



Review

Specificity in Legume-Rhizobia Symbioses

Mitchell Andrews * and Morag E. Andrews

Faculty of Agriculture and Life Sciences, Lincoln University, PO Box 84, Lincoln 7647, New Zealand;
moragandrews@gmail.com

* Correspondence: mitchell.andrews@lincoln.ac.nz; Tel.: +64-3-423-0692

Academic Editors: Peter M. Gresshoff and Brett Ferguson

Received: 12 February 2017; Accepted: 21 March 2017; Published: 26 March 2017

Abstract: Most species in the Leguminosae (legume family) can fix atmospheric nitrogen (N_2) via symbiotic bacteria (rhizobia) in root nodules. Here, the literature on legume-rhizobia symbioses in field soils was reviewed and genotypically characterised rhizobia related to the taxonomy of the legumes from which they were isolated. The Leguminosae was divided into three sub-families, the Caesalpinoideae, Mimosoideae and Papilionoideae. *Bradyrhizobium* spp. were the exclusive rhizobial symbionts of species in the Caesalpinoideae, but data are limited. Generally, a range of rhizobia genera nodulated legume species across the two Mimosoideae tribes Ingeae and Mimoseae, but *Mimosa* spp. show specificity towards *Burkholderia* in central and southern Brazil, *Rhizobium/Ensifer* in central Mexico and *Cupriavidus* in southern Uruguay. These specific symbioses are likely to be at least in part related to the relative occurrence of the potential symbionts in soils of the different regions. Generally, Papilionoideae species were promiscuous in relation to rhizobial symbionts, but specificity for rhizobial genus appears to hold at the tribe level for the Fabeae (*Rhizobium*), the genus level for *Cytisus* (*Bradyrhizobium*), *Lupinus* (*Bradyrhizobium*) and the New Zealand native *Sophora* spp. (*Mesorhizobium*) and species level for *Cicer arietinum* (*Mesorhizobium*), *Listia bainesii* (*Methylobacterium*) and *Listia angolensis* (*Microvirga*). Specificity for rhizobial species/symbiovar appears to hold for *Galega officinalis* (*Neorhizobium galegeae* sv. *officinalis*), *Galega orientalis* (*Neorhizobium galegeae* sv. *orientalis*), *Hedysarum coronarium* (*Rhizobium sullae*), *Medicago laciniata* (*Ensifer meliloti* sv. *medicaginis*), *Medicago rigiduloides* (*Ensifer meliloti* sv. *rigiduloides*) and *Trifolium ambiguum* (*Rhizobium leguminosarum* sv. *trifolii*). Lateral gene transfer of specific symbiosis genes within rhizobial genera is an important mechanism allowing legumes to form symbioses with rhizobia adapted to particular soils. Strain-specific legume rhizobia symbioses can develop in particular habitats.

Keywords: Leguminosae; N_2 fixation; nodulation; *nod* genes; lateral gene transfer

1. Introduction

The Leguminosae (Fabaceae, the legume family) is comprised of ca. 19,300 species within 750 genera that occur as herbs, shrubs, vines or trees in mainly terrestrial habitats and are components of most of the world's vegetation types [1–3]. Currently, the legume family is divided into three sub-families, the Caesalpinoideae, Mimosoideae and Papilionoideae [3,4]. Members of the Caesalpinoideae are grouped into four tribes, the Caesalpinieae, Cassieae, Cercideae and Detarieae comprising ca. 170 genera and 2250 species. The Mimosoideae are grouped into two tribes, the Ingeae and Mimoseae with ca. 80 genera and 3270 species, while the Papilionoideae consists of 28 tribes with ca. 480 genera and 13,800 species. However, a new classification of the legumes has been proposed with six sub-families based on the plastid *matK* gene sequences from ca. 20% of all legume species across ca. 90% of all currently recognized genera [5]. The six sub-families proposed are a re-circumscribed Caesalpinoideae, Cercidoideae, Detarioideae, Dialioideae, Duparquetioideae and

Papilioideae. In this system, the currently recognized Mimosoideae is a distinct clade nested within the re-circumscribed Caesalpinoideae. Species within the Cercidoideae, Detarioideae, Dialioideae and Duparquetioideae do not nodulate [5,6].

Most legume species can fix atmospheric nitrogen (N_2) 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 [7,8]. Furthermore, N_2 fixation by legumes can be a major input of N into natural and agricultural ecosystems [9–12]. Generally, legume nodules can be classified as indeterminate or determinate in growth [13]. Indeterminate nodules maintain meristematic tissue, while determinate nodules have a transient meristem. Nodule type is dependent on host plant, and legume species that can produce both determinate and indeterminate nodules are rare [14,15]. All genera examined in the Caesalpinoideae and Mimosoideae had indeterminate nodules [13]. Within the Papilioideae, most tribes had indeterminate nodules, but the Desmodieae, Phaseoleae, Psoraleae and some members of the Loteae show “desmodioid” determinate nodules and the Dalbergieae “aeschnomenoid” determinate nodules [13]. Desmodioid nodules have lenticels, and rhizobia “infected” tissue within them also contains uninjected cells. Aeschynomenoid nodules do not have lenticels, have uniform infected tissue and are always associated with lateral or adventitious roots. Where tested, species within the Desmodieae, Phaseoleae and Psoraleae had ureides as the main N-containing compound transported from nodules, but species in the Dalbergieae and Loteae transported amides/amino acids [13]. Indeterminate nodules have a single or branched apical meristem, and a few genera, such as *Lupinus* (Genisteae) and *Listia* (Crotalaria), have “lupinoid” nodules with two or more lateral meristems, which in some cases completely surround the subtending root [16,17]. Generally, indeterminate nodules have a mixture of infected and uninjected cells in the central nodule tissue, but lupinoid nodules, as for aeschnomenoid nodules (Dalbergiae), have uniformly-infected cells.

The nodulation process for almost all legumes studied is initiated by the legume production of a mix of compounds, mainly flavonoids, which induce the synthesis of NodD protein in rhizobia [18,19]. Different legumes produce different types/mixes of compounds. The NodD protein activates the transcription of other genes involved in the nodulation process, including those required to produce Nod factors, the signal molecules produced by the rhizobia and detected by the plant, which induce nodule organogenesis [20]. The *nodABC* genes encode for the proteins required to make the core Nod factor structure [18]. Nod factors from different rhizobia have a similar structure of a chitin-like N-acetyl glucosamine oligosaccharide backbone with a fatty acyl chain at the non-reducing end, but differ in their length of N-acetyl glucosamine oligosaccharide backbone and the length and saturation of the fatty acid chain. The Nod-factor core is modified by species-specific proteins, which results in various substitutions, including acetylation, glycosylation, methylation and sulfation. Perception of the Nod-factor signal in legumes is mediated by Nod factor receptors, which are plasma membrane localized serine/threonine receptor kinases in the case of the model legumes *Lotus japonicus* and *Medicago truncatula* [18,19].

The available data indicate that rhizobia enter the roots of most legume species via root hair infection [13]. Here, rhizobia enter root hairs, and host cell wall material grows around the developing “infection”, forming an infection thread, which grows through the cortex of the root, branching repeatedly. Generally, rhizobia are released from the tips of these infection threads into membrane-bound structures within host cells called symbiosomes where they differentiate into their N_2 -fixing form known as bacteroids. However, all species examined in the Caesalpinoideae, except herbaceous *Chamaecrista* spp. and a few species in the Papilioideae, retain their rhizobia within infection threads [2,13]. Bacteroids vary greatly in their level of differentiation and viability depending on the legume host [13,21]. The process of root hair infection can lead to the formation of either indeterminate or desmodioid determinate nodules. A second mode of rhizobial infection occurs with species in the Dalbergiae (aeschnemonoid nodules) where rhizobia enter roots at the sites of lateral root emergence (“crack” entry), and infection threads are not involved in the infection process [22,23].

Thirdly, for at least some members of the Genisteae (e.g., *Lupinus* spp.) and Crotalariae (e.g., *Listia* spp.), rhizobia enter the roots directly through the root epidermis at the junction between epidermal cells, and again, infection threads are not involved in the infection process [17,21,24].

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 the symbiosis have been developed as a “standard approach” [15,25,26]. The 16S rRNA gene sequence on its own can delineate rhizobia at the genus level [27]. The main symbiosis genes studied are the “*nif*” genes, which encode the subunits of nitrogenase, the rhizobial enzyme that fixes N₂, and the “*nod*” genes, which encode Nod factors that induce various symbiotic responses on legume roots. Specific *nod* genes have been shown to be major determinants of legume host specificity [28,29]. 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 [30–32]. Almost all rhizobia tested had *nod* genes. However, a few *Bradyrhizobium* strains, which do not possess *nodABC* genes, can form N₂ fixing nodules on particular *Aeschynomene* spp. [33,34]. Bacterial species from a range of genera in the α-proteobacteria (most commonly *Bradyrhizobium*, *Ensifer* (*Sinorhizobium*), *Mesorhizobium* and *Rhizobium*) and two genera in the β-proteobacteria (*Burkholderia* (*Paraburkholderia*) and *Cupriavidus*) can form functional (N₂ fixing) nodules on specific legumes (Tables 1–4). Reports that *Achromobacter* and *Herbaspirillum* (β-proteobacteria) produce N₂ fixing nodules on *Prosopis juliflora* and *Aspalathus linearis*, respectively [35,36] and *Pseudomonas* (Gammaproteobacteria) produces N₂ fixing nodules on *Robinia pseudoacacia* [37] and *Acacia confusa* [38] have not been confirmed. Furthermore, for *Lotus corniculatus*, *Geobacillus* (phylum Firmicutes), *Paenibacillus* (Firmicutes) and *Rhodococcus* (Actinobacteria) were for the first time reported as rhizobial symbionts [39]. These bacterial species had similar *nodA* gene sequences to *Mesorhizobium* isolated from the same plants, and it was concluded that the lateral gene transfer of these genes had occurred from the *Mesorhizobium*. However, lateral gene transfer of symbiosis genes is much less common between than within genera, and this work needs to be independently verified.

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

Mimosoideae Tribes and Genera	Rhizobia-Field
Ingeae	
<i>Acacia auriculiformis</i>	<i>Bradyrhizobium</i> [40–42]
<i>Acacia mangium</i>	<i>Bradyrhizobium</i> [40,41,43,44], <i>Ochrobactrum</i> [44], <i>Rhizobium</i> [44]
<i>Acacia mangium</i> × <i>A. auriculiformis</i>	<i>Bradyrhizobium</i> [43]
<i>Acacia mearnsii</i>	<i>Ensifer</i> [45,46]
<i>Acacia melanoxylon</i>	<i>Bradyrhizobium</i> [47]
<i>Acacia saligna</i>	<i>Bradyrhizobium</i> [42,48], <i>Ensifer</i> [49], <i>Rhizobium</i> [48]
<i>Acaciella angustissima</i>	<i>Ensifer</i> [50,51]
<i>Calliandra calothyrsis</i>	<i>Ensifer</i> [52], <i>Rhizobium</i> [52]
<i>Calliandra grandiflora</i>	<i>Ensifer</i> [53], <i>Mesorhizobium</i> [53], <i>Rhizobium</i> [53]
<i>Faidherbia albida</i>	<i>Bradyrhizobium</i> [54]
<i>Inga edulis</i>	<i>Bradyrhizobium</i> [55]
<i>Inga laurina</i>	<i>Bradyrhizobium</i> [56]
<i>Mariosousa acatlensis</i>	<i>Ensifer</i> [57]
<i>Senegalia laeta</i>	<i>Ensifer</i> [45]
<i>Senegalia macilenta</i>	<i>Ensifer</i> [57],
<i>Senegalia senegal</i>	<i>Ensifer</i> [45,46], <i>Rhizobium</i> [45,58], <i>Mesorhizobium</i> [58]

Table 1. Cont.

Mimosoideae Tribes and Genera	Rhizobia-Field
Mimoseae	
<i>Anadenanthera peregrina</i>	Burkholderia [59]
<i>Desmanthus illinoensis</i>	Rhizobium [60]
<i>Desmanthus paspalaceus</i>	Mesorhizobium [61], Rhizobium [61]
<i>Desmanthus virgatus</i>	Rhizobium [43]
<i>Leucaena leucocephala</i>	Ensifer [52,62,63], Mesorhizobium [52,62,63], Rhizobium [52,62,64]
<i>Microlobius foetidus</i>	Bradyrhizobium [59], Rhizobium [59]
~50 <i>Mimosa</i> spp.	Burkholderia [65–77]
<i>Mimosa affinis</i>	Rhizobium [72]
<i>Mimosa albida</i> , <i>M. biuncifera</i> , <i>M. borealis</i> , <i>M. dysocarpa</i> , <i>M. polyantha</i> , <i>M. tricephala</i> , <i>Mimosa</i> sp.	Ensifer [74], Rhizobium [74]
<i>Mimosa asperata</i>	Cupriavidus [78]
<i>Mimosa benthamii</i> , <i>M. goldmanii</i> , <i>M. monancistra</i> , <i>M. robusta</i> , <i>M. tequilana</i>	Rhizobium [74]
<i>Mimosa borealis</i> , <i>M. lacerata</i> , <i>M. luisana</i> , <i>M. similis</i>	Ensifer [74]
<i>Mimosa ceratonia</i>	Rhizobium [72]
<i>Mimosa cruenta</i> , <i>M. magentea</i> , <i>M. ramulosa</i> , <i>M. reptans</i> , <i>M. schleidenii</i>	Cupriavidus [79]
<i>Mimosa diplotricha</i>	Burkholderia [74], Cupriavidus [65,75,76], Rhizobium [65,72]
<i>Mimosa hamata</i> , <i>M. himalayana</i>	Ensifer [77]
<i>Mimosa invisa</i>	Rhizobium [70]
<i>Mimosa pigra</i>	Burkholderia [68], Cupriavidus [67,69]
<i>Mimosa polyantha</i>	Rhizobium [74]
<i>Mimosa pudica</i>	Bradyrhizobium [70], Burkholderia [74], Cupriavidus [65,69,72,75–77], Rhizobium [69,70]
<i>Mimosa skinneri</i>	Burkholderia [74], Rhizobium [74]
<i>Mimosa strigillosa</i>	Ensifer [78]
<i>Neptunia natans</i>	Allorhizobium [80], Devosia [81]
<i>Parapiptadenia pterosperma</i>	Burkholderia [59]
<i>Parapiptadenia rigida</i>	Burkholderia [59], Cupriavidus [82], Rhizobium [59]
<i>Piptadenia adiantoides</i> , <i>P. flava</i>	Rhizobium [59]
<i>Piptadenia gonoacantha</i> , <i>P. paniculata</i>	Burkholderia [59], Rhizobium [59]
<i>Piptadenia stipulacea</i> , <i>P. trisperma</i> , <i>P. vividiflora</i>	Burkholderia [59]
<i>Prosopis alba</i>	Bradyrhizobium [83], Ensifer [83,84], Mesorhizobium [83,85], Rhizobium [84]
<i>Prosopis chilensis</i>	Ensifer [46,86]
<i>Prosopis cineraria</i>	Ensifer [87]
<i>Prosopis farcta</i>	Ensifer [88], Mesorhizobium [88]
<i>Prosopis juliflora</i>	Ensifer [35], Rhizobium [35]
<i>Pseudopiptadenia contorta</i>	Burkholderia [59]
<i>Stryphnodendron</i> sp.	Bradyrhizobium [59]
<i>Vachellia abyssinica</i>	Mesorhizobium [89], Ensifer [90]
<i>Vachellia cochliacantha</i> , <i>V. farnesiana</i> , <i>V. pennatula</i>	Ensifer [57]
<i>Vachellia gummosa</i>	Ensifer [49]
<i>Vachellia horrida</i>	Ensifer [45,49]
<i>Vachellia jacquemontii</i>	Ensifer [87,91]
<i>Vachellia macracantha</i>	Ensifer [92], Rhizobium [92]
<i>Vachellia nubica</i>	Bradyrhizobium [54]
<i>Vachellia seyal</i>	Rhizobium [45], Ensifer [90]
<i>Vachellia tortilis</i>	Ensifer [45,49,90,93], Mesorhizobium [45,54,89,93], Rhizobium [93]
<i>Vachellia xanthophloea</i>	Mesorhizobium [54]
<i>Xyilia xylocarpa</i>	Bradyrhizobium [40,43]

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.

Papilionoidieae Tribes and Genera	Rhizobia-Field
Ciceraceae	
<i>Cicer arietinum</i>	<i>Mesorhizobium</i> [94–101]
<i>Cicer canariense</i>	<i>Mesorhizobium</i> [102]
Fabeae	
<i>Lathyrus aphaca</i> , <i>L. nissolia</i> , <i>L. pratensis</i>	<i>Rhizobium</i> [103]
<i>Lathyrus japonicus</i>	<i>Rhizobium</i> [104]
<i>Lathyrus odoratus</i>	<i>Rhizobium</i> [105]
<i>Lens culinaris</i>	<i>Rhizobium</i> [101,106,107]
<i>Pisum sativum</i>	<i>Rhizobium</i> [101,103,107,108]
<i>Vicia amoena</i> , <i>V. bungei</i> , <i>V. villosa</i>	<i>Rhizobium</i> [109]
<i>Vicia cracca</i>	<i>Rhizobium</i> [103,109,110]
<i>Vicia hirsuta</i>	<i>Rhizobium</i> [103,105,110]
<i>Vicia faba</i>	<i>Rhizobium</i> [101,103,108,109,111–114]
<i>Vicia multicaulis</i> , <i>V. sylvatica</i> , <i>V. tetrasperma</i>	<i>Rhizobium</i> [110]
<i>Vicia sativa</i>	<i>Rhizobium</i> [103,109,115–118]
<i>Vicia sepium</i>	<i>Rhizobium</i> [109,110]
Galega	
<i>Galega officinalis</i>	<i>Neorhizobium</i> [119,120]
<i>Galega orientalis</i>	<i>Neorhizobium</i> [119]
Galegeae	
<i>Astragalus adsurgense</i>	<i>Ensifer</i> [121], <i>Mesorhizobium</i> [121], <i>Rhizobium</i> [122]
<i>Astragalus aksuensis</i> , <i>A. betetovii</i>	<i>Rhizobium</i> [105]
<i>Astragalus complanatus</i>	<i>Ensifer</i> [121], <i>Mesorhizobium</i> [121], <i>Rhizobium</i> [122]
<i>Astragalus chrysopterus</i>	<i>Rhizobium</i> [122]
<i>Astragalus discolor</i> , <i>A. efoliolatus</i> , <i>A. kifonsanicus</i>	<i>Mesorhizobium</i> [121]
<i>Astragalus melilotoides</i>	<i>Ensifer</i> [121], <i>Mesorhizobium</i> [121]
<i>Astragalus membranaceus</i>	<i>Mesorhizobium</i> [121,123,124]
<i>Astragalus mongolicus</i>	<i>Mesorhizobium</i> [124]
<i>Astragalus polycladus</i>	<i>Rhizobium</i> [121]
<i>Astragalus scaberrimus</i>	<i>Mesorhizobium</i> [121], <i>Rhizobium</i> [122]
<i>Biserrula pelecinus</i>	<i>Mesorhizobium</i> [125,126]
<i>Carmichaelia australis</i> , <i>C. monroi</i> ,	<i>Mesorhizobium</i> [127]
<i>Cianthus puniceus</i>	<i>Mesorhizobium</i> [127]
<i>Colutea arborescens</i>	<i>Ensifer</i> [128], <i>Mesorhizobium</i> [128,129], <i>Rhizobium</i> [128]
<i>Glycyrrhiza eurycarpa</i>	<i>Ensifer</i> [130]
<i>Glycyrrhiza glabra</i>	<i>Mesorhizobium</i> [130,131], <i>Rhizobium</i> [130]
<i>Glycyrrhiza inflata</i>	<i>Ensifer</i> [130]
<i>Glycyrrhiza multiflora</i>	<i>Mesorhizobium</i> [132]
<i>Glycyrrhiza pallidiflora</i>	<i>Mesorhizobium</i> [133]
<i>Glycyrrhiza uralensis</i>	<i>Mesorhizobium</i> [130,132], <i>Rhizobium</i> [130]
<i>Glycyrrhiza</i> sp.	<i>Mesorhizobium</i> [130]
<i>Gueldenstaedtia multiflora</i>	<i>Mesorhizobium</i> [132], <i>Rhizobium</i> [132,134]
<i>Lessertia annulans</i> , <i>L. capitata</i> , <i>L. diffusa</i> , <i>L. excisa</i> , <i>L. frutescens</i> , <i>L. herbacea</i> , <i>L. microphylla</i> , <i>L. pauciflora</i>	<i>Mesorhizobium</i> [135]
<i>Lessertia</i> sp.	<i>Ensifer</i> [136]
<i>Montigena novae-zelandiae</i>	<i>Mesorhizobium</i> [137]
<i>Oxytropis glabra</i>	<i>Ensifer</i> [109], <i>Mesorhizobium</i> [138], <i>Rhizobium</i> [105,109]
<i>Oxytropis kansuenses</i> , <i>O. myriophylla</i> , <i>O. psammocharis</i>	<i>Rhizobium</i> [109]
<i>Oxytropis meinshausenii</i>	<i>Rhizobium</i> [105]

Table 2. Cont.

Papilionoidieae Tribes and Genera	Rhizobia-Field
<i>Oxytropis ochrocephala</i>	<i>Mesorhizobium</i> [109], <i>Rhizobium</i> [109]
<i>Oxytropis</i> sp.	<i>Phyllobacterium</i> [109]
<i>Sphaerophysa salsula</i>	<i>Ensifer</i> [139], <i>Mesorhizobium</i> [139], <i>Rhizobium</i> [139,140]
<i>Swainsona leeania, S. pterostylis</i>	<i>Ensifer</i> [141]
<i>Swainsona galegifolia</i>	<i>Mesorhizobium</i> [137]
Hedysareae	
<i>Alhagi sparsifolia</i>	<i>Mesorhizobium</i> [142]
<i>Alhagi toum</i>	<i>Rhizobium</i> [105]
<i>Caragana bicolor, C. erinacea</i>	<i>Mesorhizobium, Rhizobium</i> [143]
<i>Caragana franchetiana</i>	<i>Mesorhizobium</i> , [143]
<i>Caragana intermedia</i>	<i>Bradyrhizobium</i> [143], <i>Mesorhizobium</i> [132,143], <i>Rhizobium</i> [143]
<i>Caragana jubata</i>	<i>Rhizobium</i> [105]
<i>Caragana microphylla</i>	<i>Mesorhizobium</i> [144]
<i>Halimodendron halodendron</i>	<i>Rhizobium</i> [105]
<i>Hedysarum coronarium</i>	<i>Rhizobium</i> [120,145]
<i>Hedysarum polybotrys</i>	<i>Rhizobium</i> [122], <i>Mesorhizobium</i> [124]
<i>Hedysarum scorpiarium</i>	<i>Rhizobium</i> [122]
<i>Hedysarum spinosissimum</i>	<i>Ensifer</i> [118]
<i>Onobrychis viciifolia</i>	<i>Phyllobacterium</i> [146]
Trifolieae	
<i>Medicago archiducis-nicolai</i>	<i>Rhizobium</i> [109]
<i>Medicago intertexta</i>	<i>Ensifer</i> [147]
<i>Medicago laciniata</i>	<i>Ensifer</i> [147–150], <i>Neorhizobium</i> [147]
<i>Medicago lupulina</i>	<i>Ensifer</i> [109,151]
<i>Medicago orbicularis</i>	<i>Ensifer</i> [152]
<i>Medicago polymorpha</i>	<i>Ensifer</i> [147], <i>Neorhizobium</i> [147]
<i>Medicago rigiduloides</i>	<i>Ensifer</i> [153]
<i>Medicago ruthenica</i>	<i>Rhizobium</i> [154]
<i>Medicago sativa</i>	<i>Ensifer</i> [109,150,155–158], <i>Neorhizobium</i> [147], <i>Rhizobium</i> [156]
<i>Medicago scutellata</i>	<i>Ensifer</i> [150]
<i>Medicago truncatula</i>	<i>Ensifer</i> [149,150,152]
<i>Melilotus alba</i>	<i>Ensifer</i> [156], <i>Rhizobium</i> [156]
<i>Melilotus indicus, M. messanensis, M. siculus</i>	<i>Ensifer</i> [147]
<i>Melilotus officinalis</i>	<i>Ensifer</i> [109,151]
<i>Trigonella maritima</i>	<i>Ensifer</i> [118,147]
Trifolium	
<i>Trifolium fragiferum</i>	<i>Bradyrhizobium</i> [70], <i>Mesorhizobium</i> [70], <i>Rhizobium</i> [70]
<i>Trifolium pratense</i>	<i>Phyllobacterium</i> [159],
<i>Trifolium repens</i>	<i>Bradyrhizobium</i> [70], <i>Ensifer</i> [70], <i>Rhizobium</i> [70,160]

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

Papilioideae Tribes (Genera)	Rhizobia-Field
Abreae	
<i>Abrus precatorius</i>	<i>Ensifer</i> [161]
Amorpheae	
<i>Amorpha fruticosa</i>	<i>Bradyrhizobium</i> [162], <i>Mesorhizobium</i> [132,151,162]
<i>Dalea purpurea</i>	<i>Mesorhizobium</i> [163], <i>Rhizobium</i> [163]

Table 3. Cont.

Papilioideae Tribes (Genera)	Rhizobia-Field
Crotalarieae	
<i>Aspalathus callosa</i>	<i>Burkholderia</i> [136]
<i>Aspalathus ciliaris, A. uniflora</i>	<i>Mesorhizobium</i> [136]
<i>Aspalathus linearis</i>	<i>Bradyrhizobium</i> [36], <i>Burkholderia</i> [36], <i>Mesorhizobium</i> [36], <i>Rhizobium</i> [36]
<i>Crotalaria comosa, C. hyssopifolia, C. lathyroides</i>	<i>Bradyrhizobium</i> [164]
<i>Crotalaria pallida</i>	<i>Bradyrhizobium</i> [70], <i>Burkholderia</i> [70], <i>Rhizobium</i> [70]
<i>Crotalaria perrotteti, C. podocarpa</i>	<i>Methylobacterium</i> [164]
<i>Crotalaria</i> sp.	<i>Burkholderia</i> [136]
<i>Lebeckia ambigua</i>	<i>Burkholderia</i> [165]
<i>Listia angolensis</i>	<i>Microvirga</i> [166]
<i>Listia bainesii, L. solitudinis, L. listii</i>	<i>Methylobacterium</i> [16]
<i>Lotononis laxa, L. sparsifolia</i>	<i>Ensifer</i> [17]
<i>Lotononis</i> sp.	<i>Bradyrhizobium, Mesorhizobium</i> [17]
<i>Rafnia</i> sp.	<i>Burkholderia</i> [136]
Genisteae	
<i>Adenocarpus hispanicus</i>	<i>Phyllobacterium</i> [129]
<i>Argyrolobium uniflorum</i>	<i>Ensifer</i> [150,157]
<i>Argyrolobium</i> sp.	<i>Mesorhizobium</i> [136]
<i>Cytisus aeolicus</i>	<i>Bradyrhizobium</i> [167]
<i>Cytisus balansae, C. multiflorus, C. striatus</i>	<i>Bradyrhizobium</i> [168]
<i>Cytisus laburnum, C. purgans</i>	<i>Bradyrhizobium</i> [129]
<i>Cytisus proliferus</i>	<i>Bradyrhizobium</i> [169–172]
<i>Cytisus scoparius</i>	<i>Bradyrhizobium</i> [173,174]
<i>Cytisus villosum</i>	<i>Bradyrhizobium</i> [175]
<i>Genista hystrix</i>	<i>Bradyrhizobium</i> [168]
<i>Genista stenopetala</i>	<i>Bradyrhizobium</i> [170]
<i>Genista versicolor</i>	<i>Bradyrhizobium</i> [176]
<i>Lupinus albescens</i>	<i>Bradyrhizobium</i> [177,178]
<i>Lupinus albus</i>	<i>Bradyrhizobium</i> [172,179,180]
<i>Lupinus angustifolius</i>	<i>Bradyrhizobium</i> [172,180]
<i>Lupinus honoratus</i>	<i>Ochrobactrum</i> [181]
<i>Lupinus luteus</i>	<i>Bradyrhizobium</i> [172,180]
<i>Lupinus mariae-josephae</i>	<i>Bradyrhizobium</i> [182,183]
<i>Lupinus montanus</i>	<i>Bradyrhizobium</i> [170]
<i>Lupinus micranthus</i>	<i>Bradyrhizobium</i> [184]
<i>Lupinus polyphyllus</i>	<i>Bradyrhizobium</i> [170,185]
<i>Lupinus texensis</i>	<i>Microvirga</i> [166]
<i>Lupinus</i> sp.	<i>Bradyrhizobium</i> [172]
<i>Retama monosperma</i>	<i>Bradyrhizobium</i> [186]
<i>Retama raetam</i>	<i>Bradyrhizobium</i> [187]
<i>Retama sphaerocarpa</i>	<i>Bradyrhizobium</i> [168,186–188], <i>Phyllobacterium</i> [129]
<i>Spartium junceum</i>	<i>Bradyrhizobium</i> [129,167,189], <i>Phyllobacterium</i> [129]
<i>Ulex europeus</i>	<i>Bradyrhizobium</i> [190]
Hypocalyppteae	
<i>Hypocalypthus coluteoides, H. oxalidifolius, H. sophoroides</i>	<i>Burkholderia</i> [191]
Indigofereae	
<i>Indigofera angustifolia</i>	<i>Burkholderia</i> [136]
<i>Indigofera astragalina, I. hirsuta, I. senegalensis, I. tinctoria</i>	<i>Bradyrhizobium</i> [192]
<i>Indigofera filifolia</i>	<i>Burkholderia</i> [193]

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

Papilioideae Tribes (Genera)	Rhizobia-Field
Loteae	
<i>Coronilla varia</i>	<i>Mesorhizobium</i> [194], <i>Rhizobium</i> [132,134,194]
<i>Ornithopus compressus, O. sativus</i>	<i>Bradyrhizobium</i> [195]
Millettieae	
<i>Millettia leucantha</i>	<i>Bradyrhizobium</i> [40]
<i>Millettia pinnata</i>	<i>Rhizobium</i> [196]
<i>Tephrosia capensis</i>	<i>Bradyrhizobium</i> [136]
<i>Tephrosia falciformis</i>	<i>Bradyrhizobium</i> [87], <i>Ensifer</i> [87]
<i>Tephrosia purpurea</i>	<i>Bradyrhizobium</i> [192], <i>Ensifer</i> [87], <i>Rhizobium</i> [87]
<i>Tephrosia villosa</i>	<i>Bradyrhizobium</i> [87,192], <i>Ensifer</i> [87]
<i>Tephrosia wallichii</i>	<i>Ensifer</i> [86]
Podalyrieae	
<i>Cyclopia buxifolia, C. genistoides, C. glabra, C. intemedia, C. longifolia, C. maculata, C. meyeriana, C. pubescens, C. sessiflora, C. subternata</i>	<i>Burkholderia</i> [191]
<i>Podalyria burchelli, P. sericea</i>	<i>Burkholderia</i> [136]
<i>Podalyria calyptrata</i>	<i>Burkholderia</i> [136,191,193,197]
<i>Podalyria pinnata</i>	<i>Burkholderia</i> [193]
<i>Virgilia divaricata</i>	<i>Rhizobium</i> [136]
<i>Virgilia oroboides</i>	<i>Burkholderia</i> [136,191]
Robineae	
<i>Gliricidia sepium</i>	<i>Ensifer</i> [52], <i>Rhizobium</i> [52]
<i>Robinia pseudocacia</i>	<i>Mesorhizobium</i> [198,199], <i>Rhizobium</i> [105,198]
Sesbanieae	
<i>Sesbania aculeata, S. grandiflora, S. pachycarpa, Sesbania sp.</i>	<i>Ensifer</i> [45]
<i>Sesbania cannabina</i>	<i>Ensifer</i> [45,200–202], <i>Neorrhizobium</i> [202], <i>Rhizobium</i> [200,202]
<i>Sesbania exasperata</i>	<i>Rhizobium</i> [30]
<i>Sesbania herbacea</i>	<i>Rhizobium</i> [203]
<i>Sesbania punicea</i>	<i>Azorhizobium</i> [136,204], <i>Mesorhizobium</i> [30], <i>Rhizobium</i> [204]
<i>Sesbania rostrata</i>	<i>Azorhizobium</i> [205,206], <i>Bradyrhizobium</i> [43], <i>Ensifer</i> [45,161], <i>Rhizobium</i> [43]
<i>Sesbania sericea</i>	<i>Mesorhizobium</i> [30], <i>Rhizobium</i> [30]
<i>Sesbania sesban</i>	<i>Ensifer</i> [45,52,90], <i>Mesorhizobium</i> [52,54,89], <i>Rhizobium</i> [52,54]
<i>Sesbania virgata</i>	<i>Azorhizobium</i> [206], <i>Rhizobium</i> [204]
Sophoreae	
<i>Sophora alopecuroides</i>	<i>Ensifer</i> [207], <i>Mesorhizobium</i> [207], <i>Phyllobacterium</i> [207], <i>Rhizobium</i> [105,207]
<i>Sophora flavescens</i>	<i>Bradyrhizobium</i> [208], <i>Ensifer</i> [208], <i>Mesorhizobium</i> [208], <i>Phyllobacterium</i> [209], <i>Rhizobium</i> [208]
<i>Sophora longicarinata, S. microphylla, S. prostrata, S. tetrapetala</i>	<i>Mesorhizobium</i> [210]
<i>Sophora viciifolia</i>	<i>Mesorhizobium</i> [132]
Thermopsideae	
<i>Ammopiptanthus nanus, A. mongolicus</i>	<i>Ensifer</i> [211], <i>Neorrhizobium</i> [211], <i>Pararhizobium</i> [211], <i>Rhizobium</i> [211]
<i>Anagyris latifolia</i>	<i>Mesorhizobium</i> [212]
<i>Thermopsis lupinoides</i>	<i>Mesorhizobium</i> [213]

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

Papilionoideae Tribes and Genera	Rhizobia-Field
Dalbergieae	
<i>Adesmia bicolor</i>	<i>Rhizobium</i> [214]
<i>Aeschynomene afraspera</i> , <i>A. ciliata</i> , <i>A. elaphroxylon</i> , <i>A. scabra</i> , <i>A. sensitiva</i> , <i>A. shimperi</i>	<i>Bradyrhizobium</i> [34]
<i>Aeschynomene americana</i>	<i>Bradyrhizobium</i> [34,215]
<i>Aeschynomene indica</i>	<i>Bradyrhizobium</i> [34,216]
<i>Aeschynomene rufis</i>	<i>Bradyrhizobium</i> [34,217]
<i>Arachis duranensis</i>	<i>Bradyrhizobium</i> [218]
<i>Arachis hypogaea</i>	<i>Bradyrhizobium</i> [43,219–229], <i>Rhizobium</i> [221,222]
<i>Centrolobium paraense</i>	<i>Bradyrhizobium</i> [230,231]
<i>Dalbergia baroni</i> , <i>D. louveli</i> , <i>D. madagascariensis</i> , <i>D. maritima</i> , <i>D. monticola</i> , <i>D. purpurascens</i> , <i>Dalbergia</i> sp.	<i>Bradyrhizobium</i> [232]
<i>Pterocarpus officinalis</i>	<i>Bradyrhizobium</i> [233]
<i>Pterocarpus indicus</i>	<i>Bradyrhizobium</i> [40,43]
<i>Zornia glochidiata</i>	<i>Bradyrhizobium</i> [234]
Desmodieae	
<i>Desmodium caudatum</i> , <i>D. fallax</i> , <i>D. triflorum</i>	<i>Bradyrhizobium</i> [235]
<i>Desmodium elegans</i>	<i>Bradyrhizobium</i> [235,236], <i>Pararhizobium</i> [236]
<i>Desmodium gangeticum</i>	<i>Bradyrhizobium</i> [235,237]
<i>Desmodium heterocarpan</i>	<i>Bradyrhizobium</i> [235,237]
<i>Desmodium microphyllum</i>	<i>Bradyrhizobium</i> [235], <i>Mesorhizobium</i> [235], <i>Rhizobium</i> [235]
<i>Desmodium oldhami</i>	<i>Rhizobium</i> [236]
<i>Desmodium racemosum</i>	<i>Bradyrhizobium</i> [235], <i>Ensifer</i> [235], <i>Rhizobium</i> [235]
<i>Desmodium sequax</i>	<i>Bradyrhizobium</i> [235], <i>Ensifer</i> [235], <i>Mesorhizobium</i> [236], <i>Pararhizobium</i> [236], <i>Rhizobium</i> [235,236]
<i>Desmodium sinuatum</i>	<i>Rhizobium</i> [238]
<i>Kummerowia stipulacea</i>	<i>Bradyrhizobium</i> [151,239], <i>Rhizobium</i> [239]
<i>Kummerowia striata</i>	<i>Bradyrhizobium</i> [239], <i>Ensifer</i> [239], <i>Rhizobium</i> [239]
<i>Lespedeza bicolor</i>	<i>Bradyrhizobium</i> [240], <i>Ensifer</i> [240], <i>Mesorhizobium</i> [151] <i>Rhizobium</i> [240]
<i>Lespedeza capitata</i> , <i>L. cuneata</i> , <i>L. juncea</i> , <i>L. procumbens</i> , <i>L. stipulacea</i> , <i>L. striata</i>	<i>Bradyrhizobium</i> [240]
<i>Lespedeza cystobotrya</i>	<i>Ensifer</i> [240], <i>Rhizobium</i> [122]
<i>Lespedeza daurica</i>	<i>Bradyrhizobium</i> [240], <i>Ensifer</i> [240], <i>Mesorhizobium</i> [240]
<i>Lespedeza daviddii</i>	<i>Rhizobium</i> [122]
<i>Lespedeza inschanica</i> , <i>L. tomentosa</i>	<i>Ensifer</i> [240]
Phaseoleae	
<i>Amphicarpaea bracteata</i> , <i>A. edgeworthii</i>	<i>Bradyrhizobium</i> [241]
<i>Amphicarpaea trisperma</i>	<i>Rhizobium</i> [132]
<i>Bolusafra bituminosa</i>	<i>Burkholderia</i> [136]
<i>Cajanus cajan</i>	<i>Bradyrhizobium</i> [242]
<i>Canavalia rosea</i>	<i>Ensifer</i> [243]
<i>Centrosema pascuorum</i>	<i>Bradyrhizobium</i> [43]
<i>Centrosema pubescens</i>	<i>Bradyrhizobium</i> [42]
<i>Dipogon lignosus</i>	<i>Burkholderia</i> [15,193]
<i>Glycine max</i>	<i>Bradyrhizobium</i> [43,151,244–251], <i>Ensifer</i> [245–247,252,253], <i>Rhizobium</i> [254]
<i>Glycine soja</i>	<i>Bradyrhizobium</i> [151,255], <i>Ensifer</i> [255], <i>Rhizobium</i> [256]
<i>Lablab purpureus</i>	<i>Bradyrhizobium</i> [224,226,227]
<i>Neonotonia wightii</i>	<i>Bradyrhizobium</i> [237]
<i>Pachyrhizus erosus</i>	<i>Bradyrhizobium</i> [257–259], <i>Rhizobium</i> [257]

Table 4. Cont.

Papilioideae Tribes and Genera	Rhizobia-Field
<i>Pachyrhizus ferrugineus</i> , <i>P. tuberosus</i>	<i>Bradyrhizobium</i> [258]
<i>Phaseolus lunatus</i>	<i>Bradyrhizobium</i> [260–262], <i>Rhizobium</i> [262]
<i>Phaseolus vulgaris</i>	<i>Bradyrhizobium</i> [260,263], <i>Burkholderia</i> [264,265], <i>Ensifer</i> [263,266–268], <i>Pararhizobium</i> [263], <i>Rhizobium</i> [64,101,151,227,263,266–275]
<i>Pueraria phaseoloides</i>	<i>Bradyrhizobium</i> [276]
<i>Rhynchosia aurea</i>	<i>Ensifer</i> [87]
<i>Rhynchosia ferulifolia</i>	<i>Burkholderia</i> [277,278]
<i>Rhynchosia minima</i>	<i>Bradyrhizobium</i> [192,277]
<i>Rhynchosia totta</i>	<i>Bradyrhizobium</i> [277]
<i>Vigna angularis</i>	<i>Bradyrhizobium</i> [279], <i>Ensifer</i> [279], <i>Rhizobium</i> [279]
<i>Vigna radiata</i>	<i>Bradyrhizobium</i> [280,281], <i>Ensifer</i> [280], <i>Rhizobium</i> [280]
<i>Vigna sinensis</i>	<i>Bradyrhizobium</i> [43]
<i>Vigna subterranea</i>	<i>Bradyrhizobium</i> [227,282], <i>Burkholderia</i> [282], <i>Rhizobium</i> [282]
<i>Vigna unguiculata</i>	<i>Bradyrhizobium</i> [223,227,280,283–285], <i>Burkholderia</i> [283], <i>Microvirga</i> [286], <i>Rhizobium</i> [280,283]
Psoraleae	
<i>Otholobium bracteolatum</i> , <i>O. hirtum</i> , <i>O. virgatum</i> , <i>O. zeyhari</i> , <i>Otholobium</i> sp.	<i>Mesorhizobium</i> [136]
<i>Psoralea asarina</i>	<i>Burkholderia</i> [286]
<i>Psoralea corylifolia</i>	<i>Ensifer</i> [201]
<i>Psoralea pinnata</i>	<i>Bradyrhizobium</i> [193], <i>Burkholderia</i> [287], <i>Mesorhizobium</i> [136,193,287]
Loteae	
<i>Lotus arabicus</i> , <i>L. arinagensis</i>	<i>Ensifer</i> [157]
<i>Lotus berthelotii</i> , <i>L. callis-viridis</i> , <i>L. campylocladus</i> , <i>L. pyranthus</i>	<i>Mesorhizobium</i> [288]
<i>Lotus corniculatus</i>	<i>Mesorhizobium</i> [39,288–291]
<i>Lotus creticus</i>	<i>Ensifer</i> [118,157], <i>Mesorhizobium</i> [118,157], <i>Rhizobium</i> [118,157]
<i>Lotus frondosus</i>	<i>Mesorhizobium</i> [138], <i>Rhizobium</i> [105]
<i>Lotus halophyllus</i>	<i>Ensifer</i> [118]
<i>Lotus kunkelii</i> , <i>L. lancerottensis</i> , <i>L. maculatus</i>	<i>Ensifer</i> [292]
<i>Lotus sessilifolius</i>	<i>Ensifer</i> [292], <i>Mesorhizobium</i> [288]
<i>Lotus tenuis</i>	<i>Mesorhizobium</i> [291,293,294], <i>Rhizobium</i> [105,293]
<i>Lotus uliginosus</i>	<i>Bradyrhizobium</i> [295]

Legume species differ greatly 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 [120,145,296,297]. Both of 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 [298,299]. Almost all genera in the IRLC are temperate; all have indeterminate nodules, and where examined, their bacteroids were terminally differentiated and could not return to their bacterial form [13]. 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 [117]. 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 α- and β-proteobacteria [264,283,300]. The Phaseoleae are of tropical/subtropical origin, have desmodioid determinate nodules with bacteroids, which are not terminally differentiated [2,13].

Here, the literature on legume-rhizobia symbioses in field soils was reviewed and genotypically characterised rhizobia related to the taxonomy of the legumes from which they were isolated. The objectives of the work were to collate data on legume rhizobia symbioses and then assess to what extent legume specificity for rhizobial symbionts is related to legume taxonomy.

2. Framework and Assumptions of Study

The general classification of the Leguminosae follows Lewis et al., 2005 [1], with updates [3,4]. The sub-families Caesalpinoideae, 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 at the 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 the tables. Sequences for *nif* and *nod* genes are considered 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* [301,302], 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 that differ with respect to the legume species they effectively nodulate [303].

A comprehensive collation of published legume-rhizobia symbioses up until 30 September 2016 was carried out. Articles were collected by searching the Institute for Scientific Information (ISI) Web of Science using each legume genus partnered with each of the rhizobia, *Bradyrhizobium*, *Burkholderia*, *Cupriavidus*, *Ensifer*, *Mesorhizobium*, *Rhizobium* and *Sinorhizobium* as the keywords. Further searches were carried out on the literature quoted in the selected papers and those listed as quoting the selected papers in the 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_2 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_2 fixation were accepted. These were acetylene reduction activity, red/pink nodules (evidence of leghaemoglobin 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 [304]. 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. Caesalpinoideae-Rhizobia Symbioses

Of the three legume sub-families, the Caesalpinoideae contains the smallest proportion of nodulated genera with nodulation confirmed for *Campsandra*, *Chidlowia*, *Dimorphandra*, *Erythrophleum*, *Jacqueshuberia*, *Melanoxylon*, *Moldenhawera* and *Tachigali* in the tribe Caesalpinieae and *Chamaecrista* in the tribe Cassiaeae [2,13]. Only two studies have genotypically characterised bacteria confirmed as rhizobia of Caesalpinoideae species. Firstly, five rhizobial isolates from *Dimorphandra wilsonii* and one from *Dimorphandra jorgei* sampled in the Cerrado biome in Brazil were *Bradyrhizobium* [305]. Secondly, 166 rhizobial isolates from *Erythrophleum fordii* sampled at four sites in the Guangdong and Guangxi Provinces of the southern sub-tropical region of China were also all *Bradyrhizobium* [306]. 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 Caesalpinoideae species, but their ability to produce N_2 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 were shown to nodulate *Macroptilium atropurpureum*, were *Bradyrhizobium* [307]. 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 southeast Guinea and shown to produce functional nodules on *Macroptilium atropurpureum* [308]. 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 N₂ fixation was not reported [309]. Furthermore, there are several reports that *Bradyrhizobium* inoculum can increase nodulation of *Chamaecrista* spp. under field conditions in Australia and China [310–312]. Thus, the available evidence indicates that *Bradyrhizobium* spp. are the dominant, possibly exclusive, rhizobial symbionts of legumes in the Caesalpinoideae, but data are limited, and the degree of specificity between legumes in the Caesalpinoideae 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. 120 species from 13 genera in the tribe Mimosae within the sub-family Mimosoideae (Table 1). *Bradyrhizobium*, *Ensifer*, *Mesorhizobium* and *Rhizobium* were each reported to nodulate species in the Ingeae and the Mimosae. Furthermore, *Ochrobactrum* was reported to nodulate *Acacia mangium* (Ingeae); *Allorhizobium* and *Devosia* were reported to nodulate *Neptunia natans* (Mimosae); and there are many reports that *Cupriavidus* and *Burkholderia* nodulate *Mimosa* spp. and related species (Mimosae) (Table 1). In addition, excepting *Acacia auriculiformis* (Ingeae) and *Mimosa pigra* (Mimosae), all species that were examined in three or more separate studies, *Acacia mangium*, *Acacia saligna*, *Calliandra grandiflora* and *Senegalia senegal* (Ingeae), *Leucaena leucocephala*, *Mimosa diplosticha*, *Mimosa pudica*, *Parapiptadenia rigida*, *Prosopis alba* and *Vachellia tortilis* (Mimosae), were nodulated by at least three different rhizobial genera. Thus, a range of rhizobial genera, including both α- and β-proteobacteria, can nodulate legume species across the two Mimosoideae tribes, and generally, where tested over different studies, species within the Ingeae and Mimosae tribes were promiscuous with respect to their rhizobial symbionts.

The *Mimosa* species examined across studies were the pan-tropical invasive *Mimosa diplosticha* and *Mimosa pudica*, and findings for these species appear not to reflect the situation with most *Mimosa* spp., which are endemic with a restricted range. The evidence indicates that most *Mimosa* spp. show specificity towards the rhizobial genus depending on their distribution with *Burkholderia*, *Rhizobium/Ensifer* and *Cupriavidus*, the main rhizobial symbiont of endemic *Mimosa* spp. in central and southern Brazil, central Mexico and southern Uruguay, respectively [73,74,79]. The 16S rRNA and housekeeping gene sequences were diverse for *Mimosa* *Burkholderia* symbionts in Brazil, *Rhizobium/Ensifer* in Mexico and *Cupriavidus* in Uruguay. For *Burkholderia* in Brazil and *Rhizobium/Ensifer* in Mexico, the symbiosis gene sequences were largely congruent with the 16S rRNA and housekeeping gene sequences, indicating that these genes diverged over a long period within *Burkholderia* without substantial horizontal gene transfer between species [73,74]. For *Cupriavidus* rhizobia in Uruguay, the *nodA* gene sequences were not congruent with the housekeeping gene sequences, but grouped together in a cluster [79]. This is strong evidence that the various *Cupriavidus* species obtained their symbiosis genes via within group lateral gene transfer [32,79,313]. It is not known if endemic *Mimosa* spp. nodulated by a particular rhizobia genus can form N₂-fixing symbioses with *Mimosa* rhizobia of different genera from outside their region.

5. Papilionoideae-Rhizobia Symbioses

5.1. The IRLC

Data are available for 103 species from 27 genera/five 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* within the IRLC clade were reported to only form effective nodules with their respective symbionts *Neorhizobium galegeae* sv. *officinalis*, *Neorhizobium galegeae* sv. *orientalis* and *Rhizobium sullae* [120,145,296,297]. The data in Table 2 indicate two 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. The 16S rRNA and housekeeping gene sequences indicated that strains of *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 [100]. Across studies where tested, *nifH* and *nodC* gene sequences were similar for all *Mesorhizobium* isolates shown to produce functional nodules on *Cicer arietinum*, indicating their specificity towards this legume species and that lateral transfer of these genes had occurred between the different *Mesorhizobium* spp. [97,99,100].

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 with some varieties of *Pisum sativum*, such as cv. Afghanistan, only nodulated by specific strains of *Rhizobium leguminosarum* sv. *viciae*, which occur in soils in their native range in Afghanistan/Turkey [103]. Furthermore, 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 (“colour red”) nodules [115]. 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. fabeae* [116], *R. multihospitium* [105], *R. pisi* [111], *R. laguerreae* [314] and *R. anhuiense* [108] have been reported to effectively nodulate Fabeae species. However, the *nifH* and *nodC* gene sequences of all of these rhizobia showed high similarity, indicating their specificity towards the Fabeae species and that, in this case, lateral gene transfer had occurred between different *Rhizobium* spp. [32,108].

Within the tribe Trifolieae, 14 out of 16 *Medicago/Melilotus* spp. had *Ensifer* as symbiont, but in four cases not exclusively. The most studied species, *Medicago sativa* (lucerne), was commonly nodulated by *Ensifer meliloti*, which is the recommended inoculum for this legume crop, but it also had *Neorhizobium* and *Rhizobium* symbionts. However, *Medicago laciniata* and *Medicago rigiduloides* were found to only nodulate with *Ensifer* strains sampled in their native range in the Mediterranean Basin. These strains were formally described as *Ensifer meliloti* sv. *medicaginis* and *Ensifer meliloti* sv. *rigiduloides*, respectively [148,153]. Similarly, different *Trifolium* spp. have different compatibility with different strains of *Rhizobium leguminosarum* sv. *trifolii*, which is the recommended inoculum for most *Trifolium* crops. *Trifolium ambiguum*, in particular, has been highlighted as only forming N₂-fixing nodules with strains of *Rhizobium leguminosarum* sv. *trifolii* specific to its region of origin (the Caucasus and Eastern Europe) [315].

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), *Hedysarum* (Hedysareae) and *Trifolium*. Furthermore, *Astragalus adsurgense*, *Astragalus complanatus*, *Colutea arborescens*, *Oxytropis glabra* and *Sphaerophysa salsula* (Galegeae), *Caragana intermedia* (Hedysareae) and *Trifolium fragiferum* and *Trifolium repens* were all nodulated by three different rhizobial genera. Thus, for the IRLC, specificity for the rhizobial genus appears to hold at the tribe level for the Fabeae (*Rhizobium* spp.) and species level for *Cicer arietinum* (*Mesorhizobium* spp.). Specificity for rhizobial species or symbiovar holds for *Galega officinalis* (*Neorhizobium galegeae* sv. *officinalis*), *Galega orientalis* (*Neorhizobium galegeae* sv. *orientalis*), *Hedysarum coronarium* (*Rhizobium sullae*), *Medicago laciniata* (*Ensifer meliloti* sv. *medicaginis*), *Medicago rigiduloides* (*Ensifer meliloti* sv. *rigiduloides*) and *Trifolium ambiguum* (*Rhizobium leguminosarum* sv. *trifolii*), but it is not a characteristic of all members of the clade.

5.2. Clades with Indeterminate Nodules, Excluding the IRLC

Data are shown for 113 species from 33 genera across 13 Papilionoideae tribes with indeterminate nodules that do not show the IRLC mutation (Table 3). *Azorhizobium*, *Bradyrhizobium*, *Burkholderia*, *Ensifer*, *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 sphaeroarpa* and *Spartium junceum* (Genisteae), *Coronilla varia* (Loteae), *Tephrosia falciformis* and *Tephrosia villosa* (Millettiae), *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), *Tephrosia purpurea* (Millettiae), *Sesbania cannabina*, *Sesbania punicea*, *Sesbania rostrata* and *Sesbania sesban* (Sesbanieae), *Sophora alopecuroides* and *Sophora flavescens* (Sophoreae) and *Ammopiptanthus nanus* and *Ammopiptanthus mongolicus* (Thermopsidiae) 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. 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). Furthermore, eight out of 10 *Lupinus* spp. (Genisteae) across 11 separate studies were nodulated by *Bradyrhizobium*. These results indicate that *Bradyrhizobium* may be the main symbionts of Genisteae species, but further work is required to confirm this. Generally, 16S rRNA and housekeeping gene sequences indicate that diverse *Bradyrhizobium* spp. form N₂-fixing nodules on *Cytisus* spp. and *Lupinus* spp., but the diversity of their symbiosis genes is dependent on the geographical origin of the legumes. For example, most *Bradyrhizobium* isolates from native *Lupinus* spp. in Europe form a distinct lineage, 'clade 11', on the basis of their *nodA* gene sequences [180,195]. Similarly, different *Bradyrhizobium* spp. associated with native *Cytisus villosus* in Morocco all showed similar *nodC* and *nifH* sequences, which were closely related to those of *Bradyrhizobium japonicum* sv. *genistearum* [175]. In contrast, rhizobia sampled from invasive *Cytisus scoparius* sampled in six states in the United States, differed with respect to housekeeping and symbiosis gene sequences [174]. Specifically, one group of isolates had both housekeeping and symbiosis gene sequences similar to a *Bradyrhizobium* clade from native legumes in Western North America, but two clades had *nifD*, *nifH* and *nodC* sequences highly similar or identical to a *Cytisus scoparius* strain isolated in Spain, while their housekeeping genes were similar to American *Bradyrhizobium* clades. Thus, it appears that *Bradyrhizobium* ancestrally associated with native North American legumes have acquired symbiosis genes from European *Cytisus scoparius* *Bradyrhizobium* symbionts via lateral gene transfer.

The two exceptions to *Bradyrhizobium* as the rhizobial symbiont of *Lupinus* spp. were *Ochrobactrum* [181] and *Microvirga* [166], both of which are rare as rhizobial symbionts of legumes. The *nodD* sequence for *Ochrobactrum* and the *nodA* sequence for *Microvirga* indicated that both bacteria obtained their *nod* genes via horizontal gene transfer from more common rhizobial genera. *Microvirga* is also the only bacterial genus shown to form N₂-fixing nodules on *Listia angolensis* [17]. Similarly, *Listia bainesii* has been found to only produce N₂-fixing nodules with pink pigmented *Methylobacterium* [17]. It was suggested that the seasonally waterlogged habitat of *Listia* spp. may have resulted in the selection of unusual rhizobial symbionts adapted to their environments [17].

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) [191]. *Burkholderia* was confirmed to nodulate *Podalyria calyptera* and *Virgilia oroboides* in the CFR [136,193,197]. 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 [31], 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 *Ensifer*, *Mesorhizobium*, *Phyllobacterium* and *Rhizobium* with a wide range of symbiosis gene sequences [207,208] 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 [210,316,317]. 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 an aeschynomoid determinate nodule structure [2]. Rhizobia have been characterised for 23 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*), with *Rhizobium* also reported for *Arachis hypogaea* in two studies. Thus, on the data available, the Dalbergieae appear to be primarily nodulated by *Bradyrhizobium*. For *Arachis hypogaea*, twelve separate studies reported *Bradyrhizobium* as a rhizobial symbiont (Table 4). Across these studies, both core and symbiosis gene sequences indicated that *Arachis hypogaea* was nodulated by a diverse range of *Bradyrhizobium* spp. and are promiscuous with respect to *Bradyrhizobium* spp. Excepting *Arachis hypogaea*, data are limited for rhizobial symbionts of species in the Dalbergieae. However, the unusual ability of specific *Bradyrhizobium* strains that lack canonical *nodABC* genes to form N₂-fixing nodules on roots and/or stems of particular *Aeschynomene* spp. is highlighted [34,215].

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 a desmodioid nodule structure [2,15]. 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 α-proteobacteria, as well as *Burkholderia* in the β-proteobacteria. Across three studies, *Phaseolus lunatus* was reported to be nodulated by *Bradyrhizobium* and *Rhizobium*, while *Vigna angularis*, *Vigna radiata* and *Vigna subterranea* 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, and *Glycine soja*. Both *Glycine* spp. were nodulated by *Bradyrhizobium*, *Ensifer* and *Rhizobium*. In the one case where separate studies were carried out on one species within the Psoraleae, *Psoralea pinnata* was nodulated by *Bradyrhizobium*, *Burkholderia* and *Mesorhizobium* [136,193,287]. Thus, where tested, species within the Desmodieae, Phaseoleae and Psoraleae were promiscuous with respect to their rhizobial symbionts.

Species in the Loteae, which show a desmodioid nodule structure, are of temperate distribution [2]. 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. Overall, the available data indicate that legume species with a desmodioid determinate nodule structure are promiscuous with respect to their rhizobia symbionts.

6. Legume Specificity for Rhizobial Symbionts

The objectives of the work were to collate data on legume rhizobia symbioses and assess the extent that legume specificity for rhizobial symbiont is related to legume taxonomy. *Bradyrhizobium* spp. were the exclusive rhizobial symbionts of species in the Caesalpinoideae; but, rhizobia were characterised for only three legume species over two studies, and the degree of specificity between legumes in the Caesalpinoideae and their rhizobial symbionts cannot be assessed without further work. Generally, species within the two Mimosoideae tribes, Ingeae and Mimoseae were promiscuous with respect to their rhizobial symbionts, but *Mimosa* spp. show specificity towards the rhizobia genus depending on

their distribution, with *Burkholderia*, *Rhizobium*/*Ensifer* and *Cupriavidus* the main rhizobial symbiont of endemic *Mimosa* spp. in central and southern Brazil, central Mexico and southern Uruguay, respectively [73,74,79]. 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 specificity for rhizobial genus or species/symbiovar. Specificity for rhizobial genus appears to hold at the tribe level for the Fabeae (*Rhizobium*), the genus level for *Cytisus* (*Bradyrhizobium*), *Lupinus* (*Bradyrhizobium*) and NZ native *Sophora* spp. (*Mesorhizobium*) and the species level for *Cicer arietinum* (*Mesorhizobium*), *Listia bainesii* (*Methylobacterium*) and *Listia angolensis* (*Microvirga*). Specificity for rhizobial species/symbiovar appears to hold for *Galega officinalis* (*Neorhizobium galegeae* sv. *officinalis*), *Galega orientalis* (*Neorhizobium galegeae* sv. *orientalis*), *Hedysarum coronarium* (*Rhizobium sullae*), *Medicago laciniata* (*Ensifer meliloti* sv. *medicaginis*), *Medicago rigiduloides* (*Ensifer meliloti* sv. *rigiduloides*) and *Trifolium ambiguum* (*Rhizobium leguminosarum* sv. *trifolii*). For Papilionoideae with determinate nodules, the Dalbergieae (aeschnomenoid nodules) were primarily nodulated by *Bradyrhizobium*, while those in the Desmodieae, Phaseoleae, Psoraleae and Loteae (desmodioïd nodules) were promiscuous with respect to rhizobial genus. Thus, on the data available, species in the Papilionoideae that show specificity for rhizobial genus, species or symbiovar have indeterminate nodules and are generally (but not exclusively) of temperate distribution. However, many temperate legumes with indeterminate nodules are promiscuous with respect to the rhizobial genus indicating that high specificity for rhizobial symbiont only occurs under specific conditions [318].

For *Mimosa* spp., specificity towards rhizobial genus depending on distribution is likely to be at least in part related to the relative occurrence of the potential symbionts in soils of the different regions [74,79]. For example, evidence indicates that *Mimosa Cupriavidus* symbionts are absent from soils in central and southern Brazil, while *Mimosa Burkholderia* symbionts are absent from soils in southern Uruguay. This has been related to soil characteristics with low pH favouring *Burkholderia* over *Cupriavidus* in Brazil, but high heavy metal content favouring *Cupriavidus* over *Burkholderia* in Uruguay [73,74,79]. It was proposed that native *Mimosa* in the different regions have selected symbiotic bacteria adapted to local conditions, which resulted in the development of highly specific associations [74,79]. However, for this to occur, such rhizobia must be available in the soil. The within genus 16S rRNA and housekeeping gene sequences were diverse for *Mimosa* symbionts in all regions. For *Burkholderia* in Brazil and *Rhizobium/Ensifer* in Mexico, the symbiosis gene sequences were largely congruent with the 16S rRNA and housekeeping gene sequences [73,74]. For *Cupriavidus* rhizobia in Uruguay, the *nodA* gene sequences were not congruent with the housekeeping gene sequences, but grouped together in a cluster, indicating that the various species within the group obtained their symbiosis genes via within group lateral gene transfer [79]. Lateral gene transfer is a mechanism whereby rhizobia and non-rhizobial bacteria adapted to local soil conditions could become specific rhizobial symbionts of legumes growing in these soils. The evidence described above indicates that lateral gene transfer of symbiosis genes has been important within the Papilionoideae in relation to the development of specific relationships between the Fabeae and *Rhizobium* spp., *Cytisus* and *Bradyrhizobium* spp., *Lupinus* and *Bradyrhizobium* spp., NZ native *Sophora* and *Mesorhizobium* spp. and *Cicer arietinum* and *Mesorhizobium* spp. Data are presented for *Mesorhizobium* isolates from *Cicer arietinum* and NZ native *Sophora* spp. to emphasise this point.

Firstly, 20 *Mesorhizobium* isolates from *Cicer arietinum*, sampled across three countries in five separate studies, showed diverse 16S rRNA sequences, but highly similar *nodC* sequences (Figure 1A,B). Here, evidence is strong that native *Mesorhizobium muleiense* adapted to alkaline soils in Gansu and Xinjiang Provinces of China obtained its *Cicer arietinum*-specific symbiotic genes from *Mesorhizobium ciceri* or *Mesorhizobium mediterraneum* introduced together with *Cicer arietinum* used as a crop [100]. Secondly, 48 isolates from four NZ native *Sophora* spp. sampled at eight different field sites separated into eight groups and three individual isolates on the basis of their concatenated *recA*, *glnI1* and *rpoB* gene sequences, but showed almost identical *nodC* (and *nodA* [210]) sequences (Figure 2A,B). Seven of the groups have been formally identified as new species [316,317]. This relationship between

NZ native *Sophora* spp. and *Mesorhizobium* spp. with specific symbiosis gene sequences is highly specific as none of twenty rhizobial isolates from common weed and crop legumes in NZ produced functional nodules on the NZ native *Sophora microphylla* [190]. Furthermore, *Mesorhizobium* isolates from *Carmichaelia*, *Cianthus* and *Montigena*, the only other NZ native legume genera, did not nodulate NZ native *Sophora microphylla* or *Sophora tetraptera* [127]. *Mesorhizobium* isolates from *Carmichaelia*, *Cianthus* and *Montigena* had unique *nodC* sequences different from those of *Sophora* *Mesorhizobium* isolates (Figure 2B). However, in some cases, their 16S rRNA, *recA* and *gln11* sequences were similar to those of *Sophora* *Mesorhizobium* isolates, emphasizing the importance of the specific symbiosis genes in the NZ *Sophora* *Mesorhizobium* symbiosis [137]. Generally, *Sophora* isolates from the same field site grouped together on concatenated *recA*, *gln11* and *rpoB* gene sequences (Figure 2B). This apparent link between housekeeping gene sequences and field site is compatible with the proposal that lateral transfer of symbiosis genes to *Mesorhizobium* strains adapted to local soil conditions has occurred.

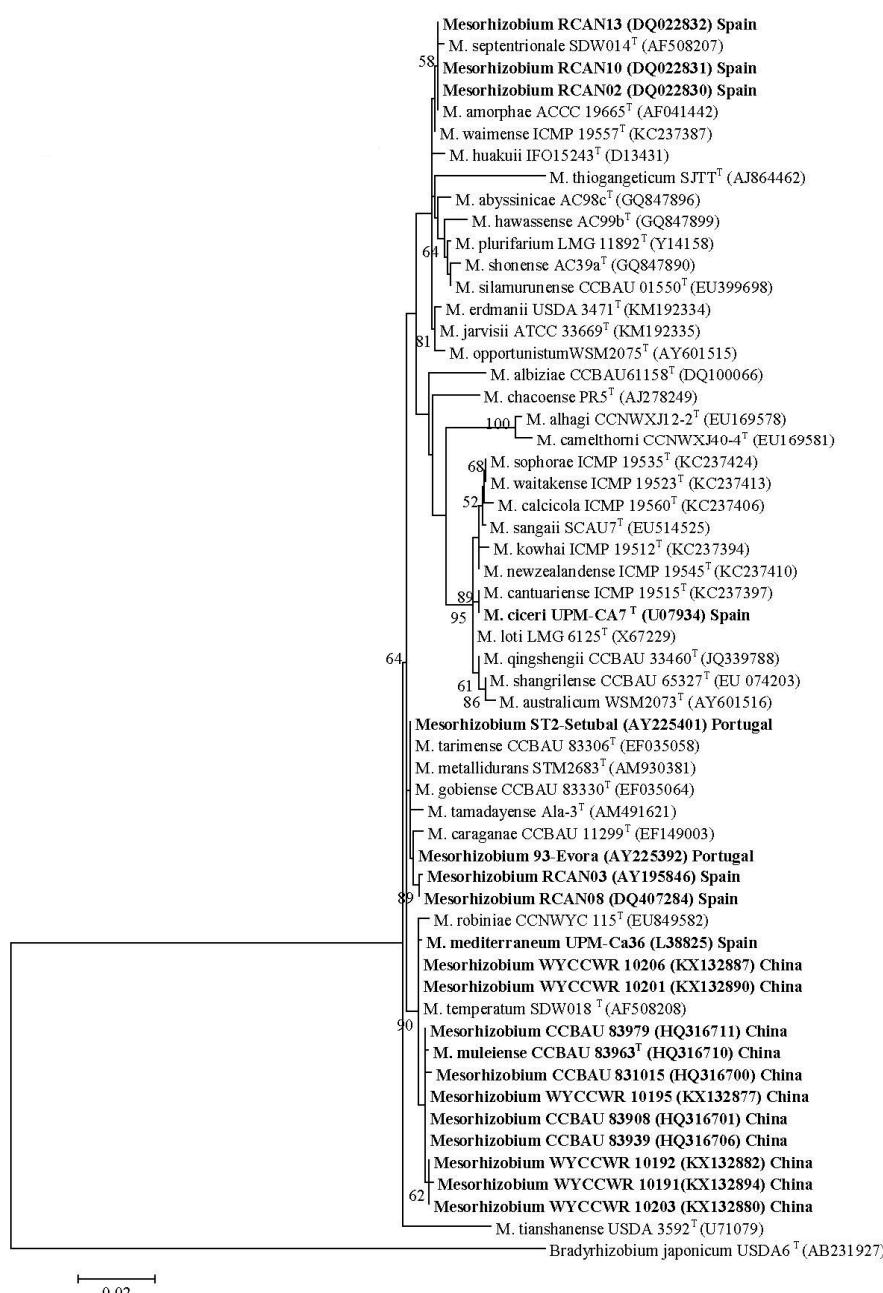
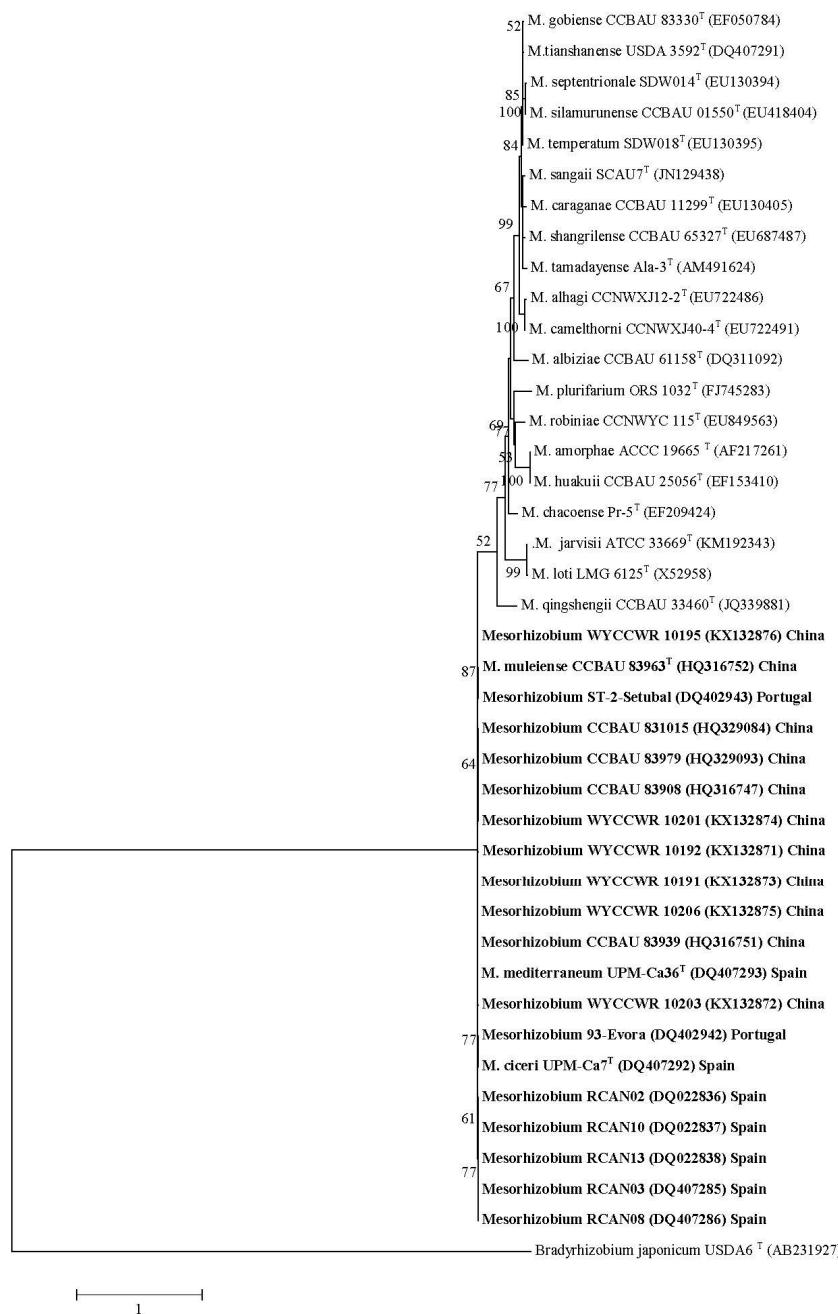


Figure 1. Cont.



1 —————— 1

Figure 1. 16S rRNA gene maximum likelihood (ML) tree (ca. 1360 bp) (A) and *nodC* gene ML tree (ca. 630 bp) (B) of rhizobial strains isolated from *Cicer arietinum* in Spain, Portugal and China (bold) and selected *Mesorhizobium* type strains [97,99,100]. Numbers on branches are bootstrap % from 1000 replicates (shown only when ≥50%).

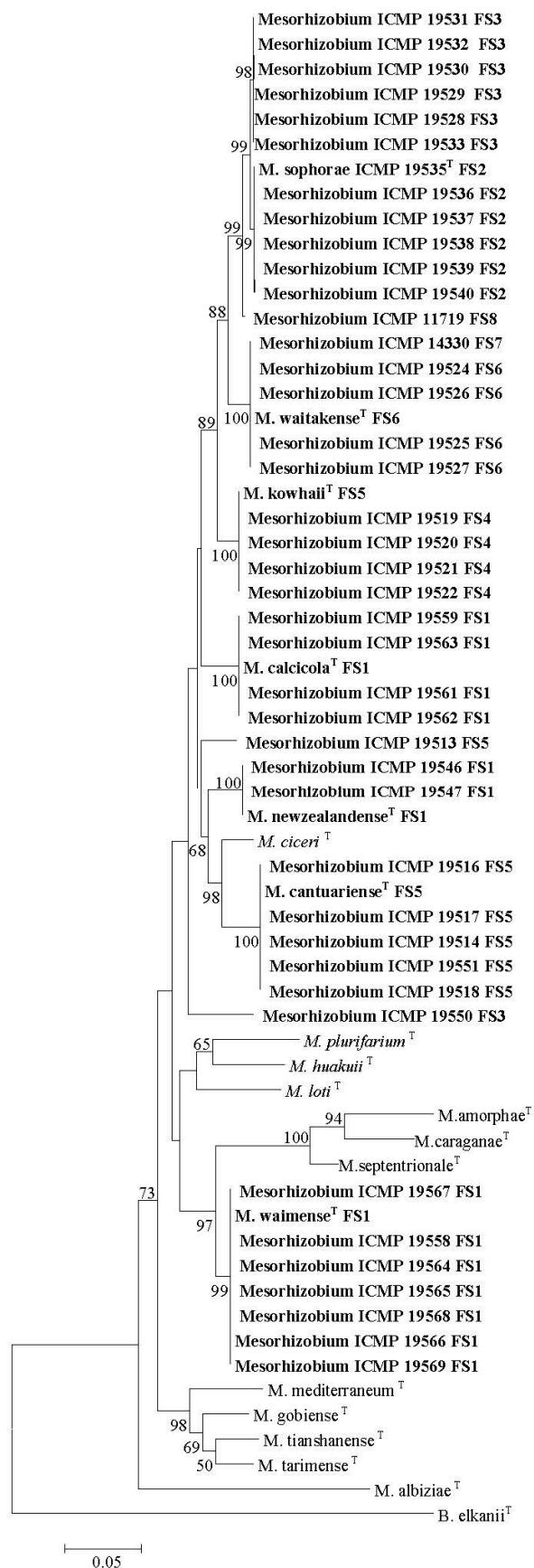


Figure 2. Cont.

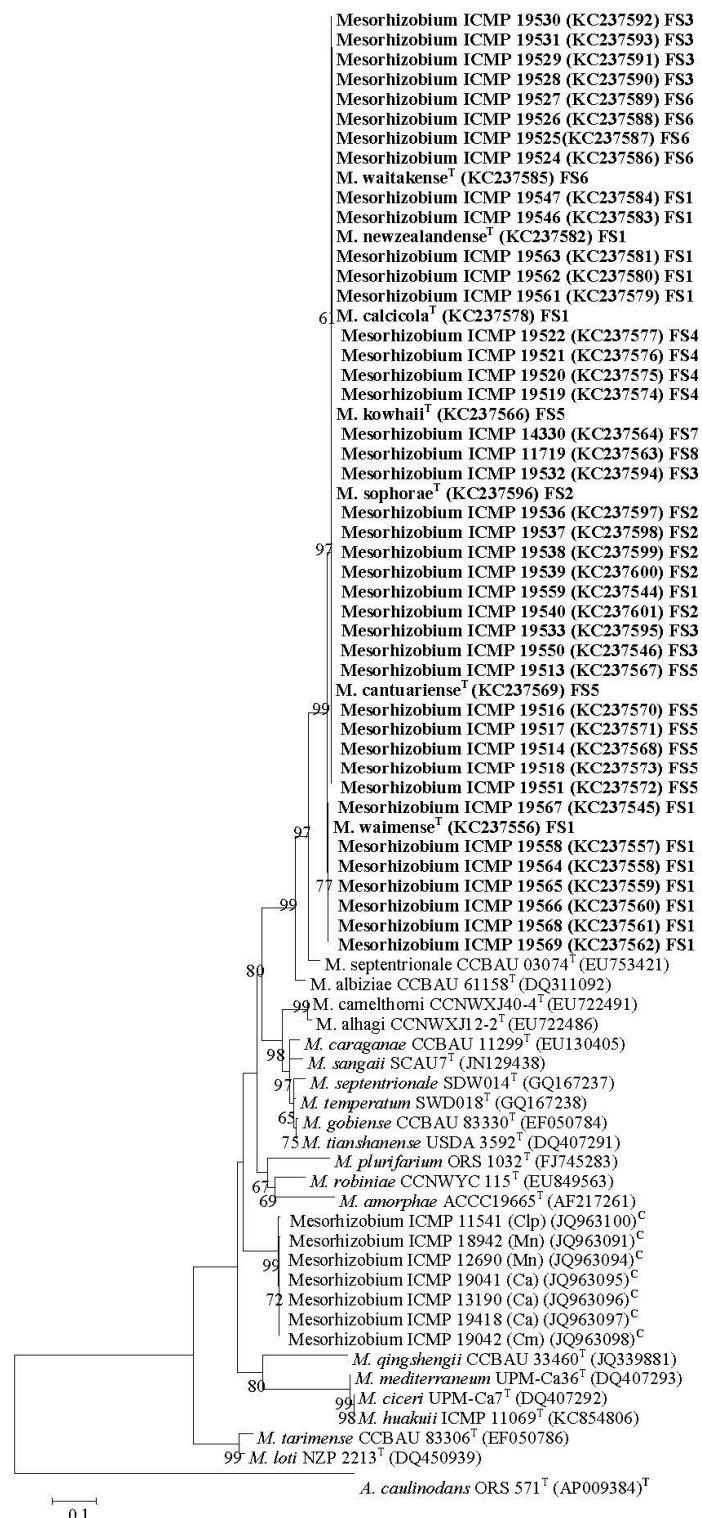


Figure 2. Concatenated *recA*, *glnI1* and *rpoB* gene maximum likelihood (ML) tree (ca. 1800 bp) (A) and *nodC* gene ML tree (ca. 650 bp) (B) of rhizobial strains isolated from New Zealand (NZ) native *Sophora* spp. (bold) and selected *Mesorhizobium* type strains. The *nodC* sequences of isolates from NZ native legumes *Cianthus puniceus* (Clp), *Montigena novozelandiae* (Mn), *Carmichaelia australis* (Ca) and *Carmichaelia monroi* (Cm) tested on NZ *Sophora* spp. are shown. Numbers on branches are bootstrap % from 500 replicates (shown only when $\geq 50\%$). FS = field site. Modified from Tan et al., 2015 [210].

Some varieties of *Pisum sativum*, such as cv. Afghanistan, are only nodulated by specific strains of *Rhizobium leguminosarum* sv. *viciae*, which occur in soils in their native range in Afghanistan/Turkey [103]. The ability of these strains to nodulate *Pisum sativum* cv. Afghanistan is controlled by a single recessive gene, *sym2* in the plant. The *sym2* allele interacts with a specific gene, *nodX*, present in *R. leguminosarum* sv. *viciae* strains able to nodulate cv. Afghanistan [319]. The *nodX* gene product acetylates a Nod factor, which mediates a specific compatible interaction with this cultivar [320,321]. Furthermore, *Medicago laciniata* and *Medicago rigiduloides* were found to only nodulate with *Ensifer meliloti* strains (*E. meliloti* sv. *medicaginis* and *E. meliloti* sv. *rigiduloides*, respectively) sampled in their native range in the Mediterranean Basin [148,153], and *Trifolium ambiguum* only forms N₂-fixing nodules with strains of *Rhizobium leguminosarum* sv. *trifolii* specific to its region of origin, the Caucasus and Eastern Europe [315]. The mechanisms of these highly specific relationships are not fully understood, but the *nodA* gene sequences of *E. meliloti* sv. *medicaginis* and *nodA*, *nodB* and *nodC* gene sequences of *E. meliloti* sv. *rigiduloides* diverged from those of *E. meliloti* strains, which nodulated other *Medicago* spp. [148,153], while the ability of certain strains of *Rhizobium leguminosarum* sv. *trifolii* to effectively nodulate *Trifolium ambiguum*, but not *Trifolium repens* (white clover) appears to be linked to a 111-bp insertion in their *nifH/fixA* intergenic region [315]. The factors that have resulted in these highly specific relationships are not known. Furthermore, it is not known if these highly specific relationships reflect adaptation of the symbioses and result in greater rates of N₂ fixation or more efficient N₂ fixation, as would be expected on theoretical grounds [322], and this warrants further study.

7. Conclusions

Overall, the data indicate that lateral gene transfer of specific symbiosis genes within rhizobial genera is an important mechanism allowing legumes to form symbioses with rhizobia adapted to particular soils. It also maintains specificity between legume species and rhizobia species with specific symbiosis genes. Strain-specific legume rhizobia symbioses can develop in particular habitats.

Acknowledgments: Lincoln University, New Zealand provided funds to cover the costs to publish in open access.

Author Contributions: Mitchell Andrews wrote the paper; Morag E. Andrews was responsible for the collation and presentation of data.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Lewis, G.A.; Schrire, B.B.; Mackinder, B.C.; Lock, M.D. *Legumes of the World*; Kew: Royal Botanic Gardens, London, UK, 2005.
2. Sprent, J.I. *Legume Nodulation A Global Perspective*; Wiley Blackwell: Chichester, UK, 2009.
3. LPWG. Legume phylogeny and classification in the 21st century: Progress, prospects and lessons for other species-rich clades. *Taxon* **2013**, *62*, 217–248.
4. Cardoso, D.; Pennington, R.T.; de Queiroz, L.P.; Boatwright, J.S.; van Wyk, B.-E.; Wojciechowski, M.F.; Lavin, M. Reconstructing the deep-branching relationships of the papilionoid legumes. *S. Afr. J. Bot.* **2013**, *89*, 58–75. [[CrossRef](#)]
5. LPWG. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* **2017**, *66*, 44–77.
6. Sprent, J.I.; Ardley, J.; James, E.K. Biogeography of nodulated legumes and their nitrogen-fixing symbionts. *New Phytol.* **2017**. [[CrossRef](#)] [[PubMed](#)]
7. Raven, J.A. Why are mycorrhizal fungi and symbiotic nitrogen-fixing bacteria not genetically integrated into plants? *Ann. Appl. Biol.* **2010**, *157*, 381–391. [[CrossRef](#)]
8. Andrews, M.; Raven, J.A.; Lea, P.J. Do plants need nitrate? The mechanisms by which nitrogen form affects plants. *Ann. Appl. Biol.* **2013**, *163*, 174–199. [[CrossRef](#)]

9. Andrews, M.; Scholefield, D.; Abberton, M.T.; McKenzie, B.A.; Hodge, S.; Raven, J.A. Use of white clover as an alternative to nitrogen fertilizer for dairy pastures in nitrate vulnerable zones in the UK: Productivity, environmental impact and economic considerations. *Ann. Appl. Biol.* **2007**, *151*, 11–23. [[CrossRef](#)]
10. Andrews, M.; James, E.K.; Sprent, J.I.; Boddey, R.M.; Gross, E.; dos Reis, F.B., Jr. Nitrogen fixation in legumes and actinorhizal plants in natural ecosystems: Values obtained using ^{15}N natural abundance. *Plant Ecol. Divers.* **2011**, *4*, 131–140. [[CrossRef](#)]
11. Jackson, L.E.; Burger, M.; Cavagnaro, T.R. Roots, nitrogen transformations, and ecosystem services. *Ann. Rev. Plant Biol.* **2008**, *59*, 341–363. [[CrossRef](#)] [[PubMed](#)]
12. Vitousek, P.M.; Menge, D.N.L.; Reed, S.C.; Cleveland, C.C. Biological nitrogen fixation: Rates, patterns and ecological controls in terrestrial ecosystems. *Philos. Trans. R. Soc. B* **2013**, *368*, 20130119. [[CrossRef](#)] [[PubMed](#)]
13. Sprent, J.I.; Ardley, J.K.; James, E.K. From north to south: A latitudinal look at legume nodulation processes. *S. Afr. J. Bot.* **2013**, *89*, 31–41. [[CrossRef](#)]
14. Fernández-López, M.; Goormachtig, S.; Gao, M.; D’Haeze, W.; van Montagu, M.; Holsters, M. Ethylene-mediated phenotypic plasticity in root nodule development on *Sesbania rostrata*. *Proc. Natl. Acad. Sci. USA* **1998**, *95*, 12724–12728. [[CrossRef](#)] [[PubMed](#)]
15. Liu, W.Y.Y.; Ridgway, H.J.; James, T.K.; James, E.K.; Chen, W.-M.; Sprent, J.I.; Young, J.P.W.; Andrews, M. *Burkholderia* sp. induces functional nodules on the South African invasive legume *Dipogon lignosus* (Phaseoleae) in New Zealand soils. *Microb. Ecol.* **2014**, *68*, 542–555. [[CrossRef](#)] [[PubMed](#)]
16. Yates, R.J.; Howieson, J.G.; Reeve, W.G.; Nandasena, K.G.; Law, I.J.; Bräu, L.; Ardley, J.K.; Nistelberger, H.M.; Real, D.; O’Hara, G.W. *Lotononis angolensis* forms nitrogen fixing, lupinoid nodules with phylogenetically unique, fast growing, pink-pigmented bacteria, which do not nodulate *L. bainesii* or *L. listii*. *Soil Biol. Biochem.* **2007**, *39*, 1680–1688. [[CrossRef](#)]
17. Ardley, J.K.; Reeve, W.G.; O’Hara, G.W.; Yates, R.J.; Dilworth, M.J.; Howieson, J.G. Nodule morphology, symbiotic specificity and association with unusual rhizobia are distinguishing features of the genus *Listia* within the southern African crotalariaoid clade *Lotononis* s.l. *Ann. Bot.* **2013**, *112*, 1–15. [[CrossRef](#)] [[PubMed](#)]
18. Wang, D.; Yang, S.; Tang, F.; Zhu, H. Symbiosis specificity in the legume-rhizobial mutualism. *Cell Microbiol.* **2012**, *14*, 334–342. [[CrossRef](#)] [[PubMed](#)]
19. Downie, J.A. Legume nodulation. *Curr. Biol.* **2014**, *24*, R184–R190. [[CrossRef](#)] [[PubMed](#)]
20. Oldroyd, G.E.; Downie, J.A. Coordinating nodule morphogenesis with rhizobial infection in legumes. *Ann. Rev. Plant Biol.* **2008**, *59*, 519–546. [[CrossRef](#)] [[PubMed](#)]
21. Czernic, P.; Gully, D.; Cartieaux, F.; Moulin, L.; Guefrachi, I.; Patrel, D.; Pierre, O.; Fardoux, J.; Chaintreuil, C.; Nguyen, P.; et al. Convergent evolution of endosymbiont differentiation in dalbergioid and inverted repeat-lacking clade legumes mediated by nodule specific cysteine rich peptides. *Plant Physiol.* **2015**, *169*, 1254–1265. [[CrossRef](#)] [[PubMed](#)]
22. Okubo, T.; Fukushima, S.; Minamisawa, K. Evolution of *Bradyrhizobium*–*Aeschynomene* mutualism: Living testimony of the ancient world or highly evolved state? *Plant Cell Physiol.* **2012**, *53*, 2000–2007. [[CrossRef](#)] [[PubMed](#)]
23. Bianco, L. Rhizobial infection in *Adesmia bicolor* (Fabaceae) roots. *Arch. Microbiol.* **2014**, *196*, 675–679. [[CrossRef](#)] [[PubMed](#)]
24. González-Sama, A.; Lucas, M.M.; de Felipe, M.R.; Pueyo, J.J. An unusual infection mechanism and nodule morphogenesis in white lupin (*Lupinus albus*). *New Phytol.* **2004**, *163*, 371–380. [[CrossRef](#)]
25. Martens, M.; Delaere, M.; Coopman, R.; de Vos, P.; Gillis, M.; Willems, A. Multilocus sequence analysis of *Ensifer* and related taxa. *Int. J. Syst. Evol. Microbiol.* **2007**, *57*, 489–503. [[CrossRef](#)] [[PubMed](#)]
26. Peix, A.; Ramírez-Bahena, M.H.; Velázquez, E.; Bedmar, E.J. Bacterial associations with legumes. *Crit. Rev. Plant Sci.* **2015**, *34*, 17–42. [[CrossRef](#)]
27. Lindström, K.; Aserse, A.A.; Mousavi, S.A. Evolution and Taxonomy of Nitrogen-Fixing Organisms with Emphasis on Rhizobia. In *Biological Nitrogen Fixation*, 1st ed.; de Bruijn, F.J., Ed.; Wiley & Sons, Inc.: Hoboken, NJ, USA, 2015; pp. 21–37.
28. Roche, P.; Maillet, F.; Plazanet, C.; Debelle, F.; Ferro, M.; Truchet, G.; Promé, J.-C.; Dénarié, J. The common *nodABC* genes of *Rhizobium meliloti* are host-range determinants. *Proc. Natl. Acad. Sci. USA* **1996**, *93*, 15305–15310. [[CrossRef](#)] [[PubMed](#)]
29. Masson-Boivin, C.; Giraud, E.; Perret, X.; Batut, J. Establishing nitrogen-fixing symbiosis with legumes: How many rhizobium recipes? *Trends Microbiol.* **2009**, *17*, 10. [[CrossRef](#)] [[PubMed](#)]

30. Vinuesa, P.; Silva, C.; Lorite, M.J.; Izaguirre-Mayoral, M.L.; Bedmar, E.J.; Martínez-Romero, E. Molecular systematics of rhizobia based on maximum likelihood and Bayesian phylogenies inferred from *rrs*, *atpD*, *recA* and *nifH* sequences, and their use in the classification of *Sesbania* microsymbionts from Venezuelan wetlands. *Syst. Appl. Microbiol.* **2005**, *28*, 702–716. [CrossRef] [PubMed]
31. Cummings, S.P.; Gyaneshwar, P.; Vinuesa, P.; Farruggia, F.T.; Andrews, M.; Humphry, D.; Elliott, G.N.; Nelson, A.; Orr, C.; Pettitt, D.; et al. Nodulation of *Sesbania* species by *Rhizobium* (*Agrobacterium*) strain IRBG74 and other rhizobia. *Environ. Microbiol.* **2009**, *11*, 2510–2525. [CrossRef] [PubMed]
32. Remigi, P.; Zhu, J.; Young, J.P.W.; Masson-Boivin, C. Symbiosis within symbiosis: Evolving nitrogen-fixing legume symbionts. *Trends Microbiol.* **2016**, *24*, 63–75. [CrossRef] [PubMed]
33. Giraud, E.; Moulin, L.; Vallenet, D.; Barbe, V.; Cytryn, E.; Avarre, J.C.; Jaubert, M.; Simon, D.; Cartieaux, F.; Prin, Y.; et al. Legumes symbioses: Absence of *Nod* genes in photosynthetic bradyrhizobia. *Science* **2007**, *316*, 1307–1312. [CrossRef] [PubMed]
34. Miché, L.; Moulin, L.; Chaintreuil, C.; Contreras-Jimenez, J.L.; Munive-Hernández, J.-A.; del Villegas-Hernandez, M.C.; Crozier, F.; Béna, G. Diversity analyses of *Aeschynomene* symbionts in tropical Africa and central America reveal that *nod*-independent stem nodulation is not restricted to photosynthetic bradyrhizobia. *Symbiosis* **2010**, *12*, 2152–2164.
35. Benata, H.; Mohammed, O.; Noureddine, B.; Abdelbasset, B.; Abdelmoumen, H.; Muresu, R.; Squartini, A.; El Idrissi, M.M. Diversity of bacteria that nodulate *Prosopis juliflora* in the eastern area of Morocco. *Syst. Appl. Microbiol.* **2008**, *31*, 378–386. [CrossRef]
36. Hassen, A.I.; Bopape, F.L.; Habig, J.; Lamprecht, S.C. Nodulation of rooibos (*Aspalathus linearis* Burm. f.), an indigenous South African legume, by members of both the α -proteobacteria and β -proteobacteria. *Biol. Fertil. Soils* **2012**, *48*, 295–303. [CrossRef]
37. Shiraishi, A.; Matsushita, N.; Hougetsu, T. Nodulation in black locust by the γ -proteobacteria *Pseudomonas* sp. and the β -proteobacteria *Burkholderia* sp. *Syst. Appl. Microbiol.* **2010**, *33*, 269–274. [CrossRef] [PubMed]
38. Huang, B.; Lv, C.; Zhao, Y.; Huang, R. A novel strain D5 isolated from *Acacia confusa*. *PLoS ONE* **2012**, *7*, e49236. [CrossRef] [PubMed]
39. Ampomah, O.Y.; Huss-Danell, K. Genetic diversity of root nodule bacteria nodulating *Lotus corniculatus* and *Anthyllis vulneraria* in Sweden. *Syst. Appl. Microbiol.* **2011**, *34*, 267–275. [CrossRef]
40. Manassila, M.; Nuntagij, A.; Kotepong, S.; Boonkerd, N.; Teamroong, N. Characterization and monitoring of selected rhizobial strains isolated from tree legumes in Thailand. *Afr. J. Biotechnol.* **2007**, *6*, 1393–1402.
41. Le Roux, C.; Tentchev, D.; Prin, Y.; Goh, D.; Japarudin, Y.; Perrineau, M.-M.; Duponnois, R.; Domergue, O.; de Lajudie, P.; Galiana, A. Bradyrhizobia nodulating the *Acacia mangium* \times *A. auriculiformis* interspecific hybrid are specific and differ from those associated with both parental species. *Appl. Environ. Microbiol.* **2009**, *75*, 7752–7759. [CrossRef] [PubMed]
42. Helene, L.C.F.; Delamuta, J.R.M.; Ribeiro, R.A.; Ormeño-Orrillo, E.; Rogel, M.A.; Martínez-Romero, E.; Hungria, M. *Bradyrhizobium viridifuturi* sp. nov., encompassing nitrogen-fixing symbionts of legumes used for green manure and environmental services. *Int. J. Syst. Evol. Microbiol.* **2015**, *65*, 4441–4448. [CrossRef] [PubMed]
43. Sinsu Wongwat, S.; Nuntagij, A.; Shuttsirung, A.; Nomura, M.; Tajima, S. Characterization of local rhizobia in Thailand and distribution of malic enzymes. *Soil Sci. Plant Nutr.* **2002**, *48*, 719–727. [CrossRef]
44. Ngom, A.; Nakagawa, Y.; Sawada, H.; Tsukahara, J.; Wakabayashi, S.; Uchiumi, T.; Nuntagij, A.; Kotepong, S.; Suzuki, A.; Higashi, S.; et al. A novel symbiotic nitrogen-fixing member of the *Ochrobactrum* clade isolated from root nodules of *Acacia mangium*. *J. Gen. Appl. Microbiol.* **2004**, *50*, 17–27. [CrossRef] [PubMed]
45. Lortet, G.; Méar, N.; Lorquin, J.; Dreyfus, B.; de Lajudie, P.; Rosenberg, C.; Boivin, C. Nod factor thin-layer chromatography profiling as a tool to characterize symbiotic specificity of rhizobial strains: Application to *Sinorhizobium saheli*, *S. teranga*, and *Rhizobium* sp. strains isolated from Acacia and Sesbania. *Mol. Plant Microbe Interact.* **1996**, *9*, 736–747. [CrossRef]
46. Räsänen, L.A.; Sprent, J.I.; Lindström, K. Symbiotic properties of sinorhizobia isolated from *Acacia* and *Prosopis* nodules in Sudan and Senegal. *Plant Soil* **2001**, *235*, 193–210. [CrossRef]
47. Lu, J.K.; Dou, Y.J.; Zhu, Y.J.; Wang, S.K.; Sui, X.H.; Kang, L.H. *Bradyrhizobium ganzhouense* sp. nov., an effective symbiotic bacterium isolated from *Acacia melanoxylon* R. Br. nodules. *Int. J. Syst. Evol. Microbiol.* **2014**, *64*, 1900–1905. [CrossRef] [PubMed]

48. Marsudi, N.D.S.; Glenn, A.R.; Dilworth, M.J. Identification and characterization of fast- and slow-growing root nodule bacteria from South-Western Australian soils able to nodulate *Acacia saligna*. *Soil Biol. Biochem.* **1999**, *31*, 1229–1238. [[CrossRef](#)]
49. Khbaya, B.; Neyra, M.; Normand, P.; Zerhari, K.; Filali-Maltouf, A. Genetic diversity and phylogeny of rhizobia that nodulate *Acacia* spp. in Morocco assessed by analysis of rRNA genes. *Appl. Environ. Microbiol.* **1998**, *64*, 4912–4917. [[PubMed](#)]
50. Lloret, L.; Ormeño-Orrillo, E.; Rincón, R.; Martínez-Romero, J.; Rogel-Hernández, M.A.; Martínez-Romero, E. *Ensifer mexicanus* sp. nov. a new species nodulating *Acacia angustissima* (Mill.) Kuntze in Mexico. *Syst. Appl. Microbiol.* **2007**, *30*, 280–290. [[CrossRef](#)] [[PubMed](#)]
51. Rincón-Rosales, R.; Lloret, L.; Ponce, E.; Martínez-Romero, E. Rhizobia with different symbiotic efficiencies nodulate *Acaciella angustissima* in Mexico, including *Sinorhizobium chiapanecum* sp. nov. which has common symbiotic genes with *Sinorhizobium mexicanum*. *FEMS Microbiol. Ecol.* **2009**, *67*, 103–117. [[CrossRef](#)] [[PubMed](#)]
52. Bala, A.; Giller, K.E. Symbiotic specificity of tropical tree rhizobia for host legumes. *New Phytol.* **2001**, *149*, 495–507. [[CrossRef](#)]
53. Rincón-Rosales, R.; Villalobos-Escobedo, J.M.; Rogel, M.A.; Martínez, J.; Ormeño-Orrillo, E.; Martínez-Romero, E. *Rhizobium calliandrae* sp. nov., *Rhizobium mayense* sp. nov. and *Rhizobium jaguaris* sp. nov., rhizobial species nodulating the medicinal legume *Calliandra grandiflora*. *Int. J. Syst. Evol. Microbiol.* **2013**, *63*, 3423–3429. [[CrossRef](#)] [[PubMed](#)]
54. Odee, D.W.; Haukka, K.; McInroy, S.G.; Sprent, J.I.; Sutherland, J.M.; Young, J.P.W. Genetic and symbiotic characterization of rhizobia isolated from tree and herbaceous legumes grown in soils from ecologically diverse sites in Kenya. *Soil Biol. Biochem.* **2002**, *34*, 801–811. [[CrossRef](#)]
55. Leblanc, H.A.; McGraw, R.L.; Nygren, P.; Le Roux, C. Neotropical legume tree *Inga edulis* forms N₂-fixing symbiosis with fast-growing *Bradyrhizobium* strains. *Plant Soil* **2005**, *275*, 123–133. [[CrossRef](#)]
56. Da Silva, K.; de Meyer, S.E.; Rouws, L.F.M.; Farias, E.N.C.; dos Santos, M.A.O.; O'Hara, G.; Ardley, J.K.; Willems, A.; Pitard, R.M.; Zilli, J.E. *Bradyrhizobium ingae* sp. nov., isolated from effective nodules of *Inga laurina* grown in Cerrado soil. *Int. J. Syst. Evol. Microbiol.* **2014**, *64*, 3395–3401. [[CrossRef](#)] [[PubMed](#)]
57. Toledo, I.; Lloret, L.; Martínez-Romero, E. *Sinorhizobium americanus* sp. nov., a new *Sinorhizobium* species nodulating native *Acacia* spp. in Mexico. *Syst. Appl. Microbiol.* **2003**, *26*, 54–64. [[CrossRef](#)] [[PubMed](#)]
58. Fall, D.; Diouf, D.; Ourarhi, M.; Faye, A.; Abdelmounen, H.; Neyra, M.; Sylla, S.N.; Missbah el Idrissi, M. Phenotypic and genotypic characteristics of *Acacia Senegal* (L.) Willd. root-nodulating bacteria isolated from soils in the dryland part of Senegal. *Lett. Appl. Microbiol.* **2008**, *47*, 85–97. [[CrossRef](#)] [[PubMed](#)]
59. Bournaud, C.; de Faria, S.M.; dos Santos, J.M.F.; Tisseyre, P.; Silva, M.; Chaintreuil, C.; Gross, E.; James, E.K.; Prin, Y.; Moulin, L. *Burkholderia* species are the most common and preferred nodulating symbionts of the Piptadenia group (Tribe Mimoseae). *PLoS ONE* **2013**, *8*, e63478. [[CrossRef](#)] [[PubMed](#)]
60. Beyhaut, E.; Tlusty, B.; van Berkum, P.; Graham, P.H. *Rhizobium giardinii* is the microsymbiont of Illinois bundleflower (*Desmanthus illinoensis* (Michx.) Mcmillan) in Midwestern prairies. *Can. J. Microbiol.* **2006**, *52*, 903–907. [[CrossRef](#)] [[PubMed](#)]
61. Fornasero, L.V.; del Papa, M.F.; López, J.L.; Albicoro, F.J.; Zabala, J.M.; Toniutti, M.A.; Pensiero, J.F.; Lagares, A. Phenotypic, molecular and symbiotic characterization of the rhizobial symbionts of *Desmanthus paspalaceus* (Lindm.) Burkart that grow in the province of Santa Fe, Argentina. *PLoS ONE* **2014**, *9*, e104636. [[CrossRef](#)] [[PubMed](#)]
62. Wang, E.T.; Martínez-Romero, J.; Martínez-Romero, E. Genetic diversity of rhizobia from *Leucaena leucocephala* nodules in Mexican soils. *Mol. Ecol.* **1999**, *8*, 711–724. [[CrossRef](#)]
63. Xu, K.W.; Penttinen, P.; Chen, Y.X.; Chen, Q.; Zhang, X. Symbiotic efficiency and phylogeny of the rhizobia isolated from *Leucaena leucocephala* in arid-hot river valley area in Panxi, Sichuan, China. *Appl. Microbiol. Biotechnol.* **2013**, *97*, 783–793. [[CrossRef](#)] [[PubMed](#)]
64. López-López, A.; Rogel-Hernández, M.A.; Baroisi, I.; Ortíz Ceballos, A.I.; Martínez, J.; Ormeño-Orrillo, E.; Martínez-Romero, E. *Rhizobium grahamii* sp. nov., from nodules of *Dalea leporina*, *Leucaena leucocephala* and *Clitoria ternatea*, and *Rhizobium mesoamericanum* sp. nov., from nodules of *Phaseolus vulgaris*, siratro, cowpea and *Mimosa pudica*. *Int. J. Syst. Evol. Microbiol.* **2012**, *62*, 2264–2271. [[CrossRef](#)] [[PubMed](#)]
65. Chen, W.-M.; Moulin, L.; Bontemps, C.; Vandamme, P.; Béna, G.; Boivin-Masson, C. Legume symbiotic nitrogen fixation by β-proteobacteria is widespread in nature. *J. Bacteriol.* **2003**, *185*, 7266–7272. [[CrossRef](#)] [[PubMed](#)]

66. Chen, W.-M.; de Faria, S.M.; Straliotto, R.; Pitard, R.M.; Simões-Araújo, J.L.; Chou, J.-H.; Chou, Y.-J.; Barrios, E.; Prescott, A.R.; Elliott, G.N.; et al. Proof that *Burkholderia* strains form effective symbioses with legumes: A study of novel *Mimosa*-nodulating strains from South America. *Appl. Environ. Microbiol.* **2005**, *71*, 7461–7471. [CrossRef] [PubMed]
67. Chen, W.-M.; James, E.K.; Chou, J.-H.; Sheu, S.-Y.; Yang, S.-Z.; Sprent, J.I. β -Rhizobia from *Mimosa pigra*, a newly discovered invasive plant in Taiwan. *New Phytol.* **2005**, *168*, 661–675. [CrossRef] [PubMed]
68. Barrett, C.F.; Parker, M.A. Prevalence of *Burkholderia* sp. nodule symbionts on four mimosoid legumes from Barro Colorado Island, Panama. *Syst. Appl. Microbiol.* **2005**, *28*, 57–65. [CrossRef] [PubMed]
69. Barrett, C.F.; Parker, M.A. Coexistence of *Burkholderia*, *Cupriavidus*, and *Rhizobium* sp. nodule bacteria on two *Mimosa* spp. in Costa Rica. *Appl. Environ. Microbiol.* **2006**, *72*, 1198–1206. [CrossRef] [PubMed]
70. Liu, X.Y.; Wang, E.T.; Li, Y.; Chen, W.X. Diverse bacteria isolated from root nodules of *Trifolium*, *Crotalaria* and *Mimosa* grown in the subtropical regions of China. *Arch. Microbiol.* **2007**, *188*, 1–14. [CrossRef] [PubMed]
71. Parker, M.A.; Wurtz, A.K.; Paynter, Q. Nodule symbiosis of invasive *Mimosa pigra* in Australia and in ancestral habitats: A comparative analysis. *Biol. Invasions* **2007**, *9*, 127–138. [CrossRef]
72. Elliott, G.N.; Chou, J.-H.; Chen, W.-M.; Bloemberg, G.V.; Bontemps, C.; Martínez-Romero, E.; Velázquez, E.; Young, J.P.W.; Sprent, J.I.; James, E.K. *Burkholderia* spp. are the most competitive symbionts of *Mimosa*, particularly under N-limited conditions. *Environ. Microbiol.* **2009**, *11*, 762–778. [CrossRef] [PubMed]
73. Bontemps, C.; Elliott, G.N.; Simon, M.F.; dos Reis, F.B., Jr.; Gross, E.; Lawton, R.C.; Neto, N.E.; Loureiro, M.deF.; de Faria, S.M.; Sprent, J.I.; et al. *Burkholderia* species are ancient symbionts of legumes. *Mol. Ecol.* **2010**, *19*, 44–52. [CrossRef] [PubMed]
74. Bontemps, C.; Rogel, M.A.; Wiechmann, A.; Mussabekova, A.; Moody, S.; Simon, M.F.; Moulin, L.; Elliott, G.N.; Lacercat-Didier, L.; Dasilva, C.; et al. Endemic *Mimosa* species from Mexico prefer α -proteobacterial rhizobial symbionts. *New Phytol.* **2016**, *209*, 319–333. [CrossRef] [PubMed]
75. Liu, X.Y.; Wu, W.; Wang, E.T.; Zhang, B.; Macdermott, J.; Chen, W.X. Phylogenetic relationships and diversity of β -rhizobia associated with *Mimosa* species grown in Sishuangbanna, China. *Int. J. Syst. Evol. Microbiol.* **2011**, *61*, 334–342. [CrossRef] [PubMed]
76. Liu, X.Y.; Wei, S.; Wang, F.; James, E.K.; Guo, X.Y.; Zagar, C.; Xia, L.G.; Dong, X.; Wang, Y.P. *Burkholderia* and *Cupriavidus* spp. are the preferred symbionts of *Mimosa* spp. in Southern China. *FEMS Microbiol. Ecol.* **2012**, *80*, 417–426. [CrossRef] [PubMed]
77. Gehlot, H.S.; Tak, N.; Kaushik, M.; Mitra, S.; Chen, W.-M.; Poweleit, N.; Panwar, D.; Poonar, N.; Parihar, R.; Tak, A.; et al. An invasive *Mimosa* in India does not adopt the symbionts of its native relatives. *Ann. Bot.* **2013**, *112*, 179–196. [CrossRef] [PubMed]
78. Andam, C.P.; Mondo, S.J.; Parker, M.A. Monophyly of *nodA* and *nifH* genes across Texan and Costa Rican populations of *Cupriavidus* nodule symbionts. *Appl. Environ. Microbiol.* **2007**, *73*, 4686–4690. [CrossRef] [PubMed]
79. Platero, R.; James, E.K.; Rios, C.; Iriarte, A.; Sandes, L.; Zabaleta, M.; Battistoni, F.; Fabiano, E. Novel *Cupriavidus* strains isolated from root nodules of native Uruguayan *Mimosa* species. *Appl. Environ. Microbiol.* **2016**, *82*, 3150–3164. [CrossRef] [PubMed]
80. De Lajudie, P.; Laurent-Fulele, E.; Willemse, A.; Torck, U.; Coopman, R.; Collins, M.D.; Kersters, K.; Dreyfus, B.; Gillis, M. *Allorhizobium undicola* gen. nov., sp. nov., nitrogen-fixing bacteria that efficiently nodulate *Neptunia natans* in Senegal. *Int. J. Syst. Bacteriol.* **1998**, *48*, 1277–1290. [CrossRef] [PubMed]
81. Rivas, R.; Velázquez, E.; Willemse, A.; Vizcaíno, N.; Subba-Rao, N.S.; Mateos, P.F.; Gillis, M.; Dazzo, F.B.; Martínez-Molina, E. A new species of *Devosia* that forms a unique nitrogen-fixing root-nodule symbiosis with the aquatic legume *Neptunia natans* (L.f.) Druce. *Appl. Environ. Microbiol.* **2002**, *68*, 5217–5222. [CrossRef] [PubMed]
82. Taulé, C.; Zabaleta, M.; Mareque, C.; Platero, R.; Sanjurjo, L.; Sicardi, M.; Frioni, L.; Battistoni, F.; Fabiano, E. New β -proteobacterial *Rhizobium* strains able to efficiently nodulate *Parapiptadenia rigida* (Benth.) Brenan. *Appl. Environ. Microbiol.* **2012**, *78*, 1692–1700. [CrossRef] [PubMed]
83. Diaz, L.C.; González, P.; Rubio, E.; Melchiorre, M. Diversity and stress tolerance in rhizobia from Parque Chaqueño region of Argentina nodulating *Prosopis alba*. *Biol. Fertil. Soils* **2013**, *49*, 1153–1165. [CrossRef]
84. Iglesias, O.; Rivas, R.; García-Fraile, P.; Abril, A.; Mateos, P.F.; Martínez-Molina, E.; Velázquez, E. Genetic characterization of fast-growing rhizobia able to nodulate *Prosopis alba* in North Spain. *FEMS Microbiol. Lett.* **2007**, *277*, 210–216. [CrossRef] [PubMed]

85. Velázquez, E.; Igual, J.M.; Willems, A.; Fernández, M.P.; Muñoz, E.; Mateos, P.F.; Abril, A.; Toro, N.; Normand, P.; Cervantes, E.; et al. *Mesorhizobium chacoense* sp. nov., a novel species that nodulates *Prosopis alba* in the Chaco Arido region (Argentina). *Int. J. Syst. Evol. Microbiol.* **2001**, *51*, 1011–1021.
86. Nick, G.; de Lajudie, P.; Eardly, B.D.; Suomalainen, S.; Paulin, L.; Zhang, X.; Gillis, M.; Lindström, K. *Sinorhizobium arboris* sp. nov. and *Sinorhizobium kostiense* sp. nov., isolated from leguminous trees in Sudan and Kenya. *Int. J. Syst. Bacteriol.* **1999**, *49*, 1359–1368. [CrossRef] [PubMed]
87. Gehlot, H.S.; Panwar, D.; Tak, N.; Tak, A.; Sankhla, I.S.; Poonar, N.; Parihar, R.; Shekhawat, N.S.; Kumar, M.; Tiwari, R.; et al. Nodulation of legumes from the Thar desert of India and molecular characterization of their rhizobia. *Plant Soil* **2012**, *357*, 227–243. [CrossRef]
88. Fterich, A.; Mahdhi, M.; Caviedes, M.A.; Pajuelo, E.; Rivas, R.; Rodriguez-Llorente, I.D.; Mars, M. Characterization of root-nodulating bacteria associated to *Prosopis farcta* growing in the arid regions of Tunisia. *Arch. Microbiol.* **2011**, *193*, 385–397. [CrossRef] [PubMed]
89. Degefu, T.; Wolde-meskel, E.; Frostegård, Å. Multilocus sequence analyses reveal several unnamed *Mesorhizobium* genospecies nodulating *Acacia* species and *Sesbania sesban* trees in Southern regions of Ethiopia. *Syst. Appl. Microbiol.* **2011**, *34*, 216–226. [CrossRef] [PubMed]
90. Degefu, T.; Wolde-meskel, E.; Frostegård, Å. Phylogenetic multilocus sequence analysis identifies seven novel *Ensifer* genospecies isolated from a less-well-explored biogeographical region in East Africa. *Int. J. Syst. Evol. Microbiol.* **2012**, *62*, 2286–2295. [CrossRef]
91. Sankhla, I.S.; Tak, N.; Meghwal, R.R.; Choudhary, S.; Tak, A.; Rathi, S.; Sprent, J.I.; James, E.K.; Gehlot, H.S. Molecular characterization of nitrogen fixing microsymbionts from root nodules of *Vachellia (Acacia) jacquemontii*, a native legume from the Thar Desert of India. *Plant Soil* **2017**, *410*, 21–40. [CrossRef]
92. Cordero, I.; Ruiz-Díez, B.; de la Peña, T.C.; Balaguer, L.; Lucas, M.M.; Rincón, A.; Pueyo, J.J. Rhizobial diversity, symbiotic effectiveness and structure of nodules of *Vachellia macracantha*. *Soil Biol. Biochem.* **2016**, *96*, 39–54. [CrossRef]
93. Ba, S.; Willems, A.; de Lajudie, P.; Roche, P.; Jeder, H.; Quatrini, P.; Neyra, M.; Ferro, M.; Promé, J.-C.; Gillis, M.; et al. Symbiotic and taxonomic diversity of rhizobia isolated from *Acacia tortilis* sp. subsp. *raddiana* in Africa. *Syst. Appl. Microbiol.* **2002**, *25*, 130–145. [CrossRef] [PubMed]
94. Nour, S.M.; Fernandez, M.P.; Normand, P.; Cleyet-Marel, J.-C. *Rhizobium ciceri* sp. nov., consisting of strains that nodulate chickpeas (*Cicer arietinum* L.). *Int. J. Syst. Bacteriol.* **1994**, *44*, 511–522. [CrossRef] [PubMed]
95. Aouani, M.E.; Mhamdi, R.; Jebara, M.; Amarger, N. Characterization of rhizobia nodulating chickpea in Tunisia. *Agronomie* **2001**, *21*, 577–581. [CrossRef]
96. Maâtallah, J.; Berraho, E.B.; Muñoz, S.; Sanjuan, J.; Lluch, C. Phenotypic and molecular characterization of chickpea rhizobia isolated from different areas of Morocco. *J. Appl. Microbiol.* **2002**, *93*, 531–540. [CrossRef] [PubMed]
97. Rivas, R.; Laranjo, M.; Mateos, P.F.; Oliveira, S.; Martínez-Molina, E.; Velázquez, E. Strains of *Mesorhizobium amorphae* and *Mesorhizobium tianshanense*, carrying symbiotic genes of common chickpea endosymbiotic species, constitute a novel biovar (*ciceri*) capable of nodulating *Cicer arietinum*. *Lett. Appl. Microbiol.* **2007**, *44*, 412–418. [CrossRef] [PubMed]
98. Ben Romdhane, S.; Trabelsi, M.; Aouani, M.E.; de Lajudie, P.; Mhamdi, R. The diversity of rhizobia nodulating chickpea (*Cicer arietinum*) under water deficiency as a source of more efficient inoculants. *Soil Biol. Biochem.* **2009**, *41*, 2568–2572. [CrossRef]
99. Zhang, J.J.; Lou, K.; Jin, X.; Mao, P.H.; Wang, E.T.; Tian, C.F.; Sui, X.H.; Chen, W.F.; Chen, W.X. Distinctive *Mesorhizobium* populations associated with *Cicer arietinum* L. in alkaline soils of Xinjiang, China. *Plant Soil* **2012**, *353*, 123–134. [CrossRef]
100. Zhang, J.; Yang, X.; Guo, C.; de Lajudie, P.; Singh, R.P.; Wang, E.; Chen, W. *Mesorhizobium muleiense* and *Mesorhizobium* gsp. Nov. are symbionts of *Cicer arietinum* L. in alkaline soils of Gansu, Northwest China. *Plant Soil* **2017**, *410*, 103–112. [CrossRef]
101. Zahran, H.H.; Chahboun, R.; Moreno, S.; Bedmar, E.J.; Abdel-Fattah, M.; Yasser, M.M.; Mahmoud, A.M. Identification of rhizobial strains nodulating Egyptian grain legumes. *Int. Microbiol.* **2013**, *16*, 157–163. [PubMed]

102. Armas-Carpote, N.; Pérez-Yépez, J.; Martínez-Hidalgo, P.; Garzón-Machado, V.; del Arco-Aguilar, M.; Velázquez, E.; Léon-Barrios, M. Core and symbiotic genes reveal nine *Mesorhizobium* genospecies and three symbiotic lineages among the rhizobia nodulating *Cicer canariense* in its natural habitat (La Palma, Canary Islands). *Syst. Appl. Microbiol.* **2014**, *37*, 140–148. [CrossRef] [PubMed]
103. Mutch, L.A.; Young, J.P.W. Diversity and specificity of *Rhizobium leguminosarum* biovar *viciae* on wild and cultivated legumes. *Mol. Ecol.* **2004**, *13*, 2435–2444. [CrossRef] [PubMed]
104. Aoki, S.; Kondo, T.; Prévost, D.; Nakata, S.; Kajita, T.; Itó, M. Genotypic and phenotypic diversity of rhizobia isolated from *Lathyrus japonicus* indigenous to Japan. *Syst. Appl. Microbiol.* **2010**, *33*, 383–397. [CrossRef] [PubMed]
105. Han, T.X.; Wang, E.T.; Wu, L.J.; Chen, W.F.; Gu, J.G.; Gu, C.T.; Tian, C.F.; Chen, W.X. *Rhizobium multihospitium* sp. nov., isolated from multiple legume species native of Xinjiang, China. *Int. J. Syst. Evol. Microbiol.* **2008**, *58*, 1693–1699. [CrossRef] [PubMed]
106. Rashid, M.H.; Schäfer, H.; Gonzalez, J.; Wink, M. Genetic diversity of rhizobia nodulating lentil (*Lens culinaris*) in Bangladesh. *Syst. Appl. Microbiol.* **2012**, *35*, 98–109. [CrossRef] [PubMed]
107. Riah, N.; Béna, G.; Djekoun, A.; Heulin, K.; de Lajudie, P.; Laguerre, G. Genotypic and symbiotic diversity of *Rhizobium* populations associated with cultivated lentil and pea in sub-humid and semi-arid regions of Eastern Algeria. *Syst. Appl. Microbiol.* **2014**, *37*, 368–375. [CrossRef] [PubMed]
108. Zhang, Y.J.; Zheng, W.T.; Everall, I.; Young, J.P.W.; Zhang, X.X.; Tian, C.F.; Sui, X.H.; Wang, E.T.; Chen, W.X. *Rhizobium anhuiense* sp. nov., isolated from effective nodules of *Vicia faba* and *Pisum sativum*. *Int. J. Syst. Evol. Microbiol.* **2015**, *65*, 2960–2967. [CrossRef] [PubMed]
109. Kan, F.L.; Chen, Z.Y.; Wang, E.T.; Tian, C.F.; Sui, X.H.; Chen, W.X. Characterization of symbiotic and endophytic bacteria isolated from root nodules of herbaceous legumes grown in Qinghai-Tibet plateau and in other zones of China. *Arch. Microbiol.* **2007**, *188*, 103–115. [CrossRef] [PubMed]
110. Ampomah, O.Y.; Huss-Danell, K. Genetic diversity of rhizobia nodulating native *Vicia* spp. in Sweden. *Syst. Appl. Microbiol.* **2016**, *39*, 203–210. [CrossRef] [PubMed]
111. Santillana, N.; Ramírez-Bahena, M.H.; García-Fraile, P.; Velázquez, E.; Zúñiga, D. Phylogenetic diversity based on *rrs*, *atpD*, *recA* genes and 16S–23S intergenic sequence analyses of rhizobial strains isolated from *Vicia faba* and *Pisum sativum* in Peru. *Arch. Microbiol.* **2008**, *189*, 239–247. [CrossRef]
112. Saïdi, S.; Chebil, S.; Gtari, M.; Mhamdi, R. Characterization of root-nodule bacteria isolated from *Vicia faba* and selection of plant growth promoting isolates. *World J. Microbiol. Biotechnol.* **2013**, *29*, 1099–1106. [CrossRef] [PubMed]
113. Youseif, S.H.; Abd El-Megeed, F.H.; Ageez, A.; Cocking, E.C.; Saleh, S.A. Phylogenetic multilocus sequence analysis of native rhizobia nodulating faba bean (*Vicia faba* L.) in Egypt. *Syst. Appl. Microbiol.* **2014**, *37*, 560–569. [CrossRef] [PubMed]
114. Xu, K.W.; Zou, L.; Penttiläinen, P.; Wang, K.; Heng, N.N.; Zhang, X.P.; Chen, Q.; Zhao, K.; Chen, Y.X. Symbiotic effectiveness and phylogeny of rhizobia isolated from faba bean (*Vicia faba* L.) in Sichuan hilly areas, China. *Syst. Appl. Microbiol.* **2015**, *38*, 515–523. [CrossRef] [PubMed]
115. Lei, X.; Wang, E.T.; Chen, W.F.; Sui, X.H.; Chen, W.X. Diverse bacteria isolated from root nodules of wild *Vicia* species grown in temperate region of China. *Arch. Microbiol.* **2008**, *190*, 657–671. [CrossRef] [PubMed]
116. Tian, C.F.; Wang, E.T.; Wu, L.J.; Han, T.X.; Chen, W.F.; Gu, C.T.; Gu, J.G.; Chen, W.X. *Rhizobium fabae* sp. nov., a bacterium that nodulates *Vicia faba*. *Int. J. Syst. Evol. Microbiol.* **2008**, *58*, 2871–2875. [CrossRef] [PubMed]
117. Alvarez-Martínez, E.R.; Valverde, Á.; Ramírez-Bahena, M.H.; García-Fraile, P.; Tejedor, C.; Mateos, P.F.; Santillana, N.; Zúñiga, D.; Peix, A.; Velázquez, E. The analysis of core and symbiotic genes of rhizobia nodulating *Vicia* from different continents reveals their common phylogenetic origin and suggests the distribution of *Rhizobium leguminosarum* strains together with *Vicia* seeds. *Arch. Microbiol.* **2009**, *191*, 659–668. [CrossRef] [PubMed]
118. Rejili, M.; Mahdhi, M.; Fterich, A.; Dhaoui, S.; Guefrachi, I.; Abdeddayem, R.; Mars, M. Symbiotic nitrogen fixation of wild legumes in Tunisia: Soil fertility dynamics, field nodulation and nodules effectiveness. *Agric. Ecosyst. Environ.* **2012**, *157*, 60–69. [CrossRef]
119. Radeva, G.; Jurgens, G.; Niemi, M.; Nick, G.; Suominen, L.; Lindström, K. Description of two biovars in the *Rhizobium galegae* species: Biovar *orientalis* and biovar *officinalis*. *System. Appl. Microbiol.* **2001**, *24*, 192–205. [CrossRef] [PubMed]

120. Liu, W.Y.Y.; Ridgway, H.J.; James, T.K.; Premaratne, M.; Andrews, M. Characterisation of rhizobia nodulating *Galega officinalis* (goat's rue) and *Hedysarum coronarium* (sulla). *NZ Plant Prot.* **2012**, *65*, 192–196.
121. Chen, W.; Sun, L.; Lu, J.; Bi, L.; Wang, E.; Wei, G. Diverse nodule bacteria were associated with *Astragalus* species in arid region of northwestern China. *J. Basic Microbiol.* **2015**, *55*, 121–128. [CrossRef] [PubMed]
122. Wei, G.H.; Zhang, Z.X.; Chen, C.; Chen, W.M.; Ju, W.T. Phenotypic and genetic diversity of rhizobia isolated from nodules of the legume genera *Astragalus*, *Lespedeza* and *Hedysarum* in northwestern China. *Microbial. Res.* **2008**, *163*, 651–662. [CrossRef] [PubMed]
123. Zhao, C.T.; Wang, E.T.; Zhang, Y.M.; Chen, W.F.; Sui, X.H.; Chen, W.X.; Liu, H.C.; Zhang, X.X. *Mesorhizobium silamurunense* sp. nov., isolated from root nodules of *Astragalus* species. *Int. J. Syst. Evol. Microbiol.* **2012**, *62*, 2180–2186. [CrossRef] [PubMed]
124. Yan, H.; Ji, Z.J.; Jiao, Y.S.; Wang, E.T.; Chen, W.F.; Guo, B.L.; Chen, W.X. Genetic diversity and distribution of rhizobia associated with the medicinal legumes *Astragalus* spp. and *Hedysarum polybotrys* in agricultural soils. *Syst. Appl. Microbiol.* **2016**, *39*, 141–149. [CrossRef] [PubMed]
125. Nandasena, K.G.; O'Hara, G.W.; Tiwari, R.P.; Yates, R.J.; Howieson, J.G. Phylogenetic relationships of three bacterial strains isolated from the pasture legume *Biserrula pelecinus* L. *Int. J. Syst. Evol. Microbiol.* **2001**, *51*, 1983–1986. [CrossRef] [PubMed]
126. Nandasena, K.G.; O'Hara, G.W.; Tiwari, R.P.; Willems, A.; Howieson, J.G. *Mesorhizobium australicum* sp. nov. and *Mesorhizobium opportunistum* sp. nov., isolated from *Biserrula pelecinus* L. in Australia. *Int. J. Syst. Evol. Microbiol.* **2009**, *59*, 2140–2147. [CrossRef] [PubMed]
127. Tan, H.W.; Weir, B.S.; Carter, N.; Heenan, P.B.; Ridgway, H.J.; James, E.K.; Sprent, J.I.; Young, J.P.Y.; Andrews, M. Rhizobia with 16S rRNA and *nifH* similar to *Mesorhizobium huakuii* but novel *recA*, *glnN1*, *nodA* and *nodC* genes are symbionts of New Zealand Carmichaelinae. *PLoS ONE* **2012**, *7*, e47677. [CrossRef] [PubMed]
128. Ourarhi, M.; Abdelmoumen, H.; Guerrouj, K.; Benata, H.; Muresu, R.; Squartini, A.; El Idrissi, M.M. *Colutea arborescens* is nodulated by diverse rhizobia in Eastern Morocco. *Arch. Microbiol.* **2011**, *193*, 115–124. [CrossRef] [PubMed]
129. Ruiz-Díez, B.; Fajardo, S.; Puertas-Mejía, M.A.; del Felipe, M.R.; Fernández-Pascual, M. Stress tolerance, genetic analysis and symbiotic properties of root-nodulating bacteria isolated from Mediterranean leguminous shrubs in Central Spain. *Arch. Microbiol.* **2009**, *191*, 35–46. [CrossRef] [PubMed]
130. Li, L.; Sinkko, H.; Montonen, L.; Wei, G.; Lindström, K.; Räsänen, L.A. Biogeography of symbiotic and other endophytic bacteria isolated from medicinal *Glycyrrhiza* species in China. *FEMS Microbiol. Ecol.* **2012**, *79*, 46–68. [CrossRef] [PubMed]
131. Wei, G.H.; Yang, X.-Y.; Zhang, Z.-X.; Yang, Y.-Z.; Lindström, K. Strain *Mesorhizobium* sp. CCNWGX035: A stress-tolerant isolate from *Glycyrrhiza glabra* displaying a wide host range of nodulation. *Pedosphere* **2008**, *18*, 102–112. [CrossRef]
132. Tan, Z.Y.; Wang, E.T.; Peng, G.X.; Zhu, M.E.; Martínez-Romero, E.; Chen, W.X. Characterization of bacteria isolated from wild legumes in the north-western regions of China. *Int. J. Syst. Bacteriol.* **1999**, *49*, 1457–1469. [CrossRef] [PubMed]
133. Chen, W.; Wang, E.; Wang, S.; Li, Y.; Chen, X.; Li, Y. Characteristics of *Rhizobium tianshanense* sp. nov., a moderately and slowly growing root nodule bacterium isolated from an arid saline environment in Xinjiang, People's Republic of China. *Int. J. Syst. Bacteriol.* **1995**, *45*, 153–159. [CrossRef] [PubMed]
134. Tan, Z.Y.; Kan, F.L.; Peng, G.X.; Wang, E.T.; Reinhold-Hurek, B.; Chen, W.X. *Rhizobium yanglingense* sp. nov., isolated from arid and semi-arid regions in China. *Int. J. Syst. Evol. Microbiol.* **2001**, *51*, 909–914. [CrossRef] [PubMed]
135. Gerding, M.; O'Hara, G.W.; Bräu, L.; Nandasena, K.; Howieson, J.G. Diverse *Mesorhizobium* spp. with unique *nodA* nodulating the South African legume species of the genus *Lessertia*. *Plant Soil* **2012**, *358*, 385–401. [CrossRef]
136. Lemaire, B.; Dlodlo, O.; Chimphango, S.; Stirton, C.; Schrire, B.; Boatwright, J.S.; Honnay, O.; Smets, E.; Sprent, J.; James, E.K.; et al. Symbiotic diversity, specificity and distribution of rhizobia in native legumes of the Core Cape Subregion (South Africa). *FEMS Microbiol. Ecol.* **2015**, *91*, 1–17. [CrossRef] [PubMed]
137. Tan, H.W.; Heenan, P.; Ridgway, H.; Andrews, M. The New Zealand alpine endemic *Montigena novae-zelandiae* (Fabaceae) shares rhizobial symbionts with *Carmichaelia* and *Clianthus*. *N. Z. J. Bot.* **2013**, *51*, 297–307. [CrossRef]

138. Han, T.X.; Han, L.L.; Wu, L.J.; Chen, W.F.; Sui, X.H.; Gu, J.G.; Wang, E.T.; Chen, W.X. *Mesorhizobium gobiense* sp. nov. and *Mesorhizobium tarimense* sp. nov., isolated from wild legumes growing in desert soils of Xinjiang, China. *Int. J. Syst. Evol. Microbiol.* **2008**, *58*, 2610–2618. [CrossRef] [PubMed]
139. Deng, Z.S.; Zhao, L.F.; Kong, Z.Y.; Yang, W.Q.; Lindström, K.; Wang, E.T.; Wei, G.H. Diversity of endophytic bacteria within nodules of the *Sphaerophysa salsula* in different regions of Loess Plateau in China. *FEMS Microbiol. Ecol.* **2011**, *76*, 463–475. [CrossRef] [PubMed]
140. Xu, L.; Shi, J.F.; Zhao, P.; Chen, W.M.; Qin, W.; Tang, M.; Wei, G.H. *Rhizobium sphaerophysae* sp. nov., a novel species isolated from root nodules of *Sphaerophysa salsula* in China. *Antonie van Leeuwenhoek* **2011**, *99*, 845–854. [CrossRef] [PubMed]
141. Yates, R.J.; Howieson, J.G.; Nandasena, K.G.; O’Hara, G.W. Root-nodule bacteria of indigenous legumes in the north-west of Western Australia and their interaction with exotic legumes. *Soil Biol. Biochem.* **2004**, *36*, 1319–1329. [CrossRef]
142. Wei, G.; Chen, W.; Young, J.P.W.; Bontemps, C. A new clade of *Mesorhizobium* nodulating *Alhagi sparsifolia*. *Syst. Appl. Microbiol.* **2009**, *32*, 8–16. [CrossRef] [PubMed]
143. Lu, Y.L.; Chen, W.F.; Wang, E.T.; Guan, S.H.; Yan, X.R.; Chen, W.X. Genetic diversity and biogeography of rhizobia associated with *Caragana* species in three ecological regions of China. *Syst. Appl. Microbiol.* **2009**, *32*, 351–361. [CrossRef] [PubMed]
144. Guan, S.H.; Chen, W.F.; Wang, E.T.; Lu, Y.L.; Yan, X.R.; Zhang, X.X.; Chen, W.X. *Mesorhizobium caraganae* sp. nov., a novel rhizobial species nodulated with *Caragana* spp. in China. *Int. J. Syst. Evol. Microbiol.* **2008**, *58*, 2646–2653. [CrossRef] [PubMed]
145. Squartini, A.; Struffi, P.; Döring, H.; Selenska-Pobell, S.; Tola, E.; Giacomini, A.; Vendramin, E.; Velázquez, E.; Mateos, P.F.; Martínez-Molina, E.; et al. *Rhizobium sullae* sp. nov. (formerly “*Rhizobium hedysari*”), the root-nodule microsymbiont of *Hedysarum coronarium* L. *Int. J. Syst. Evol. Microbiol.* **2002**, *52*, 1267–1276. [CrossRef] [PubMed]
146. Baimiev, A.K.; Baimiev, A.K.; Gubaidullin, I.I.; Kulikova, O.L.; Chemeris, A.V. Bacteria closely related to *Phyllobacterium trifolii* according to their 16S rRNA gene are discovered in the nodules of Hungarian sainfoin. *Genetika* **2007**, *43*, 587–590. [CrossRef]
147. El Batanony, N.H.; Castellano-Hinojosa, A.; Correa-Galeote, D.; Bedmar, E.J. The diversity of rhizobia nodulating the *Medicago*, *Melilotus* and *Trigonella* inoculation group in Egypt is marked by the dominance of two genetic types. *Symbiosis* **2015**, *67*, 3–10. [CrossRef]
148. Del Villegas, M.C.; Rome, S.; Mauré, L.; Domergue, O.; Gardan, L.; Bailly, X.; Cleyet-Marel, J.-C.; Brunel, B. Nitrogen-fixing sinorhizobia with *Medicago laciniata* constitute a novel biovar (bv. *medicaginiis*) of *S. meliloti*. *Syst. Appl. Microbiol.* **2006**, *29*, 526–538. [CrossRef] [PubMed]
149. Badri, Y.; Zribi, K.; Badri, M.; Huguet, T.; van Berkum, P.; Aouani, M.E. Comparison of rhizobia that nodulate *Medicago laciniata* and *Medicago truncatula* present in a single Tunisian arid soil. *Can. J. Microbiol.* **2007**, *53*, 277–283. [CrossRef] [PubMed]
150. Mnasri, B.; Badri, Y.; Saïdi, S.; de Lajudie, P.; Mhamdi, R. Symbiotic diversity of *Ensifer meliloti* strains recovered from various legume species in Tunisia. *Syst. Appl. Microbiol.* **2009**, *32*, 583–592. [CrossRef] [PubMed]
151. Wang, H.; Man, C.X.; Wang, E.T.; Chen, W.X. Diversity of rhizobia and interactions among the host legumes and rhizobial genotypes in an agricultural-forestry ecosystem. *Plant Soil* **2009**, *314*, 169–182. [CrossRef]
152. Rome, S.; Fernandez, M.P.; Brunel, B.; Normand, P.; Cleyet-Marel, J.-C. *Sinorhizobium medicae* sp. nov., isolated from annual *Medicago* spp. *Int. J. Syst. Bacteriol.* **1996**, *46*, 972–980. [CrossRef] [PubMed]
153. Gubry-Rangin, C.; Béna, G.; Cleyet-Merel, J.-C.; Brunel, B. Definition and evolution of a new symbiovar, sv. *rigiduloides*, among *Ensifer meliloti* efficiently nodulating *Medicago* species. *Syst. Appl. Microbiol.* **2013**, *36*, 490–496. [CrossRef] [PubMed]
154. Van Berkum, P.; Beyene, D.; Bao, G.; Campbell, T.A.; Eardly, B.D. *Rhizobium mongolense* sp. nov. is one of three rhizobial genotypes identified which nodulate and form nitrogen-fixing symbioses with *Medicago ruthenica* (L. Ledebour). *Int. J. Syst. Bacteriol.* **1998**, *48*, 13–22. [CrossRef] [PubMed]
155. Yan, A.M.; Wang, E.T.; Kan, F.L.; Tan, Z.Y.; Sui, X.H.; Reinhold-Hurek, B.; Chen, W.X. *Sinorhizobium meliloti* associated with *Medicago sativa* and *Melilotus* spp. in arid saline soils in Xinjiang, China. *Int. J. Syst. Evol. Microbiol.* **2000**, *50*, 1887–1891. [CrossRef] [PubMed]

156. Bromfield, E.S.P.; Tambong, J.T.; Cloutier, S.; Prévost, D.; Laguerre, G.; van Berkum, P.; Tran Thi, T.V.; Assabgui, R.; Barran, L.R. *Ensifer, Phyllobacterium* and *Rhizobium* species occupy nodules of *Medicago sativa* (alfalfa) and *Melilotus alba* (sweet clover) grown at a Canadian site without a history of cultivation. *Microbiology* **2010**, *156*, 505–520. [CrossRef] [PubMed]
157. Merabet, C.; Martens, M.; Mahdi, M.; Zakhia, F.; Sy, A.; Le Roux, C.; Domergue, O.; Coopman, R.; Bekki, A.; Mars, M.; et al. Multilocus sequence analysis of root nodule isolates from *Lotus arabicus* (Senegal), *Lotus creticus*, *Argyrolobium uniflorum* and *Medicago sativa* (Tunisia) and description of *Ensifer numidicus* sp. nov. and *Ensifer garamanticus* sp. nov. *Int. J. Syst. Evol. Microbiol.* **2010**, *60*, 664–674. [CrossRef] [PubMed]
158. Djedidi, S.; Yokoyama, T.; Tomooka, N.; Ohkama-Ohtsu, N.; Risal, C.P.; Abdelly, C.; Sekimoto, H. Phenotypic and genetic characterization of rhizobia associated with alfalfa in the Hokkaido and Ishigaki regions of Japan. *Syst. Appl. Microbiol.* **2011**, *34*, 453–461. [CrossRef] [PubMed]
159. Valverde, A.; Velázquez, E.; Fernández-Santos, F.; Vizcaíno, N.; Rivas, R.; Mateos, P.F.; Martínez-Molina, E.; Igual, J.M.; Willems, A. *Phyllobacterium trifolii* sp. nov., nodulating *Trifolium* and *Lupinus* in Spanish soils. *Int. J. System. Evol. Microbiol.* **2005**, *55*, 1985–1989. [CrossRef] [PubMed]
160. Zhang, J.J.; Jing, X.Y.; de Lajudie, P.; Ma, C.; He, P.X.; Singh, R.P.; Chen, W.F.; Wang, E.T. Association of white clover (*Trifolium repens* L.) with rhizobia of sv. *trifoli* belonging to three genomic species in alkaline soils in North and East China. *Plant Soil* **2016**, *407*, 417–427. [CrossRef]
161. Ogasawara, M.; Suzuki, T.; Mutoh, I.; Annapurna, K.; Arora, N.K.; Nishimura, Y.; Maheshwari, D.K. *Sinorhizobium indiaense* sp. nov. and *Sinorhizobium abri* sp. nov. isolated from tropical legumes, *Sesbania rostrata* and *Abrus precatorius*, respectively. *Symbiosis* **2003**, *34*, 53–68.
162. Wang, E.T.; van Berkum, P.; Sui, X.H.; Beyene, D.; Chen, W.X.; Martínez-Romero, E. Diversity of rhizobia associated with *Amorpha fruticosa* isolated from Chinese soils and description of *Mesorhizobium amorphae* sp. nov. *Int. J. Syst. Bacteriol.* **1999**, *49*, 51–65. [CrossRef] [PubMed]
163. Tlusty, B.; van Berkum, P.; Graham, P.H. Characteristics of the rhizobia associated with *Dalea* spp. in the Ordway, Kellogg-Weaver Dunes, and Hayden prairies. *Can. J. Microbiol.* **2005**, *51*, 15–23. [CrossRef] [PubMed]
164. Sy, A.; Giraud, E.; Jourand, P.; Garcia, N.; Willems, A.; de Lajudie, P.; Prin, Y.; Neyra, M.; Gillis, M.; Boivin-Masson, C.; et al. Methylotrophic *Methylobacterium* bacteria nodulate and fix nitrogen in symbiosis with legumes. *J. Bacteriol.* **2001**, *183*, 214–220. [CrossRef] [PubMed]
165. Howieson, J.G.; de Meyer, S.E.; Vivas-Marfisi, A.; Ratnayake, S.; Ardley, J.K.; Yates, R.J. Novel *Burkholderia* bacteria isolated from *Lebeckia ambigua*—A perennial suffrutescent legume of the fynbos. *Soil Biol. Biochem.* **2013**, *60*, 55–64. [CrossRef]
166. Ardley, J.K.; Parker, M.A.; de Meyer, S.E.; Trengove, R.D.; O'Hara, G.W.; Reeve, W.G.; Yates, R.J.; Dilworth, M.J.; Willems, A.; Howieson, J.G. *Microvirga lupini* sp. nov., *Microvirga lotononisidis* sp. nov. and *Microvirga zambiensis* sp. nov. are α proteobacterial root-nodule bacteria that specifically nodulate and fix nitrogen with geographically and taxonomically separate legume hosts. *Int. J. Syst. Evol. Microbiol.* **2012**, *62*, 2579–2588. [CrossRef] [PubMed]
167. Cardinale, M.; Lanza, A.; Bonnì, M.L.; Marsala, S.; Puglia, A.M.; Quatrini, P. Diversity of rhizobia nodulating wild shrubs of Sicily and some neighbouring islands. *Arch. Microbiol.* **2008**, *190*, 461–470. [CrossRef] [PubMed]
168. Rodríguez-Echeverría, S.; Pérez-Fernández, M.A.; Vlaar, S.; Finnian, T. Analysis of the legume-rhizobia symbiosis in shrubs from central western Spain. *J. Appl. Microbiol.* **2003**, *95*, 1367–1374. [CrossRef] [PubMed]
169. Vinuesa, P.; Rademaker, J.L.W.; de Bruijn, F.J.; Werner, D. Genotypic characterization of *Bradyrhizobium* strains nodulating endemic woody legumes of the Canary Islands by PCR-restriction fragment length polymorphism analysis of genes encoding 16S rRNA (16S rDNA) and 16S–23S rDNA intergenic spacers, repetitive extragenic palindromic PCR genomic fingerprinting, and partial 16S rDNA sequencing. *Appl. Environ. Microbiol.* **1998**, *64*, 2096–2104. [PubMed]
170. Vinuesa, P.; Léon-Barrios, M.; Silva, C.; Willems, A.; Jarabo-Lorenzo, A.; Pérez-Galdona, R.; Werner, D.; Martínez-Romero, E. *Bradyrhizobium canariense* sp. nov., an acid-tolerant endosymbiont that nodulates endemic genistoid legumes (Papilionoideae: Genisteae) from the Canary Islands, along with *Bradyrhizobium japonicum* bv. *genistearum*, *Bradyrhizobium* genospecies alpha and *Bradyrhizobium* genospecies beta. *Int. J. Syst. Evol. Microbiol.* **2005**, *55*, 569–575. [PubMed]

171. Jarabo-Lorenzo, A.; Velázquez, E.; Pérez-Galdona, R.; Vega-Hernández, M.C.; Martínez-Molina, E.; Mateos, P.F.; Vinuesa, P.; Martínez-Romero, E.; Léon-Barrios, M. Restriction fragment length polymorphism analysis of 16S rDNA and low molecular weight RNA profiling of rhizobial isolates from shrubby legumes endemic to the Canary Islands. *System. Appl. Microbiol.* **2000**, *23*, 418–425. [[CrossRef](#)]
172. Jarabo-Lorenzo, A.; Pérez-Galdona, R.; Donate-Correa, J.; Rivas, R.; Velázquez, E.; Hernández, M.; Temprano, F.; Martínez-Molina, E.; Ruiz-Argüeso, T.; Léon-Barrios, M. Genetic diversity of Bradyrhizobial populations from diverse geographic origins that nodulate *Lupinus* spp. and *Ornithopus* spp. *Syst. Appl. Microbiol.* **2003**, *26*, 611–623. [[CrossRef](#)] [[PubMed](#)]
173. Kalita, M.; Malek, W.; Kaznowski, A. Analysis of genetic relationship of *Sarrothamnus scoparius* microsymbionts and *Bradyrhizobium* sp. by hybridization in microdilution wells. *J. Biosci. Bioeng.* **2004**, *97*, 158–161. [[CrossRef](#)]
174. Horn, K.; Parker, I.M.; Malek, W.; Rodríguez-Echeverria, S.; Matthew, A.P. Disparate origins of *Bradyrhizobium* symbionts for invasive populations of *Cytisus scoparius* (Leguminosae) in North America. *FEMS Microbiol. Ecol.* **2014**, *89*, 89–98. [[CrossRef](#)] [[PubMed](#)]
175. Chahboune, R.; Barrijal, S.; Moreno, S.; Bedmar, E.J. Characterization of *Bradyrhizobium* species isolated from root nodules of *Cytisus villosus* grown in Morocco. *Syst. Appl. Microbiol.* **2011**, *34*, 440–445. [[CrossRef](#)] [[PubMed](#)]
176. Cobo-Díaz, J.F.; Martínez-Hidalgo, P.; Fernández-González, A.J.; Martínez-Molina, E.; Toro, N.; Velázquez, E.; Fernández-López, M. The endemic *Genista versicolor* from sierra nevada national park in Spain is nodulated by putative new *Bradyrhizobium* species and a novel symbiovar (*sierranevadense*). *Syst. Appl. Microbiol.* **2014**, *37*, 177–185. [[CrossRef](#)] [[PubMed](#)]
177. Stroschein, M.R.D.; Eltz, F.L.F.; Antoniolli, Z.I.; Lupatini, M.; Vargas, L.K.; Giongo, A.; Pontelli, M.P. Symbiotic efficiency and genetic characteristics of *Bradyrhizobium* sp. strain UFSM LA 1.3 isolated from *Lupinus albescens* (H. et Arn.). *Sci. Agric.* **2010**, *67*, 702–706. [[CrossRef](#)]
178. Granada, C.E.; Beneduzi, A.; Lisboa, B.B.; Turchetto-Zolet, A.C.; Vargas, L.K.; Passaglia, L.M.P. Multilocus sequence analysis reveals taxonomic differences among *Bradyrhizobium* sp. symbionts of *Lupinus albescens* plants growing in arenized and non-arenized areas. *Syst. Appl. Microbiol.* **2015**, *38*, 323–329. [[CrossRef](#)] [[PubMed](#)]
179. Velázquez, E.; Valverde, A.; Rivas, R.; Gomis, V.; Peix, A.; Gantois, I.; Igual, J.M.; León-Barrios, M.; Willems, A.; Mateos, P.F.; et al. Strains nodulating *Lupinus albus* on different continents belong to several new chromosomal and symbiotic lineages within *Bradyrhizobium*. *Antonie van Leeuwenhoek* **2010**, *97*, 363–376. [[CrossRef](#)] [[PubMed](#)]
180. Stępkowski, T.; Źak, M.; Moulin, L.; Króliczak, J.; Golińska, B.; Narożna, D.; Safronova, V.I.; Mađrzak, C.J. *Bradyrhizobium canariense* and *Bradyrhizobium japonicum* are the two dominant rhizobium species in root nodules of lupin and serratella plants growing in Europe. *Syst. Appl. Microbiol.* **2011**, *34*, 368–375. [[CrossRef](#)] [[PubMed](#)]
181. Trujillo, M.E.; Willems, A.; Abril, A.; Planchuelo, A.-M.; Rivas, R.; Ludeña, D.; Mateos, P.F.; Martínez-Molina, E.; Velázquez, E. Nodulation of *Lupinus albus* by strains of *Ochrobactrum lupini* sp. nov. *Appl. Environ. Microbiol.* **2005**, *71*, 1318–1327. [[CrossRef](#)] [[PubMed](#)]
182. Sánchez-Cañizares, C.; Rey, L.; Durán, D.; Temprano, F.; Sánchez-Jiménez, P.; Navarro, A.; Polajnar, M.; Imperial, J.; Ruiz-Argüeso, T. Endosymbiotic bacteria nodulating a new endemic lupine *Lupinus mariae-josephi* from alkaline soils in Eastern Spain represent a new lineage within the *Bradyrhizobium* genus. *Syst. Appl. Microbiol.* **2011**, *34*, 207–215. [[CrossRef](#)] [[PubMed](#)]
183. Durán, D.; Rey, L.; Sánchez-Cañizares, C.; Navarro, A.; Imperial, J.; Ruiz-Argüeso, T. Genetic diversity of indigenous rhizobial symbionts of the *Lupinus mariae-josephae* endemism form alkaline-limed soils within its area of distribution in Eastern Spain. *Syst. Appl. Microbiol.* **2013**, *36*, 128–136. [[CrossRef](#)] [[PubMed](#)]
184. Bourebaba, Y.; Durán, D.; Boulila, F.; Ahnia, H.; Boulila, A.; Temprano, F.; Palacios, J.M.; Imperial, J.; Ruiz-Argüeso, T.; Rey, L. Diversity of *Bradyrhizobium* strains nodulating *Lupinus micranthus* on both sides of the Western Mediterranean: Algeria and Spain. *Syst. Appl. Microbiol.* **2016**, *39*, 266–274. [[CrossRef](#)] [[PubMed](#)]
185. Ryan-Salter, T.P.; Black, A.D.; Andrews, M.; Moot, D.J. Identification and effectiveness of rhizobial strains that nodulate *Lupinus polyphyllus*. *Proc. NZ Grassland Assoc.* **2014**, *76*, 61–66.

186. Guerrouj, K.; Ruíz-Díez, B.; Chahboune, R.; Ramírez-Bahena, M.-H.; Abdelmoumen, H.; Quiñones, M.A.; El Idrissi, M.M.; Velázquez, E.; Fernández-Pascual, M.; Bedmar, E.J.; Peix, A. Definition of a novel symbiovar (*sv. retamae*) within *Bradyrhizobium retamae* sp. nov., nodulating *Retama sphaerocarpa* and *Retama monosperma*. *Syst. Appl. Microbiol.* **2013**, *36*, 218–223. [CrossRef] [PubMed]
187. Farida, B.; Géraldine, D.; Abdelghani, B.; Djellali, B.; Said, B.; Gisèle, L. *Retama* species growing in different ecological-climatic areas of northeastern Algeria have a narrow range of rhizobia that form a novel phylogenetic clade within the *Bradyrhizobium* genus. *Syst. Appl. Microbiol.* **2009**, *32*, 245–255. [CrossRef] [PubMed]
188. Rodríguez-Echeverría, S.; Moreno, S.; Bedmar, E.J. Genetic diversity of root nodulating bacteria associated with *Retama sphaerocarpa* in sites with different soil and environmental conditions. *Syst. Appl. Microbiol.* **2014**, *37*, 305–310. [CrossRef] [PubMed]
189. Quatrini, P.; Scaglione, G.; Cardinale, M.; Caradonna, F.; Puglia, A.M. *Bradyrhizobium* sp. nodulating the Mediterranean shrub Spanish broom (*Spartium junceum* L.). *J. Appl. Microbiol.* **2002**, *92*, 13–21. [CrossRef] [PubMed]
190. Liu, W.Y.Y. Characterisation of Rhizobia and Studies on N₂ Fixation of Common Weed Legumes in New Zealand. Ph.D. Thesis, Lincoln University, Lincoln, New Zealand, 2014.
191. Beukes, C.W.; Venter, S.N.; Law, I.J.; Phalane, F.L.; Steenkamp, E.T. South African papilionoid legumes are nodulated by diverse *Burkholderia* with unique nodulation and nitrogen-fixation loci. *PLoS ONE* **2013**, *8*, e68406. [CrossRef] [PubMed]
192. Doignon-Bourcier, F.; Sy, A.; Willems, A.; Torck, U.; Dreyfus, B.; Gillis, M.; de Lajudie, P. Diversity of bradyrhizobia from 27 tropical *Leguminosae* species native of Senegal. *System. Appl. Microbiol.* **1999**, *22*, 647–661. [CrossRef]
193. Lemaire, B.; Chimphango, S.B.M.; Stirton, C.; Rafudeen, S.; Honnay, O.; Smets, E.; Chen, W.-M.; Sprent, J.; James, E.K.; Muasya, A.M. Biogeographical patterns of legume-nodulating *Burkholderia* spp.: From African fynbos to continental scales. *Appl. Environ. Microbiol.* **2016**, *82*, 5099–5115. [CrossRef] [PubMed]
194. Yang, W.; Kong, Z.; Chen, W.; Wei, G. Genetic diversity and symbiotic evolution of rhizobia from root nodules of *Coronilla varia*. *Syst. Appl. Microbiol.* **2013**, *36*, 49–55. [CrossRef] [PubMed]
195. Stępkowski, T.; Moulin, L.; Krzyżanśka, A.; McInnes, A.; Law, I.J.; Howieson, J. European origin of *Bradyrhizobium* populations infecting lupins and serradella in soils of Western Australia and South Africa. *Appl. Environ. Microbiol.* **2005**, *71*, 7041–7052. [CrossRef] [PubMed]
196. Kesari, V.; Ramesh, A.M.; Rangan, L. *Rhizobium pongamiae* sp. nov. from root nodules of *Pongamia pinnata*. *Biomed. Res. Int.* **2013**, *2013*, 165198. [CrossRef] [PubMed]
197. Lemaire, B.; van Cauwenbergh, J.; Verstraete, B.; Chimphango, S.; Stirton, C.; Honnay, O.; Smets, E.; Sprent, J.; James, E.K.; Muasya, A.M. Characterization of the papilionoid-*Burkholderia* interaction in the Fynbos biome: The diversity and distribution of β-rhizobia nodulating *Podalyria calyptrata* (Fabaceae, Podalyrieae). *Syst. Appl. Microbiol.* **2016**, *39*, 41–48. [CrossRef] [PubMed]
198. Ulrich, A.; Zaspel, I. Phylogenetic diversity of rhizobial strains nodulating *Robinia pseudoacacia* L. *Microbiology* **2000**, *146*, 2997–3005. [CrossRef] [PubMed]
199. Mierzwa, B.; Wdowiak-Wróbel, S.; Malek, W. Phenotypic, genomic and phylogenetic characteristics of rhizobia isolated from root nodules of *Robinia pseudoacacia* (black locust) growing in Poland and Japan. *Arch. Microbiol.* **2009**, *191*, 697–710. [CrossRef] [PubMed]
200. Chen, W.-M.; Lee, T.-M. Genetic and phenotypic diversity of rhizobial isolates from sugarcane-*Sesbania cannabina*-rotation fields. *Biol. Fertil. Soils* **2001**, *34*, 14–20. [CrossRef]
201. Wang, Y.C.; Wang, F.; Hou, B.C.; Wang, E.T.; Chen, W.F.; Sui, X.H.; Chen, W.X.; Li, Y.; Zhang, Y.B. Proposal of *Ensifer psoraleae* sp. nov., *Ensifer sesbaniae* sp. nov., *Ensifer morelense* comb. nov. and *Ensifer americanum* comb. nov. *Syst. Appl. Microbiol.* **2013**, *36*, 467–473. [CrossRef] [PubMed]
202. Li, Y.; Li, X.; Liu, Y.; Wang, E.T.; Ren, C.; Liu, W.; Xu, H.; Wu, H.; Jiang, N.; Li, Y.; Zhang, X.; Xie, Z. Genetic diversity and community structure of rhizobia nodulating *Sesbania cannabina* in saline-alkaline soils. *Syst. Appl. Microbiol.* **2016**, *39*, 195–202. [CrossRef] [PubMed]
203. Wang, E.T.; van Berkum, P.; Beyene, D.; Sui, X.H.; Dorado, O.; Chen, W.X.; Martínez-Romero, E. *Rhizobium huautlense* sp. nov., a symbiont of *Sesbania herbacea* that has a close phylogenetic relationship with *Rhizobium galegae*. *Int. J. Syst. Bacteriol.* **1998**, *48*, 687–699. [CrossRef] [PubMed]

204. Blanco, A.R.; Csukasi, F.; Abreu, C.; Sicardi, M. Characterization of rhizobia from *Sesbania* species native to seasonally wetland areas in Uruguay. *Biol. Fertil. Soils* **2008**, *44*, 925–932. [[CrossRef](#)]
205. Dreyfus, B.; Garcia, J.L.; Gillis, M. Characterisation of *Azorhizobium caulinodans* gen. nov., sp. nov., a stem nodulating nitrogen-fixing bacterium isolated from *Sesbania rostrata*. *Int. J. Syst. Bacteriol.* **1988**, *38*, 89–98. [[CrossRef](#)]
206. De Moreira, F.M.S.; Cruz, L.; de Faria, S.M.; Marsh, T.; Martínez-Romero, E.; de Pedrosa, F.O.; Pitard, R.M.; Young, J.P.W. *Azorhizobium doeberiniae* sp. nov. microsymbiont of *Sesbania virgata* (Caz.) Pers. *Syst. Appl. Microbiol.* **2006**, *29*, 197–206. [[CrossRef](#)] [[PubMed](#)]
207. Zhao, L.; Deng, Z.; Yang, W.; Cao, Y.; Wang, E.; Wei, G. Diverse rhizobia associated with *Sophora alopecuroides* grown in different regions of Loess Plateau in China. *Syst. Appl. Microbiol.* **2010**, *33*, 468–477. [[CrossRef](#)] [[PubMed](#)]
208. Jiao, Y.S.; Liu, Y.H.; Yan, H.; Wang, E.T.; Tian, C.F.; Chen, W.X.; Guo, B.L.; Chen, W.F. Rhizobial diversity and nodulation characteristics of the extremely promiscuous legume *Sophora flavescens*. *Mol. Plant Microbe Interact.* **2015**, *28*, 1338–1352. [[CrossRef](#)] [[PubMed](#)]
209. Jiao, Y.S.; Yan, H.; Ji, Z.J.; Liu, Y.H.; Sui, X.H.; Zhang, X.X.; Wang, E.T.; Chen, W.X.; Chen, W.F. *Phyllobacterium sophorae* sp. nov., a symbiotic bacterium isolated from root nodules of *Sophora flavescens*. *Int. J. Syst. Evol. Microbiol.* **2015**, *65*, 399–406. [[CrossRef](#)] [[PubMed](#)]
210. Tan, H.W.; Heenan, P.B.; de Meyer, S.E.; Willems, A.; Andrews, M. Diverse novel mesorhizobia nodulate New Zealand native *Sophora* species. *Syst. Appl. Microbiol.* **2015**, *38*, 91–98. [[CrossRef](#)] [[PubMed](#)]
211. Zhao, L.; Wang, X.; Huo, H.; Yuan, G.; Sun, Y.; Zhang, D.; Cao, Y.; Xu, L.; Wei, G. Phylogenetic diversity of *Ammopiptanthus* rhizobia and distribution of rhizobia associated with *Ammopiptanthus mongolicus* in diverse regions of Northwest China. *Microb. Ecol.* **2016**, *72*, 231–239. [[CrossRef](#)] [[PubMed](#)]
212. Donate-Correa, J.; Léon-Barrios, M.; Hernández, M.; Pérez-Galdona, R.; del Arco-Aguilar, M. Different *Mesorhizobium* species sharing the same symbiotic genes nodulate the shrub legume *Anagyris latifolia*. *Syst. Appl. Microbiol.* **2007**, *30*, 615–623. [[CrossRef](#)] [[PubMed](#)]
213. Ampomah, O.Y.; Huss-Danell, K. Nodulation of *Thermopsis lupinoides* by a *Mesorhizobium huakuii* strain with a unique *nodA* gene in Kamtchatka, Russia. *Appl. Environ. Microbiol.* **2011**, *77*, 5513–5516. [[CrossRef](#)] [[PubMed](#)]
214. Bianco, L.; Angelini, J.; Fabra, A.; Malpassi, R. Diversity and symbiotic effectiveness of indigenous rhizobia-nodulating *Adesmia bicolor* in soils of Central Argentina. *Curr. Microbiol.* **2013**, *66*, 174–184. [[CrossRef](#)] [[PubMed](#)]
215. Noisangiam, R.; Teamtisong, K.; Tittabutr, P.; Boonkerd, N.; Toshiki, U.; Minamisawa, K.; Teaumroong, N. Genetic diversity, symbiotic evolution, and proposed infection process of *Bradyrhizobium* strains isolated from root nodules of *Aeschynomene americana* L. in Thailand. *Appl. Environ. Microbiol.* **2012**, *78*, 6236–6250. [[CrossRef](#)] [[PubMed](#)]
216. Van Berkum, P.; Eardly, B.D. The aquatic budding bacterium *Blastobacter denitrificans* is a nitrogen-fixing symbiont of *Aeschynomene indica*. *Appl. Environ. Microbiol.* **2002**, *68*, 1132–1136. [[CrossRef](#)] [[PubMed](#)]
217. Montecchia, M.S.; Kerber, N.L.; Pucheu, N.L.; Perticari, A.; García, A.F. Analysis of genomic diversity among photosynthetic stem-nodulating rhizobial strains from Northeast Argentina. *Syst. Appl. Microbiol.* **2002**, *25*, 423–433. [[CrossRef](#)] [[PubMed](#)]
218. Chen, J.Y.; Gu, J.; Wang, E.T.; Ma, X.X.; Kang, S.T.; Huang, L.Z.; Cao, X.P.; Li, L.B.; Wu, Y.L. Wild peanut *Arachis duranensis* are nodulated by diverse and novel *Bradyrhizobium* species in acid soils. *Syst. Appl. Microbiol.* **2014**, *37*, 525–532. [[CrossRef](#)] [[PubMed](#)]
219. Urtz, B.E.; Elkan, G.H. Genetic diversity among *Bradyrhizobium* isolates that effectively nodulate peanut (*Arachis hypogaea*). *Can. J. Microbiol.* **1996**, *42*, 1121–1130. [[CrossRef](#)] [[PubMed](#)]
220. Yang, J.K.; Xie, F.L.; Zou, J.; Zhou, Q.; Zhou, J.C. Polyphasic characteristics of bradyrhizobia isolated from nodules of peanut (*Arachis hypogaea*) in China. *Soil Biol. Biochem.* **2005**, *37*, 141–153. [[CrossRef](#)]
221. Taurian, T.; Ibañez, F.; Fabra, A.; Aguilar, O.M. Genetic diversity of rhizobia nodulating *Arachis hypogaea* L. in Central Argentinean soils. *Plant Soil* **2006**, *282*, 41–52. [[CrossRef](#)]
222. El-Akhal, M.R.; Rincón, A.; Arenal, F.; Lucas, M.M.; El Mourabit, N.; Barrijal, S.; Pueyo, J.J. Genetic diversity and symbiotic efficiency of rhizobial isolates obtained from nodules of *Arachis hypogaea* in northwestern Morocco. *Soil Biol. Biochem.* **2008**, *40*, 2911–2914. [[CrossRef](#)]

223. Steenkamp, E.T.; Stępkowski, T.; Przymusiak, A.; Botha, W.J.; Law, I.J. Cowpea and peanut in southern Africa are nodulated by diverse *Bradyrhizobium* strains harboring nodulation genes that belong to the large pantropical clade common in Africa. *Mol. Phylogenet. Evol.* **2008**, *48*, 1131–1144. [CrossRef] [PubMed]
224. Chang, Y.L.; Wang, J.Y.; Wang, E.T.; Liu, H.C.; Sui, X.H.; Chen, W.X. *Bradyrhizobium lablabi* sp. nov., isolated from effective nodules of *Lablab purpureus* and *Arachis hypogaea*. *Int. J. Syst. Evol. Microbiol.* **2011**, *61*, 2496–2502. [CrossRef] [PubMed]
225. Muñoz, V.; Ibañez, F.; Tonelli, M.L.; Valetti, L.; Anzuay, M.S.; Fabra, A. Phenotypic and phylogenetic characterization of native peanut *Bradyrhizobium* isolates obtained from Córdoba, Argentina. *Syst. Appl. Microbiol.* **2011**, *34*, 446–452. [CrossRef] [PubMed]
226. Wang, R.; Chang, Y.L.; Zheng, W.T.; Zhang, D.; Zhang, X.X.; Sui, X.H.; Wang, E.T.; Hu, J.Q.; Zhang, L.Y.; Chen, W.X. *Bradyrhizobium arachidis* sp. nov., isolated from effective nodules of *Arachis hypogaea* grown in China. *Syst. Appl. Microbiol.* **2013**, *36*, 101–105. [CrossRef] [PubMed]
227. Grönemeyer, J.L.; Kulkarni, A.; Berkemann, D.; Hurek, T.; Reinhold-Hurek, B. *Rhizobia* indigenous to the Okavango region in Sub-Saharan Africa: Diversity, adaptations, and host specificity. *Appl. Environ. Microbiol.* **2014**, *80*, 7244–7257. [CrossRef] [PubMed]
228. Li, Y.H.; Wang, R.; Zhang, X.X.; Young, J.P.W.; Wang, E.T.; Sui, X.H.; Chen, W.X. *Bradyrhizobium guangdongense* sp. nov. and *Bradyrhizobium guangxiense* sp. nov., isolated from effective nodules of peanut. *Int. J. Syst. Evol. Microbiol.* **2015**, *65*, 4655–4661. [CrossRef] [PubMed]
229. Chen, J.; Hu, M.; Ma, H.; Wang, Y.; Wang, E.T.; Zhou, Z.; Gu, J. Genetic diversity and distribution of bradyrhizobia nodulating peanut in acid-neutral soils in Guangdong Province. *Syst. Appl. Microbiol.* **2016**, *39*, 418–427. [CrossRef] [PubMed]
230. Baraúna, A.C.; da Silva, K.; Pereira, G.M.D.; Kaminski, P.E.; Perin, L.; Zilli, J.E. Diversity and nitrogen fixation efficiency of rhizobia isolated from nodules of *Centrolobium paraense*. *Pesq. Agropecu. Bras.* **2014**, *49*, 296–305. [CrossRef]
231. Zilli, J.E.; Baraúna, A.C.; da Silva, K.; de Meyer, S.E.; Farias, E.N.C.; Kaminski, P.E.; da Costa, I.B.; Ardley, J.K.; Willems, A.; Camacho, N.N.; et al. *Bradyrhizobium neotropicale* sp. nov., isolate from effective nodules of *Centrolobium paraense*. *Int. J. Syst. Evol. Microbiol.* **2014**, *64*, 3950–3957. [CrossRef] [PubMed]
232. Rasolomampianina, R.; Bailly, X.; Fetiarison, R.; Rabevohitra, R.; Béna, G.; Ramaroson, L.; Raherimandimbry, M.; Moulin, L.; de Lajudie, P.; Dreyfus, B.; et al. Nitrogen-fixing nodules from rose wood legume trees (*Dalbergia* spp.) endemic to Madagascar host seven different genera belonging to α- and β-proteobacteria. *Mol. Ecol.* **2005**, *14*, 4135–4146. [CrossRef] [PubMed]
233. Le Roux, C.; Muller, F.; Bouvet, J.-M.; Dreyfus, B.; Béna, G.; Galiana, A.; Bâ, A.M. Genetic diversity patterns and functional traits of *Bradyrhizobium* strains associated with *Pterocarpus officinalis* Jacq. in Caribbean islands and Amazonian forest (French Guiana). *Microb. Ecol.* **2014**, *68*, 329–338. [CrossRef] [PubMed]
234. Gueye, F.; Moulin, L.; Sylla, S.; Ndoye, I.; Béna, G. Genetic diversity and distribution of *Bradyrhizobium* and *Azorhizobium* strains associated with the herb legume *Zornia glochidiata* sampled from across Senegal. *Syst. Appl. Microbiol.* **2009**, *32*, 387–399. [CrossRef] [PubMed]
235. Gu, J.; Wang, E.T.; Chen, W.X. Genetic diversity of rhizobia associated with *Desmodium* species grown in China. *Lett. Appl. Microbiol.* **2007**, *44*, 286–292. [CrossRef] [PubMed]
236. Xu, K.W.; Zou, L.; Penttinen, P.; Zeng, X.; Liu, M.; Zhao, K.; Chen, C.; Chen, Y.X.; Zhang, X. Diversity and phylogeny of rhizobia associated with *Desmodium* spp. in Panxi, Sichuan, China. *Syst. Appl. Microbiol.* **2016**, *39*, 33–40. [CrossRef] [PubMed]
237. Delamuta, J.R.M.; Ribeiro, R.A.; Ormeño-Orrillo, E.; Parma, M.M.; Melo, I.S.; Martínez-Romero, E.; Hungria, M. *Bradyrhizobium tropiciagri* sp. nov. and *Bradyrhizobium embrapense* sp. nov., nitrogen-fixing symbionts of tropical forage legumes. *Int. J. Syst. Evol. Microbiol.* **2015**, *65*, 4424–4433. [CrossRef] [PubMed]
238. Chen, W.-X.; Tan, Z.-Y.; Gao, J.-L.; Li, Y.; Wang, E.-T. *Rhizobium hainanense* sp. nov., isolated from tropical legumes. *Int. J. Syst. Bacteriol.* **1997**, *47*, 870–873. [CrossRef] [PubMed]
239. Lin, D.X.; Man, C.X.; Wang, E.T.; Chen, W.X. Diverse rhizobia that nodulate two species of *Kummerowia* in China. *Arch. Microbiol.* **2007**, *188*, 495–507. [CrossRef] [PubMed]
240. Yao, Z.Y.; Kan, F.L.; Wang, E.T.; Wei, G.H.; Chen, W.X. Characterization of rhizobia that nodulate legume species of the genus *Lespedeza* and description of *Bradyrhizobium yuanmingense* sp. nov. *Int. J. Syst. Evol. Microbiol.* **2002**, *52*, 2219–2230. [CrossRef] [PubMed]

241. Parker, M.A.; Doyle, J.L.; Doyle, J.J. Comparative phylogeography of *Amphicarpaea* legumes and their root-nodule symbionts in Japan and North America. *J. Biogeogr.* **2004**, *31*, 425–434. [[CrossRef](#)]
242. Araujo, J.; Díaz-Alcántara, C.-A.; Velázquez, E.; Urbano, B.; González-Andrés, F. *Bradyrhizobium yuanmingense* related strains form nitrogen-fixing symbiosis with *Cajanus cajan* L. in Dominican Republic and are efficient biofertilizers to replace N fertilization. *Sci. Hort.* **2015**, *192*, 421–428. [[CrossRef](#)]
243. Chen, W.-M.; Lee, T.-M.; Lan, C.-C.; Cheng, C.-P. Characterization of halotolerant rhizobia isolated from root nodules of *Canavalia rosea* from seaside areas. *FEMS Microbiol. Ecol.* **2000**, *34*, 9–16. [[CrossRef](#)] [[PubMed](#)]
244. Xu, L.M.; Ge, C.; Cui, Z.; Li, J.; Fan, H. *Bradyrhizobium liaoningense* sp. nov., isolated from the root nodules of soybeans. *Int. J. Syst. Bacteriol.* **1995**, *45*, 706–711. [[CrossRef](#)] [[PubMed](#)]
245. Barcellos, F.G.; Menna, P.; da Batista, J.S.S.; Hungria, M. Evidence of horizontal transfer of symbiotic genes from a *Bradyrhizobium japonicum* inoculant strain to indigenous diazotrophs *Sinorhizobium (Ensifer) fredii* and *Bradyrhizobium elkanii* in a Brazilian savannah soil. *Appl. Environ. Microbiol.* **2007**, *73*, 2635–2643. [[CrossRef](#)] [[PubMed](#)]
246. Appunu, C.; Sasirekha, N.; Prabavathy, V.R.; Nair, S. A significant proportion of indigenous rhizobia from India associated with soybean (*Glycine max* L.) distinctly belong to *Bradyrhizobium* and *Ensifer* genera. *Biol. Fertil. Soils* **2009**, *46*, 57–63. [[CrossRef](#)]
247. Zhang, Y.M.; Li, Y., Jr.; Chen, W.F.; Wang, E.T.; Tian, C.F.; Li, Q.Q.; Zhang, Y.Z.; Sui, X.H.; Chen, W.X. Biodiversity and biogeography of rhizobia associated with soybean plants grown in the North China Plain. *Appl. Environ. Microbiol.* **2011**, *77*, 6331–6342. [[CrossRef](#)] [[PubMed](#)]
248. Jaiswal, S.K.; Anand, A.; Dhar, B.; Vaishampayan, A. Genotypic characterization of phage-typed indigenous soybean *Bradyrhizobia* and their host range symbiotic effectiveness. *Microb. Ecol.* **2012**, *63*, 116–126. [[CrossRef](#)] [[PubMed](#)]
249. Tang, J.; Bromfield, E.S.P.; Rodrigue, N.; Cloutier, S.; Tambong, J.T. Microevolution of symbiotic *Bradyrhizobium* populations associated with soybeans in east North America. *Ecol. Evol.* **2012**, *2*, 2943–2961. [[CrossRef](#)] [[PubMed](#)]
250. Wang, J.Y.; Wang, R.; Zhang, Y.M.; Liu, H.C.; Chen, W.F.; Wang, E.T.; Sui, X.H.; Chen, W.X. *Bradyrhizobium daqingense* sp. nov., isolated from soybean nodules. *Int. J. Syst. Evol. Microbiol.* **2013**, *63*, 616–624. [[CrossRef](#)] [[PubMed](#)]
251. Ribeiro, R.A.; Ormeño-Orrillo, E.; Dall’Agnol, R.F.; Graham, P.H.; Martinez-Romero, E.; Hungria, M. Novel *Rhizobium* lineages isolated from root nodules of the common bean (*Phaseolus vulgaris* L.) in Andean and Mesoamerican areas. *Res. Microbiol.* **2013**, *164*, 740–748. [[CrossRef](#)] [[PubMed](#)]
252. Peng, G.X.; Tan, Z.Y.; Wang, E.T.; Reinhold-Hurek, B.; Chen, W.F.; Chen, W.X. Identification of isolates from soybean nodules in Xinjiang Region as *Sinorhizobium xinjiangense* and genetic differentiation of *S. xinjiangense* from *Sinorhizobium fredii*. *Int. J. Syst. Evol. Microbiol.* **2002**, *52*, 457–462. [[CrossRef](#)] [[PubMed](#)]
253. Li, Q.Q.; Wang, E.T.; Chang, Y.L.; Zhang, Y.Z.; Zhang, Y.M.; Sui, X.H.; Chen, W.F.; Chen, W.X. *Ensifer sojae* sp. nov., isolated from root nodules of *Glycine max* grown in saline-alkaline soils. *Int. J. Syst. Evol. Microbiol.* **2011**, *61*, 1981–1988. [[CrossRef](#)] [[PubMed](#)]
254. Alam, F.; Bhuiyan, M.A.H.; Alam, S.S.; Waghmode, T.R.; Kim, P.J. Effect of *Rhizobium* sp. BARIRGm901 inoculation on nodulation, nitrogen fixation and yield of soybean (*Glycine max*) genotypes in gray terrace soil. *Biosci. Biotechnol. Biochem.* **2015**, *1660*–1668. [[CrossRef](#)] [[PubMed](#)]
255. Wu, L.J.; Wang, H.Q.; Wang, E.T.; Chen, W.X.; Tian, C.F. Genetic diversity of nodulating and non-nodulating rhizobia associated with wild soybean (*Glycine soja* Sieb. & Zucc.) in different ecoregions of China. *FEMS Microbiol. Ecol.* **2011**, *76*, 439–450. [[PubMed](#)]
256. Zhao, L.; Fan, M.; Zhang, D.; Yang, R.; Zhang, F.; Xu, L.; Wei, X.; Shen, Y.; Wei, G. Distribution and diversity of rhizobia associated with wild soybean (*Glycine soja* Sieb. & Zucc.) in Northwest China. *Syst. Appl. Microbiol.* **2014**, *37*, 449–456. [[PubMed](#)]
257. Fuentes, J.B.; Abe, M.; Uchiumi, T.; Suzuki, A.; Higashi, S. Symbiotic root nodule bacteria isolated from yam bean (*Pachyrhizus erosus*). *J. Gen. Appl. Microbiol.* **2002**, *48*, 181–191. [[CrossRef](#)] [[PubMed](#)]
258. Rodríguez-Navarro, D.N.; Camacho, M.; Leidi, E.O.; Rivas, R.; Velázquez, E. Phenotypic and genotypic characterization of rhizobia from diverse geographical origin that nodulate *Pachyrhizus* species. *Syst. Appl. Microbiol.* **2004**, *27*, 737–745. [[CrossRef](#)] [[PubMed](#)]

259. Ramírez-Bahena, M.H.; Peix, A.; Rivas, R.; Camacho, M.; Rodríguez-Navarro, D.N.; Mateos, P.F.; Martínez-Molina, E.; Willems, A.; Velázquez, E. *Bradyrhizobium pachyrhizi* sp. nov. and *Bradyrhizobium jicamae* sp. nov., isolated from effective nodules of *Pachyrhizus erosus*. *Int. J. Syst. Evol. Microbiol.* **2009**, *59*, 1929–1934. [CrossRef] [PubMed]
260. López-López, A.; Negrete-Yankelevich, S.; Rogel, M.A.; Ormeño-Orrillo, E.; Martínez, J.; Martínez-Romero, E. Native bradyrhizobia from Los Tuxtlas in Mexico are symbionts of *Phaseolus lunatus* (Lima bean). *Syst. Appl. Microbiol.* **2013**, *36*, 33–38. [CrossRef] [PubMed]
261. Durán, D.; Rey, L.; Mayo, J.; Zúñiga-Dávila, D.; Imperial, J.; Ruiz-Argüeso, T.; Martínez-Romero, E.; Ormeño-Orrillo, E. *Bradyrhizobium paxllaeri* sp. nov. and *Bradyrhizobium license* sp. nov., nitrogen-fixing rhizobial symbionts of Lima bean (*Phaseolus lunatus* L.) in Peru. *Int. J. Syst. Evol. Microbiol.* **2014**, *64*, 2072–2078. [CrossRef] [PubMed]
262. Matsubara, M.; Zúñiga-Dávila, D. Phenotypic and molecular differences among rhizobia that nodulate *Phaseolus lunatus* in the Supe valley in Peru. *Ann. Microbiol.* **2015**, *65*, 1803–1808. [CrossRef]
263. Wang, L.; Cao, Y.; Wang, E.T.; Qiao, Y.J.; Jiao, S.; Liu, Z.S.; Zhao, L.; Wei, G.H. Biodiversity and biogeography of rhizobia associated with common bean (*Phaseolus vulgaris* L.) in Shaanxi Province. *Syst. Appl. Microbiol.* **2016**, *39*, 211–219. [CrossRef] [PubMed]
264. Talbi, C.; Delgado, M.J.; Girard, L.; Ramirez-Trujillo, A.; Caballero-Mellado, J.; Bedmar, E.J. *Burkholderia phymatum* strains capable of nodulating *Phaseolus vulgaris* are present in Moroccan soils. *Appl. Environ. Microbiol.* **2010**, *76*, 4587–4591. [CrossRef] [PubMed]
265. Dall’Agnol, R.F.; Plotegher, F.; Souza, R.C.; Mendes, I.C.; dos Reis Junior, F.B.; Béna, G.; Moulin, L.; Hungria, M. *Paraburkholderia nodosa* is the main N₂-fixing species trapped by promiscuous common bean (*Phaseolus vulgaris* L.) in the Brazilian “Cerradão”. *FEMS Microbiol. Ecol.* **2016**, *92*, fiw108. [CrossRef] [PubMed]
266. Mhamdi, R.; Laguerre, G.; Aouani, M.E.; Mars, M.; Amarger, N. Different species and symbiotic genotypes of field rhizobia can nodulate *Phaseolus vulgaris* in Tunisian soils. *FEMS Microbiol. Ecol.* **2002**, *41*, 77–84. [CrossRef] [PubMed]
267. Mnasri, B.; Mrabet, M.; Laguerre, G.; Aouani, M.E.; Mhamdi, R. Salt-tolerant rhizobia isolated from a Tunisian oasis that are highly effective for symbiotic N₂-fixation with *Phaseolus vulgaris* constitute a novel biovar (bv. *mediterranense*) of *Sinorhizobium meliloti*. *Arch. Microbiol.* **2007**, *187*, 79–85. [CrossRef] [PubMed]
268. Mnasri, B.; Saïdi, S.; Chihaoui, S.-A.; Mhamdi, R. *Sinorhizobium americanum* symbiovar *mediterranense* is a predominant symbiont that nodulates and fixes nitrogen with common bean (*Phaseolus vulgaris* L.) in a Northern Tunisian field. *Syst. Appl. Microbiol.* **2012**, *35*, 263–269. [CrossRef] [PubMed]
269. Martínez-Romero, E.; Segovia, L.; Mercante, F.M.; Franco, A.A.; Graham, P.; Pardo, M.A. *Rhizobium tropici*, a novel species nodulating *Phaseolus vulgaris* L. beans and *Leucaena* sp. trees. *Int. J. System. Bacteriol.* **1991**, *41*, 417–426. [CrossRef] [PubMed]
270. Amarger, N.; Macheret, V.; Laguerre, G. *Rhizobium gallicum* sp. nov. and *Rhizobium giardini* sp. nov., from *Phaseolus vulgaris* nodules. *Int. J. Syst. Bacteriol.* **1997**, *47*, 996–1006. [CrossRef] [PubMed]
271. Mostasso, L.; Mostasso, F.L.; Dias, B.G.; Vargas, M.A.T.; Hungria, M. Selection of bean (*Phaseolus vulgaris* L.) rhizobial strains for the Brazilian Cerrados. *Field Crops Res.* **2002**, *73*, 121–132. [CrossRef]
272. Valverde, A.; Igual, J.M.; Peix, A.; Cervantes, E.; Velázquez, E. *Rhizobium lusitanum* sp. nov. a bacterium that nodulates *Phaseolus vulgaris*. *Int. J. System. Evol. Microbiol.* **2006**, *56*, 2631–2637. [CrossRef] [PubMed]
273. Wang, F.; Wang, E.T.; Wu, L.J.; Sui, X.H.; Li, Y., Jr.; Chen, W.X. *Rhizobium vallis* sp. nov., isolated from nodules of three leguminous species. *Int. J. Syst. Evol. Microbiol.* **2011**, *61*, 2582–2588. [CrossRef] [PubMed]
274. De Ribeiro, P.R.A.; dos Santos, J.V.; da Costa, E.M.; Lebbe, L.; Assis, E.S.; Louzada, M.O.; Guimarães, A.A.; Willems, A.; de Moreira, F.M.S. Symbiotic efficiency and genetic diversity of soybean bradyrhizobia in Brazilian soils. *Agric. Ecosyst. Environ.* **2015**, *212*, 85–93. [CrossRef]
275. Cao, Y.; Wang, E.-T.; Zhao, L.; Chen, W.-M.; Wei, G.-H. Diversity and distribution of rhizobia nodulated with *Phaseolus vulgaris* in two ecoregions of China. *Soil Biol. Biochem.* **2014**, *78*, 128–137. [CrossRef]
276. Sarr, P.S.; Araki, S.; Begoude, D.A.; Yemefack, M.; Manga, G.A.; Yamakawa, T.; Htwe, A.Z. Phylogeny and nitrogen fixation potential of *Bradyrhizobium* species isolated from the legume cover crop *Pueraria phaseoloides* (Roxb.) Benth. in Eastern Cameroon. *Soil Sci. Plant Nutr.* **2016**, *62*, 13–19. [CrossRef]

277. Garau, G.; Yates, R.J.; Deiana, P.; Howieson, J.G. Novel strains of nodulating *Burkholderia* have a role in nitrogen fixation with papilionoid herbaceous legumes adapted to acid, infertile soils. *Soil Biol. Biochem.* **2009**, *41*, 125–134. [[CrossRef](#)]
278. De Meyer, S.E.; Cnockaert, M.; Ardley, J.K.; Trengove, R.D.; Garau, G.; Howieson, J.G.; Vandamme, P. *Burkholderia rhynchosiae* sp. nov., isolated from *Rhynchosia ferulifolia* root nodules. *Int. J. Syst. Evol. Microbiol.* **2013**, *63*, 3944–3949. [[CrossRef](#)] [[PubMed](#)]
279. Han, L.L.; Wang, E.T.; Lu, Y.L.; Zhang, Y.F.; Sui, X.H.; Chen, W.F.; Chen, W.X. *Bradyrhizobium* spp. and *Sinorhizobium fredii* are predominant in root nodules of *Vigna angularis*, a native legume crop in the subtropical region of China. *J. Microbiol.* **2009**, *47*, 287–296. [[CrossRef](#)] [[PubMed](#)]
280. Zhang, Y.F.; Wang, E.T.; Tian, C.F.; Wang, F.Q.; Han, L.L.; Chen, W.F.; Chen, W.X. *Bradyrhizobium elkanii*, *Bradyrhizobium yuanmingense* and *Bradyrhizobium japonicum* are the main rhizobia associated with *Vigna unguiculata* and *Vigna radiata* in the subtropical region of China. *FEMS Microbiol. Lett.* **2008**, *285*, 146–154. [[CrossRef](#)] [[PubMed](#)]
281. Risal, C.P.; Djedidi, S.; Dhakal, D.; Ohkama-Ohtsu, N.; Sekimoto, H.; Yokoyama, T. Phylogenetic diversity and symbiotic functioning in mungbean (*Vigna radiata* L. Wilczek) bradyrhizobia from contrast agro-ecological regions of Nepal. *Syst. Appl. Microbiol.* **2012**, *35*, 45–53. [[CrossRef](#)] [[PubMed](#)]
282. Onyango, B.; Anyango, B.; Nyunja, R.; Koech, P.K.; Skilton, R.A.; Stomeo, F. Morphological, genetic and symbiotic characterization of root nodule bacteria isolated from Bambara groundnuts (*Vigna subterranea* L. Verdc) from soils of Lake Victoria basin, western Kenya. *J. Appl. Biol. Biotechnol.* **2015**, *3*, 1–10.
283. Guimarães, A.A.; Jaramillo, P.M.D.; Nóbrega, R.S.A.; Florentino, L.A.; Silva, K.B.; de Moreira, F.M.S. Genetic and symbiotic diversity of nitrogen-fixing bacteria isolated from agricultural soils in the Western Amazon by using cowpea as the trap plant. *Appl. Environ. Microbiol.* **2012**, *78*, 6726–6733. [[CrossRef](#)] [[PubMed](#)]
284. Bejarano, A.; Ramírez-Bahena, M.-H.; Velázquez, E.; Peix, A. *Vigna unguiculata* is nodulated in Spain by endosymbionts of Genisteae legumes and by a new symbiovar (vignae) of the genus *Bradyrhizobium*. *Syst. Appl. Microbiol.* **2014**, *37*, 533–540. [[CrossRef](#)] [[PubMed](#)]
285. Silva, F.V.; de Meyer, S.E.; Simões-Araújo, J.L.; da Barbé, T.C.; Xavier, G.R.; O'Hara, G.; Ardley, J.K.; Rumjanek, N.G.; Willems, A.; Zilli, J.E. *Bradyrhizobium manausense* sp. nov., isolated from effective nodules of *Vigna unguiculata* grown in Brazilian Amazonian rainforest soils. *Int. J. Syst. Evol. Microbiol.* **2014**, *64*, 2358–2363. [[CrossRef](#)] [[PubMed](#)]
286. Radl, V.; Simões-Araújo, J.L.; Leite, J.; Passos, S.R.; Martins, L.M.V.; Xavier, G.R.; Rumjanek, N.G.; Baldani, J.I.; Zilli, J.E. *Microvirga vignae* sp. nov., a root nodule symbiotic bacterium isolated from cowpea grown in semi-arid Brazil. *Int. J. Syst. Evol. Microbiol.* **2014**, *64*, 725–730. [[CrossRef](#)] [[PubMed](#)]
287. Kanu, S.A.; Dakora, F.D. Symbiotic nitrogen contribution and biodiversity of root-nodule bacteria nodulating *Psoralea* species in the Cape Fynbos, South Africa. *Soil Biol. Biochem.* **2012**, *54*, 68–76. [[CrossRef](#)]
288. Lorite, M.J.; Donate-Correa, J.; del Arco-Aguilar, M.; Galdona, R.P.; Sanjuán, J.; Léon-Barrios, M. *Lotus* endemic to the Canary Islands are nodulated by diverse and novel rhizobial species and symbiotypes. *Syst. Appl. Microbiol.* **2010**, *33*, 282–290. [[CrossRef](#)] [[PubMed](#)]
289. Jarvis, B.D.W.; van Berkum, P.; Chen, W.X.; Nour, S.M.; Fernandez, M.P.; Cleyet-Marel, J.C.; Gillis, M. Transfer of *Rhizobium loti*, *Rhizobium huakuii*, *Rhizobium ciceri*, *Rhizobium mediterraneum*, and *Rhizobium tianshanense* to *Mesorhizobium* gen. nov. *Int. J. Syst. Bacteriol.* **1997**, *47*, 895–898. [[CrossRef](#)]
290. Lorite, M.J.; Muñoz, S.; Olivares, J.; Soto, M.J.; Sanjuán, J. Characterization of strains unlike *Mesorhizobium loti* that nodulate *Lotus* spp. in saline soils of Granada, Spain. *Appl. Environ. Microbiol.* **2010**, *76*, 4019–4026. [[CrossRef](#)] [[PubMed](#)]
291. Marcos-García, M.; Menéndez, E.; Cruz-González, X.; Velázquez, E.; Mateos, P.F.; Rivas, R. The high diversity of *Lotus corniculatus* endosymbionts in soils of northwest Spain. *Symbiosis* **2015**, *67*, 11–20. [[CrossRef](#)]
292. Léon-Barrios, M.; Lorite, M.J.; Donate-Correa, J.; Sanjuán, J. *Ensifer meliloti* bv. lancerottense establishes nitrogen-fixing symbiosis with *Lotus* endemic to the Canary Islands and shows distinctive symbiotic genotypes and host range. *Syst. Appl. Microbiol.* **2009**, *32*, 413–420. [[CrossRef](#)] [[PubMed](#)]
293. Estrella, M.J.; Muñoz, S.; Soto, M.J.; Ruiz, O.; Sanjuán, J. Genetic diversity and host range of rhizobia nodulating *Lotus tenuis* in typical soils of the Salado River basin (Argentina). *Appl. Environ. Microbiol.* **2009**, *75*, 1088–1098. [[CrossRef](#)] [[PubMed](#)]

294. Sannazzaro, A.I.; Bergottini, V.M.; Paz, R.C.; Castagno, L.N.; Menéndez, A.B.; Ruiz, O.A.; Pieckenstain, F.L.; Estrella, M.J. Comparative symbiotic performance of native rhizobia of the Flooding Pampa and strains currently used for inoculating *Lotus tenuis* in this region. *Antonie van Leeuwenhoek* **2011**, *99*, 371–379. [CrossRef] [PubMed]
295. Lorite, M.J.; Videira e Castro, I.; Muñoz, S.; Sanjuán, J. Phylogenetic relationship of *Lotus uliginosus* symbionts with bradyrhizobia nodulating genistoid legumes. *FEMS Microbiol. Ecol.* **2012**, *79*, 454–464. [CrossRef] [PubMed]
296. Lindström, K. *Rhizobium galegae*, a new species of legume root nodule bacteria. *Int. J. Syst. Bacteriol.* **1989**, *39*, 365–367. [CrossRef]
297. Franche, C.; Lindström, K.; Elmerich, C. Nitrogen-fixing bacteria associated with leguminous and non-leguminous plants. *Plant Soil.* **2009**, *321*, 35–59. [CrossRef]
298. Wojciechowski, M.F.; Lavin, M.; Sanderson, M.J. A phylogeny of legumes (Leguminosae) based on analysis of the plastid MATK gene resolves many well-supported subclades within the family. *Am. J. Bot.* **2004**, *91*, 1846–1862. [CrossRef] [PubMed]
299. Schwarz, E.N.; Ruhlman, T.A.; Sabir, J.S.M.; Hajirah, N.H.; Alharbi, N.S.; Al-Malki, A.L.; Bailey, C.D.; Jansen, R.K. Plastid genome sequences of legumes reveal parallel inversions and multiple losses of *rps16* in papilionoids. *J. Syst. Evol.* **2015**, *53*, 458–468. [CrossRef]
300. Martínez-Romero, E. Diversity of *Rhizobium-Phaseolus vulgaris* symbiosis: Overview and perspectives. *Plant Soil* **2003**, *252*, 11–23. [CrossRef]
301. Oren, A.; Garrity, G.M. List of new names and new combinations previously effectively, but not validly, published. *Int. J. Syst. Evol. Microbiol.* **2015**, *65*, 2017–2025. [CrossRef]
302. Dobritsa, A.P.; Samadpour, M. Transfer of eleven *Burkholderia* species to the genus *Paraburkholderia* and proposal of *Caballeronia* gen. nov., a new genus to accommodate twelve species of *Burkholderia* and *Paraburkholderia*. *Int. J. Syst. Evol. Microbiol.* **2016**, *66*, 2836–2846. [CrossRef] [PubMed]
303. Rogel, M.A.; Ormeño-Orrillo, E.; Martínez-Romero, E. Symbiovars in rhizobia reflect bacterial adaptation to legumes. *Syst. Appl. Microbiol.* **2011**, *34*, 96–104. [CrossRef] [PubMed]
304. Andrews, M.; Hodge, S.; Raven, J.A. Positive plant microbial interactions. *Ann. Appl. Biol.* **2010**, *157*, 317–321. [CrossRef]
305. Fonseca, M.B.; Peix, A.; de Faria, S.M.; Mateos, P.F.; Rivera, L.P.; Simões-Araujo, J.L.; França, M.G.C.; dos Isaías, R.M.S.; Cruz, C.; Velázquez, E.; et al. Nodulation in *Dimorphandra wilsonii* Rizz. (Caesalpinoideae), a threatened species native to the Brazilian Cerrado. *PLoS ONE* **2012**, *7*, e49520. [CrossRef] [PubMed]
306. Yao, Y.; Wang, R.; Lu, J.K.; Sui, X.H.; Wang, E.T.; Chen, W.X. Genetic diversity and evolution of *Bradyrhizobium* populations nodulating *Erythrophleum fordii*, an evergreen tree indigenous to the southern subtropical region of China. *Appl. Environ. Microbiol.* **2014**, *80*, 6184–6194. [CrossRef] [PubMed]
307. Parker, M.A. Divergent *Bradyrhizobium* symbionts on *Tachigali versicolor* from Barro Colorado Island, Panama. *Syst. Appl. Microbiol.* **2000**, *23*, 585–590. [CrossRef]
308. Diabate, M.; Munive, A.; de Faria, S.M.; Ba, A.; Dreyfus, B.; Galiana, A. Occurrence of nodulation in unexplored leguminous trees native to the West African tropical rainforest and inoculation response of native species useful in reforestation. *New Phytol.* **2005**, *166*, 231–239. [CrossRef] [PubMed]
309. Lafay, B.; Burdon, J.J. Molecular diversity of legume root-nodule bacteria in Kakadu National Park, Northern Territory, Australia. *PLoS ONE* **2007**, *3*, e277. [CrossRef] [PubMed]
310. Michalk, D.L.; Zhi-Kai, H. Grassland improvement in subtropical Guangdong province, China. 1. Evaluation of pasture legumes. *Trop. Grassl.* **1994**, *28*, 129–138.
311. Keller, K.R. Mutualistic rhizobia reduce plant diversity and alter community composition. *Oecologia* **2014**, *176*, 1101–1109. [CrossRef] [PubMed]
312. Australian Centre for International Agricultural Research. Forages fact sheet. Available online: www.tropicalforages.info (accessed on 19 June 2016).
313. Sullivan, J.T.; Ronson, C.W. Evolution of rhizobia by acquisition of a 500-kb symbiosis island that integrates into a phe-tRNA gene. *Proc. Natl. Acad. Sci. USA* **1998**, *95*, 5145–5149. [CrossRef] [PubMed]
314. Saidi, S.; Ramírez-Bahena, M.H.; Santillana, N.; Zúñiga, D.; Álvarez-Martínez, E.R.; Peix, A.; Mhamdi, R.; Velázquez, E. *Rhizobium laguerreae* sp. nov. nodulates *Vicia faba* on several continents. *Int. J. Syst. Evol. Microbiol.* **2014**, *64*, 242–247. [CrossRef] [PubMed]

315. Miller, S.H.; Elliot, R.M.; Sullivan, J.T.; Ronson, C.W. Host-specific regulation of symbiotic nitrogen fixation in *Rhizobium leguminosarum* biovar trifolii. *Microbiology* **2007**, *153*, 3184–3195. [CrossRef] [PubMed]
316. De Meyer, S.E.; Tan, H.W.; Heenan, P.B.; Andrews, M.; Willems, A. *Mesorhizobium waimense* sp. nov. isolated from *Sophora longicarinata* root nodules and *Mesorhizobium cantuariense* sp. nov. isolated from *Sophora microphylla* root nodules in New Zealand. *Int. J. Syst. Evol. Microbiol.* **2015**, *65*, 3419–3426. [CrossRef] [PubMed]
317. De Meyer, S.E.; Tan, H.W.; Andrews, M.; Heenan, P.B.; Willems, A. *Mesorhizobium calcicola* sp. nov., *Mesorhizobium waitakense* sp. nov., *Mesorhizobium sophorae* sp. nov., *Mesorhizobium newzealandense* sp. nov. and *Mesorhizobium kowhaii* sp. nov. isolated from *Sophora* root nodules in New Zealand. *Int. J. Syst. Evol. Microbiol.* **2016**, *66*, 786–795. [CrossRef] [PubMed]
318. Perret, X.; Staehelin, C.; Broughton, W.J. Molecular basis of symbiotic promiscuity. *Microbiol. Mol. Bio. Rev.* **2000**, *64*, 180–201. [CrossRef]
319. Davis, E.O.; Evans, I.J.; Johnston, A.W. Identification of *nodX*, a gene that allows *Rhizobium leguminosarum* biovar *viciae* strain TOM to nodulate Afghanistan peas. *Mol. Gen. Genet.* **1988**, *212*, 531–535. [CrossRef] [PubMed]
320. Firmin, J.L.; Wilson, K.E.; Carlson, R.W.; Davies, A.E.; Downie, J.A. Resistance to nodulation of cv. Afghanistan peas is overcome by *nodX*, which mediates an O-acetylation of the *Rhizobium leguminosarum* lipo-oligosaccharide nodulation factor. *Mol. Microbiol.* **1993**, *10*, 351–360. [CrossRef] [PubMed]
321. Geurts, R.; Heidstra, R.; Hadri, A.E.; Downie, J.A.; Franssen, H.; van Kammen, A.; Bisseling, T. Sym2 of pea is involved in a nodulation factor-perception mechanism that controls the infection process in the epidermis. *Plant Physiol.* **1997**, *115*, 351–359. [CrossRef] [PubMed]
322. Ehinger, M.; Mohr, T.J.; Starcevich, J.B.; Sachs, J.L.; Porter, S.S.; Simms, E.L. Specialisation-generalisation trade off in a *Bradyrhizobium* symbiosis with wild legume hosts. *BMC Ecol.* **2014**, *14*, 8. [CrossRef] [PubMed]



© 2017 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).