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THE STATUS OF THE GENERIC NAME GLUCONOBACTER

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ABSTRACT. The generic name Acetobacter Beijerinck is accepted for the nonmotile or peritrichously flagellated acetic acid bacteria and the generic name Gluconobacter Asai for the gluconic acid bacteria. The type species proposed for Gluconobacter is G. oxydans (Henneberg 1897) DeLey 1961. It is proposed that a single species of Gluconobacter be recognized.

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The nomenclature and classification of the acetic acid bacteria appear at first sight to be rather confused. One group can, however, at once be singled out concerning which there is no dispute. It includes the peritrichously or non-flagellated, aerobic rodlike bacteria, typically oxidizing ethanol to acetic acid at a pH as low as 4.5, and acetate and/or lactate to CO₂ and water. Ability to oxidize carbohydrates is greatly diversified. They constitute three groups typified by Acetobacter peroxydans, A. oxydans and A. mesoxydans as proposed by Frateur (1950, 287). The DNA base compositions range from 55-64% GC (De Ley and Schell 1963, 243). There is general agreement that they constitute one genus, Acetobacter Beijerinck 1900, with the emended description of Leifson (1954, 102). They will not be discussed here further.

The relationships and particularly the nomenclature of the remaining acetic acid bacteria remain to be clarified. Names have been proposed as Gluconobacter (Asai 1935, 674),

the suboxydans group of Acetobacter (Frateur 1950, 287), Acetomonas (Leifson 1954) and the glycophilic group of Acetobacter (Brown and Rainbow 1956), previously called the Acetobacter viscosus group (Rainbow and Mitson 1953). Quite frequently, particularly in the biochemical literature, they are still cited as Acetobacter. Some authors use Acetomonas; others prefer Gluconobacter. The National Collection of Industrial Bacteria (NCIB), Aberdeen, catalogue splits the acetic acid bacteria into Acetobacter and Acetomonas. The American Type Culture Collection (ATCC) catalogue recognizes Gluconobacter and Acetobacter, not Acetomonas.

It is our purpose to review the origins of this heterogeneity and to show that all these names refer to the same group of organisms and are therefore synonyms. We conclude that the name Gluconobacter has priority and is the correct generic name. We will not review in detail the properties of these bacteria, on which much of physiological and biochemical work has been carried out.

In 1935 Asai proposed that the acetic acid bacteria be recognized as including two genera. From his extensive description, we present the following summary:

Acetobacter Beijerinck (1900, 495): optimal growth temperature at 30°C; grows at 39-40°C, not at 7-9°C; the oxidation of ethanol to acetic acid is pronounced; the oxidation of glucose to gluconic acid is moderate to absent; acetic acid is assimilated and oxidized. It is clear that this genus is the Acetobacter of Beijerinck.

Gluconobacter Asai 1935: optimal growth temperature below 30°C; does not grow at 39-40°C, grows at 7-9°C; the oxidation of ethanol to acetic acid is weaker than with Acetobacter, and is sometimes absent; the oxidation of glucose to gluconic acid is pronounced. Acetic acid is neither assimilated nor oxidized. Some additional properties may be listed; poor growth on sake or beer; red or red-brown pigments produced; glucose, mannitol and glycerol are good carbon sources; optimal pH usually 3.4-6.3; acid production from many carbohydrates and some alcohols; 5-ketogluconate and kojic acid are produced by some strains; ketogenesis, etc. There is no doubt that most, if not all, of the organisms included by Asai were indeed acetic acid bacteria. He proposed that Gluconobacter be divided into two subgenera, Eugluconobacter (two strains investigated) and Gluconoacetobacter (23 strains investigated). The latter thus constitute the bulk of the genus Gluconobacter. These

25 strains were his own isolates. Asai also tentatively included Bacterium industrium Henneberg 1898 and Bacterium oxydans Henneberg 1897 in the latter subgenus. This placement was later (Asai, Iizuka and Komagata 1964) definitely confirmed experimentally. As an argument in favor of the identity between Gluconobacter and the suboxydans group of one of us, it may be pointed out that B. industrium and B. oxydans were considered to be identical with Acetobacter suboxydans muciparum Frateur 1950. Misled by the incomplete description and the strong action on glucose, Asai mistakenly included Acetobacter xylinum (Brown) Bergey et al. 1925 in the subgenus Gluconoacetobacter. The position of the two species of Eugluconobacter, G. liquefaciens Asai 1935, strain 16 and G. viscosus Asai 1935, strain 38 is still uncertain, as will be discussed below. Asai's 1935 paper, being written in Japanese, remained virtually unknown in the West until some 25 years later when the problem arose relative to the use of Gluconobacter versus Acetomonas. In later papers (Asai and Shoda 1958; Asai, Iizuka and Komagata 1964) the subdivision of the genus Gluconobacter into subgenera was abandoned. A brief summary of the originally proposed classification was published in the Jubilee Publication for Prof. Sakaguchi (1958). The Index Bergeyana (Buchanan, Holt and Lessel 1966) lists Gluconobacter as validly published and legitimate.

There followed the monograph by one of us (Frateur 1950). Only the suboxydans group discussed therein need concern us here. The main characteristics of these organisms are: catalase positive, acetic acid not oxidized, no CO₂ produced from lactate, strong ketogenesis, pronounced formation of gluconic acid from glucose, sometimes pigment produced. The suboxydans group remained within the genus Acetobacter. Unfortunately the author was not then aware of Asai's work. Table 1 shows that Gluconobacter and the suboxydans group are identical.

In 1954 Leifson found that the named suboxydans, melanogenus, capsulatus and viscosus strains, all belonging to Frateur's suboxydans group, have 3 - 8 polar multitrichous flagella. Nineteen years after Asai's first paper, Leifson proposed the recognition in acid bacteria of two genera, Acetobacter Beijerinck (peritrichous, with pronounced or weak oxidation of acetate and/or lactate) and a new genus Acetomonas (polar multitrichous with 3 - 8 flagella, acetate and lactate not oxidized). Leifson did not mention Asai's 1935 paper. Acetomonas Leifson 1954 should not be confused

with nor regarded as an orthographic variant of Acetimonas Orla-Jensen 1909, the latter being a generic name proposed to include all acetic acid bacteria. Shimwell (1958) proposed the emendation of Leifson's description of Acetomonas because a few strains showed a single polar flagellum. This alteration of diagnostic characters is only very minor and, according to Recommendation 15a of Rule 15 (International Code of Nomenclature of Bacteria 1966) no amendment should have been made. In addition the diagnosis of the newly described Acetomonas is so incomplete as to be of little value. The description (Shimwell and Carr 1959): "Bacteria oxidizing ethyl alcohol to free acetic acid, but not further to carbon dioxide and water. Motile or non-motile. If motile the cells possess one or more polar flagella." There are a few strains of Pseudomonas which fit this description. In fact every nonmotile or polarly flagellate bacterium, irrespective of its cell morphology and physiology, capable of oxidizing ethanol and with an impaired Krebs cycle would be included.

Rainbow and Mitson (1953) and Brown and Rainbow (1956) divided the acetic acid bacteria into the lactophilic (or Acetobacter mobilis) group and the glycophilic (or Acetobacter viscosus) group. The latter have a predominant glucose metabolism, are unable to oxidize acetate and lactate and display several other nutritional characteristics. It was explicitly stated by Brown and Rainbow (1956) that their glycophilic group corresponds closely to Acetomonas, but they did not mention Asai's work, nor did they accept the recognition of two genera of acetic acid bacteria.

The similarity between all these different groups is summarized in Table 1.

As a result of Leifson's reports on flagellar distribution Asai and Shoda (1958) and Asai, Iizuka and Komagata (1964) reinvestigated the gluconobacters extensively. A much greater variety of strains were included. The properties reported in 1935 were confirmed. It is noteworthy that several strains, already explicitly listed in the genus Gluconobacter in 1935, were again included, e.g., G. cerinus 24, G. roseus G-2, G. nonoxygluconicus and G. scleroideus 5. This once more shows that the original description of Gluconobacter was essentially correct. The relevant conclusions are: 1) that all the organisms considered to be Gluconobacter by Asai have polar multitrichous flagella; 2) the authors point out that Gluconobacter can be equated with Acetomonas Leifson, with the suboxydans group of Frateur, and with the

Table 1. Comparison of reported properties of Gluconobacter strains.

Only those features are included which are mentioned by at least two authors. Many other properties are described by Asai (1935); Frateur (1950); Asai and Shoda (1958); Asai, Iizuka and Komagata (1964).

The reference (1) in the table refers to later additions in the latter two papers.

	Suboxydans group, Frature (1950)	<u>Gluconobacter</u> subg. <u>Euglu-</u> <u>conobacter</u>	Asai (1935) subg. <u>Glucono-</u> <u>acetobacter</u>	<u>Acetomonas</u> Leifson (1954)	Glycophilic group, Brown and Rainbow (1956)
Morphology	rods, diplobacters	rods, diplobacters	rods, diplobacters	rods	rods
Pleomorphism	frequently	frequently	frequently	generally	
Motility	usually + in young cultures	1+ 1-	5+ 18-	9+ 1-	
Flagellation			polar multi- trichous (1)	polar multi- trichous	
Capsule or slime formation	slime:variable	frequently	frequently		
Gram stain	neg.		neg. (1)	neg.	neg.
Gelatin liquefaction	neg. or very weak	1+ 1-	6+ 17-		
Aerobiosis	+	+	+	+	
pH optimum		5.4-7.1 7.1-8.0	usually 3.4 - 6.3	better at 5-6 than at 7	
NH ₄ assimilation	variable	neg.	7+ 16-	10-	
Brown pigments	frequently		frequently	frequently	
Growth on sugars	predominant	predominant	predominant		predominant

Table 1 (continued)

	Suboxydans group, Frateur (1950)	Gluconobacter Asai (1935)		Acetomonas Leifson (1954)	Glycophilic group, Brown and Rainbow (1956)
		subg. <u>Euglu-</u> <u>conobacter</u>	subg. <u>Glucono-</u> <u>acetobacter</u>		
Growth on gluconate	good	good	good		
" on acetate	very poor	neg.	neg.		
" on ethanol	rather poor to good	very poor	very poor		
Catalase	+	+	+(1)	8+ 2-	+
CH ₃ COOH → CO ₂	neg.	neg.	neg.	neg.	neg.
Lactate → CO ₂	neg.		neg. (1)	neg.	neg.
Ketogenesis	very strong		very strong		
Glycerol → dihydroxy- acetone	very much	1+ 1-	very much		
Mannitol → fructose	very much	1+ 1-	very much		
Glucose → 5-ketogluconate	usually very much	neg.	usually very much		
Glucose → other reducing compounds	+	neg.	+		
Acid formation from ethanol to acetic acid	+(at pH 4.5)	neg.	+(at pH down to ca 3)	+(pH not stated)	+(pH not stated)
Lactose	neg.	neg.	very weak		
Starch	neg.	neg.	neg.		
Glucose to gluconic acid	very strong	very strong	very strong	+	+
Maltose	variable	usually neg.	variable		

Sucrose	variable	1+	1-	+		
Arabinose	+	+		+		
Fructose	variable	+		+		
Galactose	+	+		+		
Other sugars	frequently +			frequently +		
Species names:						
<u>albidus</u>				+(1)		
<u>capsulatus</u>	+			+(1)	+	+
<u>cerinus</u>				+		
<u>dioxyaceticus</u>				+(1)		
<u>gluconicus</u>	(?)			+(1)		+
<u>industrius</u>	+			+(1)	(?)	
<u>liquefaciens</u>		+		+		
<u>melanogenus</u>	+			+(1)	+	
<u>nonoxygluconicus</u>				+		
<u>opacus</u>				+		
<u>oxydans</u>	+			+(1)	(?)	
<u>roseus</u>	+			+		
<u>rubiginosus</u>				+(1)		
<u>rugosus</u>				+		
<u>scleroideus</u>				+		
<u>suboxydans</u>	+			+(1)	+	
<u>turbidans</u>				(?)(1)		+
<u>viscosus</u>	+	+			+	+
<u>xylinum</u>				mistake		

glycophilic group of Rainbow. They likewise point out that the creation of a new name Acetomonas was redundant. Independent investigations (see e. g. NCIB catalogue) have likewise shown the identity of both groups; this is illustrated by the fact that Asai's G. cerinus G-2 is called Acetomonas oxydans NCIB 9137.

In his papers and personal correspondence Shimwell became a vigorous proponent of the validity of the generic name Acetomonas and rejected Gluconobacter. This criticism, together with the regrettable lack of acquaintance with Asai's 1935 paper, have been largely responsible for the lack of general acceptance of the name Gluconobacter. This criticism needs to be carefully evaluated, from three aspects: a) Asai reported that two strains, Gluconobacter liquefaciens strain 16 and G. viscosus strain 38, did not oxidize ethanol to acetic acid. Shimwell and Carr (1959) and Carr and Shimwell (1961) dismissed these organisms as pseudomonads, without examining them. That certain bacteria should be grouped with the acetic bacteria even though they do not produce acetic acid, at first glance makes both organisms highly suspect. Shimwell, however, himself apparently isolated similar organisms which he never mentioned in his criticism. We quote from a letter to one of us (J.D.L.) dated September 4, 1958: "We have recently encountered a bacterium which produces just as much starch as A. pasteurianus, and is culturally a typical Acetobacter species, being a strict aerobe, growing on the surface of highly acidic media, and so on. But it does not produce acetic acid from alcohol (!)" (italics are Shimwell's). Shimwell and Carr (1960) reported on spontaneous mutants, isolated by them from A. rancens, which were otherwise typical acetobacters; but which had lost the property of producing acetic acid from ethanol. They were called "Quasi-acetobacter." These organisms were never mentioned in the criticism against Gluconobacter. These authors were thus in the paradoxical position of, on the one hand dismissing Asai's nonethanol-oxidizers without proof as pseudomonads, but on the other hand describing similar organisms. It may be added that according to numerical taxonomy, the quasi-acetobacters would be classified with the acetic acid bacteria. Asai et al. (1964) have later again reported on four Gluconobacter strains which have a very weak or no power to oxidize ethanol, e. g. G. cerinus IAM 1832. It is likewise our personal experience that some strains have a weak ethanol-oxidizing power. As reviewed by Schell and De Ley (1962)

one-step mutational losses are not uncommon amongst acetic acid bacteria and there is no reason to believe that the oxidation of ethanol might not be one of them. Summarizing this one may—and one should—be suspicious of placement of bacteria which produce no acetic acid with the acetic bacteria, but they can not be eliminated without proof. Rejection of Asai's subgeneric name Eugluconobacter does not change the status of his genus Gluconobacter, and this part of Shimwell's criticism can not be accepted.

b) There are undoubtedly three strains described in Asai and Shoda's (1958) paper which have been misplaced in the genus Gluconobacter. They are: G. liquefaciens strain G-1, G. melanogenus strains U-4 and AC8. They were originally described as having polar flagella. They are in fact peritrichous (Shimwell and Carr 1959; Stouthamer 1960; Hodgkiss, Shimwell and Carr 1962; Kimmit and Williams 1963) and were correctly reassigned to Acetobacter. These three strains constituted the bulk of Shimwell's criticism against Gluconobacter. It is obvious, however, that thereby the value of the original 1935 description is not affected.

c) Not once, however, have the 23 strains constituting the bulk of the original Gluconobacter been discussed adequately by Shimwell. Never did he mention the extensive published material on these organisms. Yet, this group constitutes the heart of the matter. Shimwell and Carr (1959) do not even mention Asai's original paper and present it as if the genus Gluconobacter was proposed after Acetomonas. Carr and Shimwell (1961) admit that the original 1935 description of Gluconobacter resembles Acetomonas and the suboxydans group. They erroneously state that the acetate oxidation was not reported by Asai (1935); the data were quite clearly tabulated for all strains examined. Another error is Shimwell and Carr's statement that Gluconobacter oxidizes ethanol slightly (*italics theirs*). They should have mentioned that the actual per cent of acetic acid production for each strain was given by Asai (1935). For 13 strains of Acetobacter the average was 1.33%, for 23 strains of Gluconobacter it was an average of 0.66%, thus quantitatively illustrating Asai's point that the gluconobacters on the whole produce less acetic acid than the acetobacters. It is not out of place to recall that on another occasion (De Ley 1963) it has been shown that Shimwell misinterpreted and distorted results from other investigators.

The situation may thus be summarized as follows:

1) Gluconobacter Asai 1935, the suboxydans group Frateur 1950, Acetomonas Leifson 1954, the Acetobacter viscosus group Rainbow and Mitson 1953, and the glyco-philic group Brown and Rainbow 1945 are all to be referred to the genus Gluconobacter.

2) In spite of two doubtful ethanol nonoxidizing strains and the mistaken inclusion of Acetobacter xylinum (Brown) Holland in the original description, Gluconobacter has been validly and legitimately published (Buchanan, Holt and Les-sel, Index Bergeyana 1966) 19 years before Acetomonas Leifson 1954.

We therefore conclude that Gluconobacter Asai 1935 is the only acceptable generic name for the group (Principle 9, International Code of Nomenclature of Bacteria 1966).

We include herewith a generic description. Some of the features involved are from our own published data, but since no drastic change results, no further amendment is proposed.

Gluconobacter Asai 1935. (J. Agr. Chem. Soc. Japan 11: 686, 1935; J. gen. appl. Microbiol. 10:95, 1964).

Synonyms: (Vernacular names of "groups" included)

Acetomonas Leifson 1954, 102; non Acetimonas Orla-Jensen 1909, 312; group suboxydans Frateur 1950, 287; The Acetobacter viscosus group Rainbow and Mitson 1953; the glycophilic group Brown and Rainbow 1956, 61.

Individual cells ellipsoidal to rods, occurring singly, in pairs or in short or long chains. Involution forms frequently filamentous. Motile with 3 - 8 polar flagella (sometimes only one) or nonmotile. Gram-negative. No endospores. DNA composition: 60-64% GC (one exception with 57%). Obligate aerobes. As a rule strongly catalase positive. Oxidizes ethanol to acetic acid, sometimes weakly and slowly, even at pH 4.5. Does not oxidize acetate and lactate to CO₂. Grows in beer and wine, but better on glucose-containing media. Growth occurs at pH 4 - 4.5. Temperature optimum: 25-30°C. Ketogenesis, acid formation from carbohydrates, acid and ketone formation from glycols, usually very pronounced. Many strains produce much 2- and 5-ketogluconic acid; a water soluble brown pigment and γ -pyrones (violet ferric chloride reaction). Many oxidative enzymes are linked to the cell wall. Widely distributed in nature (beer, wine, fruits). Of industrial importance. From Greek glykos, sweet; Latin bactrum, rod.

The type species is Gluconobacter oxydans (Henneberg) De Ley 1961.

The Type Species. Asai (1935) did not propose a type species for the new genus. As far as we could trace it, Asai used the name Gluconobacter for the first time in 1934. He included a single species G. viscosus nov. spec. However, he used Gluconobacter at that time as a group, not a generic name. It is evident from later papers that he distinguished quite clearly between a "group" and a "genus," e.g. in his 1935 paper he subordinates the group Gluconobacter to the genus Gluconobacter. Therefore it seems to us that G. viscosus is not a type species. Leifson (1954) proposed Acetomonas suboxydans (Kluyver and de Leeuw) Leifson 1954. Shimwell and Carr (1959) pointed out that Bacterium oxydans Henneberg (1897) appeared to be the first recognizable representative of the bacterial group considered here and proposed as a type species Acetomonas oxydans (Henneberg) Shimwell and Carr. Frateur (1950) had already pointed out that Henneberg's organism appeared to belong in the suboxydans group and probably corresponded to Acetobacter suboxydans var. muciparum. De Ley (1961) recognized only one species in Gluconobacter, namely G. oxydans (Henneberg) comb. nov. Asai, Iizuka and Komagata (1964) came to the same conclusion but called it Gluconobacter oxydans (Henneberg) Asai.

It is our conclusion that for priority reasons the type species should be Gluconobacter oxydans (Henneberg 1897) De Ley 1961.

A number of authors (Shimwell and Carr 1959; De Ley 1961; Asai, Iizuka and Komagata 1964) have concluded that this genus should contain only one species. This should thus encompass all previous species names, G. albidus, G. capsulatus, G. cerinus, G. dioxyaceticus, G. gluconicus, G. industrius, G. liquefaciens, G. melanogenus, G. non-oxygluconicus, G. opacus, G. oxydans, G. roseus, G. rubiginosus, G. rugosus, G. scleroideus, G. suboxydans and G. viscosus, which would thereby become subjective synonyms of G. oxydans.

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