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## Specificity in Legume-Rhizobia Symbioses — [Source link](#)

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Review

# Specificity in Legume-Rhizobia Symbioses

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**Abstract:** The Leguminosae (legume family) is divided into three sub-families, the Caesalpinioideae, Mimosoideae and Papilionoideae. Here, the literature on legume-rhizobia symbioses was reviewed, and genotypically characterised rhizobia related to the taxonomy of the legumes they were isolated from. Only data from field soils were considered. The objective of the work was to assess to what extent legume specificity for rhizobial symbiont is related to legume taxonomy. *Bradyrhizobium* spp. were the exclusive rhizobial symbionts of species in the Caesalpinioideae but data are limited. Where tested, species within the two Mimosoideae tribes, Ingeae and Mimoseae were nodulated by different rhizobial genera. Generally, Papilionoideae species with indeterminate nodules were promiscuous in relation to rhizobial symbionts but high specificity for rhizobial partners appears to hold at tribe level for the Fabae (*Rhizobium* spp.), genus level for *Medicago* (*Ensifer* spp.), *Cytisus* (*Bradyrhizobium* spp.) and *Lupinus* (*Bradyrhizobium* spp.), and species level for *Galega* spp. (*Neorhizobium galegeae*), *Hedysarum coronarium* (*Rhizobium sullae*), *Cicer arietinum* (*Mesorhizobium* spp.) and New Zealand native *Sophora* spp. (*Mesorhizobium* spp.). High legume specificity for rhizobial symbionts was linked to specific rhizobial symbiosis genes. For Papilionoideae species with determinate nodules, the Dalbergieae were primarily nodulated by *Bradyrhizobium* but were promiscuous with respect to *Bradyrhizobium* spp. while those in the Desmodieae, Phaseoleae, Psoraleae and Loteae were promiscuous across different rhizobial genera. Possible advantages and disadvantages of high specificity or promiscuity are discussed.

**Keywords:** Leguminosae; N<sub>2</sub> fixation; nodulation

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## 1. Introduction

The Leguminosae (= Fabaceae, the legume family) is comprised of ca 19,300 species within 750 genera which occur as herbs, shrubs, vines or trees in mainly terrestrial habitats and are components of most of the world's vegetation types [Lewis et al. 2005; Sprent 2009; LPWG 2013]. Currently, the legume family is divided into three sub-families, the Caesalpinioideae, Mimosoideae and Papilionoideae [LPWG 2013, Cardoso et al. 2013]. Members of the Caesalpinioideae are grouped in four tribes, the Caesalpinieae, Cassieae, Cercideae and Detarieae comprising ca 170 genera and 2,250 species. The Mimosoideae are grouped in two tribes, the Ingeae and Mimoseae with ca 80 genera and 3,270 species while the Papilionoideae consists of 28 tribes with ca 480 genera and 13,800 species.

Most legume species can fix atmospheric nitrogen (N<sub>2</sub>) via symbiotic bacteria (general term 'rhizobia') in root nodules and this can give them an advantage under low soil nitrogen (N) conditions if other factors are favourable for growth [Raven 2010; Andrews et al. 2013]. Also, N<sub>2</sub> fixation by legumes can be a major input of N into natural and agricultural ecosystems [Andrews et al. 2007, 2011; Jackson et al. 2008; Vitousek et al. 2013]. Generally, legume nodules can be classified as indeterminate or determinate in growth [Sprent 2009]. Indeterminate nodules maintain meristematic tissue while determinate nodules have a transient meristem. Nodule type is dependent on host plant, and legume species which can produce both determinate and indeterminate nodules are rare [Fernández-Lopez et al. 1998; Liu et al. 2014]. All genera examined

in the Caesalpinioideae and Mimosoideae had indeterminate nodules (Sprent, 2009). Within the Papilionoideae, most tribes had indeterminate nodules but the Desmodieae, Phaseoleae, Psoraleae and some members of the Loteae show 'desmodoid' determinate nodules and the Dalbergieae 'aeschynomenoid' determinate nodules [Sprent 2009]. Most indeterminate nodules have a single persistent apical meristem, however, a few genera such as *Lupinus* (tribe Genisteae, Papilionoideae) and *Listia* (tribe Crotalaria, Papilionoideae), have nodules with two or more lateral meristems which in some cases completely surround the subtending root [Yates et al. 2007; Sprent 2009]. Rhizobia 'infected' tissue within desmodoid nodules always contains uninfected cells while aeschynomenoid nodules have uniform infected tissue and are always associated with lateral or adventitious roots (Sprent 2009).

Over the past twenty-five years, DNA based methods have become increasingly used to characterize rhizobia. In particular, phylogenetic analyses of sequences of the 16S ribosomal RNA (rRNA) gene, a range of 'housekeeping' genes and genes involved in symbiosis have been developed as a 'standard approach' [Martens et al. 2007; Liu et al. 2014; Peix et al. 2015]. The main symbiosis genes studied are the '*nif*' genes which encode the subunits of nitrogenase, the rhizobial enzyme that fixes N<sub>2</sub>, and the '*nod*' genes which encode Nod factors that induce various symbiotic responses on legume roots. The *nod* genes are activated by plant root exudates mainly flavonoids [Masson-Boivin et al. 2009]. The 16S rRNA gene sequence on its own can delineate rhizobia at the genus level [Lindstrom et al. 2015]. The *nif* and *nod* genes are often carried on plasmids or symbiotic islands and these genes can be transferred (lateral transfer) between different bacterial species within a genus and more rarely across genera [Vinuesa et al. 2005b; Cummings et al. 2009; Remigi et al. 2016]. Bacterial species from a range of genera in the alphaproteobacteria (most commonly *Bradyrhizobium*, *Ensifer* (= *Sinorhizobium*), *Mesorhizobium*, and *Rhizobium*) and two genera in the betaproteobacteria (*Burkholderia* (= *Paraburkholderia*) and *Cupriavidus*) can form functional (N<sub>2</sub> fixing) nodules on specific legumes (Tables 1-4). *Pseudomonas* in the gammaproteobacteria was reported to nodulate *Robinia pseudoacacia* [Shiraishi et al. 2010] and *Acacia confusa* [Huang et al. 2012] but this has not been confirmed.

Legume species differ in their specificity for rhizobial symbionts. *Galega officinalis* (tribe Galegeae) and *Hedysarum coronarium* (tribe Hedysareae) have been highlighted as being highly specific with respect to their rhizobial symbionts [Lindström 1989; Squartini et al. 2002; Franche et al. 2009; Liu et al. 2012]. Both these species are in the inverted repeat lacking clade (IRLC). The IRLC is marked by the loss of one copy of the inverted region of the plastid genome (Wojciechowski et al. 2004; Schwarz et al. 2015). Almost all genera in the IRLC are temperate and all have indeterminate nodules. The IRLC contains several important temperate grain (e.g. *Pisum sativum* and *Vicia faba*) and forage (e.g. *Trifolium* spp. and *Medicago* spp.) legumes. There is evidence that at least some of these crop legumes have a high degree of rhizobial specificity. For example, an analysis of core and symbiotic genes of rhizobia nodulating *Vicia faba* and *Vicia sativa* from different continents showed that they belong to a phylogenetically compact group indicating that these species are restrictive hosts [Álvarez-Martínez et al. 2009]. In contrast, *Macroptilium purpureum* and the grain legumes *Phaseolus vulgaris* and *Vigna unguiculata* in the tribe Phaseoleae are nodulated by rhizobia from different genera across the alpha- and beta-proteobacteria [Martínez-Romero 2003; Elliot et al. 2007; Guimarães et al. 2012; Table 4]. The Phaseoleae are of tropical/subtropical origin and have determinate (desmodoid) nodules [Sprent 2009].

Here, the literature on legume-rhizobial symbioses was reviewed, and genotypically-characterised rhizobia related to the taxonomy of the legumes they were isolated from. Only data from field soils were considered. The objective of the work was to assess to what extent legume specificity for rhizobial symbiont is related to legume taxonomy.

## 2. Framework and assumptions of study

The general classification of the Leguminosae follows Lewis *et al.* 2005 [Lewis et al. 2005] with updates [LPWG 2013; Cardoso et al. 2013]. The sub-families Caesalpinioideae, Mimosoideae and Papilionoideae are considered separately. The Papilionoideae is split into those that show

indeterminate nodules and those that show determinate nodules. Those that show indeterminate nodules are further split into the IRLC, and all other clades.

Nodulating bacteria were classified to genus level, on the basis of sequences of the 16S rRNA gene (almost all cases), and/ or the 16S-23S DNA intergenic spacer region, and/ or common house-keeping genes, and/ or DNA-DNA hybridisations and these results are presented in tables. Cases where legume specificity for rhizobial symbiont appeared to occur at genus level are considered further in the text. Rhizobial genus and species names validated in the International Journal of Systematic and Evolutionary Microbiology were used with one exception; *Burkholderia* was retained as opposed to using *Paraburkholderia* [Oren & Garrity 2015; Dobritsa & Samadpour 2016] as a case to reinstate *Burkholderia* is being prepared by workers in the field. The term symbiovar (sv.) is used when describing rhizobial strains within the same species which differ with respect to the legume species they effectively nodulate [Rogel et al. 2011].

A comprehensive collation of published legume-rhizobia symbioses was carried out. Articles were collected by searching the ISI Web of Science using each legume genus partnered with each of rhizobia, *Bradyrhizobium*, *Burkholderia*, *Cupriavidus*, *Ensifer*, *Mesorhizobium*, *Rhizobium* and *Sinorhizobium* as key words. Further searches were carried out on the literature quoted in the selected papers and those listed as quoting the selected papers in ISI Web of Science. Only data for plants sampled under field conditions, or for plants grown in soils taken from the field, or supplied field soil extracts, were used. Bacteria isolated from legume nodules were accepted as rhizobia if they were shown to produce functional (N<sub>2</sub> fixing) nodules on inoculation of their original legume host or a species within the original host legume genus under axenic conditions. The range of measurements and visual assessments used as evidence of the occurrence of N<sub>2</sub> fixation were accepted. These were acetylene reduction activity, red/pink nodules (evidence of haemoglobin and hence nodules assumed to be active), increased total plant or shoot dry matter or N content, visually greener (increased chlorophyll) and increased plant vigour. However, it is acknowledged that in some cases, greater growth, vigour and/ or greenness could have been caused by plant hormone production by the bacterium [Andrews et al. 2003]. All data obtained for all species are presented with three exceptions. Representative data are presented for *Glycine max*, *Phaseolus vulgaris* and *Vigna unguiculata* due to the large number of publications on these three species.

### 3. Caesalpinioideae-Rhizobia Symbioses

Of the three legume sub-families, the Caesalpinioideae contains the smallest proportion of nodulated genera with nodulation confirmed for *Campsiandra*, *Chidlowia*, *Dimorphandra*, *Erythrophleum*, *Melanoxylon*, *Moldenhauvera* and *Tachigali* in the tribe Caesalpinieae and *Chamaecrista* in the tribe Cassieae [Sprent 2009]. Only two studies have genotypically characterised rhizobia of Caesalpinioideae species. Firstly, five rhizobial isolates from *Dimorphandra wilsonii* and one from *Dimorphandra jorga* sampled in the Cerrado biome in Brazil were *Bradyrhizobium* [Fonseca et al. 2012]. Secondly, 166 rhizobial isolates from *Erythrophleum fordii* sampled at four sites in the Guangdong and Guangsii Provinces of the southern sub-tropical region of China were also all *Bradyrhizobium* [Yao et al. 2014]. In both studies, core and symbiosis gene sequences indicated that there were diverse and novel strains amongst the isolates.

Data are available for bacterial isolates from nodules of other Caesalpinioideae species but their ability to produce N<sub>2</sub> fixing nodules on their legume host under axenic conditions was not tested. Specifically, three isolates from *Tachigali versicolor* sampled on Barro Colorado Island, Panama which were not tested on their original host plant but shown to nodulate *Macroptilium atropurpureum* were *Bradyrhizobium* [Parker 2000]. Similarly, strain STM934, stated to be confirmed as *Bradyrhizobium* was isolated from nodules of *Erythrophleum guineensis* growing in natural forests of the Ziama reservation in S.E. Guinea and shown to produce functional nodules on *Macroptilium atropurpureum* [Diabate et al. 2005]. In this case, a re-inoculation experiment was carried out on the original host but the substrate was non-sterile forest soil. *Bradyrhizobium* was isolated from and shown to nodulate *Chamaecrista* sampled in Kakadu National Park, Northern Territory, Australia but N<sub>2</sub> fixation was not reported [Lafay & Burdon 2007]. Also, there are several reports that

*Bradyrhizobium* inoculum can increase nodulation of *Chamaecrista* spp. under field conditions in Australia and China [Michalk and Zhi-Kai 1994; Keller 2014; www.tropicalforagesinfo]. Thus, overall, the available evidence indicates that *Bradyrhizobium* spp. are the dominant, possibly exclusive, rhizobial symbionts of legumes in the Caesalpinioideae but the degree of specificity between legumes in the Caesalpinioideae and their rhizobial symbionts cannot be assessed without further work.

#### 4. Mimosoideae-Rhizobia Symbioses

Rhizobia have been characterized from 15 species across seven genera in the tribe Ingeae and ca 90 species from 13 genera in the tribe Mimoseae within the sub-family Mimosoideae (Table 1). *Bradyrhizobium*, *Ensifer*, *Mesorhizobium* and *Rhizobium* were each reported to nodulate species in the Ingeae and the Mimoseae. Also, *Ochrobactrum* was reported to nodulate *Acacia mangium* (Ingeae), *Allorhizobium* and *Devosia* were reported to nodulate *Neptunia natans* (Mimoseae), and there are many reports that *Cupriavidus* and *Burkholderia* nodulate *Mimosa* spp. and related species (Mimoseae) (Table 1). In addition, with the exception of *Acacia auriculiformis* (Ingeae) and *Mimosa diplotricha* (Mimoseae), all species which were examined in three or more separate studies, *Acacia mangium*, *Acacia saligna*, *Calliandra grandiflora* and *Senegalia senegal* (Ingeae), *Leucaena leucocephala*, *Mimosa pudica*, *Parapiptadenia rigida*, *Prosopis alba* and *Vachellia tortilis* (Mimoseae), were nodulated by at least three different rhizobial genera. Thus, a range of rhizobial genera, including both alpha- and beta-proteobacteria, can nodulate legume species across the two Mimosoideae tribes and, generally, where tested over different studies, species within the Ingeae and Mimoseae tribes were promiscuous with respect to their rhizobial symbionts.

Despite their ability to form symbioses with different rhizobial genera, *Mimosa* spp. appear to be predominantly nodulated by *Burkholderia* in Brazil, *Ensifer/Rhizobium* in Mexico and *Cupriavidus* in Uruguay [Bontemps et al. 2010, 2016, dos Reis et al. 2010, Platero et al. 2016]. This is likely to be at least in part related to the relative occurrence of the potential symbionts in the different soils due, for example, to differences in soil pH [Bontemps et al 2016, Platero et al 2006]. However, it has been reported that in competition studies between a *Burkholderia* strain, a *Cupriavidus* strain and three *Rhizobium* strains which were all potential rhizobial symbionts of three *Mimosa* spp., the *Burkholderia* strain outcompeted the other strains to the point of exclusion in flooded soils [Elliott et al. 2009]. This advantage of the *Burkholderia* strain could not be explained by differences in initial inoculum levels, growth rate, growth inhibition of the other rhizobia or nodulation rate but the advantage decreased if 0.5 mM nitrate was added to the system. These data show that the competitive ability of different potential rhizobial strains can be greatly dependent on environmental conditions.

#### 5. Papilionoideae-Rhizobia Symbioses

##### 5.1. The IRLC

Data are available for 110 species from 29 genera within six tribes in the IRLC with *Ensifer*, *Mesorhizobium*, and *Rhizobium* commonly, and *Bradyrhizobium*, *Neorhizobium* and *Phyllobacterium* rarely, reported to nodulate species within this clade (Table 2). There are no reports of *Burkholderia* or *Cupriavidus* symbionts within the IRLC. Previously, *Galega officinalis*, *Galega orientalis* and *Hedysarum coronarium* were reported to only form effective nodules with their respective symbionts *Neorhizobium galegeae* sv. *officinalis*, *Neorhizobium galegeae* sv. *orientalis* and *Rhizobium sullae* [Lindström 1989; Squartini et al. 2002; Franche et al. 2009; Liu et al. 2012]. Several mechanisms maintain these highly specific legume-rhizobia symbioses [Suominen et al. 2003; Franche et al 2009; Gharzouli et al. 2013]. For example, in the *Galega orientalis* – *Neorhizobium galegeae* sv. *orientalis* interaction, the first recognition between the flavonoid inducer secreted from the roots of *Galega orientalis* and the NodD protein of *N. galegeae* sv. *orientalis* is specific for these organisms [Suominen et al 2003].

The data in Table 2, indicate three other specific relationships between IRLC legumes and rhizobia. Firstly, eight separate studies on *Cicer arietinum* carried out over different countries and



continents, reported *Mesorhizobium* as the only symbiont (Table 2). *Mesorhizobium ciceri* and *M. mediterraneum* were common but not exclusive *Mesorhizobium* symbionts of *Cicer arietinum* in most studies outside China with *M. muleiense* the main symbiont in Northwest China [Zhang et al 2016]. In the three studies where tested, *Mesorhizobium* symbionts other than *M. ciceri*, *M. mediterraneum* and *M. muleiense* showed *nifH* and *nodC* gene sequences similar to these three common symbionts indicating that *Cicer arietinum* strongly selects rhizobia with specific symbiotic genes [Rivas et al 2006; Zhang et al 2012, 2016].

Secondly, for the tribe Fabeae, seventeen studies across five *Lathyrus* species, *Lens culinaris*, *Pisum sativum* and eleven *Vicia* spp. reported *Rhizobium* as the only symbiont. Across these studies, *Rhizobium leguminosarum* and where tested, *R. leguminosarum* sv. *viciae* was the most common symbiont. Also, in a study of 154 isolates of 18 *Vicia* species grown in 16 Chinese provinces, only 17 representative *Rhizobium leguminosarum* sv. *viciae* isolates, from a wide range of potential rhizobia, produced fully developed, effective ('color red') nodules [Lei et al. 2008]. Thus, a highly specific relationship has developed between species in the Fabeae and *R. leguminosarum* sv. *viciae* but it is not an exclusive relationship as *R. fabae* [Tian et al 2008], *R. multihospitium* [Han et al 2008b], *R. pisi* [Santillana et al 2008], *R. laguerreae* [Said et al 2014] and *R. anhuiense* [Zhang et al 2015] have been reported to effectively nodulate Fabeae species. However, the *nifH* and *nodC* gene sequences of all these rhizobia show high similarity indicating specificity towards the Fabeae species [Zhang et al. 2015].

Thirdly, within the tribe Trifolieae, 12 out of 13 separate studies across 11 *Medicago* spp. reported *Ensifer* as symbiont although in some cases not exclusively. In particular, highly specific relationships have developed between *Medicago* spp. and the closely related (core and symbiosis genes) *E. meliloti* and *E. medicae* with symbiovars of these rhizobial species associated with particular *Medicago* spp. (Villegas et al. 2006; Gubry Rangin et al. 2013).

In relation to other members of the IRLC, *Ensifer*, *Mesorhizobium* and *Rhizobium* were shown to nodulate species within *Astragalus*, *Colutea*, *Glycyrrhiza*, *Oxytropis* and *Sphaerophyceae* (Galegeae), *Caragana* (Hedysareae), *Tephrosia* (Millettiae) and *Trifolium* (Trifolieae). Also, *Astragalus adsurgense*, *Astragalus complanatus*, *Colutea arborescens*, *Oxytropis glabera* and *Sphaerophysia sabula* (Galegeae), *Caragana intermedia* (Hedysareae), *Tephrosia purpurea* (Millettiae) and *Trifolium fragiferum* and *Trifolium repens* (Trifolieae) were all nodulated by three different rhizobial genera. Thus, for the IRLC, high specificity in relation to rhizobial partners appears to hold at tribe level for the Fabeae, genus level for *Medicago* and species level for *Galega officinalis*, *Galega orientalis*, *Hedysarum coronarium* and *Cicer arietinum* but it is not a characteristic of all members of the clade.

## 5.2. Clades with indeterminate nodules, excluding the IRLC

Data are available for approximately 100 species from 50 genera across 11 Papilionoideae tribes with indeterminate nodules which do not show the IRLC mutation (Table 3). *Azorhizobium*, *Bradyrhizobium*, *Burkholderia*, *Ensifer*, *Herbaspirillum*, *Mesorhizobium*, *Methylobacterium*, *Microvirga*, *Neorhizobium*, *Ochrobactrum*, *Pararhizobium*, *Phyllobacterium* and *Rhizobium* were all reported to nodulate species within this group. *Amorpha fruticosa* and *Dalea purpurea* (Amorpheae), *Retama sphaerocarpa* and *Spartium junceum* (Genisteae), *Coronilla varia* (Loteae), *Gliricidia sepium* and *Robinia pseudoacacia* (Robineae) and *Sesbania sericea* and *Sesbania virgata* (Sesbanieae) were nodulated by two rhizobial genera. *Aspalathus linearis* and *Crotalaria pallida* (Crotalarieae), *Sesbania cannabina*, *Sesbania punicea*, *Sesbania rostrata* and *Sesbania sesban* (Sesbanieae), *Sophora alopecuroides* and *Sophora flavescens* (Sophoreae) and *Ammopiptanthus nanus* and *Ammopiptanthus mongolicus* (Thermopsidae) were all nodulated by at least three different rhizobial genera. Thus, generally, where tested, Papilionoideae species with indeterminate nodules excluding the IRLC were promiscuous in relation to rhizobial symbiont. However, within the Genisteae, *Bradyrhizobium* was the only symbiont reported for nine *Cytisus* spp. across ten separate studies and three *Genista* spp. across three separate studies (Table 3). Also, 10 *Lupinus* spp. (Genisteae) across 11 separate studies were predominantly nodulated by *Bradyrhizobium*. These results indicate that *Bradyrhizobium* may be the main symbionts of Genisteae species but further work is required to confirm this. The relationship

between *Cytisus* spp. and *Lupinus* spp. and their *Bradyrhizobium* symbionts is highly specific and dependent on geographical origin of the legumes. For example, most *Bradyrhizobium* isolates from *Lupinus* spp. in Europe form a distinct lineage, 'clade 11', on the basis of their *nodC* gene sequences [Stepkowski et al. 2007, 2011]. Similarly, different *Bradyrhizobium* spp. associated with *Cytisus villosus* in Morocco all showed similar *nodC* and *nifH* sequences which were closely related to those of *Bradyrhizobium japonicum* sv. *genistearum* [Chahboune et al. 2011].

On more limited data (one study), *Bradyrhizobium* was found to be the exclusive symbiont of four *Indigofera* spp. [Doignon-Bourcier et al. 1999] although in a separate study *Burkholderia* was reported to be the symbiont of *Indigofera angustifolia* [Lemaire et al. 2015]. Also, in one study, in the Cape Floristic Region (CFR) of South Africa, *Burkholderia* was reported to be the exclusive symbiont of ten *Cyclopia* spp., *Podalyria calyptera* and *Virgilia oroboides*, all species in the Podalyrieae plus three *Hypocalyptus* spp. (Hypocalypteae) [Beukes et al. 2013]. *Burkholderia* was confirmed to nodulate *Podalyria calyptata* and *Virgilia oroboides* in the CFR [Lemaire et al. 2015]. The majority of *Burkholderia* isolates had unique *nifH* and *nodA* gene sequences and the specificity of these symbioses needs testing.

Previously, *Sesbania sesban* was reported to be highly promiscuous with respect to rhizobial symbionts [Cummings et al. 2009] and the data here indicate that this could be a genus level trait (Table 3). However, the reports that *Sophora alopecuroides* and *Sophora flavescens* sampled in China are nodulated by a wide range of rhizobial genera with a wide range of symbiosis gene sequences [Zhao et al. 2010; Jiao et al. 2015a] contrasts with the finding that New Zealand (NZ) native *Sophora* spp. were exclusively nodulated by *Mesorhizobium* spp. with almost identical unique *nodA* and *nodC* gene sequences [Tan et al. 2015; De Meyer et al. 2015, 2016]. Also, none of twenty rhizobial isolates from common weed and crop legumes in NZ produced functional nodules on the NZ native *Sophora microphylla* [Liu 2014]. This emphasises that species within the same genus can vary greatly with respect to their specificity for rhizobial symbionts.

### 5.3. Clades with Determinate Nodules

The Dalbergieae are almost exclusively of tropical/ sub-tropical distribution and show aeschynomenoid determinate nodule structure (Sprent 2009). Rhizobia have been characterised for 24 species from seven genera in the Dalbergieae, *Adesmia*, *Aeschynomene*, *Arachis*, *Centrolobium*, *Dalbergia*, *Pterocarpus* and *Zornia* (Table 4). *Bradyrhizobium* was found to nodulate all species except *Adesmia bicolor* (*Rhizobium*) and *Dalbergia odorifera* (*Burkholderia*), with *Rhizobium* also reported for *Arachis hypogaea*. For *Arachis hypogaea*, twelve separate studies reported *Bradyrhizobium* as a rhizobial symbiont with two of these also reporting *Rhizobium*. Thus, on the data available, *Arachis hypogaea* and the Dalbergieae, in general, appear to be primarily nodulated by *Bradyrhizobium*. However, across studies, both core and symbiosis gene sequences indicate that *Arachis hypogaea*, *Arachis duranensis* and *Aeschynomene* spp. are nodulated by a diverse range of *Bradyrhizobium* spp. and are promiscuous with respect to *Bradyrhizobium* spp.

The closely related tribes Desmodieae, Phaseoleae and Psoraleae are also mainly of tropical/ sub-tropical distribution and, with rare exceptions, species within these tribes showed desmodoid nodule structure (Sprent 2009; Liu et al. 2014). Rhizobia have been characterized for 25 species from three genera, *Desmodium*, *Kummerowia* and *Lespedeza*, in the Desmodieae (Table 4). Species from all three genera, *Desmodium microphyllum*, *Desmodium racemosum*, *Desmodium sequax*, *Kummerowia striata*, *Lespedeza bicolor* and *Lespedeza daurica* were nodulated by rhizobia from three separate genera. Similarly, for 28 species across 14 genera within the Phaseoleae, there was no strong evidence for high specificity for rhizobial symbiont (Table 4). *Phaseolus vulgaris* and *Vigna unguiculata* have been highlighted as being promiscuous with respect to their rhizobial symbionts under field conditions. Data in Table 4 show that both species can be nodulated by different rhizobial genera in the alphaproteobacteria as well as *Burkholderia* in the betaproteobacteria. Across three studies, *Phaseolus lunatus* was reported to be nodulated by *Bradyrhizobium* and *Rhizobium* while on one study each, both *Vigna sangularis* and *Vigna subterranean* were reported to be nodulated by three separate rhizobial genera. Data are limited for other genera/ species within the Phaseoleae with the

exception of *Glycine max* which is the main grain/ oil seed legume grown worldwide. *Glycine max* was nodulated by *Bradyrhizobium*, *Ensifer* and *Rhizobium*. Data are limited for Psoraleae but in the one case where two separate studies were carried out on the one species (*Psoralea pinnata*) it was nodulated by *Burkholderia* and *Mesorhizobium* [Kanu & Dakora 2012; Lemaire et al. 2015]. Thus, where tested, species within the Desmodieae, Phaseoleae and Psoraleae were promiscuous with respect to their rhizobial symbionts.

Species in the Loteae which show desmodoid nodule structure are of temperate distribution [Sprent 2009]. Data are available for 16 *Lotus* spp. within the Loteae across 13 separate studies.. For all species examined in two or more studies at least two rhizobia genera were reported as symbionts. In the case of *Lotus corniculatus*, *Geobacillus*, *Paenibacillus* and *Rhodococcus* were for the first time reported as rhizobial symbionts (Ampomah and Huss-Danell 2011). These bacterial species had similar symbiosis gene sequences to *Mesorhizobium* isolated from the same plants and it was concluded that lateral gene transfer of these genes had occurred from the *Mesorhizobium*. However, this work needs to be independently verified. Overall, the available data indicate that legume species with desmodoid determinate nodule structure are promiscuous with respect to their rhizobia symbionts.

## 6. Legume Specificity for Rhizobial Symbionts

High specificity or promiscuity of legumes with respect to rhizobial symbionts are both likely to have advantages and disadvantages to the legume [Ehinger et al. 2014]. For example, promiscuity could allow a legume to participate in a wider range of beneficial interactions and hence possibly occupy more environments. However, high specificity is likely to result in increased 'fitness', e.g. increased N<sub>2</sub> fixation, within a narrower range of conditions [Ehinger et al 2014]. In an agricultural situation, the degree of crop legume specificity for rhizobial symbiont is an important factor in determining the level of success of applied rhizobial inoculant [Andrews et al. 2009].

The objective of the work was to assess to what extent legume specificity for rhizobial symbiont is related to legume taxonomy. The legume sub-families, Caesalpiinoideae, Mimosoideae and Papilionoideae were considered separately with species in the Papilionoideae split in relation to whether they show indeterminate or determinate nodules. *Bradyrhizobium* spp. were the exclusive rhizobial symbionts of species in the Caesalpiinoideae but rhizobia were authenticated for only three legume species over two studies and the degree of specificity between legumes in the Caesalpiinoideae and their rhizobial symbionts cannot be assessed without further work.

In relation to the Mimosoideae, generally, where examined in three or more studies, species within both the Ingeae and Mimoseae tribes were promiscuous with respect to their rhizobial symbionts and there is no strong evidence for high specificity for rhizobial symbionts for any species in this sub-family. For Papilionoideae species with determinate nodules, the Dalbergieae were primarily nodulated by *Bradyrhizobium* but were promiscuous with respect to *Bradyrhizobium* spp. while those in the Desmodieae, Phaseoleae, Psoraleae and Loteae were promiscuous across different rhizobial genera. Papilionoideae species with indeterminate nodules were split into the IRLC, and all other clades. A range of species within both groups nodulated with different rhizobia genera but there was also strong evidence that some species within both groups showed high specificity for rhizobial symbiont. High specificity for rhizobial symbiont appears to hold at tribe level for the Fabae (*Rhizobium* spp.), genus level for *Medicago* (*Ensifer* spp.), *Cytisus* (*Bradyrhizobium* spp.) and *Lupinus* (*Bradyrhizobium* spp.), and species level for *Galega* spp. (*Neorhizobium galegeae*), *Hedysarum coronarium* (*Rhizobium sullae*), *Cicer arietinum* (*Mesorhizobium* spp.) and NZ native *Sophora* spp. (*Mesorhizobium* spp.). In all cases, this high specificity involved rhizobial species within the alphaproteobacteria and was associated with specific symbiosis genes of the rhizobial symbiont (Sections 5.1, 5.2). The legume species which show high specificity in rhizobial symbionts have common features in that they are all within the Papilionoideae, have indeterminate nodules and are of temperate distribution.



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**Table 1.** Legume-rhizobia symbioses in the legume sub-family Mimosoideae. All species have indeterminate nodules.

Mimosoideae Tribes and genera	Rhizobia – field
<b>Ingeae</b>	
<i>Acacia auriculiformis</i>	<i>Bradyrhizobium</i> [Manassila et al. 2007; Le Roux et al. 2009; Helene et al. 2015]
<i>Acacia mangium</i>	<i>Bradyrhizobium</i> [Sinsuwongwat et al. 2002; Ngom et al. 2004; Manassila et al. 2007; Le Roux et al. 2009], <i>Ochrobactrum</i> [Ngom et al. 2004], <i>Rhizobium</i> [Ngom et al. 2004]
<i>Acacia mangium</i> × <i>A. auriculiformis</i>	<i>Bradyrhizobium</i> [Le Roux et al. 2009]
<i>Acacia mearnsii</i>	<i>Ensifer</i> [Lortet et al. 1996; Räsänen et al. 2001]
<i>Acacia melanoxylon</i>	<i>Bradyrhizobium</i> [Lu et al. 2014]
<i>Acacia saligna</i>	<i>Bradyrhizobium</i> [Marsudi et al. 1999; Helene et al. 2015], <i>Ensifer</i> [Khbaya et al. 1998], <i>Rhizobium</i> [Marsudi et al. 1999]
<i>Acaciella angustissima</i>	<i>Ensifer</i> [Lloret et al. 2007; Rincon-Rosales et al. 2009]
<i>Calliandra calothyrsis</i>	<i>Ensifer</i> [Bala & Giller, 2001], <i>Rhizobium</i> [Bala & Giller, 2001]
<i>Calliandra grandiflora</i>	<i>Ensifer</i> [Rincón-Rosales et al. 2013], <i>Mesorhizobium</i> [Rincón-Rosales et al. 2013], <i>Rhizobium</i> [Rincón-Rosales et al. 2013]
<i>Faidherbia albida</i>	<i>Bradyrhizobium</i> [Odee et al. 2002]
<i>Inga edulis</i>	<i>Bradyrhizobium</i> [Leblanc et al. 2005]
<i>Inga laurina</i>	<i>Bradyrhizobium</i> [da Silva et al. 2014]
<i>Mariosousa acatlensis</i>	<i>Ensifer</i> [Toledo et al. 2003]
<i>Senegalia laeta</i>	<i>Ensifer</i> [Lortet et al. 1996]
<i>Senegalia macilentata</i>	<i>Ensifer</i> [Toledo et al. 2003],
<i>Senegalia senegal</i>	<i>Ensifer</i> [Lortet et al. 1996; Räsänen et al. 2001], <i>Rhizobium</i> [Lortet et al. 1996; Fall et al. 2008], <i>Mesorhizobium</i> [Fall et al. 2008]
<b>Mimoseae</b>	
<i>Anadenanthera peregrina</i>	<i>Burkholderia</i> [Bournaud et al. 2013]

<i>Desmanthus illinoensis</i>	<i>Rhizobium</i> [Beyhaut et al. 2006]
<i>Desmanthus paspalaceus</i>	<i>Mesorhizobium</i> [Fornasero et al. 2014], <i>Rhizobium</i> [Fornasero et al. 2014]
<i>Desmanthus virgatus</i>	<i>Rhizobium</i> [Sinsuwongwat et al. 2002]
<i>Leucaena leucocephala</i>	<i>Ensifer</i> [Wang et al. 1999a; Bala & Giller, 2001; Xu et al. 2013], <i>Mesorhizobium</i> [Wang et al. 1999a; Bala & Giller, 2001; Xu et al. 2013], <i>Rhizobium</i> [Wang et al. 1999a; Bala & Giller, 2001; López-López et al. 2012]
<i>Microlobius foetidus</i>	<i>Bradyrhizobium</i> [Bournaud et al. 2013], <i>Rhizobium</i> [Bournaud et al. 2013]
~ 50 <i>Mimosa</i> spp.	<i>Burkholderia</i> [Chen et al. 2003, 2005a,b; Barrett & Parker 2005, 2006; Liu et al. 2007; Parker et al. 2007; Elliott et al. 2009; Bontemps et al. 2010; Liu et al. 2011; Liu et al. 2012; Gehlot et al. 2013].
<i>Mimosa affinis</i>	<i>Rhizobium</i> [Elliot et al. 2009]
<i>Mimosa asperata</i>	<i>Cupriavidus</i> [Andam et al. 2007]
<i>Mimosa borealis</i>	<i>Ensifer</i> [Bontemps et al. 2016]
<i>Mimosa ceratonia</i>	<i>Rhizobium</i> [Elliot et al. 2009]
<i>Mimosa cruenta</i>	<i>Cupriavidus</i> [Platero et al. 2016]
<i>Mimosa diplotricha</i>	<i>Cupriavidus</i> [Chen et al. 2003, Liu et al. 2011; Liu et al. 2012], <i>Rhizobium</i> [Chen et al. 2003; Elliott et al. 2009]
<i>Mimosa hamata</i> , <i>Mimosa himalayana</i>	<i>Ensifer</i> [Gehlot et al. 2013]
<i>Mimosa invisa</i>	<i>Rhizobium</i> [Liu et al. 2007]
<i>Mimosa magnate</i>	<i>Cupriavidus</i> [Platero et al. 2016]
<i>Mimosa pigra</i>	<i>Cupriavidus</i> [Chen et al. 2005b; Barrett & Parker 2006]
<i>Mimosa polyantha</i>	<i>Rhizobium</i> [Bontemps et al. 2016]
<i>Mimosa pudica</i>	<i>Bradyrhizobium</i> [Liu et al. 2007], <i>Cupriavidus</i> [Chen et al. 2003; Barrett & Parker, 2006; Elliott et al. 2009; Liu et al. 2011; Liu et al. 2012; Gehlot et al. 2013], <i>Rhizobium</i> [Barrett & Parker, 2006; Liu et al. 2007]
<i>Mimosa ramulosa</i> , <i>Mimosa reptans</i> , <i>Mimosa schleidenii</i>	<i>Cupriavidus</i> [Platero et al. 2016]
<i>Mimosa strigillosa</i>	<i>Ensifer</i> [Andam et al. 2007]
<i>Mimosa tequilana</i>	<i>Rhizobium</i> [Bontemps et al. 2016]
<i>Neptunia natans</i>	<i>Allorhizobium</i> [de Lajudie 1998], <i>Devosia</i> [Rivas et al. 2002]
<i>Parapiptadenia pterosperma</i>	<i>Burkholderia</i> [Bournaud et al. 2013]
<i>Parapiptadenia rigida</i>	<i>Burkholderia</i> [Bournaud et al. 2013], <i>Cupriavidus</i> [Taulé et al. 2012], <i>Rhizobium</i> [Bournaud et al. 2013]
<i>Piptadenia adiantoides</i> , <i>Piptadenia flava</i>	<i>Rhizobium</i> [Bournaud et al. 2013]
<i>Piptadenia gonoacantha</i>	<i>Burkholderia</i> [Bournaud et al. 2013], <i>Rhizobium</i> [Bournaud et al. 2013]
<i>Piptadenia paniculata</i>	<i>Burkholderia</i> [Bournaud et al. 2013], <i>Rhizobium</i> [Bournaud et al. 2013]
<i>Piptadenia stipulacea</i> , <i>Piptadenia trisperma</i> , <i>Piptadenia vividiflora</i>	<i>Burkholderia</i> [Bournaud et al. 2013]
<i>Prosopis alba</i>	<i>Bradyrhizobium</i> [Diaz et al. 2013], <i>Ensifer</i> [Iglesias et al. 2007; Diaz et al. 2013], <i>Mesorhizobium</i> [Velázquez et al. 2001; Diaz et al. 2013], <i>Rhizobium</i> [Iglesias et al. 2007]
<i>Prosopis chilensis</i>	<i>Ensifer</i> [Nick et al. 1999; Räsänen et al. 2001]

<i>Prosopis cineraria</i>	<i>Ensifer</i> [Gehlot et al. 2012]
<i>Prosopis farcta</i>	<i>Ensifer</i> [Fterich et al. 2011], <i>Mesorhizobium</i> [Fterich et al. 2011]
<i>Prosopis juliflora</i>	<i>Achromobacter</i> [Benata et al. 2008], <i>Ensifer</i> [Benata et al. 2008], <i>Rhizobium</i> [Benata et al. 2008]
<i>Pseudopiptadenia contorta</i>	<i>Burkholderia</i> [Bournaud et al. 2013]
<i>Stryphnodendron</i> sp.	<i>Bradyrhizobium</i> [Bournaud et al. 2013]
<i>Vachellia abyssinica</i>	<i>Mesorhizobium</i> [Degefu et al. 2011], <i>Ensifer</i> [Degefu et al. 2012]
<i>Vachellia cochliacantha</i> , <i>Vachellia farnesiana</i>	<i>Ensifer</i> [Toledo et al. 2003]
<i>Vachellia gummifera</i>	<i>Ensifer</i> [Khbaya et al. 1998]
<i>Vachellia horrida</i>	<i>Ensifer</i> [Lortet et al. 1996; Khbaya et al. 1998]
<i>Vachellia jacquemontii</i>	<i>Ensifer</i> [Gehlot et al. 2012; Sankhla et al. 2016]
<i>Vachellia macracantha</i>	<i>Ensifer</i> [Cordero et al. 2016], <i>Rhizobium</i> [Cordero et al. 2016]
<i>Vachellia nubica</i>	<i>Bradyrhizobium</i> [Odee et al. 2002]
<i>Vachellia seyal</i>	<i>Rhizobium</i> [Lortet et al. 1996], <i>Ensifer</i> [Degefu et al. 2012]
<i>Vachellia pennatula</i>	<i>Ensifer</i> [Toledo et al. 2003]
<i>Vachellia tortilis</i>	<i>Ensifer</i> [Lortet et al. 1996; Khbaya et al. 1998; Ba et al. 2002; Degefu et al. 2012], <i>Mesorhizobium</i> [Lortet et al. 1996; Ba et al. 2002; Odee et al. 2002; Degefu et al. 2011], <i>Rhizobium</i> [Ba et al. 2002]
<i>Vachellia xanthophloea</i>	<i>Mesorhizobium</i> [Odee et al. 2002]
<i>Xylia xylocarpa</i>	<i>Bradyrhizobium</i> [Sinsuwongwat et al. 2002; Manasila et al. 2007]

**Table 2.** Legume-rhizobia symbioses in the inverted repeat lacking clade (IRLC) of the legume sub-family Papilionoideae. All species in the IRLC have indeterminate nodules.

Papilionoideae Tribes and genera	Rhizobia – field
<b>Cicereae</b>	
<i>Cicer arietinum</i>	<i>Mesorhizobium</i> [Nour et al. 1994; Aouani et al. 2001; Maâtallah et al. 2002; Rivas et al. 2007; Ben Romdhane et al. 2009; Zhang et al. 2012; Zahran et al. 2013; Zhang et al. 2016]
<i>Cicer canariense</i>	<i>Mesorhizobium</i> [Armas-Capote et al. 2014]
<b>Fabeae</b>	
<i>Lathyrus aphaca</i> , <i>Lathyrus nissolia</i> , <i>Lathyrus pratensis</i>	<i>Rhizobium</i> [Mutch & Young, 2004]
<i>Lathyrus japonicus</i>	<i>Rhizobium</i> [Aoki et al. 2010]
<i>Lathyrus odoratus</i>	<i>Rhizobium</i> [Han et al. 2008b]
<i>Lens culinaris</i>	<i>Rhizobium</i> [Rashid et al. 2012; Zahran et al. 2013; Riah et al. 2014]
<i>Pisum sativum</i>	<i>Rhizobium</i> [Mutch & Young, 2004; Zahran et al. 2013; Riah et al. 2014; Zhang et al. 2015]
<i>Vicia amoena</i>	<i>Rhizobium</i> [Kan et al. 2007]
<i>Vicia bungei</i>	<i>Rhizobium</i> [Kan et al. 2007]
<i>Vicia cracca</i>	<i>Rhizobium</i> [Mutch & Young, 2004; Kan et al. 2007; Ampomah & Huss-Danell, 2016]
<i>Vicia hirsuta</i>	<i>Rhizobium</i> [Mutch & Young, 2004; Han et al. 2008b; Ampomah & Huss-Danell, 2016]
<i>Vicia faba</i>	<i>Rhizobium</i> [Mutch & Young, 2004; Kan et al. 2007;

	Santillana et al. 2008; Saidi et al. 2013; Zahran et al. 2013; Youseif et al. 2014; Xu et al. 2015; Zhang et al. 2015]
<i>Vicia multicaulis</i>	<i>Rhizobium</i> [Ampomah & Huss-Danell, 2016]
<i>Vicia sativa</i>	<i>Rhizobium</i> [Mutch & Young, 2004; Kan et al. 2007; Lei et al. 2008; Tian et al. 2008; Alvarez-Martinez et al. 2009; Rejili et al. 2012]
<i>Vicia sepium</i>	<i>Rhizobium</i> [Kan et al. 2007; Ampomah & Huss-Danell, 2016]
<i>Vicia sylvatica</i>	<i>Rhizobium</i> [Ampomah & Huss-Danell, 2016]
<i>Vicia tetrasperma</i>	<i>Rhizobium</i> [Ampomah & Huss-Danell, 2016]
<i>Vicia villosa</i>	<i>Rhizobium</i> [Kan et al. 2007]
<b>Galegeae</b>	
<i>Astragalus adsurgense</i>	<i>Ensifer</i> [Chen et al. 2015], <i>Mesorhizobium</i> [Chen et al. 2015], <i>Rhizobium</i> [Wei et al. 2008b]
<i>Astragalus aksuensis</i>	<i>Rhizobium</i> [Han et al. 2008b]
<i>Astragalus betetovii</i>	<i>Rhizobium</i> [Han et al. 2008b]
<i>Astragalus complanatus</i>	<i>Ensifer</i> [Chen et al. 2015], <i>Mesorhizobium</i> [Chen et al. 2015], <i>Rhizobium</i> [Wei et al. 2008b]
<i>Astragalus chrysopterus</i>	<i>Rhizobium</i> [Wei et al. 2008b]
<i>Astragalus discolor</i> , <i>Astragalus efoliolatus</i> , <i>Astragalus kifonsanicus</i>	<i>Mesorhizobium</i> [Chen et al. 2015]
<i>Astragalus melilotoides</i>	<i>Ensifer</i> [Chen et al. 2015], <i>Mesorhizobium</i> [Chen et al. 2015]
<i>Astragalus membranaceus</i>	<i>Mesorhizobium</i> [Zhao et al. 2012; Chen et al. 2015; Yan et al. 2016]
<i>Astragalus mongholicus</i>	<i>Mesorhizobium</i> [Yan et al. 2016]
<i>Astragalus polycladus</i>	<i>Rhizobium</i> [Chen et al. 2015]
<i>Astragalus scaberrimus</i>	<i>Mesorhizobium</i> [Chen et al. 2015], <i>Rhizobium</i> [Wei et al. 2008b]
<i>Biserrula pelecinus</i>	<i>Mesorhizobium</i> [Nandasena et al. 2001; Nandasena et al. 2009]
<i>Carmichaelia australis</i> , <i>Carmichaelia monroi</i> ,	<i>Mesorhizobium</i> [Tan et al. 2012]
<i>Clianthus puniceus</i>	<i>Mesorhizobium</i> [Tan et al. 2012]
<i>Colutea arborescens</i>	<i>Ensifer</i> [Ourarhi et al. 2011], <i>Mesorhizobium</i> [Ruiz-Diéz et al. 2009; Ourarhi et al. 2011], <i>Rhizobium</i> [Ourarhi et al. 2011]
<i>Galega officinalis</i>	<i>Neorhizobium</i> [Radeva et al. 2001; Liu et al. 2012]
<i>Galega orientalis</i>	<i>Neorhizobium</i> [Radeva et al. 2001]
<i>Glycyrrhiza eurycarpa</i>	<i>Ensifer</i> [Li et al. 2012]
<i>Glycyrrhiza glabra</i>	<i>Mesorhizobium</i> [Wei et al. 2008a; Li et al. 2012], <i>Rhizobium</i> [Li et al. 2012]
<i>Glycyrrhiza inflata</i>	<i>Ensifer</i> [Li et al. 2012]
<i>Glycyrrhiza multiflora</i>	<i>Mesorhizobium</i> [Tan et al. 1999]
<i>Glycyrrhiza pallidiflora</i>	<i>Mesorhizobium</i> [Chen et al. 1995]
<i>Glycyrrhiza uralensis</i>	<i>Mesorhizobium</i> Tan et al. 1999; Li et al. 2012], <i>Rhizobium</i> [Li et al. 2012]
<i>Glycyrrhiza</i> sp.	<i>Mesorhizobium</i> [Li et al. 2012]
<i>Gueldenstaedtia multiflora</i>	<i>Mesorhizobium</i> [Tan et al. 1999], <i>Rhizobium</i> [Tan et al. 1999; Tan et al. 2001]
<i>Lessertia annulans</i> , <i>Lessertia capitata</i> , <i>Lessertia diffusa</i> , <i>Lessertia excisa</i> , <i>Lessertia frutescens</i> , <i>Lessertia herbacea</i> ,	<i>Mesorhizobium</i> [Gerding et al. 2012]



<i>Lessertia microphylla</i> , <i>Lessertia pauciflora</i>	
<i>Lessertia</i> sp.	<i>Ensifer</i> [Lemaire et al. 2015]
<b><i>Montigena novae-zelandiae</i></b>	<i>Mesorhizobium</i> [Tan et al. 2013]
<b><i>Oxytropis glabra</i></b>	<i>Ensifer</i> [Kan et al. 2007], <i>Mesorhizobium</i> [Han et al. 2008a], <i>Rhizobium</i> [Kan et al. 2007; Han et al. 2008b]
<i>Oxytropis kansuenses</i>	<i>Rhizobium</i> [Kan et al. 2007]
<i>Oxytropis meinshausenii</i>	<i>Rhizobium</i> [Han et al. 2008b]
<i>Oxytropis myriophylla</i>	<i>Mesorhizobium</i> [Kan et al. 2007]
<i>Oxytropis ochrocephala</i>	<i>Mesorhizobium</i> [Kan et al. 2007], <i>Rhizobium</i> [Kan et al. 2007]
<i>Oxytropis psammocharis</i>	<i>Rhizobium</i> [Kan et al. 2007]
<i>Oxytropis</i> sp.	<i>Phyllobacterium</i> [Kan et al. 2007]
<b><i>Sphaerophysa salsula</i></b>	<i>Ensifer</i> [Deng et al. 2011], <i>Mesorhizobium</i> [Deng et al. 2011], <i>Rhizobium</i> [Deng et al. 2011; Xu et al. 2011]
<b><i>Swainsona leana</i></b> , <i>Swainsona pterostylis</i>	<i>Ensifer</i> [Yates et al. 2004]
<i>Swainsona galegifolia</i>	<i>Mesorhizobium</i> [Tan et al. 2013]
<b>Hedysareae</b>	
<b><i>Alhagi sparsifolia</i></b>	<i>Mesorhizobium</i> [Wei et al. 2009]
<i>Alhagi toum</i>	<i>Rhizobium</i> [Han et al. 2008b]
<b><i>Caragana bicolor</i></b> , <i>Caragana erinacea</i>	<i>Mesorhizobium</i> , <i>Rhizobium</i> [Lu et al. 2009]
<i>Caragana franchetiana</i>	<i>Mesorhizobium</i> , [Lu et al. 2009]
<i>Caragana intermedia</i>	<i>Bradyrhizobium</i> [Lu et al. 2009], <i>Mesorhizobium</i> [Tan et al. 1999; Lu et al. 2009], <i>Rhizobium</i> [Lu et al. 2009]
<i>Caragana jubata</i>	<i>Rhizobium</i> [Han et al. 2008b]
<i>Caragana microphylla</i>	<i>Mesorhizobium</i> [Guan et al. 2008]
<b><i>Halimodendron halodendron</i></b>	<i>Rhizobium</i> [Han et al. 2008b]
<b><i>Hedysarum coronarium</i></b>	<i>Rhizobium</i> [Squartini et al. 2002; Liu et al. 2012]
<i>Hedysarum polybotrys</i>	<i>Rhizobium</i> [Wei et al. 2008b], <i>Mesorhizobium</i> [Yan et al. 2016]
<i>Hedysarum scoparium</i>	<i>Rhizobium</i> [Wei et al. 2008b]
<i>Hedysarum spinosissimum</i>	<i>Ensifer</i> [Rejilli et al. 2012]
<b><i>Onobrychis viciifolia</i></b>	<i>Phyllobacterium</i> [Baimiev et al. 2007]
<b>Millettieae</b>	
<b><i>Milletia leucantha</i></b>	<i>Bradyrhizobium</i> [Manassila et al. 2007]
<i>Milletia pinnata</i>	<i>Rhizobium</i> [Kesari et al. 2013]
<b><i>Tephrosia capensis</i></b>	<i>Bradyrhizobium</i> [Lemaire et al. 2015]
<i>Tephrosia falciformis</i>	<i>Bradyrhizobium</i> [Gehlot et al. 2012], <i>Ensifer</i> [Gehlot et al. 2012]
<i>Tephrosia purpurea</i>	<i>Bradyrhizobium</i> [Doignon-Bourcier et al. 1999], <i>Ensifer</i> [Gehlot et al. 2012], <i>Rhizobium</i> [Gehlot et al. 2012]
<i>Tephrosia villosa</i>	<i>Bradyrhizobium</i> [Doignon-Bourcier et al. 1999; Gehlot et al. 2012], <i>Ensifer</i> [Gehlot et al. 2012]
<i>Tephrosia wallichii</i>	<i>Ensifer</i> [Gehlot et al. 2012]
<b>Trifolieae</b>	
<b><i>Medicago archiducis-nicolai</i></b>	<i>Rhizobium</i> [Kan et al. 2007]
<i>Medicago intertexta</i>	<i>Ensifer</i> [El Batanony et al. 2015]
<i>Medicago laciniata</i>	<i>Ensifer</i> [Villegas et al. 2006; Badri et al. 2007; Mnasri et al. 2009; El Batanony et al. 2015], <i>Neorhizobium</i> [El Batanony et al. 2015]
<i>Medicago lupulina</i>	<i>Ensifer</i> [Kan et al. 2007; Wang et al. 2009]
<i>Medicago orbicularis</i>	<i>Ensifer</i> [Rome et al. 1996]

<i>Medicago polymorpha</i>	<i>Ensifer</i> [El Batanony et al. 2015], <i>Neorhizobium</i> [El Batanony et al. 2015]
<i>Medicago rigiduloides</i>	<i>Ensifer</i> [Cubry-Rangin et al. 2013]
<i>Medicago ruthenica</i>	<i>Rhizobium</i> [van Berkum et al. 1998]
<i>Medicago sativa</i>	<i>Ensifer</i> [Yan et al. 2000; Kan et al. 2007; Mnsasri et al. 2009; Bromfield et al. 2010; Merabet et al. 2010; Djedidi et al. 2011], <i>Neorhizobium</i> [El Batanony et al. 2015], <i>Rhizobium</i> [Bromfield et al. 2010]
<i>Medicago scutellata</i>	<i>Ensifer</i> [Mnsasri et al. 2009]
<i>Medicago truncatula</i>	<i>Ensifer</i> [Rome et al. 1996; Badri et al. 2007; Mnsasri et al. 2009]
<i>Melilotus alba</i>	<i>Ensifer</i> [Bromfield et al. 2010], <i>Rhizobium</i> [Bromfield et al. 2010]
<i>Melilotus indicus</i> , <i>Melilotus messanensis</i>	<i>Ensifer</i> [El Batanony et al. 2015]
<i>Melilotus officinalis</i>	<i>Ensifer</i> [Kan et al. 2007; Wang et al. 2009]
<i>Melilotus siculus</i>	<i>Ensifer</i> [El Batanony et al. 2015]
<i>Trifolium fragiferum</i>	<i>Bradyrhizobium</i> [Liu et al. 2007], <i>Mesorhizobium</i> [Liu et al. 2007], <i>Rhizobium</i> [Liu et al. 2007]
<i>Trifolium pratense</i>	<i>Phyllobacterium</i> [Valverde et al. 2005],
<i>Trifolium repens</i>	<i>Bradyrhizobium</i> [Liu et al. 2007], <i>Ensifer</i> [Liu et al. 2007], <i>Rhizobium</i> [Liu et al. 2007; Zhang et al. 2016]
<i>Trigonella maritima</i>	<i>Ensifer</i> [Rejili et al. 2012; El Batanony et al. 2015]

**Table 3.** Legume-rhizobia symbioses of species in the sub-family Papilionoideae with indeterminate nodules excluding the inverted repeat lacking clade.

Papilionoideae Tribes (genera)	Rhizobia – field
<b>Abreae</b>	
<i>Abrus precatorius</i>	<i>Ensifer</i> [Ogasawara et al. 2003]
<b>Amorpheae</b>	
<i>Amorpha fruticosa</i>	<i>Bradyrhizobium</i> [Wang et al. 1999b], <i>Mesorhizobium</i> [Tan et al. 1999; Wang et al. 1999b; Wang et al. 2009]
<i>Dalea purpurea</i>	<i>Mesorhizobium</i> [Tlusty et al. 2005], <i>Rhizobium</i> [Tlusty et al. 2005]
<b>Crotalariaeae</b>	
<i>Aspalathus callosa</i>	<i>Burkholderia</i> [Lemaire et al. 2015]
<i>Aspalathus ciliaris</i> , <i>Aspalathus uniflora</i>	<i>Mesorhizobium</i> [Lemaire et al. 2015]
<i>Aspalathus linearis</i>	<i>Bradyrhizobium</i> [Hassen et al. 2012], <i>Burkholderia</i> [Hassen et al. 2012], <i>Herbaspirillum</i> [Hassen et al. 2012], <i>Mesorhizobium</i> [Hassen et al. 2012], <i>Rhizobium</i> [Hassen et al. 2012]
<i>Crotalaria comosa</i> , <i>Crotalaria hyssopifolia</i> , <i>Crotalaria lathyroides</i>	<i>Bradyrhizobium</i> [Sy et al. 2001]
<i>Crotalaria pallida</i>	<i>Bradyrhizobium</i> [Liu et al. 2007], <i>Burkholderia</i> [Liu et al. 2007], <i>Rhizobium</i> [Liu et al. 2007]
<i>Crotalaria perrotteti</i> , <i>Crotalaria podocarpa</i>	<i>Methylobacterium</i> [Sy et al. 2001]
<i>Crotalaria</i> sp.	<i>Burkholderia</i> [Lemaire et al. 2015]
<i>Lebeckia ambigua</i>	<i>Burkholderia</i> [Howieson et al. 2013]
<i>Listia angolensis</i>	<i>Microvirga</i> [Ardley et al. 2012]
<i>Listia bainesii</i> , <i>Listia solitudinis</i> , <i>Listia listii</i>	<i>Methylobacterium</i> [Yates et al. 2007]
<i>Rafnia</i> sp.	<i>Burkholderia</i> [Lemaire et al. 2015]

<b>Genisteae</b>	
<i>Adenocarpus hispanicus</i>	<i>Phyllobacterium</i> [Ruiz-Diéz et al. 2009]
<i>Argyrolobium uniflorum</i>	<i>Ensifer</i> [Mnasri et al. 2009; Merabet et al. 2010]
<i>Argyrolobium</i> sp.	<i>Mesorhizobium</i> [Lemaire et al. 2015]
<i>Cytisus aeolicus</i>	<i>Bradyrhizobium</i> [Cardinale et al. 2008]
<i>Cytisus balansae</i>	<i>Bradyrhizobium</i> [Rodriguez-Echeverria et al. 2003]
<i>Cytisus laburnum</i>	<i>Bradyrhizobium</i> [Ruiz-Diez et al. 2009]
<i>Cytisus multiflorus</i>	<i>Bradyrhizobium</i> [Rodriguez-Echeverria et al. 2003]
<i>Cytisus proliferus</i>	<i>Bradyrhizobium</i> [Vinuesa et al. 1998; Jarabo-Lorenzo et al. 2000; Jarabo-Lorenzo et al. 2003; Vinuesa et al. 2005a]
<i>Cytisus purgans</i>	<i>Bradyrhizobium</i> [Ruiz-Diez et al. 2009]
<i>Cytisus scoparius</i>	<i>Bradyrhizobium</i> [Kalita et al. 2004; Horn et al. 2014]
<i>Cytisus striatus</i>	<i>Bradyrhizobium</i> [Rodriguez-Echeverria et al. 2003]
<i>Cytisus villosus</i>	<i>Bradyrhizobium</i> [Chahboune et al. 2011]
<i>Genista hystrix</i>	<i>Bradyrhizobium</i> [Rodriguez-Echeverria, 2003]
<i>Genista stenopetula</i>	<i>Bradyrhizobium</i> [Vinuesa et al. 2005a]
<i>Genista versicolor</i>	<i>Bradyrhizobium</i> [Cobo-Diaz et al. 2014]
<i>Lupinus albescens</i>	<i>Bradyrhizobium</i> [Stroschein et al. 2010; Granada et al. 2015]
<i>Lupinus albus</i>	<i>Bradyrhizobium</i> [Jarabo-Lorenzo 2003, Velazquez et al. 2010; Stepkowski et al. 2011]
<i>Lupinus angustifolius</i>	<i>Bradyrhizobium</i> [Jarabo-Lorenzo 2003; Stepkowski et al. 2011]
<i>Lupinus honoratus</i>	<i>Ochrobactrum</i> [Trujillo et al. 2005]
<i>Lupinus luteus</i>	<i>Bradyrhizobium</i> [Jarabo-Lorenzo et al. 2003; Stepkowski et al. 2011]
<i>Lupinus mariae-josephae</i>	<i>Bradyrhizobium</i> [Sánchez-Cañizares et al. 2011; Duran et al. 2013]
<i>Lupinus montanus</i>	<i>Bradyrhizobium</i> [Vinuesa et al. 2005]
<i>Lupinus polyphyllus</i>	<i>Bradyrhizobium</i> [Vinuesa et al. 2005; Ryan-Salter et al. 2014]
<i>Lupinus texensis</i>	<i>Microvirga</i> [Ardley et al. 2012]
<i>Lupinus</i> sp.	<i>Bradyrhizobium</i> [Jarabo-Lorenzo et al. 2003]
<i>Retama monosperma</i>	<i>Bradyrhizobium</i> [Guerrouj et al. 2013]
<i>Retama raetam</i>	<i>Bradyrhizobium</i> [Farida et al. 2009]
<i>Retama sphaerocarpa</i>	<i>Bradyrhizobium</i> [Rodriguez-Echeverria, 2003; Farida et al. 2009; Guerrouj et al. 2013; Rodriguez-Echeverria, 2014], <i>Phyllobacterium</i> [Ruiz-Diez et al. 2009]
<i>Spartium junceum</i>	<i>Bradyrhizobium</i> [Quatrini et al. 2002; Cardinale et al. 2008; Ruiz-Diéz et al. 2009], <i>Phyllobacterium</i> [Ruiz-Diez et al. 2009]
<i>Ulex europaeus</i>	<i>Bradyrhizobium</i> [Liu 2014]
<b>Hypocalypteae</b>	
<i>Hypocalyptus coluteoides</i> , <i>Hypocalyptus oxalidifolius</i> , <i>Hypocalyptus sophoroides</i>	<i>Burkholderia</i> [Beukes et al. 2013]
<b>Indigofereae</b>	
<i>Indigofera angustifolia</i>	<i>Burkholderia</i> [Lemaire et al. 2015]
<i>Indigofera astragalina</i>	<i>Bradyrhizobium</i> [Doignon-Bourcier et al. 1999]
<i>Indigofera hirsuta</i>	<i>Bradyrhizobium</i> [Doignon-Bourcier et al. 1999]
<i>Indigofera senegalensis</i>	<i>Bradyrhizobium</i> [Doignon-Bourcier et al. 1999]
<i>Indigofera tinctoria</i>	<i>Bradyrhizobium</i> [Doignon-Bourcier et al. 1999]

<b>Loteae</b>	
<i>Coronilla varia</i>	Mesorhizobium [Yang et al. 2013], Rhizobium [Tan et al. 1999; Tan et al. 2001; Yang et al. 2013]
<i>Ornithopus compressus, Ornithopus sativus</i>	<i>Bradyrhizobium</i> [Stepkowski et al. 2005]
<b>Podalyrieae</b>	
<i>Cyclopia buxifolia, Cyclopia genistoides, Cyclopia glabra, Cyclopia intemedia, Cyclopia longifolia, Cyclopia maculata, Cyclopia meyeriana, Cyclopia pubescens, Cyclopia sessiflora, Cyclopia subternata</i>	<i>Burkholderia</i> [Beukes et al. 2013]
<i>Podalyria burchelli</i>	<i>Burkholderia</i> [Lemaire et al. 2015]
<i>Podalyria calyptrata</i>	<i>Burkholderia</i> [Beukes et al. 2013; Lemaire et al. 2015; Lemaire et al. 2016]
<i>Podalyria sericea</i>	<i>Burkholderia</i> [Lemaire et al. 2015]
<i>Virgilia divaricata</i>	<i>Rhizobium</i> [Lemaire et al. 2015]
<i>Virgilia oroboides</i>	<i>Burkholderia</i> [Beukes et al. 2013; Lemaire et al. 2015]
<b>Robineae</b>	
<i>Gliricidia sepium</i>	<i>Ensifer</i> [Bala & Giller, 2001], <i>Rhizobium</i> [Bala & Giller, 2001]
<i>Robinia pseudocacia</i>	<i>Mesorhizobium</i> [Ulrich & Zaspel 2000; Mierzwa et al. 2009], <i>Rhizobium</i> [Ulrich & Zaspel 2000; Han et al. 2008b]
<b>Sesbanieae</b>	
<i>Sesbania aculeata</i>	<i>Ensifer</i> [Lortet et al. 1996]
<i>Sesbania cannabina</i>	<i>Ensifer</i> [Lortet et al. 1996; Chen & Lee, 2001; Wang et al. 2013a; Li et al. 2016], <i>Neorhizobium</i> [Li et al. 2016], <i>Rhizobium</i> [Chen & Lee 2001; Li et al. 2016]
<i>Sesbania exasperata</i>	<i>Rhizobium</i> [Vinuesa et al. 2005b]
<i>Sesbania grandiflora</i>	<i>Ensifer</i> [Lortet et al. 1996]
<i>Sesbania herbacea</i>	<i>Rhizobium</i> [Wang et al. 1998]
<i>Sesbania pachycarpa</i>	<i>Ensifer</i> [Lortet et al. 1996]
<i>Sesbania punicea</i>	<i>Azorhizobium</i> [Blanco et al. 2008; Lemaire et al. 2015], <i>Mesorhizobium</i> [Vinuesa et al. 2005b], <i>Rhizobium</i> [Blanco et al. 2008]
<i>Sesbania rostrata</i>	<i>Azorhizobium</i> [Dreyfus et al. 1988; Moreira et al. 2006], <i>Bradyrhizobium</i> [Sinsuwongwat et al. 2002], <i>Ensifer</i> [Lortet et al. 1996; Ogasawara et al. 2003], <i>Rhizobium</i> [Sinsuwongwat et al. 2002]
<i>Sesbania sericea</i>	<i>Mesorhizobium</i> [Vinuesa et al. 2005b], <i>Rhizobium</i> [Vinuesa et al. 2005b]
<i>Sesbania sesban</i>	<i>Ensifer</i> [Lortet et al. 1996; Bala & Giller, 2001; Degefu et al. 2012], <i>Mesorhizobium</i> [Bala & Giller 2001; Odee et al. 2002; Degefu et al. 2011], <i>Rhizobium</i> [Bala & Giller 2001; Odee et al. 2002]
<i>Sesbania virgata</i>	<i>Azorhizobium</i> [Moreira et al. 2006], <i>Rhizobium</i> [Blanco et al. 2008]
<i>Sesbania sp.</i>	<i>Ensifer</i> [Lortet et al. 1996]
<b>Sophoreae</b>	
<i>Sophora alopecuroides</i>	<i>Ensifer</i> [Zhao et al. 2010] <i>Mesorhizobium</i> [Zhao et al. 2010], <i>Phyllobacterium</i> [Zhao et al. 2010], <i>Rhizobium</i> [Han et al. 2008b; Zhao et al. 2010]
<i>Sophora flavescens</i>	<i>Bradyrhizobium</i> [Jiao et al. 2015a], <i>Ensifer</i> [Jiao et al. 2015a], <i>Mesorhizobium</i> [Jiao et al. 2015a], <i>Phyllobacterium</i> [Jiao et al. 2015b], <i>Rhizobium</i> [Jiao et



	al. 2015a]
<i>Sophora longicarinata</i> , <i>S. microphylla</i> , <i>S. prostrata</i> , <i>S. tetraptera</i>	<i>Mesorhizobium</i> [Tan et al. 2015]
<i>Sophora vicifolia</i>	<i>Mesorhizobium</i> [Tan et al. 1999]
<b>Thermopsidae</b>	
<i>Ammopiptanthus nanus</i> , <i>Ammopiptanthus mongolicus</i>	<i>Ensifer</i> [Zhao et al. 2016], <i>Neorhizobium</i> [Zhao et al. 2016], <i>Pararhizobium</i> [Zhao et al. 2016], <i>Rhizobium</i> [Zhao et al. 2016]
<i>Anagyris latifolia</i>	<i>Mesorhizobium</i> [Donate-Correa et al. 2007]
<i>Thermopsis lupinoides</i>	<i>Mesorhizobium</i> [Ampomah & Huss-Danell, 2011]

**Table 4.** Legume-rhizobia symbioses of species in the sub-family Papilionoideae with determinate nodules.

Papilionoideae Tribes and genera	Rhizobia – field
<b>Dalbergieae</b>	
<i>Adesmia bicolor</i>	<i>Rhizobium</i> [Bianco et al. 2013]
<i>Aeschynomene afraspera</i>	<i>Bradyrhizobium</i> [Miché et al. 2010]
<i>Aeschynomene americana</i>	<i>Bradyrhizobium</i> [Miché et al. 2010; Noisangian et al. 2012]
<i>Aeschynomene ciliata</i> , <i>Aeschynomene elaphroxylon</i>	<i>Bradyrhizobium</i> [Miché et al. 2010]
<i>Aeschynomene indica</i>	<i>Bradyrhizobium</i> [Van Berkum & Eardly, 2002; Miché et al. 2010]
<i>Aeschynomene rudis</i>	<i>Bradyrhizobium</i> [Montecchia et al. 2002; Miché et al. 2010]
<i>Aeschynomene scabra</i> , <i>Aeschynomene sensitiva</i> , <i>Aeschynomene shimperi</i>	<i>Bradyrhizobium</i> [Miché et al. 2010]
<i>Arachis duranensis</i>	<i>Bradyrhizobium</i> [Chen et al. 2014]
<i>Arachis hypogaea</i>	<i>Bradyrhizobium</i> [Urtz & Elkan, 1996; Sinsuwongwat et al. 2002; Yang et al. 2005; Taurian et al. 2006; El-Akhal et al. 2008; Steenkamp et al. 2008; Chang et al. 2011; Munoz et al. 2011; Wang et al. 2013b; Grönemeyer et al. 2014; Li et al. 2015; Chen et al. 2016], <i>Rhizobium</i> [Taurian et al. 2006; El-Akhal et al. 2008]
<i>Centrolobium paraense</i>	<i>Bradyrhizobium</i> [Baraúna et al. 2014; Zilli et al. 2014]
<i>Dalbergia baroni</i> , <i>Dalbergia louveli</i> , <i>Dalbergia madagascariensis</i> , <i>Dalbergia maritima</i> , <i>Dalbergia monticola</i> ,	<i>Bradyrhizobium</i> [Rasolomampianina et al. 2005]
<i>Dalbergia odorifera</i>	<i>Burkholderia</i> [Lu et al. 2012]
<i>Dalbergia purpurascens</i>	<i>Bradyrhizobium</i> [Rasolomampianina et al. 2005]
<i>Dalbergia</i> sp.	<i>Bradyrhizobium</i> [Rasolomampianina et al. 2005]
<i>Pterocarpus officinalis</i>	<i>Bradyrhizobium</i> [Le Roux et al. 2014]
<i>Pterocarpus indicus</i>	<i>Bradyrhizobium</i> [Sinsuwongwat et al. 2002; Manassila et al. 2007]
<i>Zornia glochidiata</i>	<i>Bradyrhizobium</i> [Gueye et al. 2009]
<b>Desmodieae</b>	
<i>Desmodium caudatum</i>	<i>Bradyrhizobium</i> [Gu et al. 2007]
<i>Desmodium elegans</i>	<i>Bradyrhizobium</i> [Gu et al. 2007; Xu et al. 2016], <i>Pararhizobium</i> [Xu et al. 2016]

<i>Desmodium fallax</i>	<i>Bradyrhizobium</i> [Gu et al. 2007]
<i>Desmodium gangeticum</i>	<i>Bradyrhizobium</i> [Gu et al. 2007; Xu et al. 2016]
<i>Desmodium heterocarpan</i>	<i>Bradyrhizobium</i> [Gu et al. 2007; Delamuta et al. 2015]
<i>Desmodium microphyllum</i>	<i>Bradyrhizobium</i> [Gu et al. 2007], <i>Mesorhizobium</i> [Gu et al. 2007], <i>Rhizobium</i> [Gu et al. 2007]
<i>Desmodium oldhami</i>	<i>Rhizobium</i> [Xu et al. 2016]
<i>Desmodium racemosum</i>	<i>Bradyrhizobium</i> [Gu et al. 2007], <i>Ensifer</i> [Gu et al. 2007], <i>Rhizobium</i> [Gu et al. 2007]
<i>Desmodium sequax</i>	<i>Bradyrhizobium</i> [Gu et al. 2007], <i>Ensifer</i> [Gu et al. 2007], <i>Mesorhizobium</i> [Xu et al. 2016], <i>Pararhizobium</i> [Xu et al. 2016], <i>Rhizobium</i> [Gu et al. 2007; Xu et al. 2016]
<i>Desmodium sinuatum</i>	<i>Rhizobium</i> [Chen et al. 1997]
<i>Desmodium triflorum</i>	<i>Bradyrhizobium</i> [Gu et al. 2007]
<i>Kummerowia stipulacea</i>	<i>Bradyrhizobium</i> [Lin et al. 2007; Wang et al. 2009], <i>Rhizobium</i> [Lin et al. 2007]
<i>Kummerowia striata</i>	<i>Bradyrhizobium</i> [Lin et al. 2007], <i>Ensifer</i> [Lin et al. 2007], <i>Rhizobium</i> [Lin et al. 2007]
<i>Lespedeza bicolor</i>	<i>Bradyrhizobium</i> [Yao et al. 2002], <i>Ensifer</i> [Yao et al. 2002], <i>Mesorhizobium</i> [Wang et al. 2009] <i>Rhizobium</i> [Yao et al. 2002]
<i>Lespedeza capitata</i> , <i>Lespedeza cuneata</i>	<i>Bradyrhizobium</i> [Yao et al. 2002]
<i>Lespedeza cystobotrya</i>	<i>Ensifer</i> [Yao et al. 2002], <i>Rhizobium</i> [Wei et al. 2008b]
<i>Lespedeza daurica</i>	<i>Bradyrhizobium</i> [Yao et al. 2002], <i>Ensifer</i> [Yao et al. 2002], <i>Mesorhizobium</i> [Yao et al. 2002]
<i>Lespedeza davidii</i>	<i>Rhizobium</i> [Wei et al. 2008b]
<i>Lespedeza inschanica</i>	<i>Ensifer</i> [Yao et al. 2002]
<i>Lespedeza juncea</i> , <i>Lespedeza procumbens</i> , <i>Lespedeza stipulacea</i> , <i>Lespedeza striata</i>	<i>Bradyrhizobium</i> [Yao et al. 2002]
<i>Lespedeza tomentosa</i>	<i>Ensifer</i> [Yao et al. 2002]
<b>Phaseoleae</b>	
<i>Amphicarpaea bracteata</i> , <i>Amphicarpaea edgeworthii</i>	<i>Bradyrhizobium</i> [Parker et al. 2004]
<i>Amphicarpaea trisperma</i>	<i>Rhizobium</i> [Tan et al. 1999]
<i>Bolusafra bituminosa</i>	<i>Burkholderia</i> [Lemaire et al. 2015]
<i>Cajanus cajan</i>	<i>Bradyrhizobium</i> [Araujo et al. 2015]
<i>Canavalia rosea</i>	<i>Ensifer</i> [Chen et al. 2000]
<i>Centrosema pascuorum</i>	<i>Bradyrhizobium</i> [Sinsuwongwat et al. 2002]
<i>Centrosema pubescens</i>	<i>Bradyrhizobium</i> [Hélène et al. 2015]
<i>Dipogon lignosus</i>	<i>Burkholderia</i> [Liu et al. 2014]
<i>Glycine max</i>	<i>Bradyrhizobium</i> [Xu et al. 1995; Sinsuwongwat et al. 2002; Barcellos et al. 2007; Appunu et al. 2009; Wang et al. 2009; Zhang et al. 2011; Jaiswal et al. 2012; Tang et al. 2012; Wang et al. 2013c; Ribeiro et al. 2015], <i>Ensifer</i> [Peng et al. 2002; Barcellos et al. 2007; Appunu et al. 2009; Li et al. 2011; Zhang et al. 2011], <i>Rhizobium</i> [Alam et al. 2015]
<i>Glycine soja</i>	<i>Bradyrhizobium</i> [Wang et al. 2009; Wu et al. 2011], <i>Ensifer</i> [Wu et al.

	2011], <i>Rhizobium</i> [Zhao et al. 2014]
<i>Lablab purpureus</i>	<i>Bradyrhizobium</i> [Chang et al. 2011; Wang et al. 2013b; Grönemeyer et al. 2014]
<i>Neonotonia wightii</i>	<i>Bradyrhizobium</i> [Delamuta et al. 2015]
<i>Pachyrhizus erosus</i>	<i>Bradyrhizobium</i> [Fuentes et al. 2002; Rodriguez-Navarro et al. 2004; Ramirez-Bahena et al. 2009], <i>Rhizobium</i> [Fuentes et al. 2002]
<i>Pachyrhizus ferrugineus</i>	<i>Bradyrhizobium</i> [Rodriguez-Navarro et al. 2004]
<i>Pachyrhizus tuberosus</i>	<i>Bradyrhizobium</i> [Rodriguez-Navarro et al. 2004]
<i>Phaseolus lunatus</i>	<i>Bradyrhizobium</i> [López-López et al. 2013; Durán et al. 2014; Matsubara & Zúñiga-Dávila 2015], <i>Rhizobium</i> [Matsubara & Zúñiga-Dávila 2015]
<i>Phaseolus vulgaris</i>	<i>Bradyrhizobium</i> [López-López et al. 2013; Wang et al. 2016], <i>Burkholderia</i> [Talbi et al. 2010; Dall'Agnol et al. 2016], <i>Ensifer</i> [Mhamdi et al. 2002; Mnasri et al. 2007; Mnasri et al. 2012; Wang et al. 2016], <i>Pararhizobium</i> [Wang et al. 2016], <i>Rhizobium</i> [Martinez-Romero et al. 1991; Amarger et al. 1997; Mhamdi et al. 2002; Mostasso et al. 2002; Valverde et al. 2006; Mnasri et al. 2007; Wang et al. 2009; Wang et al. 2011; López-López et al. 2012; Mnasri et al. 2012; Ribeiro et al. 2013; Zahran et al. 2013; Cao et al. 2014; Grönemeyer et al. 2014; Wang et al. 2016]
<i>Pueraria phaseoloides</i>	<i>Bradyrhizobium</i> [Sarr et al. 2016]
<i>Rhynchosia aurea</i>	<i>Ensifer</i> [Gehlot et al. 2012]
<i>Rhynchosia ferulifolia</i>	<i>Burkholderia</i> [Garau et al. 2009; De Meyer et al. 2013]
<i>Rhynchosia minima</i>	<i>Bradyrhizobium</i> [Doignon-Bourcier et al. 1999; Garau et al. 2009]
<i>Rhynchosia totta</i>	<i>Bradyrhizobium</i> [Garau et al. 2009]
<i>Vigna angularis</i>	<i>Bradyrhizobium</i> [Han et al. 2009], <i>Ensifer</i> [Han et al. 2009], <i>Rhizobium</i> [Han et al. 2009]
<i>Vigna radiata</i>	<i>Bradyrhizobium</i> [Zhang et al. 2008; Risal et al. 2012], <i>Ensifer</i> [Zhang et al. 2008], <i>Rhizobium</i> [Zhang et al. 2008]
<i>Vigna sinensis</i>	<i>Bradyrhizobium</i> [Sinsuwongwat et al. 2002]
<i>Vigna subterranea</i>	<i>Bradyrhizobium</i> [Grönemeyer et al. 2014; Onyango et al. 2015], <i>Burkholderia</i> [Onyango et al. 2015], <i>Rhizobium</i> [Onyango et al. 2015]
<i>Vigna unguiculata</i>	<i>Achromobacter</i> [Guimarães et al. 2012], <i>Bradyrhizobium</i> [Steenkamp et al. 2008; Zhang et al. 2008; Guimarães et al. 2012; Bejarano et al. 2014; Grönemeyer et al. 2014; Silva et al. 2014], <i>Burkholderia</i> [Guimarães et al. 2012], <i>Rhizobium</i> [Zhang et al. 2008; Guimarães et al. 2012]
<b>Psoraleae</b>	
<i>Otholobium bracteolatum</i> , <i>Otholobium hirtum</i> , <i>Otholobium virgatum</i> , <i>Otholobium zeyhari</i> , <i>Otholobium</i> sp	<i>Mesorhizobium</i> [Lemaire et al. 2015]
<i>Psoralea asarina</i>	<i>Burkholderia</i> [Kanu & Dakora, 2012]
<i>Psoralea corylifolia</i>	<i>Ensifer</i> [Wang et al. 2013a]
<i>Psoralea pinnata</i>	<i>Burkholderia</i> [Kanu & Dakora, 2012], <i>Mesorhizobium</i> [Kanu & Dakora, 2012; Lemaire et al. 2015]
<b>Loteae</b>	
<i>Lotus arabicus</i> , <i>Lotus arinagensis</i>	<i>Ensifer</i> [Merabet et al. 2010]
<i>Lotus bertheloti</i> , <i>Lotus callis-viridis</i> , <i>Lotus campylocladus</i>	<i>Mesorhizobium</i> [Lorite et al. 2010a]
<i>Lotus corniculatus</i>	<i>Geobacillus</i> [Ampomah & Huss-Danell, 2011], <i>Mesorhizobium</i> [Jarvis et al. 1997; Lorite et al. 2010a; Lorite et al. 2010b; Ampomah & Huss-Danell, 2011; Marcos-Garcia et al. 2015], <i>Paenibacillus</i>

	[Ampomah & Huss-Danell, 2011], <i>Rhodococcus</i> [Ampomah & Huss-Danell, 2011]
<i>Lotus creticus</i>	<i>Ensifer</i> [Merabet et al. 2010; Rejili et al. 2012], <i>Mesorhizobium</i> [Merabet et al. 2010; Rejili et al. 2012], <i>Rhizobium</i> [Merabet et al. 2010; Rejili et al. 2012],
<i>Lotus frondosus</i>	<i>Mesorhizobium</i> [Han et al. 2008a], <i>Rhizobium</i> [Han et al. 2008b]
<i>Lotus halophyllus</i>	<i>Ensifer</i> [Rejili et al. 2012]
<i>Lotus kunkeli</i> , <i>Lotus lancerottensis</i> , <i>Lotus maculatus</i>	<i>Ensifer</i> [Léon-Barrios et al. 2009]
<i>Lotus pyranthus</i>	<i>Mesorhizobium</i> [Lorite et al. 2010a]
<i>Lotus sessilifolius</i>	<i>Ensifer</i> [Léon-Barrios et al. 2009], <i>Mesorhizobium</i> [Lorite et al. 2010a]
<i>Lotus tenuis</i>	<i>Mesorhizobium</i> [Estrella et al. 2009; Lorite et al. 2010b; Sannazzaro et al. 2011], <i>Rhizobium</i> [Han et al. 2008b; Estrella et al. 2009]
<i>Lotus uliginosus</i>	<i>Bradyrhizobium</i> [Lorite et al. 2012]



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