Published in final edited form as:
Arch Virol. 2010 April ; 155(4): 445–453. doi:10.1007/s00705-010-0600-9.

Clarification and guidance on the proper usage of virus and virus species names

Jens H. Kuhn and
Integrated Research Facility at Fort Detrick (IRF-Frederick), Division of Clinical Research (DCR), National Institute of Allergy and Infectious Diseases (NIAID), National Institutes of Health (NIH), B-8200 Research Plaza, Fort Detrick, Frederick, MD 21702, USA, IRF-Frederick contract employee of Tunnell Consulting, Inc., King of Prussia, PA 19406, USA

Peter B. Jahrling
Integrated Research Facility at Fort Detrick (IRF-Frederick), Division of Clinical Research (DCR), National Institute of Allergy and Infectious Diseases (NIAID), National Institutes of Health (NIH), B-8200 Research Plaza, Fort Detrick, Frederick, MD 21702, USA

Jens H. Kuhn: kuhnjens@mail.nih.gov

Abstract

A pivotal step in the development of a consistent nomenclature for virus classification was the introduction of the virus species concept by the International Committee on Taxonomy of Viruses (ICTV) in 1991. Yet, almost two decades later, many virologists still are unable to differentiate between virus species and actual viruses. Here we attempt to explain the origin of this confusion, clarify the difference between taxa and physical entities, and suggest simple measures that could be implemented by ICTV Study Groups to make virus taxonomy and nomenclature more accessible to laboratory virologists.

Introduction

In 1989, van Regenmortel defined a virus species as "…a polythetic class of viruses constituting a replicating lineage and occupying a particular ecological niche" [33]. In 1991, the International Committee on Taxonomy of Viruses (ICTV), the body empowered by the International Union of Microbiological Societies (IUMS) to make decisions on matters of virus classification and nomenclature, adopted this definition [27,35]. According to the rules of nomenclature set forth by the ICTV, virus species names are to be italicized with the first letter of the name being capitalized (e.g. *Rabbit hemorrhagic disease virus*). Virus names, on the other hand, are to be written in lower case (except if a part of the virus name is a proper noun) and in standard, non-italicized, script (e.g. rabbit hemorrhagic disease virus) [23,36]. Abbreviations (e.g. RHDV), recommended by the ICTV Study Groups, always should refer to virus names, but not to species names [40,42]. With the exception of the term "polythetic," which still is the cause of ongoing confusion among virus taxonomists [19], van Regenmortel's species concept is reminiscent of those adopted for cellular organisms. Consequently, virus taxonomists are frustrated by the observation that, on the one hand, most laboratory virologists write with ease that a particular virus infects, for instance, "European rabbits (*Oryctolagus cuniculus*)" (rather than erroneously writing that the virus infects "*Oryctolagus cuniculus*"),

---

Correspondence to: Jens H. Kuhn, `kuhnjens@mail.nih.gov`.

while on the other hand having obvious difficulties writing that a particular animal is infected with “rabbit hemorrhagic disease virus (species *Rabbit hemorrhagic disease virus*).” Current ill-practice is that most laboratory virologists either ignore the species name completely, which in itself is only negligent, or they substitute the (non-italicized) virus name for the (italicized) species name, which is incorrect. Calisher poignantly asked why “…so many otherwise intelligent people have so much difficulty understanding and applying [virus taxonomy]” [10]. van Regenmortel and others [9,15,39,41,42] have not tired of repeating that taxonomic classes, such as virus orders, families, genera or species (taxa), are *abstract* concepts, i.e., “…constructions fabricated by the mind and not real entities located in space and time” [42], whereas viruses are *real* objects. The majority of laboratory virologists seem to understand and/or accept this instinctively in the case of virus orders, families, and genera, but many do not in the case of virus species [7,18]. In this article, we will not discuss how the species concept evolved or where its shortcomings may lie, as this is the task of taxonomists (for reviews on the concept of species in general and virus species in particular see [12,24, 34,45]). Likewise, we will not discuss the basis of classification, as this is the task of, increasingly, phylogeneticists who provide the basic sequence comparison data that allow for evolutionary classification. Instead, we will attempt to explain the differences between virus species and viruses and how the *current* definitions and nomenclature ought to be applied, and provide suggestions to virus taxonomists on how to gain wider acceptance of *current* nomenclature among laboratory virologists.

Virus species versus viruses

Accepting the risk of offending the specialists, we judge virus taxonomy to be nothing but the very important effort to group a particularly large set of objects, namely viruses, into categories, aiming to illustrate tangible relationships among them, as well as to simplify communication among international scientists. To quote Condit: “…all of nature is a continuum, and the business of taxonomy has the obligation of drawing boundaries within this continuum, an artificial and illogical task, but necessary nevertheless” [13].

The usefulness of classification should be obvious. To build on one of van Regenmortel's analogies [42]: although there are de facto millions of colors, most people get by in daily life by knowing the names of fewer than a dozen. The majority of people have a distinct idea of what is meant when somebody refers to a “green” object, although the exact color referred to (which shade of green) remains undefined. Modern taxonomic schemes are frameworks in which different classes are arranged hierarchically. The classes themselves are created to roughly reflect the evolutionary connection of their members [21]. They make use of hierarchical categories (the taxonomic classes), such as domains or kingdoms at the higher levels and genera and species at the lower levels, to allow for an even more precise way of conversation. Ideally, a taxonomic scheme is established in a way that allows the majority of experts in the pertaining field to extrapolate a sophisticated profile of a novel organism only based on its taxonomic description. For instance, zoologists should have a distinct idea of what is meant when a researcher reports the discovery of a hitherto unrecognized green “rabbit.” In this particular case, a novel living object, namely an actual mammal, would have certain characteristics that it shares with other known mammals. All of these known animals had been placed by taxonomists into a category, namely the mammalian family “Leporidae,” for which the common vernacular name is “rabbits/hares” (note that it is not “*the* rabbits/hares”).

In his most recent book, Dawkins beautifully describes the dilemma of classifying forms of life. Paraphrasing Mayr's statement that “[b]iology…is plagued by its own version of essentialism…,” Dawkins elaborates that “[t]he rabbits that we see are wan shadows of the perfect ‘idea’ of rabbit, the ideal, essential Platonic rabbit, hanging somewhere out in conceptual space… Flesh-and-blood rabbits may vary, but their variations are always to be seen as flawed deviations from the ideal essence of rabbit" [14]. Dawkins used these sentences to explain that nature (i.e. tangible reality) is different from human attempts at categorizing it, but with them he also explained the concept of a taxonomic class clearer than most taxonomists: although there are many different varieties of rabbit we (hopefully) recognize a rabbit as such even if it is one never seen before because it satisfies our criteria for the idea of rabbit. Nobody would hunt an idea, inject an idea, cuddle an idea, or feed an idea. One could do that with the actual newly discovered animal, however.

The difference between idea and physical entity is the clearer to people the wider the delineations of the taxonomic class are cast. Most children can follow the idea of animals (kingdom Animalia) or plants (kingdom Plantae). Most high-schoolers understand the idea of mammals (the animal class Mammalia). The problem is that the lower the class in a taxonomic ranking scheme, the more sophisticated its definition. This explains why quite a few people make the error of grouping rabbits, hares, and pikas (order Lagomorpha) with rodents (order Rodentia). It is even more difficult for them to understand the difference between rabbits/hares (family Leporidae) and pikas (family Ochotonidae). Only dedicated rabbit aficionados are able to differentiate the 11 leporid genera [47] (or disagree on the number 11) and only experts can differentiate members of various rabbit species. However, this increase in complexity of categorical ranks does not change the fact that all of them, including species, remain ideas. Hence, it follows that, if a taxonomist determined the newly found green rabbit to be a member of the species *Oryctolagus cuniculus*, that *Oryctolagus cuniculus* could still not be hunted, injected, cuddled or fed. *Oryctolagus cuniculus* would also not be green, the rabbit at hand would be. The green color would be a very unusual trait for a rabbit, but it would not change the fact that the animal is a member of *Oryctolagus cuniculus* as long as this green animal still fulfills the definition of rabbit experts for that particular leporid species. In other words, "[a] species taxon has spatiotemporal referents in the form of organisms, which are the actual instances that satisfy the membership conditions of the [taxonomic] class" [45]. From this, it logically follows that taxa only can be established, discussed, or defined (since they are ideas), whereas the actual organisms only can be described, or identified. A species cannot go extinct (except if humanity develops amnesia) but it can cease to have members when those go extinct. A species also cannot be discovered (except if amnesia gets reversed), but a newly discovered organism can require the creation of a new species. On the other hand, an organism cannot be defined because it exists as it is [39].

Virus taxonomy is organized similarly to animal taxonomy (although the highest taxonomic class in virus taxonomy is currently that of the order) but it is more difficult to grasp because viruses (or, properly, virions) are not everyday objects that can be seen and touched. The notion that broader categories can be grasped more easily than more narrow ones holds true for virus taxonomy as well. While non-virologists are probably lost even at the level of order, virologists should have a distinct idea of what is meant when a colleague reports the discovery of a hitherto undetected member of the order *Mononegavirales* that induces green fluorescence in infected cells. Accordingly, a virologist would assume that a novel object, namely the novel virus, would have a monopartite single-stranded RNA genome of negative polarity, a genome with the characteristic organization 3′ -UTR-*N*-*G*-*L*-5′-UTR, and that its virions would be enveloped. These characteristics, among important others, such as natural host range, had been used by virus taxonomists to define the virus order *Mononegavirales* [28–30]. The most precise vernacular name is "mononegavirads" (note that it is not "*the* mononegavirads") [46]. Some virologists might know the differences between the mononegavirad families *Borna-viridae, Filoviridae, Paramyxoviridae*, and *Rhabdoviridae* [29]. Fewer are educated in the intricacies of different paramyxovirid genera. Experts would be called upon to assign this novel virus to a particular paramyxovirid species, *Measles virus* for instance. Again, the increase in complexity of categorical ranks does not change the fact that all of them, including species, remain ideas. Neither the species *Measles virus* nor the family *Paramyxoviridae* could be injected, centrifuged, isolated, or visualized by electron microscopy. The species *Measles virus* would also not induce green fluorescence in infected cells—the virus at hand would. Thorough investigation might reveal that the novel virus is in fact *a* measles virus (and not the measles virus)—because, of course, there are several, but this measles virus would never be the species Measles *virus. A variant* or *type* designation would then be assigned to the novel virus to differentiate it during communication from other variants. If the novel measles virus remains phenotypically different, i.e. inducing green fluorescence, over generations then the new variant could be elevated to *strain*, which "…is a biological variant of a given virus that is recognizable because it possesses some unique phenotypic characteristics that remain stable under natural conditions" [42]. It is important to remember this definition as currently many laboratory virologists use the words isolates, variants, and strains indiscriminately. A strain is always a variant, but a variant is most often not a strain. Both strains and variants are represented by isolates (experimental material corresponding to an instance of a given virus). Two isolates of the same variant, for instance isolated at two different time points during infection from the same animal, can be identical or different in sequence [44] because of the presence of a quasispecies, i.e. a mixture of related genotypes that exist in an environment of high mutation rate, in the animal (note that the word quasispecies does not have a taxonomic connotation and in fact is unrelated to the term species). Measles isolates, variants, and strains are physical entities. Therefore, they can be described, identified, or discovered. They can also be centrifuged or injected into animals. Importantly, they cannot be defined. The species *Measles virus*, on the other hand, cannot emerge, be isolated, or be identified. However, it can be (and currently is) defined [22]. From this, it follows that the definition of taxa such as species are a "…matter of opinion and adjudication rather than logical necessity" [43,45], i.e. species demarcation criteria differ drastically among the different established categories of viruses depending on currently available information. In biological classifications, species cannot be defined as immutable natural kinds in terms of necessary and sufficient properties as is done in physics and chemistry. Species are *invented* by the ICTV Study Groups who *stipulate* species demarcation criteria. This also means that species can be dissolved or absorbed by other taxa, whereas actual viruses remain what they are—only their descriptions and designations can be can changed.

Explanations for the current confusion

In 2007, van Regenmortel wrote that his species proposal and the described nomenclature of species-name italicization "…was accepted by the ICTV…and [that] this italicized typography is now applied in all virology journals and books" [42]. Unfortunately, this statement has been too optimistic, as a glance into current issues of common virology journals irrefutably demonstrates. Many authors, including those of ICTV Study Groups, do not adhere to taxonomic standards despite journals' requests to do so, and reviewers and editors often do not enforce correct nomenclature—possibly because they themselves do not understand or accept it. The fact that GenBank's Entrez software assigns by default any new virus name in the field "Organism" to a new virus species if the same name is absent from the ICTV Species Master list added considerably to the confusion [16], as of course a genomic sequence characterizes an actual virus rather than a species, a genus or a family. Calisher and Mahy threw their hands in the air and seemingly conceded that "[v]irus taxonomy…is extremely complex and may be best left to the compulsive types who devise it. Unfortunately, all of us have to use taxonomy, so it is in our best interest to have at least a working understanding of taxonomy" [9]. They recommended that laboratory virologists should name the virus, list in parentheses the taxon of which it is a member, and then "leave it [taxonomy] alone" [9]—a view also shared by van Regenmortel [40].

We think, however, that there are some simple explanations for the fact that so many virologists "do not understand" the concept of an idea versus a physical object, and we think there are some rather simple solutions to make virus taxonomy more accessible and convenient for non-taxonomists.

Hypothesis 1: the purpose of the taxonomic class "species" is unclear to many virologists

We submit that a scientific concept that is not accepted by the greater scientific community is useless and should either be explained better, modified to gain acceptance, or be replaced. It seems to us that the problem with the distinction of virus species versus actual viruses is *not* that laboratory virologists do not understand the distinction itself, but rather that they do not a priori comprehend what benefit would stem from such a distinction. Consequently, laboratory virologists are reluctant to apply the distinction. Ill-applied nomenclature is the logical consequence. Virus taxonomists should therefore educate the virologist community in more detail about the usefulness of taxa.

In zoology, the concept of hypothetical taxonomic classes is easily understandable from the highest category (kingdom) to the lowest (species): the more similar an animal is to another the more those two are most likely related; the more related they are, the lower the taxonomic class which they share. An animal species is still a clearly discernible and thus useful taxonomic class *because it groups many very different animals*. For instance, most children would correctly identify both a (standard) poodle and a German shepherd as "(domestic) dogs," the vernacular name for the *entirety* of members of the species *Canis lupus familiaris* [47]. "Domestic dogs" thus remains a taxonomic class and therefore an idea—particular domestic dogs can be petted, but one cannot do that with the category domestic dogs, i.e. all existing and theoretical domestic dogs. While both dog types (standard poodle and German shepherd) are so closely related on genomic and other levels to justify their grouping in a common species, it is plainly obvious that both dog types are still very different indeed—a fact that is also reflected genomically [3]. From this, it follows that the taxonomic class species is useful in daily life ("dogs bark") and also to specialists: many different objects share a (large) number of properties to allow them to be grouped together and thereby to refer to them together in communication. The grouping of similar objects often does not stop at the species level. Pitbulls and German shepherds are different dog *breeds*, roughly the artificial-selection equivalent of the natural-selection term *strain* (or *race* or *lineage*). Of course, the rather pronounced divergence of different dog breeds [3] has been emphasized through artificial selection, but the principle continues to hold true for undomesticated animals as well, as the black panther/melanistic jaguar (black) and the jaguar (spotted) are obviously very different felids (different strains) but belong to the same species, *Panthera onca*. Even within a breed/strain, interindividual differences exist. In the case of large pets, humans usually assign names to emphasize these differences ("*this* poodle's name is Buddy" —i.e. not all poodles are (named) "Buddy"). In the case of other life forms, individual specimens are assigned numbers, acronyms, abbreviations or otherwise distinct designations ("*Escherichia coli* K-12").

Many virologists, it seems to us, have not yet seen their viruses as different types of dogs. Virology is a relatively young specialty and molecular methodologies have only recently been devised to truly characterize nanoscopic subjects. Hence, the overall number of known viruses (and their different variants or types) is still very small and, consequently, many virus species currently have only one member, often represented by only one or a few variants. If one understands a species as the theoretical average of all existing and imagined members (the *ideal abstract* domestic dog being something between the standard poodle, the German shepherd, and all the other breeds of domestic dogs) then it is understandable that differentiating species (idea) and member (entity) may seem pointless to many once a species has only one member. It seems nonsensical to discuss, for instance, simian hemorrhagic fever viruses (as a vernacular name for the species *Simian hemorrhagic fever virus*) if in fact there is only one member of that species, namely simian hemorrhagic fever virus (SHFV), and only one recognized variant thereof (SHFV-LVR42-0) [32]. This is what we think happens among laboratory virologists: research on one particular virus that is currently represented only by one variant leads to the impression that there is, i.e. exists, only this one virus. If so, so may many bench virologists ask, then of what use is a species as a group designation? However, this one virus necessarily always consists of a very large number of potential mutants and variants circulating in nature (and even within the animal infected with this one variant), which might not yet have been isolated and recognized. We do know that they exist, though. Every one of those variants, even if not in our hands yet, is a physical entity. The theoretical average of all these physical entities is the group designation, i.e. the species. Therefore, one needs to distinguish conceptually between the taxonomic class species (which does not and cannot have a sequence) and the myriads of possible variants that may not be available as isolates yet, but each one possessing a sequence and other physical properties not found in species.

But even in virology, it is common that a virus of a particular species is represented by many relatives. For instance, in the case of feline calicivirus (currently the only member of the species *Feline calicivirus*) there are dozens of variants that differ slightly in their genomic sequence. Most of them (the standard poodles) cause a relatively benign disease in domestic cats (*Felis catus*), but a few others (the German shepherds) cause a hemorrhagic fever with high lethality, although their genomic sequences do not differ drastically from those of the less virulent (standard poodle) variants [1,20,26,31]. Clearly, all these viruses are related and belong to the same species—but it is equally clear that these two groups of feline caliciviruses are as different as two different dog breeds, i.e. the German shepherd variants represent different strains of feline caliciviruses. van Regenmortel correctly pointed out that “[o]nly when the properties of many members of a…species are compared, is it possible to discover which diagnostic property or set of properties will discriminate between the members of that species and other species…” [45].

Solution 1—Although not a mandate of the ICTV, the virology community, through the ICTV Study Groups, should more strongly emphasize variants, pay more attention to proper delineations of strains, and clearly distinguish them from each other and mere isolates. Laboratory virologists should be educated to understand that different virus variants and strains are de facto different entities that share many common properties, justifying the creation of an abstract group for them, the species. Laboratory virologists should thereby understand that the species is a very useful means of communication when referring to an entire group of viruses in publications or during seminars.

Hypothesis 2: the identical spelling of taxa, their vernacular names, and viruses is confusing to laboratory virologists

Until fairly recently, animal and plant taxonomy had an undeniable and rather trivial advantage over virus taxonomy from a user's point of view, namely the existence of vernacular names for members of those species that are sizeable enough to be known by most people. *Importantly, those vernacular names are different from the species names*. For instance, the English vernacular name for the animal(s) assigned to the species “*Oryctolagus cuniculus*” is “European rabbit(s)” (not the European rabbit(s)) [47]. If asked which animal is hopping around in the lettuce seedlings most people would suggest “*a* rabbit” (not *the* rabbit) instead of “*a* leporid” (not *the* leporid) although both answers would be correct. More knowledgeable people would correctly say “a European rabbit,” but would not incorrectly say “*Oryctolagus cuniculus*.” The use of the indefinite article “a” rather than the definite article “the” demonstrates an intuitive understanding of the species concept by most people, namely that any given European rabbit is but one of many other slightly different European rabbits. Due to the availability of vernacular names, taxon names and animal or plant names rarely get confused, even if the person pointing to the rabbit has not enjoyed a taxonomical education. It is elephants (note the zero article) that roam Africa and Asia and not Elephantidae; and in the same realm it is a spotted garden slug (species *Limax maximus*) that competes with that European rabbit for the lettuce seedlings and not the species *Limax maximus*. Unfortunately, this advantage of having different taxon and organism names is only available for a small percentage of animal and plants. The majority does not have vernacular names, probably because they are not common topics of lay conversation. In those cases, zoological and botanic taxonomy is as convoluted as virus and bacterial taxonomy as scientists and other people have to use species names in lieu of organism names to refer to them ("here we infect with *Escherichia coli* K-12…"). Calisher and van Regen-mortel recently suggested a simple and elegant solution for this dilemma: if biologists were to follow current (correct) virus nomenclature they could solve the species–organism problem by simply not italicizing a species name and therefore de facto creating a vernacular name ("here we infect with Escherichia coli K-12, a member of the species *Escherichia coli*…") [11]. Of course, while this proposal would give biologists at least the possibility to use correct nomenclature in their descriptions, it creates the very problem that plagues virology right now: since both species and organism name are identical in spelling, knowledge of the difference between (theoretical) species and (actual) organisms would be necessary so that both do not get confused. Nevertheless, Calisher and van Regenmortel's proposal makes sense for the taxonomic systems established for all organisms of all six branches of life: the sheer number of organisms assigned to them is so large that the creation of distinct vernacular names for them would be an enormous effort with little benefit considering that the vast majority would only be used by a handful of experts in specialized journals. Calisher and van Regenmortel's system would satisfy nomenclatural requirements and improve the current situation. In virus taxonomy, however, the establishment of the very same system, i.e. identical species and virus names, was not beneficial, as it did not solve an existing problem but rather created one. In virology, vernacular names existed long *before* the creation of species names and hence laboratory virologists are accustomed to using them already. However, laboratory virologist are not yet used to using species names. Virus taxonomists "solved" the problem of lacking species names by asking to italicize the vernacular names, rather than creating novel distinct species names—a possible violation of the International Code of Virus Classification and Nomenclature that, in Article 3.24, clearly states that "[a] species name must provide an appropriately unambiguous identification of the species" [17]. If the group of members of each higher taxon is assigned a vernacular name (order *Mononegavirales*: mononegavirads; family *Paramyxoviridae*: paramyxovirids; subfamily *Paramyxovirinae*: paramyxovirins; genus *Morbillivirus*: morbilliviruses [46]), then it logically follows that this should hold true for species as well. In some cases (clearly not the majority), a virus species has several members. For instance, Amur virus, Da Bie Shan virus, and Hantaan virus are currently considered members of the species *Hantaan virus* (*Bunyaviridae: Hantavirus*) [25]. A (correct) sentence such as "Amur virus is a member of the species *Hantaan virus*" could potentially be replaced by "Amur virus is a Hantaan virus" if one uses "Hantaan viruses" as the vernacular name for the group of members of the species *Hantaan virus*. On the other hand, it becomes instantly clear where the confusion among virologists about taxonomy originates when one writes "Hantaan virus is a member of the species *Hantaan virus*" and of course a sentence such as "Hantaan virus is *a* Hantaan virus" sounds just plain silly. This example is but one that uncovers the problem of laboratory virologists when referring to taxa versus viruses in writing and speaking. van Regenmortel and others realized that [16,42], but for some reason, Fauquet and Fargette wrote that "[i]t is particularly unfortunate that we are in this situation and that different names have not been created for virus species, but this is a reality that cannot be changed, at least in the short term…" [16]. Virus taxonomists did not suggest the straightforward solution of simply creating species names that differ from the virus names in use. To do so would have been and still is easy even in the short term, since most laboratory virologists do not use species names in the first place and hence a change of existing species names to novel ones would hardly have a negative impact on the virology community, while at the same time rectifying an obviously very confusing problem. Such a change is also less radical than it sounds initially because, as mentioned above for the example of Amur virus, Da Bie Shan virus, and Hantaan virus, there already are several instances in which more than one virus have been assigned to one species, ipso facto creating a discrepancy between (some) virus and species names.

Virus taxonomists initiated a still ongoing debate by suggesting that virus taxonomy ought to follow the Linnaean binomial species system [2,4–6,37,38,42]. If binomial names were to be introduced for all virus species, then the species names would be different from the actual (vernacular) virus names, thereby solving the current problem. Since species names of microorganisms, animals and plants are binomials that include a genus designation, virologists should have no difficulty in recognizing and accepting that virus binomials with a genus designation are the names of the virus species while the vernacular names they use constantly are the names of the viruses. However, although surveys among laboratory virologists have revealed support for the introduction of binomial species names, it is possible that this system would not be followed by the same virologists once implemented by the ICTV, reminiscent of the current situation in which laboratory virologists do not follow current ICTV mandates due to misperceptions or misunderstandings. While it is possible that the virology community will accept a binomial system in the future, it seems imperative that it first comprehend the difference between taxa and entities, then accept vernacular names for the members of taxa, and then accept and correctly use species names. Species names should differ sufficiently from virus names as to make confusion impossible and could be chosen by the ICTV Study Groups in such a way that binomialization in the future would be straightforward, while at the same time not suggesting a “radical break” from current ways of communication about viruses. A similar proposal has recently been submitted to the ICTV by Brister [8].

Solution 2—The ICTV Study Groups should consider changing current virus species names to new names whose word stems are not present in either other taxa or virus/strain/variant/isolate names. In fact, any duplication of word stems (*Picornavirales* ↔ *Picornaviridae; Paramyxoviridae* ↔ *Paramyxovirinae; Rabbit hemorrhagic disease* virus ↔ rabbit hemorrhagic disease virus) should be avoided to decrease confusion. Existing duplications should be eliminated by changing the name of the higher taxon, even if such a change collides with Article 3.9 of the International Code of Virus Classification and Nomenclature (“Existing names of taxa and viruses shall be retained whenever feasible”) [17]. At the very least, Vetten and Haenni's suggestion to use taxon-specific suffixes for vernacular names, such as “-virads” for orders, “-virids” for families, and “-virins” for subfamilies, should be followed to decrease confusion (since “paramyxoviruses” could refer to both members of the family *Paramyxoviridae* or only to members of the subfamily *Paramyxovirinae*, whereas the designation paramyxovirids versus paramyxovirins does not allow for this confusion) [46]. The introduction of binomial species names should be postponed until laboratory virologists have accepted the nonidentity of species and viruses.

Hypothesis 3: the overemphasis of species not having properties is causing more harm than good and is not clarifying

As mentioned above, most laboratory virologists either do not use taxon names in their articles or they do not use them in accordance with correct nomenclature. It is thus not surprising that virus taxonomists reacted to the ensuing chaos by overemphasizing the difference between abstract concepts, such as taxa, and real entities, such as virions [9,15,39,41,42]. The argumentation usually revolves around examples such as that one cannot centrifuge a species and inevitably ends in a grave reminder that species do not have properties since they are abstractions. In our opinion, this overemphasis did not help the confusion and in fact may have aggravated it. Of course, at least to us, it is clear what was meant: namely that abstract concepts cannot have any *physical* properties. However, abstract concepts still have a definition, and these definitions are characteristic for each individual concept. One cannot centrifuge (the idea of) mononegavirads—but mononegavirads "have" (meaning, "the members are characterized by") negative-sense single-stranded RNA genomes. Or, as written in the 8th ICTV Report, "… the members of a virus species are defined collectively by a consensus group of properties" [17]. Once that has been clarified, and once taxonomists exert leniency in regard to the "misuse" of words such as "have" in the context of taxa, virologists will most likely embrace rather than reject taxa as they allow for poignant introductions to groups of viruses of interest ("mononegavirads have a particular gene order. Here we describe a potential new member, which challenges this idea…").

Suggestion 3—The ICTV should point out more clearly that, whereas taxa are not physical entities and therefore do not have physical properties, their members (the viruses studied by virologists) do have such properties which can be used for the general description of groups of viruses. The ICTV or the ICTV Study Groups should consider publishing examples of sentences correctly using taxa names, their vernacular names, and actual virus names and opposing them with sentences in which these terms are ill-applied, such as depicted in Table 1, *for each taxonomical class and each virus group*.

Acknowledgments

We thank Charles H. Calisher (Colorado State University, Ft. Collins, CO, USA) and Marc H. V. van Regenmortel (CNRS/Université de Strasbourg, Illkirch, France) for many stimulating and thought-provoking discussions on virus taxonomy and nomenclature. We are also indebted to Thomas S. Postler (New England Primate Research Center, Southborough, MA, USA) and Victoria M. Wahl-Jensen (Integrated Research Facility at Fort Detrick, Frederick, MD, USA) for editorial comments and suggestions.

References

1. Abd-Eldaim M, Potgieter L, Kennedy M. Genetic analysis of feline caliciviruses associated with a hemorrhagic-like disease. J Vet Diagn Invest 2005;17:420–429. [PubMed: 16312232]
2. Agut H. Back to Latin and tradition: a proposal for an official nomenclature of virus species. Arch Virol 2002;147:1465–1470. [PubMed: 14700061]
3. Akey JM, Ruhe AL, Akey DT, Wong AK, Connelly CF, Madeoy J, Nicholas TJ, Neff MW. Tracking footprints of artificial selection in the dog genome. Proc Natl Acad Sci USA 2010;107:1160–1165. [PubMed: 20080661]
4. Bos L. The naming of viruses: an urgent call to order. Arch Virol 1999;144:631–636. [PubMed: 10226627]
5. Bos L. Structure and typography of virus names. Arch Virol 2000;145:429–432. [PubMed: 10752565]
6. Bos L. International naming of viruses—a digest of recent developments. Arch Virol 2002;146:1471–1477. [PubMed: 14700062]
7. Bos L. Virus nomenclature; continuing topicality. Arch Virol 2003;148:1235–1246. [PubMed: 12756628]
8. Brister, JR. Proposal 2010.001aG.N.v1: Unique taxonomy names. International Committe on Taxonomy of Viruses Online. 2009. http://talk.ictvonline.org/media/p/1232/download.aspx
9. Calisher CH, Mahy BWJ. Taxonomy: get it right or leave it alone. Am J Trop Med Hyg 2003;68:505–506. [PubMed: 12812333]
10. Calisher CH. Taxonomy: what's in a name? Doesn't a rose by any other name smell as sweet? Croat Med J 2007;48:268–270. [PubMed: 17436393]
11. Calisher CH, van Regenmortel MHV. Should all other biologists follow the lead of virologists and stop italicizing the names of living organisms? A proposal. Zootaxa 2009;2113:63–68.
12. Claridge, MF.; Dawah, HA.; Wilson, MR. Species: the units of biodiversity. Chapman and Hall; London: 1997.
13. Condit, RC. Principles of Virology. In: Knipe, DM., editor. Fields Virology. Lippincott Williams & Wilkins; Philadelphia: 2007. p. 25-57.

14. Dawkins, R. The Greatest Show on Earth - The Evidence for Evolution. Free Press; New York: 2009.
15. Drebot MA, Henchal E, Hjelle B, Le Duc JW, Repik PM, Roehrig JT, Schmaljohn CS, Shope RE, Tesch RB, Weaver SC, Calisher CH. Improved clarity of meaning from the use of both formal species names and common (vernacular) virus names in virological literature. Arch Virol 2002;147:2465–2471. [PubMed: 12491112]
16. Fauquet CM, Fargette D. International Committee on Taxonomy of Viruses and the 3, 142 unassigned species. Virol J 2005;2:64. [PubMed: 16105179]
17. Fauquet, CM.; Mayo, MA.; Maniloff, J.; Desselberger, U.; Ball, LA., editors. Virus Taxonomy: Eighth Report of the International Committee on Taxonomy of Viruses. Academic Press; San Diego, California: 2005.
18. Gibbs AJ. Virus nomenclature descending into chaos. Arch Virol 2000;145:1505–1507. [PubMed: 10963355]
19. Gibbs AJ, Gibbs MJ. A broader definition of ‘the virus species’. Arch Virol 2006;151:1419–1422. [PubMed: 16718358]
20. Hurley KF, Pesavento PA, Pedersen NC, Poland AM, Wilson E, Foley JE. An outbreak of virulent systemic feline calicivirus disease. J Am Vet Med Assoc 2004;224:241–249. [PubMed: 14736069]
21. Kingsbury DW. Biological concepts in virus classification. Intervirology 1988;29:242–253. [PubMed: 2461915]
22. Lamb, RA.; Collins, PL.; Kolakofsky, D.; Melero, JA.; Nagai, Y.; Oldstone, MBA.; Pringle, CR.; Rima, BK. Family Paramyxoviridae. In: Fauquet, CM.; Mayo, MA.; Maniloff, J.; Desselberger, U.; Ball, LA., editors. Virus Taxonomy: Eighth Report of the International Committee on Taxonomy of Viruses. Elsevier; San Diego: 2005. p. 655-668.
23. Mayo MA, Horzinek MC. A revised version of the international code of virus classification and nomenclature. Arch Virol 1998;143:1645–1654.
24. Mayr, E. The Growth of Biological Thought; Diversity Evolution and Inheritance. Harvard University Press; Cambridge, Massachusetts: 1982.
25. Nichol, ST.; Beaty, BJ.; Elliott, RM.; Goldbach, R.; Plyusnin, A.; Schmaljohn, CS.; Tesh, RB. Family Bunyaviridae. In: Fauquet, CM.; Mayo, MA.; Maniloff, J.; Desselberger, U.; Ball, LA., editors. Virus Taxonomy: Eighth Report of the International Committee on Taxonomy of Viruses. Elsevier; San Diego: 2005. p. 695-716.
26. Pedersen NC, Elliott JB, Glasgow A, Poland A, Keel K. An isolated epizootic of hemorrhagic-like fever in cats caused by a novel and highly virulent strain of feline calicivirus. Vet Microbiol 2000;73:281–300. [PubMed: 10781727]
27. Pringle CR. The 20th meeting of the executive committee of the international committee on virus taxonomy - Virus species, higher taxa, a Universal Virus Database, and other matters. Arch Virol 1991;119:303–304.
28. Pringle CR. The order *Mononegavirales*. Arch Virol 1991;117:137–140. [PubMed: 2006902]
29. Pringle CR. The order *Mononegavirales*: current status. Arch Virol 1997;142:2321–2326. [PubMed: 9672597]
30. Pringle, CR. Order Mononegavirales. In: Fauquet, CM.; Mayo, MA.; Maniloff, J.; Desselberger, U.; Ball, LA., editors. Virus Taxonomy: Eighth Report of the International Committee on Taxonomy of Viruses. Elsevier; San Diego: 2005. p. 609-614.
31. Schorr-Evans EM, Poland A, Johnson WE, Pedersen NC. An epizootic of highly virulent feline calicivirus disease in a hospital setting in New England. J Feline Med Surg 2003;5:217–226. [PubMed: 12878149]
32. Snijder, EJ.; Brinton, MA.; Faaberg, KS.; Godeny, EK.; Gorbalenya, AE.; MacLachlan, NJ.; Mengeling, WL.; Plagemann, PGW. Family Arteriviridae. In: Fauquet, CM.; Mayo, MA.; Maniloff, J.; Desselberger, U.; Ball, LA., editors. Virus Taxonomy: Eighth Report of the International Committee on Taxonomy of Viruses. Elsevier; San Diego: 2005. p. 965-974.
33. van Regenmortel MHV. Applying the species concept to plant viruses. Arch Virol 1989;104:1–17. [PubMed: 2647059]
34. van Regenmortel MHV. Virus Species, a much overlooked but essential concept in virus classification. Intervirology 1990;31:241–254. [PubMed: 2272775]

35. van Regenmortel MHV, Maniloff J, Calisher CH. The concept of virus species. Arch Virol 1991;120:313–314. [PubMed: 1958131]
36. van Regenmortel MHV. How to write the name of virus species. Arch Virol 1999;144:1041–1042. [PubMed: 10447501]
37. van Regenmortel MHV. On the relative merits of italics, Latin and binomial nomenclature in virus taxonomy. Arch Virol 2000;145:433–441. [PubMed: 10752566]
38. van Regenmortel MHV. Perspectives on binomial names of virus species. Arch Virol 2001;146:1637–1640. [PubMed: 11676425]
39. van Regenmortel MHV. Viruses are real, virus species are man-made taxonomic constructions. Arch Virol 2003;148:2481–2488. [PubMed: 14648301]
40. van Regenmortel MHV, Mahy BW. Emerging issues in virus taxonomy. Emerg Infect Dis 2004;10:8–13. [PubMed: 15078590]
41. van Regenmortel MHV. Virologists, taxonomy and the demands of logic. Arch Virol 2006;151:1251–1255. [PubMed: 16799770]
42. van Regenmortel MHV. Virus species and virus identification: past and current controversies. Infect Genet Evol 2007;7:133–144. [PubMed: 16713373]
43. van Regenmortel, MHV. Virus species. In: Mahy, BWJ.; van Regenmortel, MHV., editors. Desk Encyclopedia of General Virology. Elsevier; Oxford: 2009. p. 37-41.
44. van Regenmortel, MHV. The nature of viruses. In: Mahy, BWJ.; van Regenmortel, MHV., editors. Desk Encyclopedia of General Virology. Elsevier; Oxford: 2009. p. 23-29.
45. van Regenmortel MHV. Logical puzzles and scientific controversies: The nature of species, viruses and living organisms. Syst Appl Microbiol 2010;33:1–6. [PubMed: 20005655]
46. Vetten HJ, Haenni A-L. Taxon-specific suffixes for vernacular names. Arch Virol 2006;151:1249–1250. [PubMed: 16721512]
47. Wilson, DE.; Reeder, DM., editors. Mammal species of the world A taxonomic and geographic reference. 3rd. The Johns Hopkins University Press; Baltimore: 2005.

Table 1

Application of taxonomic nomenclature

Incorrect usage	Correct usage	Explanation
Characterization of *Measles virus* Characterization of the *Measles virus* Characterization of *measles virus*	Characterization of measles virus	Species is a taxon. Taxa are ideas and do not exist physically. Taxa are italicized and capitalized. Taxa cannot be discovered or characterized, they can only be created. Taxa refer to theoretical averages of groups of viruses; hence taxa are not preceded by articles. Viruses do exist physically and can be discovered and described. Virus names are not italicized and not capitalized
A new arenavirus species, Machupo virus, was discovered in Bolivia A new arenavirus species, *Machupo virus*, was discovered in Bolivia	A new arenavirus, Machupo virus, was discovered in Bolivia and required the creation of a new species (*Machupo virus*)	See above. Taxa cannot be discovered, they can only be established. Species are italicized, viruses are not
The Kyasanur Forest disease virus is virulent in Bonnet macaques	Kyasanur Forest disease virus(es) is/are virulent in Bonnet macaques. The 63696 variant of Kyasanur Forest disease virus (KFDV-63696) is virulent in Bonnet macaques	There are many different Kyasanur Forest disease viruses (isolates, variants, and possibly strains). Even if they haven't been described yet we can be certain that they exist. Kyasanur Forest disease virus(es) is not italicized because the sentence refers to the actual virus(es) and not to the species *Kyasanur Forest disease virus*. Definite articles refer to definite entities, i.e. individual isolates, variants or strains
Nidovirales possess a positive-stranded RNA genome with a particular gene order	Nidovirads are (defined as) viruses with a positive-stranded RNA genome with a particular gene order	Nidoviruses, or more precisely nidovirads, is the vernacular name for all members of the order *Nidovirales*. Since taxa such as orders are concepts they cannot have (possess) physical properties
The families Comoviridae, Dicistroviridae, Marnaviridae, Picornaviridae, and Sequiviridae, and the genera Cheravirus, Iflavirus, and Sadwavirus are members of the order Picornavirales	The families *Comoviridae, Dicistroviridae, Marnaviridae*, *Picornaviridae*, and *Sequiviridae*, and the genera *Cheravirus, Iflavirus*, and *Sadwavirus* are members of the order *Picornavirales* Comovirids, dicistrovirids, marnavirids, picornavirids, and sequivirds, and cheraviruses, iflaviruses, and sadwaviruses are members of the order *Picornavirales* Comovirids, dicistrovirids, marnavirids, picornavirids, and sequivirds, and cheraviruses, iflaviruses, and sadwaviruses are picornavirads	Families and genera are taxa (ideas) and have to be italicized, except when their vernacular names are used