EVOLUTION AND THE SPECIES CONCEPT

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Keywords: Allopatric speciation, biological species concept, cohesion species concept, ecological species concept, evolutionary species concept, individual species concept, isolating mechanisms, monophyly, phylogenetic species concept, recognition species concept.

Contents

Summary

Since time immemorial, humankind has recognized and described species of animals and plants, yet, up to the present time, we still cannot agree on a universal definition or concept of species. The history of the species debate parallels the growth and development of evolutionary and pre-evolutionary biological thought, with substantial inputs from most of the great fathers of taxonomy and evolution (e.g., Linnaeus, Darwin, Wallace, Dobzhansky and Mayr). Darwin's theory of evolution, and the subsequent "Modern Synthesis" liberated the species from idealistic, teleological and typological notions of species as being created, purposeful entities with unique invariant

"essences". The Biological Species Concept (BSC), born out of the Modern Synthesis, was long regarded to be a panacea, being firmly based on the widely accepted notion of allopatric speciation. The architects of the BSC, Mayr and Dobzhansky, recognized several limitations, such as its restricted application to sexually reproducing organisms, borderline cases of incomplete speciation, and its arbitrariness in multidimensional situations (allopatric and allochronic populations). During the latter part of the twentieth century, the BSC has been subject to numerous refinements (Evolutionary, Cohesion and Ecological Species Concepts) and direct challenges (Recognition and Phylogenetic Species Concepts). Criticisms against the BSC, and its singular criterion, absence of interbreeding (or reproductive isolation), include concerns that isolating "mechanisms" originate only through the theoretically implausible process of reinforcement in hybrid zones, and the observation that reproductive isolation bears only a loose relationship with historical genealogical relationships. The application of cladistic methods to group individuals into "natural" monophyletic species is still controversial, but these Phylogenetic Species Concepts have enjoyed considerable attention in recent years. Recent debate concerns whether there exists a single kind of species (and species concept) or whether several kinds and species (and hence species concepts) apply in nature.

1. Introduction

The living world is comprised of more or less distinct entities, which we call species (Latin for "kinds"). The ease with which these entities can be identified in nature varies from simple to virtually impossible without sophisticated methods. Nobody would have any trouble distinguishing a lion from a tiger. On the other hand, even a rodent taxonomist would balk at having to distinguish two common species of African rodents, the vlei rat (*Otomys irroratus*) and the Angoni vlei rat (*Otomys angoniensis*), on external appearance (morphology) alone. The former species, the vlei rat, can be further sub-divided into five geographical entities that are chromosomally distinct from one another. Different taxonomists would differ considerably in how many, if any, of these chromosomal entities would qualify as species (see case study discussed later).

This then, is the essence of the species problem: the inability of biologists to arrive at a universal definition of the term "species" or a general method of discovering species. The species problem has been described as the Gordian knot of systematics. In part, the species problem results from the diversity of approaches and methods employed by systematists working in widely varying fields. A geneticist, a paleontologist and a physiologist could hardly be expected to define and recognize species in a uniform manner.

But why is it so important to untie this Gordian knot - to be able to objectively define and discover species? Although Charles Darwin himself considered species to be man-made, arbitrary constructs, most modern biologists agree that species are real entities that are the fundamental units of taxonomy, biodiversity and evolution. In a sense, species are the "currency" of biology, allowing biologists in all fields to communicate and compare their results meaningfully with each other. This also satisfies the human urge to ask ‘what kind of animal or plant is that?’

Are modern biologists any closer to solving the species problem than their illustrious predecessors such as Linnaeus (the father of biological taxonomy), Darwin (the father of the evolution), or Mayr (one of the fathers of the Modern Synthesis of evolutionary theory)? This article documents various alternative approaches and suggested "solutions" to the species problem, in an attempt to discover whether we are any closer to reaching a solution. It will be shown that the currently widely accepted paradigm, the Biological Species Concept, with its emphasis on the criterion of interbreeding, has come under heavy fire in recent years, particularly since the advent of the cladistic school of systematics.

From the outset, it is important to avoid confusing two distinct usages of the word species: the species-as-a-taxon (e.g., *Homo sapiens* or *Drosophila melanogaster*) and the species-as-a-category (i.e., a level in the taxonomic hierarchy, distinct from genus or family). In discussing the species problem, earlier writers clouded the debate by confusing these two usages. The criteria used to diagnose a particular species in nature (sorting) need not be the same as the criteria used to assign that particular entity to the category of species (ranking).

2. Historical Aspects

2.1 Pre-Darwin

Prior to the publication of Darwin's *Origin of Species* in 1859, the prevailing philosophical viewpoint of species was both ideological and teleological; each species was considered to be divinely created and unchanging, to be specially equipped by the Creator for a specific role in the Divine Plan (i.e., teleological), and to continue to breed true to form. The frequently observed sterility of hybrids between different species (e.g., the mule) was considered to be the means by which the Creator protected the integrity of each species. Species were expected to look different from one another and hence were described on morphological grounds. Variation in form (morphology) within a species was considered by many to represent aberrations of the original created "type" or "essence" of the species, giving rise to the so-called typological or essentialistic concept of species (Table 1).

Species concept	Key reference	Species definition
Typological-morphological	Linnaeus (1751) in Mayr (1982)	There are as many species as the infinite being created diverse forms in the beginning, which, following the laws of generation, produced as many others but always similar to them: Therefore there are as many species as we have different structures before us today.
Darwin's view	Darwin (1859)	I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms.
Nominalistic		Nature produces individuals and nothing more.
Biological	Mayr (1942)	Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups.

Evolutionary	Simpson (1961)	An evolutionary species is a lineage (an ancestral-descendant sequence of populations), evolving separately from others and with its own unitary evolutionary role and tendencies.
Individual	Ghiselin (1974)	Species may be defined as the most extensive units in the natural economy such that reproductive competition occurs among their parts.
Evolutionary (revised)	Wiley (1978) Figure 1-"successive species"	A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.
Phenetic	Sneath and Sokal (1973)	Loosely defined as a set of organisms that cluster at a certain distance from other such clusters.
Ecological	Van Valen (1976)	A lineage (or a closely related set of lineages) 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.
Recognition	Paterson (1985) Figure 2 – SMRS	We can, therefore, regard as a species that most inclusive population of individual of biparental organisms which share a common fertilization system.
Cohesion	Templeton (1989)	A species in the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability.
Phylogenetic	Cracraft (1983) Figure 3 – bird eggs	A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.

Table 1. Summary of species definitions and sources of major recognized species concepts.

This concept of species as divinely-created, constant, real entities probably had its origins in the Scholastic school of Aristotle and, as a species concept, can be traced at least as far back as the writings of John Ray (1627-1705) and Carolus Linnaeus (1707-78), at least, as revealed by the following quote from Linnaeus in 1751:

> "*There are as many species as the infinite being created diverse forms in the beginning, which, following the laws of generation, produced as many others but always similar to them: Therefore there are as many species as we have different structures before us today*".

Linnaeus's famous *Systema Naturae* (10^{th} edition) provided the framework for our modern system of biological classification and nomenclature. Each species of animal and plant is named according to Linnaeus' binomial system (Latinized genus and species, e.g., *Homo sapiens*). Linnaeus's advocacy of a typological and teleological concept of species was therefore widely accepted by many taxonomists and naturalists and it was not surprising that this viewpoint prevailed into the twentieth century (see *Historical Review of Systematic Biology and Nomenclature*).

In stressing that species were real and stable, Linnaeus played a vital role in the historical development of a modern scientific interpretation of species. In the pre-Linnaean period, prior to about 1750, most writers believed in the transmutation of species, the possibility that the seed of one species could occasionally produce an individual of another species. Species were regarded to be unstable and ephemeral. In arguing for the reality and stability of species, and thereby overturning unscientific perceptions about the nature of species, Linnaeus' ideas helped to set the stage, historically, for the advent of a species concept consistent with evolutionary theory.

2.2 Darwin's View

Ironically, Darwin's *Origin of Species* published in 1859 had very little to say about species or their origin and multiplication. The species problem remained unsolved. This was because, in sharp contrast to Linnaeus' view about species being real entities, Darwin regarded species to be highly subjective, man-made constructs:

> "*I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms*".

Although Darwin doubted the very existence of species as basic units of nature, his theory of evolution had profound implications for future interpretations of species. By stressing the importance of natural selection acting blindly on random individual variation, Darwin contributed towards replacing the prevailing teleological view of species with one that was empirically-based, and completely free of teleology (i.e., intended design or purpose). In particular, he regarded the sterility of hybrids to be an incidental bi-product of natural selection and not a device to preserve the "integrity" of species. Intraspecific variation was acknowledged to form an integral part of the process of natural selection and not merely imperfections of a hidden "type" or "essence" (see *The Darwinian View of Life*).

2.3 Post-Darwin (Modern Synthesis)

Spearheaded by the likes of Ronald A. Fisher, J. B. S. Haldane, Julian Huxley, Sewall Wright and later, Theodosius Dobzhansky, Ernst Mayr and George Gaylord Simpson, the so-called Modern Synthesis of evolution of the early part of the 20^{th} century challenged Darwin's idea that species were arbitrary and subjective mental constructs. Many biologists of the late nineteenth and early twentieth century had followed a view similar to that of Darwin, that "Nature produces individuals and nothing more" (the so-called Nominalistic Species Concept). On the other hand, many Mendelian geneticists opposed Darwin's theory and maintained that evolution proceeds by macromutations. In a view expressed in 1940, the geneticist, Goldschmidt, regarded gross macromutations as being capable of generating new species out of "hopeful monsters". The Modern Synthesis eventually reconciled Darwinism and genetics by showing that morphological variation could be derived from the principles of Mendelian genetics. The dispute was put to rest since Darwin's theory could now lie on the firm foundations of Mendel's laws of inheritance (see *History of Evolutionary Theory*).

Arising from the Modern Synthesis, Mayr, Dobzhansky and others argued that species were the units of evolution, and that these units were marked by the ability to interbreed among their members, but not with members of a separate species. This Biological Species Concept, as an important result of the Modern Synthesis, became the current paradigm throughout the latter half of the twentieth century, but has recently been challenged from several quarters, as shown below.

3. Current Paradigms and Challenges

3.1 Philosophical Perspectives: The Individual Species Concept

Much of the voluminous scientific debate on species has centered on philosophical discourse, to the point that one biologist lamented the fact that the debate on species has left the "solid ground of biology" and strayed into the "swampy mire of philosophy".

Nevertheless, philosophical viewpoints on the species have helped to clarify issues such as the reality (ontology) of the species. As first argued in the 1970s by Michael Ghiselin and David Hull, if species are arbitrary aggregations of individuals, they behave logically as "classes". On the other hand, if species are real evolutionary lineages they behave logically as "individuals". In fact, species do have many properties that qualify them as individuals and hence real entities in nature. They have a distinct beginning (speciation) and end (extinction). They have proper names (e.g., *Homo sapiens*). There cannot be instances of them. Thus, by analogy, the class of United States of America can have instances or examples (e.g., California), but the state of California is an individual concept; there are no examples of it. Like individuals, species do not have defining properties, and their constituent organisms can be regarded as parts and not members.

Many modern writers have pointed out that early species concepts, like the Nominalistic Species Concept and the Typological-Morphological Species Concept, treat species as classes. Authors of most currently debated species concepts agree that species should be regarded as individuals having ontological reality.

3.2 Current Paradigm: The Biological Species Concept

In 1942, Mayr formulated the Biological Species Concept as:

> "*Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such populations*".

Although Mayr later altered this basic definition slightly – by omitting the "actual or potentially" clause (in 1969), or adding an ecological clause relating to species occupying "a specific niche in nature" (in 1982) – the basic element remains: reproductive isolation. Interbreeding between species is prevented by isolating barriers or "mechanisms". The term "mechanism" should perhaps be avoided as it has teleological connotations that have been criticized by opponents of the Biological Species Concept (BSC). Since the process of reproductive isolation was critical to the process of speciation (termed allopatric speciation) advocated by Dobzhansky, Mayr, and their followers, it followed that the units produced by this process were real evolutionary units, and not arbitrary human constructs as argued by Darwin.

Although the BSC is defined in terms of reproductive isolation, it makes extensive use of morphological discontinuity and geographical criteria in the practical application to delimiting biological species in nature.

3.2.1 Isolating Barriers

Dobzhansky described two classes of isolating barriers: prezygotic and postzygotic. Prezygotic isolating mechanisms prevent the formation of hybrid zygotes, and four general types were recognized.

(a) Ecological or habitat isolation. The populations concerned occur in different habitats in the same general region. For example, the toad species, *Bufo fowleri and B. americanus* occur in different habitats throughout the same regions in Central and Eastern USA. They do not normally interbreed with the exception of a few populations in Michigan and Indiana where they occupy the same human-modified habitats and here produce fertile hybrids.
(b) Seasonal or temporal isolation. Mating or flowering times occur in different seasons. For example, the toad *Bufo fowleri* breeds later in the year than *B. americanus* (except where the two occur together in the same habitat)
(c) Sexual or ethological isolation. Mutual attraction between the sexes of different species is weak or absent, for example, in some frogs and crickets where females are attracted specifically to the croaks or calls of males of their own (but not other) species.
(d) Mechanical. Physical non-correspondence of the genitalia or the flower parts prevents copulation or the transfer of pollen.

Prezygotic barriers	Potential mates (although sympatric) do not meet	Temporal isolation (by season or time of day)
		Habitat isolation
	Potential mates meet but do not mate (etholgical, behavioural or sexual isolation)	
	Copulation occurs but no transfer of male gametes takes place (mechanical isolation)	
	Gamete transfer takes place, but egg is not fertilized (gametic incompatibility)	
Postzygotic barriers	Zygote dies (zygotic mortality soon after fertilization)	
	F_1 hybrid has reduced viability (hybrid inviability)	
	F_1 hybrid viable but had reduced fertility (hybrid sterility)	

	Reduced viability or fertility in F_2 or backcross generations (F_2 breakdown)	

Table 2. A classification of barriers to gene flow (“isolating mechanisms”). (After Futuyma 1998).

Postzygotic isolating mechanisms (see also Table 2) can involve hybrid inviability (growth and survival of F_1 hybrids impaired) or hybrid sterility (F_1 hybrids fail to produce functional gametes). Certain classes of chromosomal rearrangements, such as tandem fusions, may result in hybrids that, due to meiotic malsegregation, are sterile, partly sterile, or have reduced viability in the heterozygous state. For example, two populations of vlei rats, *Otomys irroratus* occupying the KwaZulu-Natal midlands of South Africa differ from one another in a tandem fusion chromosomal rearrangement (of chromosome pairs 7 and 12) which results in hybrids between the two populations having slower growth rates than their parents, as well as being virtually sterile (see *Speciation and Intraspecific Taxa*).

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Biographical Sketch

Peter John Taylor - Born 25th January 1963, a Zimbabwean citizen by birth, married with four young children, Peter Taylor obtained his B.Sc. from the University of Cape Town in 1983, with Zoology and Botany as majors. His B.Sc. (Honours), also from University of Cape Town, was obtained in 1984. His Ph.D., on "Infraspecific systematics of the yellow mongoose (*Cynictis penicillata*)", was obtained from the University of Natal Durban in 1990.

Peter Taylor was a volunteer/student at the Mammal Department of the Transvaal Museum and later Scientific Assistant to the late Prof. J. A. Meester, at the University of Natal. He took up his present post as Curator of Mammals at the Durban Natural Science Museum in July 1989. His research at the Museum is centered on the evolution, classification and conservation of small mammals including vlei rats, bats, shrews and mongooses.

Peter Taylor has published 48 scientific papers and 10 popular science articles since 1985 and presented scientific papers at six overseas conferences (in Britain, Rome, Israel, Brazil, Australia and France), as well as at several local conferences. His book on "The smaller mammals of KwaZulu-Natal" was published by University of Natal Press in 1998, and a full color popular field guide on "Bats of Southern Africa" was published in November 2000. He belongs to the Wildlife Society of Southern Africa, the Zoological Society of Southern Africa, the Natal Evolutionary Biology Society and the Southern African Museums Association (Natal Branch).

Peter Taylor founded the Durban Bat Interest Group (DBIG) in February 1994. The group currently numbers some 150 individuals, and was nominated for the "Conservationist of the Year" award by the KwaZulu-Natal Nature Conservation Service.