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

Y. Yamada (✉)
Department of Applied Biological Chemistry, Faculty of Agriculture, Shizuoka University, 836 Ohya, Suruga-ku, Shizuoka 422-8529, Japan
e-mail: yamada333@kch.biglobe.ne.jp

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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).

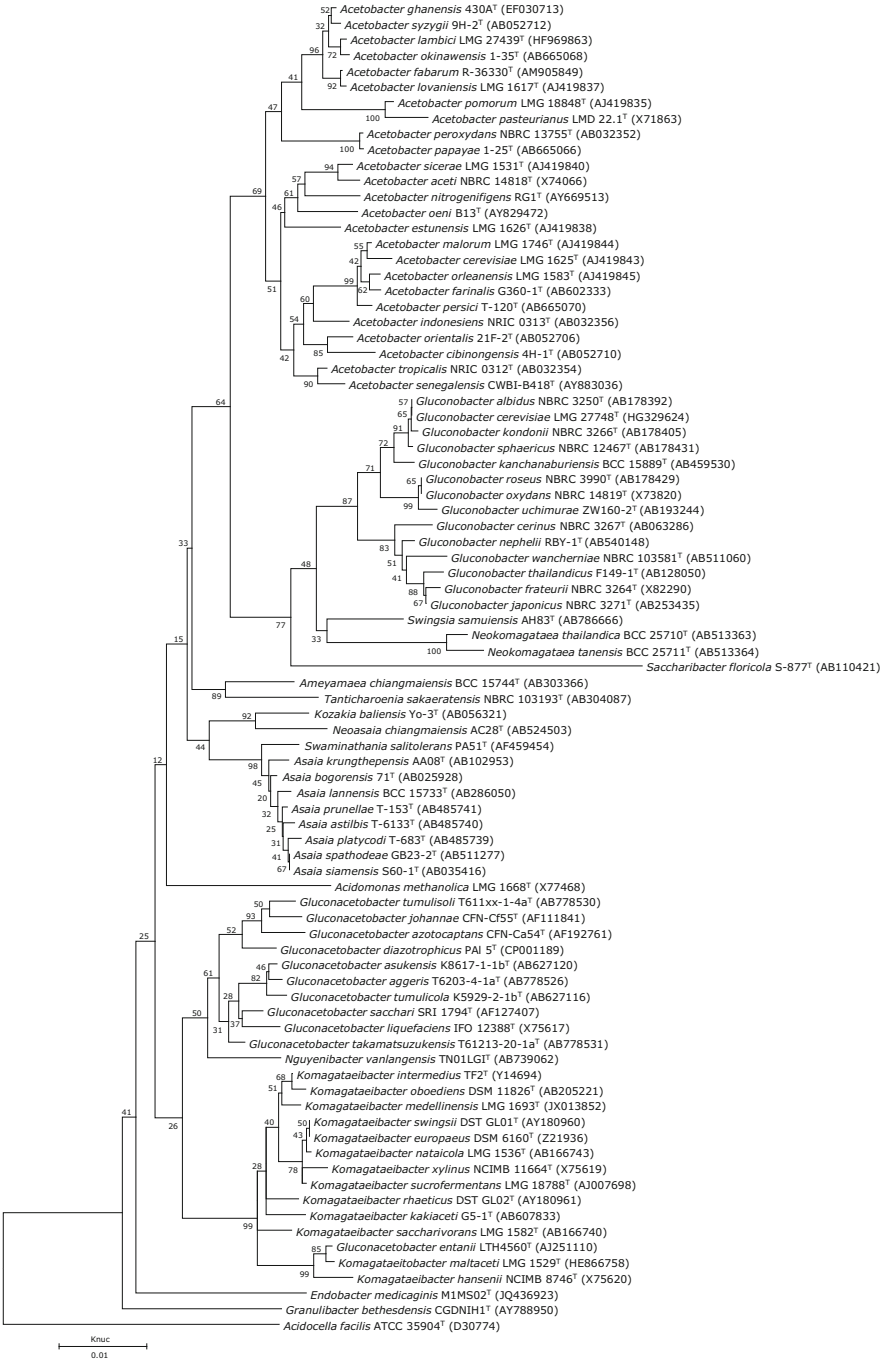

Fig. 1.1 A neighbor-joining phylogenetic tree of acetic acid bacteria. The phylogenetic tree based on 16S rRNA gene sequences of 1213 bases was constructed by using MEGA 5.05 (Tamura et al. 2011). *Numerals* at the nodes of respective branches indicate bootstrap values (%) derived from 1000 replications

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 cryoconservation 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

	Acetobacter	*Gluconobacter*	*Acidomonas*	*Gluconacetobacter*	*Asaia*	*Kozakia*	*Swaminathania*	*Saccharibacter*	*Neoasaia*	*Granulibacter*	*Tanticharoenia*	*Ameyamaea*	*Neokomagataea*	*Komagataeibacter*	*Endobacter*	*Nguyenibacter*	*Swingsia*
Characteristic	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	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 $C_{18:1}\omega7c$. 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%.

1.4.4.3 *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 sugarcane and from the pink sugarcane mealybug. The DNA G+C content of the type strain is 65 mol%.

1.4.4.4 *Gluconacetobacter johannae* Fuentes-Ramírez, Bustillos-Cristales, Tapia-Hernández, Jiménez-Salgado, Wang, Martínez-Romer 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%.

1.4.4.5 *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%.

1.4.4.6 *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%.

1.4.4.7 *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 northeast 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%.

1.4.4.8 *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 a spider 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%.

1.4.4.9 *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 the dismantling work of Takamatsuzuka Tumulus in Asuka village, Nara Prefecture, Japan. The DNA G+C content of the type strain is 66.6 mol%.

1.4.4.10 *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%.

1.4.5 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, that is, in Thailand, the Philippines, and Indonesia (Yamada and Yukphan 2008). However, the *Asaia* strains were isolated in the temperate zone, in Japan (Suzuki et al. 2010). The strains of the genus *Asaia* produced no or a very small amount of acetic acid from ethanol and did not grow in the presence of 0.35 % acetic acid (v/w).

Cells are gram negative, rod shaped, measuring 0.4–1.0 by 1.0–2.5 μm, and motile with peritrichous flagella. Colonies are smooth, entire, raised, shiny, and light brown, 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-keto-D-gluconate and 5-keto-D-gluconate from D-glucose, but not 2,5-diketo-D-gluconate. Acid is produced from D-glucose, D-galactose, D-fructose, or other sugars and sugar alcohols. Grows on D-glucose, D-fructose, or D-mannitol. Ammoniac nitrogen is assimilated on D-glucose or D-mannitol.

Grows on 30 % D-glucose (w/v), but not in the presence of 0.35 % 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 $C_{18:1}\omega 7c$. The major quinone is Q-10. The DNA G+C content is 58.6–61.0 mol%. 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.

1.4.5.1 *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%.

1.4.5.2 *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%.

1.4.5.3 *Asaia krungthepensis* Yukphan, Potacharoen, Tanasupapwat, 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 0535^T = TISTER 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%.

1.4.5.4 *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%.

1.4.5.5 *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 (*Sapathodea campanulata*) in Thailand. The DNA G+C content of the type strain is 59.7 mol%.

1.4.5.6 *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, Japan. The DNA G+C content of the type strain is 58.9 mol%.

1.4.5.7 *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, Japan. The DNA G+C content of the type strain is 60.0 mol%.

1.4.5.8 *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, Japan. The DNA G+C content of the type strain is 58.9 mol%.

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

Cells are gram negative, rod shaped, and non motile, measuring 0.6–0.8 by 2.0–3.0 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. D-Gluconate, 2-keto-D-gluconate, and 5-keto-D-gluconate are produced from D-glucose, but 2,5-diketo-D-gluconate is not. A water-soluble brown pigment is not produced from D-glucose. Acid is produced from L-arabinose, D-xylose, D-glucose, D-galactose, D-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. A levan-like mucous substance is produced from sucrose or D-fructose. γ-Pyrone is produced from D-fructose but not from D-glucose.

Growth is not inhibited by 0.35 % acetic acid (v/v) at pH 3.5. Does not grow on 30 % D-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 Q-10. The DNA G+C content is 56.8–57.2 mol%. For more details of characteritics, see Komagata et al. (2014).

1.4.6.1 *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%.

1.4.7 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 semisolid LGI medium at pH 5.5 from the rhizosphere, roots, and stems of salt-tolerant, mangrove-associated wild rice, were phylogenetically related especially to those of the genus *Asaia*. However, the genus was distinguished phenotypically from the genus *Asaia* by growth on 0.35 % acetic acid (v/v) and 3 % NaCl (w/v) or 1 % KNO_3 (w/v).

Cells are gram negative, straight rods with round ends, measuring approximately 0.7–0.9 by 1.9–3.1 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, D-glucose, D-galactose, D-mannose, D-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 % acetic acid (v/v) at pH 3.5 and 3 % NaCl using 1 % KNO_3 (w/v) as a nitrogen source.

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

1.4.7.1 *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.

1.4.8 Saccharibacter *Jojima, Miura, Suzuki, Yokozeki, Yamanaka and Fudo 2004*

Sac.cha.ri.bac'ter. L. neut. n. *sacchrum* or *saccharon*, sugar; N. L. masc. n. *bacter*, rod; N. L. masc. n. *Saccharibacter*, a sugar rod or a rod that grows intensely in a sugar-rich environment.

The strains of the genus *Saccharibacter* that were isolated from the pollen of a Japanese flower were quite remote phylogenetically from the strains of any other genera of acetic acid bacteria. The strains of the genus were osmophilic, showing no growth on 1 % glutamate agar (w/v) but growing on 7 % glutamate agar (w/v). The phylogenetically related genera are *Neokomagataea*, *Swingsia*, and *Gluconobacter*.

Cells are gram negative, straight rods, measuring 0.8–1.0 by 2.5–4.0 μm, and non motile. Colonies are circular, entire, and pale in color on yeast extract/glucose/peptone agar.

Strictly aerobic. Catalase positive and oxidase negative. Produces negligible or very little acetic acid from ethanol. Acetate is not oxidized to carbon dioxide and water, and lactate is weakly oxidized. Grows on mannitol agar and glutamate agar supplemented with 7 % substrates (w/v). Does not grow on common mannitol agar and glutamate agar with 1 % substrates (w/v). Dihydroxyacetone is not produced from glycerol. D-Gluconate, 2-keto-D-gluconate, and 5-keto-D-gluconate are produced from D-glucose. Acid is produced from L-arabinose, D-xylose, D-glucose, D-galactose, D-mannose, melibiose, sucrose, or D-mannitol. Methanol is not utilized. Ammoniac nitrogen is not assimilated on Hoyer–Frateur medium with D-glucose, D-mannitol, or ethanol. Cellulosic pellicles and water-soluble mucous substances are not produced. Not pigmented.

Grows in the glucose range between 2 % and 40 % (w/v), with an optimum around 10 % (w/v). High glucose concentration, for example, 10 % D-glucose (w/v), is preferable for growth. Osmophilic. No growth occurs in the presence of 0.35 % acetic acid (v/v) at pH 3.5. Temperature for growth ranges from 20 ° to 33 °C; the optimum is around 25–30 °C. The growth pH ranges from pH 4.0 to pH 7.5; the optimum pH is around pH 5.0 to pH 7.0. No growth is observed below pH 4.0. The major cellular fatty acids are $C_{16:0}2OH$ (31.1–41.0 %) and $C_{18:1}\omega7c$ (22.0–29.8 %). The major quinone is Q-10. The DNA G+C content is 52–53 mol%. For more details of characteristics, see Komagata et al. (2014).

1.4.8.1 *Saccharibacter floricola* Jojima, Mihara, Suzuki, Yokozeki, Yamanaka and Fudo 2004

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

The type strain is S-877^T (= AJ 13480^T = DSM 15669^T = JCM 12116^T), isolated from pollen collected in Kanagawa Prefecture, Japan. The DNA G+C content of the type strain is 52.3 mol%.

1.4.9 Neoasaia *Yukphan, Malimas, Potacharoen, Tanasupawat, Tanticharoen and Yamada 2006*

Ne.o.a.sa'i.a. Gr. adj. *neos*, new; N. L. fem. n. *Asaia*, a bacterial name after Professor Asai, Japan; N. L. fem. n. *Neoasaia*, new *Asaia*.

The strain of the genus *Neoasaia* that was isolated from a flower of red ginger was closely related phylogenetically to those of the genera *Kozakia, Asaia*, and *Swaminathania*. However, the phenotypic characteristic was that of no oxidation of acetate and lactate, differentiating from the foregoing three genera.

Cells are gram negative, rod shaped, measuring 0.8–1.0 by 1.0–2.0 μm, and non motile. Colonies are smooth, raised, entire, shiny, and pink.

Aerobic. Acetic acid is produced from ethanol. Acetate and lactate are not oxidized. Grows on glutamate agar and mannitol agar. Dihydroxyacetone is weakly produced from glycerol. 2-Keto-D-gluconate and 5-keto-D-gluconate are produced from D-glucose. Acid is produced from D-arabinose weakly, L-arabinose, D-xylose, L-rhamnose weakly, D-fructose with delay, D-galactose, D-glucose, D-mannose, melibiose, sucrose, raffinose, D-mannitol weakly, D-sorbitol with delay, dulcitol weakly, *meso*-erythritol, glycerol, or ethanol.

Grows on D-arabinose weakly, L-arabinose, D-xylose, D-fructose, L-sorbose, D-galactose, D-glucose, D-mannose weakly, sucrose, raffinose, D-mannitol, D-sorbitol, dulcitol, *meso*-erythritol, or glycerol. Ammoniac nitrogen is hardly assimilated in the presence of D-glucose or D-mannitol as a carbon source. A water-soluble brown pigment is not produced on a glucose/peptone/yeast extract/calcium carbonate medium, and a levan-like polysaccharide is not produced on a sucrose medium. However, the production of fructan is reported by *Neoasaia chiangmaiensis* NBRC 101099^T (Jacob et al. 2013).

Grows on 30 % D-glucose (w/v) and in the presence of 0.35 % acetic acid (v/v), but not in the presence of 1.0 % KNO_3 (w/v). The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is Q-10. The DNA G+C content is 63.1 mol%. For more details of characteristics, see Komagata et al. (2014).

1.4.9.1 *Neoasaia chiangmaiensis* Yukphan, Malimas, Potacharoen, Tanasupawat, Tanticharoen and Yamada 2006

For the characteristics of the species, refer to Yukphan et al. (2005).

The type strain is $AC28^T$ (= BCC 15763^T = NBRC 101099^T), isolated from a flower of red ginger (*Alpinia purpurata*) in Chiang Mai, Thailand, in September 2002. The DNA G+C content of the type strain is 63.1 mol%.

1.4.10 Granulibacter *Greenberg, Porcella, Orcella, Stock, Wong, Conville, Murray, Holland and Zelazny 2006*

Gra.nu.li.bac'ter. L. neut. n. *granulum*, grain; N. L. masc. n. *bacter*, rod; N. L. masc. n. *Granulibacter*, a rod that causes granules or granuloma formation.

The strain of the genus *Granulibacter* isolated first from three patients with chronic granulomatous disease was quite remote phylogenetically from other acetic acid bacteria. The strain grew at optimum temperatures of 35–37 °C and on methanol.

Gram negative, coccobacillus to rod shaped, and non motile. Colonies are convex, entire, smooth, and nondiffusible yellow on a modified glucose/yeast extract/calcium carbonate.

Strictly aerobic. Catalase positive and oxidase negative. Acetic acid is hardly produced from ethanol. Acetate and lactate are oxidized to carbon dioxide and water, but the activity of the former is weak. Grows on glutamate agar but weakly on mannitol agar. Dihydroxyacetone is not produced from glycerol. Acid is produced from D-glucose or ethanol and from glycerol weakly. Methanol can be used as a sole source of carbon. Ammoniac nitrogen is assimilated on glucose. A high concentration of D-glucose, for example, 5 % D-glucose (w/v), is preferable for growth.

Optimum temperature for growth is 35–37 °C. Optimum pH for growth is 5.0–6.5. Grows at pH 3.5. The major cellular fatty acids are $C_{18:1}\omega7c$ and $C_{16:0}$. The major quinone is Q-10 (Yukphan et al. 2009). The DNA G+C content is 59.1 mol%. For more details of characteristics, see Komagata et al. (2014).

1.4.10.1 *Granulibacter bethesdensis* Greenberg, Porcella, Stock, Wong, Conville, Murray, Holland and Zelazny 2006

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

The type strain is CGDNIH1^T (= ATCC BAA-1260^T = DSM 17861^T), which was isolated from lymph node culture from a granulomatous disease patient in Bethesda, MD, USA, in 2003. The DNA G+C content of the type strain is 59.1 mol%.

1.4.11 Tanticharoenia *Yukphan, Malimas, Muramatsu, Takahashi, Kaneyasu, Tanasupawat, Nakagawa, Suzuki, Potacharoen and Yamada 2008*

Tan.ti.cha.ro.e'nia. N. L. fem. n. *Tanticharoenia*, named after Dr. Morakot Tanticharoen, Thailand, who contributed to studies of acetic acid bacteria.

The strains of the genus *Tanticharoenia* that were isolated from soil collected in Sakaerat, Nakhon Rachashima, Thailand, constituted an independent cluster

phylogenetically. The strains did not oxidize either acetate or lactate, but grew on 30 % D-glucose (w/v).

Cells are gram negative, rod shaped, measuring 0.6–0.8 by 1.0–1.6 μm, and non motile. Colonies are creamy and smooth with entire margin when grown on glucose/ethanol/peptone/yeast extract/calcium carbonate agar.

Acetic acid is produced from ethanol. Acetate and lactate are not oxidized. Grows on glutamate agar weakly and on mannitol agar. Dihydroxyacetone is produced from glycerol. 2-Keto-D-gluconate, 5-keto-D-gluconate, and 2,5-diketo-D-gluconate are produced from D-glucose. A water-soluble brown pigment is intensely produced on glucose/peptone/yeast extract/calcium carbonate agar. Acid is produced from L-arabinose, D-xylose, D-fructose weakly, D-galactose, D-glucose, D-mannose, melibiose, sucrose weakly, raffinose weakly, *meso*-erythritol, glycerol, or ethanol. Grows on L-arabinose, D-xylose, D-fructose, D-glucose, D-galactose, *meso*-erythritol, D-mannitol, D-sorbitol, glycerol, or sucrose. Ammoniac nitrogen is not assimilated in the presence of D-glucose, D-mannitol, or ethanol as a carbon source.

Grows in the presence of 0.35 % acetic acid (v/v), but not of 1 % KNO_3. Grows on 30 % D-glucose (w/v). The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is Q-10. The DNA G+C content ranges from 64.5 to 65.6 mol%. For more details of characteristics, see Komagata et al. (2014).

1.4.11.1 *Tanticharoenia sakaeratensis* Yukphan, Malimas, Muramatsu, Takahashi, Kaneyasu, Tanasupawat, Nakagawa, Suzuki, Potacharoen and Yamada 2008

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

The type strain is AC37^T (= BCC 15772^T = NBRC 103193^T), isolated from soil collected at Sakaerat, Nakhon Ratchasima, Thailand. The DNA G+C content of the type strain is 65.6 mol%.

1.4.12 Ameyamaea *Yukphan, Malimas, Muramatsu, Takahashi, Kaneyasu, Potacharoen, Tanasupawat, Nakagawa, Hamana, Tahara, Suzuki, Tanticharoen and Yamada 2010*

A.me.ya.ma'e.a. N. L. fem. n. *Ameyamaea*, Ameyama, named after Professor Minoru Ameyama, Japan, who contributed to studies of acetic acid bacteria, especially their biochemical and systematic studies.

The strains of the genus *Ameyamaea* that were isolated from flowers of red ginger collected in Chiang Mai, Thailand, were closely related phylogenetically to strains of the genus *Tanticharoenia*. However, the strains showed oxidation of

acetate and weak oxidation of lactate and no growth on 30 % D-glucose (w/v), differing from those of the genus *Tanticharoenia*.

Cells are gram negative rods, measuring 0.6–0.8 by 1.0–1.8 μm, and motile with polar flagella. Colonies are creamy and smooth with entire margin on glucose/ethanol/peptone/yeast extract/calcium carbonate agar.

Acetic acid is produced from ethanol. Acetate is oxidized to carbon dioxide and water, but lactate is weakly oxidized. Grows on glutamate agar weakly and on mannitol agar. Dihydroxyacetone is weakly produced from glycerol. 2-Keto-D-gluconate and 5-keto-D-gluconate are produced from D-glucose. A water-soluble brown pigment is not produced on glucose/peptone/yeast extract/calcium carbonate agar.

Acid is produced from D-arabinose weakly, L-arabinose, D-xylose, L-rhamnose, D-glucose, D-mannose, D-galactose, *meso*-erythritol, glycerol weakly, melibiose, or ethanol. Grows on D-glucose, D-mannose very weakly, D-galactose, D-xylose, L-arabinose, L-rhamnose, D-fructose, L-sorbose, D-mannitol, D-sorbitol, dulcitol, *meso*-erythritol, glycerol, or melibiose very weakly. Growth is weak on methanol. Ammoniac nitrogen is very weakly assimilated in the presence of D-glucose, D-mannitol, or ethanol as a carbon source.

Grows in the presence of 0.35 % acetic acid (v/v), but not on 30 % D-glucose (w/v). The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is Q-10. The DNA G+C content is 66.0–66.1 mol%. For more details of characteristics, see Komagata et al. (2014).

1.4.12.1 *Ameyamaea chiangmaiensis* Yukphan, Malimas, Muramatsu, Takahashi, Kaneyasu, Potacharoen, Tanasupawat, Nakagawa, Hamana, Tahara, Suzuki, Tanticharoen and Yamada 2010

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

The type strain is AC04^T (= BCC 15744^T = NBRC 103196^T), isolated from a flower of red ginger (*Alpinia purpurea*) in Chiang Mai, Thailand. The DNA G+C content of the type strain is 66.0 mol%.

1.4.13 Neokomagataea *Yukphan, Malimas, Muramatsu, Potacharoen, Tanasupawat, Nakagawa, Tanasupawat and Yamada 2011*

Ne.o.ko.ma.ga.ta'ea. N. L. fem. n. *Neokomagataea*, new Komagata, named after Professor Kazuo Komagata, a Japanese microbiologist who contributed to bacterial systematics and phylogeny, especially of acetic acid bacteria.

The strains of the genus *Neokomagataea* that were isolated in Thailand from flowers of lantana and candle bush were related phylogenetically to those of the

genus *Gluconobacter*. The strains of the genus grew on 30 % D-glucose (w/v) but not in the presence of 0.35 % acetic acid (v/v), the latter of which differed from those of the genus *Gluconobacter*.

Cells are gram negative rods, measuring 0.6–0.8 by 1.0–1.6 μm, and non motile. Colonies are smooth, entire, and creamy on glucose/ethanol/peptone/yeast extract/calcium carbonate agar.

Acetic acid is weakly produced from ethanol. Acetate and lactate are not oxidized. Grows on glutamate agar and mannitol agar. Dihydroxyacetone is not produced from glycerol. 2-Keto-D-gluconate, 5-keto-D-gluconate, and 2,5-diketo-D-gluconate are produced from D-glucose. A water-soluble brown pigment is not produced. Acid is produced from L-arabinose weakly, D-xylose, D-glucose, D-galactose weakly, D-fructose, or sucrose. Grows on D-glucose, L-rhamnose weakly, or sucrose. Ammoniac nitrogen is not generally assimilated on D-glucose or ethanol as a source of carbon.

Grows between 1.0 and 30 % D-glucose (w/v). Osmotolerant. Growth does not occur in the presence of 0.35 % acetic acid (v/v) or in the presence of 1.0 % or 2.0 % NaCl (w/v), or 1.0 % KNO_3 (w/v). 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 51.2–56.8 mol%. For more details of characteristics, see Komagata et al. (2014).

The type species of the genus is *Neokomagataea thailandica* Yukphan et al. 2011. Two species are reported.

1.4.13.1 *Neokomagataea thailandica* Yukphan, Malimas, Muramatsu, Potacharoen, Tanasupawat, Nakagawa, Tanticharoen and Yamada 2011

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

The type strain is AH11^T (= BCC 25710^T = NBRC 106555^T), isolated from a flower of lantana (*Lantana camera*) at Tan Island, Hat Khanom-Mu Ko Thale Thai National Park, Nakhon-Si-Thammarat, Thailand, in 2007. The DNA G+C content of the type strain is 56.8 mol%.

1.4.13.2 *Neokomagataea tanensis* Yukphan, Malimas, Muramatsu, Potacharoen, Tanasupawat, Nakagawa, Tanticharoen and Yamada 2011

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

The type strain is AH13^T (= BCC 25711^T = NBRC 106556^T), isolated from a flower of candle bush (*Senna alata*) at Tan Island, Hat Khanom-Mu Ko Thale Thai National Park, Nakhon-Si-Thammarat, Thailand, in 2007. The DNA G+C content of the type strain is 51.2 mol%.

1.4.14 Komagataeibacter *Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013*

Ko.ma.ga.ta.e.i.bac'ter. N. L. fem. n. *Komagataea*, Komagata, the name of a Japanese microbiologist; N. L. masc. n. bacter, rod; N. L. masc. n. *Komagataeibacter*, Komagata rod, which is named after Professor Kazuo Komagata, Japan, who contributed to the bacterial systematics, especially of acetic acid bacteria.

The genus *Komagataeibacter* was introduced for the *Gluconacetobacter xylinus* group of the genus *Gluconacetobacter* based on 16S rRNA gene sequence analysis and morphological, physiological, and ecological characterizations. The 11 species of the genus *Gluconacetobacter* were transferred to the genus *Komagataeibacter* as new combinations. Recently, three new combinations were additionally reported. The phenotypic characteristics of the genus *Komagataeibacter* were generally no motility, no production of 2,5-diketo-D-gluconate from D-glucose, and no water-soluble brown pigment production on glucose/peptone/yeast extract/calcium carbonate medium.

Cells are gram negative rods, measuring 0.5–0.8 by 1.0–3.0 μm, occurring singly, in pairs, or in chains. Non motile. Colonies are circular, smooth, or rough, raised to convex or umbonate, entire, glistening, and white-creamy to beige.

Aerobic. Catalase positive and oxidase negative. Acetic acid is produced from ethanol. Acetate and lactate are oxidized to carbon dioxide and water. Grows on glutamate agar and mannitol agar. Dihydroxyacetone is generally produced from glycerol. D-Gluconate, 2-keto-D-gluconate, and/or 5-keto-D-gluconate are produced from D-glucose, but 2,5-diketo-D-gluconate is not produced.

Acid is produced from L-arabinose, D-xylose, D-glucose, D-galactose, or ethanol. Grows on D-glucose, D-fructose, maltose, sucrose, or D-mannitol. Ammoniac nitrogen is generally assimilated on D-mannitol. Cellulosic materials are produced by some strains, that is, of *Komagataeibacter xylinus* and *Komagataeibacter nataicola*. A water-soluble brown pigment is not produced on glucose/yeast extract/calcium carbonate medium. γ-Pyrone compounds are not produced.

Grows generally in the presence of 0.35 % acetic acid (v/v). Some species require acetic acid for growth. Grows at pH 3.0. The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is Q-10. The DNA G+C content ranges from 58 to 64 mol%. For more details of characteristics, see Komagata et al. (2014).

The type species of the genus is *Komagataeibacter xylinus* (Brown 1886) Yamada et al. 2013. Fourteen species are reported.

1.4.14.1 *Komagataeibacter xylinus* (Brown 1886) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Acetobacter aceti* subsp. *xylinus* corrig. (Brown 1886) De Ley and Frateur 1974.

Synonyms: *Acetobacter xylinus* (Brown 1886) Yamada 1984; *Gluconacetobacter xylinus* (Brown 1886) Yamada, Hoshino and Ishikawa 1998; '*Bacterium xylinum*' Brown 1886.

For the characteristics of the species, refer to Gosselé et al. (1983b), Lisdiyanti et al. (2006), Navarro and Komagata (1999), Yamada (1983), Sievers and Swings (2005c), and Komagata et al. (2014).

The type strain is NCIMB 11664^T (= DSM 6513^T = JCM 7644^T = LMG 1515^T = NBRC 15237^T = BCC 49175^T), isolated from mountain ash berry by Professor G. Bertrand. The DNA G+C content of the type strain is 62.5 mol%.

1.4.14.2 *Komagataeibacter hansenii* (Gosselé et al. 1983) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Acetobacter hansenii* Gosselé, Swings, Kersters, Pauwels and De Ley 1983.

Synonyms: *Gluconacetobacter hansenii* (Gosselé et al. 1983) Yamada, Hoshino and Ishikawa 1998; *Gluconacetobacter kombuchae* Dutta and Gachhui 2007.

For the characteristics of the species, refer to Gosselé et al. (1983b), Lisdiyanti et al. (2006), Dutta and Chchhui (2007), Cleenwerck et al. (2009), Komagata et al. (2014), and Sievers and Swings (2005c).

The type strain is NCIMB 8746^T (= DSM 5602^T = JCM 7643^T = LMG 1527^T = NBRC 14820^T = BCC 6318^T), isolated from a local vinegar in Jerusalem, Israel. The DNA G+C content of the type strain is 59.0 mol%.

1.4.14.3 *Komagataeibacter europaeus* (Sievers et al. 1992) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Acetobacter europaeus* Sievers, Sellmer and Teuber 1992.

Synonym: *Gluconacetobacter europaeus* (Sievers et al. 1992) Yamada, Hoshino and Ishikawa 1998.

For the characteristics of the species, refer to Sievers et al. (1992).

The type strain is DES11^T (= DSM 6160^T = JCM 16935^T = BCC 36446^T), isolated from a submerged culture vinegar generator at a factory in Esslingen in the southern part of Germany. The DNA G+C content of the type strain is not described. The range of DNA G+C content is 56.2–57.3 mol%.

1.4.14.4 *Komagataeibacter oboediens* (Sokollek et al. 1998) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Acetobacter oboediens* Sokollek, Hertel and Hammes 1998.

Synonym: *Gluconacetobacter oboediens* (Sokollek et al. 1998) Yamada 2000.

For the characteristics of the species, refer to Sokollek et al. (1998) and Yamada (2000).

The type strain is LTH 2460^T (= DSM 11826^T = JCM 16937^T = LMG 18849^T = BCC 36445^T), isolated from a submerged red wine vinegar fermentation at a factory in the southern part of Germany. The DNA G+C content of the type strain is 59.9 mol%.

1.4.14.5 *Komagataeibacter intermedius* (Boesch et al. 1998) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Acetobacter intermedius* Boesch, Trček, Sievers and Teuber 1998.

Synonym: *Gluconacetobacter intermedius* (Boesch et al. 1998) Yamada 2000.

For the characteristics of the species, refer to Boesch et al. (1998) and Yamada (2000).

The type strain is TF2^T (= DSM 11804^T = JCM 16936^T = BCC 36447^T = LMG 18909^T), isolated from a commercially available tea fungus beverage (Kombucha) in Switzerland. The DNA G+C content of the type strain is 61.55 mol%.

1.4.14.6 *Gluconacetobacter entanii* Schüller, Hertel and Hammes 2000

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

The type strain is LTH 4560^T (= BCRC 17196^T = DSM 13536^T = LMG 20950^T = LMG 21788^T), isolated from submerged high-acid industrial vinegar fermentations. The DNA G+C content of the type strain is 58 mol%. The type strain is not available in any culture collections (Yamada et al. 2012b). This species is not listed as a new combination, according to Rule 27 of the Bacteriological Code (Tindall et al. 2006).

1.4.14.7 *Komagataeibacter swingsii* (Dellaglio et al. 2005) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Gluconacetobacter swingsii* Dellaglio, Cleenwerck, Felis, Engelbeen, Janssens and Marzotto 2005.

For the characteristics of the species, refer to Dellaglio et al. (2005).

The type strain is DST GL01^T (= DSM 16373^T = JCM 17123^T = LMG 22125^T = BCC 36451^T), isolated from apple juice in South Tyrol region, Italy. The DNA G+C content of the type strain is 61.7 mol%.

1.4.14.8 *Komagataeibacter rhaeticus* (Dellaglio et al. 2005) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Gluconacetobacter rhaeticus* Dellaglio, Cleenwerck, Felis, Engelbeen, Janssens and Marzotto 2005.

For the characteristics of the species, refer to Dellaglio et al. (2005).

The type strain is DST GL02^T (= DSM 16663^T = JCM 17122^T = LMG 22126^T = BCC 36452^T), isolated from apple juice in South Tyrol region, Italy. The DNA G+C content of the type strain is 63.4 mol%.

1.4.14.9 *Komagataeibacter saccharivorans* (Lisdiyanti et al. 2006) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Gluconacetobacter saccharivorans* Lisdiyanti, Navarro, Uchimura and Komagata 2006.

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

The type strain is LMG 1582^T (= BCC 36444^T = JCM 25121^T = NRIC 0614^T = BCC 36444^T), isolated from beet juice in Germany in 1927. The DNA G+C content of the type strain is 61 mol%.

1.4.14.10 *Komagataeibacter nataicola* (Lisdiyanti et al. 2006) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Gluconacetobacter nataicola* Lisdiyanti, Navarro, Uchimura and Komagata 2006.

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

The type strain is LMG 1536^T (= JCM 25120^T = NRIC0616^T = BCC 36443^T), isolated from nata de coco in the Philippines. The DNA G+C content of the type strain is 62 mol%.

1.4.14.11 *Komagataeibacter sucrofermentans* (Toyosaki et al. 1996) Yamada, Yukphan, Vu, Muramatsu, Ochaikul, Tanasupawat and Nakagawa 2013

Basonym: *Acetobacter xylinus* subsp. *sucrofermentans* Toyosaki, Kojima, Tsuchida, Hoshino, Yamada and Yoshinaga 1996.

Synonym: *Gluconacetobacter sucrofermentans* (Toyosaki et al. 1996) Cleenwerck, De Vos and De Vuyst 2010.

For the characteristics of the species, refer to Toyosaki et al. (1995) and Cleenwerck et al. (2010).

The type strain is LMG 18788^T (= DSM 15973^T = JCM 9730^T = BCC 7227^T), isolated from a cherry. The DNA G+C content of the type strain is 62.7 mol%.

1.4.14.12 *Komagataeibacter kakiaceti* (Iino et al. 2012) Yamada 2014

Basonym: *Gluconacetobacter kakiaceti* Iino, Suzuki, Tanaka, Kosako, Ohkuma, Komagata and Uchimura 2012.

For the characteristics of the species, refer to Iino et al. (2012b) and Yamada (2014).

The type strain is G5-1^T (= JCM 25156^T = NRIC 0798^T = LMG 26206^T), isolated from kaki vinegar collected in Kumamoto Prefecture, Japan in 2005. The DNA G+C content of the type strain is 63.6 mol%.

1.4.14.13 *Komagataeibacter medellinensis* (Castro et al. 2013) Yamada 2014

Basonym: *Gluconacetobacter medellinensis* Castro, Cleenwerck, Trček, Zuluaga, De Vos, Caro, Aguirre, Putaux and Gañán 2013.

For the characteristics of the species, refer to Castro et al. (2013), Yamada et al. (1969b), and Yamada (2014).

The type strain is LMG 1693^T (= NBRC 3288^T = Kondo 51^T), isolated from vinegar by K. Kondo, Japan. The DNA G+C content of the type strain is 60.7 mol%.

1.4.14.14 *Komagataeibacter maltaceti* (Slapšak et al. 2013) Yamada 2014

Basonym: *Gluconacetobacter maltaceti* Slapšak, Cleenwerck, De Vos and Trček 2013.

For the characteristics of the species, refer to Slapšak et al. (2013) and Yamada (2014).

The type strain is LMG 1529^T (= NBRC 14815^T = NCIMB 8752^T), isolated from malt vinegar brewery acetifier by T.K. Walker in 1956. The DNA G+C content of the type strain is 62.5 mol%.

1.4.15 Endobacter *Ramírez-Bahena, Teijedor, Martín, Velázquez and Peix 2013*

En.do.bac'ter. Gr. pref. *endo*, within; N. L. masc. n. *bacter*, rod; N. L. masc. n. *Endobacter*, a rod isolated from the inside of a root nodule of alfalfa.

The strain of the genus *Endobacter* was isolated from a surface-sterilized nodule of alfalfa in Spain; it is quite remote phylogenetically from other acetic acid bacteria and constituted an independent cluster in a phylogenetic tree based on 16S rRNA gene sequences.

Cells are gram negative, coccoid to rod shaped. Motile with subpolar flagella. Colonies are white and mucoid on modified yeast extract mannitol agar.

Aerobic. Catalase positive and oxidase negative. Acetate and lactate are not oxidized. Acetic acid is produced from ethanol. Grows on glutamate agar and mannitol agar. Dihydroxyacetone is produced from glycerol. Acid is produced from D-xylose, D-glucose, glycerol, or ethanol. Grows between 20 ° and 37 °C with an optimum temperature for growth of 28 °C. Ammoniac nitrogen is assimilated on D-glucose. Optimal pH for growth ranges from 5.0 to 7.0, but growth occurs at pH 3.5.

The major cellular fatty acids are $C_{18:1}\omega7c$ (39.94 %), $C_{19:0}$cyclo$\omega8c$ (12.15 %), and $C_{16:0}$ (13.40 %). The major quinone is Q-10. The DNA G+C content is 60.3 mol%. For more details of characteristics, see Komagata et al. (2014).

1.4.15.1 *Endobacter medicaginis* Ramírez-Bahena, Teijedor, Martín, Velázquez and Peix 2013

For the characteristics of the species, refer to Ramírez-Bahena (2013).

The type strain is M1MS02^T (= CECT 8088^T = LMG 26838^T), isolated from a surface-sterilized nodule of alfalfa (*Medicago sativa*), Spain. The DNA G+C content of the type strain is 60.3 mol%.

1.4.16 Nguyenibacter *Vu, Yukphan, Chaipitakchonlatarn, Malimas, Muramatsu, Bui, Tanasupawat, Duong, Nakagawa, Pham and Yamada 2013*

Ngu.ye.ni.bac'ter. N. L. masc. n. *Nguyenius*, Nguyen, the name of a famous Vietnamese microbiologist; N. L. masc. n. bacter, rod; N. L. masc. n. *Nguyenibacter*, a rod, which is named after Professor Dung Lan Nguyen, Vietnam, who contributed to the study of microorganisms, especially of strains isolated in Vietnam.

The two strains of the genus *Nguyenibacter* were isolated by the use of nitrogen-free LGI medium. The strains were related phylogenetically to those of the genera *Gluconacetobacter* and *Acidomonas*.

Cells are gram negative rods, measuring 0.6–0.8 by 1.0–1.6 μm. Motile with peritrichous flagella. Colonies are smooth, entire, transparent, and creamy to brownish.

Aerobic. Catalase positive and oxidase negative. Acetic acid is not produced from ethanol. Acetate is oxidized to carbon dioxide and water, but lactate is not oxidized. Grows on glutamate agar and mannitol agar. Dihydroxyacetone is not produced from glycerol. 2-Keto-D-gluconate and 2,5-diketo-D-gluconate are produced from D-glucose. A water-soluble brown pigment is produced. Acid is produced from L-arabinose, D-xylose, D-glucose, D-galactose, D-fructose weakly, maltose, melibiose, sucrose, or raffinose weakly. Grows on D-glucose, D-galactose, L-arabinose weakly, D-xylose weakly, D-fructose weakly, L-sorbose weakly, maltose, melibiose weakly, sucrose, raffinose, D-mannitol weakly, D-sorbitol weakly, or glycerol. Ammoniac nitrogen is utilized on D-mannitol, but not on D-glucose or ethanol. Growth occurs on N_2-free medium. γ-Pyrone compound is weakly produced. Levan-like polysaccharides are produced from sucrose.

Grows weakly on 30 % D-glucose (w/v), and weakly in the presence of 0.35 % acetic acid (v/v). Growth does not occur on 1.0 % KNO_3 (w/v). The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is Q-10. The DNA G+C content range is 68.1–69.4 mol%. For more details of characteristics, see Komagata et al. (2014).

1.4.16.1 *Nguyenibacter vanlangensis* Vu, Yukphan, Chaipitakchonlatarn, Malimas, Muramatsu, Bui, Tanasupawat, Duong, Nakagawa, Pham and Yamada 2013

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

The type strain is TN01LGI^T (= BCC 54774^T = NBRC 109046^T = VTCC-B-1198^T), isolated from the rhizosphere of Asian rice collected in Vietnam. The DNA G+C content of the type strain is 69.4 mol%.

1.4.17 Swingsia *Malimas, Chaipitakchonlatarn, Vu, Yukphan, Muramatsu, Tanasupawat, Potacharoen, Nakagawa, Tanticharoen and Yamada 2014*

Swing'si.a. N. L. fem. n. *Swingsia*, Swings, named after Professor Jean Swings, Belgium, who contributed to the systematics of bacteria, especially of acetic acid bacteria.

The two strains of the genus *Swingsia* were isolated from flowers in Thailand and located at an intermediary position phylogenetically between the genera

Gluconobacter and *Neokomagataea*. The strains grew on 30 % D-glucose (w/v) and at 37 °C, but not in the presence of 0.35 % acetic acid (v/v), and acetic acid was sometimes produced weakly from ethanol.

Cells are gram negative rods, measuring 0.6–0.8 by 1.0–1.8 μm. Non motile. Colonies are brownish and smooth with entire margin.

Aerobic. Catalase positive and oxidase negative. Acetic acid is produced weakly from ethanol. Acetate and lactate are not oxidized. Grows on glutamate agar and mannitol agar. Dihydroxyacetone is produced from glycerol. 2-Keto-D-gluconate, 5-keto-D-gluconate, and 2,5-diketo-D-gluconate are produced from D-glucose. A water-soluble pigment is produced. Acid is produced from L-arabinose weakly, D-arabinose weakly, D-xylose weakly, L-rhamnose weakly, D-glucose, D-mannose weakly, D-galactose, D-fructose weakly, D-arabitol weakly, D-mannitol, maltose weakly, lactose weakly, melibiose, sucrose, or raffinose weakly. Grows on D-glucose, D-fructose, sucrose, L-arabitol weakly, D-arabitol weakly, or D-mannitol. Ammoniac nitrogen is utilized on D-mannitol, but not on D-glucose or ethanol. Ammonic nitrogen is assimilated on D-mannitol but not on D-glucose or ethanol. Levan-like polysaccharides are not produced.

Grows on 30 % D-glucose (w/v), but not in the presence of 0.35 % acetic acid (v/v). Growth occurs in the presence of 1.0 % KNO_3 (w/v). The major cellular fatty acid is $C_{18:1}\omega7c$. The major quinone is Q-10. The DNA G+C content range is 46.9–47.3 mol%.

1.4.17.1 *Swingsia samuiensis* Malimas, Chaipitakchonlatarn, Vu, Yukphan, Muramatsu, Tanasupawat, Potacharoen, Nakagawa, Tanticharoen and Yamada 2014

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

The type strain is AH83^T (= BCC 25779^T = NBRC 107927^T), isolated from a flower of golden trumpet. The DNA G+C content of the type strain is 46.9 mol%.

1.5 Genus and Species in Pseudacetic Acid Bacteria

Several strains were once isolated and named '*Acetobacter aurantium*' by Kondo and Ameyama (1958). According to the description of the species, the strains were not able to oxidize acetate.

Asai et al. (1964) reinvestigated the strains for phenotypic characteristics and found that they had polar flagellation and oxidized acetate and lactate to carbon dioxide and water, and the strains were named the polarly flagellated intermediate strains. Additional three strains were then newly isolated and confirmed to have polar flagellation and the capability of oxidizing acetate and lactate (Ameyama and Kondo 1967).

In the isoprenoid quinone analysis of the polarly flagellated intermediate strains, Q-8 was detected as the major quinone, indicating that the quinone system obtained was quite different chemotaxonomically from either Q-9 of *Acetobacter* strains or Q-10 of *Gluconobacter* strains (Yamada et al. 1969a, 1976). In the cellular fatty acid composition of the polarly flagellated intermediate strains, *iso*-$C_{15:0}$ acid was found as the major, indicating that the strains were quite different similarly from $C_{18:1}\omega7c$ acid of *Acetobacter* and *Gluconobacter* strains (Yamada et al. 1981a).

For such unique bacterial strains equipped with Q-8 and *iso*-$C_{15:0}$ acid, the name of pseudacetic acid bacteria was given (Yamada 1979; Yamada et al. 1981a, b; Lisdiyanti et al. 2003a). The genus *Frateuria* was later introduced for these strains by Swings et al. (1980). The genus is accommodated in the class *Gammaproteobacteria* Stackebrandt et al. 1988.

1.5.1 Frateuria *Swings, Gillis, Kersters, De Vos, Gosselé and De Ley 1980 emend. Zhang, Liu and Liu 2011*

Fra.teu'ri.a. N. L. fem. n. *Frateuria*, Frateur, named after Professor Joseph Frateur, Belgium, especially in recognition of the study of acetic acid bacteria.

The genus *Frateuria* was long thought to be monotypic. However, a second species was recently reported.

Cells are gram negative, rod shaped, measuring 0.4–0.8 by 0.8–2.0 μm, singly or in pairs, motile with a single polar or subpolar flagellum when motile. Shows luxuriant growth on glucose/yeast extract/calcium carbonate agar. Colonies are flat or circular, and medium turning to brown.

Aerobic. Catalase positive or negative. Oxidase negative or positive. Oxidizes lactate but not acetate (Swings et al. 1980; Lisdiyanti et al. 2003a). Grows on glutamate agar and mannitol agar. Dihydroxyacetone is generally produced from glycerol. Produces D-gluconate, 2-keto-D-gluconate, and 2,5-diketo-D-gluconate from D-glucose but not 5-keto-D-gluconate. Produces a water-soluble brown pigment. Acid is produced from D-arabinose, L-arabinose, D-ribose, D-xylose, L-rhamnose, D-galactose, D-glucose, D-mannose, D-fructose, glycerol, or ethanol. Does not grow on methanol. Assimilates ammoniac nitrogen on D-mannitol.

No growth is observed in the presence of 0.35 % acetic acid (v/v). Grows on 20 % D-glucose (w/v) at 34 °C and at pH 3.5. The major cellular fatty acid is *iso*-$C_{15:0}$. The major quinone is Q-8. The DNA G+C content is 62–68 mol%. *Frateuria* strains are isolated from flowers of lily, rose, ladybell, and coconut and fruits of raspberry, mango, rambai, and jackfruit. For more details of characteristics, see Komagata et al. (2014) and Swings and Sievers (2005).

The type species is *Frateuria aurantia* (ex Kondo and Ameyama 1958) Swings et al. 1980. Two species are reported.

1.5.1.1 *Frateuria aurantia* (ex Kondo and Ameyama 1958) Swings, Gillis, Kersters, De Vos, Gosselé and De Ley 1980

Synonym: '*Acetobacter aurantius*' corrig. Kondo and Ameyama 1958.

For the characteristics of the species, refer to Swings et al. (1980), Yamada et al. (1969a, 1976, 1981a, b), and Lisdiyanti et al. (2003a, b).

The type strain is G-6^T (= Kondo 67^T = NBRC 3245^T = ATCC 33424^T = DSM 6220^T = LMG 1558^T), isolated from a flower of lily. The DNA G+C content of the type strain is 65.0 mol%.

1.5.1.2 *Frateuria terrea* Zhang, Liu and Liu 2011

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

The type strain is VA24^T (= CGMCC 1.7053^T = NBRC 104236^T), isolated from forest soil of the Changbai Mountains, Heilongjiang Province, China. The DNA G+C content of the type stran is 67.4 mol%.

1.6 Closing Remarks

More than 100 years have already passed since the genus *Acetobacter* Beijerinck 1898 was introduced with the only known species, *Acetobacter aceti* (Pasteur 1864) Beijerinck 1898, for vinegar-producing acetic acid bacteria. Up to 1960, acetic acid bacteria were believed to constitute a quite small taxonomic group, that is, only the one genus. However, their circumstances have entirely changed.

Acetic acid bacteria, including the vinegar-producing bacteria and their relatives, have been found in large numbers by expanding their possible living environments, viz., activated sludge, rhizosphere soils, soils, pollen, human patients, mosquitoes, stone chambers of tumuluses, and nodules of plants, in addition to sugary and alcoholic materials.

Up to the present, the acetic acid bacteria have numbered 17 genera and 84 species. These numbers will be greatly increased in future, pushing back the frontiers of their living environments and their isolation sources, and many new taxa, that is, new genera and new species, will be reported.

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