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The species paradigm in bacteriology: proposal for a cross-disciplinary species concept

Lindström, Kristina

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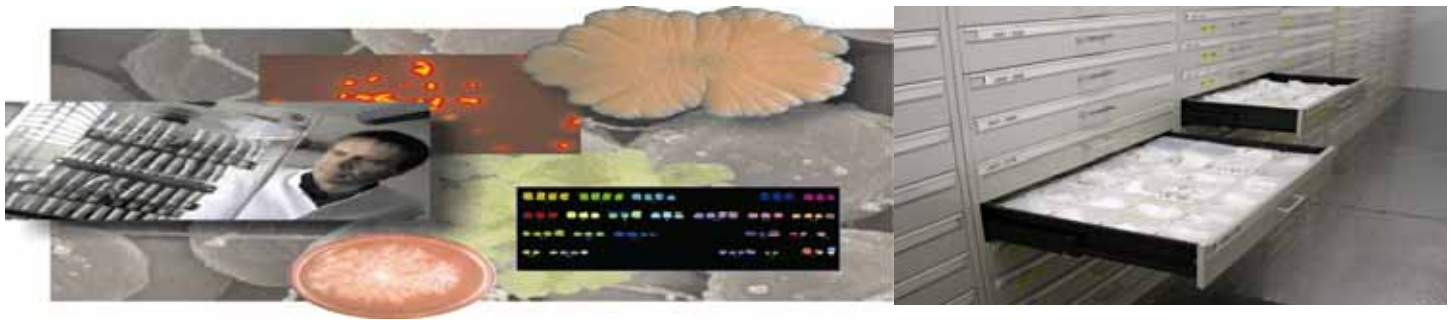
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WORLD FEDERATION OF CULTURE COLLECTIONS

Newsletter – JULY 2006

GBIF Data Portal Survey Results Summary

From March 17 to April 30, GBIF offered a survey on "Feedback and Requirements for Use of GBIF Data Portal".

Summary of the first GBIF Data Portal Survey results can be located at:

<http://www.surveymonkey.com/s.asp?u=279441780723>

<http://www.surveymonkey.com/s.asp?u=279441780723>

The following URL links to a brief summary of the survey results to date
http://circa.gbif.net/Public/irc/gbif/dadi/library?l=/surveys/portalusersurveysummary_1/

http://circa.gbif.net/Public/irc/gbif/dadi/library?l=/surveys/portalusersurveysummary_1/

UPDATES FROM WORK PROGRAMS

Quality Matters Work Program (ECWP) (Contact: Dr David Smith, U.K.)

The WFCC has continued to work closely with the OECD Biological Resource Centre Task Force (BRCTF) to develop appropriate standards for the operations of culture collections. Member collections will be asked to comment on the OECD documents during a pilot phase that will take place in the latter part of this year. A number of collections will be involved in the closer testing of recommended procedures and comment on the development of a Global Network. The WFCC will work to:

- Assess the impact of the general and domain specific standards developed by the OECD BRC Task Force
- Examine the different mechanisms of certification/accreditation recommended by the BRCTF.
- Test the implementation of the principles of biosecurity, ownership and management of IP through MTAs and other mechanisms and as such work closely with the EU projects MOSAICS and the Postal, quarantine and biosafety regulations work Program.

11th International Congress on Culture Collections (ICCC-11)

7-11 October, 2007, GOSLAR, GERMANY

<http://www.iccc11.de/>

The output of the OECD BRC pilot study will be taken into account in the revision of the WFCC Guidelines on the establishment and operation of culture collections and, in close collaboration with the Capacity Building Work Program, address the capacity building needs to put in place appropriate mechanisms for these quality management procedures.

Endangered Culture Collections (Contact: Dr Peter Green, UK)

Mission:

- To provide a focal point or first port of call for any collection (industrial/private/academic) which considers itself to be endangered or in need of help or advice with respect to its future sustainability.
- To assess the requirements of endangered collections who seek assistance and to provide any support, advice or practical help to facilitate the continued survival of that collection; preferably in situ.
- In the event of a culture collection being in imminent danger of being lost, to visit, or by means of correspondence, assess the holdings of that collection and attempt to find an alternative home for all or part of said collection.
- To seek additional levels of funding to build upon those achieved previously.

Progress Report:

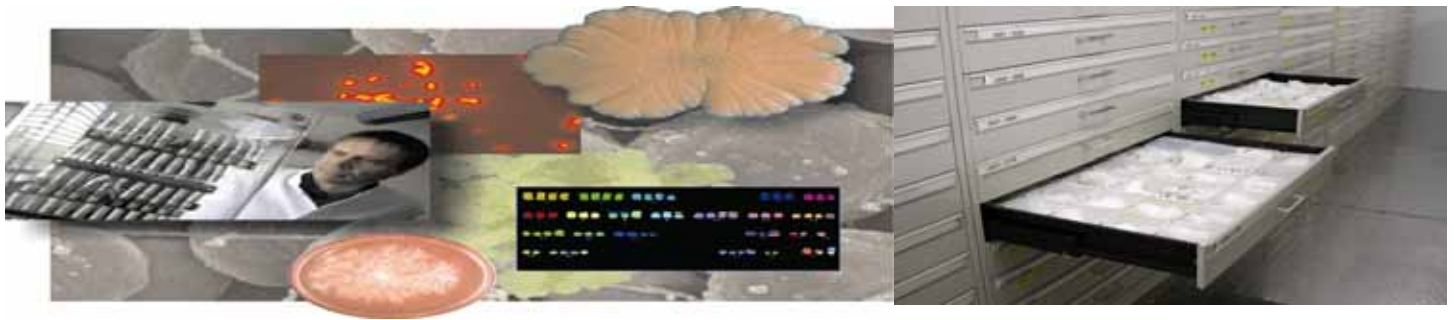
Dr Green has just about to visited a small mixed collection of bacteria and fungi in Los Banos, Philippines to administer the most recent SfAM grant of £2500. With this fund the Collection will be purchasing a number of consumables including urgently needed materials to repair their freeze drier. Dr Green will also deliver some lectures in various culture collections topics including preservation methods to maximize the potential of the cultures assets maintained in these collections.

He has also been invited to attend the 5th Asia-Pacific biotechnology Conference and give a talk on the role of the CBD within the scientific community.

An interesting aside is that a previous recipient of funding from the Endangered Collection Task Group, Dr Dilfuza Egamberdiyeva who managed the Industrial and Agriculture Collections of Microorganisms in Tashkent, is now benefiting from a sabbatical in Manchester as a result of contacts and exchange of ideas which resulted from the visit. Indirectly this will further benefit and help capacity building within her collection and perhaps lead to funded projects, which will also help underpin the future sustainment of the collection.

Capacity Building (Contact: Dr. David Smith, U.K.)

Capacity building in biodiversity management, conservation and sustainable utilisation has been neglected, although it is on the agenda of many national and international initiatives. The human resources, facilities, technologies and knowledge necessary need development to meet the demands to complete the world's biodiversity inventory, to harness the world's genetic resources for the benefit of humankind and to develop the bio-economy. The WFCC has offered training courses many associated with their International Congress for Culture Collections and some one off as requested and funds were available. The courses are normally general in nature covering management of culture collections and preservation of organisms. Member collections of the WFCC offer individual training, often tailor made to requirements. Although the WFCC has a mandate from its members to co-ordinate activities to date it has not done so, it provides *ad hoc* training as requested in addition to the courses associated with its meetings. It held two training courses on the occasion of ICC09 in Brisbane and similar courses were held at ICC10. A training course to support collections in Morocco was held in Rabat in 2004, and



special workshops are often arranged for example on *Microbial Resources and Biodiscovery* held in Melbourne, Australia in 2003.

The WFCC wishes to work with others to try and target its efforts so that they have long-term impact.

To facilitate the development of culture collections and their role in conservation and utilisation of biodiversity and enhance coverage, quality and output there is a requirement for capacity building in several key areas:

- Taxonomy, classifying, naming and identifying elements of biodiversity; a need to focus on neglected groups, e.g. microbial, especially mycological, and entomological
- Information storage, analysis and distribution
- Co-ordinated acquisition programmes including targeted isolation strategies
- Improved technologies e.g. molecular techniques to elaborate classification systems including sequencing, microarray technologies, gene chips etc.
- Characterisation and screening for useful properties
- Policies and strategies to comply with international agreements and conventions

Initiatives currently in place to address the needs:

- Training programmes covering taxonomy training, technical cooperation and networking implemented by WFCC: UKFCC; MIRCENS; CABI; National networks e.g. Thailand, Philippines, Cuba through
- Government investment e.g. Japan; Thailand; Vietnam; Taiwan; China
- Data access and distribution initiatives include GBIF; BioCASE; WDCM; BioNET; GTI; Projects: e.g. SYNTHES NAB

The drive to enhance collections are quality management, biodiversity needs, biosecurity, health and safety, and international networking initiatives e.g. OECD BRC Initiative. Some of the programmes to support development are included in the remits of: UNIDO; UNESCO; UNEP; World Bank; Asian Development Bank etc.

The WFCC believes that to maximise effort and prevent duplication these activities must be better co-ordinated. The opportunity arises to

focus these efforts around the OECD BRC initiative. This programme will endeavour to achieve these ends.

Biodiscovery (Contact: Dr Ipek Kurtböke, Australia)

Biodiscovery is based on search for exploitable and diverse biological resources. In this search the screening of microbial natural products still continues to represent an important route to the discovery of novel chemicals for development of new therapeutic agents, and the evaluation of the potential of lesser-known and/or new bacterial taxa is of increasing interest. However, selection of novel bioactive producing microorganisms from nature requires a sound microbial taxonomical knowledge and fuller understanding of microbial ecology and physiology as means for revealing novelty. Therefore, taxonomic expertise combined with Microbial Genetic Resources Networks will provide a stronger platform to novel discoveries.

The current work program involves the following:

1] Stress the importance of the economic value of microbial diversity with reference to the CBD and making recommendations towards global regulations on access and benefit sharing;

2] Improve understanding towards the needs of the key players and establishment of common grounds between the public sectors, private sectors, intermediaries, communities involved in the chain of biodiscovery;

3] Overview of training schemes and methods used during the building of the source-country's institutional capacity in relation to scientific and technological trends;

4] Overview of conservation policies and wise-management of global resources and benefits associated with the use of traditional knowledge;

5] Focus on social, environmental and ethical issues and the need for the conservation of microhabitats;

6] Organization of workshops and special sessions on the current program during the WFCC Congresses and facilitation of networking among the interested parties.

Progress Report:

In line with the goals of the Work Program and in collaboration with the *Australian Society for Microbiology* a special issue has been produced dedicated to "Management of Global Biological Resources".



Issue contains the following articles:

First Words:

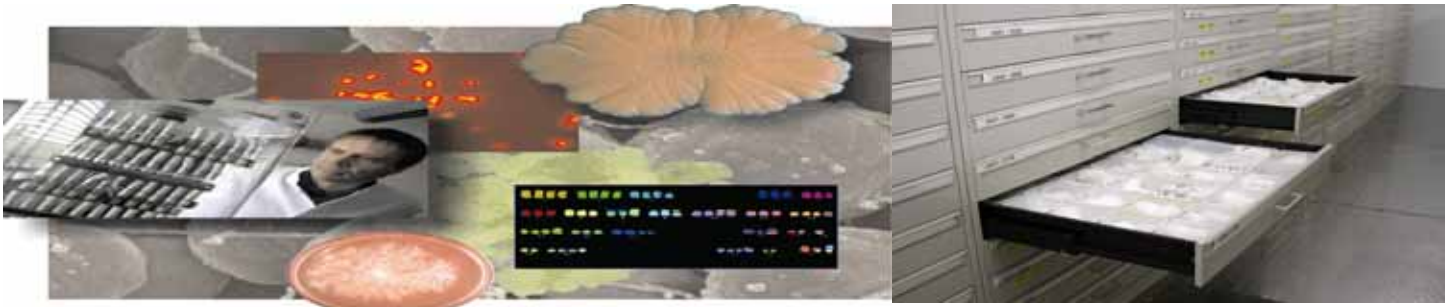
- From Culture Collections to Biological Resources Centres (Ipek Kurtböke, Australia)

In Focus:

- AMRIN: Working Together for Australian Microbial Resources (Lindsay Sly, Australia)
- The World Federation for Culture Collections and BRC's (David Smith, UK)
- WFCC – MIRCEN World Data Centre for Microorganisms (Hideaki Sugawara, Japan)

Under the Microscope:

- Global Taxonomy Initiative – Building capacity in taxonomy to underpin the conservation of biological diversity (Junko Shimura and Kaduo Hiraki, Japan)
- Biosecurity responsibilities of Biological Resources Centres (Ronald Atlas, USA)
- Microbes in transit: International Shipping Requirements in Brief (Christine Rohde, Germany)
- Information Infrastructure for Global Biological Networks (Meredith Lane, Denmark)
- Unesco's perspective on Biological Resource Centers (Lucy Hoareau and Julia Hasler, France)
- The European Initiatives: MINE, CABRI, EBRCN and ENBI (Dagmar Fritze, Germany)
- Quality management an BRCs (Vera Wehs, Germany)
- NBRC: A National BRC of Japan (Ken-ichiro Suzuki, Japan)



- Connecting Industry and the Bioresource Collection and Research Center (BCRC) in Taiwan (Yu-Fen Chen, Gwo-Fang Yuan and Chii-Cherng Liao, Taiwan)
- The Three Cornerstones for BRCs (Virginie Storms, Philippe Desmeth and Jean Swings, Belgium)
- The OECD Initiative: Towards a Global Biological Resource Centre network (GBRCN) (Iain Gillespie, France)

CONTRIBUTIONS AND NEWS FROM MEMBERS

AMRIN

Exciting developments have happened in Australia with the launch of the web site for the

Australian Microbial Resources information Network.

Network is introduced and maintained by Assoc. Prof. Lindsay Sly (Past-President of the WFCC) at the University of Queensland.

He can be contacted at: l.sly@uq.edu.au



Assessment of National and International Models for the Development of Sustainable Biodiscovery Programs in Queensland

Cherine Bootland and Ipek Kurtböke

University of the Sunshine Coast, Faculty of Science, Health and Education, Maroochydore DC, QLD 4558, Australia

Background

Queensland is one of the most biodiverse States in Australia (1, 2 & 3) and the State Government, academic and research Institutions of the State have now started to make a dedicated move towards building a strong and lasting biodiscovery industry based on these resources (4 & 5).

The Queensland Government has made significant progress in Biodiscovery thanks to the development of laws and regulations that support the industry and conservation efforts through access and benefit sharing agreements to provide many future benefits to all Queenslanders (4 & 5). Further progress in the area will be facilitated by:

1] The Australian Microbial Resources Research Network,

Which aims *ex-situ* conservation of industrially important Australian microorganisms and patent deposits as well as storage and distribution of data on the unique Australian microbial diversity to support research, industrial and bio-business activities (6).

2] Taxonomy development

The development of expertise in the field of taxonomy supported by biodiscovery activities

3] Biodiscovery Promotion

Production of directories that promote and facilitate communication among enterprises to provide a snapshot of the companies within the State's biotechnology industry (e.g. *Directory of Biotechnology in Queensland Australia 2005*).

Online networking tools for investors and biodiscovery programs in Queensland that require investment through electronic databases with contact details.

Creation of biodiscovery investor packs that include information on the processes involved in access and benefit sharing agreements.

Participation in biodiscovery events for further promotion and network formation within the global bioindustry.

4] Investment

Australia is mega-diverse along with 18 other nations and it is competing with these other nations for investment. Queensland already hosts many events to attract international and national scientists while it also promotes the growth of skills and expertise as well as equipment within the State through funding (e.g. *Smart State Research Facility Fund*).

Further awareness of price-based competition in other mega-diverse countries may be necessary to ensure benefit undercutting does not occur.

5] Capacity-building

Expansion of the communication network between industry, research and Government agencies;

Capacity building initiatives for indigenous Australians for mutual benefit sharing from traditional knowledge.

6] Regulation

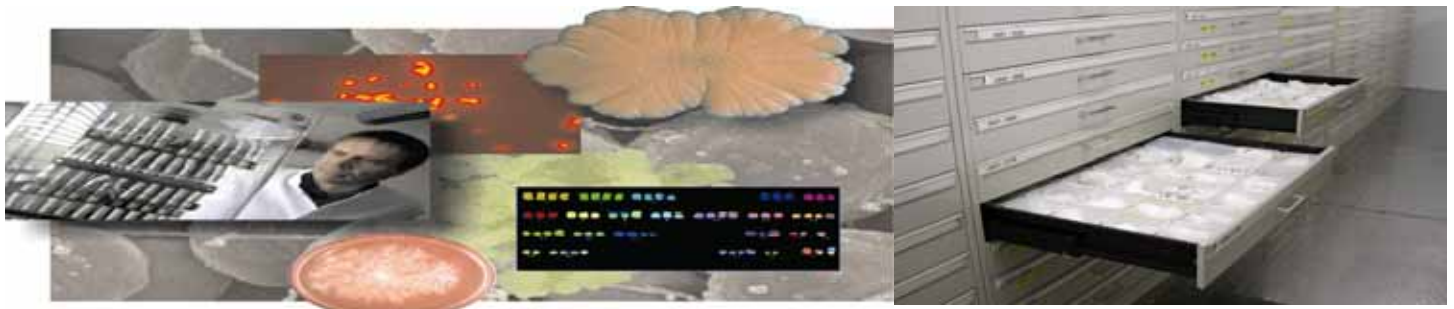
Invitation to other States and Territories to follow Queensland's Biodiscovery Regulations as an example to create similar regulations in accordance with the Commonwealth's Nationally Consistent Approach for access to and the utilisation of Australia's native genetic and biochemical resources.

Combined efforts in the Queensland biodiscovery industry and elsewhere will ensure a sustainable program facilitating information exchange between industry members, communicating and solving problems in a timely manner and working to build capacity for industry growth.

Acknowledgement: Authors thank Mrs Sue Coke, Queensland Government for the advice provided.

References:

- 1] Kurtböke D.I. (2004a). Uniqueness of the Smart State's Microbial Diversity: From a Microbial Library to Biodiscovery, an academic initiative complementing Queensland Government's action plan. In *Microbial Genetic Resources and Biodiscovery* (Kurtböke, I. & Swings, J. Eds). Queensland Complete Printing Services: Australia, pp. 236-248.
- 2] Kurtböke D.I. (2004b). Uniqueness of the Smart State's Microbial Diversity: From an Actinomycete Collection to Biodiscovery at the University of the Sunshine Coast. *Microbiology Australia*, **25**: 36-38.
- 3] Kurtböke D.I. (2004c). Actino-Rush on the Sunshine Coast: prospects for bioprospecting. In *Innovative Roles of Biological Resources Centres* (Watanabe, M.M., Suzuki, K. and Seki, T. Eds.), Japan Society for Culture Collections and World Federation of Culture Collections, pp. 319-322.



4] Queensland Government (2003a). *Queensland Biodiscovery Bill Fact Pack* (2003). Queensland Government, Department of Innovation and Information Economy.

5] Queensland Government (2003b). *Queensland Government Biodiversity Policy Framework* (2003). Environmental Protection Agency, Brisbane.

6] Sly, L.I. (2004): Australian Microbial Resources Research Network: Underpinning Biodiversity, Biodiscovery and Biotechnology Research. In *Microbial Genetic Resources and Biodiscovery* (Kurtböke, I. & Swings, J. Eds). Queensland Complete Printing Services: Australia, pp. 89-105.

ENDANGERED CULTURE COLLECTIONS: THE BABY OR THE BATH WATER

Dr. Peter N. Green

NCIMB Ltd., Aberdeen, UK

Almost all westernised countries and many countries in the developing world maintain collections of micro-organisms. These are biological resources, maintained for the benefit of current and future generations of scientists. Such collections may be specialist collections of marine algae or plant pathogenic fungi or whatever. They may be national collections of international standing with a wide client base, or they may be institutional collections reflecting research programmes or personal or industrial collections which are the life's work of a single person. Alternatively, they may be an in-house collection within an industrial or pharmaceutical company. Whatever their origins or purpose, large or small, multi-staffed or one-man shows, they are highly likely to be of some scientific value. Most will contain some unique organisms which are unlikely to be held in other collections and may have come from a specialised microbial niche (e.g. the Great Barrier Reef).

Most of the scientific community, whether they use culture collections or not, see the value or necessity in maintaining them as a supply source for valuable reference material. The problem starts and finishes with, like many things in life, finances. Culture collections are not cheap to maintain and require a reliable, realistic and long-term means of funding and/or other forms of revenue generation to be maintained. The levels of governmental or industrial support for culture collections vary from country to country and sometimes even within the same country. Problems arise when researchers retire, institutes are closed or their remit changes or government department cut direct or indirect financial support. This then places a previously viable collection into crisis

and they take on an "endangered" status. Some such collections can down resource and survive on a lower level of activity whereas other cannot. For those collections that try to continue best they can on a severely reduced or restricted budget, their whole existence becomes something of a lottery. In many cases they do not have the staff, equipment, or consumables to ensure best practise and the result is many cultures are lost, become contaminated or are preserved sub-optimally which can cause mutational changes. In such cases the World Federation of Culture Collections (WFCC) Endangered Collection Task Group (ECTG) can sometimes help. This help can be in the form of lobbying funding bodies or senior management, offering advice on optimal collection management given the resources available; through to providing small grants for urgent consumables and basic equipment. As a last resort, re-housing the culture collection as part of a "rescue mission" may have to be an option. The ECTG can be contacted through its chair (p.green@ncimb.com) or via regional members (see

www.wdcm.nig.ac.jp/wfcc/committee/endangered/home.html). Collections in danger are encouraged to contact the ECTG and may be asked to complete a questionnaire in confidence to allow their status to be evaluated and any appropriate help or advice given to try to ensure the long term survival of that collection in some form or another. Of course the ECTG are not able to help in all cases, especially if there is a fundamental and irresolvable funding problem and hence, inevitably, some collections are lost. Indeed parent institutions may well order the collection to be mothballed or destroyed or may, in an attempt to preserve some remnant of it severely prune the holdings and cherry pick what are deemed the more "desirable" cultures. But what exactly are "desirable" cultures? Are they cultures, which are "best sellers" or most frequently requested strains? What about cultures which are rarely used; are they the bath water which can safely be discarded or might they retrospectively contain the baby, yet to be discovered? These are difficult and complex decisions, which are often forced upon us, but in most cases there is no quick or easy fix. What is important is that the proper and appropriate advice is sought and given to ensure all avenues are explored. The aim of this review process is to ensure that, as little as possible of our microbial heritage is lost. It is an odd fact of life that because bacteria, fungi and the like are microscopic, there is the perception among some that they are of little importance. Were it a collection of fluffy cuddly mammals in danger of extinction, then much more pressure and public outcry would be brought to bear to ensure their survival. However, tomorrow's new drug in the fight against MRSA or HIV or a

new industrial enzyme worth billions of dollars, will almost certainly not come from fluffy cuddly mammals they will come from smaller life forms; including micro-organisms. It is the duty of all of us to ensure that as many as possible of these collections of smaller life forms survive and are properly maintained for future generations to access.

THE SPECIES PARADIGM IN BACTERIOLOGY: PROPOSAL FOR A CROSS-DISCIPLINARY SPECIES CONCEPT

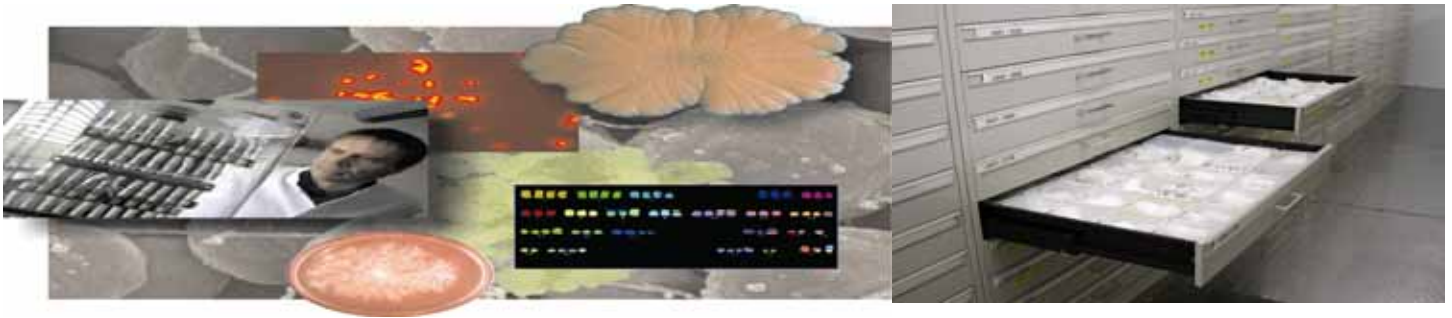
Kristina Lindström and Helge G. Gyllenberg

Department of Applied Chemistry and Microbiology, University of Helsinki, Biocenter 1, P.O.Box 56, FIN-00014 Helsinki, Finland

Abstract

For centuries species concepts for living organisms have been proposed, modified and rejected over and over again. In bacteriology consensus has been particularly difficult to reach. This is partly due to the nature of the bacteria to be sorted into species, but partly to the nature and various needs of man. We argue that so far, prokaryotic taxonomy had no philosophical concept or theoretical framework. New scientific and theoretical approaches and new methods for the dissection of cells and genomes have led to proposals of new species definitions, but the search for a unified species concept seems to have remained a "mission impossible".

The first part of this essay is a review of the philosophical, biological, technical and social basis of species concepts and definitions in bacteriology. Our conclusion is that there are conflicting views between a search for the evolutionary truth and the practical needs in the various fields of applied bacteriology. This conclusion is further elaborated in the second part of the essay, which deals with a specific kind of prokaryotes, the symbiotically nitrogen fixing rhizobia. Finally, we propose a new, cross-disciplinary species concept in bacteriology. This concept accommodates both the nature of bacteria and the nature and needs of man, and incorporates bacterial evolution, biodiversity, population genetics and bioinformatics. In addition, it emphasizes the role of social learning. It thus combines philosophy, biology and social sciences – a combination we think revitalises the field and gives it a proper theoretical framework within which to develop further.



Introduction

The need for species concepts derives from the inherent need of man to structure the world and to classify and name things. Therefore, the species has been an object of thinking already for the earliest natural philosophers. Thus, for centuries species concepts and definitions in biology have been proposed, modified and rejected over and over again. In bacteriology consensus has been particularly difficult to reach. This is partly due to the nature of the bacteria to be sorted into species, but partly to the nature and various needs of man, and the wish to stick to the Linnean nomenclature with binomial species designations. New scientific and theoretical approaches and new methods for the dissection of cells and genomes have led to proposals of new species definitions, but the search for a unified species concept seems to have remained a "mission impossible".

Background - the problem

The following citations illustrate the species dilemma in bacteriology:

"The boundaries of the species, whereby men sort them, are made by men," (John Locke, An Essay Concerning Human Understanding, 1689).

"The species: A concept: that it is useful cannot be denied, but the user must realize that the species does not exist and is not an entity," (S.T. Cowan, A dictionary of microbial taxonomic usage, 1968)

But even for the much more uniform higher organisms the species problem is not trivial. Ernst Mayr (1957), zoologist and taxonomist, has commented: "... there is still much uncertainty and widespread divergence of opinion on many aspects of the species problem. It is rather surprising that not more agreement has been reached during the past two hundred years in which these questions have been tossed back and forth. This certainly cannot be due to lack of trying, for an immense amount of time and thought has been devoted to the subject during this period." Forty years later Hull (1997) gave the following explanation: "Any species concept, no matter which one we choose, will have some shortcoming or other. Either it is narrowly applicable, or if applicable in theory, not in practice, and so on. The trouble is that we have several criteria that we would like an ideal species concept to meet, and these criteria tend to conflict. Most importantly, if a species concept is theoretically significant, it is hard to apply, and if it is easily applicable, too often it is theoretically trivial."

Hull's paper is included as a chapter in an anthology, *Species: The units of biodiversity*. In another chapter of that book Mayden (1997) described and discussed not less than twenty-two species concepts used in biological sciences,

a convincing evidence of the invested amount of time and thought Mayr mentioned. One of Mayden's points is that the term species has two meanings, which have to be differentiated in order to avoid confusion and misunderstanding. One is the species as a taxonomic category, and the other is the species as the actual individuals, which are observed and described, and sorted, in the taxonomic category (*classification*). According to Mayden the species as a taxonomic category is spatiotemporally unbounded, lacks cohesion, is not self-replicating, does not participate in any biological process, has members, and can be defined. On the other hand, the species as a group of individuals is spatiotemporally bounded, has intrinsic cohesion, is self-replicating, participates in biological processes, has part-whole relationships, but cannot be defined (individuals can only be described not defined, since they change over time, and individuals exist as parts or wholes, hence a category of individuals does not have members).

The species as a taxonomic category can be seen as a file for the records on the actual individuals of a given cluster. Such a file needs a label (*nomenclature*), which facilitates communication, and is useful in *identification*, which gives a hitherto unknown item a place in a known cluster of organisms (species), but also its record a place in an existing file (species as a taxonomic category).

Can taxonomy and evolution meet? – Mayr revisited

In an obituary in honour of Ernst Mayr (1904-2005), Coyne (2005) listed three major contributions of Mayr's to understanding biodiversity, which, according to Coyne make Mayr "the Darwin of the 20th century": (i) Why is nature divided into discrete groups – species – and how could the gradual and continuous process of Darwinian natural selection produce these discontinuities? With these questions Mayr made "the species problem" a central concern of evolutionary biology. (ii) Mayr proposed "the biological species concept", defining species as groups of interbreeding populations in nature, unable to exchange genes with other such groups living in the same area. The barriers to gene exchange he calls reproductive isolating mechanisms. Thus, origin of species becomes equivalent to the origin of isolating mechanisms. (iii) Finally, Mayr showed how these barriers could arise. Geographically isolated populations of a single species undergo independent evolutionary divergence, and the reproductive barriers arise as by-products of the differentiation (allopatric speciation). According to Mayr (1957), the biological species concept is a combination of two philosophical concepts applicable to the species rank: The non-dimensional concept, which is relational and based on distinction, i.e. the presence or

absence of interbreeding (reproductive gap), and the multidimensional concept, involving gene flow among interbreeding populations in a multidimensional system. However, he abandons the typological concept, which is related to Plato's idea concept, is static and stresses differences between species. Instead, we think that the biological species concept finds some response in Aristotle's more dynamic philosophical views; there is an interaction between form and material and this combination is subject to change.

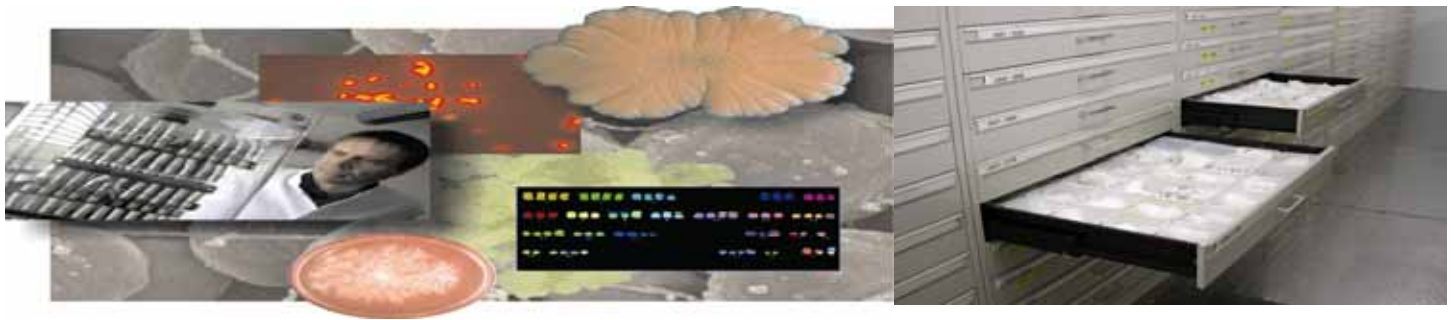
Is the biological species concept applicable to prokaryotes?

Mayr's biological species concept was formulated based on studies of higher organisms. Mayr himself was an expert on birds. In higher eukaryotes mating and breeding are coupled to the reproductive mechanisms of the organisms. Geographic isolation is a consequence of migration. The life style of prokaryotes is different. Breeding and recombination is not part of reproduction, and migration is a rule and can take place all the time. Is then the biological species concept applicable to prokaryotes, or are there other more suitable concepts? This question has awaited an answer for a long time. We argue that the taxonomy of prokaryotes until now has had no species concept at all. What is the reason?

Bacterial species: only useful or even existing?

The recent division of the living world, including the micro-organisms, into three domains: Bacteria, Archaea, and Eukarya (e.g. Woese *et al.* 1990) specifies "bacteriology" as a distinct branch of biology. Prior to this milestone in biology, the phylogenetic position of bacteria in relation to other organisms was floating. S.T. Cowan (1905-1976) was an expert and philosopher on bacterial taxonomy, hence "microbial" in his texts refers to bacteria. In many of his papers Cowan strongly criticized the use of the species concept in bacteriology. He was both elegant and arrogant in his formulations: "all classifications are subjective, and like religious and political opinions, have a large element of aesthetic unreason about them" (1955) or "with so much regimentation and officialdom, will the bacterium's life be worth living, and will it, at last, bow to man's will and remain docile and unchanged long enough to justify the fulfilment of man's perpetual wish to stick a label on it?" (1956).

As last speaker at a symposium on microbial classification 1962, Cowan presented a paper ("The microbial species - a macromyth?") where he expressed an extremely strong critique of the usage of the species concept in bacteriology. Cowan stressed the subjectivity of that concept, and argued that every one of the



previous nineteen speakers at the meeting had used the term, but in nineteen different meanings. Cowan's other arguments were the asexuality of bacteria, which excludes interbreeding as a species criteria and the lack of reproductive isolation. Cowan's strong point was that "the microbial species ... is impossible to define except in terms of a nomenclatural type, and it is one of the greatest myths in microbiology."

What did Cowan suggest? He discussed some substitutes for the species concept, but concluded that "none of them assumes that living things can be arranged in a hierarchical system". Cowan's final conclusion was: "... it is to the geneticists that we must look for future advances in phylogeny". Cowan's despair is understandable. Earlier microbiologists achieved fantastic results in fields such as bacterial metabolism, physiology, ultrastructure and genetics. But until Woese's groundbreaking work, there were no good methods for reconstruction of bacterial phylogeny and tracking evolution in a longer time perspective.

Current species definitions for prokaryotes

Buchanan (1955) defined the bacterial species as "the type culture together with such other cultures or strains of bacteria as are accepted by bacteriologists as sufficiently closely related". This definition can be traced back to Plato's typology, and was criticized by i.e. Cowan. It is still in use in some microbiological textbooks and is also used by taxonomists. The Bacteriological Code (Sneath, 1992) instructs that a bacterial species has to be defined (represented) by a type strain, which should be registered and deposited in an official culture collection. Ward (1998) criticized the species concept as based on conserved strains: "Many (most?) of our impressions are based on what could be considered to be observations of rare species maintained in zoos. How much does this tell us about the diverse prokaryotic species that are now known to occur in nature..."

However, Cowan's hope for the future has now been fulfilled. The scientific development in the last decades, with the breakthrough of molecular biology and genetics, has influenced general views and evaluations of bacteriological concepts, including the species concept. The "molecular revolution" has put utmost emphasis on bacterial phylogeny, and there is now a tendency to approach bacterial taxonomy from the point of view of 16S ribosomal gene (SSU) phylogeny (e.g. Woese, 1987, 1994, Woese *et al.* 1994). In combination with the 16S gene phylogeny, one of the most used bacterial species definitions is that of Wayne *et al.* (1987): A species can be defined as an assemblage of strains sharing 70% or more DNA similarity (relative homology). In addition, to have a new species validly described, a

phenotypic diagnostic feature is necessary (Gillis *et al.* 2001).

A recent species definition in bacteriology is that of Rosello-Mora and Amann (2001). This phylo-phenetic approach circumscribes the species as a monophyletic and genomically coherent cluster of individual organisms that show a high degree of overall similarity in many independent characteristics, and is diagnostically by a discriminative phenotypic property. This definition summarizes the pragmatic or polyphasic approach definition (e.g. Wayne *et al.* 1987, Vandamme *et al.* 1996). Rosello-Mora's and Amann's definition is very descriptive and treats bacteria as individuals. However, it is close to the criteria required when descriptions and claims of a new species are published.

A species concept based on evolution?

Mayden (1997) evaluated the twenty-two species concepts listed by him using four criteria: theoretical significance, generality, operationality, and applicability. Based on such an analysis Mayden arrived at a hierarchy of species concepts where the *evolutionary species concept* (ESC, originally suggested by Simpson, 1961) is the "most appropriate primary concept". According to Mayden ESC, in order to be fully implemented must be supplemented with more operational, accessory notions of biological diversity, other concepts that Mayden refers to as secondary species concepts. The conclusion is that ESC, and secondary species concepts have to be applied together to reveal species diversity. Whereas the primary concept gives the theoretical framework, the secondary concepts provide the practical or applied definitions, guidelines or tools needed to obtain a clear picture of what can be accepted as a species. Can Mayden's theories be useful for bacteriology?

Stackebrandt *et al.* (2002) when attempting to re-evaluate the species definition in bacteriology mainly dealt with methods for description and definition, but did not propose new concepts and was thus primarily stuck with Rosello-Mora's and Amann's (2001) definition. In a recent lecture Stackebrandt (2003) listed four important criteria to be considered when defining taxonomic categories in the future: The tempo and mode of evolution, 2) the rate of recombination, 3) the effect of lateral gene transfer, and 4) the recognition of discrete units of biodiversity ("lumpy diversity"). Here a problem remains. What is the "unit of biodiversity"? Diversity has been defined as the number of species and their relative abundance in a community. Would not this lead to the use of "species" to define diversity, which we in turn try to use for the definition of the species? A more attractive description/definition of diversity is the amount of and distribution of

information in a community. We will turn to this point in later paragraphs.

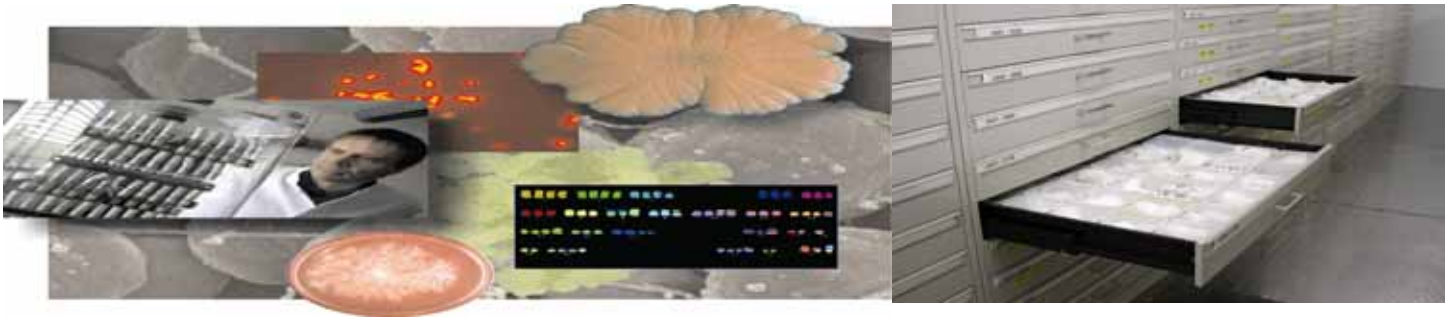
The microbiologists' species perception

In a thorough analysis Moreno (1997) discussed also other approaches to and perceptions of the bacterial species concept. Moreno describes and compares what he calls the phylogenetic, the taxonomic and the biological approaches. In addition he analyses "the microbiologist's" and "the fixed species" perceptions. The above-mentioned "approaches" correspond to three of Mayden's (1997) twenty-two species concepts. Mayden considered similar approaches as stressed by Moreno as secondary concepts (supplements to the primary evolutionary species concept). As such they may be general, operational or applicable, but not theoretically significant. Moreno's "search of a bacterial species definition" is clarifying in many respects, but in fact it provides just three alternative "approaches" for the reader to consider.

Two further comments are needed. First, close to the biological approach is an ecological approach (also one of Mayden's twenty-two concepts). Many bacteria appear in a given environment, but not elsewhere. Hence they are defined by their unique habitat (e.g. animal parasites or plant symbionts) and described as separate "species", although they according to another approach would seem inseparable from strains, which do not react, to the same animal or plant hosts. Torsvik *et al.* (2002) recommended a strict ecological definition according to which a species consists of the organisms occupying the same niche. We will return to this matter below, and discuss the taxonomy of symbiotic, nitrogen-fixing bacteria in more detail.

Second, the Moreno's "microbiologist's perception" deals with the "usefulness" of the bacterial species. The bacterial species in some way exists because it is useful. With present day methods of characterization one can hardly argue that there is aesthetic unreason about the bacterial species concept. On the other hand, the interests of the society may influence considerations of bacterial species, or as Moreno (1997) put it: "in many cases the celerity for naming a new bacteria is based on the grounds of pure anthropocentric arguments. For instance in the case of some 'unimportant' soil bacteria, endosymbionts or the pathogens of some marine animals there is no rush to provide a species name". On this point Moreno comes close to Cowan's views; Moreno (1997): "Our human self-centered view of the world frequently makes us forget that bacteria themselves are not susceptible to systematics as we are".

Goodfellow *et al.* (1997) have presented convincing examples in this respect. Between



the years 1974 and 1995 the number of "official" *Lactobacillus* species (industrially important bacteria) increased from 27 to 60, of *Staphylococcus* species (medically important bacteria) from 3 to 33, but the number of *Azotobacter* species (ecologically interesting bacteria) remained as 6 during the same twenty years.

Ravin (1963) introduced the use of the concepts genospecies, taxospecies, and nomen-species for bacteria. Ravin's taxospecies to some extent correlates with the taxonomic approach referred to above. The genospecies can be compared with the biological approach where the search for a genotype based species concept dominates. The nomen-species, finally, represents what is defined by the *nomen* (or the "file label"), the scientific name attached to a taxonomic category (in this case the species). The name, the label, is useful and purposeful, especially as a tool for communication, but it is largely normative. What is referred to as *Escherichia coli* is easily considered and accepted as *E. coli*. Wrong names can thus cause confusion and misunderstandings.

From the preceding discussion it can be concluded that the bacterial species is utmost useful. There is a bacterial species concept for any use and any need. But does the bacterial species really exist? Even a superficial reading of the enormous literature available on the bacterial species concept leaves a sense of circular evidence: Most writers consider, already at start, the species as an axiom which is there and needs no further definition. The bacterial species is a bacterial species! No further questions or comments. Very few authors develop an actual discussion of the logic of the existence of the bacterial species, and what it could be from the theoretical (or practical) point of view. Cowan's points, almost 50 years ago, are still valid: the bacterial species is extremely useful, an unavoidable tool. It can be approached from many angles, it can be defined in many different ways, but can we consider the bacterial species as a clear-cut entity, or should we accept that it is a multitude, a conglomerate of various views and considerations?

"One bacterium" is a clone

In botany and zoology individual specimens can be observed and investigated for the purpose of definition and circumscription of species. However, also in botany and zoology it is discussed whether one has to consider a several individuals or concentrate the study on populations (Mayr, 1957). Individual bacterial cells are impossible to take as an object of study already because of their limited life span and small size. Thus, in bacteriology the basic unit is not an individual but a clone. In theory a clone is static and consists of identical cells, but

in practice we are dealing with mixtures of clones, populations.

Populations are by no means uniform: there is always smaller or bigger variation within them. What we define as a bacterial specimen or item, a bacterial strain, or a pure culture, is, therefore, a mixture of individual cells, containing a common gene pool with a "sister" specimen, but anyway differing from that to some extent. Moreover, bacteria are in a continuous evolution process, and as Cowan (1962) put it, the populations we observe in order to circumscribe bacterial species are just stations or short stops in such an on-going process.

Will population genetics resolve bacterial taxonomy?

Bacterial population and molecular genetic studies have recently enormously advanced our understanding of the dynamic processes that shape the populations. The word speciation is often used to describe a process when populations diversify enough to warrant them new species names. The barrier the speciation process must pass for a new species to be born can be different depending on which organisms are considered, but the species formed during the speciation process must have some basic traits that can be used to delineate the species. If a biological species is formed, it is separated from its sister species by the inability to breed and recombine with it. At a molecular level this is seen as congruence of phylogenetic trees constructed based on genes present in both populations (Vinuesa *et al.* 2005).

Maynard Smith *et al.* (2000) emphasised that the most surprising feature of bacterial population genetics is that most bacteria (species) have a worldwide distribution, but a local population may contain the full range of variation that exists worldwide (the migration problem). By introducing the population geneticist's view on bacteria Maynard Smith *et al.* add something fresh to the bacterial species soup. A dynamic aspect is the introduction of the concept-evolvingevolving unit". Since phenotypically recognised species often do not correspond to evolving populations, sharing a common gene pool, isolated from the other species, the species definition of Rosello-Mora and Amann cannot be supported. Maynard Smith's conclusions are drawn from studies on *Salmonella* and *Neisseria* species. The former showed a strict clonal behaviour, whereas the latter showed a reticulate pattern of evolution and frequently recombine even across species. Maynard Smith *et al.* proposed that a study of the genetic and phenotypic variation in a taxon such as *Neisseria* "should be compulsory for all philosophers who believe in the existence of natural kinds, for all cladists who believe in the universal validity of phylogenetic classification, and for all pheneticists whatever they believe".

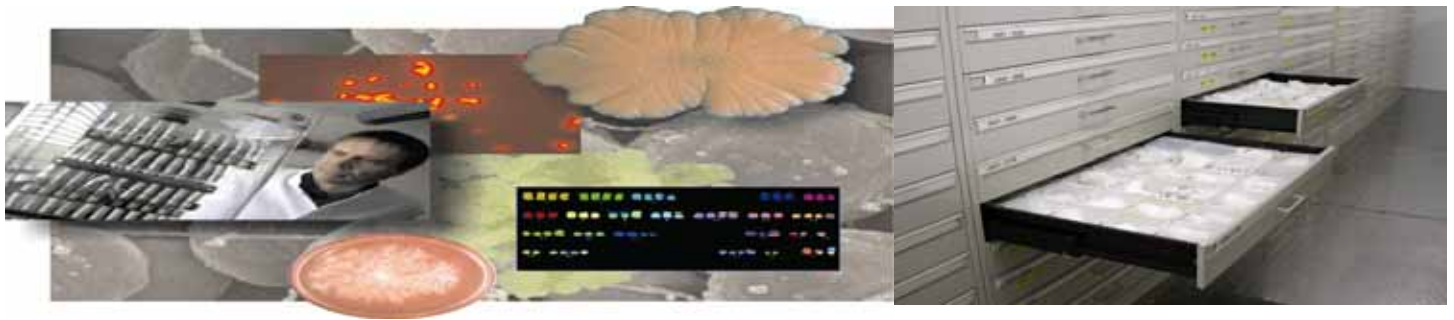
According to Maynard Smith, bacteria either fall into groups that hardly ever recombine, like *Salmonella*, or recombine freely, like *Neisseria*. The frequency of recombination seems to fall off continuously with genetic distance, and there is no discontinuity that can be used to delineate species.

"When does a clone deserve a name" is a provocative question asked by Lan and Reeves (2001). The question arose from studies on *E. coli* and the closely related *Shigella*. Strains representing these genera form a continuum of genetic and phenotypic properties, with shiga-toxin producing, but metabolically uniform shigellas at one end and metabolically diverse, non-toxic *E. coli* at the other end and combinations of these two (toxigenic, metabolically less diverse *E. coli*) in between. This observation was a confirmation of the work done by H.G. Gyllenberg *et al.* (1997), who in a taxonomic approach (minimization of stochastic complexity) found no less than ten clusters of *Escherichia coli* (in a material including data on 1708 strains of *E.coli*). Without clear gaps these clusters showed a continuously decreasing biochemical activity. At the ultimate end of inactivity *E. coli* was close to strains defined as *Shigella*. This as well as other relationships within *Enterobacteriaceae* can be explained by the reticulate horizontal exchange of genes among these organisms. Recently, this phenomenon has also been documented at the genome level (Kotewicz *et al.*, 2003). For a taxonomist relying on a strict biological species concept, the barrier separating species is here less obvious. Since *Shigella* differs from *E. coli* only by some horizontally acquired pathogenicity genes, which may have counteracted the function of other metabolic genes, there is no clear gap between the two that would warrant their separation into two species by the biological species definition.

Application of an ecological species concept could be fruitful in terms of justifying species boundaries drawn based on genes involved in pathogenicity (niche adaptation). Also the closely related *Salmonella* seems to be a collection of clones mainly differentiated by pathogenicity genes, but otherwise evolved via lateral transfer of essential genes in the past (Ochman *et al.* 2000). The numbers of different pathogenicity islands and islets in *Salmonella* are however not always "on the move", but allows classification of clones based on pathogenicity traits.

Horizontal gene transfer: A final obstacle for proper taxonomy?

The classical mechanisms for genetic evolution are point mutations, rearrangements of DNA sequences, gene gain through horizontal gene transfer and gene loss. In general these processes take place at random and the



environment selects. Arber (1999) discusses these processes and the role of evolutionary genes in bacterial evolution. These genes act as variation generators and as modulators of the frequency of genetic variation. As discussed above, putative horizontal gene transfer in the past can explain many of the “aberrations” observed in the composition of bacterial genomes. For bacteria with frequent recombination horizontally transferred genes may become incorporated in the genome of the recipient, with mosaic genomic structures as a result. Horizontal gene transfer may also add separate, accessory elements to target genomes.

Applying bioinformatics to sequences of whole genomes led e.g. Doolittle (1999) to propose that horizontal gene transfer was the essence of the phylogenetic process. This conclusion was challenged by Kurland *et al.* (2003), who pointed out that many premature conclusions have been made by simply applying the BLAST algorithm. Even though horizontal gene transfer may be frequent at the cellular level, they conclude that Darwinian lineages are the essence of genome evolution for contemporary organisms. Also reports by Tekaiia *et al.* (1999) and Brown *et al.* (2001), support this view; whole-genome phylogenies are in good agreement with SSU based phylogenies.

In conclusion, horizontal gene transfer is a major player in evolution, but no obstacle for a modern taxonomy. With proper sampling and analyses, especially bioinformatics, phylogenies of diverse organismal groups based on whole genomes can give a solid base for further dissection of taxonomic hierarchies.

Are selective sweeps a driving speciation force?

Cohan (2001, 2002), based on studies by Palys *et al.* (1997, 2000), developed a species definition based on the ecological species concept. They mainly used *Bacillus* species as models while showing that phylogenies based on protein-coding genes were better suited for species delineation than phylogenies based on SSU genes. They concluded that speciation took place by the formation of ecological populations, results of selective sweeps during which adaptive mutations give rise to superior populations that outcompeted the resident ones. In the later papers Cohan calls these taxa ecotypes, which are kept together by genomic cohesion.

Berg and Kurland (2002) challenged this theory as being too simplistic. Related bacterial populations occur as patches (metapopulations). Selective sweeps can take place within patches and through migration new genetic combinations can transfer to other patches where they either confer an advantage (adaptive mutation) and becomes manifested in

the new population or become extinct because they are dispensable. These authors also emphasise the role of gene loss in the evolution of species.

Rhizobia - can we ever sequence out the species?

We want to exemplify some points in the above discussion with a brief review of taxonomical problems in a certain group of bacteria. The nitrogen-fixing, plant-inter-acting bacteria (here called rhizobia) constitute a challenge to bacterial taxonomists. The rhizobia have adapted to an ecological niche, normally the leguminous root nodule, which they enter to form a symbiotic relationship. Thus, if the ecological species definition is applied, all rhizobia would constitute only one species. But, because there are different legume taxa, the leguminous root nodule niches are also different. Suominen *et al.* (2001) have shown that the phylogeny of rhizobium genes involved in nodulation is incongruent with the phylogeny of SSU genes of the bacteria, but congruent with host plant phylogeny. Accordingly, if parts of genomes would define a species, part of the rhizobial genome - the symbiotic genes - could be considered as defining an ecological species or an ecotype according to Cohan. The nodulation genes are very potent in creating both a phenotype and in helping the bacteria invade an ecological niche. However, they are labile and very prone to horizontal gene transfer. Therefore, we call them accessory genes in contrast to housekeeping or core genes, which serve the general maintenance of the cells. Housekeeping genes are distributed vertically in a “clonal” way from the ancestor to the descendant, but accessory genes may be transmitted horizontally (or laterally) between clones.

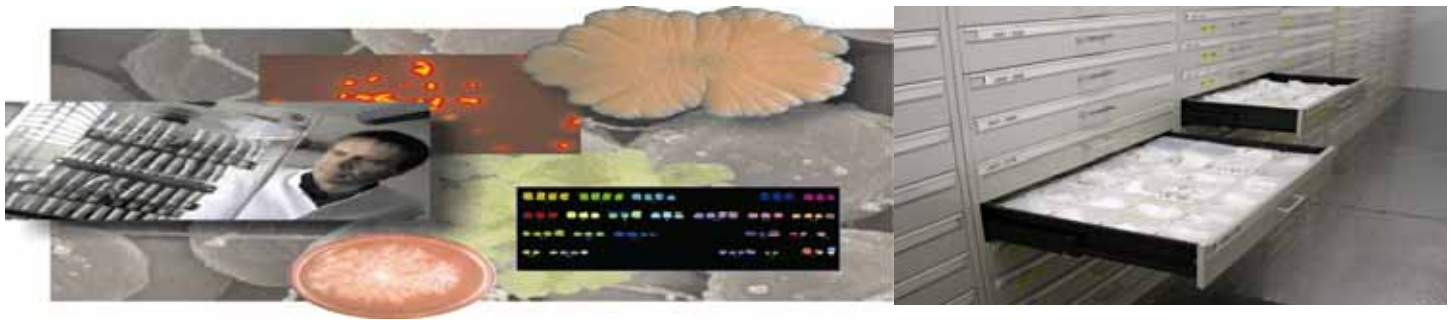
What about the rest of the rhizobial genomes? Based on the phylogeny of SSU genes, the rhizobia occur in several different clades of the alpha-proteobacteria. More than 20 species have been described, and they are classified into seven genera (Euzéby 2005). Recently also members of beta-proteobacterial genera have been isolated from leguminous root nodules and found to possess symbiotic genes (e.g. Moulin *et al.* 2001). The tighter SSU clusters of rhizobia in the subgroup 2 of the alpha-proteobacteria are intermingled with non-rhizobia. Nonsymbiotic relatives of rhizobia lack symbiotic genes, but sometimes share another of the ecological niches of rhizobia, the rhizosphere. The best-known example of this is the genus *Agrobacterium*, which consists of plant-pathogenic and non-pathogenic species.

Dealing with rhizobia the genus delineations have created problems. Rhizobia, one the one hand, show niche adaptation, but on the other hand often seem to have a mosaic structure even in their SSU genes (Van Berkum *et al.*

2003). Thus, with so much recombination in the past, should all these genera be combined into one? In the past, rhizobia were named after the host they occupy. Nowadays we know that the symbiotic genes are mobile, often residing on either symbiotic plasmids or on (genomic) symbiotic islands, which are perhaps frequently lost and gained. Thus, from the human and natural point of view the important and attractive plant nodulation phenotype is of little use in a taxonomic world that requires stable phenotypic traits for species identification.

Will the sequencing of entire genomes help rhizobium taxonomists? The full-length sequences of *Sinorhizobium meliloti* 2011 and *Mesorhizobium loti* MAFF 303099 (which has been misclassified and should be *M. huakuii*, Turner *et al.*, 2002), as well as the taxonomically related plant pathogen *Agrobacterium tumefaciens* C 58 give the opportunity to compare not only gene phylogenies but also the order of genes on the replicons. The *S. meliloti* genome is organised in three replicons: the circular chromo- some, pSymA and pSymB. The plasmid pSymA carries many genes necessary for symbiosis, whereas pSymB has both symbiotic and other genes, some of them essential. So even though this plasmid has a plasmid-type mode of replication, it is essential for the survival of the bacterium. *A. tumefaciens* has one circular and one linear chromosome, and one linear plasmid, the pTi responsible for plant virulence and transformation. The synteny (similarity of gene order) between the circular chromosomes of *S. meliloti* and *A. tumefaciens* is high, indicating that these two organisms are closely related. The synteny of these chromosomes to the *M. loti* chromosome is much lower, confirming the more distant relationship. The symbiotic genes of *M. loti* are located on a genomic island, and genes located there show some similarity to pSymA of *S. meliloti*. (Kaneko *et al.* 2000, Galibert *et al.* 2001, Goodner *et al.* 2001, Wood *et al.* 2001)

The comparison of full-length sequences of obligately parasitic bacteria shows that the genomes of taxonomically close bacteria have very similar genomes (Tamas *et al.*, 2002). Generally, a genome reduction seems to be going on in evolution, leading to the silencing and deletion of redundant genes. Frequent recombination might indicate ongoing adaptation to changing environments/ecological niches. The genomes of rhizobia and agrobacteria are large, about 5 to 8 megabases, compared to less than one for obligate parasites. The symbiotic genes of rhizobia account for about 0.5 megabases (Galibert *et al.* 2001), so what do these bacteria need the rest of their genes for? The answer to this question still has to wait for the future. On pSymB there were nine new loci discovered involved in the biosynthesis of polysaccharides, in addition to



two new chromosomal loci. Why do the bacteria need so many polysaccharide genes? Are they housekeeping or accessory genes? The sequencing of the genome of a strain is more a starting point than an end point. With the availability of the sequences it is now possible to design microarray experiments to investigate the occurrence in other bacteria of genes found in the sequenced model organisms. Hopefully, these experiments with rhizobia will give as clear-cut answers as with some pathogenic bacteria, in which the presence or absence of genes can be elegantly displayed (Joyce *et al.* 2002). The requirements of rhizobia to be able to live in a range of environmental conditions and not just inside the plant let us anticipate that there is a larger variation and magnitude of accessory genes in rhizobia. These genes will tell us something about the life of the rhizobia and add to the known gene pool of biotechnologically interesting genes, but will they be helpful for taxonomy?

The sequencing of several well-conserved rhizobial housekeeping genes seems to be able to provide us with information that can be used for grouping these bacteria into a taxonomic category equal to what is currently defined as a genus (e.g. Gaunt *et al.* 2001, Vinuesa *et al.* 2005). We may have to accept that rhizobia have recombined in the past, as they do today, and it might be impossible to get a neat display of all evolutionary events that have led to what rhizobia are today. If we ask the question "where do they come from?", Turner and Young (1999) have shown that rhizobia were there already before there were plants to nodulate; the origin of the symbiotic genes is still obscure. If we ask where the rhizobia are going, the answer is even more vague. As far as the rhizobia are concerned neither their whole history nor a forecast for their future is yet written.

What is the outcome if we apply Cohan's (2001, 2002) ecotype theory to rhizobia? Also Cohan divides the genome composition of bacteria into housekeeping (loci functionally interchangeable across populations) and accessory (loci responsible for population-specific adaptations) genes. He defines the bacterial species as the evolutionary lineage held together by ecotype specific periodic selection. Eardly and Van Berkum (2005) applied the star clade computer simulation eBURST developed by Feil *et al.* (2004) for MLST data on a dataset of MLEE results for two related *Sinorhizobium* species, and found good support for the ecotype theory. Vinuesa *et al.* (2005) on the other hand found no support for this theory in their studies of *Bradyrhizobium* populations. In their studies, proper sampling and focussing on a group of bradyrhizobia, enabled the delineation of species in the classical biological manner; two sister species had undergone speciation even in

a sympatric context. Among the two sister species, ecotypes (biovars) were detected. These were consistent with the plant nodulation phenotype and symbiotic genotype. However, these ecotypes did not arise according to Cohan's theories, but might be viewed as patches or metapopulations.

An account on gene transfer among rhizobia was published by Haukka *et al.* (1998). Several levels at which gene transfer might occur were discovered, ranging from transfer of symbiotic plasmids in the rhizosphere to probable gene transfer in the past followed by migration. In rhizobial taxonomy horizontal transfer of accessory genes is likely to rule out the applicability of the ecotype species definition.

Can taxonomy and biology meet?

If Samuel Cowan could attend a symposium on microbial classification today, he might not complain to have heard the term "species" used in nineteen different meanings. We cannot know if he would be satisfied with the present state of discussion on the species concept. Certainly the situation has improved during the four decades since Cowan's "Macromyth-lecture" (1962). There occurs at least an intensive exchange of views. However, an esoteric "taxonomy for taxonomists" is still there. Bacterial taxonomy may have risen to a higher intellectual or technological level, but it is not a challenge for bacteriologists outside the narrow compartment of taxonomy professionals, it rather has caused confusion.

We extracted some species definitions from the papers on molecular evolution and population microbiology cited above:

Palys *et al.* (1997) equals a species to a "sequence similarity cluster"

Palys *et al.* (2000): "sequence clustering in protein-coding genes could be the primary criterion for discovering and identifying ecologically distinct groups, and classifying them as separate species"

Cohan (2001): "A species in the bacterial world may be understood as the evolutionary lineage held together by ecotype-specific periodic selection"

Ochman *et al.* (2001): "lateral gene transfer can redefine the ecological niche of a micro-organism, which will, in effect, promote bacterial speciation"

Berg and Kurland (2002): "We stress the influence of sequence loss on the isolation and divergence (speciation) of novel patches from a global population"

Lan and Reeves (2001): "We suggest that the species definition in bacteria should be based on analysis of sequence variation in

housekeeping genes, and also that the 'clone' be give official status in bacterial nomenclature"

Gogarten *et al.* (2002) citing Levin (1981): ". early models for understanding adaptation, evolution and speciation in these organisms often focussed on clonality and periodic selection. According to such models, all individuals within a species resemble each other because they descend from a single ancestor..." Gogarten *et al.* (2002) "Here we use 'species' to designate assemblages of related organisms to which microbiologists have attached specific names, rather than natural kinds."

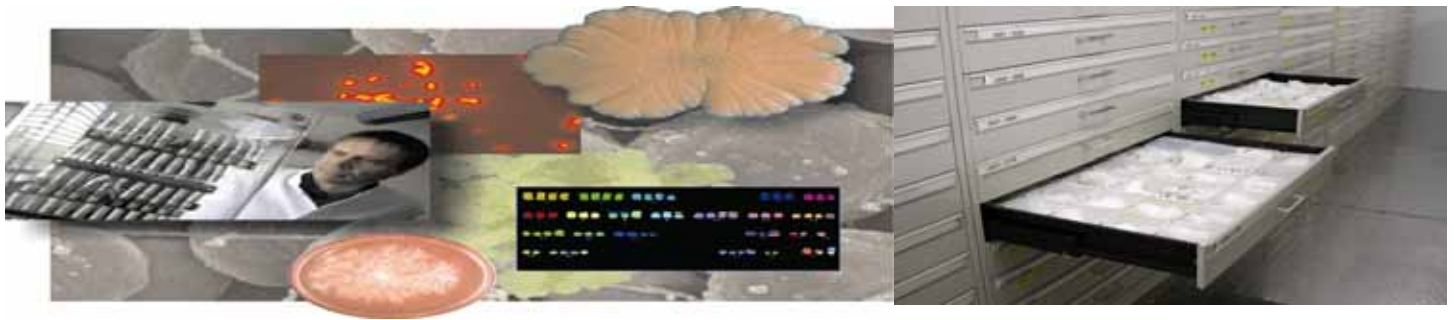
It is obvious, that evolutionary microbiologists go around the species concept and need to define it for their own purposes. Current species definitions are very technical; "use these and these techniques, measure your specimens and see whether they are similar or different". It is more of an engineering science than biology. Current taxonomic methods are in addition laborious and expensive to perform, and there is little funding for taxonomic work with micro-organisms. Controversies arise when taxonomists rename taxa or when new, or even worse, old taxa must be named according to the rules and not to common sense. Here we specifically call attention to the genus *Sinorhizobium*, which according to the rules should be renamed *Ensifer* (J.M. Young 2003).

Taxonomic work should unravel speciation

There is a need for a species concept for prokaryotes, which could give the framework, and direction for future development of their taxonomy. Evolution, change, is an inherent property of the living world, as already noticed by Aristotle. We propose that the evolutionary, species concept (ESG; Mayden 1997, Simpson 1961) is the primary philosophical concept on which to build the taxonomy of prokaryotes. As seen from the examples cited above, tracking prokaryotic evolution is a complex enterprise that requires an input from not just microbiologists, but also from population geneticists, molecular geneticists and bioinformaticists.

Since different organisms have a different evolutionary biology they require different approaches. The theories developed during the classical and the modern work referred to in this essay can help future taxonomists to choose the most appropriate approach and methodology for their purpose. Bioinformatics is a key methodology but also the data treated should be of high quality and cover the diversity expected to occur.

The diversification of assemblages of clones (populations) is commonly called speciation, and one stop in the speciation process is the species. Taxonomic work of good quality should unravel the evolutionary speciation process as



truthfully as possible. Studies aimed at demonstrating speciation should take into account the biology of the organisms under study in order to give the taxonomic work a solid biological foundation. In bacteriology, allopatric (geographical barriers) as well as sympatric (recombination restricting barriers) speciation can occur.

Evolution can only be reconstructed by proper sampling to cover the extent of diversity assumed to exist among the organisms under study, thus maximising the information content collected for the samples. The methods used for examining the samples should depend on previous knowledge of the organisms. An obvious first choice for unknown organisms is the sequencing of the SSU gene, which as been shown to fairly truthfully reflect the evolution of higher taxa. It is also the basis for the Roadmap of the second edition of Bergey's Manual of Systematic Bacteriology (Garrity and Holt 2001). In the future, sequencing and comparisons of whole genomes might become common practice, but at the moment this is unrealistic (Dubchak and Frazer 2003). However, gene sequences of commonly agreed genes are very useful and can be stored in databases and thus accessible for biologists all over the world. Multi Locus Sequence Typing (MLST) and more recently Multi Locus Sequence Analysis (MLSA) are concepts used for the analysis of sequences of a selection of housekeeping genes within a genus in order to display a speciation process (Maiden *et al.* 1998, Feil *et al.* 2003, 2004). These approaches seem very appropriate tools for speciation studies and should already preferentially be used instead of DNA:DNA hybridisations for species delineations.

The role of bioinformatics

Bioinformatics has long been an important tool in taxonomy, and was previously called numerical taxonomy and used for phenotypic binary data (Sokal and Sneath 1963). Mathematical methods to improve bacterial classification have been developed since (e.g. M. Gyllenberg *et al.* 1997, 1999, 2002), with the aim of maximizing the information content of the data, to cover its full diversity, but minimizing its complexity. A review of the methods used to construct phylogenies based on sequence data is beyond the scope of this essay. However, we want to emphasize careful analysis of data and the development of new tools for studies of population dynamics (e.g. Feil *et al.* 2003, 2004). If we consider biodiversity to be the amount of information contained in a biome, we realize the importance of adequate mathematical approaches for the analysis of its diversity and the evolution of diversity, including speciation.

Nomenclature

There is no need to abandon the binomial nomenclature in use for species, but how should the name labels be put on the results of the speciation processes uncovered? With many bacteria a trinomial nomenclature could be proposed, the first name standing for genus affiliation, the second for species and the third for ecological niche adaptation (Cohen's ecological species). The third name, biovar, pathovar, serovar or similar, would indicate functions encoded by accessory genes but important for those who work with the organisms. At this stage we should namely not forget about the end-users, those who use the names (the microbiologist's species concept). Microbiologists and others who need the names for communication should have a say especially in controversial cases. Because the species cannot be universally defined by using concepts from natural sciences, we should turn to the social scientists for help.

Communities of practice

In social sciences, communities of practice are people working in a similar context (Wenger 1998). The social theory of learning sees learning as a participatory process producing meaning. The collective learning becomes the vehicle for evolution of practices in these communities. It can be demonstrated that these communities produce artefacts – abstract objects jointly agreed upon, which in a decisive manner aid in learning and communication in daily life. The counterpart of participation is reification, which means that knowledge becomes fixed and cannot evolve. The dual relationship between participation and reification in the social theory of learning can be viewed as corresponding to the dialectic dialogue between taxonomists and end-users of bacterial names. The final naming of species could be a dialogue between reification and participation, learning as negotiation; the named species would represent knowledge, an artefact of a community of practice.

A community of practice is e.g. all those people who in their work deal with *Salmonella*, everything from evolution to clinical diagnostics. In microbiology, a taxon name can be considered an artefact of a community of practice, e.g. *Salmonella enterica*. It has also been agreed that former *Salmonella* species now are called serovars instead. So far, *Shigella* retains its genus name even though it might strictly taxonomically speaking, according to current species definitions be *Escherichia coli*. If taxonomists, scientists and other end-users agree, there is no need to make changes just for the sake of taxonomy.

From the end-user's point of view *Agrobacterium* is different from *Rhizobium* – one is pathogenic and the other symbiotic.

Strictly taxonomically speaking, by applying current species definitions, at least *Agrobacterium rhizogenes* equals *Rhizobium tropici*. Here, the question of naming becomes a question of species concepts, which are not mainly biological. For those interested in this controversy we refer to J. Young *et al.* (2003) and Farrand *et al.* (2003).

A cross-disciplinary species concept

If a species is described according to current rules and the description is validly published, the name proposed is also valid. The List of Bacterial Names maintained by Euzéby (2005), contains all validly described species but does not make preferences as to which names to use in controversial cases. It is up to the individual scientist to choose which names to use, but there is no scientific basis guiding his choice. This practice is confusing for those who want to use the names.

We propose a scientific, theoretical framework for making this choice. The naming of the species (a result of a demonstrated speciation process) should be more participatory for the taxonomy to have a real purpose. Van Berkum *et al.* (2003) criticized the use of only SSU to classify rhizobia, because they could demonstrate a mosaic structure of ribosomal genes in these bacteria. Broughton (2003) picked up the message and called for a more conservative taxonomic approach for these organisms. We extend this call to actively involve the end-users to develop a more participatory process.

Scientists working with specific groups or organisms should set the standards and propose guidelines for how to deal with the taxonomy of that group. This happens already with the aid the subcommittees of the International Committee of Systematic Bacteriology proposing the standards (e.g. Graham *et al.* 1991; Martínez *et al.* 2005 for rhizobia).

The ICSP subcommittees exist for discussions on taxonomic issues for diverse bacterial groups. The subcommittee on the taxonomy of *Agrobacterium* and *Rhizobium* meets regularly and publishes minutes from the meetings (e.g. Lindström and Martínez 2002, 2005). By including the meetings into the species concept, we can avoid having arguments about issues that are not plainly a question for natural sciences, but as much a question of social learning.

We call this species concept a cross-disciplinary concept, since it involves philosophy, biology and social sciences. The three cornerstones of the cross-disciplinary species concept are shown in Figure 1, whereas Figure 2 outlines a working scheme for species definition in various organismal groups according to the concept.

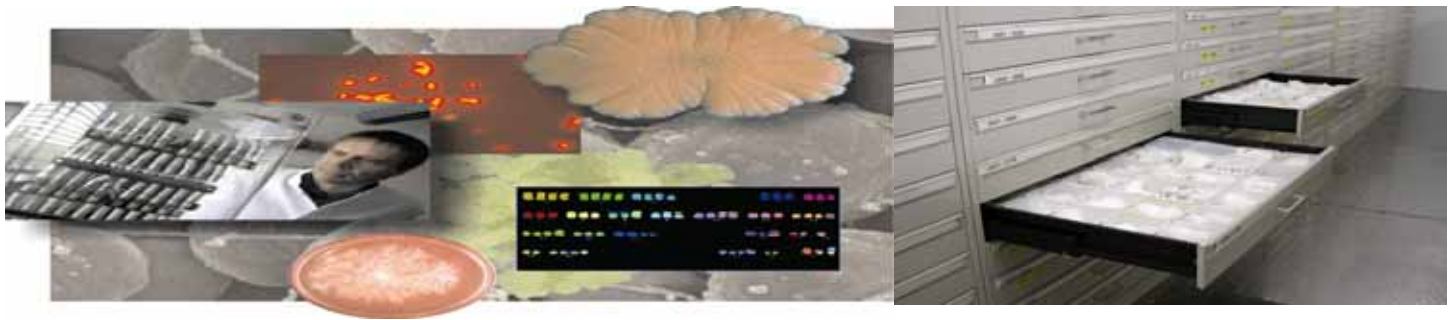


Figure 1: A cross-disciplinary species concept

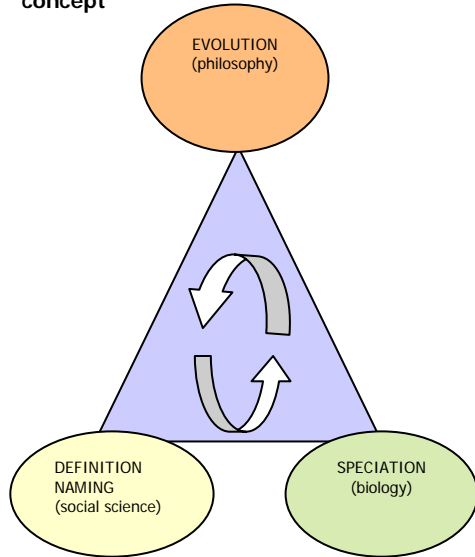


Fig. 2. A working scheme for the cross-disciplinary species concept and the corresponding definitions.

PROCESS	DISCIPLINE
DEFINE SPECIES IN ORGANISM GROUP OF INTEREST	SOCIAL SCIENCE (social theory of learning)
SAMPLING POPULATIONS OF ORGANISMS OF INTEREST	BIOLOGY
APPLICATION OF APPROPRIATE METHODS TO UNCOVER DIVERSITY AND PHYLOGENY	BIOLOGY, MOLECULAR GENETICS, BIOINFORMATICS
DEMONSTRATION OF SPECIATION OR CORRESPONDING FEATURES TO WARRANT THE NAMING OF A NEW SPECIES	POPULATION GENETICS, BIOINFORMATICS
NAMING THE SPECIES	SOCIAL SCIENCE (social theory of learning)

Acknowledgements

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References

Arber, W. 1999. Involvement of gene products in bacterial evolution. *Ann. NY Acad. Sci.* 870: 36-44.

Berg, O.G. and Kurland, C.G. 2002. Evolution of microbial genomes: Sequence acquisition and loss. *Mol. Biol. Evol.* 19: 2265-2276.

Bergey, D.H. 1939. Manual of Determinative Bacteriology. 5th Edition. Baltimore, Williams & Wilkins.

Broughton, W.J. 2003. Roses by other names: Taxonomy of the *Rhizobiaceae*. *J. Bacteriol.* 185:2975-2979.

Buchanan, R.E. 1955. Taxonomy. *Ann. Rev. Microbiol.* 9:1-20.

Claridge, M.F., Dawah, H.A., and Wilson, M.R. 1997. Practical approaches to species concepts for living organisms. p. 1-14. In M.F. Claridge, H.A. Dawah, and M.R. Wilson (ed.) *Species. The units of biodiversity*. Chapman & Hall, London, U.K.

Cohan, F. M. 2001. Bacterial species and speciation. *Syst. Biol.* 50:513-524.

Cohan, F. M. 2002. What are bacterial species? *Annu. Rev. Microbiol.* 56: 457-487.

Cowan, S.T. 1955. The philosophy of classification. *J. Gen. Microbiol.* 12:314-819.

Cowan, S.T. 1956. "Ordnung in das Chaos." *MIGULA Can. J. Microbiol* 2:212-219.

Cowan, S.T. 1962. The microbial species – a macromyth? *Microbial Classification. Symposia of the Society for General Microbiology* 12:433-453. Cambridge University Press, Cambridge.

Cowan, S.T. 1968. A dictionary of microbial taxonomic usage. Oliver & Boyd, Edinburgh.

Coyne, J.A. 2005. Ernst Mayr (1904-2005). *Science* 307: 1212-1213.

Doolittle, W.F. 1999. Phylogenetic classification and the universal tree. *Science* 284: 2124-2129.

Dubchak, I. and Frazer, K. 2003. Multi-species sequence comparisons: the next frontier in genome annotation. *Genome Biology* 4: 122.

Eardly, B. and Van Berkum, P. 2006. Use of population genetic structure to define species limits in the *Rhizobiaceae*. *Symbiosis* 38. In press.

Euzéby, J.P. 2005. List of bacterial names with standing in nomenclature. <http://www.bacterio.cict.fr/>. Last full update 14 May 2005.

Farmer, J.J.III, Davis, B.R., Hickman-Brenner, F.W., McWhorter, A., Huntley-Carter, G.P., Ashbury, M.A., Riddle, C., Wathen-Grady, H.G., Elias, C., Fanning, G.R., Steigerwalt, A.G., O'Hara, C.M., Morris, G.K., Smith, P.B., and D.J. Brenner. 1985. Bio-chemical identification of new species and biogroups of *Enterobacteriaceae* isolated from clinical specimen. *J. Clin. Microbiol.* 21:46-76.

Farrand, S.K., Van Berkum, P. and Oger, P. 2003. *Agrobacterium* is a definable genus of the family *Rhizobiaceae* *Int. J. Syst. Evol. Microbiol.* 53: 1681-1687.

Feil, E.J., Cooper, .E., Grundmann, H., Robinson, D.A., Enright, M.C., Berendt, T., Peacock, S.J., Maynard Smith, J., Murphy, M., Brian G. Spratt, B.G., Moore, C.E. and Day, N.P.J. 2003. How clonal is *Staphylococcus aureus*? *J. Bacteriol.* 185: 3307-3316.

Feil, E.J., Li, B.C., Aanensen, D.M., Hanage, W.P. and Spratt, B.G. 2004. eBURST: Inferring patterns of evolutionary descent among clusters of related bacterial genotypes from multilocus sequence typing data. *J. Bacteriol.* 186: 1518-1530.

Galibert, F., Finan, T.F., Long, S.R., Pühler, A., Abola, P., Ampe, F., Barloy-Hubler, F., Barnett, M.J., Becker, A., Boistard, P., Bothe, G., Boutry, M., Bowser, Leah, Buhrmester, J., Cadieu, E., Capela, D., Chain, P., Cowie, A., Davis, R.W., Dréano, S., Federspiel, N.A., Fisher, R.F. Gloux, S., Godrie, T., Goffeau, A., Golding, B., Gouzy, J., Gurjal, M., Hernandez-Lucas, I., Hong, A., Huizar, L., Hyman, R.W., Jones, T., Kahn, D., Kahn, M.L., Kalman, S., Keating, D.H., Kiss, E., Komp, C., Lelaure, V., Masuy, D., Palm, C., Peck, M.C., Pohl, T.M., Portetelle, D., Purnelle, B., Ramsperger, U., Surzycki, R., Thébault, P., Vandenbol, M., Vorholter, F.-J., Weidner, S., Wells, D.H., Wong, K., Yeh, K.-C., and J. Batut. 2001. The composite genome of the legumes symbiont *Sinorhizobium meliloti*. *Science* 293:668-672.

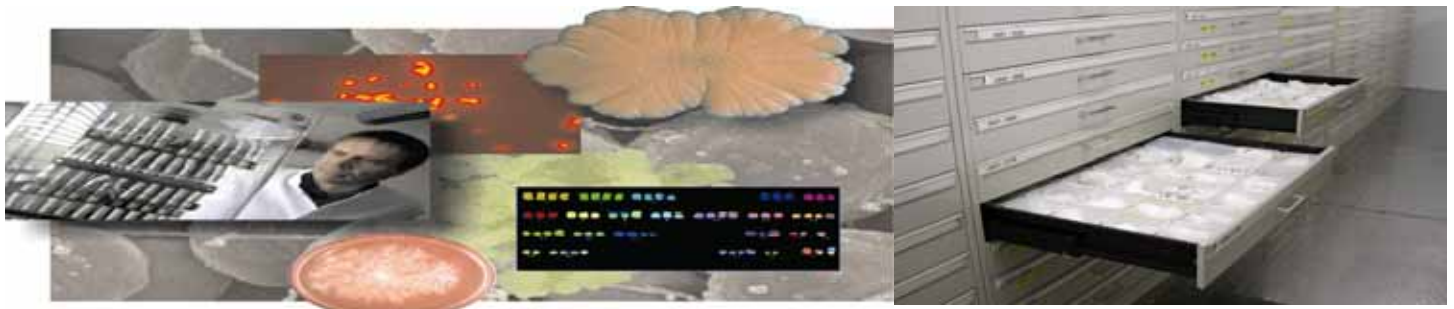
Garrity, G.M. and Holt, J.G. 2001. The road map to the Manual. In: Boone, D.R. and Castenholz, R.W. (ed). *Bergey's Manual of Systematic Bacteriology*. Springer-Verlag. New York, pp. 119-166.

Gaunt, M.W., Turner, S.L., Rigotier-Gois, L., Lloyd-Macgilp, S.A., and J.P.W. Young. 2001. Phylogenies of *atpD* and *recA* support the small subunit rRNA-based classification of rhizobia. *Int. J. Syst. Evol. Microbiol.* 51:2037-2048.

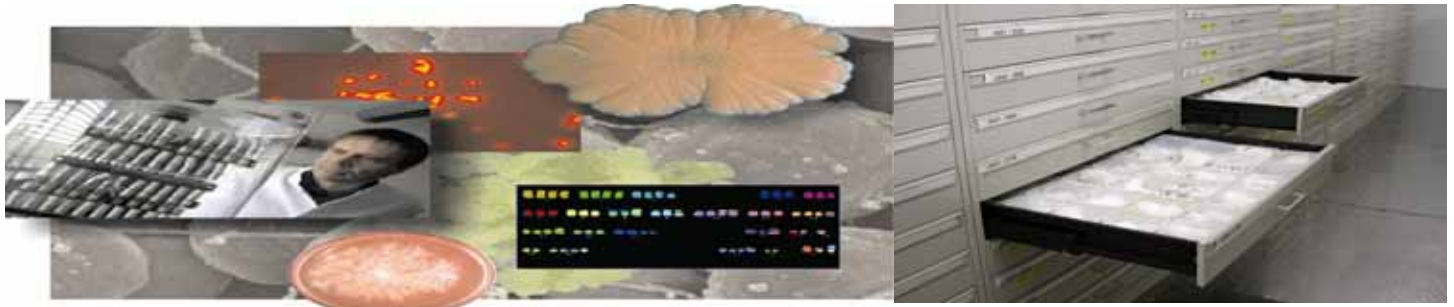
Gillis, M., Vandamme, P., De Vos, P., Swings, J. and Kersters, K. 2001. Polyphasic taxonomy. In: Boone, D.R. and Castenholz, R.W. (ed). *Bergey's Manual of Systematic Bacteriology*. Springer-Verlag. New York, pp. 43-48.

Gogarten, J.P., Doolittle, W.F. and Lawrence, J.G. 2002. Prokaryotic evolution in light of gene transfer. *Mol. Biol. Evol.* 19: 2226-2238.

Goodfellow, M., Manfio, G.P., and Chun, J. 1997. Towards a practical species concept for cultivable bacteria. p. 25-60. In M.F. Claridge, H.A. Dawah, and M.R. Wilson (ed.) *Species. The units of biodiversity*. Chapman & Hall, London, U.K.



- Goodner, B., Hinkle, G., Gattung, S., Miller, N., Blanchard, M., Quorollo, B., Goldman, B.S., Cao, Y., Askenazi, M., Halling, C., Mullin, L., Houmiel, K., Gordon, J., Vaudin, M., Iartchouk, O., Epp, A., Liu, F., Wollam, C., Allinger, M., Doughty, D., Scott, C., Lappas, C., Markelz, B., Flanagan, C., Crowell, C., Gurson, J., Lomo, C., Sear, C., Strub, G., Cielo, C., and S. Slater. 2001. Genome sequence of the plant pathogen and biotechnology agent *Agrobacterium tumefaciens* C58. *Science* 294:2323-2328.
- Gower, J.C. 1974. Maximal predictive classification. *Biometrics* 30:643-654.
- Graham, P. H., Sadowsky, M. J., Keyser, H. H., Barnett, Y. M., Bradley, R. S., Cooper, J. E., De Ley, J., Jarvis, B. D. W., Roslycky, E. B., Strijdom, B. W. and Young, J. P. W. 1991. Proposed minimal standards for the description of new genera and species of root- and stem-nodulating bacteria. *Int. J. Syst. Bacteriol* 41: 582-587.
- Gyllenberg, H.G., Gyllenberg, M., Koski., Lund, T., Schindler, J., and M. Verlaan. 1997. Classification of *Enterobacteriaceae* by minimization of stochastic complexity. *Microbiology* 143:721-732.
- Gyllenberg, M., Koski, T. and M. Verlaan. 1997. Identification of binary vectors by stochastic complexity. *J. Multivariate Anal.* 63:47-72.
- Gyllenberg, M., Koski, T., Lund, T., and H.G. Gyllenberg. 1999. Bayesian predictive identification and cumulative classification of bacteria. *Bull. Mathematical Biol.* 61:85-111.
- Gyllenberg, M., Koski, T., Dawyndt, P., Lund, T., Thompson, F., Austin, B. and J.Swings. 2002. New methods for the analysis of binarized BIOLOG GN data of *Vibrio* species: Minimization of stochastic complexity and cumulative classification. *System. Appl. Microbiol.* 25:403-415.
- Haukka, K., Lindström, K. and Young, P. 1998. Three phylogenetic groups of *nodA* and *nifH* genes in *Sinorhizobium* and *Mesorhizobium* isolates from leguminous trees growing in Africa and Latin America. *Appl. Environ. Microbiol.* 64: 419-426.
- Hull, D.L. 1997. The ideal species concept – and why we can't get it. p. 357-380. In M.F. Claridge, H.A. Dawah, and M.R. Wilson (ed.) *Species. The units of biodiversity.* Chapman & Hall, London, U.K.
- Joyce, E.A., Chan, K., Salama, N.R., and S. Falkow. 2002. Redefining bacterial populations: A post-genomic reformation. *Nature Reviews Genetics* 3:42-473. [Online.]
- Kaneko, T., Nakamura, Y., Sato, S., Asamizu, E., Kato, T., Sasamoto, S., Watanabe, A., Idesawa, K., Ishikawa, K., Kawashima, K., Kimur, T., Kishhida, Y., Kiyokawa, C., Kohara, M., Matsumoto, M., Matsuno, A., Mochizuki, Y., Nakayama, S., Nakazaki, N., Shimpo, S., Sugimoto, M., Takeuchi, C., Yamada, M. and S. Tabata. 2000. *DNA Res.* 7:331-338, Supplement: 381-406.
- Kotewicz, M.L., Brown, E.W., LeClerc, J.E. and Cebula. T. A. 2003. Genomic variability among enteric pathogens: the case of the *mutS-rpoS* intergenic region. *TRENDS Microbiol.* 11:2-6.
- Kurland, C.G., Canback, B. and Berg, O.G. 2003. Horizontal gene transfer: A critical view. *PNAS* 100: 9658-9662.
- Lan, R., and P.R. Reeves. 2001. When does a clone deserve a name? A perspective on bacterial species based on population genetics. *TRENDS Microbiol.* 9:419-424.
- Lindström, K. and E. Martínez-Romero. 2002. International Committee on Systematics of Prokaryotes Subcommittee on the taxonomy of *Agrobacterium* and *Rhizobium*. Minutes of the meeting, 4 July 2001, Hamilton, Canada. *Int. J. Syst. Evol. Microbiol.* 52: 2337.
- Lindström, K. and E. Martínez-Romero. 2005. International Committee on Systematics of Prokaryotes Subcommittee on the taxonomy of *Agrobacterium* and *Rhizobium*. Minutes of the meeting, 26 July, 2004, Toulouse, France. *Int. J. Syst. Evol. Microbiol.* 55: 1383.
- Locke, J. 1689. An essay concerning human understanding. Book III, Chapter, 6th Edition, *ILT Classics.*
- Maiden, M.C.J., Bygraves, J.A., Feil, E., Morelli, G., Russell, J.E., Urwin, R., Zhang, Q., Zhou, J., Zurth, K., Caugant, D.A., Ian M. Feavers, I. M., Achtman, M. and Spratt, B.G. 1998. Multilocus sequence typing: A portable approach to the identification of clones within populations of pathogenic microorganisms. *PNAS* 95: 3140-3145.
- Martínez-Romero, E., Vinuesa, P., Young, P.J.W., Chen W.X., de Lajudie, P., Eardly, B., Graham, P., Laguerre G., van Berkum, P., Willems, A., Jarvis, B.D.W. and K. Lindström, K. 2005. Guidelines to propose new rhizobial species. Manuscript.
- Mayden, R.L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem, pp. 31-424. In M.F. Claridge, H.A. Dawah, and M.R. Wilson (ed.) *Species. The units of biodiversity.* Chapman & Hall, London, U.K.
- Maynard Smith, J., Feil, E., and N.H. Smith. 2000. Population structure and evolutionary dynamics of pathogenic bacteria. *BioEssays* 22:1115-1122. [Online.]
- Mayr, E. 1957. Species concepts and definitions. p. 1-22. In E. Mayr (ed.) *The species problem. The American Association for the Advancement of Science, Washington D.C.*
- Moreno, E. 1997. In search of a bacterial species definition. *Rev. Biol. Trop.* 45:753-771.
- Moulin, L., Munive, A., Dreyfus, B., and C. Boivin-Masson. 2001. Nodulation of legumes by members of the beta-subclass of Proteobacteria. *Nature* 411:948-950.
- Ochman, H., Lawrence, J.G. and Groisman, E.A. 2000. Lateral gene transfer and the nature of bacterial innovation. *Nature* 405: 299-304.
- Palys, T., Nakamura, L.K. and Cohan, F.M. 1997. Discovery and classification of ecological diversity in the bacterial world: the role of DNA sequence data. *Int. J. Syst. Bacteriol.* 47: 1145-1156.
- Palys, T., Berger, E., Mitrica, I., Nakamura, L.K. and Cohan, F.M. 2000. Protein-coding genes as molecular markers for ecologically distinct populations: the case of two *Bacillus* species. *Int. J. Syst. Evol. Microbiol.* 50: 1021-1028.
- Ravin, A.W. 1963. Experimental approaches to the study of bacterial phylogenies. *Am. Naturalist* 97:307-318.
- Roselló-Mora, R., and R. Amann. 2001. The species concept for prokaryotes. *FEMS Microbiol. Rev.* 25:39-67.
- Silva, C., Vinuesa, P., Eguiarte, L.E., Martínez-Romero, E. and Souza, V. 2003. *Rhizobium etli* and *Rhizobium gallicum* nodulate common bean (*Phaseolus vulgaris*) in traditionally managed Milpa plot in Mexico: Populatio genetics and biogeographic implications. *Appl. Environ. Microbiol.* 69:884-893.
- Simpson, G.G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York.
- Sneath, P.H.A. 1992. International code of nomenclature of bacteria: Bacteriological Code, 1990, Revision. American Society for Microbiology, Washington D.C. 232 pp.
- Sokal, R.R. and P.H.A. Sneath. 1963. Principles of numerical taxonomy. Freeman, San Francisco.
- Stackebrandt, E. 2003. The richness of prokaryotic diversity: There must be a species somewhere. *Food Technol. Biotechnol.* 41:17-22.
- Stackebrandt, E., Fredericksen, W., Garrity, G.M., Grimont, P.A.D., Kämpfer, P., Maiden, M.C.J., Nesme, X., Roselló-Mora, R., Swings, J., Trüper, H.G., Vauterin, L., Ward, A.C., and W.B. Whitman. 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.
- Suominen, L., Lortet, G., Roos, C. Paulin, L. and K. Lindström. 2001. Identification and structure of the *Rhizobium galegae* common nodulation genes: evidence for horizontal gene transfer. *Mol. Biol. Evol.* 18:906-916.



Tamas, I., Klasson, L., Canbäck, B., Näslund, A.K., Eriksson, A.-S., Wernegreen, J.J., Sandström, J.P., Moran, N.A. and S.G.E. Andersson. 2002. 50 million years of genomic stasis in endosymbiotic bacteria. *Science* 296: 2376-2379.

Tekaia, F., Lazcano, A. and Dujon, B. 1999. The genomic tree as revealed from whole proteome comparisons. *Genome Res.* 9: 550-557.

Terefework, Z., Nick, G., Suomalainen, S., Paulin, L., and K. Lindström. 1998. Phylogeny of Rhizobium galegae with respect to other rhizobia and agrobacteria. *Int. J. Syst. Bacteriol.* 48:349-356.

Torsvik, V., Övreås, L., and T.F. Thingstad. 2002. Prokaryotic diversity – magnitude, dynamics and controlling factors. *Science* 296:1064-1066.

Turner, S.L. and J.P.W. Young. 1999. The glutamine synthetases of rhizobia: phylogenetics and evolutionary implications. *Mol. Biol. Evol.* 17:309-319.

Turner, S.L., Zhang, X.-X., Li, F.-D. and J.P.W. Young. 2002. What does a bacterial genome sequence represent? Misassignment of MAFF 303099 to the genospecies *Mesorhizobium loti*. *Microbiology* 148:3330-3331.

Van Berkum, P., Terefework, Z., Paulin, L., Suomalainen, S., Lindström, K., and B.D. Eardley. 2003. Discordant phylogenies within the *rrn* loci of rhizobia. *J. Bacteriol.* 185: 2975-9

Vandamme, P., Pot, B., Gillis, M., De Vos, P., Kersters, K., and J. Swings. 1996. Polyphasic taxonomy, a consensus approach to bacterial systematics. *Microbiol. Rev.* 60:407-438.

Vinuesa, P., Silva, C., Werner, D. and Martinez-Romero, E. 2005. Population genetics and phylogenetic inference in bacterial molecular systematics: the roles of migration and recombination in *Bradyrhizobium* species cohesion and delineation. *Mol. Phylogenetics and Evolution* 34: 29-54.

Ward, D.M. 1998. A natural species concept for prokaryotes. *Curr. Opinion Microbiol.* 1: 271-277.

Wayne, L.G., Brenner, D.J., Colwell, R.R., Grimont, P.A.D., Kandler, O., Krichevsky, L., Moore, L.H., Moore, W.C., Murray, R.G.E., Stackebrandt, E., Starr, M.P., and H.G. Trüper. 1987. Report of the ad hoc committee on reconciliation of approaches to bacterial systematics. *Int. J. Syst. Bacteriol.* 37: 463-464.

Wenger, W. 1998. Communities of practice: learning, meaning and identity. Cambridge University Press. Cambridge.

Woese, C.R. 1987. Bacterial evolution. *Microbiol. Rev.* 51:221-271.

Woese, C.R. 1994. There must be a prokaryote somewhere: Microbiology's search for itself. *Microbiol. Rev.* 58: 1-9.

Woese C.R., Kandler, O., and M.L. Wheelis. 1990. Towards a natural system of organisms: Proposal for the domains *Archaea*, *Bacteria* and *Eucarya*. *Proc. Nat. Acad. Sci. USA*, 87: 4576-4579.

Wood, D.W., Setubal, J.C., Kaul, R., Monks, D., Kitajima, J.P., Okura, V.K., Zhou, Y., Chen, L., Wood, G.E., Almeida, N.F. Jr., Woo, L., Chen, Y., Paulsen, I.T., Eise, J.A., Karp, P.D., Bovee, D. Sr., Chapman, P., Clendenning, J., Deatherage, G., Gilet, W., Grant, C., Kutuyavin, T., Levy, R., Li, M.-J., McClelland, E., Palmieri, A., Raymond, C., Rouse, G., Saenphimmachak, C., Wu, Z., Romero, P., Gordon, D., Zhang, S., Yoo, H., Tao, Y., Biddle, P., Jung, M., Krespan, W., Perry, M., Gordon-Kamm, B., Liao, L., Kim, S., Hendrick, C., Zhao, Z.-Y., Dolan, M., Chumley, F., Tingeny, S.v., Tomb, J.-F., Gordon, M.P., Olson, M.V., and E.W. Nester. 2001. The genome of the natural genetic engineer *Agrobacterium tumefaciens* C58. *Science* 294: 2317-2323.

Young, J.M., Kuykendall, L.D., Martínez-Romero, E., Kerr, A., and H. Sawada. 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. 2003. The genus name *Ensifer* Casida 1982 takes priority over *Sinorhizobium* Chen *et al.* 1988, and *Sinorhizobium morelense* Wang *et al.* 2002 is a later synonym of *Ensifer adhaerens* Casida 1982. Is the combination '*Sinorhizobium adhaerens*' (Casida 1982) Willems *et al.* 2003 legitimate? Request for an opinion. *Int. J. Syst. Evol. Microbiol.* 53: 1207-1217.

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ECDC is a very important organisation expressing again a harmonised European activity. The young European agency should strengthen Europe's defences against infectious diseases like SARS, influenza, HIV, avian flu and other possible outbreaks and pandemics. In spring 2004, the EU Parliament and Council passed a law creating ECDC designed to be a small but effective EU agency, working in partnership with national health protection bodies across Europe. Keywords are disease surveillance and early warning systems to pool Europe's health knowledge. Emerging diseases are the centres of interest. ECDC's inaugural meeting was held in Stockholm where the headquarters are located. The Mission Statement sub-page is worth to read: The European Council Regulation 851/2004 is the founding document and contains the ECDC's missions. The ECDC work programme can be downloaded as well as a general presentation of ECDC' mission and other relevant legal documents in the context.

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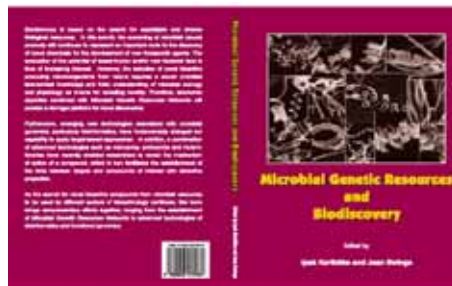
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