphan 2008).

In strains to be assigned to the genus *Acetobacter*, a deep blue color appears quickly 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 aforementioned four genera, and the color change is very slow in acetate and lactate oxidation. The two conventional tests just described are useful, especially when a large number of isolates are routinely identified or classified at the generic level.

To isolate acetic acid bacteria, sugary and alcoholic materials have widely been utilized as isolation sources. In such cases, the habitats of the acetic acid bacteria are to be the isolation sources (Komagata et al. 2014; Kersters et al. 2006; Sievers and Swings 2005a). Recently, acetic acid bacteria have been found ecologically in a

wide variety of isolation sources, such as activated sludges, rhizosphere soils, soils, pollen, human patients, mosquitoes, a stone chamber of a tumulus, and nodules (Komagata et al. 2014; Kersters et al. 2006; Sievers and Swings 2005a). In addition, acetic acid bacteria that grow on nitrogen-free media have been found (Gillis et al. 1989; Fuentes-Ramírez et al. 2001; Samaddar et al. 2011; Vu et al. 2013).

Most acetic acid bacteria can be maintained at 4 °C for 1 month on agar slants containing an appropriate medium. Long-term preservation of acetic acid bacteria can be achieved by lyophilization or by storage in liquid nitrogen, or by cryo-conservation at −80 °C by the use of low-temperature refrigerators and appropriate cryoprotectants (Komagata et al. 2014; Kersters et al. 2006; Sievers and Swings 2005a).

1.3 Identification of Acetic Acid Bacteria

When a certain strain of acetic acid bacteria is isolated, the strain will be assigned to a proper or suitable systematic or taxonomic position. Such a process is called identification. The identification consists of two levels, genus level and species level.

To select acetic acid bacteria from a number of the strains isolated, it is suitable to test the strains for growth on a pH 3.5 medium, which contains, for example, 1.0 % D-glucose (w/v), 0.5 % ethanol (99.8 %) (v/v), 0.3 % peptone (w/v), and 0.2 % yeast extract (w/v); the pH is adjusted to 3.5 with hydrochloric acid (Yamada et al. 1999). A pH 4.0 medium can be used for the growth test. If a certain strain is an acetic acid bacterium, appropriate growth can be seen. If the pH of the medium is adjusted to 4.5, bacteria other than acetic acid bacteria sometimes can grow.

For generic-level identification, the candidates of the acetic acid bacteria obtained are in general subjected to 16S rRNA gene sequence analysis, especially to the construction of phylogenetic trees based on 16S rRNA gene sequences (Komagata et al. 2014). When the phylogenetic trees are constructed by the three methods, viz., the neighbor-joining, maximum parsimony, and maximum likelihood methods, the candidates may be assignable to new taxa, such as new genera (Yamada and Yukphan 2008). On the other hand, some phenotypic feature analyses are applicable to the routine identification of the candidates (Table 1.1).

For specific-level identification, whole-genome DNA–DNA hybridization is necessary and inevitable for the precise identification of the strains that have already been identified or classified at the generic level (Komagata et al. 2014). Of the phenotypic features used for the specific-level identification, acid production from different carbon sources and growth on different carbon sources are generally utilized; however, precise identification would hardly be expected.

Recently, many taxonomic methods have been reported (Komagata et al. 2014; Sievers and Swings 2005a; Cleenwerck and De Vos 2008), for example, isoprenoid quinone analysis and fatty acid composition analysis as chemotaxonomic methods and DNA base composition determination, and 16S–23S rRNA gene internally

Table 1.1 Phenotypic characteristics differentiating the genera of acetic acid bacteria

Characteristic	*Acetobacter* 1	*Gluconobacter* 2	*Acidomonas* 3	*Gluconacetobacter* 4	*Asaia* 5	*Kozakia* 6	*Swaminathania* 7	*Saccharibacter* 8	*Neoasaia* 9	*Granulibacter* 10	*Tanticharoenia* 11	*Ameyamaea* 12	*Neokomagataea* 13	*Komagataeibacter* 14	*Endobacter* 15	*Nguyenibacter* 16	*Swingsia* 17
Flagellation	per[a]	pol[a]	n[c]	per	per	n	per	n	n	n	n	pol	n	n	spol	per	n
Oxidation of																	
Acetate	+	–	+	+	w	w	w	–	–	w	–	+	–	+	–	+	–
Lactate	+	–	–	+	w	w	w	w	–	+	–	w	–	+	–	–	–
Growth on:																	
30 % D-Glucose (w/v)	–	–[b]	+	–	+	–	+	+	+	nd	+	–	+	nd	nd	w	+
1 % D-Glucose (w/v)	+	+	+	+	+	+	nd	–	nd	nd	nd	+	+	+	+	+	+
Glutamate agar	–	–	nd	+	+	–	+	–[e]	+	+	w	w	+	+	+	+	+
Mannitol agar	vw	+	nd	+	+	+	+	–[e]	+	w	+	+	+	+	+	+	+
Raffinose	–	–	–	–	+	w	nd	nd	+	nd	–	–	–	nd	nd	+	–
Growth in the presence of																	
0.35 % acetic acid (w/v)	+	+	+	+	–	+	+	–	+	nd	+	+	–	+	nd	w	–
1 % KNO_3 (w/v)	–	–	+	–	–	–	+	nd	–	nd	–	–	–	nd	nd	–	+
Production of acetic acid from ethanol	+	+	+	+	–	+	+	w/–	+	vw	+	+	w	+	+	–	w
Water-soluble brown pigment production	–	–[b]	–	+	–	–	+	–	–	nd	+	–	–	–	nd	+	+
Production of dihydroxyacetone from glycerol	+	+	–	+	w	+	+	–	w	–	+	w	–	+	+	–	+
Production of levan-like polysaccharide	–	–	–	–	–	+	nd	–	–	nd	–	–	–	–	nd	+	–
Assimilation of ammoniac nitrogen on																	
D-Glucose	–	+	w	+	+	–	nd	–	–	+	–	vw	vw	+	+	–	–
D-Mannitol	–	+	w	+	+	–	nd	–	w	nd	–	vw	–	+	nd	w	+
Ethanol	w	–	w	–	–	–	nd	–	–	nd	–	vw	vw	nd	nd	–	–
Production of																	
2-Keto-D-gluconate	+	+	–	+	+	+	nd	+	+	nd	+	+	+	+	nd	+	+

(continued)

Table 1.1 (continued)

Characteristic	*Acetobacter* 1	*Gluconobacter* 2	*Acidomonas* 3	*Gluconacetobacter* 4	*Asaia* 5	*Kozakia* 6	*Swaminathania* 7	*Saccharibacter* 8	*Neoasaia* 9	*Granulibacter* 10	*Tanticharoenia* 11	*Ameyamaea* 12	*Neokomagataea* 13	*Komagataeibacter* 14	*Endobacter* 15	*Nguyenibacter* 16	*Swingsia* 17
5-Keto-D-gluconate	+	+	−	+	+	+	nd	+	+	nd	+	+	+	+	nd	−	+
2,5-Diketo-D-gluconate	−	−[b]	−	+	−	−	nd	−	−	nd	+	−	+	−	nd	+	+
Acid production from																	
D-Mannitol	−	+	w	−	+	−	−	+	w	−	−	−	−	−	−	−	+
D-Sorbitol	−	+	−	−	+(d)	−	+	−	+(d)	−	−	−	−	−	−	−	−
Dulcitol	−	w	−	−	+(d)	−	v	−	w	−	−	−	−	nd	−	−	−
Glycerol	−	+	+	−	+	+	+	−	+	w/-	+	w	−	−	+	−	−
Raffinose	−	−	−	−	+	+	nd	−	+	nd	w	−	−	nd	nd	w	w
Ethanol	+	+	+	+	−	+	+	−	+	+	+	+	−	+	+	−	−
Major quinone	Q-9	Q-10	Q-10	Q-10	Q-10	Q-9	Q-10	Q-10	Q-10	Q-10	Q-10	Q-10	Q-10	Q-10	Q-10	Q-10	Q-10
DNA G+C (mol%)	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	69.4	46.9

The characteristics mentioned here are mainly based on those of the type strains of the type species of the respective genera: 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

pol polar, *per* peritrichous, *spol* subpolar, *n* none, + positive, − negative, *w* weakly positive, *vw* very weakly positive, *d* delayed, *v* variable, *nd* not determined

[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 at 7 % glutamate but not at 1 % glutamate

transcribed spacer (ITS) sequencing and restriction analysis of ITS as DNA-based molecular methods, in addition to the phenotypic feature analysis, 16S rRNA gene sequence analysis, and the whole-genome DNA–DNA hybridization. The combination of these methods gives more precise information for the identification and the classification of acetic acid bacteria.

1.4 Genera and Species in Acetic Acid Bacteria

The acetic acid bacteria classified in the acetous group constitute the family *Acetobacteraceae* Gillis and De Ley 1980, the class *Alphaproteobacteria* Stackebrandt et al. 1988, together with the acidophilic group (Komagata et al. 2014; Sievers and Swings 2005a; Gillis and De Ley 1980; Stackebrandt et al. 1988). The type genus of the family is *Acetobacter*. Seventeen genera are reported (Table 1.1). The genera and the species listed below are ordered chronologically, because they have their own respective long (or not so long) histories in transitions of generic and specific circumscriptions and in selection of isolation sources.

1.4.1 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*, and *Saccharibacter*. In the genus *Acetobacter*, there are two phylogenetically different groups: the *Acetobacter aceti* group and the *Acetobacter pasteurianus* group.

Cells are gram negative, ellipsoidal to rod shaped, measuring 0.4–1.0 by 1.2–3.0 μm, rarely longer. Cells occur singly or in 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. Does not grow on glutamate agar and very weakly on mannitol agar. Dihydroxyacetone is not usually produced from glycerol, but is produced by a few species. D-Gluconate is produced from D-glucose by all the

species, 2-keto-D-gluconate by a considerable number of species, and 5-keto-D-gluconate by a few species. 2,5-Diketo-D-gluconate 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, D-xylose, D-glucose, D-galactose, D-mannose, or ethanol (Lisdiyanti et al. 2000). Ammoniac nitrogen is in general hardly utilized.

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

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

1.4.1.1 *Acetobacter aceti* (Pasteur 1864) Beijerinck 1898

For the characteristics of the species, refer to Lisdiyanti et al. (2000), Gosselé et al. (1983b), Komagata et al. (2014), and Sievers and Swings (2005b).

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%.

1.4.1.2 *Acetobacter pasteurianus* (Hansen 1879) Beijerinck and Folpmers 1916

For the characteristics of the species, refer to Beijerinck and Folpmers (1916), Lisdiyanti et al. (2000), Gosselé et al. (1983b), Komagata et al. (2014), and Sievers and Swings (2005b).

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

1.4.1.3 *Acetobacter peroxydans* Visser't Hooft 1925

For the characteristics of the species, refer to Visser't Hooft (1925), Lisdiyanti et al. (2000), Gosselé et al. (1983b), Komagata et al. (2014), and Sievers and Swings (2005b).

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%.

1.4.1.4 *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%.

1.4.1.5 *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%.

1.4.1.6 *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%.

1.4.1.7 *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%.

1.4.1.8 *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 fruit of zirzak (*Annona muricata*) in Indonesia. The DNA G+C content of the type strain is 53.7 mol%.

1.4.1.9 *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%.

1.4.1.10 *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%.

1.4.1.11 *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%.

1.4.1.12 *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%.

1.4.1.13 *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%.

1.4.1.14 *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%.

1.4.1.15 *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%.

1.4.1.16 *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%.

1.4.1.17 *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%.

1.4.1.18 *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%.

1.4.1.19 *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%.

1.4.1.20 *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%.

1.4.1.21 *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%.

1.4.1.22 *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 a stem of sugarcane, Okinawa, Japan. The DNA G+C content of the type strain is 59.3 mol%.

1.4.1.23 *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%.

1.4.1.24 *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%.

1.4.1.25 *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%.

1.4.2 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 of acetic acid bacteria and found two taxonomic groups in the isolated strains on the oxidation of ethanol and D-glucose. One had intense ethanol oxidizability rather than D-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 its five subspecies (Skerman et al. 1980). The DNA G+C content of the species was 54.2–62.8 mol%, with the range of 8.6 mol% (Yamada et al. 1981b).

Cells are gram negative, ellipsoidal to rod shaped, measuring 0.4–1.2 by 1.0–3.0 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. D-Gluconate, 2-keto-D-gluconate, and 5-keto-D-gluconate are produced from D-glucose, and a few strains produce 2,5-diketo-D-gluconate. A water-soluble brown pigment is produced in strains of a few species. Acid is produced from L-arabinose, D-xylose, D-glucose, D-galactose, D-mannose, D-fructose, melibiose, D-mannitol, D-sorbitol, glycerol, and ethanol. Grows on D-glucose, D-fructose, D-mannitol, D-sorbitol, and glycerol. Strains of several species require nicotinic acid for growth.

Optimum temperature for growth is 25 °–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 species grow at pH 3.5. acid is $C_{18:1}\omega 7c$. The major ubiquinone is Q-10. The DNA G+C content is 54.0–61.5 mol%. 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.

1.4.2.1 *Gluconobacter oxydans* (Henneberg 1897) De Ley 1961

For the characteristics of the species, refer to Asai et al. (1964), Yamada et al. (1981a, b), Gosselé et al. (1983a), Yamada and Akita (1984), Tanaka et al. (1999), Katsura et al. (2002), Komagata et al. (2014), and Sievers and Swings (2005d).

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%.

1.4.2.2 *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), Mason and Claus (1989), and 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%.

1.4.2.3 *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%.

1.4.2.4 *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%.

1.4.2.5 *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*) Bangkok, Thailand. The DNA G+C content of the type strain is 55.8 mol%.

1.4.2.6 *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%.

1.4.2.7 *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%.

1.4.2.8 *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) and 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%.

1.4.2.9 *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%.

1.4.2.10 *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%.

1.4.2.11 *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%.

1.4.2.12 *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%.

1.4.2.13 *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 10606^T), isolated from rambutan (*Nephelium lappaceum*). The DNA G+C content of the type strain is 57.2 mol%.

1.4.2.14 *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%.

1.4.3 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. 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 sufficiently remote to establish the new genus (Bulygina et al. 1992; Yamada et al. 1997; Yamashita et al. 2004).

Cells are gram negative, short rods, measuring 0.5–0.8 by 1.5–2.0 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, beige to pink, and 1–3 mm in diameter on glucose/peptone/yeast extract/malt

extract (PYM) agar (pH 4.5) after 5 days 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. D-Gluconate is produced from D-glucose. 2-Keto-D-gluconate, 5-keto-D-gluconate, or 2,5-diketo-D-gluconate is not produced in culture media. Acid is produced from L-arabinose, D-xylose, D-ribose, D-glucose, D-galactose, D-mannose, glycerol, ethanol, or methanol. Methanol, ethanol, D-glucose, D-mannose, glycerol, or succinic acid is utilized as a sole source of carbon. Pantothenic acid is essentially required for growth.

Grows on 30 % D-glucose (w/v) and 0.35 % 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 Q-10. The DNA G+C content is 62–63 mol%. 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).

1.4.3.1 *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), and 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 nonsterile 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%.

1.4.4 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 Q-10-equipped *Acetobacter* species. Phylogenetically, the genus *Gluconacetobacter* consisted of two groups: the *Gluconacetobacter liquefaciens* group and the *Gluconacetobacter xylinus* group. For the latter group, the genus *Komagataeibacter* Yamada et al. 2013 was proposed.

Cells are gram negative rods, measuring 0.6–0.9 by 1.2–2.0 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-Keto-D-gluconate is produced from D-glucose. Most of species produce 2,5-diketo-D-gluconate, and a few species produce 5-keto-D-gluconate. Most of the species produce a water-soluble brown pigment. Acid is produced from L-arabinose, D-xylose, D-glucose, D-mannose, or ethanol. Grows on D-glucose, D-fructose, sucrose, D-mannitol, or ethanol. Ammoniac nitrogen is used as a sole nitrogen source. Strains of most species have the activity of nitrogen fixation.

Most of the species grow on 30 % D-glucose (w/v). Grows between 15 ° 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 Q-10. The DNA G+C content is 58–65 mol%. 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.

1.4.4.1 *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), Gosselé et al. (1983b), Yamada and Kondo (1984), Navarro and Komagata (1999), Sievers and Swings (2005c), and 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%.

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

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

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

The type strain is Döbereiner PAl 5^T (= ATCC 49037^T = CCUG 37298^T = CIP 103539^T = DSM 5601^T = LMG 7603^T), isolated from roots and stems of sugarcane in Alagoas, Brazil. The DNA G+C content of the type strain is 61 mol%.