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Request for an Opinion

Proposal that *Agrobacterium radiobacter* has priority over *Agrobacterium tumefaciens*. Request for an Opinion

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It is proposed that *Agrobacterium radiobacter* has priority as the earlier heterotypic (subjective) synonym when it is united with *Agrobacterium tumefaciens*. The nomenclatural status of *A. tumefaciens* as a later heterotypic synonym of the united species is not lost and it remains the type species of the genus. Request for an Opinion.

The specific epithet '*radiobacter*' was first proposed in the combination *Bacillus radiobacter* by Beijerinck & van Delden (1902) in a study of saprobic soil bacteria associated with nitrogen utilization. Subsequently, the species was reclassified successively in the genera *Bacterium*, *Rhizobium*, *Achromobacter* and *Alcaligenes* (Buchanan *et al.*, 1966) before being transferred by Conn (1942) to the new genus *Agrobacterium*. The specific epithet '*tumefaciens*' was first proposed in the combination *Bacterium tumefaciens* by Smith & Townsend (1907) for the pathogen of crown gall and was successively transferred to the genera *Pseudomonas* and *Phytomonas* (Buchanan *et al.*, 1966) before Conn (1942) proposed transfer to the genus *Agrobacterium*, designating *Agrobacterium tumefaciens* as the type species.

The similarity and probable synonymy of *Agrobacterium radiobacter* and *A. tumefaciens* has been widely acknowledged (reviewed by Kersters & De Ley, 1984). Holmes & Roberts (1981) proposed synonymy of the two species and this is now unquestioned (Sawada *et al.*, 1993; Bouzar, 1994; Young *et al.*, 2001, 2005). Although the epithet '*radiobacter*' has priority over '*tumefaciens*' according to the *International Code of Nomenclature of Prokaryotes* ['the Code' – hitherto the *International Code of Nomenclature of Bacteria*; Lapage *et al.* (1992)] by reason of its earlier publication (the Code; Rule 38), Holmes & Roberts (1981) noted that *A. tumefaciens* was the type species of the genus and concluded that the union of the species would require that this name be retained over *A. radiobacter*.

Kersters & De Ley (1984) strongly supported the classification of Holmes & Roberts (1981), accepting a concept of phenotypic species and differentiating pathogen populations as infrasubspecies, but they nevertheless adopted an alternative species nomenclature based on pathogenic characters. This was contrary to the taxonomic concept guiding the inclusion of names in the Approved Lists of Bacterial Names (Skerman *et al.*, 1980), and endorsed in subsequent considerations of classification, that species should be supported by circumscriptions as natural taxa (Wayne *et al.*, 1987; Murray *et al.*, 1990; Stackebrandt *et al.*, 2002). Pathogenicity is not an essential species characteristic of a species named with the epithet '*tumefaciens*', nor, of itself, the basis for species discrimination, especially where pathogenic characters are borne on transmissible plasmids with acquisition, exchange or loss leading to a change in species identity (Kersters & De Ley, 1984). Kersters & De Ley (1984) could have adopted a natural classification, even involving the epithet '*tumefaciens*' (Holmes & Roberts, 1981; Bradbury, 1986; Moore *et al.*, 2001, Young *et al.*, 2001, 2005), but they claimed that the Judicial Commission of the International Committee on Systematic Bacteriology (1970) had designated *A. tumefaciens* as the type species and therefore this name must be used. They appear to have assumed, mistakenly (Sneath, 1984), that names are descriptive and that the epithet '*tumefaciens*' was reserved for a species based on pathogenic characters.

Sawada *et al.* (1993) reviewed the nomenclatural relationship of *A. radiobacter* and *A. tumefaciens* and, in a Request for an Opinion (Sawada *et al.*, 1993), proposed rejection of *A. tumefaciens* and acceptance of *A. radiobacter* (the Code; Rule 38). Their proposal makes it clear that they did not intend rejection according to Rule 56a (Rejection of names and placement in a list of *nomina rejicienda*) but that, believing that only one name could be applied to a species, the correct name should be *A. radiobacter*. Sawada *et al.* (1993) did not take account of the earlier discussion (Holmes & Roberts, 1981; Kersters & De Ley, 1984).

Subsequently, Bouzar (1994) reviewed the nomenclatural case and argued, *contra* Sawada *et al.* (1993) and reiterating the conclusion of Kersters & De Ley (1984), that, because *A. tumefaciens* was the type species, *A. tumefaciens* took priority over *A. radiobacter*. However, Bouzar's specific Request for

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an Opinion was confined to the proposal that *A. tumefaciens* be confirmed as the type species of *Agrobacterium* and a response (by Oyaizu and Sawada; Authors' reply in Bouzar, 1994) conceded the validity of this claim. With this accord, the Judicial Commission decided that there was no need for a formal response to either Request (Frederiksen, 1995) and therefore the question of the relative priority of the naming of the species, either as *A. radiobacter* or *A. tumefaciens*, was not considered by the Commission. Subsequently, Young *et al.* (2001, 2005) followed the interpretation that *A. tumefaciens* was the correct name for the united species.

The Code is not transparent on the attributes of synonymy (the Code; Rule 24a) and, as follows, it is easy to see how the above interpretation was arrived at. A species may have only one validly published name (the Code; Rule 23a). If the two species are united, the species name *A. radiobacter*, as the earlier heterotypic (subjective) synonym, should be the name of all strains identified as members of the species, including those previously named as *A. tumefaciens* (the Code; Rule 38). Consequently: (i) all strains of *A. tumefaciens* would be identified as *A. radiobacter*; (ii) the type species of the genus would cease to have strain representation and thus (iii) the name *A. tumefaciens* would cease to have nomenclatural standing. However, this creates a paradox because the type 'is that element of the taxon with which the name is permanently associated' (the Code; Rule 15) and loss of identity of the type species would imply loss of the genus name. Therefore, the type strain of *A. tumefaciens* must continue to be named *A. tumefaciens* and the name of the species containing the type strain must be *A. tumefaciens*. Because the epithet '*tumefaciens*' is closely associated with identification of the species as a pathogen (Kersters & De Ley, 1984), this line of reasoning has gone unquestioned and has been instrumental in inhibiting the development of a phenotypic concept for species in *Agrobacterium* for more than 20 years.

Neither the *International Code of Botanical Nomenclature* (Greuter *et al.*, 2000) nor the *International Code of Zoological Nomenclature* (2000) support this interpretation. Although the Bacteriological Code was established with the intention that the special needs of microbiologists be recognized, an early principle in the development of the Code was that 'insofar as they are applicable and appropriate, the nomenclatural codes of Botany and Zoology should be followed in the naming of micro-organisms' (Editorial Board, 1958). Furthermore, if the intention to amalgamate all biological codes in a single International Biocode (Greuter *et al.*, 1996) is pursued, then the determinations of these codes are likely to be applied in bacterial nomenclature.

The contention that *A. tumefaciens* must be the correct name of a united species because it is the name of the type species of the genus *Agrobacterium* arises from confusion between two independent principles; the principle of nomenclatural priority and the principle of the application of types. The proposition on which the present Request for an Opinion is based is that nomenclature in which *A. tumefaciens* has priority over *A. radiobacter* is inconsistent with the Code in respect to these two principles.

1. The correct nomenclature for the genus is

Agrobacterium Conn 1942

Type species: *Agrobacterium tumefaciens* (Smith & Townsend 1907) Conn 1942 [=a later heterotypic synonym of *A. radiobacter* (Beijerinck & van Delden 1902) Conn 1942].

2. In the decision of the Judicial Commission (1970) to conserve the genus name *Agrobacterium* over *Polymonas*, they did not 'designate' (Kersters & De Ley, 1984) the type species, merely noting that the type species was *A. tumefaciens* by the original designation of Conn (1942). Furthermore, conservation of names was explicitly denied in the *Introduction to the Approved Lists*. This type species is not conserved (the Code; Rule 56b) and the epithet '*tumefaciens*' has not been conserved over the epithet '*radiobacter*'.

3. The application of names is determined by means of nomenclatural types, which are 'that element of the taxon with which the name is permanently associated' (the Code; Principle 5). Nomenclatural types, usually of genera for taxa at higher taxonomic levels, species for genera and strains for species and subspecies, are the name-bearers of those taxa. A type species of a genus, in this case *A. tumefaciens*, is always associated with the name of the genus (the Code; Rule 15).

4. When species are amalgamated, there is only one name for the united species (the Code; Rule 23a). The principle of priority, central to ordered nomenclature (the Code; Principle 6), is that the *correct name* of the united species is chosen by priority of publication, embodied in Rule 38. However, the name of a species that is united as a later heterotypic synonym *does not lose standing in nomenclature* (the Code; Rule 24a); all such synonyms are maintained with their individual type strains. Although a type strain may be correctly named after the earlier synonym of a united species, its status as the type of a type species is not affected. The point is not clearly expressed in the Code because the relevant text (the Code; Rule 24a, Note 3) is in the context of synonyms published in the Approved Lists. This should be clarified in a future edition of the Code.

5. In the case of a united species amalgamating *A. radiobacter* and *A. tumefaciens*, the correct name is *A. radiobacter* (as earlier heterotypic synonym) and the type strain of the united species is the original type strain of the name *A. radiobacter*. The name *A. tumefaciens* is a later heterotypic synonym, but nevertheless retains its original type strain and remains the type species of the genus *Agrobacterium*.

6. This proposal is in accord with the codes of botanical and zoological nomenclature.

7. This revision will reduce the confusion of nomenclature in *Agrobacterium* [but not of the genus itself (Young *et al.*,

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2001)] by permitting the application of a species name that does not have ambiguous connotations (Holmes & Roberts, 1981; Kersters & De Ley, 1984).

A Request for an Opinion is sought.

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References

Beijerinck, M. W. & van Delden, A. (1902). Ueber die Assimilation des freien Stickstoffs durch Bakterien. *Zentralb Bakteriol Parasitenkd Infekt* **2**, 3–43 (in German).

Bouzar, H. (1994). Request for a judicial opinion concerning the type species of *Agrobacterium*. *Int J Syst Bacteriol* **44**, 373–374.

Bradbury, J. F. (1986). *Guide to Plant Pathogenic Bacteria*. Kew, UK: CAB International Mycological Institute.

Buchanan, R. E., Holt, J. G. & Lessel, E. F. (editors) (1966). *Index Bergeyana – an Annotated Alphabetical Listing of Names of Taxa of the Bacteria*. Baltimore: Williams & Wilkins.

Conn, H. J. (1942). Validity of the genus *Alcaligenes*. *J Bacteriol* **44**, 353–360.

Editorial Board (1958). Foreword to the first edition. In *International Code of Nomenclature of Bacteria* (1976), pp. xiv–xxv. Edited by S. P. Lapage, P. H. A. Sneath, E. F. Lessel, V. B. D. Skerman, H. P. R. Seeliger & W. A. Clark. Washington, DC: American Society for Microbiology.

Frederiksen, W. (1995). Judicial Commission of the International Committee on Systematic Bacteriology. Minutes of the meetings, 2 and 6 July, 1994, Prague, Czech Republic. *Int J Syst Bacteriol* **45**, 195–196.

Greuter, W., Hawksworth, D. L., McNeill, J., Mayo, M. A., Minelli, A., Sneath, P. H. A., Tindall, B. J., Trehane, P. & Tubbs, P. (1996). Draft BioCode: the prospective international rules for the scientific names of organisms. *Taxon* **45**, 349–372.

Greuter, W., McNeill, J., Barrie, F. R. & 9 other authors (2000). *International Code of Botanical Nomenclature* (*Saint Louis Code*). *Regnum Vegetabile* series, volume 138. Königstein, Germany: Koeltz Scientific Books.

Holmes, B. & Roberts, P. (1981). The classification, identification and nomenclature of agrobacteria. *J Appl Bacteriol* **50**, 443–467.

International Code of Zoological Nomenclature (2000). 4th edition. http://www.iczn.org/code.htm

Judicial Commission (1970). Opinion 33. Conservation of the generic name *Agrobacterium* Conn 1942. *Int J Syst Bacteriol* **20**, 10.

Kersters, K. & De Ley, J. (1984). Genus III. *Agrobacterium* Conn 1942, 359[AL]. In *Bergey's Manual of Systematic Bacteriology*, vol. 1, pp. 244–254. Edited by N. R. Krieg & J. G. Holt. Baltimore: Williams & Wilkins.

Lapage, S. P., Sneath, P. H. A., Lessel, E. F., Skerman, V. B. D., Seeliger, H. P. R. & Clark, W. A. (editors) (1992). *International Code of Nomenclature of Bacteria (1990 Revision). Bacteriological Code.* Washington, DC: American Society for Microbiology.

Moore, L. W., Bouzar, H. & Burr, T. (2001). *Agrobacterium*. In *Laboratory Guide for the Identification of Plant Pathogenic Bacteria*, 3rd edn, pp. 17–35. Edited by N. W. Schaad, J. B. Jones & W. Chun. St Paul, MN: American Phytopathological Society.

Murray, R. G. E., Brenner, D. J., Colwell, R. R., De Vos, P., Goodfellow, M., Grimont, P. A. D., Pfennig, N., Stackebrandt, E. & Zavarzin, G. A. (1990). Report of the ad hoc committee on approaches to taxonomy within the Proteobacteria. *Int J Syst Bacteriol* **40**, 213–215.

Sawada, H., Ieki, H., Oyaizu, H. & Matsumoto, S. (1993). Proposal for rejection of *Agrobacterium tumefaciens* and revised descriptions for the genus *Agrobacterium* and for *Agrobacterium radiobacter* and *Agrobacterium rhizogenes*. *Int J Syst Bacteriol* **43**, 694–702.

Skerman, V. B. D., McGowan, V. & Sneath, P. H. A. (editors) (1980). Approved lists of bacterial names. *Int J Syst Bacteriol* **30**, 225–420.

Smith, E. F. & Townsend, C. O. (1907). A plant-tumor of bacterial origin. *Science* **25**, 671–673.

Sneath, P. H. A. (1984). Bacterial nomenclature. In *Bergey's Manual of Systematic Bacteriology*, vol. 1, pp. 19–23. Edited by N. R. Krieg & J. G. Holt. Baltimore: Williams & Wilkins.

Stackebrandt, E., Frederiksen, W., Garrity, G. M. & 10 other authors (2002). Report of the ad hoc committee for the re-evaluation of the species definition in bacteriology. *Int J Syst Evol Microbiol* **52**, 1043–1047.

Wayne, L. G., Brenner, D. J., Colwell, R. R. & 9 other authors (1987). Report of the ad hoc committee on the reconciliation of approaches to bacterial systematics. *Int J Syst Bacteriol* **37**, 463–464.

Young, J. M., Kuykendall, L. D., Martínez-Romero, E., Kerr, A. & Sawada, H. (2001). A revision of *Rhizobium* Frank 1889, with an emended description of the genus, and the inclusion of all species of *Agrobacterium* Conn 1942 and *Allorhizobium undicola* de Lajudie *et al.* 1998 as new combinations: *Rhizobium radiobacter*, *R. rhizogenes*, *R. rubi*, *R. undicola* and *R. vitis*. *Int J Syst Evol Microbiol* **51**, 89–103.

Young, J. M., Kerr, A. & Sawada, H. (2005). Genus *Agrobacterium* Conn 1942, 359[AL]. In *The Proteobacteria, Bergey's Manual of Systematic Bacteriology*, 2nd edn, vol. 2, pp. 340–345. Edited by D. J. Brenner, N. R. Krieg, J. T. Staley & G. Garrity. New York: Springer.

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