Symbiosis (2017) 71:91–109
DOI 10.1007/s13199-016-0462-3

Recent changes to the classification of symbiotic, nitrogen-fixing, legume-associating bacteria: a review

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Received: 6 June 2016 / Accepted: 27 October 2016 / Published online: 18 November 2016

Abstract The Rhizobia are collectively comprised of gram negative soil bacteria that have the ability to form symbiotic nitrogen-fixing root and/or stem nodules in association with leguminous plants. The taxonomy of these bacteria is continually in a state of flux, in large part due to rapid development of refined molecular biology techniques. The isolation and characterization of new, and often different, legumes-nodulating bacteria on a variety of plant hosts has resulted in the naming of many new rhizobial species. Here we update the taxonomy of the legume-nodulating bacteria and describe newly identified rhizobia capable of nodulating edible legumes and legume trees. In 1990, there was only one bacterial species that was known to nodulate common bean worldwide (*Rhizobium leguminosarum* sv. *phaseoli*), one species that nodulated faba bean (*Rhizobium leguminosarum* sv. viciae), and two species that nodulated soybean (*Bradyrhizobium japonicum* and *Rhizobium fredii*). Today, nearly 14, 11, 6, 5, 5, 4, 3 and 2 species have been defined that are capable of nodulating common bean, soybean, cowpea, chickpea, peanut, lentils, faba bean and pea, respectively. The recent use of whole genome based taxonomy (genomotaxonomy) will surely change how we define this important group of bacteria. The identification of several rhizobial species that are able to nodulate and fix nitrogen with edible legumes may enhance the production of these crops and can compensate for worldwide deficiencies in human nutritional needs in the future.

Keywords Legumes · Nodulation · Nitrogen fixation · Taxonomy · Classification

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1 Introduction

Legumes belong to three subfamilies of the family-*Fabaceae*, including the *Caesalpinioideae*, *Mimosideae* and *Papilionoideae*. These subfamilies have received great attention because they can establish specific symbioses with rhizobia in the soil. The rhizobia, collectively referred to as the root and stem nodule bacteria of legumes, consist of 238 species in 18 genera and two clades. Under nitrogen (N) deficient conditions these microorganisms fix atmospheric nitrogen and transfer N-containing compounds to the legume plant through the process of symbiotic nitrogen fixation (Sprent 2001). In this biological process leading to symbiosis. The legumes excrete different types of flavonoid molecules, which subsequently induce bacterial strains to produce different types of Nod factors. The later molecules facilitate recognition and penetration of bacteria into root hairs, eventually leading to the production of root/stem nodules. Inside the nodule tissue, the bacteria live in a bacteroid state and are capable of fixing atmospheric dinitrogen. Until the early 980s, all symbiotic nitrogen-fixing bacteria from leguminous plants were classified as belonging to the genus *Rhizobium,* with six named species: *R. leguminosarum, R. meliloti, R. trifolii, R. phaseoli, R. lupine* and *R. japonicum* (Somasegaran and Hoben 1985). This taxonomy, however changed in 1984, and continues to evolve today.

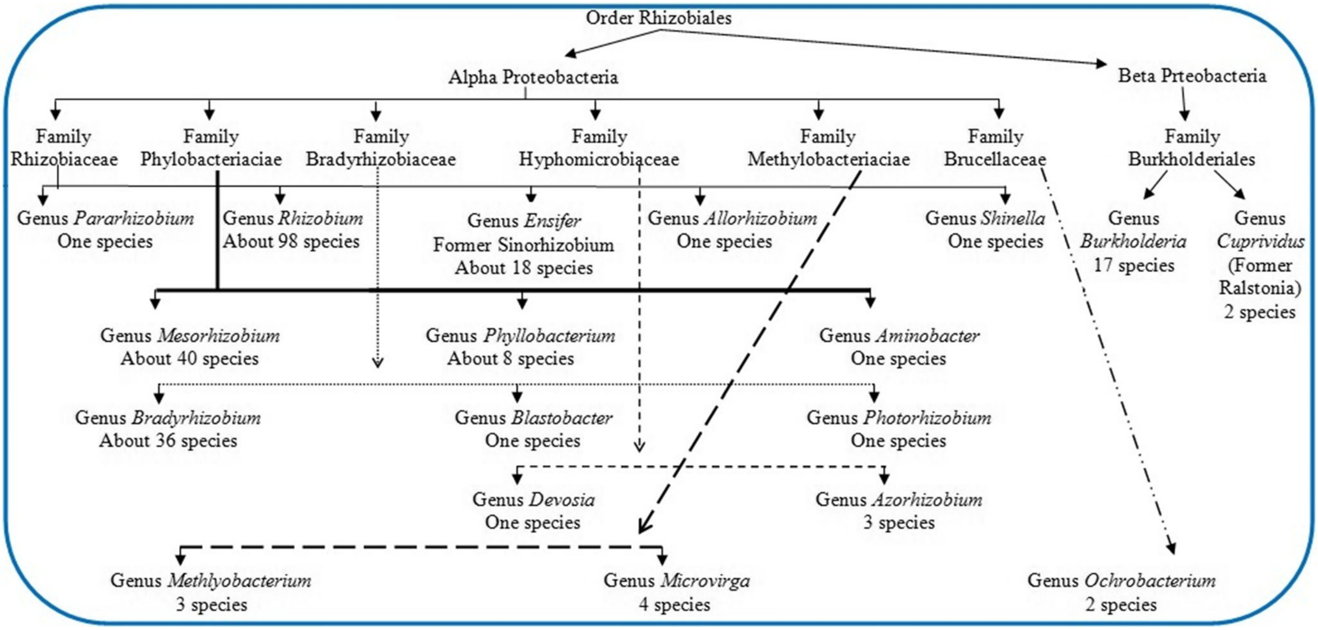

Fig. 1 Schematic diagram to explain the numbers and distribution of legume-nodulating bacterial species in the classes of α- and β-Proteobacteria.

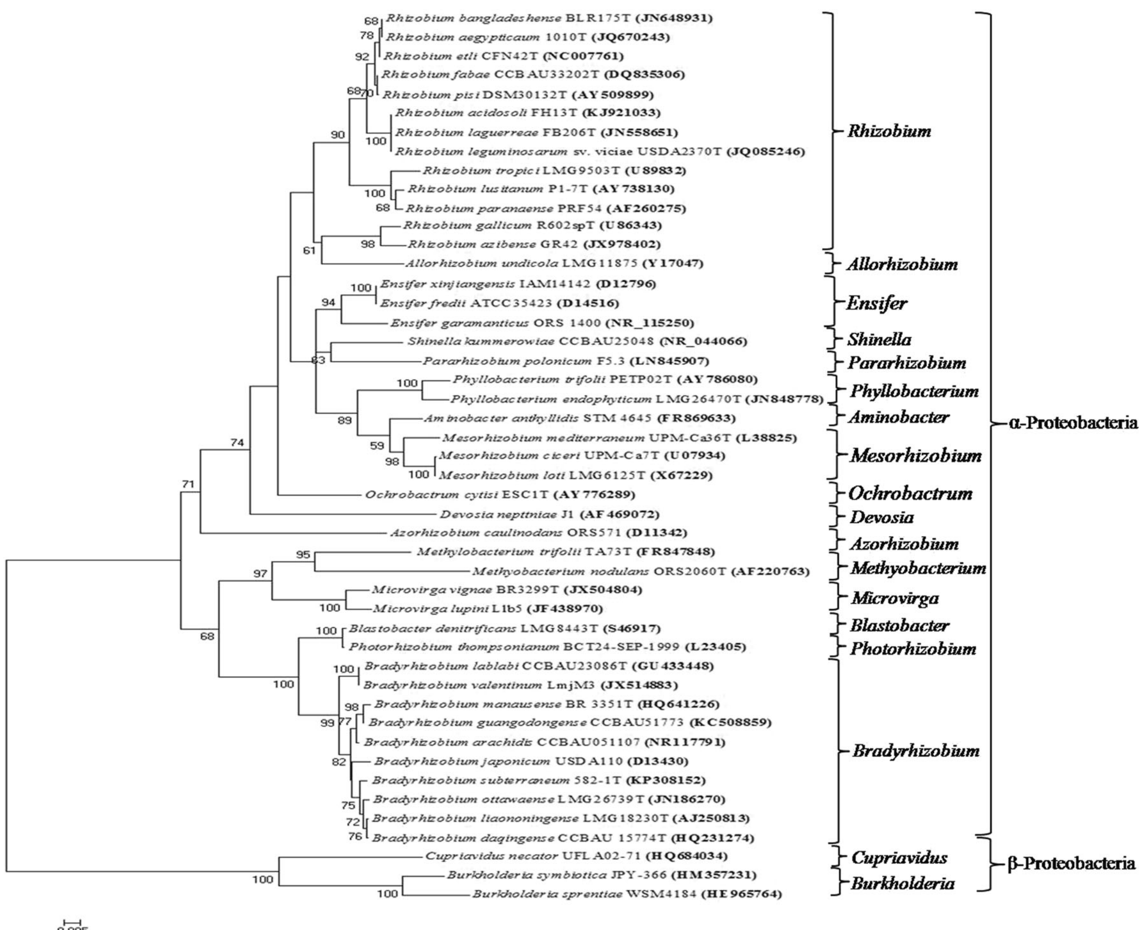

Fig. 2 Neighbor-Joining phylogenetic sequence analysis of 16S rRNA (1,450 bp) of for 47 representative species of 18 genera of root-nodulating bacteria. Values of bootstrap probaility greater than 50% are indicated

Table 1 Species within the family *Rhizobiaceae*

Class α-Proteobacteria		
I Order Rhizobiales		
I Family *Rhizobiaceae*		
Genus *Rhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Allorhizobium*, *Shinella* and *Pararhizobium*		
Genus *Rhizobium*		
Species	Host or source	Reference
Rhizobium leguminosarum	Different host	Frank 1889
Rhizobium trifolii	Clover	
Rhizobium lupine	Lupine	Eckhardt et al. 1931
Rhizobium japonicum	Soybean	Jordan 1982
Rhizobium loti	*Lotus corniculatus*	Jarvis et al. 1982
Rhizobium fredii	*Glycine max*	Scholla and Elkan 1984
Rhizobium galegae	*Galega orientalis*	Lindstrom 1989
Rhizobium leg. bv. phaseoli	*Phaseolus vulgaris*	Segovia et al. 1991
Rhizobium tropici	*Phaseolus vulgaris*	Martinez-Romero et al. 1991
Rhizobium huakuii	*Astragalus sinucus*	Chen et al. 1991
Rhizobium etli	*Phaseolus vulgaris*	Segovia et al. 1993
Rhizobium cireri	Chickpea	Nour et al. 1994b
Rhizobium tianshanense	Isolated from saline desert soil	Chen et al. 1995
Rhizobium mediterrraneum	Chickpea	Nour et al. 1995
Rhizobium gallicum	*Phaseolus vulgaris*	Amarger et al. 1997
Rhizobium giardinii	*Phaseolus vulgaris*	
Rhizobium hainanense	Tropical legumes	Chen et al. 1997
Rhizobium huautlense	*Sesbania herbacea*	Wang et al. 1998
Rhizobium mongolense	*Medicago ruthenica*	Van Berkum et al. 1998
Rhizobium etli bv. mimosa	*Mimosa affinis*	Wang et al. 1999a
Rhizobium yanglingense	Isolated from soils (NS)	Tan et al. 2001
Rhizobium radiobacter	Human pathogenic (NS)	Young et al. 2001
Rhizobium rhizogenes		
Rhizobium rubi		
Rhizobium undicola		
Rhizobium vitis		
Rhizobium indigoferae	*Indigofera spp*	Wei et al. 2002
Rhizobium sullae	*Hedysarum coronarium*	Squartini et al. 2002
Rhizobium meliloti		Young 2003
Rhizobium loessense	*Astragalus lespedeza*	Wei et al. 2003
Rhizobium larrymoorei	*Ficus benjamina* (NS)	Willems and Collins 1993, Young 2004
Rhizobium daejeonense	Isolated from cyanide bioreactor	Quan et al. 2005
	Form nodules on *Medicago sativa*	
Rhizobium lusitanum	*Phaseolus vulgaris*	Valverde et al. 2006
Rhizobium cellulosilyticum	*Populus alba*	Garcia-Fraile et al. 2007
Rhizobium selenitireducens	Bioreactor (NS)	Hunter et al. 2007
Rhizobium fabae	*Vicia faba*	Tian et al. 2008
Rhizobium miluonense	Lespedeza	Gu et al. 2008
Rhizobium multihospitium	Multiple legume	Han et al. 2008a
Rhizobium oryzae	*Oryza alta*	Peng et al. 2008

Table 1 (continued)

Class α-Proteobacteria		
I Order Rhizobiales		
I Family *Rhizobiaceae*		
Genus *Rhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Allorhizobium*, *Shinella* and *Pararhizobium*		
Genus *Rhizobium*		
Species	Host or source	Reference
	Nodulate *Phsaeolus vularis and Glycine max*	
Rhizobium pisi	Clover but nodulate bea	Ramirez-Bahena et al. 2008
Rhizobium mesosinicum	Albizia, Kummerowia and Dalbergia	Lin et al. 2009
Rhizobium alamii	Legumes and non	Berge et al. 2009
Rhizobium alkalisoli	*Caragana intermedia*	Lu et al. 2009a
Rhizobium tibeticum	*Trigonella archiducis-nicolai*	Hou et al. 2009
Rhizobium endophyticum	from rhizosphere (NS)	Lopez-Lopez et al. 2010
Rhizobium soli	Soil (NS)	Yoon et al. 2010
Rhizobium kunmingense	From rizosphere (NS)	Shen et al. 2010
Rhizobium rosettiformans	HCH contaminated groundwater (NS)	Kaur et al. 2011
Rhizobium aggregatum		
Rhizobium borbori	Activated sludge (NS)	Zhang et al. 2011b
Rhizobium herbae	Various wild legumes in China	Ren et al. 2011a
Rhizobium pseudooryzae	Wild rice oryza (NS)	Zhang et al. 2011c
Rhizobium pusense	Rhizosphere of chickpea (NS)	Panday et al. 2011
Rhizobium sphaerophysae	*Sphaerophysa salsula*	Xu et al. 2011
Rhizobium tubonense	*Oxytropis glabra*	Zhang et al. 2011a
Rhizobium vallis	*Phaseolus vulgaris*	Wang et al. 2011
	Mimosa pudica	
Rhizobium vignae	*Mung bean, Vigna radiata*	Ren et al. 2011b
Rhizobium phenanthrenilyticum	Petroleum contaminant site (NS)	Wen et al. 2011
Rhizobium halophytocola	*Rosa rugosa*	Bibi et al. 2012
Rhizobium leucaenae	*Leucaena leucocephala*	Ribeiro et al. 2012
Rhizobium petrolearium	Soil samples mixed with oil (NS)	Zhang et al. 2012b
Rhizobium skierniewicense	Tumours on (NS) chrysanthemum	Puławska et al. 2012a
Rhizobium grahamii	*Dalea leporina*, *Leucaena leucocephala*	Lopez-Lopez et al. 2012
Rhizobium mesoamericanum	and *Clitoria ternatea*	
	Phaseolus vulgaris, siratro, cowpea and *Mimosa pudica*.	
Rhizobium nepotum	Tumor on different plants (NS)	Puławska et al. 2012b
Rhizobium naphthalenivorans	Sediment of a polychlorinated (NS)	Kaiya et al. 2012
Rhizobium helanshanense	*Sphaerophysa salsula*	Qin et al. 2012
Rhizobium cauense	Herbaceous	Liu et al. 2012
Rhizobium taibaishanense	*Kummerowia stiata*	Yao et al. 2012
Rhizobium subbaraonis	Beach sand (NS)	Ramana et al. 2013
Rhizobium tarimense	Soil (NS)	Turdahon et al. 2013
Rhizobium paknamense	*Lemna aequinoctialis*	Kittiwongwattana and Thawai 2013
Rhizobium calliandrae	*Calliandra grandiflora*	Rincón-Rosales et al. 2013

Table 1 (continued)

Class α-Proteobacteria		
I Order Rhizobiales		
I Family *Rhizobiaceae*		
Genus *Rhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Allorhizobium*, *Shinella* and *Pararhizobium*		
Genus *Rhizobium*		
Species	Host or source	Reference
Rhizobium mayense *Rhizobium jaguaris* *Rhizobium qilianshanense*	*Oxytropis ochroephala*	Xu et al. 2013
Rhizobium freirei	*Phaseolus vulgaris*	Dall'Agnol et al. 2013
Rhizobium pongamiae	*Pongamia pinnata*	Kesari et al. 2013
Rhizobium halotolerans	Chloroethylenes Contaminated Soil (NS)	Diange and Lee 2013
Rhizobium azibense	*Phaseolus vulgaris*	Mnsari et al. 2014
Rhizobium laguerreae	*Vicia faba*	Saidi et al. 2014
Rhizobium rhizoryzae	Rice roots (NS)	Zhang et al. 2014a
Rhizobium flavum	Soil (NS)	Gu et al. 2014
Rhizobium lemnae	*Lemna aequinoctialis* (NS)	Kittiwongwattana and Thawai 2014
Rhizobium pakistanensis	*Arachis hypogaea*	Khalid et al. 2014
Rhizobium paranaense	*Phaseolus vulgaris*	Dall'Agnol et al. 2014
Rhizobiun populi	Endophtic from *Populus euphratica* (NS)	Rozahon et al. 2014
Rhizobium smilacinae	Endophtic from leaf of *Smilacina japonica* (NS)	Zhang et al. 2014b
Rhizobium straminoryzae	Surface of rice straw (NS)	Lin et al. 2014
Rhizobium yantingense	weathered rock (NS)	Chen et al. 2015
Rhizobium oryzicola	Surface sterilized Rice roots (NS)	Zhang et al. 2015
Rhizobium bangladeshense *Rhizobium binae* *Rhizobium lentis*	Lentil	Rashid et al. 2015
Rhizobium alvei	River water (NS)	Sheu et al. 2015
Rhizobium puerariae	*Pueraria candollei*	Boonsnongcheep et al. 2016
Rhizobium acidosoli	*Phaseolus vulgaris*	Román-Ponce et al. 2016
Rhizobium ipomoeae	Water convoevueus field (NS)	Sheu et al. 2016
Genus *Ensifer* (formerly *Sinorhizobium*)		
Ensifer adhaerens	From soil	Casida 1982
Ensifer fredii	*Glycine soja*	Scholla and Elkan 1984
Ensifer saheli *Ensifer teranga*	*Sesbania cannabina* *Acacia laeta*	de Lajudie et al. 1994
Ensifer meliloti com *Ensifer medicae*	*Medicago sativa* *Medicago spp*	Rome et al. 1996
Ensifer kostiensis *Ensifer arboris*	*Acacia Senegal* *Prosopis chilensis*	Nick et al. 1999
Ensifer kummerowiae	*Kimmerowia stipulacea*	Wei et al. 2002
Ensifer morelense	*Leucaena leucocephala*	Wang et al. 2002
Ensifer xinjiangensis	Glycine	Young 2003
Ensifer americanum	Native acacia	Toledo et al. 2003
Ensifer abri	*Abrus precatorius*	Ogasawara et al. 2003

Table 1 (continued)

Class α-Proteobacteria		
I Order Rhizobiales		
I Family *Rhizobiaceae*		
Genus *Rhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Allorhizobium*, *Shinella* and *Pararhizobium*		
Genus *Rhizobium*		
Species	Host or source	Reference
Ensifer indiaense	*Sesbania rostrata*	
Ensifer mexicanus	*Acacia angustissima*	Lloret et al. 2007
Ensifer garamanticus	*Lotus arabicus*	Merabet et al. 2010
Ensifer numidicus	*Argyrolobium uniflorum*	
Ensifer americanum comb	Native acacia	Wang et al. 2013c
Ensifer morelense comb	*Sesbania cannabina*	
Ensifer sesbaniae	*Psoralea corylifolia*	
Ensifer psoraleae		
Genus *Allorhizobium*		
Allorhizobium undicola	*Neptunia natans*	de Lajudie et al. 1998a
Genus *Shinella*		
Shinella kummerowiae	*Kummerowia stipulacea*	Lin et al. 2008
Genus *Pararhizobium*		
Pararhizobium giardinii comb.		Mousavi et al. 2015
Pararhizobium herbae comb.		
Pararhizobium sphaerophysae comb.		
Pararhizobium capsulatum comb.		
Pararhizobium polonicum	Tumor of fruits (NS)	Puławska et al. 2016

HCH hexachlorocyclohexane, *Leg* leguminosarum, *Ns* non symbiotic

2 Phenotypic and genotypic characteristics used for taxonomy of legume-nodulating bacteria

There are several phenotypic characteristics which have been used to identify and differentiate among bacteria capable of nodulating-legumes (Jordan 1984). Rhizobia were subsequently reclassified into two groups, the fast-growing, acid-producing group (the *Rhizobium* sp. strains) and a slow-growing, alkaline-producing group (*Bradyrhizobium*) based on their generation time and pH reaction on yeast extract mannitol medium containing bromophenol blue (Vincent 1970). Nodulation of specific host plants was one of main criteria used to differentiate among the *Rhizobium* species, as was known as cross inoculation group concept (Somasegaran and Hoben 1985). However, it soon became apparent that this character was not useful to classify species of rhizobia due to the possibility of natural transfer of symbiotic plasmids among bacterial strains in the soil (Mergaert et al. 1997; Finan 2002; Nakatsukasa et al. 2008). The location of symbiotic genes was also used as a genotypic tool to differentiate between the fast and slow-growing legume-nodulating bacteria, they are typically chromosome-located for the slow-growing bradyrhizobia and on plasmids for fast-growing *Rhizobium* strains. Recently, however a slow growing *Bradyrhizobium* strain DOA9 was found to carry symbiotic genes on a megaplasmid (Teamtisong et al. 2013).

Subsequent molecular biology tools developed over several decades were used in polyphasic approaches to classify rhizobia and included the mole %G + C content of the bacterial genome, and later the sequencing of 16S rRNA gene. This led to the description of large number of rhizobia in a non-systematic way. In 1991 Graham and colleagues published the minimal standards for the description of rhizobial species (Graham et al. 1991). After

Table 2 Species within the family *Phylobactericiae*

Class α-Proteobacteria		
I Order Rhizobiales		
II Family *Phylobactericiae*		
Genus *Mesorhizobium,* Genus *phyllobacterium* and *Aminobacter*		
Genus *Mesorhizobium*		
Species	Host or source	Reference
Mesorhizobium tianshanense	*Different hosts*	Chen et al. 1995
Mesorhizobium mediterraneum	Chickpea	Jarvis et al. 1997
Mesorhizobium ciceri	*Cicer artinium*	
Mesorhizobium loti	*Lotus* spp.	
Mesorhizobium huakui	*Astragalus sinicus*	
Mesorhizobium plurifarium	*Leucaena leucocephala Sesbania herbacea*	de Lajudie et al. 1998b
Mesorhizobium amorphae	*Amorpha fructicosa*	Wang et al. 1999b
Mesorhizobium chacoense	*Prosopis alba*	Velazquez et al. 2001
Mesorhizobium septentrionale	*Astragalus adsurgens*	Gao et al. 2004
Mesorhizobium temperatum	*Astragalus adsurgens*	
Mesorhizobium thiogangeticum	Rhizosphere (NS)	Ghosh and Roy 2006
Mesorhizobium albiziae	*Albizia kalkora*	Wang et al. 2007
Mesorhizobium caraganae	*Caragana spp*	Guan et al. 2008
Mesorhizobium gobiense	*Astragalus filicauls*	Han et al. 2008b
Mesorhizobium tarimense	*Lotus frondosus*	
Mesorhizobium australicum	*Biserrula pelecinus*	Nandasena et al. 2009
Mesorhizobium opportunistum		
Mesorhizobium shangrilense	*Caragana spp*	Lu et al. 2009b
Mesorhizobium metallidurans	*Anthyllis vulneraria,*	Vidal et al. 2009
Mesorhizobium robiniae	*Robinia pseudoacacia*	Zhou et al. 2010
Mesorhizobium alhagi	*Alhagi sparsifolia*	Chen et al. 2010
Mesorhizobium camelthorni	*Alhagi sparsifolia*	Chen et al. 2011
Mesorhizobium tamadayense	*Anagyris latifolia*	Ramirez-Bahena et al. 2012
Mesorhizobium muleiense	*Cicer arietinum* L	Zhang et al. 2012a
Mesorhizobium silamurunense	*Astragalis species*	Zhao et al. 2012
Mesorhizobium shonense	Agroforestry legume tree	Degefu et al. 2013
Mesorhizobium hawassense		
Mesorhizobium abyssinicae		
Mesorhizobium qingshengi	*Astragalus sinicus*	Zheng et al. 2013
Mesorhizobium sangaii	*Astragalus luteolus*	Zhou et al. 2013
Mesorhizobium acaciae	*Acacia melanoxylon*	Zhu et al. 2015
Mesorhizobium waimense	*Sophora longicarinata Sophora microphylla*	De Meyer et al. 2015
Mesorhizobium cantuariense		
Mesorhizobium jarvisii	*Lotus corniculatus*	Martinez-Hidalgo et al. 2015
Mesorhizobium erdmanii		
Mesorhizobium calcicola	*Sophora*	De Meyer et al. 2016
Mesorhizobium waitakense		
Mesorhizobium sophorae		
Mesorhizobium newzealandense		
Mesorhizobium kowhaii		
Genus *Phyllobacterium*		
Phyllobacterium trifolii	*Phyllobacterium trifolii*	Valverde et al. 2005

Table 2 (continued)

Class α-Proteobacteria		
I Order Rhizobiales		
II Family *Phylobactericiae*		
Genus *Mesorhizobium,* Genus *phyllobacterium* and *Aminobacter*		
Genus *Mesorhizobium*		
Species	Host or source	Reference
Phyllobacterium ifriqiyense	*Lathyrus numidicus*	Mantelin et al. 2006
Phyllobacterium leguminum	*Argyrolobium uniflorum*	
Phyllobacterium bourgognense	*Astragalus algerianus*	
Phyllobacterium brassicacearum	*Brassica napus*	
Phyllobacterium endophyticum	*Phaseolus vulgaris*	Flores-Félix et al. 2013
Phyllobacterium loti	*Lotus corniiculatus*	Sánchez et al. 2014
Phyllobacterium sophorae	*Sophora flavescens*	Jiao et al. 2015
Genus Aminobacter		
Aminobacter anthyllidis	*Anthyllis tightly*	Maynaud et al. 2012

this, RFLP analyses of the 16S rRNA gene, the phylogenetic analysis of 16 rRNA gene sequences (Willems and Collins 1993; Yanagi and Yamasato 1993) and DNA-DNA hybridization percentage were being proposed as needed tools for the identification of nitrogen-fixing, legume-nodulating bacteria (Stackebrandt and Gobel 1994). Moreover, strain similarity could be easily assessed by using the REP PCR DNA fingerprinting technique (De Bruijn 1992; Ishii and Sadowsky 2009). Although the sequencing of 16S rRNA gene is still used widely to propose and describe new species of legume-nodulating bacteria; it has some limitation and cannot be solely used to differentiate among the closest *Rhizobium* species (Ramirez-Bahena et al. 2008). Therefore, researchers suggest using chromosomal housekeeping genes, such as *atpD*, *recA,* and *glnII* to help with speciation of closest-related species of *R. leguminosarum* sv. trifolii, *R. leguminosarum* sv. phaseoli, and *R. leguminosarum* sv. viceae. Multilocus sequence analysis (MLSA) and multilocus sequence typing (MLST) has also been used to differentiate and identify new rhizobial taxa (Ribeiro et al. 2009). Other methods have been used to explain the differences among species, such as extracellular polysaccharide composition (Huber et al. 1984), fatty acid profiles (Tighe et al. 2000). Recently, two new methods have been used for studying the taxonomy of legume-nodulating bacteria: comparative genomics (Ormeno-Orrillo et al. 2015) and average nucleotide identity (ANI) of genome comparisons (Rashid et al. 2015).

3 Taxonomy of symbiotic, nitrogen-fixing bacteria

Currently the legume-nodulating bacteria belong to three different bacterial classes; the α, β and γ-Proteobacteria. The largest class, the alphaproteobacteria, is composed of six families, including *Rhizobiaceae*, *Phylobactericiae*, *Bradyrhizobiaceae*, *Hyphomicrobiaceae*, *Methylobacteriiaceae* and *Brucellaceae*. The second class comprised of the betaproteobacteria, currently contains one family the *Burkholderiales*, and contains two genera (Fig. 1).

The classification of symbiotic, legume-nodulating bacteria is in great state of flux, more so than ever before. Zakhia and de Lajudie (2001) subsequently summarized the classification of these bacteria into six *Rhizobium* genera with 28 recognized species. By 2003 however, Sawada et al. (2003) reported that 44 bacterial species distributed in 12 genera can form nitrogen-fixing symbiosis with legumes. Subsequently, Willems (2006) stated that rhizobia are comprised of 53 bacterial species that are distributed as follows: 16, 11, 11, 7, 5, 2 and 1 species belonging to the genera *Rhizobium*, *Sinorhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Agrobacterium*, *Azorhizobium,* and *Allorhizobium,* respectively. The further subdivisions of rhizobia continue and Berrada and Fikri-Benbrahim (2014) recently reported that there are 98 species of legume nodulating bacteria belonging to 14 genera. Here we described about 238 species distributed among 18 genera. Results in Fig. 2 describe 18 genera of root nodulating bacteria with some representative species of each genus. The largest two genera are *Rhizobium* and

Table 3 Species within the family *Bradyrhizobiaceae*

Class α-Proteobacteria		
I Order Rhizobiales		
III Family *Bradyrhizobiaceae*		
Genus *Bradyrhizobium, Blastobacter and Photorhizobium*		
Genus *Bradyrhizobium*		
Species	Host or source	Reference
Bradyrhizobium japonicum	*Glycine max*	Jordan 1982
Bradyrhizobium elkani	*Vigna unguiculata*	Kuykendall and Saxena 1992
Bradyrhizobium liaononingense	*Glycine max*	Xu et al. 1995
Bradyrhizobium yuanmingense	*Lepspedeza spp*	Yao et al. 2002
Bradyrhizobium betae	*Beta vulgaris*	Rivas et al. 2004
Bradyrhizobium canariense	Endemic genistoid	Vinuesa et al. 2005
Bradyrhizobium denitrificans	NM	Van Berkum et al. 2006
Bradyrhizobium iriomotense	*Entada koshunensis,*	Islam et al. 2008
Bradyrhizobium jicamae	*Pachyrhizus erosus*	Ramirez-Bahena et al. 2009
Bradyrhizobium pachyrhizi	*Pachyrhizus erosus*	
Bradyrhizobium lablabi	*Lablab purpureus*	Chang et al. 2011
	Arachis hypogaea	
Bradyrhizobium cytisi	*Cytisus villosus*	Chahboune et al. 2011
Bradyrhizobium huanghuaihaiense	*Glycine max*	Zhang et al. 2012c
Bradyrhizobium rifense	*Cytisus villosus*	Chahboune et al. 2012
Bradyrhizobium daqingense	*Glycine max*	Wang et al. 2013a
Bradyrhizobium arachidis	*Arachis hypogaea*	Wang et al. 2013b
Bradyrhizobium retamae	*Retama sphaerocarpa*	Guerrouj et al. 2013
	Retama monosperma	
Bradyrhizobium diazoefficience	Soybean	Delamuta et al. 2013
Bradyrhizobium oligotrophicum comb.	*Aeschynomene indica*	Ramirez-Bahena et al. 2013
Bradyrhizobium ganzhouense	*Acacia melanoxylon*	Lu et al. 2014
Bradyrhizobium ingae	*Inga laurina*	da Silva et al. 2014
Bradyrhizobium valentinum	Lupin	Durán et al. 2014
Bradyrhizobium paxllaeri	*Phaseolus lunatus* L.	Duran et al. 2014
Bradyrhizobium icense		
Bradyrhizobium manausense	Cowpea	Silva et al. 2014
Bradyrhizobium ottawaense	Soybean	Yu et al. 2014
Bradyrhizobium neotropicale	*Centrolobium paraense*	Zilli et al. 2014
Bradyrhizobium erythrophlei	*Erythrophleum fordii*	Yao et al. 2015
Bradyrhizobium ferriligni		
Bradyrhizobium subterraneum	*Arachis hypogaea*	Gronemeyer et al. 2015a
Bradyrhizobium guangodongense	Peanut	Li et al. 2015
Bradyrhizobium guangxiense		
Bradyrhizobium tropicagri	*Neonotonia wightii*	Delamuta et al. 2015
Bradyrhizobium embrapense	*Desmodium heterocarpon*	
Bradyrhizobium lupini comb	Lupinus	Peix et al. 2015
Bradyrhizobium kavagense	Traditional Namibian pulses	Gronemeyer et al. 2015b
Bradyrhizobium vignae	*Vigna*	Gronemeyer et al. 2016
	Arachis	
Genus *Blastobacter*		

Table 3 (continued)

Class α-Proteobacteria		
I Order Rhizobiales		
III Family *Bradyrhizobiaceae*		
Genus *Bradyrhizobium, Blastobacter and Photorhizobium*		
Genus *Bradyrhizobium*		
Species	Host or source	Reference
Blastobacter denitrificans	*Aeschynomene indica*	Van Berkum and Eardly 2002
Genus Photorhizobium		
Photorhizobium thompsonianum	*Aeschynomene indica*	Molouba et al. 1999

NM not mentioned

*Bradyrhizobiu*m and we focus here on species that nodulate edible legumes.

4 Whole genome sequence alignments

Ormeno-Orrillo et al. (2015) established a new trend of using whole genome sequence comparisons to define new taxa of rhizobia, which they called genomotaxonomy. Using this approach, they confirmed that the phylogenomic analysis provided support for the revival of *Allorhizobium* as a bona fide genus within the *Rhizobiaceae*, the distinctiveness of *Agrobacterium* and the recently proposed genus *Neorhizobium*, and suggested that *R. giardinii* be transferred to a novel genus.

The recent revision of rhizobial taxonomy by Mousavi et al. (2015) led to the description of the novel genus *Pararhizobium,* comprised of 4 new species combinations and 9 other species combinations belonging to the genus *Allorhizobium*.

5 Species of rhizobia within the class α-Proteobacteria

Despite these proposed changes, the *Rhizobiaceae* represent perhaps the most cohesive and preserved among the six families of legume-nodulating bacteria (Fig. 1). The family *Rhizobiaceae* is a common and widely distributed family containing five genera: *Rhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Allorhizobium, Shinella* and *Pararhizobium*. The genus *Rhizobium* has about 98 species, 69 of which were isolated from various legume hosts around the world and 29 species that are non-symbiotic (Table 1). Recently Shamseldin et al. (2016) identified *Rhizobium aegypticaum* as a new species which effectively nodulated Egyptian clover (*Trifolium alexandrinum* L.).

Table 4 Species within the family *Hyphomicrobiaceae*

Class α-Proteobacteria		
I Order Rhizobiales		
IV Family *Hyphomicrobiaceae*		
Genus *Devosia* and Genus *Azorhizobium*		
Genus *Devosia*		
Species	Host or source	Reference
Devosia neptunia	*Neptunia natans*	Rivas et al. 2003
Genus *Azorhizobium*		
Azorhizobium caulinodans	*Sesbania rostrata*	Dreyfus et al. 1988
Azorhizobium doebereinerae	*Sesbania virgata*	Moreira de Souza et al. 2006
Azorhizobium oxalatiphilum	Macerated petioles (NS)	Lang et al. 2013

Table 5 Species within the family *Methylbacteriiaceae*

Class α-Proteobacteria		
Order Rhizobiales		
V Family *Methylobacteriiaceae*		
Genus *Methylobacterium* and Genus *Microvirga*		
Genus *Methylobacterium*		
Species	Host or source	Reference
Methyobacterium nodulans	*Crotalaria galaucoides*	Jourand et al. 2004
Methylobacterium trifolii	*Phylosphere of Trifolium repens*	Wellner et al. 2013
Methylobacterium thuringiense		
Genus Microvirga		
Microvirga lupini	*Lupinus texensis*	Ardley et al. 2012
Microvirga lotononidis	*Listia angolensis*	
Microvirga zambiensis	*Listia angolensis*	
Microvirga vignae	cowpea	Radl et al. 2014

The genus *Ensifer* (formerly *Sinorhizobium)* has about 18 species (Table 1). Gubry-Rangin et al. (2013) proposed a new bacterial symbiovar *Ensifer meliloti* sv. rigiduloides, that fixes nitrogen efficiently on *Medicago rigiduloides*, but not on *Medicago truncatula*. Each of the other three genera *Allorhizobium, Shinella* and *Pararhizobium* contain a single species (Table 1).

The second family *Phylobactericiae* contains three genera: *Mesorhizobium*, *Phyllobacterium* and *Aminobacter*. The genus *Mesorhizobium* contains about 40 species, while the genus *Phyllobacterium* has 8 species, and the genus *Aminobacter* only one species (Table 2).

The third family, the *Bradyrhizobiaceae*, contains three genera *Bradyrhizobium*, *Blastobacter* and *Photorhizobium*. The genus *Bradyrhizobium* includes 36 species, while both *Blastobacter* and *Photorhizobium* contain only a single species (Table 3). Guerrouj et al. (2013) proposed a novel symbiovar named *Bradyrhizobium retamae* sp. nov., nodulating *Retama sphaerocarpa* and *Retama monosperma*.

Table 6 Species within the family *Brucellaceae*

Class α-Proteobacteria		
Order Rhizobiales		
VI Family *Brucellaceae*		
Genus *Ochrobacterium*		
Species	Host or source	Reference
Ochrobactrum lupini	*Lupinus albus*	Trujillo et al. 2005
Ochrobactrum cytisi	*Cytisi scoparius*	Zurdo-Pineiro et al. 2007

The fourth family is the *Hyphomicrobiaceae* and includes *Devosia* and *Azorhizobium* as the two known genera. The genus *Devosia* has only one species, while genus *Azorhizobium* has three species (Table 4).

The fifth family, *Methylobacteriiaceae*, is comprised of genera *Methylobacterium* and *Microvirga.* The genus *Methylobacterium* includes 3 species and *Microvirga* includes 4 species (Table 5). Lastly, the family *Brucellaceae* contains only a single genus, *Ochrobacterium*, which has 2 species (Table 6).

6 Species of legume-nodulating bacteria within the β- and γ-Proteobacteria classes

While most rhizobia were originally placed in the α-Proteobacteria, more recent studies showed that the legume-nodulating bacteria belong to a much wider group (Gyaneshwar et al. 2011; Shiraishi et al. 2010). There are about 18 species of rhizobia belonging to two genera of the β-Proteobacteria, *Burkholderia* with 17 species and *Ralstonia* (former *Cupriavidus*) with 2 species (Table 7). More recently, Shiraishi et al. (2010) noted that there is a *Pseudomonas* sp. belonging to the γ-Proteobacteria that can nodulate *Robinia pseudoacacia*.

7 Non-symbiotic bacteria

There are about 33 non-symbiotic bacterial species reported here that are related to the nodule bacteria and are distributed in different genera. The majority of them belong to the genus *Rhizobium* (29), although non-nodulating *Bradyrhizobium*

Table 7 Species of symbiotic strains of β-Proteobacteria

Class β-Proteobacteria		
Order Burkholderiales		
Family *Burkholderiales*		
Genus *Burkholderia* and Genus *Cupriavidus* former Ralstonia		
Genus *Burkholderia*		
Species	Host or source	Reference
Burkholderia carbensis	Soil	Achouak et al. 1999
Burkholderia fungorum	Different hosts	Coenye et al. 2001
Burkholderia caledonica		
Burkholderia cepacia	*Dalbergia sp.*	Rasolomampianina et al. 2005
Burkholderia tuberum	Tropical legumes	Vandamme et al. 2002
Burkholderia phymatum	*Machaerium lunatum*	
Burkholderia mimosarum	*Mimosa sp.*	Chen et al. 2006
Burkholderia nodosa	*Mimosa bimucronata*	Chen et al. 2007
	Mimosa scabrella	
Burkholderia sabiae	*Mimosa caesalpiniifolia*	Chen et al. 2008
Burkholderia contaminans	Different hosts	Vanlaere et al. 2009
Burkholderia lata		
Burkholderia symbiotica	*Mimosa sp.*	Sheu et al. 2012
Burkholderia diazotrophica	*Mimosa sp.*	Sheu et al. 2013
Burkholderia sprentiae	*Lebeckia ambigua*	De Meyer et al. 2013
Burkholderia dilworthii	*Lebeckia ambigua*	De Meyer et al. 2014
Burkholeria aspalathi	*Aspalathus abietina*	Mavengere et al. 2014
Burkholderia kirstenboschensis	Papilionoid legumes	Steenkampa et al. 2015
Cupriavidus former *Ralstonia*		
Cupriavidus taiwanesis	*Mimosa sp*	Chen et al. 2001
Cupriavidus necator	*Phaseolus vulgaris*	da Silva et al. 2012
	Leucaena leucocephala	

have been isolated (Pongsilp et al. 2002). Each of the genera *Pararhizobium*, *Mesorhizobium*, *Azorhizobium* and *Burkholderia* has one species. Kimes et al. (2015) identified a novel genus, *Pseudorhizobium pelagicum* which had 95.6 to 97 % a sequence similarity to members of genera *Neorhizobium* and *Rhizobium*, but this new species lacked symbiosis-related genes.

8 Conclusions

The considerable and continued development of molecular biology tools over the last 20 years has facilitated the identification of new legume-nodulating bacteria and resulted in considerable changes in the classification and proposal of new and different species. Although in this review we described about 238 species distributed in 18 genera, larger efforts from researchers around the world are needed. This is, in large part, due to our lack of understanding of legume-*Rhizobium* interactions. For example, the description of rhizobia species above comprises only about 23 % of legumes, and it has been estimated that there are roughly 19,000 legume species. Hopefully, the discovery and designation of new different species of bacteria-nodulating edible legumes can contribute to improve productivity, especially in developing countries which suffer from a lack of protein.

Acknowledgments The authors thank the STDF of Egypt for funding this work through project no. 1268. This projected was also funded, in part, by the Minnesota Agricultural Experiment Station (to MJS).

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