

Minutes

Kristina Lindström, *Secretary*
 J. P. W. Young, *Acting*
 Chairperson

International Committee on Systematics of Prokaryotes

Subcommittee on the taxonomy of *Agrobacterium* and *Rhizobium*

Minutes of the meeting, 7 September 2010, Geneva, Switzerland

Minute 1. Call to order. The closed meeting opened at 21:00 on 7 September 2010, during the 9th European Nitrogen Fixation Conference in Geneva, Switzerland. J. P. W. Young was elected to serve as a chairperson in the absence of E. Martínez-Romero, the usual chairperson.

Minute 2. Record of attendance. The members present were P. de Lajudie, G. Laguerre, K. Lindström and J. P. W. Young. All subcommittee members had the opportunity to participate in the online discussions.

Minute 3. Acceptance of the previous minutes. The minutes from the meeting on 31 August 2008, Gent, Belgium, were accepted (Lindström & Young, 2009).

Minute 4. Membership issues. The recruitment of new members was discussed. A wider geographical representation of subcommittee members would be valuable.

Minute 5. New taxa described since the last meeting. The new taxa are listed in Table 1.

Minute 6. Current status of *Agrobacterium* spp. The inclusion of all *Agrobacterium* species in the genus *Rhizobium*, proposed by Young *et al.* (2001) since neither genus was monophyletic, was contested by Farrand *et al.* (2003) who proposed to maintain the two genera. This introduced uncertainties in taxonomic papers where *A. tumefaciens* is sometimes called *A. radiobacter* or *R. radiobacter*. Nomenclatural uncertainties also surround the classification of strain K84, a famous non-pathogenic *Agrobacterium* strain used as a biocontrol agent. Strain K84 is variously called *A. radiobacter*, *A. rhizogenes* or *R. rhizogenes*.

i) To resolve the polyphyletic status of the genus *Agrobacterium*, it is sufficient to transfer the one most remotely related species – the so-called biovar 2 of *Agrobacterium* (Keane *et al.*, 1970) – into the genus *Rhizobium*. As a result, *Rhizobium rhizogenes* is a valid designation for biovar 2 (Costechareyre *et al.*, 2010). Notably, as strain K84 is a biovar 2 strain, strain K84 should be called *R. rhizogenes* instead of *A. radiobacter* (Velázquez *et al.*, 2010).

ii) The emended genus *Agrobacterium* is monophyletic and can be conserved as a genus (Costechareyre *et al.*, 2010). It

contains several biovars, but it should be noted that, in the *Agrobacterium* literature, the term ‘biovar’ does not have the usual meaning of a specific phenotypic form within a species. Instead, it is generally agreed that biovars correspond to biological species in this genus (Kerstens & De Ley, 1984). In this respect, *A. vitis* (i.e. biovar 3), *A. rubi* and *A. larrymoorei* are acceptable designations for three homogeneous genomic species (Ophel & Kerr, 1990; Popoff *et al.*, 1984; Bouzar & Jones, 2001). Hybridization studies have revealed, however, that biovar 1 is not a homogeneous species but a complex of several genomic species or genomovars (Popoff *et al.*, 1984; Kersters & De Ley, 1984).

iii) Most biovar 1 genomovars have not yet received accepted Latin binomials and are currently designated genomovar G1 to G9 or G13. Genomovar G4 is an exception because it includes the type strains of both *A. radiobacter* and *A. tumefaciens* (i.e. ATCC 19358^T and B6, respectively), causing nomenclatural uncertainties (Mougel *et al.*, 2002; Portier *et al.*, 2006; Costechareyre *et al.*, 2010). Although Bouzar (1994) proposed that *A. tumefaciens* should be retained because it is the type species of the genus, Young *et al.* (2006) stipulated that, despite this, the epithet *radiobacter* has priority over *tumefaciens*. For this reason, *A. radiobacter* is a valid name for genomovar G4, with ATCC 19358^T as the type strain (Costechareyre *et al.*, 2010).

iv) The name *A. radiobacter* is only valid for genomovar G4, but not for other biovar 1 genomovar members, such as the completely sequenced strains C58 and H13-3, which belong to genomovars G8 and G1, respectively. For this reason, it was proposed that the biovar 1 species complex should be collectively called the *Agrobacterium tumefaciens* species complex (Costechareyre *et al.*, 2010). This seems a good interim solution until genomovars can be formally named. Strains C58, H13-3, B6 and ATCC 19358^T all belong to the *A. tumefaciens* species complex, but only the latter two belong to the bona fide species *A. radiobacter*. The type strain of *A. radiobacter* is ATCC 19358^T (=CFBP 2414^T=LMG 140^T). Strain B6 was the type strain of *A. tumefaciens* but as this is no longer a species, strain B6 should no longer be a type strain.

v) Although *Allorhizobium undicola* appears to be related to the genus *Agrobacterium* (Costechareyre *et al.*, 2010), its generic status is not yet clearly ascertained.

Table 1. Novel species described since the last meeting of the committee in August 2008

Species	Reference	Host plants nodulated	Comments
<i>Bradyrhizobium denitrificans</i> comb. nov.	van Berkum <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 61 (2011) 1011–1013]		
<i>Bradyrhizobium iriomotense</i>	Islam <i>et al.</i> [<i>Biosci Biotechnol Biochem</i> 72 (2008) 1416–1429]	Isolated from nodules of <i>Entada koshunensis</i> . Nodulates <i>Macroptilium atropurpureum</i>	Validation List No. 132 in IJSEM
<i>Bradyrhizobium jicamae</i>	Ramirez-Bahena <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 1929–1934]	<i>Pachyrhizus erosus</i> , <i>Lespedeza</i> spp.	
<i>Bradyrhizobium pachyrhizi</i>	Ramirez-Bahena <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 1929–1934]	<i>Pachyrhizus erosus</i>	
<i>Devosia yakushimensis</i>	Bautista <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 60 (2010) 627–632]	Isolated from nodules of <i>Pueraria lobata</i> ; no nodulation reported	
<i>Ensifer adhaerens</i>	Merabet <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 60 (2010) 664–674]; Willems <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 53 (2003) 2107–2110]	<i>Sesbania grandiflora</i> , <i>Medicago sativa</i> , <i>Leucaena leucocephala</i> , <i>Pithecellobium dulce</i> , <i>Lotus arabicus</i>	
<i>Ensifer garamanticus</i>	Merabet <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 60 (2010) 664–674]	<i>Argyrobium uniflorum</i> , <i>Medicago sativa</i>	Based on MLSA (calibrated for <i>Sinorhizobium</i> by Martens <i>et al.</i> 2007)
<i>Ensifer numidicus</i>	Merabet <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 60 (2010) 664–674]	<i>Argyrobium uniflorum</i> , <i>Lotus creticus</i>	Based on MLSA (calibrated for <i>Sinorhizobium</i> by Martens <i>et al.</i> 2007)
<i>Mesorhizobium alhagi</i>	Chen <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 60 (2010) 958–962]	<i>Alhagi sparsifolia</i> , <i>Sophora alopecuroides</i> , <i>Glycyrrhiza inflata</i> , <i>Medicago sativa</i> , <i>Indigofera endecaphylla</i> , <i>Vicia cracca</i> , <i>Sophora flavescens</i>	
<i>Mesorhizobium australicum</i>	Nandasena <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 2140–2147]	<i>Biserrula pelecinus</i> , <i>Astragalus membranaceus</i> , <i>Macroptilium atropurpureum</i>	
<i>Mesorhizobium camelthorni</i>	Chen <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 61 (2011) 574–579]	<i>Alhagi sparsifolia</i> , <i>Sophora alopecuroides</i> , <i>Glycyrrhiza inflata</i> , <i>Medicago sativa</i>	
<i>Mesorhizobium metallidurans</i>	Vidal <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 850–855]	<i>Anthyllis vulneraria</i>	
<i>Mesorhizobium opportunum</i>	Nandasena <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 2140–2147]	<i>Biserrula pelecinus</i> , <i>Astragalus adsurgens</i> , <i>Astragalus membranaceus</i> , <i>Lotus peregrinus</i> , <i>Macroptilium atropurpureum</i>	
<i>Mesorhizobium robiniae</i>	Zhou <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 60 (2010) 2552–2556]	<i>Robinia pseudoacacia</i>	
<i>Mesorhizobium shangrilense</i>	Lu <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 3012–3018]		
<i>Rhizobium alamii</i>	Berghe <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 367–372]	Most strains isolated from <i>Arabidopsis</i> rhizosphere. Nodulates <i>Medicago ruthenica</i>	New comparative studies including strains of both taxa must be performed to confirm that <i>R. alamii</i> and <i>R. mesosinicum</i> are two really different species.
<i>Rhizobium alkalisoli</i>	Lu <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 3006–3011]	<i>Caragana intermedia</i> , <i>Caragana microphylla</i> , <i>Phaseolus vulgaris</i> , <i>Vigna radiata</i>	
<i>Rhizobium endophyticum</i>	López-López <i>et al.</i> [<i>Syst Appl Microbiol</i> 33 (2010) 322–327]	Isolated from <i>Phaseolus vulgaris</i> . No nodulation reported	Validation List No. 139 in IJSEM.
<i>Rhizobium mesosinicum</i>	Lin <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 1919–1923]	<i>Albizia julibrissin</i> , <i>Kummerowia stipulacea</i> , <i>Kummerowia striata</i> , <i>Dalbergia</i> spp.	New comparative studies including strains of both taxa must be performed in order to confirm that <i>R. alamii</i> and <i>R. mesosinicum</i> are two really different species.

Table 1. cont.

Species	Reference	Host plants nodulated	Comments
<i>Rhizobium phaseoli</i>	Ramirez-Bahena <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 58 (2008) 2484–2490]	<i>Phaseolus vulgaris</i> , <i>Trifolium repens</i>	Emended species.
<i>Rhizobium pisi</i>	Ramirez-Bahena <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 58 (2008) 2484–2490]	<i>Pisum sativum</i> , <i>Trifolium repens</i> , <i>Phaseolus vulgaris</i>	<i>R. pisi</i> is closely related to <i>R. fabae</i> . In case the two species are merged, <i>R. pisi</i> has priority as a name.
<i>Rhizobium soli</i>	Yoon <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 60 (2010) 1387–1393]	Isolated from soil, no plant hosts reported	
<i>Rhizobium tibeticum</i>	Hou <i>et al.</i> [<i>Int J Syst Evol Microbiol</i> 59 (2009) 3051–3057]	<i>Trigonella archiducis-nicolai</i> , <i>Medicago lupulina</i> , <i>Medicago sativa</i> , <i>Melilotus officinalis</i> , <i>Phaseolus vulgaris</i> , <i>Trigonella foenum-graecum</i>	
' <i>Sinorhizobium abri</i> '	Ogasawara <i>et al.</i> [<i>Symbiosis</i> 34 (2003) 53–68]	<i>Abrus precatorius</i>	Not a validly published name. This species belongs to the <i>Ensifer</i> phylogenetic cluster but was described before the transfer of <i>Sinorhizobium</i> to <i>Ensifer</i> (Young, 2003).
' <i>Sinorhizobium indiaense</i> '	Ogasawara <i>et al.</i> [<i>Symbiosis</i> 34 (2003) 53–68]	<i>Sesbania rostrata</i>	Not a validly published name. This species belongs to the <i>Ensifer</i> phylogenetic cluster but was described before the transfer of <i>Sinorhizobium</i> to <i>Ensifer</i> (Young, 2003).

vi) *Rhizobium galegae* and related species cluster with the genus *Agrobacterium* in some phylogenetic analyses (e.g. Young *et al.*, 2001) but not others (e.g. Velázquez *et al.*, 2010). The phylogenetic position of these species relative to the genera *Rhizobium*, *Agrobacterium* and *Ensifer* (*Sinorhizobium*) is currently uncertain. While they may eventually be removed from the genus *Rhizobium*, it would be premature to suggest that they should be transferred to the genus *Agrobacterium*.

Minute 7. *Aeschynomene* photosynthetic bradyrhizobia.

Photosynthetic bradyrhizobia were isolated from *Aeschynomene* spp. plant root and stem nodules in Africa (Alazard, 1990) and Central America (Miché *et al.*, 2010), from African wild rice roots (Chaintreuil *et al.*, 2000) and from lake water (Hirsch & Muller, 1985). *Aeschynomene* spp. plants are nodulated by photosynthetic (PB) and non-photosynthetic (NPB) bradyrhizobial strains with distinct host ranges on *Aeschynomene* spp. (Alazard, 1990). Some NPB strains lack the canonical nodulation genes and nodulate *Aeschynomene* spp. plants via a Nod factor-independent system; among these are the two sequenced model strains BTAi1 and ORS 278 (Giraud *et al.*, 2007). Nod gene-independent symbiosis is linked to *Aeschynomene* host species but not strictly to photosynthetic ability (Miché *et al.*, 2010). Photosynthesis is active in bacteroids (Eaglesham & Szalay, 1983) and is generally reported as playing a role in symbiotic infectivity and effectiveness (Evans *et al.*, 1990; Yurkov & Beatty, 1998; Giraud *et al.*, 2000; Giraud & Fleischman, 2004), although efficient *Aschynomene* stem nodulating NPB strains have also

been isolated (Montecchia *et al.*, 2002; Miché *et al.*, 2010). Miché *et al.* (2010) hypothesized that stem nodulating bradyrhizobial evolution may involve an ancestral nod-independent nodulation coupled with a photosynthetic trait, followed by occasional lateral acquisitions of *nod* genes and loss of photosynthetic ability.

Early 16S rRNA gene-based phylogenetic studies indicated that PB strains were separate from NPB (van Berkum *et al.*, 1995; Molouba *et al.*, 1999). This was later confirmed by ribosomal 16S–23S rRNA internal transcribed spacer (ITS) region phylogenies (Willems *et al.*, 2003), AFLP and MLSA (Nzoué *et al.*, 2009; Miché *et al.*, 2010). However PB strains may harbour multiple rRNA operons that are heterogeneous in ITS size and sequence (Willems *et al.*, 2003). The phylogenetic distance between PB and other *Bradyrhizobium* spp. is such that several authors (So *et al.*, 1994; Fleischman & Kramer, 1998; Nzoué *et al.*, 2009) even discussed the possibility that the PB clade should be considered to be a separate genus. Several authors have highlighted the genetic diversity of photosynthetic bradyrhizobia (Willems *et al.*, 2000; Miché *et al.*, 2010).

Comparative genomics of the two model photosynthetic bradyrhizobium strains ORS278 and BTAi1 has demonstrated high plasticity within genomes, as reflected by large variations in genome sizes and composition (Giraud *et al.*, 2007).

According to DNA–DNA hybridization data, Willems *et al.* (2001) distinguished two genospecies, VI and VIII, among PB strains. However, genospecies VI, comprising the model

strain ORS 278, is heterogeneous, with strains having DNA–DNA hybridization values ranging from 43 to 100 % between them and belonging to several AFLP groups (Willems *et al.*, 2000). Photosynthetic bradyrhizobia genospecies VI may represent several emerging separate genospecies (Rivas *et al.*, 2009; Nzoué *et al.*, 2009). The species status of ORS 278 remains unclear.

van Berkum *et al.* (2006) proposed the inclusion of *Blastobacter denitrificans* in the genus *Bradyrhizobium* and *Blastobacter denitrificans* as a synonym of *Bradyrhizobium denitrificans*. Later MLSA (3–9 housekeeping genes) data of Rivas *et al.* (2009) and Nzoué *et al.* (2009) added further arguments to this proposal, including photosynthetic bradyrhizobia genospecies VIII, comprising the genome sequenced BTAi1 strain in *Bradyrhizobium denitrificans*.

Minute 8. The home page. The subcommittee home page can be accessed at <http://edzna.ccg.unam.mx/rhizobial-taxonomy>. It would be very useful to list genome sequenced type strains on the website.

Minute 9. Biovar designations. Rogel *et al.* (2011) proposed that the term ‘symbiovar’ be used rather than ‘biovar’ to designate a set of *Rhizobium* strains that have similar host specificity because they share closely related nodulation genes. The same biovar may be found in more than one species as a result of horizontal transfer of these genes.

We recommend this change in nomenclature because it specifies that symbiosis is the property that is being used to describe the strains. Based on current understanding of bacterial genomes, it is clear that the phenotypic properties that define a biovar are conferred by a set of accessory genes that are carried by some members of a species but absent from others. Bacterial genomes normally include many different sets of accessory genes, so a strain could be classified in different ways depending on the phenotypic trait that was the focus of attention. ‘Biovar’ is a useful general term for such classifications, whereas ‘symbiovar’ refers specifically to symbiotic properties, just as ‘pathovar’ refers to pathogenic host range.

Minute 10. Current membership. The current members of the subcommittee are E. Martínez-Romero (Mexico) (Chairperson), K. Lindström (Finland) (Secretary), P. van Berkum (USA), B. Eardly (USA), W. X. Chen (China), B. D. W. Jarvis (New Zealand), G. Laguerre (France), P. de Lajudie (France), K. Nandasena (Australia), X. Nesme (France), P. Vinuesa (Mexico), G. Wei (China), A. Willems (Belgium) and J. P. W. Young (UK).

Minute 11. Next meeting. The time and location of the next meeting will be announced at a later date.

Minute 12. Adjournment. The meeting was adjourned at 22:30 on 7 September 2010. The meeting was continued online and closed on 31 May 2011.

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