



History and current taxonomic status of genus *Agrobacterium*

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ABSTRACT

The genus *Agrobacterium* was created a century ago by Conn who included it in the family *Rhizobiaceae* together with the genus *Rhizobium*. Initially, the genus *Agrobacterium* contained the non-pathogenic species *Agrobacterium radiobacter* and the plant pathogenic species *Agrobacterium tumefaciens* and *Agrobacterium rhizogenes*. At the end of the past century two new pathogenic species, *Agrobacterium rubi* and *Agrobacterium vitis*, were added to the genus. Already in the present century these species plus *Agrobacterium larrymoorei* were reclassified into genus *Rhizobium*. This reclassification was controversial and for a time both genus names were used when new species were described. Few years ago, after a taxonomic revision based on genomic data, the old species *A. rhizogenes* was maintained in the genus *Rhizobium*, the old species *A. vitis* was transferred to the genus *Allorhizobium* and several *Rhizobium* species were transferred to the genus *Agrobacterium*, which currently contains 14 species including the old species *A. radiobacter*, *A. tumefaciens*, *A. rubi* and *A. larrymoorei*. Most of these species are able to produce tumours in different plants, nevertheless the genus *Agrobacterium* also encompasses non-pathogenic species, one species able to nodulate legumes and one human pathogenic species. Taking into account that the species affiliations to five *Agrobacterium* genomospecies have not been determined yet, an increase in the number of species within this genus is expected in the near future.

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The *Agrobacterium* taxonomy in the past century

The genus *Agrobacterium* was created by Conn [9] who included it within the family *Rhizobiaceae* [8] together with the genus *Rhizobium* [14]. In the 5th edition of the Bergey's Manual of Determinative Bacteriology, the species included into the genus *Agrobacterium* were *Agrobacterium radiobacter*, *Agrobacterium tumefaciens* and *Agrobacterium rhizogenes*. In the 6th edition of this Manual the plant tumorigenic species *Agrobacterium rubi* [17,48] was included, being differentiated from *A. tumefaciens* on the basis of the ability to reduce nitrate to nitrite [6]. In the 7th edition of this Manual the species *Agrobacterium stellulatum*, *Agrobacterium pseudotsugae* and *Agrobacterium gypsophilae* were added to the genus [7], but this inclusion was later considered

unjustified because they probably belong to other genera [23]. Therefore, in the subsequent 8th edition of the Bergey's Manual only four species were included, *A. radiobacter*, which was non-pathogenic, *A. rhizogenes*, which induced hairy roots, and *A. tumefaciens* and *A. rubi*, which induced plant galls. The differentiation of these species was based on some phenotypic characteristics together with their ability to produce diverse symptoms in different plants [1]. These four species were included in the validation lists of Skerman et al. [45], who indicated that *A. tumefaciens* is the type species of genus *Agrobacterium*.

During the 70 and 80s of the past century, several studies including strains isolated from different sources were performed and the existence of different varieties, biovars and/or biotypes was deeply revised by Young [58]. Some authors proposed that the species *A. tumefaciens* and *A. radiobacter* constitute a single species, *A. radiobacter* [20], later named *A. radiobacter* var. *tumefaciens* [21]. However, considering that *A. tumefaciens* was considered the type species of the genus *Agrobacterium* by Skerman et al. [45], Holmes and Roberts considered that the correct name for the unified taxon is *A. tumefaciens* [18].

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Nonetheless, in the 1st edition of the Bergey's Manual of Systematic Bacteriology published in 1984, Kersters and de Ley [22] maintained the four species, but they included three biovars in the species *A. tumefaciens* and two biovars in the species *A. radiobacter*, assigning the species *A. rhizogenes* to a namely biovar 2 and maintaining the species *A. rubi*. In this edition of the Bergey's Manual a higher number of phenotypic characteristics were recorded for the *Agrobacterium* species, but their differentiation continued to be mainly based on phenotypic and phytopatogenicity tests [22].

At the beginning of the 90s several changes were proposed within the genus *Agrobacterium* including the description of new species, nevertheless none of these changes were recorded in the 9th and last edition of the Bergey's Manual of Determinative Bacteriology published in 1994, which included the same species that the previous version of this Manual [19]. In year 1990 the strains from the biovar 3 of *A. tumefaciens* producing tumours in *Vitis vinifera* were included into a new species of genus *Agrobacterium* named *A. vitis* [32]. In the description of this species, in addition to the classic phenotypic and phytopatogenicity tests, the authors carried out DNA–DNA hybridization among the type strains of the *Agrobacterium* species described to date and among several strains of the new proposed ones. The results obtained in this work showed that the type strain of *A. vitis* presented less than 50% DNA–DNA relatedness with respect to the type strains of the remaining *Agrobacterium* species, whereas the analysed strains of *A. vitis* presented values ranging from 80 to 92% among them. Surprisingly, the type strains *A. tumefaciens* NCPPB 2437^T and *A. radiobacter* ATCC 19358^T also presented DNA–DNA relatedness values within this range [32].

In 1992, Rügner and Höfle [41] included several strains isolated from marine sources in several species of the genus *Agrobacterium* recovering the names *A. stellulatum*, *Agrobacterium ferrugineum* and *Agrobacterium gelatinovorum*, which were not included in the validation lists of Skerman et al. [45], and proposing the new species *Agrobacterium atlanticum* and *Agrobacterium meteori*. In this work the *Agrobacterium* species previously described were not included and the classification of the new proposed ones was based in the initial assignment of *A. stellulatum* to the genus *Agrobacterium* [47] being differentiated the new species on the basis of phenotypic traits and the low DNA–DNA relatedness found among them [41]. All these species were later reclassified in other genera. The species *Agrobacterium atlanticum* and *Agrobacterium meteori* were reclassified into *Ruegeria atlantica* [51,52]. The type strain of *Agrobacterium ferrugineum* was reclassified into *Pseudorhodobacter ferrugineus* [50,53] and the strain LMG 128 into *Hoeflea marina* [37]. *Agrobacterium stellulatum* was reclassified into *Stappia stellulata* [51,52] and *Agrobacterium gelatinovorum* was reclassified into *Ruegeria gelatinovorans* [51,52] and later into *Thalassobius gelatinovorans* [2].

A year after, Sawada et al. [43] revised the taxonomic status of *Agrobacterium* species described until year 1990. In this work the 16S rRNA (*rrs*) gene sequences of representative strains of the biovar 1 (*A. tumefaciens*–*A. radiobacter*), biovar 2 (*A. rhizogenes*), biovar 3 (*A. vitis*) and *A. rubi* were obtained and compared with those of the several species from different alpha Proteobacteria genera, including the genus *Rhizobium*. The analysis of this gene showed that the strains from biovar 1 were related to *A. rubi*, but those from the biovars 2 and 3 were phylogenetically divergent being the strains from the biovar 2 very closely related to the type strain of *Rhizobium tropici*. Nevertheless, despite the species *A. rhizogenes* was emended, it was maintained within the genus *Agrobacterium*. Moreover, it was reported that the type strains of *A. tumefaciens* NCPPB 2437^T and *A. radiobacter* IAM 12048^T have 87% DNA–DNA relatedness in agreement with the results from Ophel and Kerr [32] for *A. tumefaciens* NCPPB 2437^T and *A. radiobacter* ATCC 19358^T. Therefore, Sawada et al. concluded that these two strains cannot be placed in different species and they indicated that according to the Rule 38 of the

International Code of Nomenclature of Bacteria the species established earlier should be maintained [28]. Since *A. radiobacter* was described in 1902 (as *Bacillus radiobacter*) by Beijerinck and van Delden [4] and *A. tumefaciens* was described in 1907 (as *Bacterium tumefaciens*) by Smith and Townsend [46], Sawada et al. [43] proposed to name the strains of biovar 1 as *A. radiobacter* and to reject the species name *A. tumefaciens*. Thus, at the end of the past century *A. radiobacter*, *A. rhizogenes*, *A. rubi* and *A. vitis* were considered the valid species of genus *Agrobacterium*.

The taxonomy of genus *Agrobacterium* from 2000 onwards

The most relevant and conflictive change in the taxonomic status of genus *Agrobacterium* took place in year 2001 when Young et al. [60] proposed the reclassification of the complete genus *Agrobacterium* into the genus *Rhizobium*. This reclassification was based on the results of Sawada et al. [43] and, therefore, the *Agrobacterium* species were reclassified as *Rhizobium radiobacter*, *Rhizobium rhizogenes*, *Rhizobium rubi* and *Rhizobium vitis*. The reclassification, which was based on the *rrs* gene sequences analysed by Maximum-likelihood and Neighbour-joining methods, was not accepted by many authors who signed the letter of Farand et al. [13]. These authors considered that only the biovar 2 belongs to genus *Rhizobium* and that classical and molecular data support that *Agrobacterium* and *Rhizobium* are different genera. This letter was later replied by Young et al. [61] and the controversy was settled by keeping the reclassification. Considering this decision, Young [57] also proposed the reclassification of the species *Agrobacterium larrymoorei*, which was described in 2001 [5], as *Rhizobium larrymoorei*. Nevertheless, this species was not included in the 2nd edition of the Bergey's Manual which only included the species *A. tumefaciens*, *A. rhizogenes*, *A. rubi* and *A. radiobacter*. Curiously, in this edition of Bergey's Manual the official reclassification of *Agrobacterium* species into the genus *Rhizobium* was disregarded, although the authors make a historical review of the nomenclature problems affecting the genus *Agrobacterium* over the time [59].

Due to the confusion generated after the reclassification of genus *Agrobacterium* into genus *Rhizobium*, the new species described since 2001 outside the official journal for description of new taxa of Prokaryotes (IJSEM) were named *Agrobacterium*, as occurred in the case of *Agrobacterium albertimagni* isolated from aquatic plants, in whose description, as occurred in the case of *A. larrymoorei* described a year before, only the *rrs* gene was included [42]. However, the species described outside the mentioned journal were named *Rhizobium* and the analysis of several housekeeping genes was included in their descriptions in addition to that of the *rrs* gene. These species were *Rhizobium pusense*, isolated from chickpea rhizosphere [35], *Rhizobium nepotum*, isolated from tumours of different plants [38] and *Rhizobium skierniewicense* isolated from tumours of chrysanthemum and cherry plum [39].

In parallel, the *Agrobacterium* strains from different species were distributed into the genomic groups (genomic species, genomospecies, genomovars) G1 to G9, G11, two unnamed genomic groups and G13 [10,11,30]. At the time of these works, the G4 included the type strains of *A. tumefaciens* and *A. radiobacter*, the G11 that of *A. rubi*, the G10 that of *A. rhizogenes* and the two unnamed groups included several strains of *A. larrymoorei* and *A. vitis* [30]. Later it was shown that the G8 corresponds to the species *A. fabrum* [29], the G2 to the species *R. pusense* [3,35] and a new genomovar, named G14, corresponds to the species *R. nepotum* [38,44].

The taxonomic status of these species was changed again when Mousavi et al. [31] based on the analysis of the *rrs*, *recA*, *atpD* and *rpoB* genes proposed to transfer *R. pusense*, *R. nepotum* and *R. skierniewicense* to genus *Agrobacterium* and *R. vitis* (initially *A. vitis*) to genus *Allorhizobium*, as new combinations, which were

Table 1
Species currently included in the genus *Agrobacterium* and species causing tumours or hairy roots currently included in other genera of Family *Rhizobiaceae*.

Species	Source of isolation	Pathogenicity symptoms	References
Genus <i>Agrobacterium</i>			
<i>A. radiobacter</i> ^a	Soil and plant rhizosphere	Non-pathogenic	[4,9]
<i>A. tumefaciens</i> ^a	<i>Malus</i> sp. tumours	Tumours	[9,46]
<i>A. rubi</i>	<i>Rubus</i> sp. tumours	Tumours	[17,48]
<i>A. larrymoorei</i>	<i>Ficus benjamina</i> tumours	Tumours	[5]
' <i>A. albertimagni</i> '	<i>Potamogeton pectinatus</i>	No data	[42]
' <i>A. fabrum</i> '	<i>Prunus</i> sp., <i>Humulus lupulus</i> , <i>Euonymus alata</i> , <i>Rubus macropetalus</i> tumours	Tumours	[29]
<i>A. pusense</i>	<i>Cicer arietinum</i> rhizosphere	No data	[31,35]
<i>A. nepotum</i>	<i>Prunus</i> , <i>Vitis</i> and <i>Rubus</i> tumours	Tumours	[31,38]
<i>A. skiemiewicence</i>	<i>Chrysanthemum</i> and <i>Prunus</i> tumours	Tumours	[39]
<i>A. arsenijevecii</i>	<i>Prunus</i> and <i>Rubus</i> tumours	Tumours	[25]
' <i>A. deltaense</i> '	<i>Sesbania cannabina</i> nodules	No data	[55]
<i>A. salinitolerans</i>	<i>Sesbania cannabina</i> nodules	No data	[56]
' <i>A. bohemicum</i> '	<i>Papaver somniferum</i>	Non-pathogenic	[62]
<i>A. rosae</i>	<i>Rosa x hybrida</i> tumours	Tumours	[26]
Genus <i>Allorhizobium</i>			
<i>A. vitis</i>	<i>Vitis vinifera</i> tumours	Tumours	[31,32]
Genus <i>Rhizobium</i>			
<i>R. rhizogenes</i>	<i>Malus</i> sp.	Hairy roots	[9,40]
' <i>R. tumorigenes</i> '	<i>Rubus</i> sp. tumours	Tumours	[27]

^a We have included these two species names taking into account the current decision of the Judicial Commission [49]. Gan et al. [22] proposed that they belong to different subspecies of the species *A. radiobacter*. The quoted names correspond to species that have not been officially validated to date.

later validated in IJSEM [33]. The old species *A. rhizogenes* was maintained as *Rhizobium rhizogenes* in the genus *Rhizobium*, which currently also contains the new species *Rhizobium tumorigenes* able to induce plant tumours [27]. Mousavi et al. [31] did not consider the species *Agrobacterium fabrum* isolated from tumours of various plants [29] because it was not officially proposed, although the complete genome of its type strain C58 was the first obtained for a member of the genus *Agrobacterium* and it was sequenced twice independently due to the importance of this strain for plant genetic engineering [16,54].

Since 2015, several new species of genus *Agrobacterium* have been described based on the analyses of the *rrs* and several housekeeping genes and, in some cases, the complete genomes. Some of these species were isolated from plant tumours, such as *Agrobacterium arsenijevecii* [25] and *Agrobacterium rosae* [26], but others were isolated from legume nodules, such as *Agrobacterium deltaense* [55] and *Agrobacterium salinitolerans* [56], or plant wastes, such as *Agrobacterium bohemicum* [62]. In some of these works a strain named KB-105 (ATCC31113) from *Agrobacterium viscosum* was mentioned [12], nevertheless this species has not been officially proposed and moreover the strain KB-105, which is not a type strain, is currently included in a patent (U.S. Patent Number 4,028,185). Therefore, *A. viscosum* cannot be considered a valid species to date and then it has not been included in the present study.

Concerning to the old species of genus *Agrobacterium* that were not transferred to other genera by Mousavi et al. [31], they return to their initial names *A. tumefaciens*, *A. radiobacter*, *A. rubi* and *A. larrymoorei*. Nevertheless, there is a problem with the names of the two first species as was pointed out by Sawada et al. [43] who, considering that the name *A. radiobacter* has priority, proposed the rejection of the name *A. tumefaciens*. Nevertheless, according to Rule 56a of the International Code of Nomenclature of Bacteria, only the Judicial Commission can place a name on the list of rejected names [28,36]. After years of discussion about this issue, the last decision of this Commission taken in 2014 is that "the combination *Agrobacterium radiobacter* (Beijerinck and van Delden 1902) Conn 1942 has priority over the combination *Agrobacterium tumefaciens* (Smith and Townsend 1907) Conn 1942 when the two are treated as members of the same species based on the principle of priority as applied to the corresponding specific epithets. The type species of the genus is *Agrobacterium tumefaciens* (Smith and Townsend 1907) Conn 1942, even if treated as a later heterotypic

synonym of *Agrobacterium radiobacter* (Beijerinck and van Delden 1902) Conn 1942. *Agrobacterium tumefaciens* (Smith and Townsend 1907) Conn 1942 is typified by the strain defined on the Approved Lists of Bacterial Names and by strains known to be derived from the nomenclatural type" [49].

In 2014, the same year the decision of the Judicial Commission was published, Zhang et al. [63] sequenced the genome of the type strain of *A. radiobacter* held in DSMZ culture collection (DSM 30147^T) and proposed the emendation of this species in order to include the results of assimilation of different carbon sources, the production of several enzymes and the fatty acid profile. These authors indicated that the genome of the strain DSM 30147^T was unusually large, since it has more than 7 Mb whereas the remaining analysed genomes have sizes ranging from 4.8 to 6.8 Mb. Nevertheless, in the present year 2019, Gan et al. [15] reported the reason of this difference, which was a contamination of the genome of the strain DSM 30147^T (GCF.000421945) with part of the genome of the strain TS43 also isolated by Zhang et al. [63] (GCF.001526605). The genomic data were not included in the protologue of the emended species *A. radiobacter*, but in any case the emendation is not valid to date since it was not officially performed.

In the work of Gan et al. [15] the genomes of the type strains of *A. tumefaciens* B6^T (LMVK01000030.1, FCNL01000034.1) and *A. radiobacter* NCPPB 3001^T (LMVJ01000011.1) were obtained and compared with the available genome of the strain *A. radiobacter* LMG 140^T (MRDG01000013.1) concluding that the type strains of *A. tumefaciens* and *A. radiobacter* represent two subspecies from the same species. These authors, taking into account that the combination *Agrobacterium radiobacter* has priority over the combination *Agrobacterium tumefaciens* [49], proposed that *A. tumefaciens* B6^T should be reclassified into a new subspecies of *A. radiobacter*. However, this proposal can not be accepted because the protologues of the two proposed subspecies were not included in the paper of Gan et al. [15] and moreover it is necessary a new emendation of the species *A. radiobacter*. In any case, this proposal does not modify the resolution of the Judicial Commission given that the specific name *Agrobacterium tumefaciens* can not be rejected as long as this Commission has not made such decision.

Therefore, the genus *Agrobacterium* currently contains 14 species if we consider the names *A. radiobacter* and *A. tumefaciens* and the species *A. fabrum*, although this species has not been still proposed (Table 1). One of them, *A. albertimagni*, is more closely related to some *Rhizobium* species forming a *rrs* gene cluster

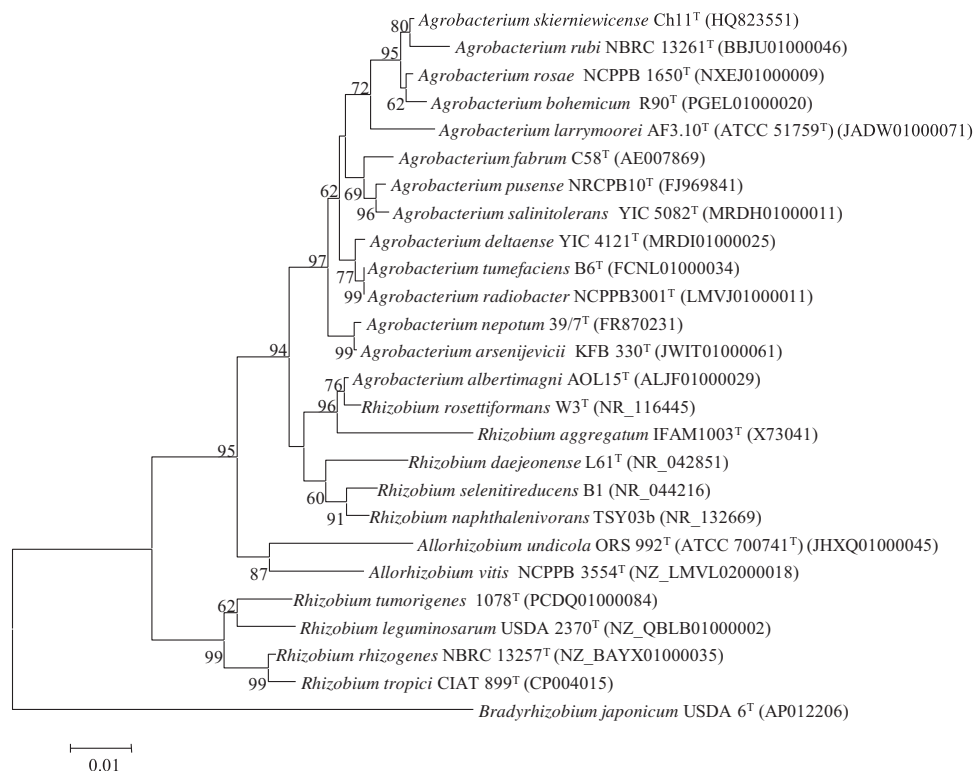


Fig. 1. Neighbour-joining phylogenetic rooted tree based on *rrs* gene sequences (1380 nt) showing the taxonomic location of the species from *Agrobacterium*, *Rhizobium* and *Allorhizobium* able to induce pathogenic symptoms in plants. Bootstrap values calculated for 1000 replications are indicated. Bar, 1 nt substitution per 100 nt. Accession numbers from Genbank are given in brackets.

(Fig. 1) that belong to neither *Agrobacterium* nor *Rhizobium* but to a separate genus [12,34]. Nevertheless, the reclassification of *A. albertimagni* in a new genus will need further studies since currently the genomes of several *Rhizobium* species belonging to this putative new genus are not available. The remaining species currently included within genus *Agrobacterium* formed a *rrs* cluster phylogenetically divergent to genera *Allorhizobium* and *Rhizobium* also containing plant pathogenic species (Fig. 1). Most of *Agrobacterium* species are able to produce tumours in different plants (Table 1), nevertheless the number of non-pathogenic species had increased in the last two years, with one of them, *A. salinitolerans*, able to nodulate the legume *Sesbania cannabina* [56] and other, *A. pusense*, frequently isolated from clinical sources [3], able to cause human sepsis [24]. If we take into account that the strains belonging to five defined genomospecies have not been assigned to an *Agrobacterium* species yet, a significant increase in its number is expected in a near future.

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