Review of the taxonomy of the genus *Arthrobacter*, emendation of the genus *Arthrobacter sensu lato*, proposal to reclassify selected species of the genus *Arthrobacter* in the novel genera *Glutamicibacter* gen. nov., *Paeniglutamicibacter* gen. nov., *Pseudoglutamicibacter* gen. nov., *Paenarthrobacter* gen. nov. and *Pseudarthrobacter* gen. nov., and emended description of *Arthrobacter roseus*

Hans-Jürgen Busse

Institute of Microbiology, Department of Pathobiology, University of Veterinary Medicine Vienna, Veterinärplatz, 1A-1210 Vienna, Austria

In this paper, the taxonomy of the genus *Arthrobacter* is discussed, from its first description in 1947 to the present state. Emphasis is given to intrageneric phylogeny and chemotaxonomic characteristics, concentrating on quinone systems, peptidoglycan compositions and polar lipid profiles. Internal groups within the genus *Arthrobacter* indicated from homogeneous chemotaxonomic traits and corresponding to phylogenetic grouping and/or high 16S rRNA gene sequence similarities are highlighted. Furthermore, polar lipid profiles and quinone systems of selected species are shown, filling some gaps concerning these chemotaxonomic traits. Based on phylogenetic groupings, 16S rRNA gene sequence similarities and homogeneity in peptidoglycan types, quinone systems and polar lipid profiles, a description of the genus *Arthrobacter sensu lato* and an emended description of *Arthrobacter roseus* are provided. Furthermore, reclassifications of selected species of the genus *Arthrobacter* into novel genera are proposed, namely *Glutamicibacter* gen. nov. (nine species), *Paeniglutamicibacter* gen. nov. (six species), *Pseudoglutamicibacter* gen. nov. (two species), *Paenarthrobacter* gen. nov. (six species) and *Pseudarthrobacter* gen. nov. (ten species).

The genus *Arthrobacter* was proposed by Conn & Dimmick (1947) to encompass three species, including the type species of the genus, *Arthrobacter globiforme*. The type species was later renamed as *Arthrobacter globiformis* (Skerman et al., 1980); the second species, *Arthrobacter tumescent*, was reclassified in another genus (Collins et al., 1989; Manaia et al., 2004), and the third species, *Arthrobacter helvolum*, was never mentioned again in a taxonomic paper. It has to be emphasized here that it was not reclassified as *Pseudoclaviibacter helvolum*, as stated by Busse et al. (2012). Originally, the genus was described as follows:

**Abbreviations:** DGDG, digalactosyldiacylglycerol; DMDG, dimannosyldiacylglycerol; DMS, dimannosylglyceride; DPG, diphosphatidylglycerol; MDMGG, monoacyldimannosylmonooacylglycerol; MGDG, monogalactosyldiacylglycerol; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PI, phosphatidylinositol; TeMDG, tetramannosyldiacylglycerol; TMDG, trimannosyldiacylglycerol.

**Morphology.** Varied, with a tendency to go through a more or less definite life cycle, the most characteristic features of which are Gram-negative rods in young cultures and Gram-positive coccoid forms (arthrospheres?) in old cultures, with intermediate stages that may be clubs, branched forms, or short unbranched filaments. Large (1 to 2 μ) spherical bodies are sometimes observed which have been termed ‘cystites’.

**Cultural characteristics.** Growth on surface of solid media soft and smooth, not dry and wrinkled or hard and leathery, as ordinarily in Mycobacterium and the Actinomycetaceae. Colonies on poured plates orderly small (punctiform). Growth in broth usually slow and never profuse.

**Physiology.** Can ordinarily use either ammonium salts or nitrates as sole sources of nitrogen. Can utilize
glucose and sometimes other sugars as sources of carbon and energy, but ordinarily without producing sufficient quantities of acid to have appreciable effect on the pH of highly buffered media (e.g. containing peptone). Gelatin usually slowly liquefied. Ordinarily cause blackening of Mueller’s tellurite agar.

Habitat. Primarily soil.

Type species. A. globiforme (Conn) Conn and Dimmick.

Concerning the description of the genus Arthrobacter, the Approved Lists of Bacterial Names (Skerman et al., 1980) refer to Keddie (1974), which concentrates on cultural, morphological and physiological characteristics. This description has been the basis for the classification of numerous novel species of the genus Arthrobacter.

Cells which in complex medium undergo a marked change in form during the growth cycle. Older cultures (generally 2–7 days) are composed entirely or largely of coccoid cells. In some strains the coccoid cells are uniform in size and spherical, and resemble micrococci; in others they are spherical to ovoid or slightly elongate. In some cultures larger coccoid cells some 2–4 times the size of the remainder may occur; these may predominate under some cultural conditions. On transfer to fresh complex medium growth occurs by enlargement (swelling) of the coccoid cells followed by elongation from one or occasionally two parts of the cell to give rods which usually have a diameter less than that of the enlarged coccoid cell (referred to a figure). In the larger coccoid cells outgrowth may occur at two, three or rarely four parts of the cell (referred to a figure). In both cases subsequent growth and division give rise to irregular rods which vary considerably in size and shape and include straight, bent and curved, wedge-shaped and club-shaped forms (referred to a figure). A proportion of the rods are arranged at an angle to each other giving V formations but more complex angular arrangements often occur. Post-fission outgrowths, usually from the proximal ends of one or both cells of a pair of rods (referred to a figure), and bud-like outgrowths from segments of septate rods (referred to a figure), especially in richer media, may give the appearance of rudimentary branching but true mycelia are not formed. As the exponential phase proceeds the rods become shorter and are eventually replaced by the coccoid cells characteristic of stationary phase cultures (referred to a figure). The coccoid cells are formed either by a gradual shortening of the rods at each successive division or, especially in richer media, by multiple fragmentation of larger rods (referred to a figure). The rods are non-motile or motile by one subpolar or a few lateral flagella. Do not form endospores.

Gram-positive. However, the rods may be readily decolorized and may show only Gram-positive granules in otherwise Gram-negative cells. Coccoid cells are Gram-positive but may be weakly so. Not acid-fast.

The cell walls do not contain both meso-diaminopimelic acid and arabinose.

Chemoorganotrophs: Metabolism respiratory, never fermentative. Molecular oxygen is the terminal electron acceptor.

Little or no acid is produced from glucose in peptone medium. Do not attack cellulose. Catalase-positive.

All species grow in a medium containing soil extract and yeast extract. Nutrient agar (peptone + meat extract) is suitable for laboratory strains which do not require terregens factor or vitamin B₁₂ but may be inhibitory to newly isolated strains (Topping, 1937).

Strict aerobes.

Temperature optimum 20–30 °C; most strains grow at 10 °C but usually not at 37 °C. Do not survive heating at 63 °C for 30 min in skim milk. Grow best at a neutral to slightly alkaline pH.

The G + C content of the DNA of the species examined ranges from ca. 60–72 moles % (Tₘ).

Type species: Arthrobacter globiformis (Conn) Conn and Dimmick 1947, 301.


With the reclassification of Micrococcus agilis in the genus Arthrobacter as Arthrobacter agilis, the description of the genus Arthrobacter was emended as follows (Koch et al., 1995):

‘a marked rod-coccus growth cycle occurs during growth in complex media; stationary-phase cultures (generally after 2 to 7 days) are composed entirely or largely of coccoid cells that are 0.6 to 1.0 μm in diameter; one species forms only spherical cells.’

Another 51 species of the genus Arthrobacter have since been described, including four novel species assigned to the genus since 2012, namely Arthrobacter cryoconitii (Margesin et al.,
Collins 2012, Arthrobacter cupressi (Zhang et al., 2012), Arthrobacter siccitolerans (SantaCruz-Calvo et al., 2013) and Arthrobacter geryonensis (Hoang et al., 2014). However, none of these descriptions considered the phylogenetic and chemotaxonomic heterogeneities found among species of the genus *Arthrobacter* that have been known for some decades (Fiedler, 1971; Schleifer & Kandler, 1972; Stackebrandt et al., 1983, 1988; Collins et al., 1982b; Collins & Kroppenstedt, 1983; Koch et al., 1994). More often than not, novel species were described as members of the genus only when an established species of the genus *Arthrobacter* was identified as the nearest relative, the peptidoglycan was shown to contain the diagnostic diamino acid lysine and a rod–coccus life cycle was observed.

At the time of writing, the genus *Arthrobacter* contains 70 species, including *Arthrobacter viscosus*, which is obviously misnamed, because it shares the highest 16S rRNA gene sequence similarity with members of the genus *Rhizobium* such as *Rhizobium gallicum* (98.1 % 16S rRNA gene sequence similarity to the type strain), *Rhizobium mongolense* (98.0 %) and *Rhizobium leguminosarum* (97.6 %) (Heyman et al., 2005). This affiliation is in agreement with chemotaxonomic traits of this species, including its quinone system (ubiquinone Q-10 predominant), fatty acid profile (hydroxy fatty acids present, C\text{18:1} and C\text{19:0 \alpha} cyclo predominant) and a polar lipid profile that suggests the presence of phosphatidylethanolamine (PE), monomethyl ethanolamine, phosphatidylglycerol (PG), diphosphatidylglycerol (DPG) and phosphatidylcholine (Collins, 1986). Phylogenetic analyses employing the neighbour-joining algorithm and embracing the vast majority of species of the genus *Arthrobacter* (Ding et al., 2009; Ganzert et al., 2011; Yassin et al., 2011b; Margesin et al., 2012) do not indicate a stable internal structure of the genus. This is indicated by the fact that many branching nodes are not supported by high bootstrap values (>70 %) and numerous nodes were not found with the maximum-likelihood or maximum-parsimony algorithm. Furthermore, certain species occupy varying positions in different trees, including *A. crystallopoietes*, *Arthrobacter nasiphocae*, *Arthrobacter roseus*, *Arthrobacter russicus*, *Arthrobacter sanguinis* and *Arthrobacter wolwensis*. However, it is worth mentioning deeply branching subline in all trees, often loosely associated with the ‘*Arthrobacter sulpureus*’ group (Fig. 1).

When representatives of additional members of the family *Micrococcaceae* are included in tree reconstructions in addition to species of the genus *Arthrobacter* (Busse et al., 2012), the phylogenetic relationships become more unclear. In this maximum-likelihood tree (Busse et al., 2012), several representatives of other genera branch within the radiation of established species of the genus *Arthrobacter*, indicating that the genus is not monophyletic.

In order to examine the phylogenetic arrangements within the genus *Arthrobacter*, including the most recently described species, 16S rRNA gene sequences were extracted from gene banks, multiply aligned using CLUSTAL_X (Thompson et al., 1997) and edited manually to remove gaps and ambiguous nucleotides using BioEdit (Hall, 1999). Phylogenetic calculations were carried out applying the maximum-likelihood, maximum-parsimony and neighbour-joining algorithms implemented in the PHYLIP package (Felsenstein, 2009). Confidence levels of branchings were determined by bootstrap analysis implemented in the PHYLIP package. The results from phylogenetic calculations carried out in the present study, including all established species of the genus *Arthrobacter* and the type species of other members of the family *Micrococcaceae*, applying the maximum-likelihood algorithm, are shown in Fig. 1. In this tree, only the branching of a few major lines is supported by high bootstrap values or by the same branching order in the maximum-parsimony and neighbour-joining algorithms. One of these sublines is designated the ‘*Arthrobacter protophormiae* group’, comprising the species *Arthrobacter creatinolyticus*, *Arthrobacter soli*, *A. protophormiae*, *A. uratoydanas*, *A. nicotianae*, *Arthrobacter arlaitensis*, *A. mysoensis*, *Arthrobacter bergerei* and *Arthrobacter ardeleyensis*. Within this subline, close relatedness is suggested from a relatively high bootstrap value between *A. ardeleyensis* and *A. bergerei*. The second subline, designated the ‘*Arthrobacter psychrolactophilus* group’, embraces the species *Arthrobacter alpinus*, *A. cryoconiti*, *Arthrobacter psychrochitinophilus*, *Arthrobacter livingstonensis*, *Arthrobacter stackebrandti* and *Arthrobacter psychrolactophilus*, and several internal nodes are supported by high bootstrap values. The third subline is designated the ‘*Arthrobacter agilis* group’ and contains the species *Arthrobacter flavus*, *A. agilis*, *Arthrobacter subterraneus*, *Arthrobacter tecti*, *Arthrobacter tumbae* and *Arthrobacter parietis*. High bootstrap support suggests that the latter four species form the stable core of the group. A fourth subline comprises *A. citreus*, *Arthrobacter luteolus*, *Arthrobacter koreensis* and *Arthrobacter gandavensis*. A deeply branching subline designated the ‘*Arthrobacter albus/cumminsii* group’ comprises the species *Arthrobacter albus* and *Arthrobacter cumminsii*. A rather stable branching position within the tree suggests a close relatedness between the pairs of species *Arthrobacter niigatensis/Arthrobacter deflueli*, *Arthrobacter gangotriensis/Arthrobacter antarcticus*, *Arthrobacter castellii/Arthrobacter pigmenti* and *Arthrobacter oryzae/Arthrobacter humicola*. It has to be mentioned here that the latter two species can be considered to be the nearest relatives of *A. pascens* and *A. globiformis* (the type species of the genus), with which they also share >98 % 16S rRNA gene sequence similarity, and the common branching node is also found with a second treeing algorithm (Fig. 1). The representatives of the ‘*Arthrobacter pigmenti* group’, the ‘*Arthrobacter citreus* group’ and the ‘*A. albus/cumminsii* group’ and *A. russicus*, *A. nasiphocae* and *A. crystallopoietes* are most distantly related to the type species of the genus and, apparently, more closely related to other members of the family *Micrococcaceae*. Rather separate positions within the tree are occupied by *A. wolwensis* and *A. sanguinis*. The existence of these major sublines is also shown in other phylogenetic
In a study on the diversity of isolates of the genus *Arthrobacter* from terrestrial deep-subsurface sediments, van Waasbergen et al. (2000) also investigated the recA phylogeny of their isolates in relation to 12 established species of the genus. On the basis of a fragment of the recA gene (360 bases), they showed that the reference species were separated into at least six groups. These authors could also show that the 16S rRNA gene and recA phylogenies were well in accordance with each other. Reanalysis of the recA-based phylogeny including sequences of type strains of the genus *Arthrobacter* from van Waasbergen et al. (2000) supplemented with additional sequences since available from gene banks supported the earlier study (Fig. 2), and is also in agreement with the 16S rRNA gene-based analyses, even though the complete set of species of the genus *Arthrobacter* was not always included in these calculations (Ganzert et al., 2011; Busse et al., 2012; Zhang et al., 2012).
phylogeny (Fig. 1). With the exception of Arthrobacter chlorophenolicus, all species were grouped in accordance with their 16S rRNA gene-based phylogeny. A. uratoxydans, A. arilaitensis, A. protophormiae and A. nicotianae form one clade corresponding to the ‘A. protophormiae group’. Another clade is formed by A. aurescens, A. ureafaciens, A. histidinolovorans and A. nicotinovorans, all assigned to the ‘Arthrobacter aurescens group’. A third clade is formed by Arthrobacter phenantherinivorans, A. oxydans and A. polychromogenes, which are members of the ‘Arthrobacter oxydans group’. Within this tree, species of the genus Micrococcus represent the deepest branching line of descent.

Chemotaxonomically, members of the genus Arthrobacter are rather diverse with respect to peptidoglycan structure, and differences in the quinone system and polar lipid profiles are also observed.

All species of Arthrobacter analysed contain the diagnostic diaminoc acid lysine, and the peptidoglycan type of arthrobacters is either A3α (only monocarboxylic amino acids present in the interpeptide chain) or A4α (dicarboxylic amino acids present in the interpeptide chain), as defined by Schleifer & Kandler (1972). However, additional differences occur in the presence of amino acids in the cross-linking interpeptide chain of both peptidoglycan types A3α and A4α (Table 1). To some extent, these amino acid compositions reflect relatedness as indicated by 16S rRNA gene sequence analyses. Where analysed, the amino acids of the interpeptide chain usually occur in the L-form. Among species that show the A3α peptidoglycan type, the interpeptide chain is composed of either Lys–Ala–Ser–Ala3 (only found in species of Arthrobacter reclassified in the genus Sinomonas and in Arthrobacter...
**Table 1. Overview of groupings within the genus *Arthrobacter***

In the descriptions of the quinone system, MK-8, MK-9 and MK-10 indicate a menaquinone with eight, nine and ten isoprenoic units in the side chain and (H2) indicates that one isoprenoic unit is dihydrogenated.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group designation</strong></td>
<td><strong>Peptidoglycan type</strong></td>
<td><strong>Quinone system</strong></td>
</tr>
<tr>
<td>'Globiformis' group† or 'A. globiformis citreus group'‡</td>
<td>A3x (Lys–Ala1–4 or Lys–Ala–Thr–Ala or Lys–Ser–Thr–Ala2–3) or Lys–Ser–Thr–Ala or Lys–Thr–Ala2</td>
<td>MK-9(H2)</td>
</tr>
<tr>
<td>Group I</td>
<td>Lys–Ser–Thr–Ala</td>
<td>'A. psychroactophilus group'</td>
</tr>
<tr>
<td>Group II</td>
<td>Lys–Ala–Thr–Ala</td>
<td>'A. aureus group'</td>
</tr>
<tr>
<td>Group III</td>
<td>Lys–Ala1–4</td>
<td>'A. globiformis group'</td>
</tr>
<tr>
<td>Group IV</td>
<td>Lys–Ser–Ala2–3</td>
<td>'Sinomonas group'</td>
</tr>
<tr>
<td>Group V</td>
<td>Lys–Thr–Ala2</td>
<td>'A. agilis group'</td>
</tr>
<tr>
<td>'Nicotianae' group† or 'A. nicotianae group'‡</td>
<td>A4x (Lys–Ala–Glu or Lys–Glu)</td>
<td>MK-8 and MK-9, MK-9 or MK-9 and MK-10</td>
</tr>
<tr>
<td>Group VI</td>
<td>Lys–Ala–Glu</td>
<td>'A. proteus group'</td>
</tr>
<tr>
<td>Group VII</td>
<td>Lys–Glu</td>
<td>'A. sulfureus group'</td>
</tr>
</tbody>
</table>

*Only considered by Keddie et al. (1986).
†According to Stackebrandt et al. (1983).
‡According to Keddie et al. (1986).
castellii), Lys–Ala2–Gly3,3–Ala(Gly) (only reported for A. nasiphoeae; Collins et al., 2002a) or Lys–Gly–Ala3 (only reported for A. roseus; Reddy et al., 2002). Peptidoglycan A4x variations detected in arthrobacters are Lys–Ala–Glu, Lys–Glu, Lys–Ser–Glu (only reported for A. cumminsiis; Funke et al., 1996), Lys–Ala–Glu (only reported for Arthrobacter rhombii; Osorio et al., 1999) or Lys–d–Asp (only reported for A. wolinensis; Funke et al., 1996). The quinone system of the majority of species of Arthrobacter contains predominantly the monosaturated menaquinone MK-9(H2), but a smaller number of established species contain the completely unsaturated menaquinones MK-8, MK-9 and/or MK-10. Rather unusual quinone systems were reported for Arthrobacter scleromae and A. phenanthrenivorans. They are composed of a combination of monosaturated and completely unsaturated menaquinones that also differ in the length of the isoprenoic side chains. A. scleromae was reported to contain MK-8(H2) and MK-10 (Huang et al., 2005), whereas A. phenanthrenivorans contains MK-8 and MK-9(H2) (Kallimanis et al., 2009). Combinations of completely unsaturated and monosaturated quinones are well known among the class Actinobacteria, but they usually share the same length of isoprenoic side chain. Hence, there are some reservations about the reproducibility of the quinone systems of these two species.

A fatty acid profile that contains predominantly iso- and anteiso-branched fatty acids with the major compound anteiso-C15:0 is common to all species of Arthrobacter. Usually, relatively large amounts of iso-C15:0, anteiso-C17:0 and/or iso-C16:0 are also present. Some species may also contain significant amounts of the straight-chain fatty acid C16:0. Unfortunately, based on the available data, the importance of fatty acid profiles for identification or differentiation of species of Arthrobacter cannot be evaluated. Fatty acid profiles of species of Arthrobacter have been reported that were analysed from biomass that was grown at different temperatures, with different medium compositions and without indication of the physiological age of the cells, were grown at different temperatures, with different medium compositions and without indication of the physiological age at which the cells were harvested. Dependence of the fatty acid composition in bacteria on cultural conditions and physiological age has been known for a long time, as demonstrated for representatives of different lines of descent, including cyanobacteria, aerobic endospore-formers, enterobacteria and the genera Listeria and Shewanella (Marr & Ingraham, 1962; Olson & Ingraham, 1975; Gill & Suisted, 1978; Bezbauh et al., 1988; Suzuki & Komagata, 1983; Abu Hatab & Gaugler, 1997; Nichols et al., 2000, 2002), and the importance of standardization of growth conditions and physiological age is also emphasized for fatty acid-based identification of bacteria (Sassar, 2009).

Keddie & Jones (1981) discussed the heterogeneity among species of Arthrobacter and, based mainly on the diamino acid in the peptidoglycan and differences in the DNA G+C content, they subdivided arthrobacters into three groups (Table 1). Species with lysine in the peptidoglycan were placed in the first category, designated the ‘globiformis’ group and A. citreus (assigned to this first group despite nutritional and other differences) or Arthrobacter sensu stricto, including the species Sinomonas atrocyanea (formerly Arthrobacter atrocyaneus), A. aurescens, A. crystalllopoietes, A. globiformis, A. histidinolovorans, A. ilicis (formerly Corynebacterium ilicis), A. nicotianae, A. oxydans, A. pascens, A. polychromogenes, A. ramosus, A. sulfureus (formerly ‘Brevibacterium sulfureum’), A. ureafaciens and A. citreus. The second group, designated the ‘simplex/tumescens’ group, comprised the species Pimelobacter simplex (formerly Arthrobacter simplex) and Terrabacter tumescens (formerly Arthrobacter tumescens), with l-diaminopimelic acid as the characteristic peptidoglycan diamino acid, a tetrahydrogenated menaquinone with eight isoprenoic acids in the side chain [MK-8(H4)] and a substantially higher DNA G+C content than those of the ‘globiformis’ group. The major characteristics of the third group, represented by Microbacterium terregens (formerly Arthrobacter terregens) and Microbacterium flavescens (formerly Arthrobacter flavescens) and hence designated the ‘terregens/flavescens’ group, were the presence of ornithine in the peptidoglycan and a DNA G+C content higher than that of the type strain of A. globiformis. Considering these differences, Keddie & Jones (1981) stated that the latter two groups should be removed from the genus Arthrobacter.

Stackebrandt et al. (1983) proposed the subdivision of the species of the genus Arthrobacter into two groups on the basis of their heterogeneity with respect to peptidoglycan types (A3x or A4x) and quinone systems [menaquinone MK-9(H2) or MK-8 and/or MK-9]. Species with monosaturated menaquinone MK-9(H2) and peptidoglycan type A3x were placed in the ‘globiformis’ group, including A. globiformis, A. oxydans, S. atrocyanea (formerly A. atrocyaneus) and A. ureafaciens. Species with completely unsaturated menaquinone MK-8 and/or MK-9 and peptidoglycan type A4x were placed in the ‘nicotianae’ group, including A. nicotianae, A. mysores, A. protophormiae, A. ura voxodans and A. sulfureus.

Also based on different quinone systems (monosaturated or completely unsaturated menaquinones) and variations in the interpeptide chain of the peptidoglycan (A3x or A4x), Keddie et al. (1986) divided the genus into the ‘A. globiformis/A. citreus group’ [S. atrocyanea (formerly A. atrocyaneus), A. aurescens, A. citreus, A. crystalllopoietes, A. globiformis, A. histidinolovorans, A. ilicis, A. oxydans, A. pascens, A. ramosus and A. ureafaciens] and the ‘A. nicotianae group’ (A. nicotianae, A. protophormiae, A. ura voxodans and A. sulfureus) (Table 1).

A subdivision of the genus Arthrobacter into seven groups (Table 1) was proposed by Komagata & Suzuki (1987) based on the detailed amino acid composition of the peptidoglycan interpeptide chain: group I with Lys–Ser–Thr–Ala (A. oxydans, A. polychromogenes); group II with Lys–Ala–Thr–Ala (A. aurescens, A. histidinolovorans, A. ilicis, A. nicotianae, A. ureafaciens); group III with Lys–Ala–Glu (A. crystalllopoietes, A. globiformis, A. pascens, A. ramosus); group IV with Lys–Ser–Ala2,3 (S. atrocyanea, formerly A. atrocyaneus); group V with Lys–Thr–Ala2
(A. citreus); group VI with Lys–Ala–Glu (A. nicotianae, A. creatinolyticus, A. uratoxidan, A. protophormiae); and group VII with Lys–Glu (A. sulfureus).

Though the first studies on polar lipids in arthrobacters were published more than 40 years ago, and interesting differences in the polar lipid compositions of arthrobacters were reported approximately 30 years ago, this approach has only rarely been considered in the description of novel species of *Arthrobacter* and their differentiation. In an early study, Shaw & Stead (1971) examined the polar lipid profiles of the type strains of *A. crystalllopoietes* and *A. pascens* and *A. globiformis* strain 616 and reported no significant qualitative differences. Major lipids in the three species were reported to be the phospholipids DPG, PG and phosphatidylinositol (PI) and the glycolipids monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol (DGDG) and dimannosyldiacylglycerol (DMDG) and probably also small amounts of trimannosyldiacylglycerol (TMDG) and tetramannosyldiacylglycerol (TeMDG). The three major glycolipids showed properties identical to those of three glycolipids of *A. globiformis* strain 616 identified earlier by Walker & Bastl (1967) as 3-O-β-D-galactosylglycerol-sn-1,2-diglyceride (MGDG), 3-[O-β-D-galactosylglycerol-(1→6)-O-β-D-galactosylglycerol]-sn-1,2-diglyceride (DGDG) and 3-[O-α-D-mannopyranosyl-(1→3)-O-α-D-mannopyranosyl]-sn-1,2-diglyceride (DMDG). Kostiw et al. (1972) also detected the glycolipids MGDG and DGDG in *A. crystalllopoietes*, but no indication of the presence of DMDG, TMDG or TeMDG was reported.

*A. ilicis* was the first species of the genus *Arthrobacter* to be described with the inclusion of the polar lipid profile (Collins et al., 1981). This species was described to contain DPG, PG, PI and two glycolipids designated G4 and G5 and supposed to represent the diglycosyldiacylglycerols DGDG or DMDG and the monoglycosyldiacylglycerol MGDG, respectively. Very similar polar lipid profiles were reported for the type strain of *A. aurescens*, a close relative of *A. ilicis*, and the more distantly related species *A. polychromogenes* (Collins et al., 1982b). The latter authors also detected two major glycolipids in *A. crystalllopoietes* that show chromatographic motilities similar to the monoglycosyldiacylglycerol and diglycosyldiacylglycerol of *A. ilicis*. In the same study, Collins et al. (1982b) reported on the polar lipid profiles of the type strain of *A. globiformis* and two strains of *A. citreus*, including the type strain. The type strain of *A. globiformis* showed a polar lipid profile that is qualitatively in agreement with that reported by Shaw & Stead (1971) for *A. globiformis* strain 616. It contains DPG, PG, PI and four glycolipids that exhibit different degrees of hydrophobicity, as indicated from their chromatographic motilities. One glycolipid spot shows high chromatographic motility, corresponding to the monoglycosyldiacylglycerol (G4) of *A. ilicis* and indicating the highly hydrophobic nature of the lipid. Another spot shows low chromatographic motility, indicating low hydrophobicity, and two spots show medium chromatographic motility, indicating medium hydrophobicity. One of these latter spots exhibits slightly higher chromatographic motility than the diglycosyldiacylglycerol (G5) of *A. ilicis*. The two strains of *A. citreus* were shown to contain DPG, PG, PI, a major glycolipid of medium hydrophobicity corresponding to the chromatographic motility of a diglycosyldiacylglycerol (G4) of *A. ilicis* and minor amounts of a second glycolipid of high hydrophobicity exhibiting the chromatographic motilities of monoglycosyldiacylglycerol (G4).

Amadi & Alderson (1982) reported that the type strains of *A. globiformis*, *A. crystalllopoietes*, *A. oxydans*, *A. polychromogenes* and *A. ramosus* all contain DPG, PG and PI in their polar lipid profiles, and they reported the variable presence of an unidentified phospholipid and the glycolipids G1 (supposed to represent MGDG, G3 (supposed to represent DMDG), G4 (supposed to represent DGDG) and G5 (supposed to represent TMDG). Reservations exist concerning the assumption that glycolipid G4 represents DGDG because, relative to the mannolipid DMDG, the chromatographic motility of the corresponding spot is in disagreement with that indicated by Shaw & Stead (1971) and Collins et al. (1982b). In *A. globiformis* and *A. oxydans*, four glycolipids were detected, G1, G3 and G5 in *A. crystalllopoietes* and *A. ramosus*, the glycolipids G1 and G3 were detected; and, in *A. polychromogenes*, the glycolipids G1, G3 and G5 were detected. The polar lipid profile of *A. ramosus* is well in agreement with its close relatedness to *A. ilicis* and *A. aurescens* (Fig. 1). The polar lipid profiles of *A. globiformis* and *A. polychromogenes* are most similar to those reported for these two species by Collins et al. (1982b). Though *A. oxydans* and *A. polychromogenes* are close phylogenetic relatives (Fig. 1), G4 was not reported for the latter species. Like in the report of Kostiw et al. (1972), *A. crystalllopoietes* was shown to contain only two glycolipids but, instead of DGDG, the presence of DMDG was reported. Collins & Kroppenstedt (1983) confirmed only the presence of the glycolipid of medium hydrophobicity in *A. citreus*. These authors also showed that the type strains of *A. nicotianae*, *A. protophormiae* (formerly *Brevibacterium protophormiae*) and *A. sulfureus* (formerly *Brevibacterium sulfureum*) lack PI and contain a single glycolipid of medium hydrophobicity. However, the glycolipid of *A. nicotianae* and *A. protophormiae* shows a chromatographic motility different from that of the glycolipid of *A. sulfureus*. Considering the information given by Keddie et al. (1986) and the report of Shaw & Stead (1971), the identity of the different glycolipids shown by Collins et al. (1982b) and Collins & Kroppenstedt (1983) can be determined. The glycolipid with the highest hydrophobicity corresponds to MGDG. The glycolipid with the lowest hydrophobicity corresponds to TMDG, because, in the first chromatographic dimension [corresponding to the solvent system applied by Shaw & Stead (1971)], it shows the same motility as PG (Shaw & Stead, 1971). Since the glycolipid of medium hydrophobicity of *A. sulfureus* was suggested to correspond to DGDG, whereas all other species of *Arthrobacter* studied contain DMDG (Keddie et al., 1986), the medium-hydrophobic glycolipid with the slightly higher Rf in both chromatographic
dimensions represents DGDG, whereas the other one corresponds to DMDG.

More recently, the chemical structures of the two major glycolipids of *A. globiformis* were analysed by Paściak *et al.* (2010). These authors confirmed the identity of one major glycolipid in *A. globiformis* to be monogalactosyldiacylglycerol but, in contrast to earlier reports, the other major glycolipid was identified as a monoacyldimannosylmonoaoylglycerol (MDMMG). The same two major glycolipids were also found in *A. scleromae*. Interestingly, MDMMG was also reported to be a major lipid in other members of the family *Micrococcaceae*, including the type strains of *S. atrocyanea* (Niepel *et al.*, 1997) and *Rothia dentocariosa*, and it was demonstrated that *Rothia mucilaginosa*, *Rothia amarae* and *M. luteus* contain a major glycolipid (Paściak *et al.*, 2002, 2010) that shows the same chromatographic motility as MDMMG detected in *A. globiformis*, *A. scleromae* and *R. dentocariosa*. For *A. globiformis* and *M. luteus*, this result is surprising, because Walker & Bastl (1967), Shaw & Stead (1971) and Pakkiri *et al.* (2004) reported that the major mannolipid of *A. globiformis* strain 616 and the type strain of *M. luteus* is DMDG. It appears unlikely that these species switch between DMDG and MDMMG depending on environmental conditions and/or physiological age, because it can be supposed that different enzymes would be required to transfer a fatty acid to the mannose and the glycerol. Hence, it has to be supposed that the result from one structural analysis of this mannolipid is due to an error.

*Arthrobacter psychrophenolicus*, a close phylogenetic relative of *A. sulfureus*, was reported to contain PG, DPG, PI and an unidentified glycolipid (Margesin *et al.*, 2004). The presence of PI in *A. psychrophenolicus* is surprising; this lipid would be expected to be absent, as in its close relative *A. sulfureus*. Since no image of the total lipid profile of this species was provided, it is not possible to evaluate whether the unidentified glycolipid corresponds to DGDG, found in *A. sulfureus*.

The most recently described species, *A. gyeryongensis* (Hoang *et al.*, 2014), was described to contain DPG, two unidentified glycolipids and two unidentified phospholipids. The two glycolipids show chromatographic motilities similar to a mono-glycosyldiacylglycerol and diglycosyldiacylglycerol and the two phospholipids might represent PG and PI. This polar lipid profile is similar to that of *A. ramosus*, with which *A. gyeryongensis* shares the highest 16S rRNA gene sequence similarity (98.2 % between the type strains).

The polar lipid profiles of *Arthrobacter castelli*, *Arthrobacter monumenti*, *A. pigmenti* and *A. parietis* (Heyrman *et al.*, 2005) share the presence of the lipids PG, DPG and PI and one or two unidentified glycolipids with many species of *Arthrobacter*. Unidentified phospholipids were also reported in some of these species. In contrast, *A. tecti* and *A. tumbae* possess, in addition to PG, DPG and PI, one unidentified phospholipid but no glycolipids (Heyrman *et al.*, 2005). *A. russicus* was reported to contain exclusively DPG, PG and PI (Li *et al.*, 2004b). The absence of any glycolipid in *A. russicus*, *A. tecti* and *A. tumbae* is most surprising, because the presence of a diglycosyldiacylglycerol is apparently a characteristic of members of the family *Micrococcaceae*. Hence, reanalyses of the polar lipid profiles of these three species would be desirable in order to confirm these unexpected traits. *A. livingstonensis* and *Arthrobacter cryotolerans* were reported to contain PG only (Ganzert *et al.*, 2011), but a polar lipid profile with only a single lipid appears unlikely, because bacterial cytoplasmic membranes are generally composed of several different lipid components. However, in the corresponding paper, the polar lipid profiles of the latter two species were incomplete. In addition to PG, HPLC-MS-MS analyses of the polar lipid profiles demonstrated that *A. livingstonensis* also contains PI, DPG and two types of unidentified glycolipid, and that *A. cryotolerans* contains DPG and an unidentified glycolipid (Kai Mangelsdorf, personal communication).

The detection of PE, as reported for *A. phenanthrenivorans*, *A. antarcticus*, *A. cupressi*, *A. flavus* and *A. roseus* (Kallimanis *et al.*, 2009; Pindi *et al.*, 2010; Reddy *et al.*, 2000, Zhang *et al.*, 2012), like the absence of any glycolipid, is surprising for representatives of the family *Micrococcaceae* because, like the presence of at least one glycolipid, the absence of PE appears to be a common trait in polar lipid profiles of members of the family. Hence, reanalyses of the polar lipids of these five species would also be desirable. However, exceptions concerning the presence of PE may occur in selected strains of *Arthrobacter*, as indicated from the observation that, in the genome of *Arthrobacter* sp. MA-N2, a sequence was annotated to encode a putative phosphatidylserine decarboxylase (Rüdiger Pukall, personal communication), which catalyses the formation of PE from phosphatidylserine. However, when compared to sequences of almost the same length in a FASTA search (Pearson & Lipman, 1988), the amino acid sequence showed the highest similarity to the phosphatidylserine decarboxylase of the epsilonproteobacterium *Sulfurimonas gotlandica* (50.6 %). Among hits sharing 40–50 % sequence identity, numerous betaproteobacterial strains, a few alpha-, gamma- and deltaproteobacterial strains and several fungal strains were found, but only two actinobacterial strains assigned to the genus *Frankia*. Two additional actinobacterial strains assigned to the genus *Streptomyces* show only 36.2 and 37.7 % identity. This observation suggests that this type of phosphatidylserine decarboxylase is not common among the actinobacteria. Hence, annotation as a phosphatidylserine decarboxylase in *Arthrobacter* sp. MA-N2 can be considered to be questionable.

In a pioneering study dealing with the dissection of the genus *Micrococcus* (Stackebrandt *et al.*, 1995), the authors also provided polar lipid data of groups I and II of *Arthrobacter*, corresponding to the ‘*A. globiformis*/*A. citreus* group’ and the ‘*A. nicotianae* group’, respectively. With reference to Jones & Collins (1986), the two groups were listed to contain DMDG and PI. Since no information
concerning lipids is provided in the cited chapter of Bergey’s Manual of Systematic Bacteriology except that the two groups of Arthrobacter differ with respect to their lipid composition; citation of this paper concerning the presence of DMDG and PI in both groups is apparently due to an error. This information is also not provided in the following chapter in Bergey’s Manual of Systematic Bacteriology dealing with the genus Arthrobacter (Keddie et al., 1986). These latter authors indicated that the majority of species of Arthrobacter analysed for polar lipids, including two species of the ‘A. nicotianae’ group, namely A. nicotianae and A. protophormiae, contain DMDG, whereas a single representative of the ‘A. nicotianae’ group, A. sulfureus, instead contains DGDG. Keddie et al. (1986) also emphasized the absence of PI in the representatives of the ‘A. nicotianae’ group. Hence, the information that both groups of the genus Arthrobacter are characterized by the presence of DMDG and PI in the polar lipid profile is misleading, because the members of the ‘A. nicotianae’ group lack PI and contain either DMDG or DGDG. It is important to point out this error because, to date, Stackebrandt et al. (1995) only has cited in eight papers in the IJSEM for the presence of DMDG and PI in both groups of Arthrobacter (Stackebrandt & Schumann, 2000; Altenburger et al., 2002; Li et al., 2004a, 2005c; Zhang et al., 2007; Schumann et al., 2009; Zhou et al., 2009; Yassin et al., 2011a).

Phylogenetic calculations have clearly demonstrated that the genus is not monophyletic but is mixed with other representatives of the family Micrococccaceae, including the genera Acaricocides, Auritidibacter, Citrococcus, Micrococcus, Nesterenkonia, Renibacterium, Sinomonas, Yaniella and Zhühengliuella (Munoz et al., 2011; Busse et al., 2012). Hence, careful evaluation of the taxonomy of the genus Arthrobacter is desirable. In this context, it is interesting that certain groupings within the radiation of the genus Arthrobacter, as indicated from comparative 16S rRNA gene sequence analyses, are also reflected by identical or at least highly similar chemotaxonomic traits.

The first move was made by Busse et al. (2012), by dissecting the genus Arthrobacter into 11 groups, mainly on the basis of robust phylogenetic clusters or high 16S rRNA gene sequence similarities and group-specific chemotaxonomic traits. A phylogenetic tree showing these groups and including most recently described novel species of Arthrobacter is shown in Fig. 1.

The ‘A. globiformis’ group contains candidates for the genus Arthrobacter sensu stricto. It is composed of the type species of the genus, A. globiformis, and A. pascens, which are closely related in all phylogenetic trees. A. humicola and A. oryzae were assigned to this group on the basis of high 16S rRNA gene sequence similarity to A. globiformis (>98%), similar peptidoglycan composition (Lys–Ala–Thr–Ala) corresponding to peptidoglycan structures A11.5/A11.6 (Schumann, 2011; http://www.dsmz.de/?id=449) and the quinone system menaquinone MK-9(H2). A. crystalllopoietes was tentatively assigned to the group on the basis of high 16S rRNA gene sequence similarity (97.6% between the type strains) and similar chemotaxonomic traits. However, in phylogenetic trees, A. crystalllopoietes is usually the sole species on a separate branch (Fig. 1; Ding et al., 2009; Ganzert et al., 2011; Yassin et al., 2011b; Margesin et al., 2012; Busse et al., 2012). The peptidoglycan structure also does not assign this species clearly to the ‘A. globiformis’ group. Hence, A. crystalllopoietes might be considered as the sole species of an-as-yet undefined group.

Though placed phylogenetically separate from the ‘A. globiformis’ group but without bootstrap support for the branching node (Zhang et al., 2012; Fig. 1), the recently described species A. cupressi might be considered another member of this group. The type strain shares the highest 16S rRNA gene sequence similarity with two members of the group, A. oryzae (97.7%) and A. humicola (97.3%), and 96.9 and 96.8% similarity with the type strains of A. pascens and A. globiformis, respectively. Like in species of the ‘A. globiformis’ group, its peptidoglycan structure shows the interpeptide bridge Lys–Alaβ, but the presence of a glycine bound to the α-carboxyl group of d-glutamic acid distinguishes it from other members of the group.

The ‘A. aurescens’ group is defined based on high 16S rRNA gene sequence similarity among its members (>97.5%), the presence of the major respiratory menaquinone MK-9(H2) and peptidoglycan of type A3α (Lys–Ala–Thr–Ala) corresponding to peptidoglycan structure A11.17. The group comprises six species, A. aurescens, A. histidinolovorans, A. ilicis, A. nicotinovorans, Arthrobacter nitroguajacolicus and A. ureafaciens.

The ‘A. oxydans’ group contains the species A. chlorophenolicus, A. delfluvii, A. niigatensis, A. oxydans, A. phenantherenivorans, A. polychromogenes, A. scleromae and Arthrobacter sulfonivorans, which share high 16S rRNA gene sequence similarities (>97%), MK-9(H2) as a major quinone [except A. scleromae, which was reported to contain predominantly MK-8(H2)] and a peptidoglycan type with Lys–Ser–Thr–Ala in the interpeptide corresponding to peptidoglycan structure A11.23 chain (A. phenantherenivorans was not analysed for its peptidoglycan type).

Arthrobacter equi, which was described recently by Yassin et al. (2011b), can be assigned to the ‘A. oxydans’ group for several reasons. It shares the highest 16S rRNA gene sequence similarity (97.9–99.2%) with members of this group, as well as the quinone system and the peptidoglycan structure A11.23. Another recently described species, A. siccitolerans (SantaCruz-Calvo et al., 2013), can also be considered to belong to the ‘A. oxydans’ group. It shows the same characteristic peptidoglycan structure and quinone system and shares high 16S rRNA gene sequence similarity with species of the ‘A. oxydans’ group (>98%).

Species of the ‘A. protophormiae’ group (including A. rhombi) were reported to share 95.5–99.7% 16S rRNA gene sequence similarity. The core of this group is composed
of the species A. aridicola, A. arilaitensis, A. bergeri, A. mycofem, A. nicotianae, A. protophormiae, A. soli and A. uratoydys, which share 96.7–99.7 % 16S rRNA gene sequence similarity. Except A. soli, which was not analysed for this trait, all species show peptidoglycan type A4z (Lys–Ala–Glu) corresponding to peptidoglycan structure A11.35. According to Stackebrandt et al. (1983), the glutamic acid in the interpeptide bridge of A. nicotianae, A. protophormiae and A. uratoydys occurs in the L-configuration. The quinone system contains exclusively completely unsaturated menaquinones, always with MK-8 as a major component (no data are available for A. arilaitensis, A. bergeri and A. soli). A. rhombi and A. creatinolyticus had been assigned to this group because they share 16S rRNA gene sequence similarity of >96.5 % with at least one representative of the group and show the presence of the group-specific peptidoglycan composition and/or quinone system. However, the presence of a quinone system menaquinone MK-9(H2) was later reported for the type strain of A. rhombi (Chen et al., 2009). Furthermore, the glutamic acid in the interpeptide chain occurs in the D-configuration (Osorio et al., 1999) and not in the L-configuration, like other members of the group. These two chemotaxonomic traits clearly distinguish A. rhombi from members of the ‘A. protophormiae group’. Hence, A. rhombi should not be considered to be a member of the ‘A. protophormiae group’. Since the combination of menaquinone MK-9(H2) and a peptidoglycan type A4z (variation Lys–Ala–D-Glu) is unique among arthrobacters, A. rhombi can be considered to be a representative of another group of the genus Arthrobacter that was not defined by Busse et al. (2012). Arthrobacter halodurans, which was described by Chen et al. (2009) to share its quinone system with A. rhombi and to belong to the same line of descent but with peptidoglycan type A4z (variation Lys–Ala–L–Glu), should hence not be considered a second species of this unnamed group of the genus Arthrobacter.

The ‘A. sulfureus group’ contains the species A. antarcticus, A. gangotrensis, Arthrobacter kerguelensis, Arthrobacter psychrophilonicus and A. sulfureus. In many trees, these species form a clade though, in Fig. 1, this branch is not supported by a significant bootstrap value (37 %). However, the same degree of branching is also shown in the neighbour-joining and maximum-parsimony tree (results not shown). 16S rRNA gene sequence similarity among the species is >97.0 %. All species share a peptidoglycan type A4z corresponding to peptidoglycan structure A11.54. According to Stackebrandt et al. (1983) and Margesin et al. (2004), the glutamic acid in the interpeptide bridge of A. sulfureus and A. psychrophilonicus occurs in the L-configuration. Quinone systems of representatives of this group exclusively contain completely unsaturated menaquinones (MK-8, MK-9 and/or MK-10).

Recently, the species Arthrobacter cryotolerans was described, which was placed phylogenetically at the root of the branch comprising the members of the ‘A. sulfureus group’ (Ganzert et al., 2011). This species contains a quinone system with MK-9 predominant and lesser amounts of MK-10, MK-8 and MK-7 and peptidoglycan type Lys–Glu. Since these traits are in accordance with the characteristics of the ‘A. sulfureus group’, the assignment of A. cryotolerans to this group appears to be justified.

Members of the ‘A. agilis group’ form a stable clade, as indicated by a high bootstrap value (89 %). The group contains the species A. agilis, A. flavus, A. parietis, A. subterraneus, A. tecti and A. tumbae, which share 97.3–99.6 % 16S rRNA gene sequence similarity, a peptidoglycan Lys–Thr–Ala2–3 corresponding to peptidoglycan structures A11.27/A11.28 and a quinone system with the predominant menaquinone MK-9(H2).

The four species of the ‘A. citreus group’, A. citreus, A. gandavensis, A. koreensis and A. luteolus, show high 16S rRNA gene sequence similarity (97.6–98.9 %), a peptidoglycan Lys–Thr–Ala2 corresponding to peptidoglycan structure A11.27 and the major menaquinone MK-9(H2).

The ‘A. psychrolactophilus group’ was defined based on 16S rRNA gene sequence similarities of >97.0 % among its members, a peptidoglycan with either Lys–Thr–Ala1–3 or Lys–Ala2 corresponding to peptidoglycan structures A11.25/A11.27/A11.28 and A11.5, respectively, and MK-9(H2) as the major respiratory quinone. Also, the ability of all members of this group to grow at low temperatures (0–4 °C) was also pointed out as a common characteristic. This group comprises the species A. psychrolactophilus, A. stackebrandtii, A. psychrochitiniphilus and A. alpinus.

Recently, two species of Arthrobacter, A. livingstonensis and A. cryoconiti, have been described and placed phylogenetically among the species representing the ‘A. psychrolactophilus group’ (Ganzert et al., 2011; Margesin et al., 2012). The two species share 97.0–97.9 and 97.7–98.3 % 16S rRNA gene sequence similarity, respectively, with the members of this group and exhibit the same quinone system and grow at low temperatures (6 and 1 °C, respectively). Data from analysis of the peptidoglycan of A. livingstonensis suggest that it is Lys–Thr–Ala2 (A11.25). This peptidoglycan type is similar to those found in A. psychrolactophilus, A. psychrochitiniphilus and A. alpinus. The peptidoglycan of A. cryoconiti is Lys–Ala4 (A11.7), resembling that of A. stackebrandtii, with Lys–Ala2 (A11.5).

Because of their almost identical quinone systems and peptidoglycan variations, the ‘A. agilis group’, the ‘A. citreus group’ and several species of the ‘A. psychrolactophilus group’ are distinguishable from each other only on the basis of 16S rRNA gene sequence similarity (94.2–96.8 %) and phylogenetic clustering. Each of these three groups forms a stable clade (Fig. 1). Hence, they can be considered to represent taxonomic entities separate from the core of the genus, Arthrobacter sensu stricto.

The ‘A. pigmei group’ comprises the two core species A. castelli and A. pigmeni, the type strains of which share 97.9 % 16S rRNA gene sequence similarity. Though sharing only 96.5 % 16S rRNA gene sequence similarity with
these two species and slightly higher similarity values with species of other groups, *A. monumenti* is placed at the root of this group in many phylogenetic trees. Common to the three species is a quinone system with the major menaquinone MK-9(H₂), the presence of the cell-wall sugars galactose and rhamnose and a peptidoglycan with four alanines in the interpeptide bridge. However, *A. castelli* shows a peptidoglycan type Lys–Ala–Ser–Ala 3 (not listed by Schumann, 1999). *A. pigmenti* and *A. monumenti* have peptidoglycan type Lys–Ala₄ corresponding to peptidoglycan structure A11.7.

The ‘*A. albus/cumminsi*’ group contains only the two species *A. albus* and *A. cumminsi*. The type strains of the two species share 99.1 % 16S rRNA gene sequence similarity and form a rather deeply branching subline within the genus *Arthrobacter* in phylogenetic trees. The two species possess peptidoglycan type A4G (Lys–Ala–Glu or Lys–Ser–Glu) corresponding to peptidoglycan structures A11.35 and A11.58, respectively. Analysis of the quinone system revealed the presence of the major menaquinone MK-8(H₂) in the two species. This menaquinone distinguishes this group unambiguously from the vast majority of species of the genus *Arthrobacter*. Only *A. scleromae* was reported to exhibit a similar quinone system, but this species is assigned to the ‘*A. oxydans*’ group, which shares the peptidoglycan type (Huang et al., 2005) and 16S rRNA gene sequence similarity.

The ‘*Sinomonas*’ group, as defined recently (Busse et al., 2012), harbours species of the genera *Sinomonas* and *Arthrobacter*. After reclassification of *Arthrobacter albidus* and *Arthrobacter echigonensis* as *Sinomonas albida* and *Sinomonas echigonensis* (Zhou et al., 2012), the ‘*Sinomonas*’ group no longer contains species of *Arthrobacter*, and hence it is not dealt with further in this discussion.

All other established species of the genus *Arthrobacter* not mentioned above were only tentatively assigned to certain groups or remained unassigned.

During this study on the taxonomy and chemotaxonomy of the genus *Arthrobacter*, reanalyses of the quinones and polar lipids of several species of *Arthrobacter* were carried out due to availability, including *A. globiformis*, *A. pascens*, *A. histidinolovorans*, *A. roseus*, *A. agilis*, *A. nicotinovorans*, *A. psychrophilenicus*, *A. polychromogenes*, *A. alpinus* and *A. cryoconitii*. Additionally, the polar lipids and quinones of *A. cumminsi* and *A. albus*, which had been described without including these traits, were also analysed. Extraction and analyses of quinones and polar lipids were carried out as described by Tindall (1990a, b). For HPLC analyses of quinones, the equipment described by Altenburger et al. (1996) or Stolz et al. (2007) was used.

*A. globiformis* DSM 20124ᵀ showed a polar lipid profile that was composed of the major lipids DPG, PG and glycolipid GL3 and moderate amounts of PI and glycolipid GL1 (Fig. 3a). Furthermore, minor to trace amounts of glycolipids GL2, GL4 and GL5 and two polar lipids (L1, L2) were detected. *A. pascens* WS 1766ᵀ showed a rather similar profile, differing mainly from *A. globiformis* DSM 20124ᵀ with respect to the amounts of certain lipids including DPG, PI and PI, glycolipids GL1, GL3, GL4 and GL5 and the polar lipids L2 and L3. The major differing characteristic of the lipid profile of *A. pascens* was the presence of the second highly hydrophobic glycolipid GL6 and absence of a second diglycosyldiacylglycerol (GL2; Fig. 3b) that was previously reported to be present in this species (Shaw & Stead, 1971). The qualitative polar lipid composition of *A. globiformis* DSM 20124ᵀ was in good agreement with the data reported by Shaw & Stead (1971). In contrast, equal amounts of the two diglycosyldiacylglycerols (GL2 and GL3) were not found, which might be related to the fact that, in the present study, the type strain of *A. globiformis* was subjected to analysis and not *A. globiformis* strain 616, which had been examined by the latter authors. The quinone system of *A. globiformis* DSM 20124ᵀ was composed of 85 % MK-9(H₂), 6 % MK-8(H₂), 6 % MK-10(H₂), 3 % MK-9 and traces (<1 %) of MK-7(H₂) and the quinone system of *A. pascens* WS 1766ᵀ was composed of 69 % MK-9(H₂), 28 % MK-10(H₂), 2 % MK-8(H₂) and 2 % MK-7(H₂).

The polar lipid profile of *A. polychromogenes* WS 1989ᵀ consisted of the major lipids DPG, PI, GL1 and GL3 and minor amounts of PG, three unidentified lipids (L1, L2 and L7) and GL5 (Fig. 3c). This profile is in excellent agreement with data reported for this species by Collins et al. (1992b). The quinone system was composed of 80 % MK-9(H₂), 13 % MK-10(H₂), 5 % MK-8(H₂), 1 % MK-7(H₂) and traces (<1 %) of MK-8, MK-9 and MK-10, which is similar to previous results for this species (Collins et al., 1979).

In *A. histidinolovorans* WS 1798ᵀ, the polar lipid profile was composed of the major lipids DPG, GL1, GL2 and PI and minor amounts of L1, L2 and GL5 (Fig. 3d). This polar lipid composition is most similar to those of *A. aurescens* (Collins et al., 1982b) and *A. ilicis* (Collins et al., 1981), close phylogenetic relatives of *A. histidinolovorans* (Fig. 1) that were placed in the ‘*A. aurescens*’ group (Busse et al., 2012). The quinone system was composed of 83 % MK-9(H₂), 9 % MK-8(H₂), 4 % MK-7(H₂), 3 % MK-10(H₂), 1 % MK-9 and traces (<1 %) of MK-7, MK-8 and MK-10; this quinone system confirms that MK-9(H₂) is the major menaquinone (Kodama et al., 1992), but other menaquinones are also present in significant amounts.

*A. agilis* DSM 20550ᵀ showed a rather simple polar lipid profile that consisted of the major lipids DPG, PG, PI and GL3 and minor amounts of GL5, L1 and L2. Furthermore, a reddish pigment spot could be detected (Fig. 3e). The fact that PE was not detected, which is in accordance with the majority of species of the genus *Arthrobacter*, but contrasts with its reported presence in the next phylogenetic relative, *A. flavus* (Reddy et al., 2000), supports concerns about the reliable identification of PE in the latter species.
The detection of PE and the absence of a diglycosyl diacylglycerol and other glycolipids in species of the family Micrococcaceae including species of the genus Arthrobacter is most surprising. The type strain of *A. roseus*, reported to contain PE and accessible in the course of this study, was subjected to reanalysis of its polar lipid profile. The results did not provide any indication of the presence of PE (Fig. 3f). Like other arthrobacters, it had a polar lipid profile containing predominantly DPG and PG, moderate amounts of PI, GL3 and three polar lipids (L1, L2, L4) and minor amounts of GL5 and two unidentified highly polar glycolipids GL8 and GL9, which so far are unique among polar lipid profiles of members of the genus *Arthrobacter*. These results suggest the need to emend the description of the species *A. roseus*.

The most complex polar lipid profiles were detected in *A. cumminsii* DSM 10493T (Fig. 3g) and *A. albus* DSM 13068T (results not shown). They were composed of the major lipids DPG, PG and GL3, unidentified phospholipids PL1, PL3 and PL5 and moderate to minor amounts of PI, two unidentified phospholipids (PL2 and PL4), two glycolipids (GL1, GL5) and four polar lipids (L1, L3, L5, L6). *A. albus* DSM 13068T contained minor amounts of an additional phospholipid. The quinone system of *A. cumminsii* DSM 10493T was composed of 85% MK-8(H2), 6% MK-8, 5% MK-7(H2), 3% MK-9(H2) and 1% MK-7 and the quinone system of *A. albus* DSM 13068T was composed of 83% MK-8(H2), 2% MK-8, 3% MK-7(H2) and 11% MK-9(H2).

The polar lipid profile of *A. nicotianae* WS1765T (Fig. 3h) consisted of the major lipids DPG, PG and GL3, moderate amounts of GL1 and polar lipids L1 and L2 and minor amounts of GL5. In agreement with the observation of Collins & Kroppenstedt (1983), PI was not detected, whereas the presence of GL1, GL5, L1 and L2 was not reported by these authors. The quinone system of *A. nicotianae* WS1765T contained 65% MK-8, 31% MK-9, 3% MK-7 and 1% MK-10, confirming earlier results published for this species (Yamada et al., 1976; Collins & Kroppenstedt, 1983).

In *A. psychrophenolicus* AG31T, the next phylogenetic relative of *A. sulfureus*, and the close relative *A. cryotolerans* LI3T, less complex polar lipid profiles were detected (Fig. 3i, j), showing only three major lipids, namely DPG, PG and GL2. Additionally, in *A. cryotolerans* LI3T, minor amounts of L1 roseus DSM 14508T (f), *A. cumminsii* DSM 10493T (g), *A. nicotianae* WS 1765T (h), *A. psychrophenolicus* AG31T (i) and *A. cryotolerans* LI3T (j) after two-dimensional TLC and detection with molybdatophosphoric acid. DPG, Diphosphatidylglycerol; PG, Phosphatidyglycerol; PI, phosphatidylinositol; GL1, monogalactosyldiacylglycerol (MGDG); GL2, digalactosyldiacylglycerol (DGDG); GL3, dimannosyldiacylglycerol (DMG); GL5, trimannosyldiacylglycerol (TMDG); GL4, GL6–GL9, unidentified glycolipids; L1–L5, unidentified lipids; PL1–PL4, unidentified phospholipids.
and L2 were detectable. As suggested from the very close phylogenetic relationship to A. sulfureus, which was reported to lack PL (Collins & Kroppenstedt, 1983), this lipid could also not be detected in A. psychrophilicus AG31T and A. cryotolerans LI3T. For A. psychrophilicus AG31T, this observation is in contrast to the data reported by Margesin et al. (2004). The quinone system of A. psychrophilicus AG31T was composed of 81 % MK-10, 13 % MK-9, 5 % MK-7, 1 % MK-8 and traces (<1 %) of MK-11, which is similar to that reported by Margesin et al. (2004).

Simple polar lipid profiles were detected in A. alpinus S6-3T and A. cryoconiti Cr6-08T (results not shown). Both strains exhibited a polar lipid profile consisting of DPG, PG, PI and GL3. Minor amounts of PL5 were detected in A. alpinus S6-3T. The similarity in the polar lipid profiles is in agreement with their close phylogenetic relationship (Margesin et al., 2012).

In order to identify the motility of DMDG in our chromatographic system, the type strain of Micrococcus luteus, which was reported to contain DMDG (Lennarz & Talamo, 1966; Pakkiri et al., 2004), was subjected to polar lipid analysis. The chromatographic motility of DMDG of M. luteus was compared by co-chromatography in a mixture of extracts of A. globiformis DSM 20124T and A. polychromogenes WS 1989T. After staining with α-naphthol, only a single positive spot was detected (results not shown), demonstrating that the diglycosylglycerides of M. luteus, A. globiformis and A. polychromogenes show the same chromatographic motility. Applying sophisticated methods, A. globiformis was described to contain MDMMG (Paściak et al., 2010) and M. luteus to contain DMDG (Pakkiri et al., 2004), but the results from the present study indicate either that MDMMG and DMDG show identical chromatographic motility in the system applied here or that, in one of the studies on the structure of the diglycosylglycerides of A. globiformis and M. luteus, the data from MS analysis were misinterpreted. Since the detailed chemical structure of the mannolipid cannot be clarified here, nor can the question be answered whether MDMMG and DMDG show the same chromatographic motility, the mannolipid will be designated dimannosylglyceride (DMG).

Except A. psychrophilicus and A. cryotolerans, all representatives of Arthrobacter examined in this study showed the presence of a major glycolipid (GL3) with chromatographic motility corresponding to DMG in A. globiformis and A. polychromogenes. Hence, it is justified to conclude that they all contain DMG. A. psychrophilicus showed the presence of a glycolipid with the chromatographic motility of a diglycosydialcglycerol corresponding to glycolipid Gb reported to be present in close phylogenetic relative A. sulfureus (Collins & Kroppenstedt, 1983). Glycolipid Gb was supposed to represent DGDG (Keddie et al., 1986). Hence, glycolipid GL2 of A. psychrophilicus and A. cryotolerans can also be identified as DGDG. This finding suggests extending the statement of Keddie et al. (1986) that, among arthrobacters, only A. sulfureus contains DGDG, to species included in the ‘A. sulfureus group’ as defined by Busse et al. (2012).

Using information concerning the chromatographic motility of glycolipids reported in the literature (Shaw & Stead, 1971; Collins et al., 1982b; Collins & Kroppenstedt, 1983; Keddie et al., 1986) and the results presented in this study, another two glycolipids (GL1 and GL5; Fig. 3) can be preliminarily identified. Glycolipid GL1 corresponds to MGDG, indicated by the highly hydrophobic chromatographic motility reported for this lipid (Shaw & Stead, 1971) and its presence in A. globiformis, A. pascens and A. crystallinopoietes. GL5 corresponds to TMDG, as it exhibits the same Rf as PG in the first chromatographic dimension (Shaw & Stead, 1971).

The presence of DGDG in arthrobacters that also contain DMG deserves closer consideration. Shaw & Stead (1971) reported almost equal amounts of these two diglycosyldiaclyglycerols in A. globiformis strain 616 and the type strains of A. pascens and A. crystallinopoietes (Shaw & Stead, 1971). In contrast, Collins et al. (1982b) showed a polar lipid profile for the type strain of A. globiformis that contained a major lipid with the chromatographic motility of DGDG and significantly smaller amounts of a lipid with the chromatographic motility of DMG whereas, in the present study, DMG was the predominant glycolipid in A. globiformis and DGDG was detected only in minor amounts (Fig. 3a). The presence of almost equal amounts of DGDG and DMG in A. pascens (Shaw & Stead, 1971) could not be reproduced in the present study, in which A. pascens showed DMG as the major glycolipid (Fig. 3b). For the type strain of A. crystallinopoietes, Collins et al. (1982b) could not reproduce the relatively large amounts of DGDG reported by Shaw & Stead (1971). This variability of the amounts of DGDG in polar lipid profiles of A. globiformis, A. pascens and A. crystallinopoietes may suggest that the expression of this glycolipid depends on growth conditions and/or the physiological age of biomass that was subjected to extraction of polar lipids. Hence, the presence of DGDG in arthrobacters that also contain significant amounts of DMG should not be given too much importance in drawing taxonomic conclusions.

Reservations concerning the polar lipid profiles reported for certain species of the genus Arthrobacter are based on the consideration that major polar lipids are rather conserved traits and are usually shared by all members of a genus or even family. The details were already discussed above and are summarized below. The polar lipid profiles reported for the majority of arthrobacters and other members of the family Micrococcaceae including representatives of the genera Auritidibacter, Citrococcus, Enteractinococcus, Kocuria, Micrococcus, Nesterenkonia, Rothia, Sinomonas, Yaniella and Zhichengliuella (Embley et al., 1984; Kovács et al., 1999; Altenburger et al., 2002; Wieser et al., 2002; Li et al., 2004a; 2005b; Zhang et al., 2007; Yassin et al., 2011a; Zhou et al., 2012; Cao et al., 2012) suggest that they generally contain a core polar lipid profile that is composed of DPG, PG and at least one glycolipid (either a
dimannosyl lipid or a digalactosyl lipid) and that PE is absent. The majority of species of *Arthrobacter* also contain PI, but members of the ‘*A. nicotianae* group’ (Keddie et al. 1986), recently split into the ‘*A. protophormiae* group’ and the ‘*A. sulfureus* group’ (Busse et al., 2012), do not. Species reported to deviate from these two core polar lipid profiles include *A. antarcticus* (Pindi et al., 2010), *A. cupressi* (Zhang et al., 2012), *A. flavus* (Reddy et al., 2000), *A. phenanthrenivorans* (Kallimanis et al., 2009), *A. psychrophenicolicus* (Margesin et al., 2004), *A. roseus* (Reddy et al., 2002), *A. russicus* (Li et al., 2004b), *A. tecti* and *A. tumbae* (Heyrman et al., 2005).

*A. phenanthrenivorans*, *A. antarcticus*, *A. flavus* and *A. roseus* were reported to contain PE and to lack any glycolipid. The close relatives of *A. phenanthrenivorans* (*A. oxydans* and *A. polychromogenes*), *A. antarcticus* (*A. sulfureus*) and *A. flavus* (*A. agilis, A. parietis, A. tecti* and *A. tumbae*) were shown to lack PE, and most of them have been shown to contain at least one glycolipid (Amadi & Alderson, 1982; Collins & Kroppenstedt, 1983; Heyrman et al., 2005; Fig. 3c, f, g, i, j). Hence, there is some probability that the named species contain at least one glycolipid and lack PE. The absence of PE and any other aminophospholipid and the presence of four glycolipids in the profile of *A. roseus* was shown in the present study (Fig. 3f), which is in line with the core polar lipid profile supposed to characterize members of the family *Micrococccaceae*. For *A. cupressi* (Zhang et al., 2012), a polar lipid profile was shown containing PE and a glycolipid exhibiting chromatographic motility that can be supposed to represent TMGD. The PE shows a chromatographic motility that would be expected for a diglycosyldiacylglycerol and, hence, it is supposed here that the corresponding spot had been misidentified. However, the presence of PE and the absence of a diglycosyldiacylglycerol has not been shown in any of the nearest related species to *A. cupressi* (>96.5 % 16S rRNA gene sequence similarity) analysed for polar lipids, including *A. globiformis*, *A. pascens*, *A. histidinolovorans*, *A. equi* and *A. aurescens* (Shaw & Stead, 1971; Collins et al., 1982b; Yassin et al., 2011b; Fig. 3a, b, d). *A. tecti*, *A. tumbae* and *A. russicus* differ from the core polar lipid profile in the absence of any glycolipid. However, the close relatives of *A. tumbae* and *A. tecti* (*A. agilis* and *A. parietis*) were shown to contain two glycolipids (Fig. 3e; Heyrman et al., 2005). Also, *Renibacterium salmoninarum*, the nearest phylogenetic relative of *A. russicus* (Pukall et al., 2006; Munoz et al., 2011; Busse et al., 2012; Fig. 1), was reported to contain glycolipids (Collins, 1982). Hence, the presence of a glycolipid in the polar lipid profile would be also expected in *A. russicus*. *A. psychrophenicolicus* was reported to contain PI, distinguishing it from its close relative *A. sulfureus*. Reanalysis of the polar lipid profile did not show the presence of PI in *A. psychrophenicolicus* (Fig. 3i), confirming the reservations expressed above. Because of these reservations, supported in two cases by data gained in this study, the reported polar lipid profiles of the other species of the genus *Arthrobacter* mentioned above are not considered in the following taxonomic conclusions.

Chemotaxonomic data that can be considered to be sufficiently conserved to characterize genera are summarized in Table 2. These data suggest that five groups of the genus *Arthrobacter*, as recently defined (Busse et al., 2012), are characterized by traits that distinguish them from the core of the genus *Arthrobacter* (*Arthrobacter sensu stricto*), which is composed of the type species of the genus, *A. globiformis*, and the additional species *A. pascens*, *A. oryzae* and *A. humicola*, and from other groups of the genus *Arthrobacter*, including the ‘*A. aurescens* group’, the ‘*A. oxydans* group’, the ‘*A. protophormiae* group’, the ‘*A. sulfureus* group’ and the ‘*A. albus/cumminsii* group’. Except the ‘*A. oxydans* group’, these groups form clades in the phylogenetic tree, but only the branching nodes of the ‘*A. aurescens* group’ and the ‘*A. albus/cumminsii* group’ were supported by another tree-calculating algorithm. High bootstrap support was only found for the branching node of the ‘*A. albus/cumminsii* group’; the branching node of the ‘*A. protophormiae* group’ was supported by a relatively high bootstrap value (Fig. 1). Members of the ‘*A. oxydans* group’ are split into several branches, with the core consisting of *A. oxydans*, *A. scleromae* and *A. polychromogenes* and the neighbouring species *A. defluvii*, *A. sulfonivorans* and *A. niigatensis*. The species pair *A. chlorophenicolicus*/*A. phenanthrenivorans* and the single species *A. equi* and *A. siccitolerans* each occupy separate positions in the vicinity of the core species of the group. However, each of the species *A. chlorophenicolicus*, *A. phenanthrenivorans*, *A. equi* and *A. siccitolerans* shares high 16S rRNA gene sequence similarity (98.4–98.9, 97.9–99.2, 97.6–99.2 and 98.4–99.3 %, respectively) with the core species and their closest neighbours. These data demonstrate that the high 16S rRNA gene sequence similarities between the species of the group are not well reflected in the phylogenetic tree (Fig. 1) and, hence, the splitting of the members of the ‘*A. oxydans* group’ is of little or no significance for taxonomic reorganization of the genus.

In conclusion, it is proposed to reclassify members of these five groups within the genus *Arthrobacter* in the novel genera *Paenarthrobacter* gen. nov. (the ‘*A. aurescens* group’), *Pseudarthrobacter* gen. nov. (the ‘*A. oxydans* group’), *Glutamicibacter* gen. nov. (the ‘*A. protophormiae* group’), *Paeniglutamicibacter* gen. nov. (the ‘*A. sulfureus* group’) and *Pseudoglutamicibacter* gen. nov. (the ‘*A. albus/cumminsii* group’).

The species *A. aurescens*, *A. histidinolovorans*, *A. ilicis*, *A. nicotinovorans*, *A. nitroguajacolicus* and *A. ureafaciens* are reclassified in the genus *Paenarthrobacter* gen. nov. The species *A. chlorophenicolicus*, *A. defluvii*, *A. equi*, *A. niigatensis*, *A. oxydans*, *A. phenanthrenivorans*, *A. polychromogenes*, *A. scleromae*, *A. siccitolerans* and *A. sulfonivorans* are reclassified in the genus *Pseudarthrobacter* gen. nov. The species *A. ardleyensis*, *A. arilaitensis*, *A. bergerei*, *A. creatinolyticus*, *A. mysores*, *A. nicotianae*, *A. protophormiae*, *A. soli* and *A. uratoxydans* are reclassified in the genus *Glutamicibacter* gen. nov. The species *A. antarcticus*, *A. cryotolerans*,
Table 2. Chemotaxonomic traits that distinguish *Paenarthrobacter* gen. nov., *Pseudarthrobacter* gen. nov., *Glutamicibacter* gen. nov., *Paeniglutamicibacter* gen. nov. and *Pseudoglutamicibacter* gen. nov. from each other and from *Arthrobacter sensu stricto* and other groups of the genus *Arthrobacter*

For the peptidoglycan composition, the three-digit code (Latin letter A/number/Greek letter $\alpha$) is that used by Schleifer & Kandler (1972). Information in parentheses indicates the type of interpeptide bridge. The four-digit code (Latin letter A/number/dot/number) specially indicates the composition of the interpeptide bridge (http://www.dsmz.de/?id=449). Data for reference genera were taken from the following studies: *Auritidibacter* (Yassin et al., 2011a); *Acaricomes* (Pukall et al., 2006); *Citricoccus* (Altenburger et al., 2002; Li et al., 2005a); *Kocuria* (Stackebrandt et al., 1995; Kovács et al., 1999; Reddy et al., 2003; Kim et al., 2004; Tvrzová et al., 2005; Li et al., 2006; Mayilraj et al., 2008); *Micrococcus* (Stackebrandt et al., 1995; Wieser et al., 2002; Liu et al., 2000, 2007); *Nesterenkonia* (Stackebrandt et al., 1995; Collins et al., 2002b; Li et al., 2004c, 2005b, 2008; Delgado et al., 2002; Li et al., 2004b; Chou et al., 2013). V, Variable; NA, no data available; MMK, menhlaquinone.

<table>
<thead>
<tr>
<th>Trait</th>
<th><em>Arthrobacter sensu stricto</em> ('<em>A. globiformis</em> group')</th>
<th><em>Paenarthrobacter</em> gen. nov. ('<em>A. aureus</em> group')</th>
<th><em>Pseudarthrobacter</em> gen. nov. ('<em>A. oxydans</em> group')</th>
<th><em>Glutamicibacter</em> gen. nov. ('<em>A. protophormiae</em> group')</th>
<th><em>Paeniglutamicibacter</em> gen. nov. ('<em>A. safraninii</em> group')</th>
<th><em>Pseudoglutamicibacter</em> gen. nov. ('<em>A. allius</em> commensali* group')</th>
<th><em>Arthrobacter sensu lato</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Quinone(s)</td>
<td>MK-9(H2)</td>
<td>MK-9(H2)</td>
<td>MK-9(H2)*</td>
<td>MK-8, MK-9</td>
<td>MK-8(H2)</td>
<td>NA</td>
<td>MK-8(H2)</td>
</tr>
<tr>
<td>Polar lipids</td>
<td>+</td>
<td>+</td>
<td>v</td>
<td>v</td>
<td>+</td>
<td>v</td>
<td>+</td>
</tr>
</tbody>
</table>

*Not listed at http://www.dsmz.de/?id=449.
†Glycolipid(s) was detected but chromatographic motility was not shown, which would be required in order to assign them to those identified as present in other species.
§Chromatographic motilities of two glycolipids detected in *Nesterenkonia suensis* suggest that they correspond to MGDG and DMG (Govender et al., 2013).
A. gangotriensis, A. kerguelensis, A. psychrophilicus and A. sulfureus are reclassified in the genus Paeniglutamicibacter gen. nov. Finally, the species A. cuminisi and A. albus are reclassified in the genus Pseudoglobatamicibacter gen. nov.

**Description of Paenarthrobacter gen. nov.**


The peptidoglycan type is A3\(\alpha\) (variation Lys–Ala–Thr–Ala; A11.17). The quinone system contains menaquinone MK-9(H\(_2\)) predominately. The polar lipid profile is composed of the major compounds diphosphatidylglycerol, phosphatidylglycerol, phosphatidylglycidoil, dimannosylglyceride and monogalactosyldiacylglycerol and minor amounts of trimannosyldiacylglycerol (Collins *et al.*, 1981, 1982b; this study). The major fatty acid is anteiso-C\(_{15}:0\). Large amounts of iso-C\(_{15}:0\), iso-C\(_{16}:0\), anteiso-C\(_{17}:0\) and iso-C\(_{14}:0\) may also be present. The G+C content of the genomic DNA is in the range 61.3–62.5 mol\%. The type species is *Paenarthrobacter aurescens*.

**Description of Paenarthrobacter aurescens comb. nov.**

*Paenarthrobacter aurescens* (au.res’cens. L. v. auresco to become golden; L. part. adj. aurescens becoming golden).


The description is as provided by Phillips (1953) for *Arthrobacter aurescens* with the following additional properties. Shares the characteristics listed in the genus description. According to Kodama *et al.* (1992), the predominant fatty acid of the type strain (IAM 12340\(^T\)) is anteiso-C\(_{15}:0\) followed by anteiso-C\(_{17}:0\). Minor fatty acids are iso-C\(_{15}:0\), iso-C\(_{16}:0\), iso-C\(_{17}:0\) and C\(_{16}:0\). Starch is hydrolysed. L-Arginine, L-asparagine, L-histidine, L-arabinose, D-galactose, D-glucose, D-ribose, D-xylose, histidinol, inositol, 4-aminoxybutyrate and \(p\)-hydroxybenzoate are utilized as carbon sources, but not \(L\)-leucine, butanediol or malonate. Citric acid, formic acid, propionic acid and uric acid are assimilated, but not adipic acid, benzoic acid, malonic acid or pimelic acid. Utilization of \(L\)-rhamnose and assimilation of glutaric acid are weak. Urea is formed from creatinine and uric acid. Nitrate is not reduced to nitrite, and no growth occurs in the presence of 10% (w/v) NaCl. Starch is not hydrolysed. Does not produce nicotine blue.

The type strain is ATCC 11442\(^T\)=CCUG 23888\(^T\)=CIP 106988\(^T\)=DSM 20115\(^T\)=IFO (now NBRC) 15510\(^T\)=JCM 2520\(^T\)=LMG 3822\(^T\)=VKM Ac-1978\(^T\). The G+C content of the DNA of the type strain is 62.6 mol\% (HPLC; Kodama *et al.*, 1992).

**Description of Paenarthrobacter histidinolovorans comb. nov.**

*Paenarthrobacter histidinolovorans* (his’ti.di.no.lo.vor’an. N.L. n. histidinolum histidinol; L. part. adj. vorans devouring, consuming; N.L. part. adj. histidinolovorans histidinol destroying).


The description is as provided by Adams (1954) for *Arthrobacter histidinolovorans* with the following additional properties. In addition, it shares the characteristics listed in the genus description. According to Kodama *et al.* (1992), the predominant fatty acids of the type strain (JCM 2520\(^T\)) are anteiso-C\(_{15}:0\), followed by anteiso-C\(_{17}:0\). Minor amounts of iso-C\(_{14}:0\), iso-C\(_{15}:0\), iso-C\(_{16}:0\), iso-C\(_{17}:0\), C\(_{14}:0\) and C\(_{16}:0\) and traces of C\(_{18}:0\) may also be present. L-Arginine, L-asparagine, L-histidine, L-arabinose, D-galactose, D-glucose, D-ribose, D-xylose, histidinol, inositol, 4-aminoxybutyrate and \(p\)-hydroxybenzoate are utilized as carbon sources, but not \(L\)-leucine, butanediol or malonate. Citric acid, formic acid, propionic acid and uric acid are assimilated, but not adipic acid, benzoic acid, malonic acid or pimelic acid. Utilization of \(L\)-rhamnose and assimilation of glutaric acid are weak. Urea is formed from creatinine and uric acid. Nitrate is not reduced to nitrite, and no growth occurs in the presence of 10% (w/v) NaCl. Starch is not hydrolysed. Does not produce nicotine blue.

The type strain is ATCC 11442\(^T\)=CCUG 23888\(^T\)=CIP 106988\(^T\)=DSM 20115\(^T\)=IFO (now NBRC) 15510\(^T\)=JCM 2520\(^T\)=LMG 3822\(^T\)=VKM Ac-1978\(^T\). The G+C content of the DNA of the type strain is 62.6 mol\% (HPLC; Kodama *et al.*, 1992).

**Description of Paenarthrobacter ilicis comb. nov.**

*Paenarthrobacter ilicus* (i.li’cis. N.L. n. Ilex -icus a scientific botanical genus name; N.L. gen. n. ilicus of Ilex).


The description is as provided by Collins *et al.* (1981) for *Arthrobacter ilicus* with the following additional properties. Shares the characteristics listed in the genus description. Predominant fatty acid of the type strain is anteiso-C\(_{15}:0\) followed by anteiso-C\(_{17}:0\). Minor fatty acids are iso-C\(_{15}:0\), iso-C\(_{16}:0\), and C\(_{16}:0\) and traces of iso-C\(_{14}:0\) may also be present (Kodama *et al.*, 1992). According to Kodama *et al.* (1992), the type strain is positive for utilization of the carbon sources \(L\)-arginine, \(L\)-asparagine, \(L\)-histidine, \(L\)-arabinose, \(D\)-galactose, \(D\)-glucose, \(D\)-ribose, \(D\)-xylose, histidinol, inositol, 4-aminoxybutyrate and \(p\)-hydroxybenzoate, but negative for \(L\)-leucine, butanediol and malonate. Citric acid, propionic acid and uric acid are assimilated, but not adipic acid, benzoic acid, glutaric acid, malonic acid or pimelic acid. Utilization of \(L\)-rhamnose and histidinol and assimilation of formic acid are weak. Urea is formed from uric acid but not from creatinine. Does not reduce nitrate to nitrite. Does not hydrolyse starch.

http://ijs.microbiologyresearch.org
not grow in the presence of 10 % (w/v) NaCl. Does not produce nicotine blue. According to Kotoučková et al. (2004), the type strain uses D-xylose, uridine and sucrose for respiration and uses propanoic acid, melibiose, 3-methyl glucose, raffinose and salicin weakly. Glucuronate is not utilized and arbutin and α-cyclodextrin are not utilized for respiration. Positive for pyrrolidonyl arylamidase and negative for elastase and oxidase. Aesculin and starch are not hydrolysed.

The type strain is ATCC 14264T = DSM 20138T = NCPPB 1228T.

**Description of Paenarthrobacter nicotinovorans** comb. nov.

*Paenarthrobacter nicotinovorans* (ni.co.ti.no.vo.ran.s. N. L. n. *nicotinum* nicotine; L. part. adj. *vorans* devouring, destroying; N.L. part. adj. *nicotinovorans* nicotine devouring).


The description is as provided by Kodama et al. (1992) for *Arthrobacter nicotinovorans* with the following additional properties. Shares the characteristics listed in the genus description, but the polar lipid profile is unknown.

The type strain is SAM 1563T (= ATCC 49919T = CIP 106990T = DSM 420T = IFO (now NBRC) 15511T = JCM 3874T = LMG 16253T = VKM Ac-1988T).

**Description of Paenarthrobacter nitroguajacolicus** comb. nov.

*Paenarthrobacter nitroguajacolicus* (ni.tro.gua.ja.co.li.cus. N.L. neut. n. *nitroguajacolum* nitroguajacol; L. suff. -icis -a -um used with the sense of belonging to; N.L. part. adj. *nitroguajacolicus* pertaining to nitroguaiacol).


The description is as provided by Kotoučková et al. (2004) for *Arthrobacter nitroguajacolicus* with the following additional properties. Shares the characteristics listed in the genus description, but the polar lipid profile is unknown.

The type strain is G2-1T (= CCM 4924T = DSM 15232T = JCM 14115T), isolated from forest soil.

**Description of Paenarthrobacter ureafaciens** comb. nov.

*Paenarthrobacter ureafaciens* (u.re.a.fa.ci.en.s. N.L. n. *urea* urea; L. v. *facio* to make, to produce; N.L. part. adj. *ureafaciens* urea-producing).

Basonym: *Arthrobacter ureafaciens* Clark 1955.

The description is as provided by Clark (1955) for *Arthrobacter ureafaciens* with the following additional properties. Shares the characteristics listed in the genus description, but the polar lipid profile is unknown. Predominant fatty acid of the type strain is anteiso-C₁₅ :₀ followed by anteiso-C₁₇ :₀. Minor fatty acids are iso-C₁₄ :₀, iso-C₁₅ :₀, iso-C₁₆ :₀, iso-C₁₇ :₀, C₁₆ :₀ and C₁₈ :₀ (Kodama et al., 1992). According to Kodama et al. (1992), the type strain does not reduce nitrate to nitrite, does not hydrolyse starch and does not grow in the presence of 10 % (w/v) NaCl. Utilizes L-arginine, L-asparagine, L-arabinose, D-galactose, D-glucose, D-xylose, inositol, 4-amino butyrate and p-hydroxy b enzoate, but not L-histidine, L-leucine, L-rhamnose, butanediol or malonate. Citric acid, formic acid, propanic acid and uric acid are hydrolysed, but not adipic acid, benzoic acid, malonic acid or pimelic acid. Utilization of D-ribose and histidinol and assimilation of glutaric acid are weak. Does not reduce nitrate to nitrite. Does not produce nicotine blue.

The type strain is ATCC 7562T = CIP 67.3T = DSM 20126T = IFO (now NBRC) 12140T = JCM 1337T = LMG 3812T = VKM Ac-1121T. The G + C content of the DNA of the type strain is 63.6 mol% (HPLC; Kodama et al., 1992).

**Description of Pseudarthrobacter gen. nov.**


The peptidoglycan type is A3α (variation Lys–Ser–Thr–Ala; A11.23). The quinone system contains major amounts of MK-9(H₄) but one species, *Pseudarthrobacter scleromae*, was originally described to contain predominantly MK-8(H₄). The polar lipid profile contains the major compounds diphasphatidylglycerol, phosphatidyl inositol, dimannosylglyceride, monogalactosyldiacylglycerol, moderate to major amounts of phosphatidylglycerol and minor amounts of trimannosyldiacylglycerol (Collins et al. 1982b; Amadi & Alderson, 1992; this study) may also be present. The major fatty acid is anteiso-C₁₅ :₀. Large amounts of iso-C₁₅ :₀, iso-C₁₆ :₀, anteiso-C₁₇ :₀ and iso-C₁₄ :₀ may also be present. The G + C content of the genomic DNA is in the range 62.0–71 mol%. The type species is *Pseudarthrobacter polychromogenes*.

**Description of Pseudarthrobacter polychromogenes** comb. nov.

*Pseudarthrobacter polychromogenes* (po.ly.chro.mo.ne.es. Gr. adj. *polys* many; Gr. n. *chroma* colour; Gr. v. *genname* produce; N.L. part. adj. *polychromogenes* producing many colours).


The description is as provided by Schippers-Lammertse et al. (1963) for *Arthrobacter polychromogenes* with the following additional properties. Shares the characteristics listed in the genus description. The predominant fatty acid is anteiso-C₁₅ :₀ followed by anteiso-C₁₇ :₀ and C₁₆ :₀. Minor fatty acids are iso-C₁₄ :₀, iso-C₁₅ :₀, iso-C₁₆ :₀, iso-C₁₄ :₀ and C₁₅ :₀ (Kodama et al., 1992).
The type strain is positive for utilization of the carbon sources L-arginine, L-asparagine, L-histidine, L-arabinose, D-galactose, D-glucose, L-rhamnose, D-ribose, D-xylene and malonate, but does not utilize inositol. Utilization of L-leucine and butanediol is weak. Citric acid, formic acid, propionic acid and uric acid are assimilated, but not adipic acid, benzoic acid, glutaric acid, malonic acid or pimelic acid. Reduces nitrate to nitrite. Does not produce nicotine blue (Kodama et al. 1992).

The type strain is ATCC 15216<sup>T</sup>=BCRC 12114<sup>T</sup>=CCUG 23891<sup>T</sup>=CIP 106989<sup>T</sup>=CGMCC 1.1927<sup>T</sup>=DSM 20136<sup>T</sup>=IFO (now NBRC) 15512<sup>T</sup>=KCTC 3384<sup>T</sup>=LMG 3821<sup>T</sup>=NCIB 10267<sup>T</sup>=VKM Ac-1955<sup>T</sup>. The G+C content of the genomic DNA of the type strain is 62.9 mol% (HPLC; Kodama et al., 1992).

### Description of *Pseudarthrobacter chlorophenolicus* comb. nov.

*Pseudarthrobacter chlorophenolicus* (chlo.ro.pheno.ni.li.cus. N.L. neut. n. *chlorophenolum* chlorophenol; L. masc. suff. -icus used with the sense of pertaining to; N.L. masc. adj. *chlorophenolicus* pertaining to chlorophenols).


The description is as provided by Westerberg et al. (2000) for *Arthrobacter chlorophenolicus* with the following additional properties. The peptidoglycan type, quinone system and fatty acid profile are in agreement with the genus description, but the polar lipid profile is unknown.

The type strain is strain A6<sup>T</sup> (=ATCC 700700<sup>T</sup>=CIP 107037<sup>T</sup>=DSM 12829<sup>T</sup>=JCM 12360<sup>T</sup>=KCTC 9906<sup>T</sup>=NCIMB 13794<sup>T</sup>).

### Description of *Pseudarthrobacter defluvii* comb. nov.

*Pseudarthrobacter defluvii* (de.flu'vi.i. L. gen. n. *defluvi* of sewage).


The description is as provided by Kim et al. (2008) for *Arthrobacter defluvii* with the following additional properties. The peptidoglycan type, quinone system and fatty acid profile are in agreement with the genus description, but the polar lipid profile is unknown.

The type strain is 4C1-a<sup>T</sup> (=KCTC 19209<sup>T</sup>=DSM 18782<sup>T</sup>).

### Description of *Pseudarthrobacter equi* comb. nov.

*Pseudarthrobacter equi* (e'qui. L. gen. n. *equi* of the horse).

Basonym: *Arthrobacter equi* Yassin et al. 2011.

The description is as provided by Yassin et al. (2011b) for *Arthrobacter equi* with the following additional properties. The peptidoglycan type, quinone system, polar lipid profile and fatty acid profile are in agreement with the genus description, but a glycolipid corresponding to trimannosyldiacylglycerol is not detected.

The type strain is IMMIB L-1606<sup>T</sup> (=CCUG 59597<sup>T</sup>=DSM 23395<sup>T</sup>).
Description of *Pseudarthrobacter phenanthrenivorans* comb. nov.


The description is as provided by Kallimanis et al. (2009) for *Arthrobacter phenanthrenivorans* with the following additional properties. In contrast to the genus description, the quinone system consists predominantly of MK-8 and relatively large amounts of MK-9(H2); the polar lipid profile contains phosphatidylethanolamine and glycolipids are absent.

The type strain is 4J27\textsuperscript{T} (=DSM 18606\textsuperscript{T}=JCM 16027\textsuperscript{T}=LMG 23796\textsuperscript{T}).

---

Description of *Pseudarthrobacter scleromae* comb. nov.

*Pseudarthrobacter scleromae* (scler.o.mae. N.L. gen. n. *scleromae* of scleroma, a hardened part).


The description is as provided by Huang et al. (2005) for *Arthrobacter scleromae* with the following additional properties. In contrast to the genus description, the major menaquinone is MK-8(H2). The polar lipid profile contains the major glycolipids dimannosylglyceride and monogalactosyldiacylglycerol, but the presence of other lipids has not been studied (Paściak et al., 2010).

The type strain is YH-2001\textsuperscript{T} (=CGMCC 1.3601\textsuperscript{T}=CIP 108992\textsuperscript{T}=DSM 17756\textsuperscript{T}=JCM 12642\textsuperscript{T}).

---

Description of *Pseudarthrobacter siccitolerans* comb. nov.


The description is as provided by SantaCruz-Calvo et al. (2013) for *Arthrobacter siccitolerans* with the following additional properties. Shares the peptidoglycan type, quinone system and fatty acid profile listed in the genus description, but the polar lipid profile is unknown.

The type strain is 4J27\textsuperscript{T} (=CECT 8257\textsuperscript{T}=LMG 27359\textsuperscript{T}). The G+C content of the genomic DNA of the type strain is 65.3 mol% (HPLC).

---

Description of *Pseudarthrobacter sulfonivorans* comb. nov.


The description is as provided by Borodina et al. (2002) for *Arthrobacter sulfonivorans* with the following additional properties. The peptidoglycan type, quinone system and fatty acid profile are in agreement with the genus description, but the polar lipid profile is unknown.

The type strain is ALL\textsuperscript{T} (=ATCC BAA-112\textsuperscript{T}=DSM 14002\textsuperscript{T}=IAM 15312\textsuperscript{T}=JCM 13520\textsuperscript{T}).

---

Description of *Glutamicibacter gen. nov.*

*Glutamicibacter* (Glut.ami.cib .ter. N.L. n. *acidum glutamicum* glutamic acid; N.L. masc. n. *bacter* a rod; N.L. masc. n. *Glutamicibacter* glutamic acid rod, referring to the presence of glutamic acid in the peptidoglycan interpeptide bridge).

Based on available data for the type species and other species assigned to the genus, the peptidoglycan type is A4\textsubscript{2} (Lys-Ala-Glu; A11.35). The quinone system contains exclusively unsaturated menaquinones (MK-8 and/or MK-9). The polar lipid profile is composed of the major compounds diphasphatidyglycerol, phosphatidyglycerol and dimannosylglyceride. Monogalactosyldiacylglycerol and minor amounts of trimannosylglyceride may also be present. Phosphatidylglycerol is absent. The major fatty acid is anteiso-C\textsubscript{17}:0. Relatively large amounts of iso-C\textsubscript{15}:0, iso-C\textsubscript{16}:0, anteiso-C\textsubscript{17}:0 and C\textsubscript{16}:0 may also be present. The G+C content of the genomic DNA is in the range 55–67 mol%. The type species is *Glutamicibacter protophormiae*.

---

Description of *Glutamicibacter protophormiae* comb. nov.

*Glutamicibacter protophormiae* (pro.to.phor‘mi.ae. N.L. gen. n. *protophormiae* of *Protophormia*, a genus of dipteran insects, referring to the isolation of the type strain from *Protophormia terraenovae*).


The description is as provided by Stackebrandt et al. (1983) for *Arthrobacter protophormiae* with the following additional properties. Shares the characteristics listed in the genus description (Collins & Kroppenstedt, 1983). According to Osorio et al. (1999), the type strain is negative for urease and \(\beta\)-galactosidase. Positive for nitrate reduction and pyrazinamidase. Assimilates cellobiose, glucosyl, maltose, turanose, D-xylene, L-arabinose, inositol, mannitol, melibiose, rhamnose, ribose,
Taxonomy of the genus Arthrobacter

Glutamicibacter ardleyensis (ard.le.yen.sis. N.L. masc. adj. ardleyensis pertaining to Ardley, where the type strain was isolated).


The description is as provided by Chen et al. (2005) for Arthrobacter ardleyensis with the following additional properties. The peptidoglycan composition, quinone system and fatty acid profile are in accordance with the genus description, but the polar lipid profile is unknown.

The type strain is An25\textsuperscript{T} (=CGMCC 1.3685\textsuperscript{T}=DSM 17432\textsuperscript{T}=JCM 12921\textsuperscript{T}).

Glutamicibacter arilaitensis (a.ri.lai.ten.sis. N.L. masc. adj. arilaitensis of Arilait, arbitrary name formed to honour Arilait, where the type strain was isolated).


The description is as provided by Irlinger et al. (2005) for Arthrobacter arilaitensis with the following additional properties. The peptidoglycan composition is in accordance with the genus description, but the quinone system and polar lipid and fatty acid profiles are unknown.

The type strain is Re117\textsuperscript{T} (=CIP 108037\textsuperscript{T}=DSM 16368\textsuperscript{T}=IAM 15318=JCM 13566\textsuperscript{T}).

Glutamicibacter bergerei (ber.ge’rei. N.L. gen. n. bergerei of Bergère, to honour Jean-Louis Bergère, a French microbiologist).


The description is as provided by Irlinger et al. (2005) for Arthrobacter bergerei with the following additional properties. The peptidoglycan composition is in accordance with the genus description, but the quinone system and polar lipid and fatty acid profiles are unknown.

The type strain is Ca106\textsuperscript{T} (=CCUG 52342=CIP 108036\textsuperscript{T}=DSM 16367\textsuperscript{T}).

Glutamicibacter creatinolyticus [cre.a.ti’no.ly’ti.cus. N.L. n. creatininum creatinine; N.L. masc. adj. lyticus (from Gr. masc. adj. lutikos) able to loose, able to dissolve; N.L. masc. adj. creatinolyticus creatinine-hydrolysing].

Basonym: Arthrobacter creatinolyticus Hou et al. 1998.

The description is as provided by Hou et al. (1998) for Arthrobacter creatinolyticus with the following additional properties. The peptidoglycan composition and quinone system are in accordance with the genus description, but the polar lipid and fatty acid profiles are unknown.

The type strain is CCM 4673\textsuperscript{T} (=CIP 105749\textsuperscript{T}=DSM 15881\textsuperscript{T}=GIFU 12498\textsuperscript{T}=JCM 10102\textsuperscript{T}=KCTC 9903\textsuperscript{T}=LMG 22054\textsuperscript{T}).

Glutamicibacter mysorens (my.so’rens. mysorens pertaining to Mysore, where the organisms were first isolated).


The description is as provided by Nand & Rao (1972) for Arthrobacter mysorens with the following additional properties. According to Wink (2012), the fatty acid profile is composed predominantly of anteiso-C\textsubscript{15:0} with moderate amounts of iso-C\textsubscript{15:0}, iso-C\textsubscript{16:0} and anteiso-C\textsubscript{17:0} and minor amounts of iso-C\textsubscript{14:0}, C\textsubscript{16:0}, iso-C\textsubscript{17:0} and C\textsubscript{18:0}. The patent strain ATCC 31021 has been shown to contain the peptidoglycan type Lys–Ala–Glu (Stackebrandt et al., 1983). Information concerning the quinone system and polar lipid profile is not available. According to Irlinger et al. (2005), the species is positive for β-galactosidase but negative for urease and gelatinase, hydrolysis of aesculin and reduction of nitrate to nitrite. It utilizes 5-aminovalerate, ((-)quinate, x-d(+)-glucose, d-xylene, d-ribose, l-arabinose, d-galactose and glycerol, but not dL-glycerate, lactose, l-rhamnose or d-xylitol.

The type strain is ATCC 33408\textsuperscript{T}=CIP 102716\textsuperscript{T}=JCM 11565\textsuperscript{T}=LMG 16219\textsuperscript{T}=NBRC 103060\textsuperscript{T}=NCIB (now NCIMB) 10583\textsuperscript{T}.

Glutamicibacter nicotianae (ni.co.ti.a’nae. N.L. gen. n. nicotianae of Nicotiana, the tobacco plant).


The description is as provided by Giovannozzi-Sermanni (1959) and emended by Stackebrandt et al. (1983) for Arthrobacter nicotianae with the following additional properties. Shares the characteristics listed in the genus.
The peptidoglycan composition and quinone system are in accordance with the genus description; the fatty acid profile is in agreement with the genus description, consisting of the major fatty acid anteiso-C₁₅:₀, followed by iso-C₁₅:₀ anteiso-C₁₇:₀ and iso-C₁₇:₀. Minor fatty acids are iso-C₁₆:₀ iso-C₁₄:₀ C₁₆:₀ and C₁₈:₀ (Funke et al., 1996). According to Osorio et al. (1999), the type strain is negative for β-galactosidase. Positive for nitrate reduction, urease and pyrazinamidase. Assimilates glycerol, ribose and N-acetylgalactosamine. Amygdalin, arbutin, cellobiose, D-arabitol, galactose, maltose, D-mannose, turanose, D-xylose, L-arabinose, mannitol, melibiose, rhamnose, salicin, starch, sucrose, trehalose, xyitol, gentiobiose and 5-ketogluconate are not assimilated.

The type strain is ATCC 21749T=CIP 102367T=DSM 20647T=IFO (now NBRC) 15515T=KCTC 3482T=NCDO 2282T=NCIMB 702282T=LMG 16220T=VKM Ac-1979T.

**Description of Paeniglutamicibacter**

*Paeniglutamicibacter* (Pae.ni.glu.ta.mi’i.bac’ter. L. adv. paene nearly, almost; N.L. masc. n. *Glutamicibacter* a bacterial genus name; N.L. masc. n. *Paeniglutamicibacter* almost *Glutamicibacter*).

The peptidoglycan type is A4(2) (Lys–Glu; A11.54). The quinone system contains exclusively unsaturated menaquinones, with MK-9 or MK-10 predominating. The polar lipid profile is composed of the major compounds diphytlyglycerol, phosphatidylglycerol and digalactosyldiacylglycerol. Phosphatidylglycerol is absent. The major fatty acid is anteiso-C₁₅:₀. Large amounts of iso-C₁₅:₀, iso-C₁₆:₀, anteiso-C₁₇:₀ and C₁₈:₀ may also be present. The G+C content of the genomic DNA is in the range 58–68 mol%. The type species is *Paeniglutamicibacter sulpfuricus*.

**Description of Paeniglutamicibacter sulpfuricus**

*Paeniglutamicibacter sulpfuricus* (sul.fu’re.us. L. masc. adj. *sulfuricus* of or like sulfur, meaning sulfur-coloured).

**Basonym:** *Arthrobacter uratoxydans* Stackebrandt et al. 1984.

The description is as provided by Stackebrandt et al. (1983) for *Arthrobacter uratoxydans* with the following additional properties. The peptidoglycan composition and quinone system are in accordance with the genus description; the fatty acid profile is in agreement with the genus description, consisting of the major fatty acid anteiso-C₁₅:₀, followed by iso-C₁₅:₀ anteiso-C₁₇:₀ and iso-C₁₇:₀. Minor fatty acids are iso-C₁₆:₀ iso-C₁₄:₀ C₁₆:₀ and C₁₈:₀ (Funke et al., 1996). According to Osorio et al. (1999), the type strain is negative for β-galactosidase. Positive for nitrate reduction, urease and pyrazinamidase. Assimilates glycerol, ribose and N-acetylgalactosamine. Amygdalin, arbutin, cellobiose, D-arabitol, galactose, maltose, D-mannose, turanose, D-xylose, L-arabinose, mannitol, melibiose, rhamnose, salicin, starch, sucrose, trehalose, xyitol, gentiobiose and 5-ketogluconate are not assimilated.

The type strain is ATCC 21749T=CIP 102367T=DSM 20647T=IFO (now NBRC) 15515T=KCTC 3482T=NCDO 2282T=NCIMB 702282T=LMG 16220T=VKM Ac-1979T.

**Description of Glutamicibacter soli comb. nov.**

*Glutamicibacter soli* (so’li. L. neut. gen. n. soli of soil).

**Basonym:** *Arthrobacter soli* Roh et al. 2008.

The type strain is as provided by Roh et al. (2008) for *Arthrobacter soli* with the following additional properties. The fatty acid profile is in accordance with the genus description. The quinone system is composed of MK-8, MK-9, MK-7 and MK-10 (55 : 36 : 2 : 1; Peter Schumann, personal communication), but neither the polar lipid profile nor the peptidoglycan composition is known.

The type strain is SYB2T (=KCTC 19291T=DSM 19449T).

**Description of Glutamicibacter uratoxydans comb. nov.**

*Glutamicibacter uratoxydans* (u.ra.to’xy.dans. N.L. n. uratum salt of uric acid; N.L. part. adj. *oxydans* oxidizing; N.L. part. adj. *uratoxydans* uric acid oxidizing).


The description is as provided by Stackebrandt et al. (1983) for *Arthrobacter uratoxydans*. Shares the properties given in the genus description.

The type strain is ATCC 19098T=CIP 106986T=DSM 20167T=IFO (now NBRC) 12678T=JCM 1338T=LMG 16694T=NRRL B-14730T.

**Description of Paeniglutamicibacter gen. nov.**

*Paeniglutamicibacter* (Pae.ni.glu.ta.mi’i.bac’ter. L. adv. paene nearly, almost; N.L. masc. n. *Glutamicibacter* a bacterial genus name; N.L. masc. n. *Paeniglutamicibacter* almost *Glutamicibacter*).

The peptidoglycan type is A4z (Lys–Glu; A11.54). The quinone system contains exclusively unsaturated menaquinones, with MK-9 or MK-10 predominating. The polar lipid profile is composed of the major compounds diphytlyglycerol, phosphatidylglycerol and digalactosyldiacylglycerol. Phosphatidylglycerol is absent. The major fatty acid is anteiso-C₁₅:₀. Large amounts of iso-C₁₅:₀, iso-C₁₆:₀, anteiso-C₁₇:₀ and C₁₈:₀ may also be present. The G+C content of the genomic DNA is in the range 58–68 mol%. The type species is *Paeniglutamicibacter sulfureus*. **Description of Paeniglutamicibacter sulfureus**

*Paeniglutamicibacter sulfureus* (sul.fu’re.us. L. masc. adj. *sulfuricus* of or like sulfur, meaning sulfur-coloured).

**Basonym:** *Arthrobacter sulfureus* Stackebrandt et al. 1984.

The description is as provided by Stackebrandt et al. (1983) for *Arthrobacter sulfureus*. Shares the properties given in the genus description.
**Description of Paeniglutamicibacter antarcticus comb. nov.**

*Paeniglutamicibacter antarcticus* (an.tarc’ti.cus. L. masc. adj. *antarcticus* southern, used to refer to the Antarctic, referring to the isolation of the type strain from Antarctic marine sediment).

Basonym: *Arthrobacter antarcticus* Pindi *et al.* 2010.

The description is as provided by Pindi *et al.* (2010) for *Arthrobacter antarcticus* with the following additional properties. Shares the quinone system and fatty acid profile listed in the genus description but, in contrast to the genus description, the polar lipid profile is reported to be composed only of phosphatidylethanolamine and diphosphatidylglycerol and not to contain any glycolipid.

The type strain is SPC26<sup>T</sup> (=LMG 24542<sup>T</sup>=NCCB 100228<sup>T</sup>).

**Additional information.** The information on the peptidoglycan composition given by Pindi *et al.* (2010) has not been added to the species description because it may cause confusion. In the species description for *Arthrobacter antarcticus*, the authors state ‘The peptidoglycan diaminoc acids are lysine and alanine and the acyl type is glutamic acid (A4<sub>x</sub> variation)’. Firstly, alanine is not a diaminoc acid. Secondly, from the presence of the amino acids lysine, alanine and glutamic acid, the peptidoglycan variation A4<sub>x</sub> cannot be concluded because the majority of bacteria with the diaminoc acid lysine also contain glutamic acid at position two of the peptide side chain. In order to reach conclusions on the peptidoglycan type, at least relative amounts of the different amino acids must be provided. Thirdly, the acyl type is never glutamic acid, but is either acetyl or glycolyl (Uchida & Seino, 1997).

**Description of Paeniglutamicibacter cryotolerans comb. nov.**

*Paeniglutamicibacter cryotolerans* (cry.o.to’ler.ans. N.L. pref. cryo from Gr. adj. kryós cold; L. part. adj. tolerans tolerating, enduring; N.L. part. adj. cryotolerans cold-tolerating).


The description is as provided by Ganzert *et al.* (2011) for *Arthrobacter cryotolerans* with the following additional properties and modifications. The peptidoglycan composition and quinone system are in accordance with the genus description. In contrast to the genus description, C<sub>18:0</sub> is the second most abundant fatty acid, and relatively large amounts of C<sub>16:0</sub>, C<sub>18:2</sub> and C<sub>18:1ω9c</sub> (5–11 %) are present. Contrary to the species description for *Arthrobacter cryotolerans*, the polar lipid profile contains diphosphatidylglycerol, phosphatidylglycerol, digalactosyldiacylglycerol and two minor lipids (Fig. 3).

The type strain is LI3<sup>T</sup> (=DSM 22826<sup>T</sup>=JCM 17806<sup>T</sup>=NCCB 100315<sup>T</sup>).

**Description of Paeniglutamicibacter gangotriensis comb. nov.**

*Paeniglutamicibacter gangotriensis* (gan.go’tri.en’sis. N.L. masc. adj. *gangotriensis* of or pertaining to the Indian Arctic station Dakshin Gangotri).


The description is as provided by Gupta *et al.* (2004) for *Arthrobacter gangotriensis* with the following additional properties. The peptidoglycan structure, fatty acid profile and quinone system are in accordance with the genus description. The polar lipid profile is unknown.

The type strain is Lz1y<sup>T</sup> (=CIP 108630<sup>T</sup>=DSM 15796<sup>T</sup>=JCM 12166<sup>T</sup>).

**Description of Paeniglutamicibacter kerguelensis comb. nov.**

*Paeniglutamicibacter kerguelensis* (ker.gu.el.en’sis. N.L. masc. adj. *kerguelensis* of or pertaining to the Kerguelen Islands, Antarctica).


The description is as provided by Gupta *et al.* (2004) for *Arthrobacter kerguelensis* with the following additional properties. The peptidoglycan structure, fatty acid profile and quinone system are in accordance with the genus description. The polar lipid profile is unknown.

The type strain is KGN15<sup>T</sup> (=CIP 108629<sup>T</sup>=DSM 15797<sup>T</sup>=JCM 12165<sup>T</sup>).

**Description of Paeniglutamicibacter psychrophenolicus comb. nov.**

*Paeniglutamicibacter psychrophenolicus* [psy.chro.phe.no’li.cus. Gr. adj. psychros cold; N.L. masc. adj. *psychrophenolicus* relating to phenol; N.L. masc. adj. *psychrophenolicus* relating to phenol (degradation) at low temperatures].


The description is as provided by Margesin *et al.* (2004) for *Arthrobacter psychrophenolicus*, except that the polar lipid profile is composed of diphosphatidylglycerol, phosphatidylglycerol and digalactosyldiacylglycerol and phosphatidylinositol is absent (Fig. 3). The type strain is AG31<sup>T</sup> (=CIP 108593<sup>T</sup>=DSM 15454<sup>T</sup>=IAM 15315<sup>T</sup>=JCM 13568=LMG 21914<sup>T</sup>).

**Description of Paeniglutamicibacter psychrophenolicus comb. nov.**

*Paeniglutamicibacter psychrophenolicus* (an.tarc’ti.cus. L. masc. adj. *antarcticus* southern, used to refer to the Antarctic, referring to the isolation of the type strain from Antarctic marine sediment).

Basonym: *Arthrobacter antarcticus* Pindi *et al.* 2010.

The description is as provided by Pindi *et al.* (2010) for *Arthrobacter antarcticus* with the following additional properties. Shares the quinone system and fatty acid profile listed in the genus description but, in contrast to the genus description, the polar lipid profile is reported to be composed only of phosphatidylethanolamine and diphosphatidylglycerol and not to contain any glycolipid.

The type strain is AG31<sup>T</sup> (=CIP 108593<sup>T</sup>=DSM 15454<sup>T</sup>=IAM 15315<sup>T</sup>=JCM 13568=LMG 21914<sup>T</sup>).
Description of *Pseudoglutamicibacter* gen. nov.


The peptidoglycan type is A4z (Lys–Ala–Glu; A11.35). The type strain is A4z (L-Lys–L-Ala–L-Glu, A11.35). Relatively large amounts of iso-C16 : 0 and anteiso-C17 : 0 are also present. The G+C content of the genomic DNA of the type strain of the type species is 60 mol%. The type species is *Pseudoglutamicibacter cumminsii*.

Status of the remaining species of the genus *Arthrobacter*

For this reason, a description of the genus *Arthrobacter* sensu lato is provided in order to cover species belonging to groups of the genus *Arthrobacter* that, so far, cannot be reclassified in novel genera. The description of *Arthrobacter* sensu lato is provided to replace the original description of Conn & Dimmick (1947) and the description given by Keddie (1974) because these descriptions are based exclusively on cultural, morphological and physiological characteristics that have to be considered not to be sufficiently conserved to characterize a genus.

**Emended description of the genus Arthrobacter**

*Conn and Dimmick 1947, emend. Koch et al. 1995 sensu lato*

Cells exhibit a rod–coccus cycle but exclusively coccoid cells may occur. The quinone system usually contains MK-9(H2) as the predominant compound, but almost equal amounts of MK-9(H2) and MK-8(H2) or MK-8(H2) as the major compound may occur. The peptidoglycan type is A3z [variations Lys–Ala–Ala–Lys–Thr–Ala–Ala, Lys–Ala–Ser–Ala, Lys–Gly–Ala–Ala, and Lys–Ala–Gly–Ala]; peptidoglycan type A4z may also be present, as reported for *Arthrobacter wolinii* (Lys–D-Asp) or in combinations with quinone system MK-9(H2) in *Arthrobacter rhombi* and *Arthrobacter halodurans* (Lys–L-Ala–D-Glu; Chen et al., 2009). The polar lipid profile contains predominantly diphosphatidylglycerol, phosphatidylglycerol, phosphatidylinositol and dimannosylglyceride. The fatty acid profile is dominated by anteiso- and iso-methyl-branched acids. The major fatty acid is usually anteiso-C15 : 0 . Fatty acids iso-C15 : 0 , iso-C16 : 0 and anteiso-C17 : 0 often contribute significantly to the profile. The type species is *Arthrobacter globiformis*.

**Emended description of Arthrobacter roseus**

*Reddy et al. 2002*

The description is as provided by Reddy et al. (2002), except that the polar lipid profile does not contain phosphahtidylethanolamine. In addition to phosphatidylglycerol and diphosphatidylglycerol, phosphatidylinositol,
dimannosyldiacylglycerol, trimannosyldiacylglycerol, three unidentified glycolipids and three polar lipids are also present.

The type strain is CMS 90rT (= CIP 107726T = CMC 90orT = CMS 90orT = DSM 14508T = JCM 11881T = MTCC 3712T = NCIMB 14039T).

Acknowledgements

The author is most grateful to Rüdiger Pukall, Peter Schuman and Ramon Rossello-Mora for critical reading of the manuscript and recommendations for improvements. Furthermore, Jean Euzéby's assistance in nomenclatural issues is highly appreciated. The author wishes to thank Peter Kämpfer, Rosa Margesin and Dirk Wagner for providing type strains.

References


Pseudoclavibacter helvolus

Int J Syst Evol Microbiol in Egypt. a novel actinobacterium isolated from a saline, alkaline desert soil

Microbiol 54

Brevibacterium helvolum bacterium, and classification of ‘

http://ijs.microbiologyresearch.org 35

http://ijs.microbiologyresearch.org 34

http://ijs.microbiologyresearch.org 33

http://ijs.microbiologyresearch.org 32

http://ijs.microbiologyresearch.org 31

http://ijs.microbiologyresearch.org 30

http://ijs.microbiologyresearch.org 29

http://ijs.microbiologyresearch.org 28

http://ijs.microbiologyresearch.org 27

http://ijs.microbiologyresearch.org 26

http://ijs.microbiologyresearch.org 25

http://ijs.microbiologyresearch.org 24

http://ijs.microbiologyresearch.org 23

http://ijs.microbiologyresearch.org 22

http://ijs.microbiologyresearch.org 21

http://ijs.microbiologyresearch.org 20

http://ijs.microbiologyresearch.org 19

http://ijs.microbiologyresearch.org 18

http://ijs.microbiologyresearch.org 17

http://ijs.microbiologyresearch.org 16

http://ijs.microbiologyresearch.org 15

http://ijs.microbiologyresearch.org 14

http://ijs.microbiologyresearch.org 13

http://ijs.microbiologyresearch.org 12

http://ijs.microbiologyresearch.org 11

http://ijs.microbiologyresearch.org 10

http://ijs.microbiologyresearch.org 9

http://ijs.microbiologyresearch.org 8

http://ijs.microbiologyresearch.org 7

http://ijs.microbiologyresearch.org 6

http://ijs.microbiologyresearch.org 5

http://ijs.microbiologyresearch.org 4

http://ijs.microbiologyresearch.org 3

http://ijs.microbiologyresearch.org 2

http://ijs.microbiologyresearch.org 1

http://ijs.microbiologyresearch.org


Yoon, J. H., Jung, S. Y., Kim, W., Nam, S. W. & Oh, T. K. (2006). Nesterenkonia jeotgalif sp. nov., isolated from jeotgal, a traditional


