Proposed minimal standards for describing new genera and species of the suborder *Micrococcineae*

Peter Schumann,¹ Peter Kämpfer,² Hans-Jürgen Busse³ and Lyudmila I. Evtushenko⁴ for the Subcommittee on the Taxonomy of the Suborder *Micrococcineae* of the International Committee on Systematics of Prokaryotes

Correspondence
P. Schumann
psc@dsMZ.de

¹DSMZ-Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Inhoffenstraße 7B, 38124 Braunschweig, Germany

²Institut für Angewandte Mikrobiologie, Justus-Liebig-Universität, 35392 Giessen, Germany

³Institut für Bakteriologie, Mykologie und Hygiene, Veterinärmedizinische Universität, A-1210 Wien, Austria

⁴All-Russian Collection of Microorganisms (VKM), G. K. Skryabin Institute of Biochemistry and Physiology of Microorganisms, RAS, Pushchino, Moscow Region 142290, Russia

The Subcommittee on the Taxonomy of the Suborder *Micrococcineae* of the International Committee on Systematics of Prokaryotes has agreed on minimal standards for describing new genera and species of the suborder *Micrococcineae*. The minimal standards are intended to provide bacteriologists involved in the taxonomy of members of the suborder *Micrococcineae* with a set of essential requirements for the description of new taxa. In addition to sequence data comparisons of 16S rRNA genes or other appropriate conservative genes, phenotypic and genotypic criteria are compiled which are considered essential for the comprehensive characterization of new members of the suborder *Micrococcineae*. Additional features are recommended for the characterization and differentiation of genera and species with validly published names.

INTRODUCTION

The suborder *Micrococcineae* was established by Stackebrandt *et al.* (1997) on the basis of a characteristic set of 16S rRNA gene signature nucleotides. Subsequent reclassifications and descriptions of additional genera have necessitated the dynamic adaptation of the originally proposed sets of signature nucleotides since new members added to the suborder have given a fresh insight into its genotypic diversity (Stackebrandt & Schumann, 2006; Zhi *et al.*, 2009). Consequently, an emended description of the suborder *Micrococcineae* was proposed on the basis of a revised set of 16S rRNA gene signatures (Zhi *et al.*, 2009): 127:234 (A–U), 598:640 (U–G), 657:749 (U–A), 953:1228 (G–C), 986:1219 (A–U), 987:1218 (A–U) and 1362 (A). At the time of writing, the suborder comprises 15 recognized families (Stackebrandt *et al.*, 1997; Stackebrandt & Schumann, 2000b; Li *et al.*, 2005, 2008; Zhi *et al.*, 2009) and 86 genera, including two pairs of genera with names that are heterotypic synonyms (*Microbacterium*/

Aureobacterium and *Rothia*/*Stomatococcus*) and one pair of homotypic synonyms (*Pseudoclavibacter*/*Zimmermannella*) (Table 1 and <http://www.the-icsp.org/taxa/micrococcinealist.htm>).

Whereas the suborder *Micrococcineae* is defined solely by the set of 16S rRNA gene signature nucleotides (Stackebrandt *et al.*, 1997; Zhi *et al.*, 2009), the affiliation of its members to genera and species requires a comprehensive investigation of genotypic and phenotypic (including chemotaxonomic) characteristics. The currently recognized organisms of the suborder *Micrococcineae* share several common phenotypic and genotypic features. Most of them are chemoheterotrophs and strict or facultative aerobes characterized by the oxidative type of metabolism. The cells are Gram-positive in terms of the cell-wall structure and do not form endospores. Although coccoid cells, branching hyphae or cell division by multiseptation are morphological features of some genera, the cells of most members of the suborder are irregular rods in an angular arrangement ('coryneform' morphology). Menaquinones are present in all members (except for the

Abbreviations: FT-IR, Fourier-transform-infrared spectroscopy; MALDI-TOF, matrix assisted laser desorption ionization time-of-flight.

Table 1. Families, genera and their type species belonging to the suborder *Micrococcineae*

Taxa	Reference
Family Beutenbergiaceae Zhi <i>et al.</i> 2009 Genus Beutenbergia Groth <i>et al.</i> 1999 (type genus) <i>Beutenbergia cavernae</i> Groth <i>et al.</i> 1999 (type species) Genus Salana Von Wintzingerode <i>et al.</i> 2001 <i>Salana multivorans</i> Von Wintzingerode <i>et al.</i> 2001 (type species)	Zhi <i>et al.</i> (2009) Groth <i>et al.</i> (1999b) Groth <i>et al.</i> (1999b) von Wintzingerode <i>et al.</i> (2001) von Wintzingerode <i>et al.</i> (2001)
Family Bogoriellaceae Schumann and Stackebrandt 2000 Genus Bogoriella Groth <i>et al.</i> 1997 (type genus) <i>Bogoriella caseilytica</i> Groth <i>et al.</i> 1997 (type species) Genus Georgenia Altenburger <i>et al.</i> 2002 emend. Li <i>et al.</i> 2007 <i>Georgenia muralis</i> Altenburger <i>et al.</i> 2002 (type species)	Stackebrandt & Schumann (2000) Groth <i>et al.</i> (1997a) Groth <i>et al.</i> (1997a) Altenburger <i>et al.</i> (2002b); Li <i>et al.</i> (2007) Altenburger <i>et al.</i> (2002b)
Family Brevibacteriaceae Breed 1953 (Approved Lists 1980) emend. Stackebrandt <i>et al.</i> 1997 Genus Brevibacterium Breed 1953 (type genus) <i>Brevibacterium linens</i> (Wolff 1910) Breed 1953 (type species)	Breed (1953); Skerman <i>et al.</i> (1980); Stackebrandt <i>et al.</i> (1997) Breed (1953) Breed (1953)
Family Cellulomonadaceae Stackebrandt and Prauser 1991 emend. Stackebrandt and Schumann 2000 Genus Cellulomonas Bergey <i>et al.</i> 1923 (type genus) <i>Cellulomonas flavigena</i> (Kellerman and McBeth 1912) Bergey <i>et al.</i> 1923 (type species) Genus Oerskovia Prauser <i>et al.</i> 1970 (Approved Lists 1980) emend. Stackebrandt <i>et al.</i> 2002 <i>Oerskovia turbata</i> (Erikson 1954) Prauser <i>et al.</i> 1970 (Approved Lists 1980) emend. Stackebrandt <i>et al.</i> 2002 (type species)	Stackebrandt & Prauser (1991); Stackebrandt & Schumann (2000) Bergey <i>et al.</i> (1923) Bergey <i>et al.</i> (1923) Prauser <i>et al.</i> (1970); Skerman <i>et al.</i> (1980); Stackebrandt <i>et al.</i> (2002a) Prauser <i>et al.</i> (1970); Skerman <i>et al.</i> (1980); Stackebrandt <i>et al.</i> (2002a)
Family Dermabacteraceae Stackebrandt <i>et al.</i> 1997 Genus Dermabacter Jones and Collins 1989 (type genus) <i>Dermabacter hominis</i> Jones and Collins 1989 (type species) Genus Brachybacterium Collins <i>et al.</i> 1988 <i>Brachybacterium faecium</i> Collins <i>et al.</i> 1988 (type species) Genus Devriesea Martel <i>et al.</i> 2008 <i>Devriesea agamarum</i> Martel <i>et al.</i> 2008 (type species)	Stackebrandt <i>et al.</i> (1997) Jones & Collins (1988) Jones & Collins (1988) Collins <i>et al.</i> (1988) Collins <i>et al.</i> (1988) Martel <i>et al.</i> (2008) Martel <i>et al.</i> (2008)
Family Dermacoccaceae Schumann and Stackebrandt 2000 Genus Dermacoccus Stackebrandt <i>et al.</i> 1995 (type genus) <i>Dermacoccus nishinomiyaensis</i> (Oda 1935) Stackebrandt <i>et al.</i> 1995 (type species) Genus Demetria Groth <i>et al.</i> 1997 <i>Demetria terragena</i> Groth <i>et al.</i> 1997 (type species) Genus Kytococcus Stackebrandt <i>et al.</i> 1995 <i>Kytococcus sedentarius</i> (ZoBell and Upham 1944) Stackebrandt <i>et al.</i> 1995 (type species)	Stackebrandt & Schumann (2000) Stackebrandt <i>et al.</i> (1995) Oda (1935); Stackebrandt <i>et al.</i> (1995) Groth <i>et al.</i> (1997b) Groth <i>et al.</i> (1997b) Stackebrandt <i>et al.</i> (1995) ZoBell & Upham (1944); Stackebrandt <i>et al.</i> (1995)
Family Dermatophilaceae Austwick 1958 Genus Dermatophilus (Van Saceghem 1915) Gordon 1964 (type genus) <i>Dermatophilus congolensis</i> (Van Saceghem 1915) Gordon 1964 (type species) Genus Kineosphaera Liu <i>et al.</i> 2002 <i>Kineosphaera limosa</i> Liu <i>et al.</i> 2002 (type species)	Austwick (1958) Van Saceghem (1915); Gordon (1964) Van Saceghem (1915); Gordon (1964) Liu <i>et al.</i> (2002) Liu <i>et al.</i> (2002)
Family Intrasporangiaceae Rainey <i>et al.</i> 1997 emend. Stackebrandt and Schumann 2000 Genus Intrasporangium Kalakoutskii <i>et al.</i> 1967 (type genus) <i>Intrasporangium calvum</i> Kalakoutskii <i>et al.</i> 1967 (type species) Genus Arsenicococcus Collins <i>et al.</i> 2004 <i>Arsenicococcus bolidensis</i> Collins <i>et al.</i> 2004 (type species) Genus Humibacillus Kageyama <i>et al.</i> 2008 <i>Humibacillus xanthopallidus</i> Kageyama <i>et al.</i> 2008 (type species) Genus Humihabitans Kageyama <i>et al.</i> 2007 <i>Humihabitans oryzae</i> Kageyama <i>et al.</i> 2007 (type species)	Stackebrandt <i>et al.</i> (1997); Stackebrandt & Schumann (2000) Kalakoutskii <i>et al.</i> (1967) Kalakoutskii <i>et al.</i> (1967) Collins <i>et al.</i> (2004) Collins <i>et al.</i> (2004) Kageyama <i>et al.</i> (2008b) Kageyama <i>et al.</i> (2008b) Kageyama <i>et al.</i> (2007) Kageyama <i>et al.</i> (2007)

Table 1. cont.

Taxa	Reference
Genus <i>Janibacter</i> Martin <i>et al.</i> 1997	Martin <i>et al.</i> (1997)
<i>Janibacter limosus</i> Martin <i>et al.</i> 1997 (type species)	Martin <i>et al.</i> (1997)
Genus <i>Knoellia</i> Groth <i>et al.</i> 2002	Groth <i>et al.</i> (2002)
<i>Knoellia sinensis</i> Groth <i>et al.</i> 2002 (type species)	Groth <i>et al.</i> (2002)
Genus <i>Kribbia</i> Jung <i>et al.</i> 2006	Jung <i>et al.</i> (2006)
<i>Kribbia dieselivorans</i> Jung <i>et al.</i> 2006 (type species)	Jung <i>et al.</i> (2006)
Genus <i>Lapillicoccus</i> Lee and Lee 2007	Lee & Lee (2007)
<i>Lapillicoccus jejuensis</i> Lee and Lee 2007 (type species)	Lee & Lee (2007)
Genus <i>Marihabitans</i> Kageyama <i>et al.</i> 2008	Kageyama <i>et al.</i> (2008a)
<i>Marihabitans asiaticum</i> Kageyama <i>et al.</i> 2008 (type species)	Kageyama <i>et al.</i> (2008a)
Genus <i>Ornithinicoccus</i> Groth <i>et al.</i> 1999	Groth <i>et al.</i> (1999a)
<i>Ornithinicoccus hortensis</i> Groth <i>et al.</i> 1999 (type species)	Groth <i>et al.</i> (1999a)
Genus <i>Ornithinimicrobium</i> Groth <i>et al.</i> 2001	Groth <i>et al.</i> (2001)
<i>Ornithinimicrobium humiphilum</i> Groth <i>et al.</i> 2001 (type species)	Groth <i>et al.</i> (2001)
Genus <i>Oryzihumus</i> Kageyama <i>et al.</i> 2005	Kageyama <i>et al.</i> (2005)
<i>Oryzihumus leptocrescens</i> Kageyama <i>et al.</i> 2005 (type species)	Kageyama <i>et al.</i> (2005)
Genus <i>Phycococcus</i> Lee 2006	Lee (2006)
<i>Phycococcus jejuensis</i> Lee 2006 (type species)	Lee (2006)
Genus <i>Serinicoccus</i> Yi <i>et al.</i> 2004	Yi <i>et al.</i> (2004)
<i>Serinicoccus marinus</i> Yi <i>et al.</i> 2004 (type species)	Yi <i>et al.</i> (2004)
Genus <i>Terrabacter</i> Collins <i>et al.</i> 1989	Collins <i>et al.</i> (1989)
<i>Terrabacter tumescens</i> (Jensen 1934) Collins <i>et al.</i> 1989 (type species)	Jensen (1934); Collins <i>et al.</i> (1989)
Genus <i>Terracoccus</i> Prauser <i>et al.</i> 1997	Prauser <i>et al.</i> (1997)
<i>Terracoccus luteus</i> Prauser <i>et al.</i> 1997 (type species)	Prauser <i>et al.</i> (1997)
Genus <i>Tetrasphaera</i> Maszenan <i>et al.</i> 2000 emend. Ishikawa and Yokota 2006	Maszenan <i>et al.</i> (2000); Ishikawa & Yokota (2006)
<i>Tetrasphaera japonica</i> Maszenan <i>et al.</i> 2000 (type species)	Ishikawa & Yokota (2006)
Family <i>Jonesiaceae</i> Stackebrandt <i>et al.</i> 1997	Stackebrandt <i>et al.</i> (1997)
Genus <i>Jonesia</i> Rocourt <i>et al.</i> 1987 (type genus)	Rocourt <i>et al.</i> (1987)
<i>Jonesia denitrificans</i> (Prévot 1961) Rocourt <i>et al.</i> 1987 (type species)	Prévot (1961); Rocourt <i>et al.</i> (1987)
Family <i>Microbacteriaceae</i> Park <i>et al.</i> 1995 emend. Rainey <i>et al.</i> 1997	Park <i>et al.</i> (1993); Stackebrandt <i>et al.</i> (1997)
Genus <i>Microbacterium</i> Orla-Jensen 1919 (Approved Lists 1980) emend. Takeuchi and Hatano 1998 (type genus)	Orla-Jensen (1919); Skerman <i>et al.</i> (1980); Takeuchi & Hatano (1998)
<i>Microbacterium lacticum</i> Orla-Jensen 1919 (type species)	Orla-Jensen (1919)
Genus <i>Agreia</i> Evtushenko <i>et al.</i> 2001	Evtushenko <i>et al.</i> (2001)
<i>Agreia bicolorata</i> Evtushenko <i>et al.</i> 2001 (type species)	Evtushenko <i>et al.</i> (2001)
Genus <i>Agrococcus</i> Groth <i>et al.</i> 1996	Groth <i>et al.</i> (1996)
<i>Agrococcus jenensis</i> Groth <i>et al.</i> 1996 (type species)	Groth <i>et al.</i> (1996)
Genus <i>Agromyces</i> Gledhill and Casida 1969 (Approved Lists 1980) emend. Zgurskaya <i>et al.</i> 1992	Gledhill & Casida (1969); Skerman <i>et al.</i> (1980); Zgurskaya <i>et al.</i> (1992)
<i>Agromyces ramosus</i> Gledhill and Casida 1969 (type species)	Gledhill & Casida (1969)
Genus <i>Aureobacterium</i> Collins <i>et al.</i> 1983. The genus name <i>Aureobacterium</i> is a later heterotypic synonym of the genus name <i>Microbacterium</i> Orla-Jensen 1919	Collins <i>et al.</i> (1983); Takeuchi & Hatano (1998)
<i>Aureobacterium liquefaciens</i> Collins <i>et al.</i> 1983 (type species)	Collins <i>et al.</i> (1983)
Genus <i>Clavibacter</i> Davis <i>et al.</i> 1984	Davis <i>et al.</i> (1984)
<i>Clavibacter michiganensis</i> (Smith 1910) Davis <i>et al.</i> 1984 (type species)	Smith (1910); Davis <i>et al.</i> (1984)
Genus <i>Cryobacterium</i> Suzuki <i>et al.</i> 1997	Suzuki <i>et al.</i> (1997)
<i>Cryobacterium psychrophilum</i> (ex Inoue and Komagata 1976) Suzuki <i>et al.</i> 1997 (type species)	Inoue & Komagata (1976); Suzuki <i>et al.</i> (1997)
Genus <i>Curtobacterium</i> Yamada and Komagata 1972	Inoue & Komagata (1976)
<i>Curtobacterium citreum</i> (Komagata and Iizuka 1964) Yamada and Komagata 1972 (type species)	Komagata & Iizuka (1964); Yamada & Komagata (1972)
Genus <i>Frigoribacterium</i> Kämpfer <i>et al.</i> 2000	Kämpfer <i>et al.</i> (2000)
<i>Frigoribacterium faeni</i> Kämpfer <i>et al.</i> 2000 (type species)	Kämpfer <i>et al.</i> (2000)
Genus <i>Frondicola</i> Zhang <i>et al.</i> 2007	Zhang <i>et al.</i> (2007b)
<i>Frondicola australicus</i> Zhang <i>et al.</i> 2007 (type species)	Zhang <i>et al.</i> (2007b)
Genus <i>Glaciibacter</i> Katayama <i>et al.</i> 2009	Katayama <i>et al.</i> (2009)

Table 1. cont.

Taxa	Reference
<i>Glaciibacter superstes</i> Katayama <i>et al.</i> 2009 (type species)	Katayama <i>et al.</i> (2009)
Genus <i>Gulosibacter</i> Manaia <i>et al.</i> 2004	Manaia <i>et al.</i> (2004)
<i>Gulosibacter molinativorax</i> Manaia <i>et al.</i> 2004 (type species)	Manaia <i>et al.</i> (2004)
Genus <i>Humibacter</i> Vaz-Moreira <i>et al.</i> 2008	Vaz-Moreira <i>et al.</i> (2008)
<i>Humibacter albus</i> Vaz-Moreira <i>et al.</i> 2008 (type species)	Vaz-Moreira <i>et al.</i> (2008)
Genus <i>Klugiella</i> Cook <i>et al.</i> 2008	Cook <i>et al.</i> (2008)
<i>Klugiella xanthotipulae</i> Cook <i>et al.</i> 2008 (type species)	Cook <i>et al.</i> (2008)
Genus <i>Labeledella</i> Lee 2007	Lee (2007)
<i>Labeledella gwakjiensis</i> Lee 2007 (type species)	Lee (2007)
Genus <i>Leifsonia</i> Evtushenko <i>et al.</i> 2000	Evtushenko <i>et al.</i> (2000)
<i>Leifsonia aquatica</i> (ex Leifson 1962) Evtushenko <i>et al.</i> 2000 (type species)	Leifson (1962); Evtushenko <i>et al.</i> (2000)
Genus <i>Leucobacter</i> Takeuchi <i>et al.</i> 1996	Takeuchi <i>et al.</i> (1996)
<i>Leucobacter komagatae</i> Takeuchi <i>et al.</i> 1996 (type species)	Takeuchi <i>et al.</i> (1996)
Genus <i>Microcella</i> Tiago <i>et al.</i> 2005 emend. Tiago <i>et al.</i> 2006	Tiago <i>et al.</i> (2005, 2006)
<i>Microcella putealis</i> Tiago <i>et al.</i> 2005 (type species)	Tiago <i>et al.</i> (2005)
Genus <i>Microterricola</i> Matsumoto <i>et al.</i> 2008	Matsumoto <i>et al.</i> (2008)
<i>Microterricola viridarii</i> Matsumoto <i>et al.</i> 2008 (type species)	Matsumoto <i>et al.</i> (2008)
Genus <i>Mycetocola</i> Tsukamoto <i>et al.</i> 2001	Tsukamoto <i>et al.</i> (2001)
<i>Mycetocola saprophilus</i> Tsukamoto <i>et al.</i> 2001 (type species)	Tsukamoto <i>et al.</i> (2001)
Genus <i>Okibacterium</i> Evtushenko <i>et al.</i> 2002	Evtushenko <i>et al.</i> (2002)
<i>Okibacterium fritillariae</i> Evtushenko <i>et al.</i> 2002 (type species)	Evtushenko <i>et al.</i> (2002)
Genus <i>Phycicola</i> Lee <i>et al.</i> 2008	Lee <i>et al.</i> (2008)
<i>Phycicola gilvus</i> Lee <i>et al.</i> 2008 (type species)	Lee <i>et al.</i> (2008)
Genus <i>Plantibacter</i> Behrendt <i>et al.</i> 2002	Behrendt <i>et al.</i> (2002)
<i>Plantibacter flavus</i> Behrendt <i>et al.</i> 2002 (type species)	Behrendt <i>et al.</i> (2002)
Genus <i>Pseudoclavibacter</i> Manaia <i>et al.</i> 2004	Manaia <i>et al.</i> (2004)
<i>Pseudoclavibacter helvolus</i> Manaia <i>et al.</i> 2004 (type species)	Manaia <i>et al.</i> (2004)
Genus <i>Rathayibacter</i> Zgurskaya <i>et al.</i> 1993	Zgurskaya <i>et al.</i> (1993)
<i>Rathayibacter rathayi</i> (Smith 1913) Zgurskaya <i>et al.</i> 1993 (type species)	Smith (1913); Zgurskaya <i>et al.</i> (1993)
Genus <i>Rhodoglobus</i> Sheridan <i>et al.</i> 2003	Sheridan <i>et al.</i> (2003)
<i>Rhodoglobus vestalii</i> Sheridan <i>et al.</i> 2003 (type species)	Sheridan <i>et al.</i> (2003)
Genus <i>Salinibacterium</i> Han <i>et al.</i> 2003	Han <i>et al.</i> (2003)
<i>Salinibacterium amurskyense</i> Han <i>et al.</i> 2003 (type species)	Han <i>et al.</i> (2003)
Genus <i>Schumannella</i> An <i>et al.</i> 2009	An <i>et al.</i> (2008)
<i>Schumannella luteola</i> An <i>et al.</i> 2009 (type species)	An <i>et al.</i> (2008)
Genus <i>Subtercola</i> Männistö <i>et al.</i> 2000	Männistö <i>et al.</i> (2000)
<i>Subtercola boreus</i> Männistö <i>et al.</i> 2000 (type species)	Männistö <i>et al.</i> (2000)
Genus <i>Yonghaparkia</i> Yoon <i>et al.</i> 2006	Yoon <i>et al.</i> (2006)
<i>Yonghaparkia alkaliphila</i> Yoon <i>et al.</i> 2006 (type species)	Yoon <i>et al.</i> (2006)
Genus <i>Zimmermannella</i> Lin <i>et al.</i> 2004. The genus name <i>Zimmermannella</i> is a later homotypic synonym of the genus name <i>Pseudoclavibacter</i> Manaia <i>et al.</i> 2004	Lin <i>et al.</i> (2004)
<i>Zimmermannella helvola</i> Lin <i>et al.</i> 2004 (type species)	Lin <i>et al.</i> (2004)
Family <i>Micrococcaceae</i> Pribram 1929 (Approved Lists 1980) emend. Stackebrandt <i>et al.</i> 1997	Pribram (1929); Skerman <i>et al.</i> (1980); Stackebrandt <i>et al.</i> (1997)
Genus <i>Micrococcus</i> Cohn 1872 (Approved Lists 1980) emend. Wieser <i>et al.</i> 2002 (type genus)	Cohn (1872); Skerman <i>et al.</i> (1980); Wieser <i>et al.</i> (2002)
<i>Micrococcus luteus</i> (Schroeter 1872) Cohn 1872 (Approved Lists 1980) emend. Wieser <i>et al.</i> 2002 (type species)	Schroeter (1872); Cohn (1872); Skerman <i>et al.</i> (1980); Wieser <i>et al.</i> (2002)
Genus <i>Acaricomes</i> Pukall <i>et al.</i> 2006	Pukall <i>et al.</i> (2006)
<i>Acaricomes phytoseiuli</i> Pukall <i>et al.</i> 2006 (type species)	Pukall <i>et al.</i> (2006)
Genus <i>Arthrobacter</i> Conn and Dimmick 1947 (Approved Lists 1980) emend. Koch <i>et al.</i> 1995	Conn & Dimmick (1947); Skerman <i>et al.</i> (1980); Koch <i>et al.</i> (1995)
<i>Arthrobacter globiformis</i> (Conn 1928) Conn and Dimmick 1947 (type species)	Conn (1928); Conn & Dimmick (1947); Koch <i>et al.</i> (1995)
Genus <i>Citricoccus</i> Altenburger <i>et al.</i> 2002	Altenburger <i>et al.</i> (2002a)
<i>Citricoccus muralis</i> Altenburger <i>et al.</i> 2002 (type species)	Altenburger <i>et al.</i> (2002a)

Table 1. cont.

Taxa	Reference
Genus <i>Kocuria</i> Stackebrandt <i>et al.</i> 1995 <i>Kocuria rosea</i> (Flügge 1886) Stackebrandt <i>et al.</i> 1995 (type species)	Stackebrandt <i>et al.</i> (1995) Flügge (1886); Stackebrandt <i>et al.</i> (1995)
Genus <i>Nesterenkonia</i> Stackebrandt <i>et al.</i> 1995 emend. Collins <i>et al.</i> 2002 <i>Nesterenkonia halobia</i> (Onishi and Kamekura 1972) Stackebrandt <i>et al.</i> 1995 (type species)	Stackebrandt <i>et al.</i> (1995); Collins <i>et al.</i> (2002) Onishi & Kamekura (1972); Stackebrandt <i>et al.</i> (1995)
Genus <i>Renibacterium</i> Sanders and Fryer 1980 <i>Renibacterium salmoninarum</i> Sanders and Fryer 1980 (type species)	Sanders & Fryer (1980) Sanders & Fryer (1980)
Genus <i>Rothia</i> Georg and Brown 1967 <i>Rothia dentocariosa</i> (Onishi 1949) Georg and Brown 1967 (type species)	Georg & Brown (1967) Onishi (1949); Georg & Brown (1967)
Genus <i>Stomatococcus</i> Bergan and Kocur 1982. The genus name <i>Stomatococcus</i> is a later heterotypic synonym of the genus name <i>Rothia</i> Georg and Brown 1967 <i>Stomatococcus mucilaginosus</i> Bergan and Kocur 1982	Bergan & Kocur (1982); Collins <i>et al.</i> (2000) Bergan & Kocur (1982)
Genus <i>Zhihengliuella</i> Zhang <i>et al.</i> 2007 <i>Zhihengliuella halotolerans</i> Zhang <i>et al.</i> 2007 (type species)	Zhang <i>et al.</i> (2007a) Zhang <i>et al.</i> (2007a)
Family <i>Promicromonosporaceae</i> Rainey <i>et al.</i> 1997 Genus <i>Promicromonospora</i> Krassil'nikov <i>et al.</i> 1961 (type genus) <i>Promicromonospora citrea</i> Krassil'nikov <i>et al.</i> 1961 (type species)	Stackebrandt <i>et al.</i> (1997) Krassil'nikov <i>et al.</i> (1961) Krassil'nikov <i>et al.</i> (1961)
Genus <i>Cellulosimicrobium</i> Schumann <i>et al.</i> 2001 emend. Brown <i>et al.</i> 2006 <i>Cellulosimicrobium cellulans</i> (Metcalf and Brown 1957) Schumann <i>et al.</i> 2001 (type species)	Schumann <i>et al.</i> (2001); Brown <i>et al.</i> (2006) Metcalf & Brown (1957); Schumann <i>et al.</i> (2001)
Genus <i>Isoptericola</i> Stackebrandt <i>et al.</i> 2004 <i>Isoptericola variabilis</i> (Bakalidou <i>et al.</i> 2002) Stackebrandt <i>et al.</i> 2004 (type species)	Stackebrandt <i>et al.</i> (2004) Bakalidou <i>et al.</i> (2002); Stackebrandt <i>et al.</i> (2004)
Genus <i>Myceligenerans</i> Cui <i>et al.</i> 2004 <i>Myceligenerans xiligouense</i> Cui <i>et al.</i> 2004 (type species)	Cui <i>et al.</i> (2004) Cui <i>et al.</i> (2004)
Genus <i>Xylanibacterium</i> Rivas <i>et al.</i> 2004 <i>Xylanibacterium ulmi</i> Rivas <i>et al.</i> 2004 (type species)	Rivas <i>et al.</i> (2004) Rivas <i>et al.</i> (2004)
Genus <i>Xylanimicrobium</i> Stackebrandt and Schumann 2004 <i>Xylanimicrobium pachnodae</i> (Cazemier <i>et al.</i> 2004) Stackebrandt and Schumann 2004 (type species)	Stackebrandt & Schumann (2004) Cazemier <i>et al.</i> (2003); Stackebrandt & Schumann (2004)
Genus <i>Xylanimonas</i> Rivas <i>et al.</i> 2003 <i>Xylanimonas cellulosilytica</i> Rivas <i>et al.</i> 2003 (type species)	Rivas <i>et al.</i> (2003) Rivas <i>et al.</i> (2003)
Family <i>Rarobacteraceae</i> Stackebrandt and Schumann 2000 Genus <i>Rarobacter</i> Yamamoto <i>et al.</i> 1988 (type genus) <i>Rarobacter faecitabidus</i> Yamamoto <i>et al.</i> 1988 (type species)	Stackebrandt & Schumann (2000) Yamamoto <i>et al.</i> (1988) Yamamoto <i>et al.</i> (1988)
Family <i>Sanguibacteraceae</i> Stackebrandt and Schumann 2000 Genus <i>Sanguibacter</i> Fernandez-Garayzabal <i>et al.</i> 1995 (type genus) <i>Sanguibacter keddiei</i> Fernandez-Garayzabal <i>et al.</i> 1995 (type species)	Stackebrandt & Schumann (2000) Fernandez-Garayzabal <i>et al.</i> (1995) Fernandez-Garayzabal <i>et al.</i> (1995)
Family <i>Yaniellaceae</i> Li <i>et al.</i> 2008* Previous illegitimate name: <i>Yaniaceae</i> Li <i>et al.</i> 2005 Genus <i>Yaniella</i> Li <i>et al.</i> 2008 (type genus)* Previous illegitimate name: <i>Yania</i> Li <i>et al.</i> 2004 <i>Yaniella halotolerans</i> Li <i>et al.</i> 2008 (type species) Previous illegitimate name: <i>Yania halotolerans</i> Li <i>et al.</i> 2004	Li <i>et al.</i> (2008) Li <i>et al.</i> (2005) Li <i>et al.</i> (2008) Li <i>et al.</i> (2004) Li <i>et al.</i> (2008) Li <i>et al.</i> (2004)
Genera unassigned to a family Genus <i>Actinotalea</i> Yi <i>et al.</i> 2007 <i>Actinotalea fermentans</i> Yi <i>et al.</i> 2007 (type species) Genus <i>Demequina</i> Yi <i>et al.</i> 2007 <i>Demequina aestuarii</i> Yi <i>et al.</i> 2007 (type species) Genus <i>Ruania</i> Gu <i>et al.</i> 2007 <i>Ruania albidiflava</i> Gu <i>et al.</i> 2007 (type species) Genus <i>Tropheryma</i> La Scola <i>et al.</i> 2001 <i>Tropheryma whipplei</i> La Scola <i>et al.</i> 2001 (type species)	Yi <i>et al.</i> (2007) Yi <i>et al.</i> (2007) Yi <i>et al.</i> (2007) Yi <i>et al.</i> (2007) Gu <i>et al.</i> (2007) Gu <i>et al.</i> (2007) La Scola <i>et al.</i> (2001) La Scola <i>et al.</i> (2001)

*The genus *Yaniella* is in most 16S rRNA gene sequence-based phylogenetic analyses a member of the family *Micrococcaceae* and it appears debatable whether it deserves the status as the type genus of its own family *Yaniellaceae* (E. Stackebrandt, W. Ludwig, personal communication).

genus *Demequina* which contains a demethylmenaquinone) as the respiratory quinones. Mycolic acids and arabinogalactan are absent and the DNA base composition is higher than 50 mol% G+C.

Many of the genera presently considered to be members of the suborder *Micrococcineae* were formerly dealt with by the Subcommittees No. 8 on *Arthrobacter* and Related Organisms and No. 9 on *Microbacterium* and Related Organisms of the International Committee on Systematic Bacteriology (now the International Committee on Systematics of Prokaryotes, ICSP). Minimal standards for the description of taxa related to the genera *Arthrobacter* and *Microbacterium* were proposed by Schumann & Prauser (1995). These minimal standards are in need of updating in the light of current taxonomic classifications, the numerous descriptions of novel taxa and the new methodological approaches to bacterial systematics. In order to comprehensively describe a new genus or species of the suborder *Micrococcineae*, to allow a clear identification of the novel taxon and to maintain the taxonomic soundness of the suborder, it is recommended that the following minimal standards are adopted.

General considerations

The general prerequisites for the description of new taxa and their designation of type genera, type species and type strains have been outlined in the Bacteriological Code (1990 Revision) (Lapage *et al.*, 1992), with several proposals for modifications (e.g. Labeda, 1997, 2000; Tindall, 1999, 2008; Tindall *et al.*, 2006; Tindall & Garrity, 2008), in previous proposals for minimal standards (e.g. Bernardet *et al.*, 2002) and in the Instructions to Authors of the *International Journal of Systematic and Evolutionary Microbiology* (<http://ijs.sgmjournals.org>). Type strains of novel species must be deposited in two publicly accessible culture collections in different countries, as recommended by the Judicial Commission on Prokaryote Nomenclature. For further details regarding the practice of valid publication of names, authors should consult Tindall *et al.* (2006), Tindall (2008) and Tindall & Garrity (2008).

It is essential that the source of the strains representing the new taxon is described comprehensively and unambiguously with respect to geographical location (country, region, mountain, lake etc., preferably with geographical coordinates) and origin of the sample (host organism, environmental sample such as type of soil, sediment, depth of water etc.). The conditions of isolation, maintenance and preservation must be reported.

The polyphasic approach, which integrates genomic and phylogenetic information with phenotypic and chemotaxonomic data (Vandamme *et al.*, 1996), is currently considered the general principle for taxonomic conclusions. Minimal standards for the description of new taxa according to Recommendation 30b of the Bacteriological

Code (1990 Revision) (Lapage *et al.*, 1992) have to be established in accordance with this principle.

The differentiation of genera of the suborder *Micrococcineae* is primarily based on 16S rRNA gene sequence comparisons in combination with chemotaxonomic characteristics. Members of the suborder are often difficult to differentiate by morphology, but show a broad chemotaxonomic diversity (Table 2). In many cases, the chemotaxonomic characteristics are consistent with the phylogenetic position of organisms (Fig. 1) and are regarded as important phenotypic traits in the differentiation of genera of this suborder. Therefore chemotaxonomic characteristics need to be carefully analysed and evaluated for descriptions of novel taxa (Stackebrandt & Schumann, 2006).

Many 'classical' phenotypic characteristics, including morphological, physiological and biochemical features used for the description of the phenotype may be affected by cultural or test conditions. A comparative experimental study of phenotypic characteristics in representatives of putative novel species and of type strains of recognized taxa in the authors' own laboratory rather than comparisons with data reported in the literature is recommended (see also paragraph on cellular fatty acids). This is of particular importance when the organisms to be compared appear highly related on the basis of 16S rRNA gene sequences and where the species description is based on only a single strain. The number and significance of differentiating phenotypic characteristics must be sufficiently high in order to delineate the species borders as reliably as possible and to ensure that a new isolate of the species will be phenotypically recognizable.

Several genera of the suborder *Micrococcineae* (*Bogoriella*, *Demequina*, *Humibacter*, *Humihabitans*, *Ruania*, *Serinicoccus*, *Terracoccus* etc.) are represented by the type strains of their type species only. The description of new taxa should preferably be based on many isolates from different sources if possible since single strains cannot reflect the full biological diversity of species and genera. However, the description of a novel taxon with extraordinary combinations of characteristics should not be inhibited by the fact that intensive isolation programs have failed to provide additional strains. The description of taxa represented by only a few isolates or even a single strain poses a special challenge as regards the selection of appropriate techniques for characterization.

Minimal standards and recommended characteristics for describing novel genera and species

The genotypic and phenotypic criteria of the minimal standards for description of genera and species (Table 3) are considered essential for the characterization and differentiation of new members of the suborder *Micrococcineae*. Additional characteristics that are not

Table 2. Chemotaxonomic characteristics of genera of the suborder *Micrococccineae*

Data from references listed in Table 1 and recent descriptions of novel species (December 2008) and genera (including Validation List no. 125). MCA, monocarboxylic amino acid; var., variable amino acid composition in the interpeptide bridge; A₂pm, 2,6-diaminopimelic acid; Lys, lysine; Orn, ornithine; Hyo, hydroxy-ornithine; Dab, 2,4-diamino butyric acid; Ala, alanine; Asp, aspartic acid; Gab, 4-aminobutyric acid; Gly, glycine; Glu, glutamic acid; D-Glu(Hyg), D-glutamic acid partially replaced by *threo*-3-hydroxy-glutamic acid; Ser, serine; Thr, threonine; MK-8, unsaturated menaquinone with 8 isoprene units; MK-8(H₄), partially saturated menaquinone with two of 8 isoprene units hydrogenated; DMK, demethylmenaquinone; DPG, diphosphatidylglycerol; PG, phosphatidylglycerol; PI, phosphatidylinositol; PIM, phosphatidylinositol mannosides; PSer, phosphatidyl serine; PL, unidentified phospholipid(s); GL, unidentified glycolipid(s); PGL, unidentified phosphoglycolipid(s); ai-C_{15:0}-DMA, 1,1-dimethoxy-anteiso-pentadecane; i-C_{16:0}-DMA, 1,1-dimethoxy-iso-hexadecane; Ch, cyclohexyl fatty acid; ND, no data available. Data in parentheses were reported for only a few species.

Genus	Diamino acid	Interpeptide bridge/[amino acid at position 3 of the peptide subunit]	Acyl type	Major respiratory quinones	Polar lipids	Characteristic cellular fatty acids	DNA G + C content (mol%)
Family Beutenbergiaceae							
<i>Beutenbergia</i>	L-Lys	L-Glu	Acetyl	MK-8(H ₄)	PI, DPG, PL	i-C _{15:0} , ai-C _{15:0}	71
<i>Salana</i>	L-Orn	L-Glu*	ND	MK-8(H ₄)	PG, DPG, PL	ai-C _{15:0} , C _{14:0} , C _{16:0}	75
Family Bogoriellaceae							
<i>Bogoriella</i>	L-Lys	L-Ala-L-Ala-L-Glu	Acetyl	MK-8(H ₄)	PI, PG, DPG, PL	ai-C _{15:0} , i-C _{15:1} , i-C _{16:0}	70
<i>Georgenia</i>	L-Lys	L-Glu or L-Ala-L-Glu	Acetyl	MK-8(H ₄)	PG, DPG, PIM, PL, GL, (PI)	ai-C _{15:0} , ai-C _{15:1} †, i-C _{14:0} , i-C _{16:0}	70–73
Family Brevibacteriaceae							
<i>Brevibacterium</i>	meso-A ₂ pm	None	Acetyl	MK-8(H ₂), MK-7(H ₂)	PI, PG, DPG, GL, PL	ai-C _{15:0} , ai-C _{17:0}	56–71
Family Cellulomonadaceae							
<i>Cellulomonas</i>	L-Orn	D-Asp or D-Glu	Acetyl	MK-9(H ₄), MK-8(H ₄)	PI, PGL, PG, DPG, (PE)	ai-C _{15:0} , C _{16:0} , i-C _{15:0} , ai-C _{17:0}	69–76
<i>Oerskovia</i>	L-Lys	L-Thr-D-Asp or L-Thr-D-Glu	Acetyl	MK-9(H ₄)	PG, DPG, PI	ai-C _{15:0} , C _{16:0} , i-C _{15:0} , C _{14:0} , ai-C _{17:0}	70–75
Family Dermabacteraceae							
<i>Dermabacter</i>	meso-A ₂ pm	D-Asp-D-Glu‡	ND	MK-9, MK-8, MK-7	PG, DPG, PL, GL	ai-C _{17:0} , ai-C _{15:0} , i-C _{16:0}	62
<i>Brachybacterium</i>	meso-A ₂ pm	D-Glu ₂ ‡ or D-Asp-D-Glu‡	Acetyl or Glycolyl	MK-7, MK-8	PG, DPG, GL, PL	ai-C _{15:0} , ai-C _{17:0}	68–73
<i>Devriesea</i>	meso-A ₂ pm	D-Asp-D-Glu‡	ND	MK-8, MK-7, MK-9	PG, PL, GL	C _{14:0} , i-C _{15:0} , ai-C _{15:0} , C _{16:0} , i-C _{16:0} , i-C _{17:0} , ai-C _{17:0}	61
Family Dermacoccaceae							
<i>Dermacoccus</i>	L-Lys	L-Ser ₁₋₂ -D-Glu or L-Ser ₁₋₂ -L-Ala-D-Glu	Acetyl	MK-8(H ₂)	PI, PG, DPG	i-C _{17:0} , i-C _{16:0} , ai-C _{17:0} , i-C _{17:1}	65–71
<i>Demetria</i>	L-Lys	L-Ser-D-Asp	Acetyl	MK-8(H ₄)	PI, PE, PG, DPG, PL	C _{18:1} , C _{18:0} , C _{17:0} , ai-C _{17:0}	66
<i>Kytococcus</i>	L-Lys	D-Glu ₂	ND	MK-8, MK-9, MK-10	PI, PG, DPG	ai-C _{17:0} , C _{17:0} , i-C _{17:1}	68–69
Family Dermatophilaceae							
<i>Dermatophilus</i>	meso-A ₂ pm	None	Acetyl	MK-8(H ₄)	PG, DPG, PI	C _{16:0} , C _{15:0} , C _{14:0}	57–59
<i>Kineosphaera</i>	meso-A ₂ pm	None	ND	MK-8(H ₄)	PG, DPG, PI, PE, PC	C _{16:0} , C _{17:1} , C _{17:0}	71

Table 2. cont.

Genus	Diamino acid	Interpeptide bridge/[amino acid at position 3 of the peptide subunit]	Acyl type	Major respiratory quinones	Polar lipids	Characteristic cellular fatty acids	DNA G + C content (mol%)
Family Intrasporangiaceae							
<i>Intrasporangium</i>	LL-A ₂ pm	Gly ₃ ‡	Acetyl	MK-8	PI, PIM, PG, DPG	i-C _{15:0} , ai-C _{15:0} , i-C _{16:0}	68
<i>Actinotalea</i>	L-Orn	D-Asp	ND	MK-10(H ₄)	ND	C _{14:0} , ai-C _{15:0} , C _{16:0}	76
<i>Arsenicococcus</i>	LL-A ₂ pm	Gly	ND	MK-8(H ₄)	ND	C _{16:1} , C _{18:1} , i-C _{15:0} , ai-C _{15:0}	72
<i>Humibacillus</i>	LL-A ₂ pm	Gly	ND	MK-8(H ₄)	PE	i-C _{15:0} , ai-C _{15:0} , i-C _{16:0} , C _{17:1}	69–70
<i>Humihabitans</i>	LL-A ₂ pm	ND	ND	MK-8(H ₄)	ND	i-C _{15:0} , i-C _{16:0} , i-C _{14:0}	70
<i>Janibacter</i>	meso-A ₂ pm	None	ND	MK-8(H ₄)	PI, PG, DPG	C _{17:1} , C _{17:0} , i-C _{16:0} , C _{18:1}	69–73
<i>Knoellia</i>	meso-A ₂ pm	None	Acetyl	MK-8(H ₄), MK-7(H ₄), MK-6(H ₄)	PI, PE, DPG	i-C _{15:0} , i-C _{17:0} , i-C _{16:0} , ai-C _{17:0}	68–69
<i>Kribbia</i>	meso-A ₂ pm	None	ND	MK-8(H ₄)	ND	10-Me-C _{18:0} , i-C _{16:0} , C _{18:1} , C _{16:0} , C _{18:0}	69–70
<i>Lapillicoccus</i>	LL-A ₂ pm	ND	Acetyl	MK-8(H ₄)	DPG, PI	i-C _{16:0} , C _{17:1} , i-C _{15:0}	74
<i>Marihabitans</i>	meso-A ₂ pm	None		MK-8(H ₄)	ND	i-C _{17:0} , C _{17:1} , i-C _{15:0} , C _{18:1} , ai-C _{17:0}	70
<i>Ornithinococcus</i>	L-Orn	Gly ₁₋₂ -D-Glu	Acetyl	MK-8(H ₄)	PI, PSer, PG, DPG, PL	i-C _{15:0} , ai-C _{15:0}	72
<i>Ornithinimicrobium</i>	L-Orn	L-Ala-Gly-D-Asp	Acetyl	MK-8(H ₄)	PI, PG, DPG, PL, GL	i-C _{15:0} , i-C _{16:0}	70–71
<i>Oryzihumus</i>	meso-A ₂ pm	None	Acetyl	MK-8(H ₄)	ND	i-C _{16:0} , i-C _{15:0} , i-C _{14:0} , ai-C _{15:0}	72–73
<i>Phycococcus</i>	meso-A ₂ pm	None	Acetyl	MK-8(H ₄)	PE, PI, PG, DPG, PL	C _{17:1} , i-C _{16:0} , i-C _{15:0} , C _{15:0} , C _{17:0}	71–74
<i>Serinococcus</i>	L-Orn	ND	Acetyl	MK-8(H ₄)	PG, DPG, PI, GL	i-C _{15:0} , i-C _{16:0} , i-C _{17:1} , ai-C _{15:0} , ai-C _{17:0}	72
<i>Terrabacter</i>	LL-A ₂ pm	Gly ₃ ‡	Acetyl	MK-8(H ₄)	PE, PI, DPG, PL	i-C _{15:0} , i-C _{14:0} , i-C _{16:0}	71–73
<i>Terracoccus</i>	LL-A ₂ pm	Gly ₃ ‡	ND	MK-8(H ₄)	PE, PI, PG, DPG	i-C _{15:0} , ai-C _{15:0} , C _{16:0}	73
<i>Tetrasphaera</i>	meso-A ₂ pm (3-hydroxy meso-A ₂ pm)	None (Asp)	ND	MK-8(H ₄)	PI, PG, DPG, PE, APL, PL	i-C _{16:0} , ai-C _{17:0} , i-C _{16:1} , i-C _{15:0} , C _{16:1} , i-C _{14:0} , C _{16:0}	68–71
Family Jonesiaceae							
<i>Jonesia</i>	L-Lys	Ser-Glu	ND	MK-9	PI, PGL	ai-C _{15:0} , i-C _{16:0} , C _{16:0}	56–58
Family Microbacteriaceae							
<i>Microbacterium</i>	L-Lys or D-Orn (Hyo)	D-Glu(Hyg)-Gly ₁₋₂ -L-Lys/D-Orn (Hyo)/[L-Hsr/L-Lys]	Glycolyl	MK-11, MK-12, MK-13, MK-14, (MK-10)	DPG, PG, GL, (PI), PGL	ai-C _{15:0} , ai-C _{17:0} , i-C _{15:0} , i-C _{16:0}	64–75
<i>Agreia</i>	L-Dab, D-Orn	ND	Acetyl	MK-10, MK-11	PG, DPG, GL	ai-C _{15:0} , i-C _{16:0} , ai-C _{17:0} , ai-C _{15:0} -DMA	65–67
<i>Agrococcus</i>	Dab	ND (Thr), (Asp)	Acetyl	MK-11, MK-12, MK-10	PG, DPG, GL, PL	ai-C _{15:0} , i-C _{16:0} , i-C _{15:0} , ai-C _{17:0}	74–75
<i>Agromyces</i>	L-Dab	D-Glu-L-Dab/[L-Dab]§	Acetyl	MK-12, MK-11, MK-13	DPG, PG, GL	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0}	69–73

Table 2. cont.

Genus	Diamino acid	Interpeptide bridge/[amino acid at position 3 of the peptide subunit]	Acyl type	Major respiratory quinones	Polar lipids	Characteristic cellular fatty acids	DNA G+C content (mol%)
<i>Clavibacter</i>	L-Dab, D-Dab	D-Glu-D-Dab/[L-Dab]	Acetyl	MK-9, MK-10	DPG, PG, GL	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0}	72–74
<i>Cryobacterium</i>	L-Dab	D-Glu-L-Dab/[L-Dab]§	Acetyl	MK-10, MK-11, MK-12	DPG, PG, GL	ai-C _{15:0} , ai-C _{15:1} †, i-C _{15:0} , ai-C _{17:0} , i-C _{16:0}	65–67
<i>Curtobacterium</i>	D-Orn	D-Glu(Hyg) (–Gly)–D-Orn/[L-Hsr]	Acetyl	MK-9	PG, GL	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0} , Ch-17:0, (at 10 °C: ai-C _{15:1})†	66–74
<i>Frigoribacterium</i>	D-Lys	D-Glu-D-Lys/[L-Hsr]	Acetyl	MK-9	PG, DPG, GL	ai-C _{15:0} , i-C _{16:0} , ai-C _{15:0} -DMA, (at <10 °C: ai-C _{15:1})†	71
<i>Fronidicola</i>	D-Orn	D-Glu-D-Orn/[L-Hsr]	Acetyl	MK-8, MK-7	PG, DPG, GL, PL	C _{18:1} , C _{14:0} 2-OH	71
<i>Gulosibacter</i>	D-Orn	ND	ND	MK-9	DPG, PG, GL	ai-C _{15:0} , i-C _{16:0} , ai-C _{17:0}	65
<i>Humibacter</i>	Orn, Dab	ND	Acetyl	MK-11, MK-12	ND	Ch-17:0, ai-C _{17:0} , i-C _{16:0}	68
<i>Klugiella</i>	Lys	ND	Acetyl	MK-12, MK-11	ND	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0}	61
<i>Labeledella</i>	Orn	ND	Acetyl	MK-10, MK-11	PG, DPG	ai-C _{15:0} , i-C _{16:0} , ai-C _{17:0}	68
<i>Leifsonia</i>	L-Dab, D-Dab	D-Glu-D-Dab/[L-Dab]	Acetyl	MK-11, MK-10, MK-12	PG, DPG, GL	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0} , (Ch-17:0)	66–71
<i>Leucobacter</i>	Dab	ND (Thr), (Gab)	Acetyl	MK-11, MK-10	DPG, PG, GL, PL	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0}	66–70
<i>Microcella</i>	Lys or D-Orn	ND	ND	MK-12, MK-13, MK-14	ND	i-C _{16:0} , ai-C _{15:0} , i-C _{14:0} , i-C _{15:0}	67–71
<i>Microterricola</i>	Dab	ND	Acetyl	MK-12, MK-11	ND	ai-C _{15:0} , ai-C _{17:0}	70
<i>Mycetocola</i>	Lys	ND	Acetyl	MK-10, MK-9, MK-11	DPG, PG, GL	ai-C _{15:0} , ai-C _{17:0}	64–70
<i>Okibacterium</i>	Lys	Glu-Lys/[Hsr]	Glycolyl	MK-10, MK-11	PG, DPG, GL	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0} , i-C _{15:0}	67
<i>Phycicola</i>	Dab	D-Glu-Dab/[Dab]	Acetyl	MK-11, MK-10	DPG, PC, PG, PI	ai-C _{15:0} , ai-C _{17:0}	70
<i>Plantibacter</i>	L-Dab	D-Glu-L-Dab/[L-Dab]§	Acetyl	MK-10, MK-11, MK-9	PG, DPG, GL	ai-C _{15:0} , i-C _{16:0} , ai-C _{17:0} , i-C _{15:0}	68–70
<i>Pseudoclavibacter</i>	L-Dab, D-Dab	D-Glu-D-Dab/[L-Dab]	Acetyl	MK-9, MK-8, MK-10	DPG, PG, GL	ai-C _{15:0} , i-C _{16:0} , ai-C _{17:0}	62–68
<i>Rathayibacter</i>	L-Dab	D-Glu-L-Dab/[L-Dab]§	ND	MK-10	PG, DPG, GL	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0}	60–69
<i>Rhodoglobus</i>	Orn	ND	ND	MK-12, MK-11	ND	ai-C _{15:0} , i-C _{16:0} , ai-C _{17:0} , (at 2 °C: ai-C _{15:1})†	62
<i>Salinibacterium</i>	Orn, Lys	ND	Acetyl	MK-11, MK-10	PG, DPG	ai-C _{15:0} , i-C _{16:0} , i-C _{14:0}	61
<i>Schumannella</i>	Dab	ND	ND	MK-11, MK-10, MK-9	ND	ai-C _{15:0} , i-C _{16:0} , ai-C _{17:0} , i-C _{14:0}	59
<i>Subtercola</i>	Dab	D-Glu(Hyg)–Dab/[Dab]	Acetyl	MK-9, MK-10	PG, DPG, PL, GL	ai-C _{15:0} , i-C _{16:0} , ai-C _{17:0} , ai-C _{15:0} -DMA, (at 4 °C: ai-C _{15:1})†	64–68
<i>Yonghaparkia</i>	Dab	D-Glu-Dab/[Dab]	ND	MK-12, MK-11	PG, DPG, PL, GL	ai-C _{15:0} , i-C _{16:0} , ai-C _{17:0}	71–72
Family Micrococcaceae							
<i>Micrococcus</i>	L-Lys	Peptide subunit‡, Asp	ND	MK-8(H ₂) or MK-8, MK-8(H ₂)	PG, DPG, PI, GL, PL	ai-C _{15:0} , i-C _{15:0}	69–74
<i>Acaricomes</i>	L-Lys	L-Ala ₃	ND	MK-10(H ₂)	PG, DPG, PI	ai-C _{15:0} , ai-C _{17:0}	58
<i>Arthrobacter, globiformis</i> group	L-Lys	MCA _{var.}	ND	MK-9(H ₂), MK-8(H ₂), MK-10(H ₂)	DPG, PG, PI, DMDG, (PE)	ai-C _{15:0} , i-C _{15:0} , i-C _{16:0} , ai-C _{17:0} , (at <10 °C: ai-C _{15:1})†	61–69
<i>Arthrobacter, nicotianae</i> group	L-Lys	Ala–Glu, Ser–Glu, Glu or Asp	ND	MK-8, MK-9, MK-10	DPG, PG, PI, DMDG	ai-C _{15:0} , ai-C _{17:0}	58–66

Table 2. cont.

Genus	Diamino acid	Interpeptide bridge/[amino acid at position 3 of the peptide subunit]	Acyl type	Major respiratory quinones	Polar lipids	Characteristic cellular fatty acids	DNA G + C content (mol%)
<i>Citricoccus</i>	L-Lys	Gly–Glu	ND	MK-9(H ₂), MK-7(H ₂), MK-8(H ₂)	DPG, PG, PI, PL, GL	ai-C _{15:0} , ai-C _{17:0} , i-C _{15:0} , i-C _{16:0}	63–68
<i>Kocuria</i>	L-Lys	L-Ala ₃₋₄	ND	MK-7(H ₂), MK-8(H ₂), MK-9(H ₂)	DPG, PG, (PI, PL, GL)	ai-C _{15:0} , ai-C _{17:0} , i-C _{15:0}	60–75
<i>Nesterenkonia</i>	L-Lys	Gly–L-Glu or L-Glu or Gly–Asp	ND	MK-8, MK-9, MK-7	DPG, PG, PI, PL, GL	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0}	64–72
<i>Renibacterium</i>	L-Lys	L-Ala–Glyll	ND	MK-9, MK-10	DPG, GL	ai-C _{15:0} , ai-C _{17:0}	52–54
<i>Rothia</i>	L-Lys	Ala ₃ , Ala, Ser, Gly or Gly–Ala	Acetyl	MK-7, (MK-6[H ₂])	DPG, PG	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0} , C _{16:0}	49–60
<i>Zhihengliuella</i>	L-Lys	L-Ala–L-Glu	ND	MK-9, MK-10, MK-8	PG, DPG, PI, PL, GL	ai-C _{15:0} , i-C _{15:0}	67
Family Promicromonosporaceae							
<i>Promicromonospora</i>	L-Lys	L-Ala–D-Glu	ND	MK-9(H ₄)	DPG, PG, PGL, PL, GL	ai-C _{15:0} , i-C _{16:0} , C _{16:0} , ai-C _{17:0}	70–75
<i>Cellulosimicrobium</i>	L-Lys	D-Ser–D-Asp	ND	MK-9(H ₄)	ND	ai-C _{15:0} , i-C _{16:0} , C _{16:0} , i-C _{15:0}	74
<i>Isoptericola</i>	L-Lys	D-Asp or D-Glu	Acetyl	MK-9(H ₄)	PG, DPG, PI, PL	ai-C _{15:0} , i-C _{15:0} , C _{14:0} , C _{16:0} , i-C _{16:0} , ai-C _{17:0}	70–72
<i>Myceligenans</i>	L-Lys	L-Thr–D-Glu	Acetyl	MK-9(H ₄), MK-9(H ₆)	PG, DPG, PI, PL, GL	ai-C _{15:0} , i-C _{15:0}	72
<i>Xylanibacterium</i>	L-Lys	L-Ala–D-Glu	ND	MK-9(H ₄), MK-8(H ₄)	PG, DPG, PI, PIM	ai-C _{15:0} , i-C _{15:0} , C _{16:0} , C _{14:0}	72
<i>Xylanimicrobium</i>	L-Lys	L-Ser–D-Glu	Acetyl	MK-9(H ₄)	PG, DPG, PI, 3PL	ai-C _{15:0} , i-C _{15:0} , C _{16:0} , C _{14:0}	70
<i>Xylanimonas</i>	L-Lys	D-Asp	ND	MK-9(H ₄), MK-8(H ₄)	PG, DPG, PI, PIM	ai-C _{15:0} , i-C _{15:0}	73
Family Rarobacteraceae							
<i>Rarobacter</i>	L-Orn	Ser–Glu or Glu	Acetyl	MK-9	ND	ai-C _{15:0} , i-C _{16:0} , C _{14:0} (aerobic)	65–66
Family Sanguibacteraceae							
<i>Sanguibacter</i>	L-Lys	Ser–D-Glu	ND	MK-9(H ₄)	ND	ai-C _{15:0} , C _{16:0} , C _{14:0}	69–73
Family Yaniellaceae							
<i>Yaniella</i>	L-Lys	Gly–L-Glu	ND	MK-8, MK-9, MK-7	DPG, PG, PI, PL, GL	ai-C _{15:0} , i-C _{14:0} , i-C _{15:0}	53–58
Genera unassigned to a family							
<i>Actinotalea</i>	L-Orn	D-Asp	ND	MK-10(H ₄)	ND	C _{14:0} , ai-C _{15:0} , C _{16:0}	76
<i>Demequina</i>	L-Orn	ND	ND	DMK-9(H ₄)	PI, DPG, PL	ai-C _{15:0} , ai-C _{15:1} †, C _{16:0} , ai-C _{17:0}	67
<i>Ruania</i>	L-Lys	Gly–L-Glu ₂	ND	MK-8(H ₄)	PG, DPG, GL	ai-C _{15:0} , ai-C _{17:0} , i-C _{16:0}	70
<i>Tropheryma</i>	ND	ND	ND	ND	ND	ND	59

*L-Ser occupies position 1 of the peptide subunit.

†The monounsaturated 12-methyl-tetradecenoic acid (ai-C_{15:1}) may also be present in organisms of other genera when grown at temperatures below 10 °C.

‡Glycine or glycine amide bound to α-carboxyl group of glutamic acid at position 2 of peptide subunit.

§Peptidoglycan structure supposed on the basis of data from Sasaki *et al.* (1998) and Behrendt *et al.* (2002).

||D-Alanine amide bound to α-carboxyl group of glutamic acid at position 2 of peptide subunit.

Fig. 1. Neighbour-joining tree showing the phylogenetic relationship of type strains of type species currently classified in the suborder *Micrococcineae* based on 16S rRNA gene sequences. Bootstrap values (expressed as percentages of 1000 replications) are given at branch points; only values >70 % are shown. *Bacillus subtilis* subsp. *subtilis* DSM 10^T was used as outgroup. Bar, 0.01 substitutions per nucleotide position.

ined in most laboratories are recommended in order to support the differentiation of special groups (Table 4). Taxonomists should feel positively encouraged to apply additional taxonomic methods to supplement those specified here and to continue to search for novel tools that are useful for the differentiation of taxa within this suborder.

CULTURAL AND BIOCHEMICAL CRITERIA

Colony appearance

Most of the 'classical' taxonomic characteristics used and recommended for the description of genera and species of the suborder *Micrococcineae* are the same as those employed for many other bacteria and are available from the literature (e.g. Smibert & Krieg, 1994). Some characteristics and methods which reflect the specificity of the suborder under consideration are outlined below.

The colony characteristics, including colour, shape, diameter, edge, elevation, surface, consistency and transpar-

ency, penetration into agar, etc., may serve for the (preliminary) differentiation of species when observed under standardized conditions (*Bergey's Manual*; Sneath *et al.*, 1986). The composition of media and growth conditions must be specified, since the colony characteristics (e.g. colony colours of related species) tend to change and depend on the growth conditions.

Growth on agar media supplemented with vitamins, Casitone (milk) and yeast extract, as well as incubation in full daylight, often induce or enhance pigment formation (Koyama *et al.*, 1974; Vidaver & Davis, 1988; Holt & Krieg, 1994; Trutko *et al.*, 2005). Attention must be paid to controlling pH values since deviations from a given pH may markedly alter the colony colour (Turner & Messenger, 1986). When organisms with alkaliphilic (alkalitolerant) or acidophilic (acidotolerant) properties and their relatives that prefer neutral pH values are compared, the colony colour should be tested at different pH values. For those representatives of the suborder which form aerial mycelia, the use of diagnostic ISP media (Shirling & Gottlieb, 1966) is often appropriate.

Table 3. Minimal standards required for the description of genera and species classified in the suborder *Micrococcineae*

Criteria
Genotypic criteria Phylogenetic position based on 16S rRNA gene sequence comparisons (different treeing methods should be applied). For species allocation within an established genus, the 16S rRNA gene sequence similarity values to the most closely related species (and the exact methods of calculation) must be given DNA base composition (mol% G + C content of the DNA) (mandatory for genus descriptions) DNA–DNA hybridizations with the most closely related species (showing a 16S rRNA gene sequence similarity >97 %) within an established genus (mandatory for species descriptions)*
Cultural and biochemical criteria General morphology Gram reaction Relation to oxygen and oxidative or fermentative metabolism Catalase activity, oxidase activity Utilization of different carbon sources, acid production from carbohydrates and other carbon sources and enzymic activities and decomposition of selected substrates which must be tested concurrently with the most closely related species on the basis of the same method
Chemotaxonomic criteria Peptidoglycan structure (qualitative amino acid composition of peptidoglycan mandatory for genus descriptions) Cellular fatty acids Polar lipids Respiratory quinone pattern

*Within the genus *Microbacterium*, it has been shown that the 16S rRNA gene sequence similarity <98 % may justify a separate species status. In these cases DNA–DNA hybridizations may not be necessary, provided that there is clear evidence that the strain(s) under study is (are) phenotypically clearly different from the most closely related species on the basis of at least five traits which must have been studied concurrently. Clear evidence may be provided by examination of several strains for which non-clonal relatedness was demonstrated. Species identity and non-clonal relatedness may be demonstrated by genomic fingerprinting (high degree of similarity but differences still present in the banding patterns).

Table 4. Recommended characteristics for characterization and differentiation of genera and species classified in the suborder *Micrococcineae*

Characteristic
Cell-wall sugars
Acyl type of peptidoglycan
Polyamines
Total protein profiles
Presence of cell-wall teichoic acids and components of cell-wall polysaccharides
Sequences of housekeeping genes, multilocus sequence analysis
DNA typing patterns
FT-IR spectroscopy
MALDI/TOF mass spectrometry
Pigments
Terminal oxidase pattern of respiratory chain
Cytochrome and haem composition

Morphology

The notion of the taxonomic value of morphological characters in the classification and differentiation of genera and species in the group under consideration has undergone changes in recent decades.

The importance of morphological characteristics seems to increase for genera since the range of available chemo-taxonomic generic criteria appears insufficient for the discrimination of some phylogenetically neighbouring coherent groups for which generic status is claimed (for examples see IJSEM, recent publications). Generalized terms such as ‘cocci’, ‘irregular rods’, ‘coryneform morphology’ and ‘nocardioform morphology’ are currently widely used in the descriptions of novel genera.

However, for both genera and species, detailed descriptions of the morphology must be provided, including cell size and shape, both at earlier and later growth phases, the type of cell division, cell arrangements, the formation of substrate (primary) and aerial (secondary) mycelium and their fragmentation, and the production and characterization of arthrospores or, if appropriate, other resting cells. As some representatives of the suborder *Micrococcineae* form spores (arthrospores), e.g. species of the genera *Arthrobacter* (Tanaka *et al.*, 2001) and *Myceligerans* (Cui *et al.*, 2004), it is recommended that it should be stated precisely which kind of spores or resting cells are observed and that the term ‘non-endospore-forming’ rather than ‘non-spore-forming’ is used in relevant cases. It is recommended that morphological changes during growth should be tested and noted and that the presence (or absence) of a specific life cycle should be determined. All of the above characteristics should be examined on at least two appropriate agar media of different compositions (e.g. rich in organics as well as chemically defined). The use of relatively old cultures or resting cells is preferable for inoculation in order to synchronize the development of subsequent populations. It is recommended that light or electron micrographs of the culture are

presented at different growth phases, particularly for the type strains of the type species of newly described genera.

Motility

The simplest method to examine motility is the ‘hanging-drop method’. Motility can be concluded from the presence of flagella as demonstrated by electron microscopy. Additional methods to test for motility and the formation of flagella were proposed by Holt & Krieg (1994). The inoculation and testing conditions may be important for some groups. Good results are usually obtained for cultures on semi-solid agar media (agar, 0.2–0.4 %) obtained after inoculation with relatively old cells (1–2 weeks) from agar media. Since not all cells in a population produce flagella, a sample taken from the periphery of colonies is preferable. It should be taken into account that in many representatives of the suborder *Micrococcineae*, flagella are formed at a later growth phase, i.e. when the cells are at the division stage and/or when the first generations of cells have already consumed the nutrient compounds around the colonies. Even for rapidly growing organisms, it is recommended that motility is examined for a growth period of up to 7–10 days. It should also be taken into account that high temperatures, the presence of glucose or low humidity may inhibit the formation of flagella (Holt & Krieg, 1994) and that cells may lose flagella during sample preparation for electron microscopy. It should be emphasized that the absence of flagella does not necessarily mean that the cells are non-motile. Members of the suborder may possess other, not yet fully elucidated mechanisms of motion, e.g. via pili (‘twitching motility’). The method used for testing motility and the type of movement observed must be clearly stated.

Gram reaction

Although members of the suborder *Micrococcineae* belong to the Gram-positive bacteria in terms of cell-wall structure, the staining reaction may be negative under special circumstances and differentiation between the terms ‘Gram reaction’ and ‘Gram type’ is necessary (Wiegel, 1981). Negative or indistinct Gram-stain has been reported for some members of the suborder, e.g. the family *Microbacteriaceae*, even in relatively young cultures. It is recommended that cultures should be subjected to the Gram staining procedure just after growth has become visible and that staining is tested again at a later exponential growth phase. As Gram-positive bacteria are in general not lysed by 3 % KOH, this simple test is recommended as an additional criterion for the classification of the Gram-reaction status of a novel strain (Ryu, 1938). The test method must be clearly stated.

Growth requirements

The data on growth requirements characterize an organism and are essential for the determination of its optimal

cultivation. Suitable media that are as different as possible, the necessary additives (vitamins and other growth factors, extracts, salt, etc.) and the range and optima of pH and growth temperature must be precisely documented. Some useful recommendations for the description of alkaliphilic and alkalitolerant organisms are outlined by Sorokin (2005).

Relationship with oxygen and oxidative or fermentative metabolism

Most members of the suborder *Micrococcineae* are strict aerobes and are characterized by the oxidative type of metabolism. There are also organisms which grow both under aerobic and anaerobic conditions and display the fermentative type of metabolism in addition to the oxidative type (e.g. representatives of the genus *Oerskovia*). Besides the aforementioned groups, there are also the microaerophilic representatives, which require low concentrations of oxygen for optimal growth (e.g. *Agromyces ramosus*) and this characteristic should be noted whenever appropriate. The examination of the capability of an organism to grow in an anaerobic chamber is recommended to demonstrate its relationship with oxygen. Anaerobic chambers are also suited to test the influence of alternative electron acceptors. For testing fermentative properties (oxidative or fermentative utilization of glucose), the oxidation–fermentation test (O/F-test, Hugh–Leifson test) is generally accepted (Leifson, 1962; Smibert & Krieg, 1994). For testing microaerophilic growth, stab cultures in semi-liquid media (0.2–0.4 % agar) can be used. Microaerophilic growth occurs primarily as a distinct or diffuse band below the agar surface (Gledhill & Casida, 1969; Smibert & Krieg, 1994).

Catalase activity

Almost all tested organisms of the considered group possess catalase activity as the main factor inactivating reactive oxygen. To test for presence of catalase, the standard method employing 3 % H₂O₂ is recommended. Although the method is very simple, it is necessary to follow exactly the general recommendations outlined by Smibert & Krieg (1994). In the case of a negative catalase test, it is advisable to characterize other factors that may be preventing oxygen damage as they might turn out to be differentiating characteristics for the organism under study.

Oxidase activity

The classical ‘oxidase test’ (Smibert & Krieg, 1994) with *N,N,N',N'*-tetramethyl-*p*-phenylenediamine (most frequently used in this group) or with *N,N*-dimethyl-*p*-phenylenediamine differentiates two types of aerobic respiratory chains (Unden, 1999). As some organisms grown under different conditions or at different growth stages may show different reactions with *N,N,N',N'*-tetramethyl-*p*-phenylenediamine, oxidase activity should

be examined in young, actively growing cultures from agar media. The term ‘negative oxidase reaction with *N,N,N',N'*-tetramethyl-*p*-phenylenediamine’ is recommended instead of ‘oxidase-negative’, since all aerobic bacteria have oxidases in the respiratory chains. The test method and growth conditions must be clearly stated.

Compared with the simple ‘oxidase test’, the determination of the terminal oxidase pattern may provide more information on respiratory chains. This characteristic has not been used regularly for taxonomic purposes. However, available data show that it may be helpful for the differentiation of some species and genera of the family *Microbacteriaceae*. For instance, species of the genus *Plantibacter* produce only the cytochrome oxidase *aa*₃, while the members of the genus *Rathayibacter* synthesize cytochrome oxidase *bb*₃ or both *bb*₃ and *aa*₃, depending on growth conditions. Some quinole oxidases, e.g. *bo*₃ or *bb*₃, may be also indicative of species (Trutko *et al.*, 2003). On the other hand, the *bd*-type oxidases seem to be of little significance for differentiation as they are synthesized at relatively low oxygen concentrations in all organisms tested so far. Growth conditions for testing this property should be standardized. The methods of determination of the terminal oxidase patterns are based on spectrophotometry (preliminary spectral characteristics) and chromatography (Trutko *et al.*, 2003).

Utilization of different carbon sources

Records of the utilization of different carbon sources, including sugars, organic acids, amino acids, etc., as sole carbon source for growth are valuable phenotypic traits in the characterization and delineation of most species within the genera of the suborder *Micrococcineae*. Several slightly varying basal media can be recommended for different groups of organisms (see e.g. Shirling & Gottlieb, 1966; Smibert & Krieg, 1994; recent publications on particular genera). Although the use of commercial test systems for the examination of the physiological characteristics of novel organisms has been controversial (Whiley & Kilian, 2003; Stackebrandt *et al.*, 2002b), their use is considered acceptable as these kits have been employed in the descriptions of many novel taxa of the suborder due to their ease of use and speed of handling. For comparative analyses it is, however, necessary to study all organisms concurrently with the same tests. Otherwise the data cannot be compared.

The utilization of organic acids is examined either by testing growth on carbon-free basal media supplemented with the compound to be tested or by classical Simmons’ citrate tests (basal medium free of additional carbon sources; bromothymol blue indicator) (Smibert & Krieg, 1994). For some groups, the basal medium should be supplemented with required additives (vitamins, salts, traces of amino acids, etc.) in order to obtain unambiguous results.

The number and type of carbon sources tested may vary depending on the group of organisms.

Acid production from carbohydrates and other carbon sources

The methods for the examination of these properties have been described by Smibert & Krieg (1994), Gordon & Mihm (1957) and in publications on particular genera. The test for acid production is performed under aerobic conditions. The following sources can be recommended: D-glucose, L-arabinose, raffinose, L-rhamnose, D-ribose, salicin, sucrose, *myo*-inositol, D-mannitol, glycerol.

The test media should meet the growth requirements of the particular organism. It is recommended that the minimal concentration of the pH indicator is used since the usually recommended concentrations (developed for other groups of organisms) may inhibit the growth of representatives of the suborder *Micrococcineae*, in particular of those of the family *Microbacteriaceae*.

With respect to this and the groups of characteristics mentioned above, it should be noted that both the terms 'utilization of carbon sources' and 'acid production from ...', which are usually used to circumscribe the respective features of members of the suborder *Micrococcineae*, are covered by the term 'utilization' and there is some confusion over this issue (and hence with the interpretation of results). Though the tests 'growth on sole carbon source' and 'acid production from ...' (carbon-free basal medium) often give the same positive or negative result, they reflect different features of the organisms. Besides, the terms 'utilization of sugars' and 'acid production from ...' are employed to report the results obtained using basal media supplemented with additional carbon sources, e.g. tryptone (API Coryne system, bioMérieux). In addition, the pH indicators (phenol red or bromothymol blue) most frequently used to test acid production show clear positive reactions at somewhat different pH values (6.8 and 6.0, respectively).

Comparisons of data generated by different methods or of author's own data with those from the literature often lead to confusion because of conflicting results. The principles of the tests must be taken into account and the results properly interpreted and described.

Enzymic activities and decomposition of selected substrates

Enzymic activities are used in almost all groups of the suborder for the circumscription of species and also of genera (e.g. *Cellulomonas*) and are determined by using particular organic substrates (e.g. aesculin, cellulose, starch, Tweens). It must be clearly indicated which method or commercial test system was applied for testing enzymic activities. The number of activities to be examined for unambiguous delineation of species may vary depending on the group of organisms.

The following minimal set of activities is recommended:

- Nitrate reduction determined by the sulfanilic acid and alpha-naphthylamine method and confirmed with zinc dust (Barrow & Feltham, 1993).
- Urease activity determined on Christensen agar (Christensen, 1946). The red-violet colour of inoculated agar is interpreted as a positive result.
- Arginine dihydrolase activity tested in tubes containing Møller medium (Møller, 1955), both with and without a covering layer of sterile paraffin oil. Tests should be read daily for a period of 5 days. Development of a violet colour is recorded as a positive result.
- Ornithine decarboxylase activity determined using basal medium with 1 % (w/v) L-ornithine dihydrochloride (Smibert & Krieg, 1994).
- Alkaline phosphatase activity determined according to Smibert & Krieg (1994).

It is recommended that decomposition (hydrolysis) is tested for the following minimal set of substrates according to methods described by Smibert & Krieg (1994): aesculin, casein, cellulose, hypoxanthine, xanthine, starch, L-tyrosine, Tween-60 and Tween-80.

H₂S production

The ability to produce H₂S is determined by using a growth medium with peptone (rich in organic sulfur) or liquid medium containing 0.05 % cysteine. The latter medium should be preferred as some members of the suborder *Micrococcineae* display a positive result only if cysteine is used as substrate. Sterile filter strips impregnated with lead acetate are used as the indicator (blackening is regarded as a positive reaction due to the formation of lead sulfide) (Smibert & Krieg, 1994).

Tolerance of NaCl and salt requirement

Representatives of many species and genera of the suborder *Micrococcineae* are well differentiated with respect to their salinity requirements. Tolerance of high concentrations of NaCl has been reported for some members of the suborder, e.g. members of the genus *Nesterenkonia*, *Yaniella halotolerans* (up to 25 % NaCl; Li *et al.*, 2004, 2008) and members of the genus *Brevibacterium* (up to 18 % NaCl; Gavrish *et al.*, 2004). The tolerance of lower salt concentrations clearly differentiates species of many genera commonly known to be non-halotolerant. The ability to grow at different concentrations of NaCl should be tested in organisms of all new taxa, particularly when strains have been isolated from marine environments, saline and alkaline soils and various desert biotopes, as well as ice and frozen soils or sediments. It is also advisable to evaluate accurately whether particular organisms are either halotolerant or halophilic. A liquid growth medium with a minimal content of essential salts is preferable for testing tolerance to NaCl and the salt requirement.

CHEMOTAXONOMIC CRITERIA

Peptidoglycan structure

The highly diverse peptidoglycan structures of members of the suborder *Micrococcineae* (Table 2) can be subdivided according to the following criteria:

- type of diagnostic diamino acid
- type of cross-linkage (A or B according to Schleifer & Kandler, 1972)
- detailed structure, including amino acid sequence of the interpeptide bridge (see Schleifer & Kandler, 1972 and http://www.dsmz.de/microorganisms/main.php?content_id=35).

Peptidoglycan structures are an important tool for the differentiation of members of the suborder *Micrococcineae* at the genus level and also at the species level within several genera (e.g. *Arthrobacter*, *Microbacterium*, *Cellulomonas*, *Oerskovia*, *Brachybacterium* and *Nesterenkonia*). On the other hand, the elucidation of the detailed peptidoglycan structure according to Schleifer & Kandler (1972) and Schleifer (1985) is a rather demanding task that requires specific experience and cannot be performed by all laboratories. For differentiation at the genus level, it is necessary to examine as a minimal requirement, the type of the diagnostic diamino acid (ornithine, lysine, diamino-butyric acid, diaminopimelic acid isomers, hydroxylated diamino acids) and other amino acids included in the peptidoglycan. The molar ratio of amino acids in peptidoglycan hydrolysates should be determined by using automated amino acid analysers (Schleifer & Kandler, 1972), HPLC (e.g. Lin *et al.*, 2004), GC (e.g. MacKenzie, 1987) or GC/MS (e.g. MacKenzie, 1984) since quantitative data allow the discrimination between many peptidoglycan structures. Additional investigations such as enantiomeric analysis of amino acids by GC (e.g. Frank *et al.*, 1980) or by HPLC (e.g. Sasaki *et al.*, 1998), the amino acid sequence of the interpeptide bridge and the determination of the *N*-terminal amino acid of the interpeptide bridge (Schleifer, 1985) also provide helpful information for the elucidation of the detailed peptidoglycan structure and the type of cross-linkage. Taxonomists are encouraged to study the detailed peptidoglycan structure for differentiation at the genus as well as at the species level or to seek cooperation for the respective analytical methods.

Acyl type of peptidoglycan

Although most of the genera of the suborder *Micrococcineae* have not yet been studied with respect to the type of acylation of the muramic acid residues in the peptidoglycan, the examination of this feature is recommended for differentiation at the genus and at the species level. Members of some genera (*Microbacterium* and *Okibacterium*) contain glycolyl (usually as well as acetyl) residues in their peptidoglycan, whereas the majority of examined genera contain only acetyl residues. The genus

Brachybacterium is inconsistent as regards the type of acylation of the muramic acid residues. Glycolylation can be detected by the procedure of Uchida & Aida (1984) or by a miniaturized method (Uchida *et al.*, 1999).

Cell-wall sugars

Only a few genera of the suborder *Micrococcineae* are consistent with respect to cell-wall sugar composition. In particular, the presence of rhamnose seems to be diagnostic for some genera. The occurrence of specific sugars in some species is desirable information in the genus description. The determination of sugars is recommended for differentiation at the species level. Since whole cells may contain incorporated sugars from the cultivation media and typically also glucose, ribose and other sugars originating from the cytoplasm or capsules, it is recommended that cell walls are isolated and purified according to Schleifer (1985) prior to the analysis. Hydrochloric acid is not suited for hydrolysis because chloro-deoxy sugars may be formed. Instead, 1 M sulfuric acid has to be used for cell-wall hydrolysis. This can be removed easily prior to sugar analysis by extraction with *N,N*-dioctylmethylamine in chloroform as described by Hancock (1994). The identification of the sugars can be performed by TLC, e.g. as described by Komagata & Suzuki (1987). Quantification of the sugars can be performed by GC or HPLC as described by Saddler *et al.* (1991) and Takeuchi & Yokota (1989), respectively.

Respiratory quinone patterns

The length and degree of saturation of the isoprenoid side chain is very variable (Table 2). The structural diversity of menaquinones and demethylmenaquinones as exclusive isoprenoid quinones in the suborder *Micrococcineae* can be analysed quantitatively by HPLC and mass spectrometric methods (Collins, 1994).

Polar lipids

Analyses of polar lipids of bacteria are performed in most laboratories by two dimensional TLC as described by Lechevalier *et al.* (1977), Komagata & Suzuki (1987) and Tindall (1990) for example. Many publications report 'unknown' phospholipid and glycolipid components (see Table 2) which could not be identified at the time of analysis. It is suggested that authors who cannot identify taxonomically relevant polar lipid components include a figure of the chromatogram in the manuscript in order to demonstrate the position of the respective spots for comparative purposes.

Polyamines

Polyamine patterns are so far available for only a limited number of genera of the suborder *Micrococcineae* including representatives of the families *Micrococcaceae*, *Intrasporangiaceae*, *Microbacteriaceae*, *Sanguibacteraceae*, *Brevi-*

bacteraceae, Bogoriellaceae, Promicromonosporaceae, Cellulomonadaceae and Dermabacteraceae. Species of the family Micrococcaceae have been shown to exhibit polyamine patterns which consist of the predominant compound spermidine often along with significant amounts of spermine (Hamana, 1994, 1995; Altenburger *et al.*, 1997, 2002a, 2002b; Gvozdiak *et al.*, 1998; Busse & Schumann, 1999; Buczolits *et al.*, 2003; Busse *et al.*, 2003). Higher variability in polyamine patterns was detected among genera of the family Microbacteriaceae (Altenburger *et al.*, 1997). Members of the genera *Curtobacterium*, *Clavibacter* and *Rathayibacter* show polyamine patterns with the major compounds spermidine and spermine, species of the genera *Agrococcus* and *Plantibacter* are characterized by the major compound spermine and *Pseudoclavibacter helvolus* contains the major compounds cadaverine and 1,3-diaminopropane. The single species of the genus *Leifsonia* analysed, *Leifsonia poae*, contains the major compound putrescine. Species of the genus *Agromyces* are characterized by very low polyamine contents. Four species of the family Intrasporangiaceae, each representing a different genus (*Intrasporangium*, *Terrabacter*, *Terracoccus* and *Janibacter*), were shown to share putrescine as a major compound. Additional major compounds such as spermidine (*Intrasporangium*), spermidine and spermine (*Terracoccus*) or cadaverine (*Janibacter*) suggest the potential of polyamine patterns to distinguish at least between groups of this complex family. Species of the genera *Promicromonospora* and *Cellulosimicrobium* (family *Promicromonosporaceae*) as well as the genera *Cellulomonas* and *Oerskovia* (family *Cellulomonadaceae*) show polyamine patterns with the predominant compound spermidine and moderate amounts of spermine, but the overall polyamine concentrations may differ by two orders of magnitude. Members of the genus *Brevibacterium* (family *Brevibacteriaceae*) exhibit polyamine patterns predominated by cadaverine and putrescine and species of the genus *Sanguibacter* (family *Sanguibacteraceae*) show only spermine as the predominant polyamine. Two species of the genus *Brachybacterium*, representing the family *Dermabacteraceae*, show a polyamine pattern consisting of the major amines spermidine and spermine and the polyamine content is quite high. *Georgenia muralis* is the only representative of the family *Bogoriellaceae* which has been examined for polyamines. The major polyamines of this species are spermidine and spermine in similar concentrations, but the overall polyamine concentrations are approximately 4–12 orders of magnitude lower than in other representatives of the suborder.

This variability among representatives of the suborder *Micrococcineae* indicates that polyamine patterns are conserved at distinctive taxonomic levels and are therefore recommended characteristics for classification and identification. According to available data, the following taxa or groups of genera within a family share common characteristics in polyamine patterns: *Clavibacter*/*Rathayibacter*/*Curtobacterium*, *Leifsonia*/*Agromyces*, *Promicromonospora*/*Cellulosimicrobium*, *Cellulomonadaceae* and *Intrasporangium*/*Terrabacter*/*Terracoccus*/*Janibacter*.

Certain polyamine patterns are found in different families but, in polyphasic classification, this approach can play an important role in distinguishing taxa which cannot be differentiated by other traits. Hence analysis of polyamine patterns can be recommended at least for those taxa listed here and data from other taxa are highly desirable to complement the classification scheme for the suborder *Micrococcineae*.

Polyamines can be easily extracted in less than two hours without any special equipment and analysed by gradient HPLC after derivatization with dansyl chloride and detection with a fluorescence detector (Altenburger *et al.*, 1997; Scherer & Kneifel, 1983) or after post-column derivatization with *o*-phthalaldehyde (Hamana, 1995).

Cellular fatty acids

The general type of cellular fatty acids (i.e. straight-chain saturated and monounsaturated type, 10-methyl-branched-chain type, iso/anteiso-branched-chain type, ω -cyclohexyl fatty acid type, complex type; Suzuki & Komagata, 1983) is of significance for classification at the genus level whereas the quantitative profile of cellular fatty acids can be used for the differentiation of species. The discriminating power of cellular fatty acid profiles differs between families of the suborder *Micrococcineae*. For instance, most organisms of the family *Microbacteriaceae* display fatty acid profiles consisting of only few components of the iso- and anteiso-branched type and the discrimination of genera and species on the basis of such patterns is hardly possible. Only representatives of particular genera have been reported to contain characteristic components as ω -cyclohexyl fatty acids (Suzuki & Komagata, 1983; Qiu *et al.*, 2007; Vaz-Moreira *et al.*, 2008), 2-hydroxy-tetradecanoic and monounsaturated octadecenoic acid (Zhang *et al.*, 2007b) or 1,1-dimethoxy-alkanes (Kämpfer *et al.*, 2000; Schumann *et al.*, 2003) (Table 2). Members of the family *Intrasporangiaceae*, on the other hand, are characterized by complex patterns consisting of many components which are well suited for their differentiation. As a conclusion from these observations, cellular fatty acid profiles are recommended as a minimal requirement for differentiation at the genus and at the species level. The comparison of fatty acid profiles necessitates the standardization of the cultivation conditions since the composition of media, the age of the culture, the temperature and the availability of oxygen have a strong influence on the fatty acid patterns. Therefore it may be necessary to analyse the fatty acids of strains for comparison in one and the same laboratory rather than to compare one's own data with those available from literature. This is particularly important when quantitative data on individual fatty acids rather than overall patterns are compared. The preferable method for analysis of cellular fatty acid profiles is capillary GC of fatty acid methyl esters. If it is the case that some fatty acid methyl

esters cannot be unambiguously identified on the basis of their retention times due to co-elution (e.g. C_{18:1}ω7c and cyclohexyl C_{17:0}; 2-OH C_{14:0} and C_{15:0}-DMA; 2-OH iso-C_{15:0} and C_{16:1}ω7c), the identification should be supported by GC/MS or hydrogenation experiments.

Total protein profiles

Whole-cell protein profiles have been proved to be useful tools for determining the coherency of species (Zlamala *et al.*, 2002a, b) and for the differentiation of species within the genus *Brachybacterium* (Buczolits *et al.*, 2003).

Cell-wall teichoic acids and related anionic polymers

Cell-wall teichoic acids have been detected in only a few genera of the suborder *Micrococcineae*, e.g. in *Brevibacterium* (Fiedler *et al.*, 1981), *Brachybacterium* (Schubert *et al.*, 1996), *Agromyces* (Naumova *et al.*, 2001), *Jonesia* (Fiedler *et al.*, 1984), *Rarobacter* (Takeuchi & Yokota, 1989), *Agromyces* (Naumova *et al.*, 2001) and in the *Arthrobacter nicotianae* group (Fiedler & Schäffler, 1987). The characteristic 'presence (absence) of teichoic acids' is recommended as a useful criterion for the differentiation of relevant genera and species.

The structure and composition of cell-wall teichoic acids and other cell-wall-associated anionic polysaccharides appear to be indicative of most of the actinomycete species where such polymers have been analysed so far (e.g. Fiedler & Schäffler, 1987; Schubert *et al.*, 1996; Ortiz-Martinez *et al.*, 2004; Potekhina *et al.*, 2003a, b, 2004, 2007; Naumova *et al.*, 2001; Shashkov *et al.*, 2004). The structural components of these polymers (glycerol, ribitol, mannitol, erythritol, galactose, glucose, rhamnose, aminosugars etc.) have been shown to be useful for the delineation of some species, e.g. in the genera *Brachybacterium* (Schubert *et al.*, 1996) and *Brevibacterium* (Gavriš *et al.*, 2004) and can be recommended as phenotypic traits for the characterization and differentiation of organisms at the species level.

Cells for the analysis of anionic phosphorus-containing polymers of cell walls can be grown in any suitable liquid media supplemented with phosphorus and should be harvested at the exponential growth phase.

The simple method for detecting the cell-wall teichoic acids is the measurement of thermostable phosphate levels, e.g. by the method of Ames (1966), combined with determination of the main structural components of polymers, mainly polyols (Bergmeyer, 1974; Endl *et al.*, 1984; Streshinskaya *et al.*, 2002). For the isolation of anionic polymers, a native cell wall is obtained from cells by fractionated centrifugation after disruption, e.g. by ultrasonication, and purified by 2 % sodium dodecyl sulfate at 100 °C for 5 min). The polymers are extracted with trichloroacetic acid (10 %, 4 °C, 48 h). The methods for the determination of the main structural components are

based on the analysis of products of acid hydrolysis (2M HCl, 100 °C, 3 h) by chemical and chromatographic methods (Archibald, 1972; Naumova *et al.*, 1980; Takeuchi & Yokota, 1989).

The main structural components of teichoic acids can be determined directly in the hydrolysates of purified cell walls without the extraction of polymers (Naumova *et al.*, 1980). Polyols can also be identified by thin-layer or paper chromatography as described for sugar analysis (e.g. Komagata & Suzuki, 1987; Becker *et al.*, 1964), with additional staining by 5 % AgNO₃ in aqueous ammonia solution (sugar spots are stained brown, while polyol spots become black). GC or HPLC analysis can also be applied (Saddler *et al.*, 1991; Takeuchi & Yokota, 1989).

Cytochrome and haem composition

Although cytochrome and haem patterns have been studied so far only in some genera of the suborder, including *Micrococcus*, *Kocuria*, *Dermacoccus*, *Agreia*, *Plantibacter*, *Rathayibacter* and *Okibacterium*, they appear to be valuable for taxonomic purposes and are recommended for the differentiation of organisms at the genus and, particularly, at the species level. The methods for testing cytochrome and haem composition are based on spectrophotometry (preliminary spectral characteristics) and chromatography (Faller *et al.*, 1980; Trutko *et al.*, 2003).

Pigments

Many representatives of the suborder *Micrococcineae* produce pigments which are typically yellow (of different tints and intensities) to orange or red. Some species of the genera *Clavibacter* and *Arthrobacter* are known to produce blue pigments. The chemical composition of pigments is not regularly determined in taxonomic studies of representatives of the suborder *Micrococcineae*. Nevertheless, the published data on the chemical nature and composition of pigments provide useful taxonomic information for species and subspecies characterization and differentiation as shown, for instance, in articles on the genera *Brevibacterium*, *Clavibacter*, *Microbacterium* and *Leucobacter* (Jones *et al.*, 1973; Gavriš *et al.*, 2004; Trutko *et al.*, 2005; Muir & Tan, 2007).

Most organisms analysed so far have been reported to produce carotenoids of different types and molecular masses (Dufossé *et al.*, 2001; Krubasik & Sadmann, 2000; Reddy *et al.*, 2003; Trutko *et al.*, 2005). In some species and subspecies of the genera *Brevibacterium*, *Leifsonia*, *Microbacterium*, *Agromyces* and *Leucobacter chromiireducens* subsp. *solipictus*, the carotenoid pigments are induced by light. The blue bipyridyl pigment indigoidine has been described in *Clavibacter michiganensis* subsp. *insidiosus* (Starr, 1958; Colwell *et al.*, 1969) and some species of the genus *Arthrobacter* (Kuhn *et al.*, 1965; Schippers-Lammertse *et al.*, 1963; Knackmuss & Beckman, 1973).

The methods for the determination of pigments are based on spectrophotometry (preliminary spectral characteristics) and chromatography (Weeks, 1981; Dufossé *et al.*, 2001; Trutko *et al.*, 2005). While analysing pigments, it should be taken into account that growth conditions may affect their formation and that the production of pigments may be strain-dependent. Qualitative and quantitative changes in the carotenoid pigments of *Curtobacterium flaccumfaciens* (basonym *Corynebacterium poinsettiae*) were observed, for instance, when the level of the required growth factor thiamine was altered in the basal medium (Starr & Saperstein, 1953).

Fourier-transform infrared (FT-IR) spectroscopy

The method and its taxonomic application were described in detail by Oberreuter *et al.* (2002). The method is particularly valuable for the differentiation of related species from similar ecological niches, which display almost identical phenotypic traits in terms of traditional physiological and biochemical criteria and similar (identical) colony colours. It should be noted that spectral similarities of strains do not necessarily correspond to their phylogenetic relationships (Kümmerle *et al.*, 1998; Oberreuter *et al.*, 2002). The method has been tested on many representatives of the suborder *Micrococcineae* (e.g. Oberreuter *et al.*, 2002; Behrendt *et al.*, 2002).

Matrix Assisted Laser Desorption Ionization Time-of-Flight mass spectrometry (MALDI/TOF)

MALDI/TOF mass spectrometry is a rapid and efficient identification method for intact whole bacteria (Holland *et al.*, 1996) which has been proven to aid medical diagnostics and risk assessment. This technique may cover a broad taxonomic range depending on the instrument conditions chosen, from the genus level up to the authentication of strains. Although reports on the application of MALDI/TOF mass spectrometry for members of the suborder *Micrococcineae* (Vargha *et al.*, 2006) are still rare, this fast method has turned out to be of great taxonomic importance when compared with gene sequence phylogenies (Stackebrandt *et al.*, 2005) and its application as a tool for characterization and differentiation at the species level is highly encouraged.

GENOTYPIC CRITERIA

Analysis of the gene sequences

16S rRNA gene sequence analysis is the current method of choice for the determination of phylogenetic relationships. The availability of the sequences of the type strains of most species with validly published names in comprehensive public databases is the main advantage of sequence analyses based on this gene. The necessity of using several different algorithms for the construction of phylogenetic dendro-

grams and for the examination of the reliability of branching points has already been outlined (Bernardet *et al.*, 2002). Whereas sequence analysis of the 23S rRNA gene provides similar phylogenetic information to 16S rRNA gene sequencing (Ward *et al.*, 2000), less information should be expected from the analysis of the smaller 5S rRNA genes. Nevertheless, 5S rRNA sequencing was applied successfully for the proposal of the family *Microbacteriaceae* (Park *et al.*, 1993). The degree of taxonomic resolution may be different when the phylogenetic analysis is based on other molecular targets, e.g. the DNA gyrase B subunit gene (Hatano *et al.*, 2003; Richert *et al.*, 2005), the tRNA intergenic spacer regions (Hinrikson *et al.*, 2000), *hrcA* (Ahmad *et al.*, 1999), *hsp60* (Kwok *et al.*, 1999), *sodA* (Poyart *et al.*, 2001), *rpoB* (Morse *et al.*, 2002) or *tuf* (Heikens *et al.*, 2005). Though there are currently only a few complete genome sequences of members of the suborder *Micrococcineae* available (<http://www.genomesonline.org/>), it can be expected that genome sequences will have increasing impact on the understanding of the phylogeny of the suborder *Micrococcineae* and in the definition of its species in future.

DNA base composition

The range of G + C values within a genus is an important taxonomic criterion. The indication of the G + C value of the type strain of the type species of a novel genus is mandatory; it is optional for type strains of novel species in established genera (Stackebrandt *et al.*, 2002b). For precise determination of G + C values, the direct quantification of nucleosides (e.g. Mesbah *et al.*, 1989; Tamaoka & Komagata, 1984) by HPLC methods is recommended. Since totally sequenced bacterial genomes with known base compositions have become available recently (<http://www.ncbi.nlm.nih.gov>), the respective strains represent excellent reference organisms for calibration purposes.

DNA–DNA hybridization

Although there are ideas for novel promising methods for the definition of bacterial species (Stackebrandt *et al.*, 2002b; Gevers *et al.*, 2005), DNA–DNA hybridization is still the established technique for species delineation. Past experience has shown that DNA–DNA hybridization is recommended for the evaluation of species status when the value for 16S rRNA gene sequence similarity is above 97 % (Stackebrandt & Goebel, 1994). In order to evaluate the stringency of the DNA–DNA hybridization, it is necessary that the experimental conditions (buffer system, ionic strength and reassociation temperature) are reported. Different methods for DNA–DNA hybridization have been described and their results compared by Grimont (1988). The filter methods using radioactive DNA showed high reproducibility but lost their importance after the worldwide introduction of strict safety regulations. The reliability of results of the spectrophotometric method is comparable to those obtained by filter techniques, as revealed by the studies of Huß *et al.* (1983). Miniaturized methods using

microtitre plates (e.g. Ezaki *et al.*, 1989; Ziemke *et al.*, 1998) offer the advantage of a higher sample throughput but can only be recommended when the reproducibility of their results is as high as those of filter or spectrophotometric techniques (Goris *et al.*, 1998).

Genomic fingerprinting

Rapid DNA-typing methods are considered appropriate tools for the determination of inter- and intraspecies relatedness by the Ad Hoc Committee for the Re-Evaluation of the Species Definition in Bacteriology (Stackebrandt *et al.*, 2002b). These methods investigate whole genomes (AFLP, RAPD, Rep-PCR, PFGE), *rrn* operons, the 16S rRNA gene (ARDRA), or the intergenic 16S–23S rRNA spacer regions (ISR). Ribotyping and methods based on whole genomes are especially recommended for the examination of whether strains belong to the same species. However, it has been shown recently for *Microbacterium paraoxydans* that ribotyping does not identify all strains of this species (Buczolits *et al.*, 2008), demonstrating that, as with other fingerprinting techniques, highly similar banding patterns are useful for species identification whereas different patterns do not necessarily indicate another species. However, further standardization of these techniques is required in order to improve the reproducibility between laboratories before these methods can be proposed as alternative minimal criteria that are equivalent to DNA–DNA hybridization. A survey of DNA fingerprinting techniques and their application in bacterial systematics is given by Pukall (2006).

Sequencing of housekeeping genes and multilocus sequence typing (MLST)

The Ad Hoc Committee for the Re-Evaluation of the Species Definition in Bacteriology (Stackebrandt *et al.*, 2002b) considers these techniques ‘methods of great promise’ for novel approaches to the species concept. Information for the differentiation of species should be obtained from the sequences of at least five genes coding for proteins of metabolic function. These genes should originate from diverse chromosomal loci and occur over a wide range of taxa. Sequencing of housekeeping genes and MLST have the advantage that discrimination at the species level could be performed by comparing the sequences available from databases instead of direct comparison of isolates to type strains by DNA–DNA hybridization or DNA-typing patterns. MLST (Maiden *et al.*, 1998) is presently mainly used in epidemiology and for the investigation of microbial populations but will have an increasing importance for bacterial systematics at the inter- and intraspecific level (Stackebrandt, 2002).

NOTE ADDED IN PROOF

The genus name *Frondicola* Zhang *et al.* 2007 was recently deemed to be illegitimate as it is a later homonym of a

fungal genus name *Frondicola* Hyde, 1992 (Fungi, Ascomycota, Sordariomycetes, Xylariomycetidae, Xylariales, Hyponectriaceae) [Principle 2 and Rule 51b(4) of the Bacteriological Code (1990 Revision)]. Therefore, a new genus name, *Frondihabitans* gen. nov., has been proposed for this taxon (Greene *et al.*, 2009). A new name was proposed for the type species, *Frondihabitans australicus* sp. nov., to replace the illegitimate combination *Frondicola australicus* Zhang *et al.* 2007.

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