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*

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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 tumescens*, 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 *'Pseudoclavi-
bacter helvolum'*, as stated by Busse et al. (2012). Originally,
the genus was described as follows:

**Arthrobacter** Fischer, emend.

**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 coccolid forms (arthro-
spores?) in old cultures, with intermediate stages that
may be clubs, branched forms, or short unbranched
filaments. Large (1 to 2 μ) spherical bodies are some-
times 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 Actinomycetecae. Colonies on poured
plates ordinarily 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

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**Abbreviations: DGDG, digalactosyldiacylglycerol; DMDG, dimannosyl-
diacylglycerol; DMG, dimannosylglyceride; DPG, diphosphatidylglycerol;
MDMMG, monoacyldimannosylmonoaoylglycerol; MGDG, monoacyl-
olglycerol; PE, phosphatidylethanolamine; PG, phosphatidyl-
glycerol; PI, phosphatidylinositol; TeMDG, tetramannosyldiacylglycerol;
TMDG, trimannosyldiacylglycerol.**

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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 % (Tₜ). 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.,...
2012), Arthrobacter cupressi (Zhang et al., 2012), Arthrobacter siccitolerans (Santa Cruz-Calvo et al., 2013) and Arthrobacter geryongensis (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 %) (Heyrman 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, C₁₈:1 and C₁₉:0 a cyclo predominant) and a polar lipid profile that suggests the presence of phosphatidylethanolamine (PE), monomethyl ethanolamine, phosphatidyglycerol (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 san- guinis and Arthrobacter wulfensis. However, it is worth mentioning that the latter species always occupies a rather deep branching subline in all trees, often loosely associated with the ‘Arthrobacter sulfureus group’ (Fig. 1). When representatives of additional members of the family Micrococaceae 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 Micrococaceae, 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. uratoxydans, A. nicotianae, Arthrobacter arlaitensis, A. mysorens, 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. cryoconitii, Arthrobacter psychrochitinophilus, Arthrobacter livingstonensis, Arthrobacter stackebrandtii 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 subturanus, 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 album/cumminsi group’ comprises the species Arthrobacter album and Arthrobacter cumminsi. A rather stable branching position within the tree suggests a close relatedness between the pairs of species Arthrobacter niagatensis/Arthrobacter deflavi, Arthrobacter gangotiensis/Arthrobacter antarcticus, Arthrobacter castelli/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. album/cumminsi 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 Micrococaceae. Rather separate positions within the tree are occupied by A. wulfensis and A. sanguinis. The existence of these major sublines is also shown in other phylogenetic
Fig. 1. Maximum-likelihood tree based on 16S rRNA gene sequences (1224 nt). The 16S rRNA gene sequence of *Microbacterium lacticum* DSM 20427 was used as an outgroup. Bootstrap values >60 based on 100 replicates are given at nodes. Bar, 0.1 substitutions per nucleotide position. The names of groups of the genus *Arthrobacter*, as defined by Busse et al. (2012), are provided in shaded rectangles. Filled squares indicate that the same branching node with bootstrap support >60% was found after analyses using either the maximum-parsimony or neighbour-joining algorithm. Type species of genera are shown in bold face.
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. histidinoluvorans* and *A. nicotinovorans*, all assigned to the ‘*Arthrobacter aurescens* group’. A third clade is formed by *Arthrobacter phenanthrenivorans*, *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 A3\(\alpha\) (only monocarboxylic amino acids present in the interpeptide chain) or A4\(\alpha\) (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 A3\(\alpha\) and A4\(\alpha\) (Table 1). To some extent, these amino acid compositions reflect relatedness as indicated by 16S rRNA gene sequences. Where analysed, the amino acids of the interpeptide chain usually occur in the L-form. Among species that show the A3\(\alpha\) peptidoglycan type, the interpeptide chain is composed of either Lys–Ala\(_{1-3}\), Lys–Ala–Thr–Ala, Lys–Ser–Thr–Ala, Lys–Thr–Ala\(_{1-3}\), Lys–Ala–Ser–Ala\(_{1}\) (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 \((\text{H}_2)\) indicates that one isoprenoic unit is dihydrogenated.

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<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–Ala–4 or Lys–Ala–Thr–Ala or Lys–Ser–Ala, or Lys–Ser–Thr–Ala)</td>
<td>MK-9((\text{H}_2))</td>
</tr>
<tr>
<td>Group I</td>
<td>Lys–Ser–Thr–Ala</td>
<td>'A. pyrophilus group'</td>
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<tr>
<td>Group II</td>
<td>Lys–Ala–Thr–Ala</td>
<td>'A. oxydans group'</td>
</tr>
<tr>
<td>Group III</td>
<td>Lys–Ala–4</td>
<td>'A. aurescens group'</td>
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<tr>
<td>Group IV</td>
<td>Lys–Ser–Ala, or Lys–Ser–Ala, or Lys–Ser–Ala</td>
<td>'Sinomonas group'</td>
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<tr>
<td>Group V</td>
<td>Lys–Thr–Ala</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, or MK-9 and MK-10</td>
</tr>
<tr>
<td>Group VI</td>
<td>Lys–Ala–Glu</td>
<td>'A. sulfureus group'</td>
</tr>
<tr>
<td>Group VII</td>
<td>Lys–Glu</td>
<td>'A. albus/cumminsii group'</td>
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*Only considered by Keddie et al. (1986).†According to Stackebrandt et al. (1983).‡According to Keddie et al. (1986).
castelli), Lys–Ala–Gly\(_{2.3}\)–Ala\(\text{Gly}\) (only reported for A. nasiphoae, Collins et al., 2002a) or Lys–Gly–Ala, (only reported for A. roseus, Reddy et al., 2002). Peptidoglycan A4\(\text{x}\) variations detected in arthrobacters are Lys–Ala–Glu, Lys–Glu, Lys–Ser–Glu (only reported for A. cumminsis; Funke et al., 1996), Lys–Ala–Glu (only reported for Arthrobacter rhombi; Orsorio et al., 1999) or Lys–Ala–Glu (only reported for A. woluwensis; Funke et al., 1996). The quinone system of the majority of species of Arthrobacter contains predominantly the monosaturated menaquinone MK-9\(\text{H}_2\), 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\(\text{H}_3\) and MK-10 (Huang et al., 2005), whereas A. phenanthrenivorans contains MK-8 and MK-9\(\text{H}_2\) (Kalimanis 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-C\(15:0\) is common to all species of Arthrobacter. Usually, relatively large amounts of iso-C\(15:0\), anteiso-C\(17:0\) and/or iso-C\(16:0\) are also present. Some species may also contain significant amounts of the straight-chain fatty acid C\(16:0\). 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 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; Bezaruruah 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. crystallopoietes, 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/tunescens’ group, comprised the species Pimelobacter simplex (formerly Arthrobacter simplex) and Terrabacter tunescens (formerly Arthrobacter tunescens), with LL-diaminopimelic acid as the characteristic peptidoglycan diamino acid, a tetrahydrogenated menaquinone with eight isoprenoic acids in the side chain [MK-8\(\text{H}_4\)] 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 (A3\(\text{x}\) or A4\(\text{x}\)) and quinone systems (menaquinone MK-9\(\text{H}_2\)) or MK-8 and/or MK-9. Species with monosaturated menaquinone MK-9\(\text{H}_2\) and peptidoglycan type A3\(\text{x}\) 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 A4\(\text{x}\) were placed in the ‘nicotianae’ group, including A. nicotianae, A. mysorens, A. protophormiae, A. ura oxydans and A. sulfureus.

Also based on different quinone systems (monosaturated or completely unsaturated menaquinones) and variations in the interpeptide chain of the peptidoglycan (A3\(\text{x}\) or A4\(\text{x}\)), Keddie et al. (1986) divided the genus into the ‘A. globiformis/A. citreus group’ [S. atrocyanea (formerly A. atrocyaneus), A. aurescens, A. citreus, A. crystallopoietes, 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 oxydans 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. protophormiae; group III with Lys–Ala\(_{1-4}\) (A. crystallopoietes, A. globiformis, A. pascens, A. ramosus); group IV with Lys–Ser–Ala\(_2\) (S. atrocyanea, formerly A. atrocyaneus); group V with Lys–Thr–Ala\(_2\)
(A. citreus); group VI with Lys–Ala–Glu (A. nicotianae, A. creatinolyticus, A. uratoxydans, 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. crystallopoietes 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 3-0-β-D-galactosylpyranosyl-sn-1,2-diglyceride (MGDG), 3-[O-β-D-galactosylpyranosyl-(1→6)-O-β-D-galactosylpyranosyl]-sn-1,2-diglyceride (DDGD) 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. crystallopoietes, 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. crystallopoietes that show chromatographic moieties 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 moieties. 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 (G₃) 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 moieties of monoglycosyldiacylglycerol (G₅).

Amadi & Alderson (1982) reported that the type strains of A. globiformis, A. crystallopoietes, 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), G₂ (supposed to represent DMG), 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, G₂, G₄ and G₅; in A. crystallopoietes 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), G₅ was not reported for the latter species. Like in the report of Kostiw et al. (1972), A. crystallopoietes 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 R₃ 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 Pasičak *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 monoacyldimannosylmonooacylglycerol (MDMMM). The same two major glycolipids were also found in *A. scleromae*. Interestingly, MDMMM 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 (Pasičak *et al.*, 2002, 2010) that shows the same chromatographic motility as MDMMM 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 MDMMM 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, 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 Systemic 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 Systemic 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. spheroides, 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 been 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 Acaricoccces, Auritidiobacter, Citrococcus, Micrococcces, Nesterenkonia, Renibacterium, Sinomonas, Yaniiella and Zhihengiue (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–2–3) 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. crystalliopoiotes 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. crystallopoietes 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. crystallopoietes 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. oxydans (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–Ala2, but the presence of a glycine bound to the z-carboxyl group of d-glutamic acid distinguishes it from other members of the group.

The ‘A. aurecens 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 A3z (Lys–Ala–Thr–Ala) corresponding to peptidoglycan structure A11.17. The group comprises six species, A. aurecens, A. histidinolovorans, A. ilicis, A. nicotinovorans, Arthrobacter nitroguajacolicus and A. ureafaciens.

The ‘A. oxydans group’ contains the species A. chloropheno- licus, A. defluvii, A. niigatensis, A. oxydans, A. phenanthreni- vorans, A. polychromogenes, A. scleromae and Arthrobacter sulfoni- vorans, 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. phenanthrenivorans 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. cicitorolans (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. protophormia 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. arlaiensis, A. arlaiensis, A. bergerei, A. mysorens, A. nicotianae, A. protophormiae, A. soli and A. uratoxidans, 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. uratoxidans 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. arlaiensis, A. bergerei 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) and a peptidoglycan 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. gaudreensis, 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).

Recently, two species of Arthrobacter, A. livingstonensis and A. cryoconitii, 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 members of this group and exhibit the same quinone system and 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.

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 % similarity between representatives of the three groups) 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. pigmeni 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–Ala3 (not listed by Schumann, 2011; http://www.dsmz.de/?id=449), whereas *A. pigmenti* and *A. monumenti* have peptidoglycan type Lys–Ala4 corresponding to peptidoglycan structure A11.7.

The ‘*A. albus/cumminsii*’ group contains only the two species *A. albus* and *A. cumminsii*. 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 A4z (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 quinone system 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’, with which it shares the peptidoglycan type (Huang et al., 2005) and high 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 echigensis* as *Sinomonas albidae* and *Sinomonas echigensis* (Zhou et al., 2012), the ‘*Sinomonas* group’ no longer contains species of *Arthrobacter*, and hence it is not be 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. psychrophilicus*, *A. polychromogenae*, *A. alpinus* and *A. cryoconiti*. Additionally, the polar lipids and quinones of *A. cumminsii* 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, PG and PI, glycolipids GL1, GL3, GL4 and GL5 and the polar lipids L2 and L3. The major differing characteristic in the lipid profile of *A. pascens* was the presence of the second highly hydrophobic glycolipid GL6 and absence of a second diglycosylglycerol (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 diglycosylglycerols (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. polychromogenae* 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. (1982b). 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. aurecens* (Collins et al., 1982b) and *A. ilicus* (Collins et al., 1981), close phylogenetic relatives of *A. histidinolovorans* (Fig. 1) that were placed in the ‘*A. aurecens* 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. psychrophilicus* 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
and L2 were detectable. As suggested from the very close phylogenetic relationship to *A. sulfureus*, which was reported to lack PI (Collins & Kroppenstedt, 1983), this lipid could also not be detected in *A. psychrophenolicus* AG31<sup>T</sup> and *A. cryotolerans* LI3<sup>T</sup>. For *A. psychrophenolicus* AG31<sup>T</sup>, this observation is in contrast to the data reported by Margesin et al. (2004). The quinone system of *A. psychrophenolicus* AG31<sup>T</sup> 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* S6-3<sup>T</sup> and *A. cryoconiit Cr6-08<sup>T</sup>* (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* S6-3<sup>T</sup>. 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 20124<sup>T</sup> and *A. polychromogenes* WS 1989<sup>T</sup>. 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 (Paščiak 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. psychrophenolicus* and *A. cryotolerans*, all representatives of *Arthrobacker* 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. psychrophenolicus* showed the presence of a glycolipid with the chromatographic motility of a diglycosylglycerol corresponding to glycolipid Gb reported to be present in its close phylogenetic relative *A. sulfureus* (Collins & Kroppenstedt, 1983). Glycolipid Gb was supposed to represent DGDG (Keddie et al., 1986). Hence, glycolipid GL2 of *A. psychrophenolicus* 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. crystallopoietes*. GL5 corresponds to TMDG, as it exhibits the same *R<sub>t</sub>* 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 diglycosyldiacylglycerols in *A. globiformis* strain 616 and the type strains of *A. pascens* and *A. crystallopoietes* (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. crystallopoietes*, 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. crystallopoietes* 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 *Arthrobacker* 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 *Zhihengliella* (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 (Keddi 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. psychrophenolicus (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. sulphureus) 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 Micrococcaceae. 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 TMDG. The PE shows a chromatographic motility that would be expected for a diglycosydialcglycerol and, hence, it is supposed here that the corresponding spot had been misidentified. However, the presence of PE and the absence of a diglycosydialcglycerol 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. histidinolivorans, 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. psychrophenolicus was reported to contain PI, distinguishing it from its close relative A. sulphureus. Reanalysis of the polar lipid profile did not show the presence of PI in A. psychrophenolicus (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. sulphureus’ 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. chlorophenolicus/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. chlorophenolicus, 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. sulphureus’ group’) and Pseudoglutamicibacter gen. nov. (the ‘A. albus/cumminsii group’).

### Table 2. Chemotaxonomic traits that distinguish *Pseudarthrobacter* 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 x) 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/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: *Auritidiibacter* (Yassin et al., 2011); *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; Maylirárová et al., 2006; Zhou 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., 2004, 2005b, 2008; Delgado et al., 2006; Yoon et al., 2006; Govender et al., 2013); *Renibacterium* (Embley et al., 1983; Kusser & Fiedler, 1983); *Rothia* (Collins et al., 2000; Fan et al., 2002; Pašciak et al., 2002; Li et al., 2004b; Chou et al., 2008); *Sinomonas* (Niewel et al., 1997; Zhou et al., 2009, 2012); *Yaniella* (Li et al., 2004a, 2005c; Chen et al., 2010); *Zhihengiuella* (Zhang et al., 2007; Tang et al., 2009; Hamada et al., 2013). V, Variable; NA, no data available; MMK, methylmenaquinone.

<table>
<thead>
<tr>
<th>Trait</th>
<th><em>Auritidiibacter</em></th>
<th><em>Acaricomes</em></th>
<th><em>Citricoccus</em></th>
<th><em>Kocuria</em></th>
<th><em>Micrococcus</em></th>
<th><em>Nesterenkonia</em></th>
<th><em>Renibacterium</em></th>
<th><em>Rothia</em></th>
<th><em>Sinomonas</em></th>
<th><em>Yaniella</em></th>
<th><em>Zhihengiuella</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Quinone(s)</td>
<td>MK-9(H$_2$)</td>
<td>MK-9(H$_2$)</td>
<td>MK-9(H$_2$)$^+$</td>
<td>MK-9 or MK-10</td>
<td>MK-8(H$_2$)</td>
<td>MK-8(H$_2$)</td>
<td>NA</td>
<td>MK-9(H$_2$)</td>
<td>MK-9(H$_2$)</td>
<td>MK-9(H$_2$)</td>
<td>MK-9(H$_2$)</td>
</tr>
<tr>
<td>Polar lipids</td>
<td>MGDG</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>v</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>TMDG</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
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<td>–</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Trait</th>
<th><em>A. pheanthreivorans</em></th>
<th><em>A. nasiphocerca</em></th>
<th><em>A. agilis</em></th>
<th><em>A. citreus</em></th>
<th><em>A. psychrotrophus</em></th>
<th><em>A. pigmenti</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Quinone(s)</td>
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<td>MK-9(H$_2$)</td>
<td>MK-9(H$_2$)</td>
<td>MK-9(H$_2$)</td>
<td>MK-9(H$_2$)</td>
<td>MK-9(H$_2$)</td>
</tr>
<tr>
<td>Peptidoglycan</td>
<td>A3x (Lys–Gly)</td>
<td>A11.56</td>
<td>A11.6</td>
<td>A11.6</td>
<td>A11.56</td>
<td>A11.56</td>
</tr>
<tr>
<td>Polar lipids</td>
<td>GL2</td>
<td>–</td>
<td>–</td>
<td>GL(s)$^+$</td>
<td>GL(s)$^+$</td>
<td>GL2</td>
</tr>
</tbody>
</table>

* A. *pheanthreivorans* was reported to contain predominantly MK-8 and MK-9(H$_2$) and A. *scleromae* to contain MK-8(H$_2$) as the predominant quinone (Huang et al., 2005; Kallimanis et al., 2009).
†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. gangotiensis, A. kerguelensis, A. psychrophenicus and A. sulfureus are reclassified in the genus Paeniglutamicibacter gen. nov. Finally, the species A. cumminsi and A. albus are reclassified in the genus Pseudoglutamicibacter gen. nov.

Description of Paenarthrobacter gen. nov.
The peptidoglycan type is A3ε (variation Lys–Ala–Thr–Ala; A11.17). The quinone system contains menaquinone MK-9(H2) predominantly. The polar lipid profile is composed of the major compounds diphosphatidyglycerol, phosphatidylglycerol, phosphatidylinositol, dimannosyglyceride 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. aurescere 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-histidine, L-arabinose, D-galactose, D-glucose, D-ribose, D-xylene, histidinol, inositol, 4-amino butyrate 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 23885^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.s. 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-xylene, histidinol, inositol, 4-amino butyrate 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 23885^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 ilicis (i.li’cis. N.L. n. Ilex -icus a scientific botanical genus name; N.L. gen. n. ilicis of Ilex).
The description is as provided by Collins et al. (1981) for Arthrobacter ilicis 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}, iso-C_{14:0} 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-xylene, histidinol, inositol, 4-amino butyrate 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. Does
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-xylene, uridine and sucrose for respiration and uses propionic acid, melibiose, 3-methyl glucose, raffinose and salcin weakly. Gluconate is not utilized and arbutin and z-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’rans. 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 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 polychromogenes comb. nov.

Pseudarthrobacter (Pseu.dar’thro.bac.ter. Gr. adj. pseudēs false; N. L. masc. n. Arthrobacter a bacterial genus name; N. L. masc. n. Pseudarthrobacter the false Arthrobacter).

The peptidoglycan type is A3α (variation Lys–Ser–Thr–Ala–11.23). The quinone system contains major amounts of MK-9(H2) but one species, Pseudarthrobacter scleromae, was originally described to contain predominantly MK-8(H2). The polar lipid profile contains the major compounds diphosphatidylglycerol, phosphatidylglycol, dimannosylglyceride, monoglactosylglyceride, 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 ureafaciens comb. nov.

Pseudarthrobacter ureafaciens (po.ly.chro.mo’ge.nes. Gr. adj. polys many; Gr. n. chroma colour; Gr. v. gennaio 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-C₁₄:₀, iso-C₁₆:₀, 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, D-ribose, D-xylose 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 15216T=BCRC 12114T=CCUG 23891T=CIP 106989T=CGMCC 1.1927T=DSM 20136T=IFO (now NBRC) 15512T=KCTC 3384T=LMG 3821T=NCIB 10267T=VKM Ac-1955T. The G+C content of the genomic DNA of the type strain is 62.9 mol% (HPLC; Kodama et al., 1992).

The description is as provided by Kim et al. 1992. The type strain is strain A6T (CCTCC AB 206012T=JCM 30147T).

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

Pseudarthrobacter chlorophenolicus (chlo.ro.phe.no’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 A6T (=ATCC 700700T=DSM 12829T=JCM 12360T=KCTC 9906T=NCIMB 13794T).

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

Pseudarthrobacter defluvii (de.flu’vi.i. L. gen. n. defluvii 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-aT (=KCTC 19209T=DSM 18782T).

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

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


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 trimannosyl-diaclyglycerol is not detected.

The type strain is IMMIB L-1606T (=CCUG 59597T=DSM 23395T).

**Description of Pseudarthrobacter niigatensis comb. nov.**

Pseudarthrobacter niigatensis (ni.i.ga.ten’sis. N.L. masc. adj. niigatensis pertaining to the Niigata region, Japan).


The description is as provided by Ding et al. (2009) for Arthrobacter niigatensis 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 LC4T (=CCTCC AB 206012T=JCM 30147T).

**Description of Pseudarthrobacter oxydans comb. nov.**

Pseudarthrobacter oxydans (o.xy’dans. N.L. part. adj. oxydans oxidizing).

Basonym: Arthrobacter oxydans Sguros 1954.

The description is as provided by Sguros (1954) for Arthrobacter oxydans with the following additional properties. The quinone system, fatty acid profile, polar lipid profile and peptidoglycan type are in accordance with the genus description but, in addition, the polar lipid profile is also reported to contain digalactosyldiacylglycerol (Amadi & Alderson, 1982). The predominant fatty acid is anteiso-C15:0 followed by anteiso-C17:0 C16:0 and iso-C16:0 and iso-C15:0. Minor fatty acids are iso-C14:0 and C14:0 and C15:0 (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 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.

The type strain is ATCC 14358T=BCRC (formerly CCRCC) 11573T=CCUG 17757T=CIP 107005T=DSM 20119T=HAMBI 1857T=IFO (now NBRC) 12138T=IMET 10684T=JCM 2521T=LMG 3816T=NCIMB 9335T=NRIC 0154T=VKM Ac-1114T. The G+C content of the genomic DNA of the type strain is 63.1 mol% (HPLC; Kodama et al., 1992).
**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 Sphe3 T (=DSM 18606 T=JCM 16027 T=LMG 23796 T).

**Description of Pseudarthrobacter scleromae comb. nov.**

*Pseudarthrobacter scleromae* (scler.o ma. 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 T (=CGMCC 1.3601 T=CIP 108992 T=DSM 17756 T=JCM 12642 T).

**Description of Pseudarthrobacter siccitolerans comb. nov.**


Basonym: *Arthrobacter siccitolerans* SantaCruz-Calvo *et al.* 2013.

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 T (=CECT 8257 T=LMG 27359 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 T (=ATCC BAA-112 T=DSM 14002 T=IAM 15312 T=JCM 13520 T).

**Description of Glutamicibacter gen. nov.**

*Glutamicibacter* (Glu.ta.mi’ce.bac’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 (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 diphosphatidylglycerol, phosphatidylglycerol and dimannosyldiacylglycerol. Monogalactosyldiacylglycerol and minor amounts of trimannosyldiacylglycerol may also be present. Phosphatidylinositol is absent. The major fatty acid is anteiso-C₁₅ : 0. Relatively large amounts of iso-C₁₅ : 0, iso-C₁₆ : 0, anteiso-C₁₇ : 0 and C₁₆ : 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 β-galactosidase. Positive for nitrate reduction and pyrazinamidase. Assimilates cellobiose, glycerol, malate, 5-ketogluconate, Amygdalin, arbutin, D-arabitol, galactose, D-mannose, turanose, D-xylose, L-arabinose, inositol, mannitol, melibiose, rhamnose, ribose, etc.
saccharose, starch, trehalose, xylitol, gentiobiose and N-acetylgalactosamine are not assimilated.

The type strain is ATCC 19271<sup>T</sup> = CIP 106987<sup>T</sup> = DSM 20168<sup>T</sup> = IFO (now NBRC) 12128<sup>T</sup> = JCM 1973<sup>T</sup> = LMG 16324<sup>T</sup> = VKM Ac-2104<sup>T</sup>.

**Description of Glutamicibacter ardleyensis**

*Glutamicibacter ardleyensis* (ard.ley.en’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<sup>T</sup> (= CGMCC 1.3685<sup>T</sup> = DSM 17432<sup>T</sup> = JCM 12921<sup>T</sup>).

**Description of Glutamicibacter arilaitensis**

*Glutamicibacter arilaitensis* (ari.lai.ten’sis. N.L. masc. adj. arilaitensis pertaining to 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 fatty acid profiles are unknown.

The type strain is Re117<sup>T</sup> (= CIP 108037<sup>T</sup> = DSM 16368<sup>T</sup> = IAM 15318 = JCM 13566<sup>T</sup>).

**Description of Glutamicibacter bergerei**

*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 fatty acid profiles are unknown.

The type strain is Ca106<sup>T</sup> (= CCUG 52342 = CIP 108036<sup>T</sup> = DSM 16367<sup>T</sup>).

**Description of Glutamicibacter creatinolyticus**

*Glutamicibacter creatinolyticus* [cre.ati’no.ly’ti.cus. N.L. n. creatinum creatinine; N.L. masc. adj. lyticus (from Gr. masc. adj. lutikos) able to loosen, able to dissolve; N.L. masc. adj. creatinolytics creatinine-hydrolysing].


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<sup>T</sup> (= CIP 105749<sup>T</sup> = DSM 15881<sup>T</sup> = Gifu 12498<sup>T</sup> = JCM 10102<sup>T</sup> = KCTC 9903<sup>T</sup> = LMG 22054<sup>T</sup>.

**Description of Glutamicibacter mysorens**

*Glutamicibacter mysorens* (mys.o’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<sub>15:0</sub> with moderate amounts of iso-C<sub>15:0</sub>, iso-C<sub>16:0</sub> and anteiso-C<sub>17:0</sub> and minor amounts of iso-C<sub>14:0</sub>, C<sub>16:0</sub>, iso-C<sub>17:0</sub> and C<sub>18:0</sub>. 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 D-glucose, D-xylose, D-ribose, D-arabinose, D-galactose and glycerol, but not D-glucuronic acid, lactose, L-rhamnose or D-xylitol.

The type strain is ATCC 33408<sup>T</sup> = CIP 102716<sup>T</sup> = JCM 11565<sup>T</sup> = LMG 16219<sup>T</sup> = NCIB (now NCIMB) 10583<sup>T</sup>.

**Description of Glutamicibacter nicotianae**

*Glutamicibacter nicotianae* (ni.co.ti’a’næ. N.L. gen. n. nicotianæ 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...
According to Margesin et al. (2004), the type strain reduces nitrate. Positive for catalase and negative for oxidase and urease. H2S is not produced from thiosulfate and indole is not produced. Alkaline phosphatase, α-glucosidase, leucine arylamidase, esterase lipase (C8), esterase (C4), pyrazinamidase and pyrrolidonyl arylamidase are present and skimmed milk is hydrolysed at 25 °C but not at 10 °C. Does not grow at pH 5 or 11. Arabinose, glucose, glutonate, maltose, malate and citrate are assimilated, but mannitol, mannose, mannotol, N-acetylglucosamine, adipate, caprate and phenylacetate are not. Arginine dihydrolase, α-galactosidase, N-acetyl-β-glucosaminidase, lipase (C14), gelatin hydrolysis, trypsin, α-chymotrypsin, α-fucosidase, β-lactamase and pectate lyase are negative. n-Hexadecane and diesel oil are not utilized for growth. Glucose, ribose, xylose, mannitol, maltose, lactose, sucrose and glycerol are not fermented. Susceptible to ampicillin (8 mg L−1), imipenem (16 mg L−1) and rifampicin (16 mg L−1) and weakly susceptible to amikacin (16 mg L−1). Resistant to aztreonam (32 mg L−1), cefamandole (16 mg L−1), cefoxitin (16 mg L−1), ceftazidime (16 mg L−1), ciprofloxacin (4 mg L−1), fleroxacin (8 mg L−1) and tetracycline (4 mg L−1). Additional traits were reported for the type strain by Osorio et al. (1999) as follows. The type strain is negative for β-galactosidase. Amygdalin, arbutin, cellobiose, D-arabitol, D-xylose, galactose, l-arabinose, maltose, ribose, salicin, starch and gentiobiose are assimilated, but not D-mannose, turanose, inositol, mannotol, melibiose, rhamnose, salicin, starch, sucrose, trehalose, xylitol, gentiobiose and 5-ketogluconate are not assimilated.

The type strain is ATCC 21749T = CIP 102367T = DSM 20647T = IFO (now NBRC) 15515T = JCM 11944T = 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).


The description 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 the major compounds diphytanylgllycerol, phosphatidylglycerol and digalactosyldiacylglycerol. Phosphatidylglycerol is absent. The major fatty acid is anteiso-C15:0. Large amounts of iso-C15:0, iso-C17:0 and C16:0 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 gen. nov.**

*Paeniglutamicibacter* (Pae.ni.glu.ti.ca’ber. 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 A4α (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 diphosphatidylglycerol, phosphatidylglycerol and digalactosyldiacylglycerol. Phosphatidylglycerol is absent. The major fatty acid is anteiso-C15:0. Large amounts of iso-C15:0, iso-C17:0 and C16:0 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 comb. nov.**

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


The description is as provided by Stackebrandt et al. (1983) for *Arthrobacter sulfureus*. 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 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 SPC26T (=LMG 24542T=NCCB 100228T).

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 diamino acids are lysine and alanine and the acyl type is glutamic acid (A4\(\alpha\) variation)'. Firstly, alanine is not a diamino acid. Secondly, from the presence of the amino acids lysine, alanine and glutamic acid, the peptidoglycan variation A4\(\alpha\) cannot be concluded because the majority of bacteria with the diamino 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. kyrıós 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\(_{18:0}\) is the second most abundant fatty acid, and relatively large amounts of C\(_{16:0}\) C\(_{18:2}\) and C\(_{18:1\alpha 9\beta}\) (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. 3j).

The type strain is Lz1yT (=CIP 108629T=DSM 15796T=JCM 12166T).

Description of *Paeniglutamicibacter gangotriensis* comb. nov.

*Paeniglutamicibacter gangotriensis* (gan.go’tri.en’sis. N.L. masc. adj. *gangotriensis* of or pertaining to the Kerguelen Islands, Antarctica).


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 KGN15T (=CIP 108629T=DSM 15797T=JCM 12165T).

Description of *Paeniglutamicibacter psychrophenolicus* comb. nov.

*Paeniglutamicibacter psychrophenolicus* [psy.chro.phe.no’ li.cus. Gr. adj. psychos cold; N.L. masc. adj. phenolicus 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. 3i).

The type strain is AG31T (=CIP 108593T=DSM 15454T=IAM 15315T=JCM 13568=LMG 21914T).
Description of Pseudoglutamicibacter gen. nov.


The peptidoglycan type is A4ς (Lys–Ala–Glu, A11.35; or Lys–Ser–Glu, A11.58). The quinone system contains predominantly menaquinone MK-8(H2). The polar lipid profile is more complex than in other arthrobacters. It is composed of the major compounds diphosphatidylglycerol, phosphatidylglycerol and dimannosyldiacylglycerol. Phosphatidylinositol, monogalactosyldiacylglycerol, trimannosyldiacylglycerol and significant amounts of five unidentified phospholipids are also present. The major fatty acid is anteiso-C15 : 0. 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

The data discussed in this study strongly suggest that the genus Arthrobacter sensu stricto should be restricted to the four species A. globiformis, A. pascens, A. oryzae and A. hunicola, which share high 16S rRNA gene sequence similarities, a quinone system with MK-9(H2) predominant and a peptidoglycan with Lys–Ala2-3 (A3ς; A11.5, A11.6). However, such a proposal would exclude numerous species from the genus Arthrobacter without the option to reclassify them in other genera, since stable diagnostic traits are not yet available. Hence, the description of Arthrobacter sensu stricto should await the availability of data allowing the assignment to other genera of species that differ from the genus description of Arthrobacter sensu stricto.

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 A3ς [variations Lys–Ala1–4, Lys–Thr–Ala1–3, Lys–Ala–Ser–Ala3, Lys–Gly–Ala3 and Lys–Ala2–Gly2–3–Ala(Gly)]; peptidoglycan type A4ς may also be present, as reported for Arthrobacter wowiunensi (Lys–D-Asp) or in combinations with quinone system MK-9(H2) in Arthrobacter rhombi and Arthrobacter halodurans (Lys–Ala–D-Glu; Chen et al., 2009). The polar lipid profile contains predominantly diphosphatidylglycerol, phosphatidylglycerol, phosphatidylinositol and dimannosyglyceride. 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 phosphatidylethanolamine. In addition to phosphatidylglycerol and diphasphatidylglycerol, phosphatidylinositol,
dimannosyldiacylglycerol, trimannosyldiacylglycerol, three unidentified glycolipids and three polar lipids are also present.

The type strain is CMS 90\(T\) (=CIP 107726\(^T\)=CMC 9009\(T\)=CMS 9009\(T\)=DSM 14508\(T\)=JCM 11881\(T\)=MTCC 3712\(T\)=NCIMB 14039\(T\)).

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.

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