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WHAT NAMES SHOULD BE USED FOR THE ORGANISMS PRODUCING NODULES ON THE ROOTS OF LEGUMINOUS PLANTS?

R. E. BUCHANAN

Strangely enough, there is even yet no agreement among those who are working with the organisms causing nodules upon the roots of leguminous plants as to the name or names to be applied to them. In consequence there is more or less confusion in the literature. At the last meeting of the Society of American Bacteriologists (Madison, Wisconsin) attention was called to the fact that in a recent issue of *Soil Science* three different names were applied to the same organism: *viz.* *Bacillus raditicola*, *Rhizobium leguminosarum* and *Rhizobium raditicolum*. It was urged that some agreement be reached.

During the past hundred and fifty years biologists have gradually formulated so-called Codes of Nomenclature to be used in determining the correct scientific names of plants and animals. The code governing the naming of plants has been developed at a series of international plant congresses. The rules laid down cannot be enforced. Anyone is at perfect liberty to use any name he pleases; however, unless the name he uses accords with these rules there is no obligation of any kind resting upon any other to follow him, in fact, it is considered good form to ignore all names so proposed. It may be well, therefore, to consider carefully what name or names should be applied to legume bacteria providing there is strict application of the rules of the code. It should be noted that provision is made in the code for making of exceptions, so that if we are not satisfied with the result secured by a strict application of rules, we may recommend the recognition of an exception.

Let us first consider what a strict interpretation of the facts will yield.

Although microscopic studies had previously been made of the contents of the nodules of legumes, and the presence of living parasites suggested, the first scientific name applied to the causal organism was *Schinzia leguminosarum* Frank. We should examine Frank's paper published in 1879 carefully to determine

whether he actually described the legume organism sufficiently to allow of its subsequent identification. Frank studied with considerable care and detail the nodules and their contents. He noted that in the nodules of most (not all) legumes threads could be observed. These infection strands he interpreted as fungus hyphae. The isolated cells, or bacterioids of later writers, he regarded as segments or abstractions from these hyphae. These infection threads and the bacterioids he carefully figured. The organism seemed to resemble in many respects the one which is found in the root nodules of the alder, which had been named *Schinzia alni* by Woronin. The fungus genus *Schinzia* had been created by Naegeli in 1842 for a fungus found in the rhizome of an *Iris*. Under the circumstances the ascription of the organism to the genus *Schinzia* would seem to have been appropriate. Further points of systematic interest are the particular legumes studied, and the emphasis upon some differences in organisms from different legumes. Most of Frank's discussion of morphology of organisms and nodules are based upon three species of leguminous plants, *Lathyrus pratensis*, *Orobus vernus*, and *Orobus tuberosus*. Of eleven figures, ten are of organisms and nodules from these, one being of *Genista germanica*. *Orobus* is now generally regarded as a subgenus of *Lathyrus* (according to Pflanzenfamilien, Engler and Prantl, and the Index Kewensis). It would seem therefore that the type of *Schinzia leguminosarum* would be the organism causing root nodules upon certain species of the genus *Lathyrus*. Frank also emphasizes that there are certain marked differences between the nodules and organisms of the type from *Lathyrus* and from *Lupinus*. The organisms of the latter he states rarely or never show infection threads in the nodules. He did not regard the differences as sufficient, however, to warrant the separation of another species.

An examination of Frank's paper can leave no question in the mind of the student but that he saw and accurately figured the legume bacteria. He did not culture them. He was mistaken in the assignment to the genus *Schinzia*. Nevertheless he described adequately for diagnosis the organism from the root nodules of *Lathyrus*, and gave it the valid specific designation *leguminosarum*. If there is more than one species of organism characteristic of the root nodules of different species of legumes, then *leguminosarum* should be the specific designation of the type found on *Lathyrus*.

The next name applied to the legume organisms was given by Schroeter (1885, p. 135) in Cohn's Kryptogamen Flora. Schroeter concluded that the closest relatives of the legume organisms were among the slime molds, and that Frank's assignment to the genus

Schinzia was an error. He therefore proposed a new generic name, *Phytomyxa*, and transferred to it the organism described by Frank, terming it *Phytomyxa leguminosarum*. He placed it in a new family *Phytomyxacei* and in a new order *Phytomyxini*. He regarded the organism as closely related to the form causing club root of cabbage; he therefore placed the genus *Phytomyxa* next to the genus *Plasmodiophora*. Schroeter regarded the infection threads as "plasma" threads, and the bacterioids in the nodules as spores. He stated that his species is present on the roots of most leguminous plants, as for example *Trifolium repens*, *Lotus corniculatus*, *Orobis vernus*, and others. It will be noted that it was from the root nodules of *Orobis vernus* that Frank (1879) developed much of his description. Schroeter also named a second species *Phytomyxa lupini* from the nodules of *Lupinus luteus* and *Lupinus angustifolius*. This species was differentiated from the first largely on the basis that plasma threads are lacking in the nodules.

It should be noted that the fact that Schroeter incorrectly placed the organism among the slime molds does not in any way invalidate the name used. There seems to be no question but what *Phytomyxa* was the first generic name proposed specifically for the microorganisms of legume nodules. Unless there is some older genus in which these organisms should be included, then from the standpoint of priority *Phytomyxa* would seem to be valid. It would follow, then, that *Phytomyxa leguminosarum* (Frank) Schroeter should constitute the type species of the genus, the organism from *Lathyrus* constituting the type of the species. If the organism of the lupine is to be regarded as specifically distinct, then for it *Phytomyxa lupini* Schroeter would have priority.

The fact however should be emphasized that the generic name *Phytomyxa* has apparently never been accepted in bacteriology. One reason undoubtedly was that Schroeter's inclusion among the *Myxomycetes* in a sense removed it from the bacteriological literature. Apparently Maire and Tison (1909, p. 241) have been alone in discussion of the name as a valid designation, and this again in an article on *Myxomycetes*. Others working later with the bacteria from legumes evidently did not know of Schroeter's name. Dr. Winslow with the Committee on Classification of Bacteria of the Society of American Bacteriologists recommended that the name be regarded as invalid, and as a synonym of names given later and more widely used.

The reasons for such a recommendation are as follows:

1. The name has never been used in articles or texts in bacteriology.
2. The family and ordinal names derived from *Phytomyxa* have been used quite regularly in floras, texts, monographs, etc., relating to the *Myxomycetes*, although the genus *Phytomyxa* itself is not included. The concurrent use of *Phytomyxa* as a genus of bacteria and *Phytomyxaceae* as a family of slime molds introduces an element of confusion.
3. The full volume of Cohn's Kryptogamen Flora containing Schroeter's name was not issued until 1889. There is some question as to the adequacy of publication and distribution of the section on *Myxomycetes* printed in 1885.

Authority for such is to be found in Article 9 of the Botanical Code which reads,

The rules and recommendations of botanical nomenclature apply to all classes of the plant kingdom reserving special arrangements for fossil plants and non-vascular plants.

A footnote to the code of 1905 states that the special arrangements noted in this rule were to be taken up in the Congress of 1910, including "Lists of *nomina conservando* for all divisions of plants other than Phanerogams." However, the special rules for the bacteria were not acted upon in 1910. It is therefore entirely appropriate that recommendations of the type offered by the committee be made to be submitted to the next congress.

Vuillemin (1888) proposed as a name for the legume organism *Cladochytrium tuberculorum*. The name is invalid on several counts.

1. The organism is incorrectly assigned to the older fungus genus *Cladochytrium*.
2. The specific name *tuberculorum* is antedated by the *leguminosarum* of Frank.
3. There is some question as to whether Vuillemin was observing the infection strands of the legume organism or the hyphae of some secondary invader of old nodules.

The next proposal was that of Beijerinck. He states in his paper of November 1888 that he proposed the name *Bacillus radicolus* at a meeting of the Akademie der Wissenschaften at Amsterdam in November 1887. No printed record of this announcement has been found by the writer. The name apparently dates from its publication in November 1888. Beijerinck apparently was familiar with Frank's article of 1879, for in a footnote he calls

attention to Frank's statement that nodules do not develop in sterile soil. However he does not mention Frank's name *Schinzia leguminosarum*. A natural inference from a perusal of the paper would be that he first named the organism. Apparently he was unaware of the names of Schroeter, at least he does not mention them.

What of the validity of Beijerinck's name? First, it will be noted that he places the organism in Cohn's genus *Bacillus*. It will be recalled that the first species described under this generic designation was *Bacillus subtilis*. As long as *Bacillus* is recognized as a genus it must of course contain the type. At the time of Beijerinck's work it should be recognized that the genus *Bacillus* was frequently defined to include rod shaped bacteria in general. There is therefore no reason to criticize this allocation of the organism. Similarly, at present, any student who believes that the natural relationships of the legume bacteria are with the group of gram positive spore producing organisms of the type of *Bacillus subtilis* is justified in using this generic name *Bacillus* to include the legume bacteria. Those who believe the relationship is not sufficiently close to *Bacillus subtilis* to justify inclusion in the same genus must seek another generic designation.

In the use of the specific designation Beijerinck was clearly in error. He was not justified in ignoring the previously published name of Frank, *leguminosarum*. The change he made is clearly and expressly forbidden in the code. Article 48 reads in part:—

When a *** species is moved into another genus, *** the first specific epithet *** must be retained or must be reestablished, ***.

In other words, when Beijerinck transferred Frank's *Schinzia leguminosarum* to the genus *Bacillus*, he should have designated it *Bacillus leguminosarum*. It is evident that Beijerinck's name *Bacillus radicolica* was clearly invalid from the beginning, and should have no standing in nomenclature.

Several objectives have been raised to this conclusion. Perhaps most important is the contention that Beijerinck was the first adequately to describe the organism, for he was the first to isolate it in pure culture, and to describe its morphology in culture. Beyond question Beijerinck did an unusually brilliant piece of work. He proved quite definitely the organisms to be bacteria. Nevertheless, Frank had previously given a description which made recognition of the organism possible. There would be grave difficulties encountered if pure cultures constituted an essential pre-

liminary to the naming of an organism. The description should be adequate to make recognition possible. Any other policy would render invalid such names as *Treponema pallidum* given by Schandinn to the causal organism of syphilis long before it was cultured. It has also been argued, as noted above, that the placing of an organism in an incorrect group should invalidate the name. This is contrary however to rule and custom.

The paper of Beyerinck contains some other material of systematic interest. Particularly does he note that the legume bacteria may be divided into two groups, which, however, he hesitates to separate as species. Under each group he enumerates certain varieties. The following outline will indicate the groups, and names used.

1. Group. Colonies on gelatin relatively large and clear. Growth on meat infusion peptone gelatin poor or lacking, increased by addition of sucrose or dextrose. Swarm cells minute. Bacteroids two branched, spherical or pear shaped. Meristem present in plant nodules. Primary coating of nodule colored. Definite infection thread present.
 - a. *Bacillus radicumicola* var. *fabae*. Described from *Vicia faba* and *V. narbonensis*. Probably those from *V. sativa* and *V. cracca* closely related, as also from *Ervum crvilia* and *E. lens*.
 - b. *B. radicumicola* var. *Viciae hirsutae*. Described from *Vicia hirsuta*. Believes the bacteria from *Medicago*, *Genista* and *Melilotus* belong here.
 - c. *B. radicumicola* var. *Trifoliorum*. Described from *Trifolium pratense*, *T. repens* and *T. procumbens*.
 - d. *B. radicumicola* var. *Pisi*. Described from *Pisum sativum*.
 - e. *B. radicumicola* var. *Lathyri*. Described from *Lathyrus tuberosus*, *L. sativus*, *L. ochrus*, *L. cicera*, *L. missolia* and *L. aphaca*.
2. Group. Colonies more cloudy white, opaque. Growth more pronounced on meat infusion peptone gelatin. Swarm cells rod shaped, usually longer. Bacteroids rodlike, rarely branched. Infection threads absent or little developed. No meristem in nodules (except in *Robinia*).
 - a. *Phaseolus* type. No varietal names given. From *Phaseolus vulgaris*, *Lotus corniculatus* and *Ornithopus perpusillus*.
 - b. *Bacillus radicumicola* var. *Lupini*. From *Lupinus polyphyllus*, *L. luteus* and *L. mutabilis*. Probably *Cytisus* type belongs here also.

- c. *Robinia* type. No varietal name given. From *Robinia acacia*. Probably the organism from *Caragana* belongs here.

It is of interest to note that Beyerinck confirmed the distinction between organisms from the lupine and from most other types. His *Bacillus radicolica* var. *Lathyri* may probably be regarded as corresponding to Frank's *Schinzia leguminosarum* in the restricted sense. His *B. radicolica* var. *Lupini* is apparently the same as Schroeter's *Phytomyxa lupini*. To the extent that Beyerinck's varietal names correspond to modern groupings, they may be used if cross inoculable groups are to be recognized as varieties.

A little less than a year after the publication of Beyerinck's article, a second contribution by Frank appeared (in October 1889). In this article he reviews the work of several investigators, particularly that of Beyerinck, and notes his use of the name *Bacillus radicolica*. He again points out that infection threads are evident in the nodules of some legumes such as peas, and are absent in those of others as lupines and beans. He recognized that his previous placing of the organism in the genus *Schinzia* was an error, and proposed the new generic name *Rhizobium* for the organism. There is no evidence that he was aware of Schroeter's name *Phytomyxa*. He also reports certain attempts at cultivation of his *Rhizobium leguminosarum* in gelatin. For the most part he studied the development of the organisms in hanging drops of gelatin. He isolated the organism from several legumes. He describes the formation of the swarm cells, and measured them and the bacteroids. He was unable to demonstrate flagella. After several days great numbers of cells were present. He then says, "Solches reines Material von Schwärmern aus Hängetropfen — Culturen habe ich nun auch auf Gelatineplatten übergeimpft. Hier entwickeln sich kleine runde convexe Gallerthäufchen von gelblichgrauer Farbe, welche meist nicht oder nur wenig die Gelatine verflüssigen und aus den nämlichen Schwärmern bestehen." From this description it is not improbable that he failed to secure pure cultures. Certainly his characterization of the colonies as yellowish-gray does not seem accurate.

In view of the preceding statements it would seem as though Löhnis has scarcely given a fair or adequate presentation of the facts in the following quotation (from Fred's translation). He says, "Two years after Beyerinck had published his findings, a German botanist, A. B. Frank gave a quite different description of what he erroneously believed to be the nodule-producing organism,

and proposed the name *Rhizobium leguminosarum* for his bacterium which was characterized by a yellow pigment. It is, of course, very incorrect to use this name instead of *B. radicola* Beij. for the genuine nodule organism as was done repeatedly." It would seem that this statement includes several inaccuracies, some important, others not.

1. Frank's paper to which reference is made appeared within a year, not two years after the complete paper of Beyerinck.
2. It is inferred that Beyerinck's description and name antedated those of Frank. In fact, Frank's specific designation *leguminosarum* antedated that of Beyerinck some eight or nine years.
3. It is inferred that an error in pure culturing should invalidate Frank's name. In the main Frank's descriptions are accurate and check well with those of Beyerinck. To state that "Frank gave a quite different description" scarcely gives justice to Frank's descriptions.
4. Far from being correct only to use *Bacillus radicola* it is evident that Beyerinck ignored a previously published and valid specific name, and *radicola* has no standing under the rules.

It is further evident that the following quotation (from Fred's translation) is essentially misleading and incorrect. Löhnis states, "Beyerinck chose as scientific name of the nodule bacteria the designation *Bacillus radicola*. According to the rules of scientific nomenclature this species name must be retained." On the contrary, it would seem that adherence to these rules would require the abandonment of this specific name.

Another contribution of some nomenclatural interest was that of Kirchner (1895). This investigator studied the root nodules from soy beans and some other legumes, and described the organisms. He believed the generic name *Rhizobium* to be invalid because of the previous use of the generic name *Rhizobius* in entomology. In this he was mistaken, as both botanical and zoological codes recognize the validity of identical names in the two fields. He proposed the new generic name *Rhizobacterium* to replace *Rhizobium*, and named a species *Rhizobacterium japonicum*. This name is of interest because of the tendency in recent years to place the bacteria of soy beans and a few other forms in a group relatively distinct from those of other legumes. If this is done it is quite possible that Kirchner's specific epithet *japonicum* might well be used. If the organism of soy beans is generically

distinct from the other forms it is possible that the generic name *Rhizobacterium* might be revived for it.

In more recent years the legume organisms have been placed in various bacterial genera by different investigators. It seems to be fairly established that the bacteria morphologically (when in the motile stage) fall into two groups (Löhnis, Hansen, Whiting, Fred), those having peritrichous and those having monotrichous flagella. The monotrichous forms have been assumed (possibly incorrectly, Conn) to be polar flagellates. Migula (1894) suggested the name *Pseudomonas* for rods with polar flagella, hence the designation *Pseudomonas radicumicola*. The discovery that many other organisms were peritrichous pushed forward again the claims of *Bacillus* as a generic designation, for Migula's definition of *Bacillus* was a peritrichous rod. Certain authors at present (Whiting, Fred) recognize the existence of the two species of legume bacteria, terming them respectively *Bacillus radicumicola*, and *Pseudomonas radicumicola*. It has already been pointed out that the specific designation *radicumicola* for the peritrichous organisms is invalidated by the previous valid name *leguminosarum* and for the specific designation of polar flagellates the specific name *japonicum* has priority over *radicumicola* and in this sense. For those who desire to follow Migula's generic differentiation the appropriate names would appear to be *Bacillus leguminosarum* and *Pseudomonas japonica*. Those who follow Erwin F. Smith in his insistence upon the priority of *Bacterium* over *Pseudomonas* the designation of the latter organism would be *Bacterium japonicum*.

The connotation of these assignments to genera should be clearly recognized. The type species of *Pseudomonas* is *Pseudomonas aeruginosa*, the organism of blue green pus. The type fixed by Erwin F. Smith for his concept of *Bacterium* was *Bact. termo* which he believed to be one of the fluorescent bacteria of the same group as the *aeruginosa*. If *Bacillus leguminosarum* (or *radicumicola*) and *Bacterium japonicum* (*Pseudomonas japonica* or *radicumicola*) are to be used for the two species, it should be understood that the writer intends to state that the peritrichous legume bacteria are so much like *Bacillus subtilis* that they belong in the same genus, and much more closely related to *B. subtilis* than to the monotrichous legume bacteria. Conversely the monotrichous forms are closely related to the other pseudomonads, more closely than to the peritrichous forms.

In conclusion, the opinion of the writer may be expressed,

1. The bacteria of leguminous plants are sufficiently distinctive

- in morphology, physiology, cultural characters and habitat to justify their separation from other bacteria into a distinct genus.
2. The resemblances among all types of bacteria producing the nodules of leguminous plants is so great as to justify the inclusion, for the present at least, of all these organisms within a single genus.
 3. Two names, *Phytomyxa* and *Rhizobium* are available for this genus. For reasons discussed, it is believed that the name *Rhizobium* is to be preferred.
 4. If a single species of legume bacteria is to be recognized, it should be termed *Rhizobium leguminosarum* Frank.
 5. If the peritrichous forms are to be separated from the monotrichous as different species, the former should bear the specific name *Rhizobium leguminosarum* Frank and the latter *Rhizobium japonicum* (Kirchner).
 6. If the various cross inoculation groups are to be recognized as varieties, they should bear the varietal names proposed by Beyerinck insofar as these are appropriate.
 7. If the cross inoculation groups are raised to the rank of species, it will be necessary to designate as the type of *Rhizobium leguminosarum* Frank the organisms from *Lathyrus* and for *Rhizobium japonicum* (Kirchner) the organisms from Soja. The remaining varietal names could then be made specific epithets.

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