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专论与综述

根瘤菌分类的新进展

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摘　要：近十多年来，根瘤菌的分类几经变迁，不断地增加一些新的属种到这个重要的细菌群体。本文综述了《伯杰氏系统细菌学手册》第2版发表至今根瘤菌分类的新进展。近年来发表的相关文献表明：从不同豆科植物分离出来的根瘤菌之间存在着极大的多样性。目前，根瘤菌多数属于α-和β-变形菌纲以及1个属于γ-变形菌纲的属，共计17个属，近100个种。它们分别是：α-变形菌纲中的 *Rhizobium* (根瘤菌属)、*Sinorhizobium* (中华根瘤菌属)、*Ensifer* (剑菌属)、*Shinella* (申氏杆菌属)、*Neorhizobium* (新根瘤菌属)、*Pararhizobium* (伴根瘤菌属)、*Mesorhizobium* (中慢生根瘤菌属)、*Bradyrhizobium* (慢生根瘤菌属)、*Phyllobacterium* (叶瘤杆菌属)、*Methylobacterium* (甲基杆菌属)、*Microvirga* (微枝形杆菌属)、*Ocrhobactrum* (苍白杆菌属)、*Azorhizobium* (固氮根瘤菌属)、*Devosia* (德沃斯氏菌属)；β-变形菌纲中的 *Burkholderia* (伯克氏菌属)、*Cupriavidus* (贪铜菌属，原青枯菌属)；γ-变形菌纲的 *Pseudomonas* (假单胞菌属)。目前世界各地约有748属19 700种豆科植物，而我国约有172属1 485种豆科植物，但在19 700种豆科植物中，只有23%的豆科植物经调查有结瘤能力。因此，有必要采用先进的方法研究不同地域的豆科植物，以此发现更多的根瘤菌新物种。

关键词：根瘤菌，豆科植物，分类学，细菌分类

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Advances in rhizobia taxonomy

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Abstract: Over the past decade, due to the addition of new genera and species to this important bacterial group, the classification of rhizobia has been gone through a substantial change. The recent progress of the classification of the rhizobia from the second edition of Bergey's Manual of Systematic Bacteriology to date was summarized in the paper. Browse our selection of published papers have shown a great diversity among nitrogen-fixing bacteria isolated from different legumes. Currently, about 100 species belonging to 17 genera of α-, β- and γ-Proteobacteria have been described as rhizobia. Class of α-Proteobacteria include the genera *Rhizobium*, *Sinorhizobium*, *Ensifer*, *Shinella*, *Neorhizobium*, *Pararhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Phyllobacterium*, *Methylobacterium*, *Microvirga*, *Ocrhobactrum*, *Azorhizobium* and *Devosia*; Class of β-Proteobacteria include *Burkholderia* and *Cupriavidus* (formerly *Ralstonia*); Class of γ-Proteobacteria include *Pseudomonas*. There are about 748 genera and 19 700 species of leguminosae plants around the world, and about 172 genera and 1 485 species of leguminosae plants in China. Among of the 19 700 species of leguminosae plants, only 23% leguminous plants have been surveyed the ablilty of nodulation. Therefore, it is necessary to survey the different regions of legumes using advanced methods, and we can obtain the new rhizobia resources.

Keywords: Rhizobia, Legume, Taxonomy, Bacterial classification

根瘤菌是一类生活在土壤中的革兰氏阴性杆状细菌，在合适的条件下，根瘤菌能侵染豆科植物并与之进行共生结瘤固氮，将空气中游离态的氮气转化成植物可以利用的化合态氮。根瘤菌与豆科植物的共生是生物固氮体系中作用最强的体系，据估计所固定的氮约占生物固氮总量的 65%。在研究根瘤菌与豆科植物共生关系的过程中，人们发现根瘤中同时定居着许多与根瘤菌不同的内生菌，这些非共生细菌生活在根瘤中，但不引起植物产生明显的病害，此类根瘤内生菌虽然不能形成根瘤，但是能产生植物激素，影响根的发育，促进植物对土壤中营养元素的吸收等[1-4]。另外，根瘤内生菌能够在没有豆科植物生长的土壤中长期存在，并可以通过接种与豆科植物相应的根瘤菌获得共生基因[5]。共生基因的横向转移在自然界普遍存在，依据种、属的不同，共生基因定位于质粒或染色体上，且可以在菌株间或种间转移[6]。这种现象最早出现在根瘤菌属 (*Rhizobium*)，之后在中华根瘤菌属 (*Sinorhizobium*)，剑菌属(*Ensifer*)，中慢生根瘤菌属 (*Mesorhizobium*) 以及慢生根瘤菌属 (*Bradyrhizobium*)，甚至在伯克氏菌属(*Burkholderia*)以及贪铜菌属(*Cupriavidus*)中均有这种现象出现[7]，这在根瘤微生态学研究上具有非常重要的意义。因此，研究人员不断地研究根瘤菌的多样性及生活习性等方面，发现了越来越多的新种：从 1932 年的 1 属 6 种，增加到现在的 17 属近 100 种；而且新的根瘤菌物种还在不断地被发现。

Zakhia 等建议使用 BNL (Bacteria nodulating legumes)来避免根瘤菌的一般术语与属名之间的混淆[8]。目前，所有描述的 BNL (根瘤菌)属于变形菌类，到目前为止共计发现 17 属。他们中的大多数，共计有 14 属都属于 α-变形菌纲。早期发现的属于 α-变形菌纲的 BNL 有根瘤菌属(*Rhizobium*)、慢生根瘤菌属 (*Bradyrhizobium*) 、固氮根瘤菌属 (*Azorhizobium*)、中慢生根瘤菌属(*Mezorhizobium*)、剑菌属(*Ensifer*)、中华根瘤菌属(*Sinorhizobium*)。此

外，他们还新发现了一些属于 α-变形菌纲的新属，即甲基杆菌属(*Methylobacterium*)、德沃斯氏菌属(*Devosia*)、微枝形杆菌属(*Microvirga*)、苍白杆菌属(*Ocrhobactrum*)、叶瘤杆菌属(*Phyllobacterium*)和申氏杆菌属(*Shinella*)。2014 年芬兰 Mousavi 等提出了一个新属，是将之前发现的几个新种合并到一起而提出的新属，属名为新根瘤菌属(*Neorhizobium*)[9]。2015 年芬兰的 Mousavi 等再次提出一个新属，属名为伴根瘤菌属(*Pararhizobium*)[10]。

Moulin 等 2001 年发现在 β-变形菌纲中也有一些细菌属于 BNL，比如：伯克氏菌属(*Burkholderia*)及贪铜菌属(*Cupriavidus*，原青枯菌属)[11]。另外，Shiraishi 等 2010 年研究发现刺槐中存在 γ-变形菌纲的假单胞菌属(*Pseudomonas*)[12]。

目前世界各地约有 748 属 19 700 种豆科植物，而我国约有 172 属 1 485 种豆科植物，但只有 23% 的豆科植物被调查过结瘤情况[13]。因此，有必要采用先进的方法研究不同地域的豆科植物，以此发现更多的根瘤菌新物种。

1 根瘤菌分类学的研究进展

早期的根瘤菌分类系统一直是以互接种族(Cross-inoculation group)为主要依据的。1926 年，Dangeard 根据宿主的种类和互接种族的关系，结合一些形态和生理性状，将根瘤菌分为若干种[14]。1932 年，Fred 等在此基础上，首次提出了根瘤菌分类系统，他们根据互接种族的关系，将全部根瘤菌分为 1 属 6 种[15]。随着研究工作的深入和结瘤豆科植物的不断发现，互接种族的概念陷入了混乱，族间结瘤的研究剧增。所以，许多学者对“互接种族”分类方法提出了质疑。

从 20 世纪 60 年代开始，细菌学家开始使用细菌形态多样性、营养代谢特征、血清学实验及简单的 DNA 特征来进行数值分类研究。《伯杰氏系统细菌学手册》第一卷(1984)进行了根瘤菌的分类系统的修订，提出了新的根瘤菌分类系统，即现代根瘤菌的分类系统。现代根瘤菌的分类系统证明了根瘤菌与农杆菌之间存在着一定的关系，Jordan 在比较了快生和慢生根瘤菌后，将慢生根瘤菌放在一个单独的属——慢生根瘤菌属(*Bradyrhizobium*)，与根瘤菌属(*Rhizobium*)并列[16]。

随着技术的发展，可以用更多具有多样性的遗传特征(DNA-DNA、DNA-rRNA 基因杂交以及 16S rDNA 序列)来区分根瘤菌与其他细菌，增加了许多新的根瘤菌属。在 16S rDNA 序列测定的基础上，目前所发现与豆科植物共生的根瘤菌可划分为 3 个纲[17]：α、β 和 γ-变形菌纲，其中 α-变形菌纲 14 个属[*Rhizobium* (根瘤菌属)、*Sinorhizobium* (中华根瘤菌属)、*Ensifer* (剑菌属)、*Shinella* (申氏杆菌属)、*Neorhizobium* (新根瘤菌属)、*Pararhizobium* (伴根瘤菌属)、*Mesorhizobium* (中慢生根瘤菌属)、*Bradyrhizobium* (慢生根瘤菌属)、*Phyllobacterium* (叶瘤杆菌属)、*Methylobacterium* (甲基杆菌属)、*Microvirga* (微枝形杆菌属)、*Ocrhobactrum* (苍白杆菌属)、*Azorhizobium* (固氮根瘤菌属)、*Devosia* (德沃斯氏菌属)]，β-变形菌纲 2 个属[*Burkholderia* (伯克氏菌属)和 *Cupriavidus* (贪铜菌属，原青枯菌属)][18-20]，还有 γ-变形菌纲 1 个属[*Pseudomonas* (假单胞菌属)] [21] (表 1)。表 1 中列出了《伯杰氏系统细菌学手册》第 2 版(2001−2007 年)以及后续发表的新种。

1.1 α-变形菌纲

1.1.1 根瘤菌属、中华根瘤菌属、剑菌属、申氏杆菌属、新根瘤菌属、伴根瘤菌属分支：根瘤菌属(*Rhizobium*)属于第 1 分支，包括 *R. yanglingense*[23]、*R. indigoferae*[25]、*R. sullae*[26]、*R. cellulosilyticum*[27]、*R. tubonense*[28]、*R. fabae*[29]、*R. miluonense*[30]、*R. multihospitium*[31]、*R. oryzae*[32] (这个新种是我们课题组 2008 年从野生稻 *Oryza alta* 中分离出的根瘤菌新种，证明了根瘤菌还能是禾本科植物内生菌，特别是谷物，并能促进水稻增产)、*R. pisi*[33]、*R. mesosinicum*[34]、*R. alamii*[35]、*R. alkalisoli*[36]、*R. tibeticum*[37]、*R. halophytocola*[37]、*R. endophyticum*[38]、*R. phaseoli*[38]、*R. sphaerophysae*[40]、

表 1 根瘤菌最新分类系统
Table 1 Advances of the rhizobia classification

属名 Genus	种名 Species	寄主植物 Host source	作者及年份 Author & Year	参考文献 References
Rhizobium	*R. radiobacter*		Young 等，2001	[22]
	R. rhizogenes		Young 等，2001	[22]
	R. rubi		Young 等，2001	[22]
	R. vitis		Young 等，2001	[22]
	R. yanglingense	*Amphicarpaea*	Tan ZY 等，2001	[23]
	R. larrymoorei	*Ficus benjamina*	Bouzart 等，2001	[24]
	R. indigoferae	*Indigofera* spp.	Wei，2002	[25]
	R. sullae	*Hedysarum coronarium*	Squartini 等，2002	[26]
	R. cellulosilyticum	*Populus alba*	García-Fraile 等，2007	[27]
	R. tubonense	*Oxytropis glabra*	El Akhal 等，2008	[28]
	R. fabae	*Vicia faba*	Tian 等，2008	[29]
	R. miluonense	*Lespedeza*	Gu 等，2008	[30]
	R. multihospitium	Multiple legume species	Han 等，2008	[31]
	R. oryzae	*Oryza alta*	Peng 等，2008	[32]
	R. pisi	*Pisum sativum*	Ramírez-Bahena 等，2008	[33]
	R. mesosinicum	*Albizia*, *Kummerowia*, *Dalbergia*	Lin 等，2008	[34]
	R. alamii	*Arabidopsis thaliana*	Berge 等，2009	[35]
	R. alkalisoli	*Caragana intermedia*	Lu 等，2009	[36]
	R. tibeticum	*Trigonella archiducis-nicolai*	Hou 等，2009	[37]
	R. halophytocola	Coastal dune plant	Hou 等，2009	[37]
	R. endophyticum	*Phaseolus vulgaris*	López-López 等，2010	[38]
	R. phaseoli	*Phaseolus*	López-López 等，2010	[38]
	R. kunmingense	*Camptotheca acuminata Decne*	Shen 等，2010	[39]
	R. sphaerophysae	*Sphaerophysa salsula*	Xu 等，2011	[40]
	R. pusense	*Chickpea*	Panday 等，2011	[41]
	R. pseudoryzae	Rice	Zhang 等，2011	[42]
	R. borbori	Sludge	Zhang 等，2011	[43]
	R. vignae	Multiple legume species	Ren 等，2011	[44]
	R. nepotum	Different plant species	Pulawska 等，2012	[45]
	R. taibaishanense	*Kummerowia striata*	Yao 等，2012	[46]
	R. skierniewicense	Chrysanthemum and Cherry plum	Pulawska 等，2012	[47]
	R. petrolearium	Oil-contaminated soil	Zhang 等，2012	[48]
	R. helanshanense	*Sphaerophysa salsula*	Qin 等，2012	[49]
	R. leucaenae	*Phaseolus*, *Medicago*, *Macroptilieum*	Ribeiro 等，2012	[50]
	R. cauense	*Kummerowia stipulacea*	Liu 等，2012	[51]
	R. pongamiae	*Pongamia pinnata*	Kesari 等，2013	[52]

(待续)

(续表)

	R. qilianshanense	*Oxytropis ochrocephala Bunge*	Xu 等，2013	[53]
	R. paknamense	*Lemna aequinoctialis*	Kittiwongwattana 等，2013	[54]
	R. subbaraonis	Beach sand	Ramana 等，2013	[55]
	R. populi	*Populus euphratica*	Rozahon 等，2014	[56]
	R. lemnae	*Lemna aequinoctialis*	Kittiwongwattana 等，2014	[57]
	R. azibense	*Phaseolus vulgaris*	Mnasri 等，2014	[58]
	R. rhizoryzae	Rice roots	Zhang 等，2014	[59]
	R. smilacinae	*Smilacina japonica*	Zhang 等，2014	[60]
	R. pakistanensis	*Groundnut*	Khalid 等，2015	[61]
	R. capsici	Green bell pepper	Lin 等，2015	[62]
Sinorhizobium[63]	*Sin. kummerowiae*	*Kummerowia stipulaceae*	Wei 等，2003	[64]
	Sin. numidicus	*Medicago sativa*	Merabet 等，2010	[65]
	Sin. garamanticus	*Medicago sativa*	Merabet 等，2010	[65]
Ensifer	*E. symbiovar acaciae*	*Acacia*	Young 等，2001	[22]
	E. americanum	*Acacia*	Toledo 等，2003	[66]
	E. mexicanus	*Acacia angustissima*	Lloret 等，2007	[67]
	E. sojae	*Glycine max*	Li 等，2011	[68]
	E. psoraleae		Wang 等，2013	[69]
	E. sesbaniae		Wang 等，2013	[69]
	E. morelense		Wang 等，2013	[69]
Shinella	*Shi. kummerowiae*	*Kummerowia stipulacea*	Lin 等，2008	[34]
	Shi. fusca	Domestic waste compost	Vaz-Moreira 等，2010	[70]
	Shi. daejeonensis	Sludge	Lee 等，2011	[71]
Neorhizobium	*R. galegae*		Mousavi 等，2014	[9]
	R. huautlense		Mousavi 等，2014	[9]
Pararhizobium	*Par. capsulatum*		Mousavi 等，2015	[10]
	Par. herbae		Mousavi 等，2015	[10]
	Par. sphaerophysae		Mousavi 等，2015	[10]
Mesorhizobium	*Mes. septentrionale*	*Astragalus adsurgens*	Gao 等，2004	[72]
	Mes. temperatum	*Astragalus adsurgens*	Gao 等，2004	[72]
	Mes. thiogangeticum	*Astragalus adsurgens*	Gao 等，2004	[72]
	Mes. albiziae	*Albzia kalkora*	Wang 等，2007	[73]
	Mes. caraganae	*Caragana* spp.	Guan 等，2008	[74]
	Mes. gobiense	Wild legumes	Han 等，2008	[31]
	Mes. tarimense	Wild legumes	Han 等，2008	[31]
	Mes. australicum	*Biserrula pelecinus*	Nandasena 等，2009	[75]
	Mes. opportunistum	*Biserrula pelecinus*	Nandasena 等，2009	[75]
	Mes. metallidurans	*Anthyllis vulneraria*	Vidal 等，2009	[76]

(待续)

(续表)

	Mes. robiniae	*Robinia pseudoacacia*	Zhou 等，2010	[77]
	Mes. alhagi	*Alhagi*	Chen 等，2010	[78]
	Mes. camelthorni	*Alhagi sparsifolia*	Chen 等，2011	[79]
	Mes. silamurunense	*Astragalus* species	Zhao 等，2012	[80]
	Mes. muleiense	*Cicer arietinum*	Zhang 等，2012	[81]
	Mes. tamadayense	*Anagyris latifolia*, *Lotus berthelotii*	Ramírez-Bahena 等，2012	[82]
	Mes. abyssinicae	Different agroforestry legume trees	Degefu 等，2013	[83]
	Mes. hawassense	Different agroforestry legume trees	Degefu 等，2013	[83]
	Mes. shonense	Different agroforestry legume trees	Degefu 等，2013	[83]
	Mes. qingshengii	*Astragalus sinicus*	Zheng 等，2013	[84]
	Mes. sangaii	*Astragalus luteolus* and *Astragalus ernestii*	Zhou 等，2013	[85]
Phyllobacterium	*P. trifolii*	*Trifolium pratense*	Valverde 等，2005	[86]
	P. endophyticum	*Phaseolus vulgaris*	Flores-Félix 等，2013	[87]
	P. loti	*Lotus corniculatus*	Sánchez 等，2014	[88]
Methylobacterium	*Met. nodulans*	*Crotalaria* spp.	Jourand 等，2004	[89]
	Met. graphalii	*Gnaphalium spicatum*	Tani 等，2012	[90]
	Met. oxalidis	*Oxalis corniculata*	Tani 等，2012	[91]
	Met. cerastii	*Cerastium holosteoides*	Wellner 等，2012	[92]
	Met. gossipiicola	Cotton phyllosphere	Madhaiyan 等，2012	[93]
	Met. haplocladii	Bryophytes	Tani 等，2013	[94]
	Met. brachythecii	Bryophytes	Tani 等，2013	[94]
	Met. tarhaniae	Arid soil	Veyisoglu 等，2013	[95]
	Met. trifolii	Leaf	Wellner 等，2013	[96]
	Met. thuringiense	Leaf	Wellner 等，2013	[96]
	Met. pseudosasicola	Bamboo leaf	Madhaiyan 等，2014	[97]
	Met. phyllostanhyos	Bamboo leaf	Madhaiyan 等，2014	[97]
	Met. murrellii	Pond water	Hoefman 等，2014	[98]
Microvirga	*Mic. lupini*	Different legume host	Ardley 等，2012	[99]
	Mic. lotononidis	Different legume host	Ardley 等，2012	[99]
	Mic. zambiensis	Different legume host	Ardley 等，2012	[99]
	Mic. vignae	Cowpea	Radl 等，2014	[100]
Ochrobactrum	*O. lupini*	*Lupinus albus*	Trujillo 等，2005	[101]
	O. cytisi	*Cytisus scoparius*	Zurdo-Piñeiro 等，2007	[102]
	O. ciceri	*Cicer arietinum*	Imran 等，2010	[103]
	O. pituitosum	Industrial environment	Huber 等，2010	[104]
	O. daejeonenso	Sludge	Woo 等，2011	[105]
	O. pecoris	Farm animals	Kämpfer 等，2011	[106]
Azorhizobium	*A. doebereinereae*	*Sesbania virgata*	de Souza Moreira 等，2006	[107]

(待续)

(续表)

	A. oxalatiphilum		Lang 等，2013	[108]
Devosia	*D. neptuniae*	*Neptunia natans*	Rivas 等，2003	[109]
	D. yakushimensis	*Pueraria lobata*	Bautista 等，2010	[110]
	D. lucknowensis	Hexachlorocydohexane	Dua 等，2013	[111]
	D. submarina	Deep-sea sediment	Romanenko 等，2013	[112]
	D. epidermidihirudinis	Medical leech	Galatis 等，2013	[113]
	D. pacifica	Deep-sea sediment	Jia 等，2014	[114]
Bradyrhizobium	*Bra. yuanmingense*	*Lespedeza*	Yao 等，2002	[115]
	Bra. betae	*Betae vulgaris*	Rivas，2004	[116]
	Bra. canariense	*Genisteae et Loteae*	Vinuesa 等，2005	[117]
	Bra. denitrificans	*Aeschynomene*	van Berkum 等，2006	[118]
	Bra. iriomotense	*Entada koshunensis*	Islam 等，2008	[119]
	Bra. jicamae	*Pachyrhizus erosus*	Ramírez-Bahena 等，2009	[120]
	Bra. pachyrhizi	*Pachyrhizus erosus*	Ramírez-Bahena 等，2009	[120]
	Bra. cytisi	*Cytisus villosus*	Chahboune 等，2011	[121]
	Bra. huanghuaihaiense	*Glycine max*	Zhang 等，2012	[122]
	Bra. daqingense	Soybean	Wang 等，2013	[123]
	Bra. oligotrophicum		Ramírez-Bahena 等，2013	[124]
	Bra. arachidis	*Arachis hypogaea*	Wang 等，2013	[125]
	Bra. retamae	*Retama sphaerocarpa* and *Monosperma*	Guerrouj 等，2013	[126]
	Bra. neotropicale	*Centrolobium paraense*	Zilli 等，2014	[127]
	Bra. ottawaense	Soybean	Yu 等，2014	[128]
	Bra. ingae	*Inga laurina*	da Silva 等，2014	[129]
Burkholderia[130]	*Bur. cepacia*	*Alysicarpus glumaceus*	Moulin 等，2001	[11]
	Bur. tuberum	Tropical legumes	Vandamme 等，2002	[131]
	Bur. phymatum	Tropical legumes	Vandamme 等，2002	[131]
	Bur. mimosarum	*Mimosa* spp.	Chen 等，2006	[132]
	Bur. rhizoxinica	*Rhizopus microsporus*	Partida-Martinez 等，2007	[133]
	Bur. endofungorum	*Rhizopus microsporus*	Partida-Martinez 等，2007	[133]
	Bur. nodosa	*Mimosa bimucronata*, *Mimosa scabrella*	Chen 等，2007	[134]
	Bur. sabiae	*Mimosa caesalpiniifolia*	Chen 等，2008	[135]
	Bur. bannensis	*Panicum repens*	Aizawa 等，2011	[136]
	Bur. symbiotica	*Mimosa* spp.	Sheu 等，2012	[137]
	Bur. diazotrophica	*Mimosa* spp.	Sheu 等，2013	[138]
	Bur. aspalathi	*Aspalathus abietina*	Mavengere 等，2014	[139]
	Bur. magalochromosomata	Grassland soil	Baek 等，2015	[140]
	Bur. susongensis	Rock surface	Gu 等，2015	[141]
Cupriavidus	*C. taiwanensis*	*Mimosa* sp.	Vandamme 等，2004	[142]
	C. yeoncheonense	Soil	Singh 等，2015	[143]
Pseuomonas	*Pseuomonas* sp.	*Robinia pseudoacacia*	Shiraishi 等，2010	[12]

R. helanshanense[49]、*R. leucaenae*[50]、*R. cauense*[51]、*R. pongamiae*[52]、*R. qilianshanense*[53]、*R. azibense*[58]、*R. pakistanensis*[61]、*R. capsici*[62]等。该属是革兰氏阴性细菌，0.5−0.9 μm 宽及 1.2−3 μm 长。这些细菌不形成芽孢，但具有 2−6 根周身鞭毛，需氧，化能有机营养型。还有一些以前属于农杆菌属的 *R. radiobacter*[22]、*R. rhizogenes* [22]、*R. rubi*[22]、*R. vitis*[22]和 *R. nepotum*[45]，它们本该属于该属，却因未被发现能够形成根瘤，不适合将其归为根瘤菌属。然而，最近有研究表明，一些农杆菌属的种也能够与豆科植物形成根瘤。例如：一些 *R. radiobacter*[22]菌株可以与菜豆属、杭子梢属、槐属[144]和紫藤[145]结瘤。Young 等在 2001 年对比分析不同的 16S rDNA 序列系统发育关系[22]，最后建议将根瘤菌、土壤杆菌属合在一个属，即根瘤菌属，包括所有属于农杆菌属与土壤杆菌属的种都归属为根瘤菌属，其中包括：*R. radiobacter*[22]、*R. rhizogenes*[22]、*R. rubi*[22]、*R. vitis*[22]和 *R. undicola*[146]。

中华根瘤菌属(*Sinorhizobium*)和剑菌属(*Ensife*r)属于第 2 分支，包括 *Sin. xingianense*[63] (这是中国农业大学陈文新院士课题组于 1988 年发表的新属新种，通讯作者在该课题组的硕士论文内容利用分子生物学方法再次确认为一个新种)，*E. symbiovar acacia*[22]、*Sin. kummerowiae*[64]、*Sin. numidicus*[65]、*Sin. garamanticus*[65]、*E. americanum*[66]和 *E. mexicanus*[67]。该支是革兰氏阴性细菌，0.5−0.9 μm 宽，1.2−3 μm 长，有极性鞭毛或周身鞭毛，需氧。Garcia 等 2012 年研究发现该支细菌的最佳生长环境：温度 25−30 °C (10−35 °C)，pH 6.0−8.0 (5.0−10.5)，能够忍受 10 g/L 的氯化钠溶液[146]。

中华根瘤菌属(*Sinorhizobium*)是陈文新院士 1988 年从根瘤菌和慢生根瘤菌中分离出来的，建议作为大豆根瘤菌的一个新属，而 2003 年 Young 等根据 16S rRNA 基因序列及其他部分看家基因的系统进化分析，发现两个属菌种的 16S rRNA 基因相似性在 99%以上，建议将中华根瘤菌属转移到剑菌属[147]。但是将两个属合并存在争议，原因在于 *Ensifer* 只包含 3 个种，且不能与豆科植物结瘤固氮，只是土壤中捕食其它细菌的细菌。*Sinorhizobium* 包含多个与豆科植物共生的根瘤菌，在名字中含有根瘤菌词根，使研究者更容易辨认属根瘤菌的范畴(http://en.wikipedia.org/wiki/Sinorhizobium)，而且 *Sinorhizobium* 是一类广为人知的种类，已经有十余个种属于 *Sinorhizobium*，在生产实践中的应用也较为广泛。经过几年的讨论，国际原核生物系统学会裁决委员会最终于 2008 年在 IJSEM 上正式发布相关的裁决结果，即 *Sinorhizobium* 与 *Ensifer* 为同物异名。

申氏杆菌属(*Shinella*)属于第 3 分支，包括 3 个物种：*Shi. kummerowiae*[34]、*Shi. fusca*[70]及 *Shi. daejeonensis*[71]。该属菌株是革兰氏阴性，严格需氧，无孢子[34]。

新根瘤菌属(*Neorhizobium*)属于第 4 分支，包括 *R. galegae*[9]、*R. huautlense*[9]、*R. alkalisoli*[36]和 *R. vignae*[44]。

伴根瘤菌属(*Pararhizobium*)属于第 5 分支，包括 *Par. capsulatum*[10]、*Par. herbae*[10]、*Par. sphaerophysae*[10]及以前属于根瘤菌属的种(*R. vitis*[22]、*R. oryzae*[32]、*R. pusense*[41]、*R. pseudoryzae*[42]、*R. borbori*[43]、*R. nepotum*[45]、*R. taibaishanense*[46]、*R. skierniewicense*[48]、*R. paknamense*[54])。

1.1.2 中慢生根瘤菌属分支：在 1997 年提出一个新属，将其命名为中慢生根瘤菌[148]，该属是革兰阴性杆菌，有鞭毛，好氧，属于叶杆菌科[86]。中慢生根瘤菌属这个分支，包括 *Mes. septentrionale*[72]、*Mes. temperatum*[72]、*Mes. thiogangeticum*[72]、*Mes. albiziae*[73]、*Mes. robiniae*[77]、*Mes. muleiense*[81]、*Mes. tamadayense*[82]及 *Mes. qingshengii*[84]等。Garcia 等 2012 年研究发现它们能够利用葡萄糖、鼠李糖和蔗糖产酸[146]。

1.1.3 固氮根瘤菌属分支：该属包括 *A. dodereinereae*[107]和 *A. oxalatiphilum*[108]，都是短杆，具有极性和周身鞭毛，只能利用葡萄糖，另外有机酸类如乳酸盐和琥珀酸盐是其良好的碳源。该属的

代时为 7−9 h。该属菌株不具有反硝化功能，能够在 43 ºC 以上的高温环境下生长。Rivas 等 2003 年发现另一个物种 *A. johannae* 与该属的典型菌株相比，具有较低的 DNA/DNA 杂交比[109]。D'Haeze 等 2004 年研究发现它不仅在根部结瘤，同样还能够在长喙田菁的地上部分结瘤[148]。此外，Garcia 等 2012 年研究发现它们对抗生素极其敏感[146]。

1.1.4 慢生根瘤菌属分支：该属包括所有慢生根瘤菌[16]，都具有单极性的短棒或鞭毛，代时为 10−12 h。该属细菌在酵母菌培养基中的菌落直径不超过 1 mm[149]，能够利用糖类及有机酸，但更倾向于利用戊糖。Garcia 等 2012 年研究发现该属细菌对抗生素的抗药性比固氮根瘤菌强[146]。Hollis 等基于获得的同源性 DNA/DNA 杂交，将慢生大豆根瘤菌分为 3 组(Ⅰ，Ⅰa 和Ⅱ)[150]。de Souza Moreira 等于 2006 年将一个新种(埃氏慢生根瘤菌，*Bradyrhizobium elkanii*)划分为Ⅱ组，它不同于其他慢生型根瘤菌[107]。慢生根瘤菌属还包括一些分类地位不明确的菌株。慢生型大豆根瘤菌和埃氏慢生型根瘤菌之间的差异是较明显的，比慢生根瘤菌属(*Bradyrhizobium*)与阿菲波菌属(*Afipia*，动物细菌病原体)、硝化菌属(*Nitrobacter*，土壤中的硝化细菌)、沼泽红假单胞菌(*Rhodopseudomonas palustris*，光合菌)和脱氮芽生杆菌(*Blastobacter denitrificans*)之间的差异更为明显[130]。Zhang 等 2012 年在中国北方(黄淮海地区)平原的不同地点采集大豆根瘤，从中分离出了一个新种(*Bra. huanghuaihaiense*)[122]，这些菌株在与野生大豆和豇豆的交叉结瘤实验中表现出较高活性。

Parker 等 2002 年发现慢生根瘤菌菌株与一种莱豆属的野生植物可以结瘤[151]。慢生根瘤菌属的其他种是从有肿瘤样变形的甜菜粘菌根中分离出来的[116],还有一些是从加那利群岛豆科植物中分离出来的[117]。许多慢生根瘤菌从其他豆科植物宿主中分离，随后根据寄主豆科植物来命名，如：Ramírez-Bahena 等 2009 年从薯类的结瘤中分离出 *Bra. pachyrhizi*[120]，Chahboune 等 2011 年从金雀儿属中分离出 *Bra. cytisi*[121]，以及 Wang 等 2013 年从大豆分离出新种 *Bra. daqingense*[123]。van Berkum 等 2006 年基于 ITS 序列数据，研究从合萌属植物茎瘤中分离出来的脱氮芽生杆菌菌株与慢生根瘤菌属，提出将脱氮芽生杆菌移到慢生根瘤菌属[118]。

1.1.5 甲基杆菌属分支：该属原来只有 1 个种，即 *Met. nodulans*[152]，可以与猪屎豆结瘤[89]。后来，随着分子生物学新技术的发展，增加了 12 个新种(*Met. pseudosasicola*、*Met. phyllostanhyos*、*Met. murrellii*、*Met. haplocladii*、*Met. brachythecii*、*Met. tarhaniae*、*Met. trifolii*、*Met. thuringiense*、*Met. graphalii*、*Met. oxalidis*、*Met. cerastii*、*Met. gossipiicola*)。该属细菌都是杆状，具有单个极性鞭毛，严格好氧菌，呈革兰氏阴性，最佳温度是 25−30 ºC。另外，甲基杆菌属菌株由于类胡萝卜素的存在，有一个典型的粉红色的色素沉着[153]，因此通常被人们称为"粉红颜料兼甲基营养菌"。

1.2 β-变形菌纲

伯克氏菌属分支：Yabuuchi 等在 1992 年基于基因组以及细胞脂质成分的考虑提出了伯克氏菌属[154]。本属有 14 个种(*Bur. cepacia*、*Bur. tuberum*、*Bur. phymatum*、*Bur. nodosa*、*Bur. sabiae*、*Bur. mimosarum*、*Bur. rhizoxinica*、*Bur. diazotrophica*、*Bur. endofungorum*、*Bur. bannensis*、*Bur. symbiotica*、*Bur. aspalathi*、*Bur. magalochromosomata*、*Bur. susongensis*)，主要表型特征是革兰氏阴性，能积聚 β-羟基丁酸，一种或多种极性鞭毛，严格需氧。Secher 等 2013 年研究了噬异源化合物伯克氏菌(原洋葱假单胞菌)和多氯联的有机联系[155]。Chen 等[132] 2006 年发现，β-变形菌纲细菌[伯克氏菌属(*Burkholderia*)和贪铜菌属(*Cupriavidus*)]及分离自豆科植物根瘤的 γ-变形菌纲细菌[假单胞菌属(*Pseudomonas*)]能够与豆科植物结瘤[21]。基于这些发现，不排除找到能够与豆科植物结瘤的其他细菌，甚至是变形杆菌范围之外的细菌[17]。

1.3 其他固氮根瘤菌

有研究者发现在传统根瘤菌范围外，存在能够

固氮的新种，它们包括 α-变形菌纲的苍白杆菌属(*Ocrhobactrum*)和微枝形杆菌属(*Microvirga*)，以及β-变形菌纲的贪铜菌属(*Cupriavidus*) [17]。Rivas 等2003 年将印度戴沃斯菌属菌株 *D.neptuniae* 归为 α-变形菌[109], Trujillo 等于 2006 年从白羽扇豆中分离出 *Ochrobactrum lupini* 菌株[101], Zurdo-Piñeiro 等于2007 年从金雀花中分离出 *Ochrobactrum cytisi* 菌株[102]，*Microvirga lupini*[99]菌株是从羽扇豆被分离出来，Ardley 等于 2012 年从不同豆科植物中分离出微枝形杆菌属菌株 *Mic. lotononidis* 和 *Mic. zambiensis*[99]。

2 根瘤菌分类方法的新进展

根瘤菌的分类同细菌分类一样，依赖于表型和遗传型特征相结合的多相分类(Polyphasic taxonomy)方法。虽然在根瘤菌的多相分类中，表型分群方法曾在根瘤菌数值分类和新种描述中起着重要作用，是新种描述的必需指标[51]，但是由于表型测定的工作繁琐，受影响条件较多，重复性不是很好，与基因型研究的结果不一致等。因此，随着根瘤菌基因组测序及比较基因组学的发展，基于基因组的分类逐渐成为提出根瘤菌新种的可靠方法。

另外，16S rDNA 全序列分析和 DNA-DNA 同源性分析存在明显的缺陷：(1) 16S rRNA 基因的高保守性，使其在种以下水平的分类具有很大局限性；(2) DNA-DNA 杂交技术缺乏一致性，差异大，无法建立一个中心数据库；(3) 基因水平转移，尤其是保守基因片段的水平转移可以引起现有细菌分类体系的混乱[156]。

然而随着核酸测序技术的迅速发展，越来越多的基因组序列已经完成测定，研究者便可以利用多个基因信息之间相互比较，综合分析得到一个全面可信的物种间的关系，相比 16S rRNA 基因的高度保守性，具有更高分化程度的看家基因更适用于菌种的鉴定。Zeigler 认为筛选过的少数看家基因序列的精确度甚至优于DNA-DNA杂交的基因组同源性分析[157]。因此，多位点序列分析(Multilocus sequence typing，MLSA)可运用于从种内到种间甚至更高级别的分析。目前，已经有十几种保守基因用于根瘤菌的系统发育研究，如 *atpD*、*dnaK*、*gap*、*glnA*、*glnII*、*gltA*、*gyrB*、*pnp*、*recA*、*rpoB* 及 *thrC*，就根瘤菌而言还包括共生基因 *nodA*、*nodC*、*nifD*、*nifH* 等。运用 MLSA 比较细菌基因组之间的差别，证明了不同遗传背景的根瘤菌之间的共生基因可通过横向转移的方式由一个菌转移到另一个菌，而且这方面的证据越来越多[7]。结瘤基因可以在不同的 *S. meliloti* 生物型之间通过横向基因转移的方式进行交换，但存在于同一环境中的 *S. meliloti* bv. meliloti 和 *S. medicae* 两个不同种之间却始终是两个不同的种[158]。随着对根瘤菌分类研究的积累及其与豆科植物互作关系研究的深入，共生基因的横向转移对未来根瘤菌分类也会产生重要影响。另外，细菌全基因核苷酸高通量测序的完成为研究者研究微生物物种的遗传特性、鉴定新种提供了一个新方法。Richter 等在对大量细菌全基因组序列分析的基础上，提出了部分或全部基因组序列 ANI (Average nucleotide identity)分析作为细菌分类的黄金标准，代替传统的 DNA 同源性分析[159]。另外，Vandamme 和 Peeters 于 2014 年提议以后的细菌多相分类中，特别是在新种的鉴定与发表中，必须增加全基因组信息，以及采用快速高效的表型鉴定系统对细菌必需特征进行测定[160]。

3 讨论与建议

近年来在根瘤菌分类方法及分类系统研究上取得了长足的发展，随着寄主范围的不断扩大和分子生物学技术的发展和应用，从早期的互接种族关系为唯一依据发展到目前以系统发育为核心的根瘤菌分类，这样有助于人们理解根瘤菌自身的进化和发育过程以及根瘤菌和相关物种之间的亲缘关系。

但是，我国对根瘤菌资源的开发利用，总体来看还是极其有限的，只有少部分根瘤菌用于制造菌剂，推广利用于农业生产和科学研究工作。因此，当前的任务除了长期有效地保护已有的菌种资源，深入研究各类菌种的特性外，还要继续从自然界中

分离筛选出新的根瘤菌种与寄主植物之间的优良组合，以不断满足共生固氮研究和根瘤菌接种剂生产对菌种资源的需要。然而，目前根瘤菌固氮效率的研究仅仅局限于根瘤菌与植物共生结瘤固氮的单个效应上，对根瘤菌与化学肥料，与其他促生菌、抑制菌等之间的协同作用、拮抗作用的研究不够深入，技术不够成熟，严重影响根瘤菌的促生效果和推广应用。因此，广泛开展根瘤菌资源调查，筛选和培育高效优良的固氮菌株(包括抗逆性菌株)，扩大固氮资源应用范围和应用效果的研究，是目前根瘤菌研究的重点。

4 结论与展望

根瘤菌分类学研究从 1932 年 1 属 6 种增加到现在的 17 属近 100 种，这是世界各国研究者共同的贡献，其中中国的根瘤菌分类专家也做出了重要的贡献，例如：陈文新院士课题组，发表根瘤菌新属 2 个，新种 15 个；谭志远教授课题组在国际上合作发表 11 个生物固氮细菌新种，1 个新属；韦革宏教授课题组发现了 3 个根瘤菌新种等。因此，随着根瘤菌资源的不断挖掘以及分子生物学技术的不断发展，今后将会有更多、更准确的方法出现，不断充实和完善着根瘤菌分类系统，使人们对根瘤菌的系统发育地位和进化本质能有更深入的认识。

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