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ScienceDirect
International Journal of Food Microbiology 125 (2008) 15–24
INTERNATIONAL JOURNAL OF Food Microbiology
www.elsevier.com/locate/ijfoodmicro

Review

Genera and species in acetic acid bacteria

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Abstract

Taxonomic studies of acetic acid bacteria were historically surveyed. The genus *Acetobacter* was first introduced in 1898 with a single species, *Acetobacter aceti*. The genus *Gluconobacter* was proposed in 1935 for strains with intense oxidation of glucose to gluconic acid rather than oxidation of ethanol to acetic acid and no oxidation of acetate. The genus "*Acetomonas*" was described in 1954 for strains with polar flagellation and no oxidation of acetate. The proposals of the two generic names were due to confusion, and "*Acetomonas*" was a junior subjective synonym of *Gluconobacter*. The genus *Acetobacter* was in 1984 divided into two subgenera, *Acetobacter* and *Gluconoacetobacter*. The latter was elevated to the genus *Gluconacetobacter* in 1998. In the acetic acid bacteria, ten genera are presently recognized and accommodated to the family *Acetobacteraceae*, the *Alphaproteobacteria*: *Acetobacteer*, *Gluconobacter*, *Acidomonas*, *Gluconacetobacter*, *Asaia*, *Kozakia*, *Swaminathania*, *Saccharibacter*, *Neoasaia* and *Granulibacter*. In contrast, the genus *Frateuria*, strains of which were once named 'pseudacetic acid bacteria', was classified into the *Gammaproteobacteria*. The genus *Gluconacetobacter* was phylogenetically divided into two groups: the *Gluconacetobacter liquefaciens* group and the *Gluconacetobacter xylinus* group. The two groups were discussed taxonomically.
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Keywords: Acetic acid bacteria; *Acetobacter*; *Acetobacteraceae*; *Frateuria*; Taxonomy; *Alphaproteobacteria*; *Gammaproteobacteria*

Contents

Abbreviations: Q-10 and Q-9, ubiquinone-10 and ubiquinone-9; ITS, internal transcribed spacer; NBRC, NITE Biological Resource Center (NBRC), Department of Biotechnology, National Institute of Technology and Evaluation, Kisarazu, Japan; IFO, Institute for Fermentation, Osaka, Osaka, Japan (On transferring IFO strains to NBRC, the numeral parts of the strain names were retained, e.g., IFO 14819^T and NBRC 14819^T); IAM, Institute of Applied Microbiology, The University of Tokyo, Tokyo, Japan.

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doi:10.1016/j.ijfoodmicro.2007.11.077

1. Introduction

More than 100 years passed, since the genus *Acetobacter* Beijerinck 1898 was set up for acetic acid bacteria with a single species, *Acetobacter aceti* (Pasteur 1864) Beijerinck 1898 (Beijerinck, 1898).

The genus *Gluconobacter* Asai 1935 was subsequently proposed 37 years after for strains with the ability to intensely oxidize glucose to gluconic acid rather than ethanol to acetic acid and no oxidation of acetate, which were different in these respects from strains of the genus *Acetobacter* (Asai, 1934, 1935). However, the new generic name was hardly known in Western countries, since the papers of Asai published in 1934 and 1935 were unfortunately described in Japanese (Buchanan, 1970).

Almost 20 years later from the publications of Asai's papers, the genus "*Acetomonas*" was proposed for polarly flagellated and non acetate-oxidizing strains (Leifson, 1954). In contrast, strains of the genus *Acetobacter* had peritrichous flagella and the capability of oxidizing acetic acid. The proposals of the two generic names, *Gluconobacter* and "*Acetomonas*" were due to confusion in naming such similar microorganisms (Asai and Shoda, 1958; Asai et al., 1964; Shimwell, 1958; Shimwell and Carr, 1959).

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

Yamada and Kondo (1984) distinguished Q-10-equipped strains from Q-9-equipped strains in the genus *Acetobacter* at the subgeneric level, and the subgenus *Gluconoacetobacter* Yamada and Kondo 1985 was proposed. However, the subgeneric name was hardly accepted, along with the name of the genus *Acidomonas* Urakami et al. 1989 for the methanol-assimilating acetic acid bacterium, *Acetobacter methanolicus* Uhlig et al. 1986 (Uhlig et al., 1986; Urakami et al., 1989; Swings, 1992; Bulygina et al., 1992; Sievers et al., 1994).

The subgenus *Gluconoacetobacter* was phylogenetically discussed on the basis of partial 16S rDNA sequences, together with the existence of the genus *Acidomonas*, and elevated to the generic level as *Gluconacetobacter* Yamada et al. 1998 (*Gluconoacetobacter* [sic]) with the type species, *Gluconacetobacter liquefaciens* (Asai 1935) Yamada et al. 1998 (Asai, 1935, Yamada et al., 1997). The genus *Acidomonas* and the genus *Gluconacetobacter* are at present listed in the family *Acetobacteraceae* Gillis and De Ley 1980 (Gillis and De Ley, 1980; Sievers and Swings, 2005; Kersters et al., 2006).

The remaining six genera, *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 and *Granulibacter* Greenberg et al. 2006 were recently described (Yamada et al., 2000; Lisdiyanti et al., 2002; Loganathan and Nair, 2004; Jojima et al., 2004; Yukphan et al., 2005; Greenberg et al., 2006). Interesting is that the recently described six genera are all monotypic except for only the genus *Asaia*. The family *Acetobacteraceae* accommodates the ten genera for the acetic acid bacteria.

In the ten genera described above, the genus *Acetobacter* is characterized chemotaxonomically by Q-9 as a major respiratory quinone, which is quite unique and exceptional. However, other genera have Q-10 (Yamada et al., 1969; Kersters et al., 2006).

In the family *Acetobacteraceae*, there are six monotypic genera, i.e., *Acidomonas*, *Kozakia*, *Swaminathania*, *Saccharibacter*, *Neoasaia* and *Granulibacter*, in which only one species is described. The occurrence of strains assigned to some of the six genera is rather rare in common isolation sources such as vinegar, wine, fruits and flowers. For example, any additional *Kozakia* and *Neoasaia* strains have not yet been isolated from the common isolation sources. In addition, *Acidomonas* strains were isolated mostly from sludge (Yamashita et al., 2004).

In the remaining four genera, *Acetobacter, Gluconobacter*, *Gluconacetobacter* and *Asaia*, the genus-level identification is not impossible phenotypically by combination of only two conventional tests comprised of acetate and lactate oxidation and acetic acid production from ethanol (Asai et al., 1964; Yamada et al., 1976).

In strains to be assigned to the genus *Acetobacter*, a deep blue color appears fast and clearly in the acetate and lactate oxidation test, and acetic acid is produced in the acetic acid production test. In acetate and lactate oxidation, strains to be assigned to the genus *Gluconobacter* generally show a clear yellow color, and the color change to blue is not so vigorous in strains to be assigned to the genus *Gluconacetobacter*, in contrast to *Acetobacter* strains. Strains to be assigned to the genus *Asaia* show no or little production of acetic acid from ethanol, differing in this respect from strains of the above-mentioned three genera, and the color change is very slow in acetate and lactate oxidation. The combination of the two phenotypic features mentioned above is very useful, especially when a large number of isolates are routinely classified at the generic level.

2. Taxonomy of acetic acid bacteria at the generic and specific levels

2.1. The genus Acetobacter Beijerinck 1898 is phylogenetically divided into two groups

Almost sixteen species are presently described in the genus *Acetobacter* (Sievers and Swings, 2005; Kersters et al., 2006; Silva et al., 2006; Dutta and Gachhui, 2006). These numbers are quite renewed for the past decade, in contrast to the only three species, *A. aceti*, *Acetobacter pasteurianus* (Hansen 1879) Beijerinck and Folpmers 1916 and *Acetobacter peroxydans* Visser't Hooft 1925, all of which were listed in the Approved List, 1980 (Skerman et al., 1980).

The species of the genus *Acetobacter* were phylogenetically divided into two groups (Fig. 1). 1) The first group corresponded to the *A. aceti* group, which included *A. aceti* (the type species), *Acetobacter orleanensis* (Henneberg 1906) Lisdiyanti et al. 2001, *Acetobacter estunensis* (Carr 1958) Lisdiyanti et al. 2001, *Acetobacter indonesiensis* Lisdiyanti et al. 2001, *Acetobacter tropicalis* Lisdiyanti et al. 2001, *Acetobacter cibinongensis* Lisdiyanti et al. 2002, *Acetobacter orientalis* Lisdiyanti et al.

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