



Species and Speciation

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ABSTRACT: Speciation refers to genetic divergence among related populations, leading to new species. The divergence is a continuous phenomenon, and the level, chosen by a taxonomist in the continuum, is a new species. The generally accepted species concept is the Biological Species Concept (BSC), which takes reproductive isolation from related forms a necessary feature of a species. During speciation reproductive isolation, among sister lineages, gradually develops. Hence the need to assess the extent of the isolation makes delimiting a species a difficult problem. Generally the extent of phenotypic deviation along a lineage is taken to assess reproductive isolation. This obviously involves some arbitrariness. To reduce the level of the arbitrariness various methods have been suggested, viz. a quantitative approach, molecular genetic criteria, phylogenetic approach etc. But, in spite of these different approaches, some arbitrariness may remain in species delimitation. Several recent authors have pleaded for an integrative approach (i.e. including phenotypic approach, phylogeny, molecular sequence study etc.) in discovery and description of new species to come closest to the species criteria set by BSC.

Key words: Reproductive isolation; Species concepts; Species delimitation; Sexual Selection; Sympatric speciation.

INTRODUCTION

A number of papers on this topic have appeared in the recent past. Still some aspects of this subject need to be emphasized and elucidated; hence this review, based mostly on recent publications.

'Species' is a very significant taxon. It has been described as an evolutionary lineage "with separate and unitary role" (Simpson, 1965). A separate and unitary role should involve reproductive isolation between the lineage in question and related lineages, including sister lineages. But then how is it that interspecific hybridizations are known to occur? Why sometimes synonymization of some described species is done? Why are there cases of a species turning out to be a 'species cluster'? Efforts have been made in this review to emphasize and elucidate such aspects of the species level taxonomy as would answer and satisfy such questions.

Species concepts

The various species concepts, as pointed out by Tobias *et al.*, (2010) are:

- (i) The biological species concept (BSC),
- (ii) The phylogenetic species concept (PSC), and
- (iii) The monophyletic species concept (MSC).

Among these species concepts the most favoured by taxonomists is BSC (Gonzalez-Forero, 2009; Tobias *et al.*, loc. cit.).

According to the Biological Species Concept of Dobzhansky (1937) and Mayr (1942), "A species is a group of interbreeding natural populations that is reproductively isolated from such other groups" (Mayr & Ashlock, 1991). As Gonzalez-Forero (loc. cit.) has stated, BSC "continues to play a central role.... specially when studying the origin of species....". Tobias *et al.*, (loc. cit.) say, "BSC ... has some advantages as a framework for a global taxonomic treatment", and also, "(the concept) applies to a relatively fixed and broadly intuitive limit to species diversity".

Hausdorf (2011) has analytically examined the various species concepts, and finds the genic concept of Wu (2001) most acceptable. This concept, as adopted by Hausdorf (loc. cit.) may be stated this way: A species is a differentiated and further differentiating group of interbreeding populations, which is able to maintain its differentiation identity despite limited gene flow between itself and similar other populations. Obviously it is a modified version of BSC, modified in view of the 'semipermeable' nature of the reproductive isolation between similar species.

Speciation and delimiting species

It is important to distinguish between speciation and species. While speciation is a continuous genetic divergence among and along sister lineages, a species is a taxon made out in the continuum of speciation. As per BSC, a species is reproductively isolated from related species. But during progress of speciation reproductive isolation very commonly gradually develops (Verma, 2006; Hendry, 2009; Gonzalez-Forero, 2009) (Fig. 1). Almost no taxonomist, before recording a new species, performs breeding experiments to ascertain reproductive isolation from related forms. Considerable phenotypic divergence is generally taken as an indicator

of reproductive isolation. As Winker (2009) has pointed out, species level taxonomy is < a categorical tool that results in discrete “bins” along a continuum of differentiation>. At the level, chosen in the continuum, for describing a new species by the taxonomist, reproductive isolation from sister lineages may not have fully developed (Fig. 1). That is why we often come across cases of interspecific hybridization. Gibbons (2011) has cited Jean-Jacques Hublin saying, “There are about 330 closely related species of mammals that interbreed, and at least a third of them can produce fertile hybrids.”.

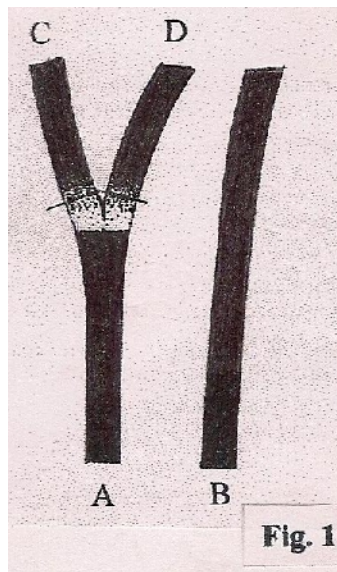


Fig. 1. Diagram to illustrate gradual development of reproductive isolation between two lineages leading to the two species ‘C’ and ‘D’. ‘B’ is a species related to ‘A’, which has been ancestral to ‘C’ and ‘D’. Solid black is meant to denote reproductive isolation, and dots and their density are indicative of growing reproductive isolation between ‘C’ and ‘D’. The lines, across the lineages, show arbitrarily chosen levels for delimiting ‘C’ and ‘D’. (From Verma, 2006).

It is obvious that the reproductive isolation part of BSC makes practical application of the concept in species level taxonomy, difficult. Gonzalez-Forero (2009) has suggested relaxation of this part of BSC. He says that this “non-discreteness” in the reproductive isolation part of BSC will make the concept applicable to the cases of “ring species”, and in addition to cases of interspecific genetic introgression.

On relaxing the reproductive isolation component of BSC, the concept should read thus <A species is a group of interbreeding natural populations that is reproductively fully or partially isolated from other such other groups, with indications of further divergence and further development of reproductive isolation>. A shortcoming of this changed version of

BSC is that the “indications” part may be misread by the working taxonomist. Hart (2010) has emphasized the importance of population studies in species level taxonomy. He has recommended studying quantitatively metapopulation differences in continuous variables, repeated at intervals. Such a study may help in making out directions in which the metapopulations are diverging. Such population studies are likely to provide firmer ‘indications’, the use of which is suggested in the modified version of BSC.

The foregoing account makes it clear that in delimiting and describing a new species on basis of BSC some arbitrariness is involved. This situation has been pointed out by Simpson (1965) and several other author.

To make the extent of arbitrariness less in species level taxonomic practice quantitative and some other methods of species delimitation have been suggested.

1. Quantitative approach to species delimitation

One quantitative method for species delimitation has been suggested by Mayr (1969). As per this method, if we want to decide whether two similar populations belong to the same species, extent of allomorphy between them should be worked out by recording the ranges of variation in a morphological feature in the two populations, and then using the following formula to calculate the coefficient of difference.

$$CD = \frac{Mb - Ma}{Sda + Sdb}$$

where CD = Coefficient of difference

Ma and Mb = Mean of the variation in the populations a and b .

Sda and Sdb = Standard deviation of the variation ranges in the populations a and b .

If between the two ranges of variation there is 75% linear overlap, the value of CD will work out to be 1.28. In such a case, if the two ranges are plotted as frequency curves, the number of individuals in the nonoverlap will be about 90%. Hence if the value of CD is found to be 1.28 or a little more, the two populations may be regarded as two subspecies of the same species. But, if it works out to be more than 1.75, the two populations may be taken as two distinct species. Some role of arbitrariness in this method, involving a statistical procedure, is obvious. Moreover, in the second edition of their book (Mayr & Ashlock, 1991), Mayr and his coauthor say that this statistical treatment may be helpful only along with other considerations, such as degree of spatial isolation between the two populations, absence of clinal variation, discordant variation of different characters etc..

Tobias *et al.*, (2010), in their significant paper, have suggested the following two steps to reduce the level of arbitrariness, when attempting making out a new species:

(a) to determine quantitatively divergence in several phenotypic traits (i.e. a polythetic approach) among a sample of well established sympatric species, and next

(b) to study the corresponding traits quantitatively in two allopatric/parapatric populations, which are suspected to represent new species. If among the allopatric/parapatric populations, under study, the divergence is equal to or more than the threshold value of divergence in the sympatric species, they may be assigned the status of new species, and if not, they may be taken as subspecies.

Tobias *et al.*, (loc. cit.) have suggested use of Cohen's d statistics for working out the degree of divergence in the chosen traits in a population. However, this method is rather complex. Perhaps it would be simpler to work out the coefficient of differences (CD) using Mayr's formula (vide supra) for such chosen traits, both for the sympatric populations of related but distinct species, as well as for allopatric/parapatric populations, the species status of which is to be determined. If the mean (\bar{x}) of the CDs of the different chosen traits in the allopatric/parapatric populations comes close to / is equal to /exceeds the \bar{x} of the CDs of the corresponding traits in the sympatric populations, the former populations may be taken and described as new species.

2. Genetic approach to species delimitation and search of a speciation gene

Coleman (2008) has suggested a molecular approach for deciding whether two populations are different species. He says, "...analyses of one locus, the second Internal Transcribed Spacer (ITS2) of the nuclear ribosomal gene cistron has suggested a high degree of predictability across eukaryotes". It is further pointed out, "As ITS2 differences between potential mates increase, sexual compatibility and zygote productivity decrease". This author recommends that species, identified through differences in morphological features, may be confirmed by comparing ITS2 differences.

Hausdorf and Hennig (2010) have suggested a molecular method for species delimitation. Dominant and codominant markers in the genome have been taken as "fields of recombination"; hence individuals, agreeing in these markers may be taken as belonging to the same species. But, while pleading for objectivity of this approach, they acknowledge that "no fully objective solution" for species delimitation is yet available. These authors agree with the opinion of Sites and Marshall (2004) that eclectic or polythetic approach in species delimitation is needed, "because all methods for species delimitation will on occasion fail".

Several authors have recommended a multilocus approach in genetic delimitation of species, and not to base the delimitation on a single genetic marker (Legrand *et al.*, 2011; Gasiz *et al.*, 2011; Morris-Pocock *et al.*, 2011).

Search of a speciation gene has long been pursued (Nosil & Schluter, 2011). By a speciation gene is meant any gene contributing to evolution of reproductive isolation, as required by BSC. Nosil & Schluter (loc. cit.) have reviewed publications suggesting discovery of a speciation gene, and have inferred that almost none fulfils the criteria for such a gene. But Hosoi *et al.*, (2010) present an instance, which comes close to the speciation gene concept. They point out that right and left torsion in snails is influenced by a single locus or gene. They have studied the case of *Satsuma* snails. Two factors seem to contribute to speciation divergence among populations of this snail; one : that dextral and sinistral individuals find mating with the opposite chirality difficult, as a result sinistrals choose sinistrals for copulation and dextrals prefer dextrals; and two: the snake *Pareas iwasaki* prefers predation on dextrals, and, thus presence of this predator favours survival of sinistrals.

Biogeography of this snail reveals that speciation, favouring sinistrals, has been accelerated in areas, in which this snake predator occurs. In this instance the single gene, influencing the direction of coiling/torsion, may behave as a speciation gene.

But in a genetic approach to species delimitation one has to study the populations, in question, genetically, including Molecular Genetics, and the whole process will be too long, and with no assurance of being infallible.

3. Phylogenetic approach to species delimitation

The fast developing phylogenetic approach to make out species is based on the cladistic analysis of Hennig (1966). In this process an evolutionary or phylogenetic tree is made out on basis of synapomorphies (= derived shared characters). According to Hennig (loc. cit.) species result from divergence of two sister lineages. As per this author a species is terminated and breaks into two new species at the point of the split, at which point two new species come into being. , *i.e.* "A species begins at a branching point and ends at the next branching point in a cladogram" (as cited by Mayr & Ashlock, 1991).

But this view of Hennig (loc. cit.) is unacceptable, as it is well realized now that that reproductive isolation only gradually develops after a split (Fig. 1).

A more acceptable view has been stated by Kergoat *et al.*, (2011). They opine that a new species is made out at a certain branch length after a split in a phylogenetic tree. The required branch length may be decided by coming to a threshold value. Presumably the threshold value may be worked out by location of some well established species in the phylogenetic tree or dendrogram, which has been based on morphological or molecular data or both.

4. An integrative approach to species delimitation

A number of recent authors have pleaded in favour of an integrative approach in making out a species, *i.e.* use of both traditional morphological/phenotypic approach as well as molecular phylogeny (Kergoat *et al.*, 2011; Barrett & Freudenstein, 2011; Lopardo *et al.*, 2011; Kenfeck, 2011; Ahyong *et al.*, 2010; Winker, 2009).

In an integrative approach use of ecological, biogeographical, population level, and behavioural data has also been suggested (Benz & Robbins, 2011; Hawlitschek *et al.*, 2011; Barrett and Freudenstein, 2011; Hart, 2010).

SPECIATION THROUGH SEXUAL SELECTION

Wenninger and Averill (2006) have categorized different modes of sexual selection. A factor, obviously operative in sexual selection, is sexual communication to invite the opposite sex for mating. The sexual communication may be chemical, visual, or acoustic.

An illustrative account is in the work of Ryan *et al.*, (2010). They have studied mating calls in the tungara frogs (*Physalaemus pustulosus*). In this species males emit a sound signal as a mating call. The sound may be a simple whine or whine ornamented with some other sound (whine chucks). Through experiments, using recorded conspecific, heterospecific, predator produced, and human made sounds, the authors have inferred that females of the species show a strong preference for ornamented whines or whine chucks to simple whine, and that males are evolving towards production of ornamented whines as their mating calls.

Shaw *et al.*, (2011) point out that sexual communication within a species is uniform in nature and quality due to stabilizing effect of selection. Any deviation from the normal communication would fail to attract the opposite sex; hence it gets negatively selected. But then how does divergence in the nature of communication occur? The authors (Shaw *et al.*, loc. cit.) opine that some mutations may pleiotropically affect the mating signal and also the preference of response by the other sex, and thus divergence, which may lead to speciation, may result.

Kraaijeveld *et al.*, (2011) say that quite long it has been believed that sexual selection has been an important factor in speciation and origin of new species, thus producing species richness among different groups of animals. To test this hypothesis these authors have extensively reviewed the published relevant data, and have analyzed the data phylogenetically and statistically.

They have inferred:

(i) that there is a small but significantly positive support for the hypothesis.

(ii) that, when sexual selection affects also ecological adaptation, it not only leads to origin of new species, but also to “maintenance of (the) species”.

(iii) that the frequency of correlation between species origin and sexual selection varies in different taxa:

(a) among available data for birds in 38 studies 24 show positive correlation,

(b) among available data for insects in 6 studies in 4 the hypothesis was found supported,

(c) among 14 studies in mammals none was found supportive.

SYMPATRIC SPECIATION

It has been traditionally believed that speciation in most cases has occurred in allopatry. But some recent studies have shown that it occurs in sympatry too, and speciation in sympatry is more common than believed earlier. On this mode of speciation there is an earlier review (Verma, 2010). To that review an addition of researches by Palma-Silva *et al.*, (2011) may be made. These authors have studied four sympatric species of *Pitcairnia* (Bromeliaceae) adapted to different inselbergs (= isolated “outcrops” or ecological islands in the tropical forests of South America) through molecular profiles of nuclear and plastid DNA. They have noted some gene flow among the four species for an extended period. But introgression through the gene flow has been extremely slow, because of an extremely low frequency of migrations of the species among the inselbergs, and because of gradual development of pre- and post-zygotic barriers between populations in the different ecological islands. Thus the four sympatric species of *Pitcairnia* have been maintaining their identity.

Speciation through hybridization and polyploidy

Often speciation is initiated by hybridization; this may be referred to as “hybrid speciation”, by which is meant

speciation in which hybridization has played “a principal role” (Mallet, 2007). Speciation may also be initiated by polyploidy.

Closely related species are most likely to hybridize. A team of scientists at Massey University, New Zealand have developed a statistical procedure to identify hybridization events in the evolutionary history of a plant group (alpine buttercup species of *Renunculus*), assuming that hybridization generally occurs between species with minimum genetic differences between them (Joly *et al.*, 2009). Their results have well confirmed their assumption of hybrid speciation hypothesis.

Speciation through hybridization is more common among plants than among animals. At an average 10% animal and 25% plant species are known to have hybridized with at least one other species (Mallet, 2007) in their history. Similar estimates of successful hybridization in the evolutionary history of plants and animals have been given by Hendry (2009). Edwards *et al.*, (2011) have studied the polar bear (*Ursus maritimus*) and the brown bear (*U. arctos*) by preparing a palaeogeographic model, showing estimation of dynamics of the two bear species, taking into account past and present geographical ranges throughout 1,20,000 years and their maternal lineages. They have inferred multiple hybridization between the two species in overlapping parts of their ranges. The authors (Edwards *et al.*, loc. cit.) have opined that the interspecific hybridization has helped their survival in marginal areas during periods of changing environment.

In many cases of interspecific hybridization result in hybrids, which are not only viable and fertile, but also capable of invading new niches, and thus diversifying from their parentals. Hendry (2009) points out that often the hybrids not only survive and reproduce, they may also take to new evolutionary trajectories, different from their ancestors.

Certain ecological conditions seem to promote hybridization. Hoban *et al.*, (2009) have studied genetically (by sequencing and analyzing chloroplast and nuclear DNA) naturally occurring two forest trees, North American butternut (*Juglans cinerea*) and Japanese walnut (*J. ailatifolia*), and got evidence of hybridization between the two species in their history. They could identify 29 F1 and 22 advanced generation hybrids of the two tree species. Out of seven locations, in which the trees had been studied, in two they found extensive hybridization.

Bank *et al.*, (2011) have developed mathematical analysis models to show how reproductive isolation develops in hybrid speciation between the hybrids and other hybrids and other species, including the parentals to complete formation of a new species. This happens due to appearance of modifiers, which are parts of the genome resulting in mate discrimination against other hybrids and heterospecifics.

Small modifiers, consisting of only one or two alleles, may have considerable/large effect in this direction. Appearance of only one mutation may even result in even total reproductive isolation. This concept has been referred to by the authors as QLD (quasi-linkage disequilibrium).

From their analysis of some fragments of nuclear DNA and also mitochondrial DNA Brelsford *et al.*, (2011) have inferred that Audubon's warbler (*Dendroica auduboni*) has resulted from hybridization between myrtle warbler (*D. coronata*) and black-fronted warbler (*D. nigrifrons*). Further by presence of a deep cline between Audubon's warbler and black-fronted warbler, absence of complete reproductive isolation between the two species has been inferred.

Polyploidy has been another source of speciation, especially among plants. As Mayrose *et al.*, (2011) have pointed out, polyploidy (i.e. duplication of the whole genome) is widespread among plants. Recent polyploids or neopolyploids are those polyploids, which have been formed since the genus origin. Among plants recent polyploidy has resulted in speciation in 15% flowering plants and 31% ferns.

Soltis and Soltis (2009), in their review on hybridization and plant speciation, have said that recent developments in genomics have revealed that seemingly all flowering plant species have gone through at least one round of polyploidization and hybridization in their evolutionary history, and that hybridization has been an important driving force in producing angiosperm diversity. Homoploidy and alleloploidy have been significant sources of plant speciation. (homoploidy = hybrids with diploidy and are recombinational; alleloploidy = duplication of chromosomes in hybrids, as defined by Mallet, 2007).

Gorelick and Olson (2011) have asked : Is lack of diversity among cycads a result of a lack of polyploidy?

CONCLUDING REMARKS

Involvement of some arbitrariness in delimitation of species, whatever be the method of the delimitation (phenotypic/quantitative/genetic/phylogenetic) cannot be denied. But even then species level taxonomy is important, as it suits the human tendency of categorization, and helps recording, expression, communication, and estimation of biodiversity.

Perhaps the relation between species and speciation can be brought out using a rough analogy. Making out a species is like filling a bin of water from a flowing stream. When the water, thus collected, is fresh, it resembles the water in the stream in all its qualities or in all parameters, except that it is stagnant and not flowing. But, if it remains in the container, in long isolated from the stream, it may differ considerably from the stream water due to contamination, pollution, and/or organic growth.

It may be added here that, in order to make out and describe a new and stable species, which is less likely to suffer from synonymization or splitting, a species level taxonomist may take to an integrative approach, which has been described under the subsection 4 of the section "Speciation and delimiting species" of this review.

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