Concepts of species and modes of speciation

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Species is a Latin word meaning 'kind'. In biology, species is a basic unit of biological classification and a taxonomic rank. Traditionally, species has been considered as a basic category of biological classification and defined as a group of similar organisms showing the same essence which is based on typological species concept (essentialism). Later on, in the eighteenth century, the typological species definition was found inappropriate for biological species so mainly in the second half of the nineteenth century an entirely new species concept (biological species concept) was developed which was elaborated in detail by Mayr and Dobzhansky in the twentieth century. Biological species concept is the most widely accepted species concept. There are a large number of species concepts proposed from time to time by various naturalists, taxonomists and evolutionists which define species in different manner. There are various models to explain the modes of speciation basically based on geographic component such as sympatric, allopatric (dichopatric and peripatric) and parapatric. Further, chromosomal models have also been suggested to explain the modes of speciation.

Keywords: Cladogenesis, evolutionary process, modes of speciation, species definitions and concepts.

WHAT is a species? This is an important question. The scientific system of naming 'kinds' of plants and animals revolves around the species level. The term 'species' is Latin for 'kinds'. Since ancient time, philosophers and naturalists realized the necessity for a basic unit by which biodiversity on this planet may be described and estimated. But the development of a scientific theory of classification is a relatively recent phenomenon. Simpson[1] and Mayr[2] have elaborated on the historical developments of taxonomy and its concepts. Early Greek philosophers and naturalists like Hippocrates, Plato and Aristotle also paid attention to biological classification. Hippocrates (460–377 BC) described types of animals, but there is no indication of useful classification in his work. Plato (427–347 BC) was, in the words of Mayr, 'the great antihero of evolution' as he believed in essentialism which is also referred to as the theory of forms. He used the term 'Eidos' for forms or types; it is of Greek origin and serves to designate any of those primary realities which came to be known as the forms. Aristotle (384–322 BC) was the father of biological classification. As far as evolution is concerned, he gave the idea of ladder of life, a series in which organisms could be arranged in the order of increasing complexity. He studied morphology of animals and also paid attention to embryology, habits and ecology. He emphasized that all the attributes of animals such as living, actions, habits and bodily parts may be taken into consideration in classification. His idea was also a kind of typological or essentialism as far as species is concerned. Linnaeus (1707–1778), a great taxonomist and sometimes called the 'father of taxonomy', adhered to downward classification. His thinking was that of an essentialist for whom species reflects the existence of fixed, unchangeable type (essence). He proposed binominal nomenclature. The typological definition of species based on the concept of Linnaeus is called the essentialist species concept. Occam and his followers suggested that nature produces individuals and nothing more, and species has no actual existence in nature; it is only a mental concept[3]. It is the basis of nominalistic species concept which was popular in France in the eighteenth century. A particular species concept is associated with a definition and definitions differ in different concepts of species. It may be mentioned here that nearly all of the older definitions of the species, including those of Buffon, Lamarck and Cuvier, refer to the morphological similarities of individuals of the same species.

An entirely new species concept had begun to emerge in the seventeenth century. Ray[4] believed in the morphological definition of species and his species characterization also contained the germ of biological species concept, which considers the reproductive relationship to be a principal species criterion[5]. As early as 1760, Koelreuter mentioned that all the individuals which are able to interbreed and produce fertile progeny belong to the same species. Hundred years before Darwin, Buffon in his *Histoire Naturelle* described everything known in the natural world and believed in organic change but did not provide

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any mechanism to explain the evolutionary change. Although initially he believed in morphological species concept, Buffon prepared the way for biological species concept using sterility barrier (instead of morphological similarities) as species criterion. Later on, the biological species concept was developed due to contributions of Merrem, Voigt, Walsh and many other naturalists and taxonomists of the nineteenth century. The biological species concept was clearly formulated by Jordan[6], Dobzhansky[7] and Mayr[8]. According to Mayr[8], a species is a group of potentially or actually interbreeding natural populations which are reproductively isolated from other such groups. However, Dobzhansky[9], being an evolutionary geneticist, defined species as a reproductive community of sexually and cross-fertilizing individuals which share in a common gene pool. The biological species concept is the most widely accepted, but it has certain difficulties in its application. Since biological species concept is applicable to non-dimensional situation, Simpson[10], faced with the problems of studying the evolution of species through time, proposed his evolutionary species concept in which a species is a lineage (an ancestral–descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies.

Darwin[11] explained the mechanisms of evolution in his book *Origin of Species* and his theory has two components: (i) descent with modification – all species living and extinct have descended from one or a few original forms of pre-existing species, and (ii) natural selection as causal agent of evolutionary change. Darwin also recognized that species not only evolve but also divide. Darwin unquestionably had adopted a biological species concept in the 1830s, even though later he largely gave it up[12]. He did not define species, but appeared to have a morphological concept of species which was central to his theory of natural selection[13]. According to Darwin, the term species is arbitrarily used for the sake of convenience to a set of individuals closely resembling each other and it does not differ from the term ‘variety’ which is given to less distinct and more fluctuating forms. Probably, Darwin believed that the concept of species is unnecessary because gradual evolutionary changes can account for the diversity of life. In this article, a number of species concepts, including those which have been rejected and are also of historical significance, have been described. Further, various modes of speciation have also been discussed with suitable examples.

Concepts of species

Species concepts originate in taxonomy in which species is the basic unit of classification according to the International Commission of Zoological Nomenclature. Survey of taxonomic literature shows that there are a large number of species concepts which have been suggested by naturalists, taxonomists and evolutionary biologists from time to time[14–20]. There are more than 20 species concepts which are listed below:

- Agamospecies: Asexual lineages, uniparental organisms (parthenogens and apomicts) that cluster together in terms of their genome, may be secondarily uniparental from biparental ancestors.
- Biological species: Mendelian population of sexually reproducing organisms, interbreeding natural populations isolated from other such groups, depending upon reproductive isolating mechanisms.
- Cladistic species: Set of organisms between speciation events or between speciation and extinction events, or a segment of a phylogenetic lineage between nodes.
- Cohesion species: Evolutionary lineages bounded by cohesion mechanisms that cause reproductive communities, particularly genetic exchange, and ecological interchangeability.
- Composite species: All organisms belonging to an internodon and their descendents until a subsequent internodon (an internodon is a set of organisms whose parent–child relations are not split).
- Ecological species: A lineage which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range.
- Evolutionary species: A lineage (ancestral–descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies.
- Evolutionary significant unit: A population (or group of populations) that is substantially reproductively isolated from other conspecific population units and represents an important component in the evolutionary legacy of the species.
- Geological concordance: Population subdivisions concordantly identified by multiple independent genetic units constitute the population units worthy of recognition as phylogenetic taxa.
- Genetic species: Group of organisms that may inherit characters from each other, common gene pool, reproductive community that forms a genetic unit.
- Genotypic cluster definition: Clusters of monotypic or polytypic biological entities, identified using morphology or genetics, forming groups that have few or no intermediates when in contact.
- Hennigian species: A tokogenetic community that arises when a stem species is dissolved into two new species and ends when it goes extinct or speciates.
- Internodal species: Organisms are conspecific in virtue of their common membership of a part of a genealogical network between two permanent splitting events or a splitting event and extinction.

- Morphological species: Similar to typological species concept of Linnaeus; species are the smallest groups that are consistently and persistently distinct and distinguishable by ordinary means.
- Nominalistic species: Only individuals exist and nothing more. Species have no actual existence in nature.
- Non-dimensional Species: Species delimitation in a non-dimensional system (a system without the dimensions of space and time).
- Nothospecies: Species formed from the hybridization of two distinct parental species, often by polyploidy.
- Phenetic species: A cluster of characters that statistically co-vary, a family resemblance concept in which possession of most characters is required for inclusion in a species, but not all. A class of organisms that share most of a set of characters.
- Phylogenetic species: A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.
- Recognition species: A species is that most inclusive population of individuals, biparental organisms which share a common fertilization system.
- Reproductive competition species: The most extensive units in the natural economy such that reproductive competition occurs among their parts.
- Successional species: Arbitrary anagenetic stages in morphological forms, mainly in the palaeontological records.
- Taxonomic species: Specimens considered by a taxonomist to be a member of a kind on the evidence or on the assumption that they are as alike as their offspring of hereditary relatives within a few generations.

Specifications of various species concepts mentioned above have been taken from Wilkins[20].

Mayr and Ashlock[15] have stated that 'The taxonomic literature reports innumerable species concepts, but they fall into four groups. The first two have mainly historical significance but are still upheld by a few contemporary authors'. These groups are: (i) typological species concept, (ii) nominalistic species concept, (iii) biological species concept and (iv) evolutionary species concept.

Typological species concept

This concept was proposed by Linnaeus and his followers and before that Plato and Aristotle also believed in this. The term 'Eidos' coined by Plato is also related to this. In nature, there are limited number of types or universals and members of a species form a class. It is also referred to as essentialism and the definition of species based on this concept is also called essentialist species concept. It is based on the degree of morphological differences used by the taxonomists. Under this concept, each species is entirely constant through time and thus the concept does not allow any change in a particular species. Since it is known that there are individual variations within the species and different species may be morphologically identical as in the case of sibling species (morphologically indistinguishable but reproductively isolated), the essentialist species concept has been rejected.

Nominalistic species concept

Occam and his followers did not believe in the existence of universals or types and for them only individuals existed and species had no real existence. This species concept was popular in France in the 18th century. According to Bessey[3], nature produces only individuals and nothing more. Species is merely a mental concept. But it is known that species are not human constructs. So this species concept has also been rejected.

Biological species concept

Jordan[6], Dobzhansky[7] and Mayr[8] clearly formulated the biological species concept. Mayr[8] defined species as a group of potentially or actually interbreeding natural populations which are reproductively isolated from other such groups. Dobzhansky[9] , being an evolutionary geneticist, added the term gene pool, and defined species as a reproductive community of sexually and cross-fertilizing individuals which share in a common gene pool. The members of a species form a reproductive community, an ecological unit and a genetic unit. These three properties (reproductive community, ecological and genetic units) show that species cannot be defined by the typological or nominalstic concepts. The biological species concept is the most widely accepted, but there are three main difficulties in its application: insufficient information, uniparental reproduction and evolutionary intermediacy. With regard to insufficient information in a particular species, there are individual variations due to sexual dimorphism, age differences, polymorphism and other types of morphological changes, but these difficulties may be overcome through a study of life histories and analysis of natural populations. In the biological species concept, interbreeding among the individuals of the same species and reproductive isolation from other species are the principal criteria. During the process of sexual reproduction, recombination of genetic materials takes place between parental individuals which leads to new combinations of genes in the progeny. However, there are many examples which do not come under this category such as hermaphroditism, automixis, parthenogenesis, gynogenesis and vegetative reproduction which show uniparental reproduction. There are numerous examples of such uniparental reproduction in invertebrates and vertebrates. Mayr[21] has given a new terminology to such uniparental lineages, i.e. paraspecies, but Grant[22] has designated such cases as agamospecies. Any terminology may be given to such cases, but they may not be considered as subdivision of biological species because they are quite different from biological species. There is difficulty in the application of biological species concept in those situations in which speciation is incomplete (evolutionary intermediacy). The species as a reproductive community exists in non-dimensional situation of a deme. As soon as it extends in dimension of space and time, the stage is set for incipient speciation. The populations may be found in the process of becoming new species which have not yet acquired the characters of entirely new species. It is difficult to assign any stage to such populations, particularly when morphological distinctness is not correlated with the acquisition of reproductive isolation. Further, there may be acquisition of reproductive isolation without the development of equivalent morphological change. Numerous difficulties may be faced by the taxonomists for such cases of evolutionary intermediacy. There are several examples of such situations which are consequences of the gradual nature of the speciation process. It is difficult to assign species status to a given population in these cases of evolutionary intermediacy. This temporal inextensibility of biological species concept makes it non-evolutionary because of its non-dimensional character. Mayr[2] has explained this limitation by stating that 'the species concept has its full meaning only where populations belonging to different species come into contact. This takes place in local situations without the dimension of space (geography) and time. The function of the species concept is to determine the status of co-existing individuals and populations.'

Evolutionary species concept

Because of non-dimensional character of the biological species concept, some palaeontologists are not satisfied with biological species definition. Their argument is that the species definition must involve evolutionary criteria. Simpson[1] proposed the evolutionary species concept and defined the species as a lineage (an ancestral–descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies. Mayr[2] has criticized the evolutionary species definition saying that it is the definition of a phyletic lineage, but not of the species. It is also applicable to incipient species or isolated populations. Further, it ignores the core of the species problem and tries to delimit species taxa in the time dimension. Wiley[23] attempted to make certain improvement in evolutionary species concept by suggesting that no presumed separate, single, evolutionary lineage may be subdivided into a series of ancestral and descendent species. But this definition is of species taxon and not of species category. Thus Mayr did not accept the evolutionary species concept and he strongly advocated for the biological species concept in spite of certain difficulties in its application.

Modes of speciation

Speciation is the evolutionary process by which new biological species arise. Darwin called it specification. The term 'speciation' was coined by Cook[24]. The basic process of evolution recognizes the existence of two processes: anagenesis – phyletic change in the course of time, and cladogenesis or speciation – the origin of new species of organisms through splitting of pre-existing ones. Darwin[11] was primarily interested in demonstrating evolutionary changes by the action of natural selection which was appropriately called the transformation of species in time by Romanes[25], and phyletic evolution by Simpson[26]. It is quite possible to have evolutionary change without any multiplication of species. The other evolutionary process is true speciation, or what Romanes in 1897 called the multiplication of species in space. It is the splitting of an originally uniform species into several daughter species[5]. Speciation is also considered as one of the main ways by which organisms adapt in order to exploit the diversity of environments available to them[27]. A number of possible modes of speciation have been suggested by various evolutionary biologists. Huxley[28] suggested three types of speciation: geographical, ecological and genetic. Mayr[29] classified the various modes of speciation into the following types: geographic speciation, semi-geographic speciation, and non-geographic or sympatric speciation – instantaneous and gradual. Wright[30] proposed seven alternative modes of speciation which are basically overlapping with each other and based on the size of the population and the number of ancestral species giving rise to new species. Mayr and Ashlock[15] proposed six possible modes of speciation: polyploidy, sympatric, parapatric, geographic or allopatric (two types – dichopatric and peripatric), and speciation in time. White[27] has considered three main sets of variables which are involved in the process of speciation: (i) genetic mechanisms generating genetic variability, (ii) genetic isolating mechanisms leading to the origin of reproductive isolation, and (iii) geographic component ranging from complete (allopatry) to absent (sympatry). These three sets of variables provide the basis for various possible models of speciation. White[27] suggested seven models to explain the mechanisms of speciation. These are:

- Strict allopatry without a narrow population bottleneck.
- Strict allopatry with a narrow population bottleneck (founder principle).
- Extinction of intermediate populations in a chain of races.

- Clinal speciation.
- Area-effect speciation (primarily genic).
- Stasipatric speciation (primarily chromosomal).
- Sympatric speciation.

The first three models are basically allopatric or geographic speciation and the next three come under semi-geographic speciation, as suggested by Mayr. White[27] has described speciation by polyploidy and asexual speciation separately. Polyploidy, which is common in plants but rare in animals, has been considered under chromosomal model of instantaneous speciation which comes under the sympatric mode of speciation. The important modes of speciation to explain the mechanism of speciation in animal species are allopatric, sympatric, parapatric and stasipatric.

Allopatric mode of speciation

Allopatric mode of speciation has also been called geographic speciation by Mayr[5]. It is of two types: dichopatric and peripatric. In allopatric speciation, evolution may take place in two spatially separated populations from a common ancestral population. These isolated populations undergo extensive genetic changes due to the action of different evolutionary forces such as mutation, selection, random genetic drift, migration and other factors and they genetically diverge. In due course of time, these isolated populations may develop reproductive isolating mechanisms and become independent species. Even if, in the long run, the ecological barrier is removed, these newly created allopatric species will become sympatric, but they will maintain their species level because they have already developed reproductive isolation. The process of allopatric species formation has long been recognized as a primary method of speciation. Within this mode of speciation, two sub-types are distinguished: (i) Traditional allopatric or dichopatric speciation or dumbbell model of Mayr[29]: In this model, a population bottleneck or founder principle is not assumed. According to this model, a substantially large geographic area is subdivided by a newly developed barrier such as ecological, geological, geographic, vegetational, which secondarily splits the original continuous range into two or more groups of populations. (ii) Peripatric speciation (with a narrow bottleneck). There is involvement of the founder principle[29] because a new population is founded by a single gravid female or a small number of founding individuals. As a result of this, genetic variation is reduced due to random genetic drift and bottleneck effect, and the isolated populations acquire genetic changes in due course of time which provide the basis for reproductive isolation. Carson[31] has explained the process of speciation in the Hawaiian-species of *Drosophila* on the basis of the founder principle, suggesting the role of flush–crash cycle. There are several interesting examples of allopatric speciation such as evolution of picture-winged *Drosophila* species on the Hawaiian Islands, evolution of Darwin's finches on the Galapagos Islands, evolution of land snails of the genus *Partula* in the Society Islands, and locusts and mammals on various islands.

Sympatric mode of speciation

This can be defined as the origin of a new species characterized by reproductive isolation within the dispersal area of the parental species[32]. Sympatric speciation involves instantaneous appearance of reproductive isolation between the segments of the same population and new species originate in the same geographical area. If one or both populations move out of the original habitat, two allopatric species would be generated. If both the populations remain in the same geographical area, sympatric species would be recognized. Although it has been criticized by Mayr[5], who stated that the geographic speciation is almost the exclusive mode of speciation among animals, there are some good examples demonstrating the occurrence of sympatric mode of speciation, particularly in host-specific plant feeders and host-specific parasites. Results of the extensive study by Bush[32,33] on fruit flies of the family Tephritidae occurring in USA have provided evidence for sympatric mode of speciation as hawthorn race gave rise to apple race sympatrically. Experimental results of Thoday and Gibson[34] have also extended evidence for sympatric speciation in *Drosophila*. Divergence for polygenic character and ethological isolation was produced simultaneously by disruptive selection for sternopleural bristle number in *Drosophila melanogaster*. There are other examples providing evidence for sympatric mode of speciation (see White[27]).

Parapatric mode of speciation

Sometimes two species completely isolated from each other may occur in geographic contact in some areas (parapatry). Under such situations of slight distributional overlap, incipient species may complete speciation because hybrids may be having lowered fitness leading to elimination of genes and chromosome arrangements which permit the interbreeding of two incipient species. This process of improving allopatrically acquired isolating mechanisms in a contact zone (a process corresponding to character displacement) can be called parapatric speciation[35]. According to Endler[36], isolating mechanisms build up in a cline, along an ecological escarpment, until the two adjacent populations are finally reproductively isolated. In many cases, the drastic belts of intergradation between two subspecies or semispecies are explained as zones of secondary contact of two previously separated populations. Nevo[37] has analysed such tension zones and found no evidence for reinforcement of reproductive isolating mechanisms. His argument was also supported by other evolutionists. For these reasons, the occurrence of parapatric mode of speciation is unlikely[38]. White[27] has also remarked that it seems undesirable to recognize the existence of a special category of parapatric mode of speciation. Parapatric species may lack behavioural isolation and hybridize, but their hybrids are sterile. This has been reported in various species of morabine grasshoppers in Australia[39]. There are different categories of hybrid zones[40], but the most significant hybrid zone from the viewpoint of speciation seems to be parapatric hybrid zones (tension zones). In general, it has been found that hybrids produced in parapatric zones are at an adaptive disadvantage[27]. Although this model has been criticized, there are few examples of ring species such as *Lurus* gulls in the north pole, *Ensatina* salamanders in central valley in California and the Greenish Warbler in the Himalaya showing evidence in favour of parapatric mode of speciation.

Stasipatric mode of speciation

It is primarily the chromosomal model of speciation as suggested by White *et al.*[41] and White[42] in order to explain those situations in which closely related species of animals having limited vagility show similar karyotypes, and where assumption of strictly allopatric speciation seems unreasonable. A daughter species is generated within the geographical range of a widespread species and the new species is characterized by new chromosomal rearrangements which play an important role in speciation by reducing the Darwinian fitness (fecundity or viability) of the heterozygous individuals. The daughter species may extend its range at the expense of original species maintaining a narrow parapatric zone of contact at the peripheral region of their distribution in which hybridization causes the production of individuals with lowered fitness[27]. Interesting examples supporting this model were provided by White[27]: Australian morabine grasshoppers of the genus *Vandiemenella* with seven species differing in their karyotypic constitution and Australian stick insects belonging to the species complex *Didymuria violescens* with 10 cytological races. Species and races of these Australian insects have essentially parapatric geographical distribution.

Conclusion

Dobzhansky[43] remarked that nothing in biology makes sense except in the light of evolution, while Mayr[2] opined that speciation is a key problem of evolution and it is remarkable how many problems of evolution cannot be fully understood until speciation is understood. Thus speciation is an important and interesting aspect of evolutionary biology. Definition of species based on biological species concept proposed by the evolutionary biologists is the most widely accepted in spite of certain difficulties in its application. Based on this concept, the species is considered as a fundamental category of biological organization. Biological species definition is still perhaps the most widely adopted, although it seems to be less popular than 30–40 years ago because of criticisms and proposed alternatives[44]. Presently, there is more disagreement among biologists about speciation than before, and also after such a long time since biological species definition was proposed, we do not have an universally accepted and clear definition of a species. The emerging solution of the species problem is an updated genetic version of Darwin's own definition which is useful for taxonomy, biodiversity and evolution[13]. During the 150th anniversary of the *Origin of Species*, we appear to be returning more and more to Darwinian views on species and to complete appreciation of what Darwin meant[45]. To explain the mechanism of speciation, different modes have been suggested. There are more examples available to support the geographical or allopatric mode of speciation compared to the sympatric mode of speciation. Nevertheless, we must have a clear definition of species if speciation is to be any different from ordinary evolution[13]. As taxonomists and systematists, we must use our available tools and knowledge to recover the natural diversity that has resulted from the process of descent with modifications and speciation[18].

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