

# Discussions > General ICTV Discussions

# Comments to proposed modification to code rule 3.21 (defining virus species)



Online admin 138.26.20.120 over 9 years ago

Below are the comments originally posted in response to the proposal:

<u>2011.002a-uG.A.v8.statute and code changes.pdf</u> that includes language to redefine the definition of a virus species.

# Comment:

# Van Regenmortel Marc Sat, Sep 22 2012 9:15 AM

The ICTV is once more proposing to modify Code Rule 3.21 that gives the definition of virus species but this time it is using a fast-track approval process which considerably reduces the time available for posting comments and objections to the proposal. I believe that the proposed change to Rule 3.21 will be detrimental to the creation of virus species in the future. Since species demarcation remains a crucial taxonomic task of the ICTV, I believe that the proposed change should not be approved.

The proposal wants to change the existing Code Rule 3.21:

"A virus species is defined as a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche"

by the following definition:

"A species is a monophyletic group of viruses whose properties can be distinguished from those of other species by multiple criteria"

This new definition is claimed to be a practical guideline for helping virologists to create new species, although the claim is actually based on erroneous taxonomic thinking. Strains or genera can equally be said to correspond to monophyletic groups of viruses derived from a single ancestor, and the species definition in fact gives no indication of how one monophyletic species can be distinguished from another,

although this information is essential for demarcating new species.

The current definition makes the important point that a virus species is a taxonomic class (all classifications consist of classes) and not simply a "group" of viruses. There have been objections in the past to species being called polythetic classes because the term "polythetic" was considered to be obscure and I have proposed that 'polythetic class' should be replaced by the more easily understood term: cluster class (Systematic Applied Microbiology 33; 1-6; 2010).

A cluster class is defined by a cluster of properties, i.e. by a variable combination of several properties of its members, with no single property being necessarily present in all the members. This is in contrast to a so-called universal class such as a virus family, which is defined by one or more properties that are universally present in everyone of its members. This is an important distinction because all the properties useful for species demarcation (i.e. host range, cell and tissue tropism, pathogenicity, mode of transmission, antigenicity, small differences in genome sequence etc) can be altered by a few mutations and may therefore vary in different members of the same species. In a cluster class, each member of the class shares a large but unspecified number of properties, each property is present in a large number of members but no property is necessarily present in all the members of the class.

It is important to define a virus species as a cluster class since this indicates that no single genotypic, phenotypic or biological property is sufficient to create new species. A combination of different types of viral properties must indeed always be used to establish new species. Unfortunately, in recent years, ICTV Study Groups have ignored the current ICTV definition of virus species as a class and have created large number of species on the basis of a single criterion, namely a certain percentage of genome similarity between individual viruses. For instance about 60 different anellovirus species were created using only genotypic criteria. A classification based only on nucleotide sequence similarities amounts to a classification of genomes rather than of viruses.

The ICTV also established 178 separate begomovirus species on the basis of a single criterion of less than 89% pairwise sequence identity in the DNA-A genome component of different viruses. Many viruses in these so-called begomovirus species infect the same host and produce very similar diseases and separate species names had to be coined by adding the geographical location of the first isolation of the virus. There is no evidence, however, that all these begomovirus species taxa correspond to separate, stable biological entities that would justify the label 'species'. If a lower threshold cut-off figure of percentage sequence identity had been chosen, the number of begomovirus species would have been considerably less. In the case of the mastreviruses in the same virus family, only 14 species were established because a cut-off figure of 75% sequence identity in the DNA-A component was used to demarcate species.

To prevent such inordinate multiplication of species, I propose that the existing Code Rule 3.21 should be retained and that the definition of species should only be slightly modified as follows:

A virus species is defined as a cluster class of viruses that constitute a replicating lineage and occupy a particular ecological niche.

Comments: Appropriate Study Groups establish species as cluster classes, using always a combination of several criteria such as host range, cell and tissue tropism, pathogenicity, vector specificity, antigenicity and degree of genome relatedness. The list of different criteria used for each species should be published in the relevant section of ICTV reports.

I believe that this definition of virus species is superior to the one that the ICTV proposes in modified code Rule 3.21 because:

1) it explains why a species cannot be demarcated by a single universally shared character such as an arbitrary degree of genome relatedness.

2) it reminds virologists that a virus species, being a cluster class, is a taxonomic construct that is not physically real and therefore cannot be transmitted to a host or sequenced. Viruses which are the members of a species, are the real objects studied by virologists which can be transmitted and sequenced. This distinction between virus (written in Roman) and species (written in italics) is not always understood and virologists often write that they have transmitted or sequenced an (italicized) species.

3) It makes clear that there are no precise cut-off points between species since the boundaries must be drawn across a continuous range of variable genotypic, phenotypic and biological properties. Although species taxa are fuzzy sets of virus populations with blurred boundaries, the absence of obvious discontinuities between individual virus species does not mean that the species concept should be abandoned. It would be equally unwarranted to refuse to distinguish colours because of the continuous nature of the spectrum of electromagnetic waves.

4) A meaningful definition is needed because the absence of a satisfactory definition of a virus species was the reason why many virologists in the past were opposed to using the concept species in viral taxonomy.

#### Comment

#### Jens H. Kuhn Mon, Sep 24 2012 10:23 AM

I agree with Marc. The new proposed species definition is much more fuzzy than the old one, and therefore less helpful to virologists. As Marc points out, it is very problematic that the polythetic (or cluster class) principle is being omitted. "Multiple criteria" does not mean that same thing as polythetic (or cluster class) and the ecological niche concept is entirely missing in the new definition. Honestly, I don't understand what the reasons are why the old definition was even under discussion, and what has led to the proposal to change it. As Marc pointed out, the discussion seemed to circle around the definition of the word "polythetic" because people seem to understand that word in different ways. However, when the old species definition was brought forward, it was explicitly explained what was meant with "polythetic" in this particular context. I therefore see no need to touch the species definition at all. At the same time, if replacing "polythetic" with "cluster class" is more acceptable to a larger community then so be it.

I am not sure whether I agree with Marc that higher taxa are universal classes whereas species is a cluster class, though. In my mind, higher taxa could be cluster classes as well. But that is just a side note as this thought has nothing to do with the species definition.

In short, I strongly recommend that the old species definition be kept, or changed subtly by replacing the word "polythetic" with "cluster class" as Marc suggests.

# Comment

Heinrich Josef Vetten Mon, Sep 24 2012 2:36 PM

I agree with the slightly modified definition proposed by Van Regenmortel (A virus species is defined as a cluster class of viruses that constitute a replicating lineage and occupy a particular ecological niche).

#### Comment

F. A. Murphy Mon, Sep 24 2012 2:48 PM Proposed wording of Code rule 3.21:

"3.21 -- Species shall be created in accordance with the following definition:

A species is the lowest taxonomic level in the hierarchy approved by the ICTV. A species is a monophyletic group of viruses whose properties can be distinguished from those of other species by multiple criteria.

Comments: The criteria by which different species within a genus are distinguished shall be established by the appropriate Study Group. These criteria may include, but are not limited to, natural and experimental host range, cell and tissue tropism, pathogenicity, vector specificity, antigenicity, and the degree of relatedness of their genomes or genes. The criteria used should be published in the relevant section of the ICTV Report and reviewed periodically by the Study Group."

I do not see how this newly suggested definition helps at all to distinguish classes of viruses that fall under

the hierarchical level of "species" from classes that might otherwise be called "strains" or "variants" or "genotypes" or such, none of which ICTV wishes to deal with. It is so vague...

My point here is that leaving the choice of criteria to a Study Group, or even an individual substituting for such, can only lead to problems, problems that might be averted by more specificity. Under the suggested definition, problematic criteria may be left out or demoted, to suit the lumper or splitter perspective of the submitter. I had always thought that the main danger lies with the splitters, giving species class designation to every damned isolate (real entity), or isolates separable only by very small genomic sequence difference. Now, I also see danger from the lumpers, as important pathogens disappear down the rabbit-hole by being called strains, variants, etc., all in the name of making lists shorter. This danger is magnified by the demise of many "international specialty groups" that formerly worked as archivists and gatekeepers.

All of this will further affect the failings to achieve overall parallelism of structure among the various taxa (and further affect ICTV's product usability as its taxonomy/nomenclature move further and further away from the useful semi-vernacular nomenclature system that was so widely liked by working virologists). I think much of the broad support for the original ICTV product was its arbitrary focus on important human, animal and plant pathogens - important viruses (real entities) were placed at the hierarchical level now held by species (classes), all by using arbitrary yet polythetic characteristics. Arbitrary as this may have been, the result was sensible to virologists who could not care less otherwise.

I applaud the intent to include phenotypic characters among the multiple criteria to be used to define species, to somehow bring more sense to the genotypy-only approach of some Study Groups/individuals. Indeed, the requirement for at least some phenotypic characters in bacterial taxonomy is instructive.

The attention to this important rule in the Code brought by Marc van Regenmortel is to be applauded. It seems to me that much more debate on this matter is called for - hopefully in a venue where full dialogue by caring virologists can be arranged. Even if the EC no longer likes the ground-breaking definition of the species class developed by Marc, I believe that the officers and EC members must at least invite Marc, and perhaps a few others, to a meeting where this matter can be hammered out - this could take hours, not the minutes available at the general meetings at the Congresses. In the days of the founding of the ICTV, such was the way many matters were dealt with. Democracy requires much discussion before decision, and as they say it is messy and inefficient, but it is still better than any known alternative.

I wish ICTV every success... and to achieve continuing success I think that the guiding perspective must continue to be service to the working virology community (the members of which don't care about taxonomy, but need the product). I also think that the guiding perspective must continue to be respect for the founders and the discoverers of the viruses – even as the technology and bases for relationships among taxa change, the continuity with the founders remains a source of pride and stability and broad support. I care much less for consistency with The BioCode.

Frederick A. Murphy, Life Member, former president of ICTV

Frederick A Murphy

Professor

University of Texas Medical Branch

Department of Pathology, Route 0609

301 University Blvd.

Galveston, TX 77555-0609 USA

(Office Tel) 409 747 2430

(Home Tel) 409 744 3143

(Cell Tel) 409 739 3332

(Email) famurphy@utmb.edu<mailto:famurphy@utmb.edu>

The Foundations of Medical and Veterinary Virology: Discoverers and Discoveries, Inventors and Inventions, Developers and Technology (.pdf, .pptx and .doc files) at www.utmb.edu/virusimages

#### Comment

Ralf Dietzgen Tue, Sep 25 2012 6:18 PM I disagree with the changes to Code Rule 3.21 proposed by the ICTV and I agree instead with the slightly modified definition proposed by Marc van Regenmortel - A virus species is defined as a cluster class of viruses that constitute a replicating lineage and occupy a particular ecological niche.

#### Comment

Tim Skern Thu, Sep 27 2012 4:11 AM I disagree with the changes to Code Rule 3.21 proposed by the ICTV and support Marc's alternative.

#### Comment

Giovanni Martelli Thu, Sep 27 2012 6:09 AM

I agree with with the slightly modified definition proposed by Van Regenmortel (A virus species is defined as a cluster class of viruses that constitute a replicating lineage and occupy a particular ecological niche).

# Comment

scottcweaver Sun, Sep 30 2012 8:32 PM I agree with Marc's suggestions.

Scott Weaver

#### Comment

Hans-W. Ackermann Tue, Oct 2 2012 10:53 PM I agree with Dr. Van Regenmortel and want to retain Code Rule 3.21.

Hans-W. Ackermann, Life Member, Viruses of Prokaryotes

#### Comment

#### Bert Rima Mon, Oct 8 2012 3:16 AM

I am of the opinion that the rule as proposed is vague and unclear. The terminology " can be distinguished " is entirely inapropriate as it is undefined and potentially allows the creation of hundreds of species based on small sequence variations. It is crucial that we deal with that threat as it will lead to a proliferation that will bring viral taxonomy into disrepute. Nobody will care anymore if we create too may species names that nobody uses. I agree that the minor modification proposed by Marc van Regenmortel is as far as we shoud go at the present.

#### Comment

Craig Pringle Tue, Oct 9 2012 4:35 PM

My opinion is that the virus species definition developed by Marc Van-Regenmortel, namely that: " A virus species is defined as a cluster class of viruses that constitute a replicating lineage and occupy a particular ecological niche', is superior to the definition proposed by the ICTV Sub-Committee.

The definition now favoured by the ICTV Sub-Committee appears to be promoting definition of species on

the basis of a single property or criterion. In reality this will have the effect of making every virus isolate a distinct virus species.

To avoid such an outcome, I favour retention of the existing definition. Personally I favour also retention of the the existing term 'polythetic.

### Comment

Brian Mahy Fri, Oct 19 2012 8:46 AM Mahy, Brian WJ

I agree with the slightly modified version of Code Rule 3.21 as proposed by Marc vanregenmortel. I do not support the change to rule 3.21 proposed by the ICTV.

#### Comment

GKeil Sun, Oct 21 2012 3:33 AM

I do not support the changes to Code Rule 3.21 suggested by the ICTV and recommend the slightly modified definition proposed by Marc van Regenmortel: A virus species is defined as a cluster class of viruses that constitute a replicating lineage and occupy a particular ecological niche.

# Comment

amqking Tue, Oct 23 2012 7:04 AM RE THE PROPOSED MODIFICATION TO CODE RULE 3.21 (DEFINING VIRUS SPECIES): A SUPPORTING CASE FROM THE PROPOSERS (Andrew King, Mike Adams, Elliot Lefkowitz and Eric Carstens)

1. DEFICIENCIES OF THE EXISTING SPECIES DEFINITION: "A virus species is defined as a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche".

1.1 "Polythetic": This term has a variety of recognised meanings. The one favoured by Professor Marc van Regenmortel, the chief protagonist of the above definition, is as follows: "a polythetic class of viruses is defined as a class based on a minimum number of shared properties, none of which must necessarily be present in every member of the class". Professor Regenmortel regards this concept as essential to understanding the nature of virus species and hence to the way species should be demarcated from each other. The reasoning can be summarised, in the words of his objection, as follows:

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Because "properties useful for species demarcation ... can be altered by a few mutations", they "may ... vary in different members of the same species". Therefore, species "are fuzzy sets of virus populations with blurred boundaries", which means that "a combination of different types of viral properties must ... always be used to establish new species".

This reasoning is questionable on a number of grounds (e.g. the leap from "may" to "are") but its main flaw arises from a confusion between two different meanings of the word "members": (a) mutants as "members" of a virus population and (b) strains/isolates as "members" of a species. Virus taxonomists classify strains and isolates, i.e. whole populations, not individual virions. Whether species are actually fuzzy sets, and whether the boundaries between them are actually blurred, can only be resolved empirically, not through specious reasoning.

In practice, it is possible to identify numerous properties that are shared by all the constituent strains/isolates of a species, despite the presumed presence of undetected mutants within their populations. Membership of the same "replicating lineage" and occupation of the same "particular ecological niche" are properties that are, by this definition, necessarily shared by all members of any particular species. Species are therefore NOT polythetic and the term "polythetic" has no place in the species definition. The same applies to its synonym, "cluster", as recently suggested by Professor Regenmortel. As for blurring at inter-species boundaries, if this were a real phenomenon, one would expect genetic drift to generate many intermediate, difficult to assign, strains whereas we see little evidence of this among species properly constituted on the basis of multiple criteria (see 3.3).

1.2 Class: Class is the taxonomic level between order and phylum. Virus taxonomy doesn't yet have a level above order, although it is conceivable that the need for it may arise in the future and that, when it does, it will be designated "class". Use of the term in connection with species is clearly inappropriate when there are alternative terms - "group", "set" – that are uncontaminated by such taxonomic associations. Everybody, including every virologist, knows what a group is.

1.3 "Replicating lineage": All living organisms replicate and are thought to belong to the same lineage. The phrase has never been defined and, as it stands, is devoid of meaning.

1.4 "Particular ecological niche": This criterion has also never been defined and it is unclear how it might be defined in a way that meaningfully applies to all virus species. The identity of the host, or a particularly limited host range, is significant in the classification of some viruses, but others have such a wide natural host range (e.g. cucumber mosaic virus, all isolates of which belong to a single species even though they are able to infect plants from over 85 distinct families) that the concept of an "ecological niche" is at best problematic. Another issue is that host range to small numbers of mutations, causing the property to be poorly correlated with phylogeny. This has been known to lead to the creation of sub-species strains adapted to distinct hosts (e.g. swine vesicular disease virus in the species Human enterovirus B). When

host was a primary criterion for new species it left an unfortunate legacy of numerous, very similar, species (Goose coronavirus, Pheasant coronavirus, Pigeon coronavirus, Turkey coronavirus, etc). In recent years a major effort has been underway to rationalise traditional species-level taxonomy into a small number of more clearly demarcated species. For all these reasons we think that any reference to niche is counter-productive in a general species definition.

2. MERITS OF THE PROPOSED SPECIES DEFINITION: "Species shall be created in accordance with the following definition: A species is the lowest taxonomic level in the hierarchy approved by the ICTV. A species is a monophyletic group of viruses whose properties can be distinguished from those of other species by multiple criteria."

2.1 "Species shall be created in accordance with the following definition": The definition is expressed as a rule. It provides virologists with the information that will be needed to propose a new species - namely to show how it differs from related species and to provide phylogenetic support. This is stated clearly and directly in plain language.

2.2 "A species is the lowest taxonomic level": Species is the basic unit of taxonomy into which all viruses are to be grouped. Since there cannot be more than one "lowest" level, it follows that all species are at the same level and, therefore, no species can be contained, wholly or in part, within another species.

2.3 "...monophyletic group of viruses": A monophyletic group is one derived from a common ancestor. Monophyly establishes two key principles. First, that species are discrete, non-overlapping groups of viruses, i.e. each species comprises only members of its defining lineage and each defining lineage comprises only members of that species. Second, the requirement for species to be monophyletic makes explicit what it is already the policy of the EC in reviewing taxonomic proposals, namely that a proper phylogenetic analysis is a fundamental requirement to justify the creation of new species (and of course, higher taxa). It is true that such analyses require interpretation and that judgements sometimes have to be made about the appropriate places for species 'boundaries' but, as the definition makes clear (see 2.4), species assignments do not rely exclusively on measures of genetic relatedness. This is discussed further in §3.3.

2.4 ".. distinguished from those of other species by multiple criteria": This provision, together with its accompanying "comments" (see text of proposal), makes it explicit that species should not be created on the basis of a single criterion, whether that is host, symptomatology or some measure of genetic distance.

3. REASONS ADVANCED FOR RETAINING THE EXISTING DEFINITION:

The following reasons have been given in support of the existing definition (or a slightly modified version):

3.1 It explains why a species cannot be demarcated by a single universally shared character such as an

arbitrary degree of genome relatedness."

Answer: On the contrary, as discussed in 1.1, it is far from obvious to us that the existing definition does explain this. In the proposed definition, by contrast, the requirement for multiple criteria is stated explicitly. Genome relatedness is not sufficient on its own to establish a new species and when it is used as one factor to support the creation of new species it is never arbitrary but is based on a careful analysis of existing data to determine where there are discontinuities.

3.2 It reminds virologists that a virus species, being a cluster class, is a taxonomic construct that is not physically real and therefore cannot be transmitted to a host or sequenced. Viruses which are the members of a species, are the real objects studied by virologists which can be transmitted and sequenced. This distinction between virus (written in Roman) and species (written in italics) is not always understood and virologists often write that they have transmitted or sequenced an (italicized) species."

Answer: This point could be made for all taxa, however defined, and is therefore not relevant to this discussion. The ICTV enforces the distinction between taxon and virus through the Rules for Orthography (International Code of Virus Classification and Nomenclature, part IX) and we are not proposing to change these.

3.3 It makes clear that there are no precise cut-off points between species since the boundaries must be drawn across a continuous range of variable genotypic, phenotypic and biological properties. Although species taxa are fuzzy sets of virus populations with blurred boundaries, the absence of obvious discontinuities between individual virus species does not mean that the species concept should be abandoned. It would be equally unwarranted to refuse to distinguish colours because of the continuous nature of the spectrum of electromagnetic waves."

Answer: We dispute the assertion that species are necessarily 'fuzzy sets'. While there are some areas of virology in which species demarcation is difficult (a situation with which taxonomists in other disciplines are familiar), in many families it is more usual for related species to be distinct in a number of properties. Two examples:

(i) All influenza viruses are assigned to just one of three species, each of which is broadly defined and distinct from the others; so distinct, indeed, that each is assigned to a separate genus. It is not possible to classify influenza viruses into a larger number of more narrowly defined mini-species because the latter would not constitute monophyletic lineages (due, at least in part, to gene reassortment between the smaller groupings).

(ii) Evidence that the species Poliovirus is actually a sub-lineage of the species Enterovirus C, and could recombine genetically with members of the latter species, posed a problem. To continue to recognise polioviruses as a separate species would be in breach of the monophyly rule (2.3, because not all members

of the enterovirus C lineage would be members of the Enterovirus C species), whereas to recognise them as a species within a species would breach the "same-level" rule (2.2). Clearly the species Poliovirus had to be abolished and its members subsumed into an enlarged Enterovirus C.

These examples illustrate how the quest to establish discrete, monophyletic species has resulted in broadly defined species whose members are readily distinguishable from those of related species according to multiple criteria. In both these examples species groupings also correspond to a clear discontinuity in measures of genetic distance which, significantly, are similar to discontinuities seen in the genome analyses of many virus families. These discontinuities are detected by the widely used PASC analysis (www.ncbi.nlm.nih.gov/.../pasc) and are found to correspond with important biological differences. This type of analysis helps to ensure that the measures of genetic distance used as one factor to support creation of new species are based on data and are not arbitrary values.

3.4 A meaningful definition is needed because the absence of a satisfactory definition of a virus species was the reason why many virologists in the past were opposed to using the concept species in viral taxonomy."

Answer: We believe that the proposed new definition is both meaningful and satisfactory while the existing one, despite its distinguished history, is not. It is also at the least interesting that other branches of biology have debated at length their species definitions (and continue to do so) but have not found it necessary to enshrine any of them in their taxonomic codes.

# 4. ALLAYING CONCERNS:

In some of the objections raised, a connection seems to have been made between the proposed change to the definition of a virus species and the relatively recent creation of 60 different anellovirus and 178 separate begomovirus species. These are quite unconnected and we refute entirely any suggestion that the desire to change the definition is driven by a wish to create large numbers of new species on an arbitrary basis.

4.1 It is true that the anellovirus species have relied heavily on genotypic criteria but with only 65% (or less) nucleotide identity and very small genome sizes, it would be difficult to argue that these should be retained within a single species. It needs to be emphasized again that these are not arbitrary values but those determined by careful analyses of the variability within the complete genome dataset that is publically available. The proposals for species creation were also supported by phylogenetic analyses.

4.2 The 178 begomovirus species are a different case, whose origins go back several years to previous ICTV administrations. In recent years, the EC has resisted the creation of any more begomovirus species while they question the justification for the 178 existing ones. As a result of this intervention, the Geminiviridae Study Group is undertaking a comprehensive review of species demarcation criteria. The

quality of the new work can be judged from the results already available for another genus in the family, Mastrevirus, which forms the basis of a proposal (<2012.019abP.A.v3.Mastrevirus-17sp,rem-2sp>) currently recommended for ratification. It appears that there are particular difficulties in defining species in the begomoviruses and the results for this genus are not yet available, but the EC recognises that the 89% value referred to in the objection was again not an arbitrary value

#### 5. LOOKING AHEAD:

The history of virus taxonomy includes many attempts to define a virus species. In practice, the decision to create a new species is often straightforward, sometimes requires a measure of judgement and is occasionally controversial. The work of the individual Study Groups in providing and reviewing their criteria is ultimately of more immediate significance than any attempt at a general definition. We do not expect or intend the definition we have proposed to be the last word on the subject, nor do we expect virologists to reach universal agreement. However, we do believe that there are clear advantages in replacing this item in the Code with a new species definition that better articulates current best practice.

#### Comment

#### Horzinek Marian C. Tue, Oct 30 2012 4:33 AM

I disagree with the changes to Code Rule 3.21 proposed by the ICTV and support Marc's alternative. I still favour his original formulation with the "polythetic class" concept included and consider the "cluster class" change a compromise. I would accept it though. When teaching virology to students, I went through a careful explanation of polytheticity, the properties of a group that cannot be defined on the basis of any single character, but rather on a combination of characters. This is lost with "cluster" that begs the association of haphazardly assembled elements rather than the association of discrete traits. This may be a linguistic rather than philosophical approach, but may I?

#### Comment

Posted by Marc Van Regenmortel Nov 15 2012

A reply to the comments posted on 23 october 2012 by Andrew King, Mike Adams, Elliot Lefkowitz and Eric Carstens

In an attempt to justify their proposal that the existing ICTV definition of virus species should be abandoned, four senior members of the ICTV Executive Committee have posted on this website a contentious and polemical document in which they argue that the official ICTV species definition is based on specious reasoning and on inappropriate, meaningless terms such as polythetic class, replicating lineage and ecological niche.

The contested species definition was proposed in 1989 (Van Regenmortel, Arch Virol 104: 1-17) and was endorsed by the ICTV in 1991 (Pringle, Arch Virol 119: 303-304) to indicate that viruses in future had to be assigned to newly created species. The category species, which previously was not recognized by the ICTV because of the absence of a satisfactory definition of the concept of species in virology, became the lowest taxonomic category in viral classification, below the categories of genus and family.

All biological classifications are human, conceptual constructions made up of classes with a hierarchical structure, the successive ranks being the species, genus, family, order etc. Class membership allows a bridge to be established between two different logical categories: the class as an abstract construct and the individual viruses which are the concrete members of the class. The relationship between a class and the higher-rank class immediately above it, is known as class inclusion (Buck & Hull 1966, Syst Zool 15: 97-111). This means that the viruses which are the members of a species are automatically also members of the genus and family classes above it.

Classification deals with classes and taxonomy deals with taxa. Classes of individual viruses are called taxa and a taxon such as a particular species is included in the genus taxon immediately above it. All classes and taxa are abstract concepts constructed by the mind and not real entities located in space and time.

It is important to distinguish two meanings of the word species. On the one hand, it refers to the numerous species taxa that have individual viruses as their members. However, the term species is also used to refer to the lowest category in an hierarchical classification, namely the class of all species taxa. These two meanings of the term species should not be confused since it would amount to confusing the element gold (the class of all gold atoms) with the concept of element (the class of all the elements). The members of the category species are all the species taxa that have been recognized by virologists so far and not the individual viruses in each species. The currently accepted definition of the concept of virus species is the following: A virus species is a polythetic class of viruses that constitutes a replication lineage and occupies a particular ecological niche. This definition of the concept should not be confused with the separate definitions of each species taxon and the guidelines for species demarcation which individual ICTV Study Groups are asked to provide when they create new species. It should also be borne in mind that the definition of the species taxon since this usually requires the use of diagnostic properties that can be selected only after the species has been created (Van Regenmortel 2011, see Book reference below).

Since King et al in their comments claim that the current definition of virus species is an assemblage of meaningless terms, I will explain the meaning of each word used in the definition.

1. Class of viruses

The term class can have many meanings in English but when used in taxonomy it refers to a conceptual collection of organisms or viruses considered to be the members of the class because they have certain properties or characters in common. If a virus has a positive strand RNA genome, it becomes automatically a member of the class of positive strand RNA viruses. Such a class which is not physically real is only a concept of the mind defined by the properties of its members and it should not be confused with the viruses themselves which are objects located in space and time studied by virologists. The abstract concept of species as a class of viruses should thus not be confused with what the concept refers to (i.e. its referents) in the same way that an object should not be confused with its conceptual or pictorial representation (Van Regenmortel 2003, Arch Virol 148: 2481-2488). A class of viruses can achieve the status of a taxon (for instance a species) in a classification scheme whereas a "group" of viruses cannot, a group being only a collection of concrete viral objects. King et al seem to be unaware that the term class which links concrete objects and conceptual taxa is universally used in taxonomy and they claim that the term class only refers to a category in the classification hierarchy situated above the category order and below the category phylum (such as Mammalia between Carnivora and Chordata in zoology). The category rank "class" is actually not used in viral taxonomy and it is ludicrous for King et al to maintain that it is not acceptable to refer to a virus species as a class of viruses.

#### 2. Polythetic class

Two types of classes are usually distinguished in taxonomy. Monothetic classes also called universal or Aristotelian classes are defined by one or more properties that are necessarily present in every member of the class and absent in other classes. A single property may thus suffice to establish membership in a monothetic class.

Polythetic classes also known as polytypic classes are defined by a variable combination of several properties, none of which must necessarily be present in every member of the class (Van Regenmortel et al 1997 Arch Virol 142: 1505-1518). There have been objections to the use of the term polythetic because it is not a word in common use and I have proposed that "polythetic class" could be replaced by the synonym "cluster class" which is widely used in taxonomy (Pigliucci 2003, BioEssays 25: 596-602; Van Regenmortel 2010, Syst Appl Micro 33: 1-6). A cluster class is defined by a cluster of properties, i.e. by a combination of phenotypic and genotypic properties without any property being necessary or sufficient for membership in the class. None of the members of a cluster class need to possess all the defining properties ascribed to the class. It must be emphasized that the term polythetic or cluster class refers to the variable distribution of the defining properties present in the members of the class. However, a variable distribution of properties is not itself a single common property of all the species members since this would turn every polythetic class into a monothetic one, which is absurd. All the members of a species share the properties of being viruses and members of a replicating lineage and they occupy a nonuniform and changeable ecological niche. They also share the genus and family-defining properties necessarily present in all the members of any species. King et al are thus mistaken to conclude that the term "polythetic" has no place in the species definition.

Properties useful for differentiating between species are obviously not those that are present in all the species of a genus such as virion morphology but are properties such as host range, cell and tissue tropism, pathogenicity, mode of transmission, certain chemical and antigenic properties of virions and differences in genome sequence. All these species-defining properties can be altered by a few mutations and therefore often vary in different members of the same species. This is one reason why species must be defined polythetically by a combination of covariant characters. It is the variable distribution of properties as well as their inherent variability in the members of a species that ensures that no single character can be used as a defining property of a virus species.

As a result there are in most cases no precise cut off points to differentiate between two species since it is necessary to draw boundaries across a continuous range of phenotypic and genotypic variability. King et al maintain that cut off points based on measures of genetic distance are not arbitrary because they are based on genome data. However, data do not speak for themselves and need to be interpreted. The selection of a particular degree of genome similarity as a single criterion to demarcate species is mostly an arbitrary decision. The arbitrary choice of using a 89 % pairwise nucleotide identity in their DNA-A genome component for species demarcation led to the creation of 178 pseudo-begomovirus species. It would also have been possible to consider that the major bimodal PASC distribution of begomovirus sequences corresponds to species and strains which would have produced a lower cut of point for species demarcation can lead to an inordinate number of species that do not correspond to biologically distinguishable stable entities justifying the label species.

#### 3. Replication lineage

The reference to replicating lineage in the definition indicates that species are not simply objects with similar properties that can be classified phenotypically as is done in numerical taxonomy. All the members of a species share descent from a common ancestor and represent an evolving lineage. Transition from one species to another during evolution occurs within the continuity of virus replication but there is usually no direct quantitative relationship between the extent of genome changes and differences in phenotypic properties of a virus. Since the biological properties of viruses are a major reason why virologists want to engage in species demarcation, it would be counterproductive to differentiate between virus species only on the basis of genome similarities. Classifying viral genomes is not the same as classifying viruses and the need to record phylogeny should not overshadow the importance of phenotypic differences for species demarcation (Drebot et al 2002, Arch Virol 147: 2465-2471). King et al erroneously claim that the concept "replicating lineage" has never been defined and is devoid of meaning which, however, does not prevent them from using the term lineage themselves and to write that "a virus species comprises only members of its defining lineage". They prefer to define a species as a monophyletic group of viruses derived from a common ancestor although "monophyly" does no more provide a guideline for demarcating species than "replicating lineage". Genera can also be defined as monophyletic lineages but this is equally irrelevant for demarcating genus as well as species taxa.

#### 4. Ecological niche

The claim of King et al that this concept has never been defined reflects their ignorance of the literature (Keller & Lloyd 1992, Keywords in Evolutionary Biology, Harvard Univ Press, Mass; Van Regenmortel et al 1997, Arch Virol 142: 1505-1518). The ecological niche refers to the biotic properties of members of a virus species such as host range and responses, tissue and vector tropism, and pathogenesis and it encompasses environmental and functional aspects. The fact that the ecological niche of a species is a highly variable biological property and is often poorly correlated with phylogeny is one reason why King et al dismiss its importance for species demarcation.

#### Conclusions

The current ICTV definition of virus species and the one proposed by King et al only define the concept of species used in viral taxonomy and are not meant to provide a practical guideline to help virologists create new species taxa. Definitions can only be provided for abstract concepts and not for objects like viruses which can only be described. The current species definition has the advantage that it makes clear that species are conceptual classes rather than simply groups or collections of viral objects. That this crucial distinction is frequently overlooked is shown by the fact that many virologists continue to confuse viruses (written in Roman) with virus species (written in italics) because these names only differ in typography. Contrary to what King et al claim, this problem does not exist with genera and families. Virologists often write that it is possible to transmit or sequence a species instead of a virus, and this persistent confusion would diminish if the ICTV introduced binomial species names that differ from virus names since this would make it easier for virologists to distinguish between species and viruses (Van Regenmortel et al 2010, Arch Virol 155: 1909-1919). In two surveys conducted in 2002, more than 80% of the virologists who responded were in favour of such binomial species names (Van Regenmortel 2011, Virus species. In: Genetics and Evolution of Infectious Diseases (Ed. Tibayrenc) pp. 3-17, available from the author on request).

The species definition proposed by King et al does not and cannot provide guidelines for species demarcation and is in no way superior to the existing ICTV species definition.

Previewing Staged Changes