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Biological Species Concept: The Most Widely Accepted Concept of Species

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Abstract: **The term species is a Latin word meaning kinds. Species is a basic unit of biological classification as well as taxonomic rank. The scientific system of giving names to kinds of plants and animals revolves around the level of species. Early Greek philosophers such as Hippocrates, Plato and Aristotle also emphasized on the biological classification. Aristotle was considered as father of biological classification and he emphasized that all the parts of the body and activity should be considered during classification. As far as species is considered his idea was basically of essentialism or typological. Later on, in eighteenth century, the typological species concept also called as essentialism was elaborated by Linnaeus who was considered as father of taxonomy and proposed binomial nomenclature. In eighteenth century, a new concept of species called as Nominalistic species concept was suggested by Occam and his followers which was very popular in France. It states that nature produces individuals and nothing else. Species has no real existence in nature and it is only a mental concept. In seventeenth century, a new species concept began to emerge and it was Ray who believed in morphological species concept, but his species characteristics also contained the germ of biological species concept because he considered the reproductive relationship to be a principal species criterion. As early as 1760, Koelreutier also emphasized that all the individuals which are able to interbreed and produce fertile offspring belong to the same species. Other naturalists and taxonomists of nineteenth century such as Buffon, Merrem, Voigt, Walsh, and many others prepared the way for development of biological species concept. Charles Darwin who proposed the theory of origin of species by means of natural selection, appeared to have a morphological concept of species which was central to his theory of natural selection. However, later he gave importance to reproductive isolation and hence biological species concept. In his transmutation notebooks, Darwin realized the reality of species on the basis of criterion of non-interbreeding. As a consequence of this, biological species concept, Darwin recognized that acquisition of reproductive isolation was the mark of completion of transformation of permanent variety to the status of good species. Later on, biological species concept was emphasized and developed by Jordan, Mayr and Dobzhansky in the twentieth century. However, it has certain difficulties in its applications. According to this species concept, species is defined as a group of potentially or actually interbreeding natural populations which are reproductively isolated from other such groups. It was accepted as a most widely accepted definition of species. However, recently it has been criticized by molecular evolutionary biologists stating that "It is the time to abandon the biological species concept". At the same time, it is also said that "No, it is not the time to abandon the BSC. The genic concept proposed by Wu goes against BSC but at the same time it has also been argued that none whole heartedly embraced the new genic concept of species. Recently, based on the work done on bacteria and viruses, it has been suggested that a single biological species definition once thought to be limited to sexually reproducing organisms, is applicable across all cellular and acellular life forms. Thus, there is a single universal definition of species across Life's domain.**

Index Terms : **biological species concept, historical development, Darwin's concept of species, difficulties in its application, criticisms by molecular evolutionary biologists, applicable to all cellular and acellular life forms**

I. INTRODUCTION

The term species was initially undefined for a long time. It is a Latin word for kinds. Even early Greek philosophers and naturalists such as Hippocrates, Plato and Aristotle felt the necessity of biological classification. Species is the basic unit of biological classification. Aristotle was considered as father of biological classification. He was also a great evolutionist and believed in the principle of "Ladder of Life". Aristotle studied morphology, embryology, habits and ecology. He also suggested that habits and bodily parts are to be taken into consideration for classification. As far as species concept is concerned, his idea was essentially a kind of typological species concept or essentialism. To compare in almost all areas of biology, species are one of the basic units from anatomy, to behavior, development, ecology, evolution, genetics, molecular biology, palaeontology, physiology, and

systematics. Largely, the importance of species stems from its significance in systematics which is a science all the branches of biology rely on (de Queiroz, 2005). Literature on systematics and taxonomy always refer to issues about species and speciation. Species are crucial in many biodiversity issues: much of conservation, biodiversity studies, ecology, and legislation concern this taxonomic level (Mallet, 2007) . There are a large number of concepts of species which define species in different ways (Mallet, 2007; Singh, 2012, 2024a; Nisha et al. 2021).

Linnaeus (1707-78), a great taxonomist and called as father of taxonomy, believed in the older essentialism (typological species concept) for whom a species has a fixed existence and is unchangeable type (essence). He also became popular for proposing binomial nomenclature. The typological concept of species based on his concept is called as essentialist species concept. After Linnaeus another concept of species was proposed by Occam which was popular in France in the 18th century. According to Occam and his supporters, nature produces only individuals and nothing more and species does not exist in nature, it is only a mental concept of human. All of the older definitions of species including those of Buffon, Launch and Cuvier stress on the morphological similarity of individuals. Both these concepts have been rejected. The presence of sibling species has clearly raised important objections to the typological species concept because different species may be morphologically similar but reproductively isolated (Mallet, 2007; Singh, 2016). In literature, there are more than twenty different concepts of species (Mallet, 2007; Singh, 2012, 2024a; Nisha et al., 2021). The important species concepts are: biological species concept, evolutionary species concept, phonetic species concept, ecological species concept, phylogenetic species concept, recognition species concept, cohesion species concept, genotypic cluster species definition, genic species concept, genetic species concept, differential fitness species concept, and gen-morph species concept which have been described by Singh (2024a).

An entirely new species concept was proposed by Hong (2020) considering the prevailing species concepts and morphological and genetic characterstics of species of plants which he has called a new and integrative species concept. The ecological species concept was supported by Anderson (1990) by arguing in its favour that ecology plays an important role in most of the species concepts. Anderson believes that there is overemphasis on reproductive isolation in biological species concept and too little attention to the role of ecology. Brothers (1985) advocated in favour of evolutionary species concept and remarked that "Nevertheless, if such a concept could be found, one applicable to all of the various types of species that may exist, each of these being a special case within a general condition, then such a concept would be of far greater usefulness than a number of different concepts." Mayden (1997) identified at least twenty-two species concepts currently in use considering different factors as important under different species concepts: reproductive isolation, morphological features, ecological requirements, genetic differences, evolutionary lineages etc. It was discussed by Ridley (1993) that the seven species concepts (phonetic, biological, recognition, ecological, cladistic, pluralistic and evolutionary) are important and concluded that a combination of four (biological, recognition, ecological and cladistic) is ideal. However, it was suggested by King (1993) that eight concepts (morphological, biological, recognition, cohesion, evolutionary, cladistic, ecological and phylogenetic) are important and finally concluding that the biological species concept is the best. Since Darwin believed in reproductive isolation, geographic speciation, interspecific hybrid sterility and transformation of varieties to the status of good species, it is rightly suggested by numerous evolutionists, biologists and naturalists that he followed the biological species concept which is widely accepted concept of species although it has certain difficulties in its applications (Singh, 2023 a). de Queiroz (1999) argues that there is single, primary species concept that is adequate –applying across biodiversity and that is the general lineage concept. Mayden (1997) and de Queiroz (999) are of the opinion that BSC and ESP are not competing rather they are complementary to each other. The biological species concept which is based on reproductive isolation, is important in so far as it identifies the kind of lineages required by the evolutionary species concept. There is no need that each concept be individually adequate, applicable across biodiversity. The biological species concept based on reproductive isolation is applicable to sexually reproducing organisms (Richards, 2013).

II. EMERGENCE OF BIOLOGICAL SPECIES CONCEPT

Although many evolutionists believed in morphological species concept, an entirely new species concept had started to emerge in seventeenth century. Here the name of Ray (1686) who believed in morphological species concept may be mentioned but his characterization of species also incorporated the germ of biological species concept and it was considered by him that the reproductive relationship to be the main species criterion (Mayr 1966). Interestingly, Koelreuter (1761) also gave stress on interbreeding and producing fertile offspring as the species criterion. The sterility barrier was also considered by Buffon as species criterion which prepared the way for biological species concept (instead of morphological similarity). After this, the biological species concept was developed resulting from the contributions of Merrem, Voist, Walsh and many other naturalists and taxonomists of nineteenth century. Historical perspectives on biological species concept has been briefly described by Singh (2024b).

III. DARWIN'S CONCEPT OF SPECIES

Darwin (1859) proposed the theory of evolution in his book "Origin of species by means of natural selection" which states that species evolved rather than being created. Darwin's materialistic, morphological definition of species was central to his theory of natural selection. Varieties have the same general characters as species but they can be distinguished by the discovery of intermediate linking forms and a certain degree of small differences (Mallet, 1959). To Darwin, species did not

differ essentially from varieties within species but were distinguishable in that they had developed gaps in formerly continuous morphological variation (Mallet, 2007). In the 150th anniversary of the Darwin's 'Origin of Species', we appear to be returning to fuller appreciation of what Darwin meant (Mallet, 2010). Kottler (1978) has clearly stated that there is definite evidence from his transmutation note books that Darwin had some sort of biological species concept accepting the reality of species in some sense, was aware of problem of speciation (the reality of species) and recognized the role of isolation in the process of speciation. Mayr (1976) has reached the conclusion in his most recent remark on Darwin's view on species and speciation that he believed in geographic speciation which was consistent with earlier concept of species as reproductively isolated populations. Interestingly, Darwin also recognized that acquisition of reproductive isolation marked the attainment by an isolated variety of species rank and hence completion of speciation (Kottler, 1978). From this it is evident that Darwin gave importance to reproductive isolation and hence biological species concept. In his transmutation note books, Darwin realized the reality of species on the basis of criterion of non-interbreeding. As a consequence of this biological species concept, Darwin recognized that acquisition of reproductive isolation was the mark of completion of transformation of permanent variety to the status of good species (Singh, 2024b). In these transmutation notebooks, Darwin came close to distinguishing the modification from the multiplication of species while using Galapagos Islands as a model, he suggested his theory of speciation based on geographic isolation (Kottler, 1978).

IV. BIOLOGICAL SPECIES CONCEPT, DEFINITIONS OF SPECIES AND DIFFICULTIES IN ITS APPLICATION

Jordan (1905), Mayr (1940) and Dobzhansky 1935) clearly formulated the biological species concept and based on biological species concept, a species is defined as a group of potentially or actually interbreeding natural populations which are reproductively isolated from other such groups (Mayr, 1940). However, Dobzhansky (1950), being an evolutionary geneticist, defined species as a reproductive community of sexually and cross-fertilizing individuals which share in a common gene pool. Although it is the most widely accepted concept of the species, it has certain difficulties in its application: such as insufficient individual information, uniparental reproduction and evolutionary intermediacy. The biological species concept became a very popular species concept in twentieth century. The individuals of a species form a reproductive community, an ecological unit and a genetic unit.

There are numerous cases showing the examples of difficulties in the application of biological species concept. They are: (i) Insufficient individual information: Within the species, there may be individual variations due to sexual dimorphism, differences in age, polymorphism and other types of morphological changes but these problems may be solved through the study of life histories and of natural populations. (ii) Uniparental reproduction: Interbreeding among the members of the same species and reproductive isolation from other species are the important criteria under biological species concept. During the process of sexual reproduction, recombination of genetic material occurs between parental members which generates new combination of genes in the offspring. On the other hand, there are certain examples, which do not fall under this category such as hermaphroditism, automixis, parthenogenesis, gynogenesis, and vegetative reproduction which demonstrate uniparental reproduction. A number of examples are known in invertebrates and vertebrates showing uniparental reproduction. Mayr (1988) has proposed a new terminology for such uniparental lineages ie. paraspecies. But Grant (1957) designated such cases as agamospecies. Certainly, these cases are different from biological species, any terminology may be assigned to them but these cannot be considered as sub division of biological species and (iii) Evolutionary intermediacy: It is also difficult to apply biological species concept in those cases where speciation is still going on and it is not completed such cases are known as evolutionary intermediacy. Such situations pose difficulties to taxonomists. Populations may be found in the process of becoming new species ie. incipient species which have not acquired the status of new species. Such species are said to be in *statu nascendi* (Singh, 2023b). It is difficult to assign any stage to such populations, particularly when morphological variation is not correlated with acquiring reproductive isolation. There problems are caused by the gradual nature of the process of speciation. Despite these difficulties in application of biological species concept, it was most widely accepted concept of species. It was remarked by Sawamura (1999). that based on biological species concept, the question how the new species evolve should be substituted by a more answerable question "how reproductive isolating mechanisms are established between populations".

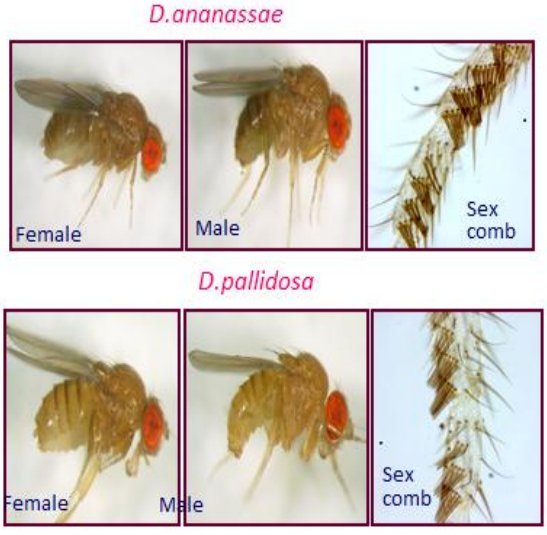

Fig. 1. Upper row: *D. ananassae*-female, male and sex comb. Lowe row: *D. pallidosa*-female, male and sex comb (From Singh, 2023b).

Singh (2023b) discussed the taxonomic status of *Drosophila pallidosa*, in the light of biological species concept. *D. pallidosa* was described as a new species just on the basis of sexual isolation with *D. ananassae*. Both these species are sympatric in certain areas of South Pacific Islands of Samoa and Fijji and their isolation in natural populations is maintained by premating or prezygotic isolation (sexual or behavioural or ethological isolation). However, they hybridize in the laboratory and produce fertile hybrids of both sexes. Further, they have identical pattern of male genitalia. Thus *D. pallidosa* is still in the process of speciation and is said to be in *statu nascendi* (Singh, 2021, 2023b). Singh's review (2016) has presented a number of cases of sibling species in the genus *Drosophila* showing evolutionary significance. There is another interesting pair of sibling species showing identical male genitalia which are basis of species identification in the sub genus *Sophophora* of genus *Drosophila*: *D. aldrichi* and *D. wheeleri* which belong to the *repleta* species group. In both these species, male genitalia are similar. These species are homosequential for banding in polytene chromosomes. These points have raised objection to their independent species status. But they have independent species status which is supported by hybrid male sterility between them which is post zygotic reproductive isolation. Further, the molecular data also support their independent status (Oliveira et al. 2008). These cases in *Drosophila* clearly support the biological species concept that sibling species are morphologically similar but reproductively isolated which goes against the typological species concept.

V. CRITICISMS OF BIOLOGICAL SPECIES CONCEPT BY MOLECULAR EVOLUTIONARY BIOLOGISTS

A new species concept was proposed by Wu (2001), a molecular evolutionary biologist which is known as genic species concept. The supporters of this concept severely criticized the biological species concept and suggested that BSC should be abandoned. According to Wu (2001), it is not the whole genome, but a gene is the unit of species differentiation. Thus, speciation depends upon genes which are designated as speciation genes. Speciation genes are those genes which show a higher frequency of differentiation during the process of cladogenesis compared to other genes which play part in differential adaptation to varying environments. He defined genic species as a group of individuals which are differentially adapted and upon contact fail to share genes controlling adaptive characters either by direct exchange or through intermediate hybrid population. In this concept, differential adaptation is a form of divergence in which alternative alleles of a gene have opposite fitness effect in two groups of individuals (Wu, 2001). Interestingly, genic species concept is applicable in both cases, biparental as well as uniparental organisms. This concept has been criticized also: it gives excessive and exclusive stress on differential adaptation caused by gene mutations and the role of random genetic drift cannot be excluded in speciation (Orr, 2001; Noor, 2021) The biological species concept has been criticized by suggesting that it is time to abandon the biological species concept by Wang et al. (2020) who believe in genic concept of species. On the other hand, Butlin and Stankowski have replied to the remark of Wang et al. by stating that it is not the time to abandon the biological species concept. In fact, Butlin and Stankowski (2020) have argued that there is actually no difference between genic concept and BSC, unless the BSC is tied to allopatric accumulation of reproductive isolation and the genic view is not. Noor (2021) has asked "Is the biological species concept is showing its age? He further remarks that many evolutionary biologists are excited by the empirical results of Wu and others, few agreeing with the abandonment of the BSC, and none wholeheartedly embracing the new genic concept (Noor, 2021). It has also been remarked that "has the biological species concept outlived its usefulness? (Ehrlich, 1961) but it is based on that fact that it has no meaning when one is dealing with asexual organisms. This limitation is there with BSC which has been clarified by the molecular work in prokaryotes.

VI. BIOLOGICAL SPECIES ARE UNIVERSAL ACROSS LIFE'S DOMAIN

Stankowski and Ravinet (2021) suggested to quantify the use of species concept. These authors considered 16 different species concepts although each concept is distinct and some differ less than others. Highly similar concepts include different forms of biological species concept in which species are recognized on the basis of reproductive isolation. According to these authors, two versions of biological species concept are fundamentally similar differing only by how much reproductive isolation is needed to recognize the species. A new species concept was proposed by Seifert (2014) designated as "pragmatic species concept" which is applicable to all eukaryotic organisms independent from their mode of reproduction or evolutionary history. The author emphasizes that Mayr does not consider the evolution and modes of reproduction of eukaryotic organisms as a whole. It is applicable to only very special conditions such as those species which are sexually reproducing and occurring sympatrically which do not exchange genes. Mayr hypothesis of reproductive isolation is not applicable to numerous groups of organisms with asexual mode of reproduction, to the frequent situations of allopatry and also to classification of fossil organisms. Seifert (2014) presented a new species concept "Pragmatic species concept" which is based on evaluation of advantages and disadvantages of different species concepts (Sonneborn, 1957; Sokal & Crovello, 1970; Cracraft, 1989; de Queiroz, 2007). "A species is a cluster of organisms which passed a threshold of evolutionary divergence". This concept is

applicable to all known groups of eukaryotic organisms independent of their mode of reproduction or evolutionary history. Xu (2020) presented evidence for fungal species concept in the genomic era. He emphasized that there are more than 140000 fungal species so far reported and they are heterogeneously defined on the basis of various criteria such as morphological, physiological, mating and molecular features. The commonly used species concepts in fungi are: biological, ecological, evolutionary, genotypic, morphological, phonetic, phylogenetic and recognition. He proposed the genomic species concept for fungi which could be similarly argued for other groups of eukaryotic microbes as well as plants and animals. Xu (2020) has also discussed that during evolutionary divergence, random mutations continuously originate and separate populations accumulate different mutations which may be fixed through the action of natural selection and random genetic drift. If the new mutations affect morphological, ecological, or sexual reproductive traits, these traits become fixed in different populations, then morphological, ecological and biological species as inferred based on their respective species concepts and criteria could be recognized. Bobay and Ochman (2017), Bobay and Ochman (2019) and Bobay (2020) have presented evidence for biological species in viral world, biological species as universal across Life's domain and prokaryotic species concept and challenges. Bobay (2020) suggested that although prokaryotic genomics is undoubtedly different from animals and plants, there is growing evidence that gene flow which is similar to sexual reproduction plays an important role in shaping the genomic cohesiveness of microbial populations extending evidence to some extent, a species definition based on biological species concept is applicable to prokaryotes. Bobay and Ochman (2017) have also suggested that there is a single species definition based on gene flow, once thought to be limited to sexually reproducing organisms, is applicable to all cellular life forms. Bobay and Ochman (2018) are of the opinion that due to their dependence on cellular organisms for metaboloism and replication, viruses are typically named and assigned to species according to their genome structure and the original host that they infect. The results obtained in viral world on the detection of gene flow within populations, give substantial evidence to these authors to define viral species according to biological species concept. These findings open the possibility to use a single, universal definition of species that is applicable across cellular as well as acellular lifeforms (Bobay & Ochman, 2018). Nauer et al. (2021) pointed out that three morphological variants of *Hypnea pseudomusciformis* (red algae) show how species delimitation is made based on DNA barcode in the taxonomy of this algae exhibiting substantial intraspecific variation. The hypothesis of these authors suggests that ecotypic and morphological variants of this species are in fact the same biological entity and thus BSC proved to be a valuable tool for responding to conflicts raised by DNA barcode technique (Nauser et al., 2021). Moreno (2002) suggested that the bacterial species concept was examined within the framework of plant and animal associated α-2 proteobacteria taking into the consideration the phylogenetic, taxonomic and biological approaches as well as microbiologist's perception. For over a century, the biological species concept in the first instance, and following this, the taxonomic species concept were the major theoretical postulates orienting the bacteriological research. These recent work in the area of molecular biology and using prokaryotes and viruses have clearly demonstrated the importance of biological species concept which does not remain confined to sexually reproducing organisms.

CONCLUSION

Early Greek philosopher and naturalist, Aristotle was considered as father of biological classification and he emphasized that all the parts of the body and activity should be considered during classification. As far as species is considered his idea was basically of essentialism or typological. Later on, in eighteenth century, the typological species concept also called as essentialism was elaborated by Linnaeus who was considered as father of taxonomy and proposed binomial nomenclature. The typological species concept was also called as morphological species concept or essentialism. This concept defines species as a group of morphologically similar individuals and it remains static and the species remains constant through time without any change. But this species concept was rejected primarily because of two reasons: there are individual variations within the species and occurrence of sibling species (morphologically indistinguishable but reproductively isolated).

Although many evolutionists believed in morphological species concept, an entirely new species concept had started to emerge in seventeenth century. Here the name of Ray (1686) who believed in morphological species concept may be mentioned but his characterization of species also incorporated the germ of biological species concept and it was considered by him that the reproductive relationship to be the main species criterion (Mayr, 1966). Interestingly, Koelreuter (1761) also gave stress on interbreeding and producing fertile offspring as the species criterion. The sterility barrier was also considered by Buffon as species criterion which prepared the way for biological species concept (instead of morphological similarity). After this, the biological species concept was developed resulting from the contributions of Merrem, Voist, Walsh and many other naturalists and taxonomists of nineteenth century. As it is apparent from his transmutation notebooks, Darwin also believed in biological species concept because of the facts that Darwin gave importance to reproductive isolation and hence biological species concept. In his transmutation note books, Darwin realized the reality of species on the basis of criterion of non-interbreeding. As a consequence of this biological species concept, Darwin recognized that acquisition of reproductive

isolation was the mark of completion of transformation of permanent variety to the status of good species (Singh, 2024 a). In these transmutation notebooks, Darwin came close to distinguishing the modification from the multiplication of species while using Galapagos Islands as a model, he suggested his theory of speciation based on geographic isolation (Kottler, 1978).

In twentieth century, Jordan (1905), Mayr (1940) and Dobzhansky (1935) clearly formulated the biological species concept and based on biological species concept, a species is defined as a group of potentially or actually interbreeding natural populations which are reproductively isolated from other such groups (Mayr, 1940). However, Dobzhansky (1950), being an evolutionary geneticist, defined species as a reproductive community of sexually and cross-fertilizing individuals which share a common gene pool. Although it is the most widely accepted concept of the species, it has certain difficulties in its application: such as insufficient individual information, uniparental reproduction and evolutionary intermediacy. The biological species concept became a very popular species concept in twentieth century. The individuals of a species form a reproductive community, an ecological unit and a genetic unit. The biological species concept has been severely criticized by the supporters of Genic Species concept and they have remarked that the BSC should be abandoned. However, it has also been remarked by other molecular evolutionary biologists that it should not be abandoned and the genic species concept also has certain demerits. This concept has been criticized also: it gives excessive and exclusive stress on differential adaptation caused by gene mutations and the role of random genetic drift cannot be excluded in speciation (Orr, 2001; Noor, 2021). Noor (2021) has asked "Is the biological species concept is showing its age? He further remarks that many evolutionary biologists are excited by the empirical results of Wu and others, few agreeing with the abandonment of the BSC, and none wholeheartedly embracing the new genic concept (Noor, 2021). Recently, the work in the area of molecular biology and using prokaryotes and viruses have clearly demonstrated the importance of biological species concept which does not remain confined to sexually reproducing organisms. Bobay and Ochman (2017), Bobay and Ochman (Bay and Ochman, 2018) and Bobay (2020) have presented evidence for biological species in viral world, biological species as universal across Life's domain and prokaryotic species concept and challenges. Bobay(2020) suggested that although prokaryotic genomics is undoubtedly different from animals and plants, there is growing evidence that gene flow which is similar to sexual reproduction plays an important role in shaping the genomic cohesiveness of microbial populations extending evidence to some extent, a species definition based on biological species concept is applicable to prokaryotes. Bobay and Ochman (2017) have also suggested that there is a single species definition based on gene flow, once thought to be limited to sexually reproducing organisms, is applicable to all cellular lifeforms. Bobay and Ochman (2018) are of the opinion that due to their dependence on cellular organisms for metabolism and replication, viruses are typically named and assigned to species according to their genome structure and the original host that they infect. The results obtained in viral world on the detection of gene flow within populations, give substantial evidence to these authors to define viral species according to biological species concept. These findings open the possibility to use a single, universal definition of species that is applicable across cellular as well as acellular lifeforms (Bay & Ochman, 2018).

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