ROLE OF TAXONOMY

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INTRODUCTION

The talk will cover the development of different species concepts, their criteria and importance to biology in general and taxonomy in particular. Furthermore there will be a discussion of the role of taxonomy - in part as an independent discipline, in part as a service function for other fields of biology with emphasis on the consistency of taxonomy and the deposition of specimens.

SPECIES CONCEPTS

The concept of a species is important to biology in general and to taxonomy in particular. You assign a name to your object of study, but it is very important to be aware of the criteria for this assignment - as will be seen from the following, these criteria vary with the context of the discussion. The following discussion is in part adopted from Mayr (1942).

The typological species concept

Using the typological species concept is the traditional way humans distinguish species in their surroundings: You use largely external features to identify and distinguish species. Even if not explicit and defined as such, it is the species concept used of every day life - when parents tell their children about animals, when you go shopping in the market etc.

The introduction of the typological species concept in biology may be ascribed to Linnaeus (1758), who formalized the concept. Linnaeus gathered as many species as possible, furnished each with a description (albeit mostly a very short and in modern contexts inadequate description), fitting into a hierarchical system in his Systema Naturae.

A definition of this kind is convenient to taxonomists (and largely the only one available to palaeontologists!) - you identify your species with the set of characters observed. The main disadvantage is that this classic definition of a species - "a species is a group of individuals with same and similar morphological characters" - presents no possibility for delimiting a species from a subspecies, nor a species from a genus. Within the study of molluscs (and of any other group of organisms, off course) this leads to the perpetual battle of "lumpers" against "splitters". Some workers (e.g. Linnaeus (1758)) have been very conservative in their use of genera - one genus contains a large number of species - whereas others, in particular more recent workers (e.g. Marshall (1987, 1988)) tend to establish a new genus and even a new family for many new species. This may evidently reflect different access to material, but is normally a matter of different approaches to taxonomy. Neither approach can be claimed to be right or wrong, the difference is a direct consequence of a "fluffy" species concept.

The practical species concept

Darwin (1859) said "...whether a form should be ranked a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow". This practical species concept is convenient, but it suggests that a species is a subjective and largely arbitrary unit. Obviously by applying this definition, species do become subjective and arbitrary, but that ruins the scope of taxonomy. A science producing subjective and arbitrary results is of no use.

Having said that, it is important to note that the experience and knowledge of a researcher is crucial in establishing new species and in
interpreting taxonomy. Experience is a valuable and indispensable tool, but it should not be the only tool nor part of the actual definition.

The genetic species concept

Lotsy (1918) introduced the genetic species concept by stating that "a species is a group of genetically identical individuals" (in the translation and interpretation of Mayr (1942)). This is obviously merely an adaptation of the typological species concept to modern techniques. A species is characterized and identified by a unique and invariable set of characters. Whether these characters are morphological or "genetic" (i.e. a number of heritable traits) makes no difference in respect to the species concept.

Today it is generally accepted that apart from identical twins there are virtually no individuals among sexually reproducing species which are genetically identical, hence the genetic species concept seems redundant and of little sense. The main reason for dealing with it is that it is the de facto species concept of many modern studies of phylogeny by means of DNA (e.g. Diamond (1988)) or immunology (e.g. Sarich (1969)). It is usual to equate a species with a fixed pattern of characters, originating from just one or at best very few individuals, and to calculate the "phylogenetic distance" between species.

This implicit emphasis of old and past virtues is evidently connected to the cost of molecular studies - the total amount of data is restricted. Though DNA techniques and immunology are "high tech" and "fancy", their theoretical counterpart - the genetic species concept - presents no conceptual innovation.

The sterility species concept

There is a certain appeal in the point, that "all forms belong to one species [if they] can produce fertile offspring" (Mayr (1942)). This species concept - like the typological species concept - has certain archaic elements and complies with our intuitive understanding of a "species": Members of the same species may have offspring with each other, members of different species may not.

The advantage of the sterility species concept relative to the preceding is that it actually encompasses a definition - with this species concept it is at least theoretically possible to assess whether two individuals belong to the same species. For technical reasons the actual experiment - attempts of crossing individuals - may often (have to) be omitted, but that is beside the point.

The sterility species concept does present some problems. Complete sterility between two species recently evolved from the same ancestor will only occur in special cases. Most models of speciation (e.g. Wright (1931), Rouhani & Barton (1987)) invoke a reduced fitness of hybrids, but do not exclude the existence of fertile hybrids. An individual, which is a fertile hybrid, will thus, though having a reduced fitness, be a member of two species at the same time!

The biological species concept

Mayr (1940) introduced the biological species concept as: "A species consists of a group of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers. Or shorter: Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups".

This is essentially an elaboration and specification of the "sterility" species concept and similar comments apply. Even if the key issue - sterility of hybrids or lack of crossability - is the same, the biological species concept
Figure 1 illustrates the difference. A and B are recent species, 1 and 2 are extinct species, 1 is an ancestor to A, 2 is an ancestor to A and B. Figure 1a represents the true pattern of evolution of the species and is the ideal goal of a phylogenetic analysis (though only rarely attainable!). In numerical taxonomy you acknowledge that elucidating the true descent is hardly ever possible (the information on fossils is to scant) and you produce a classification of characters instead. This is illustrated in fig. 1b: A and 1 are closer related to each other than either is to 2 and 2 is closer related to B than it is to 1.

emphasizes temporal and spatial variation and has been widely applied in theoretical biology. As a theoretical concept, it seems almost ideally suited for phylogeny, sensu Hennig (1966).

The Quarrel

Which species concept should then be applied? It is evident that the species concepts above represent different approaches to science. The practical species concept tends to emphasize the student rather than the study - an approach which is not in current use and must have seemed somewhat archaic even at Darwin's time.

The typological and genetic species concepts are founded in purely descriptive sciences - the actual goal is to describe natural objects, not necessarily to understand their interactions or origins. They present beautiful examples of 18th and 19th century (European) perception of Nature as something extremely complicated but essentially static, well organized and ultimately understandable.

The sterility and biological species concepts are in accordance with "modern" (i.e. current) science, emphasizing the processes shaping Nature. In their fully elaborated form (see e.g. Mayr (1942)) they take - at least claim to take - matters such as evolution and population dynamics into account. They represent the view, that Nature is dynamic and always changing.

As all of the species concepts has its fervent advocates, there is ample reason why taxonomy as a discipline is inconsistent. Inconsistencies are founded in part on personal opinion, in part on different theoretical and philosophical backgrounds. One of the major quarrels is between "phylogenetics" (sensu Hennig (1966), = cladistics) and "phenetics" (= numerical taxonomy sensu Sneath & Sokal (1973)). Phylogenetics classifies evolution (or at least evolutionary events; claiming to be a "natural" system, a phylogenetic classification should reflect the descent, evolution, of the organisms), whereas numerical taxonomy classifies characters (all characters are equally important and the distance between two species is measured by the amount of similarity).
These conceptual differences lead to lengthy and at times rather theoretical debates and amendments to the systems (e.g. Ehrlich 1961, Mayr 1974), Hennig (1974), Wiley (1979), Haszprunar (1986)) with only minor impact on our perception of Nature. The key issue is that whatever system you prefer, any kind of taxonomy is and remains an elaborate character analysis. The result you achieve depends on the characters you investigate, your interpretation of them and the weight you put on each character.

CONSISTENCY OF TAXONOMY

There is no obvious "fair" solution to differences of opinion about the theoretical background of taxonomy - i.e. it is not possible to decide whether phylogenetics or phenetics is the best. It depends strictly on what you wish to achieve with taxonomy.

Some (even some taxonomists) consider taxonomy a tool or a service function to other disciplines. The purpose of taxonomy is to record and describe species and present these descriptions in a manner, enabling others to identify their object of study. In this conceptual frame museums become libraries of material that may be used for comparison and taxonomists become their custodians. It may be considered slightly acrimonious saying so, but somehow phenetics seems ideally suited for this perception of taxonomy: The goal is organizing characters (incidentally not necessarily just morphological characters - ecological and ethological characters may be equally suitable for classification) in a system. Taxonomy becomes a question about storing and retrieving information.

Taxonomy should definitely provide this "library" function. Few if any biological studies have any value, if it is not possible to identify the species studied without doubt. Though by many biologists (privately!) described as old fashioned and "stuffy", the "library" function of taxonomy is an indispensable tool for communication between scientists. It enables us to use the results of previous investigators and to communicate our own results in a manner so they may be used by others.

In the framework of phylogenetics, taxonomy has the possibility of offering more than just being a service to other fields of biology. Phylogenetics in its modern and expanded appearance (as advocated by a.o. Haszprunar (1986)) is a dynamic sparring partner for evolution - a phylogenetic classification of organisms becomes a summary of our best interpretation of the path of evolution.

The major flaw of taxonomy - whether in the context of "library" or phylogenetics - is the lack of consequence and agreement in many fields. The taxonomy in areas of biology, yielding objects popular among collectors (a.o. sea shells, butterflies and beetles) are particularly prone to be unnecessarily elaborate due to the "opinions" of collectors and researchers alike. These opinions are not unqualified, but represent personal opinions and biases they may lead to an inconsistent taxonomy of certain groups. This is due to the principle: If it is published, it is valid! Scientific journals subject articles to review, but many articles on taxonomy are published by amateurs and collectors in popular journals with only little review. It would be a major benefit to taxonomy - and thus to biology in general - if a procedure was established for approval of new species, before they were valid.

A similar problem existed previously for the naming of new minerals - Strunz (1969) lists app. five times as many synonyms as genuine species of minerals. This plethora of names was in part due to the lack of communication, leading to the same species being described several times, in part due to differences in opinion on the definition of a mineral species. To remedy this the International Mineralogical Association (IMA) formed a Commission on New Minerals and Mineral Names, which has to approve all descriptions of new minerals for them to be valid. According to Fleischer & Mandarino (1991) virtually all descriptions of new minerals
the past few years have been approved before publication.

A similar commission on new species in biology would evidently have to be much larger - preferably there should be many commissions, each with their field of responsibility. You may evidently agree or disagree on the recommendations and decisions of such a commission, but it would within a reasonable period of time give a consistent taxonomy of e.g. Mollusca and Bryozoa. The principles behind the taxonomy of Mollusca would be different from those behind Bryozoa, but the taxonomy of either group would be consistent.

THE DEPOSITION OF SPECIMENS

It has become common usage to deposit type specimens in museums or similar major public collections in accordance with the rules of the international code of zoological nomenclature (Ride et al. (1985), recommendations 72D, 72G and 74D). In general descriptions of new species also carry information on where specimens have been deposited and how they are indexed (Ride et al. (1985), recommendations 72C, 72E and 72F).

This practice is evidently of great service to taxonomy, making it comparatively easy to locate types and use them for comparison. The task of storing and protecting types "...held in trust for science....by persons responsible for their safe keeping" (Ride et al. (1985), p. 147) is a great responsibility. Though it ads greatly to the esteem of an institution to be responsible curators of type material, it also adds to the burden in respect of finances and staff as it is also the duty of such institutions to make the specimens accessible for study (Ride et al. (1985), recommendation 72G).

Similar strict rules or general practices for the deposition do not exist for specimens used for study in other fields of biology, which is surprising in view of the value of depositing specimens (types) demonstrated by taxonomy. The results of ecological studies and monitoring of populations and species diversity may have far reaching influence on subsequent studies and decisions on management of natural resources, which emphasizes the importance of being able to verify the identification of the material studied.

In spite of dedicated efforts, errors of identification can not be avoided, not even by consulting expert taxonomists. First of all "identifying" a species is an expression of an opinion, resulting from the comparison of a specimen and a description. Descriptions used for identification may be inaccurate or grossly abbreviated (particularly older, original descriptions - see e.g. Linnaeus (1758)) and all species do show some variation. When it comes to the point, there is no alternative to forming an opinion on whether the specimen in question complies with the description at hand. This opinion may at a later point because of new methods be questioned or even proven wrong without necessarily detracting from the qualifications of the original worker, leading to the fact that particularly closely related species may be mistaken for each other. If a selection of specimens from a given survey is stored in a museum, where it may be retrieved at a later date, almost any researcher has taken an insurance for the perpetual value of his work; if all specimens are discarded, the survey may later loose its value - not because it is wrong, but simply because doubt (whether justified or not) may be cast about the identification of the material (Hylleberg & Nateewathana, 1983).

REFERENCES


QUESTIONS AND ANSWERS

Jorgen Hylleberg: How do you personally define and use the species concept?
Answer: Which species concept I use, depends wholly of the context. If the purpose is to communicate which species, I have looked at, I evidently use a rather static species concept (i.e. a de facto typological species concept). The name is intended to enable the reader/observer to understand and recognize the organism mentioned. In the context of evolutionary biology, I use a dynamic species concept - effectively the biological species concept (sensu Mayr (1940)).

The choice of species concept (which is hardly ever explicit) depends on the context. Static species concepts (typological and genetic species concepts) are quite suitable for descriptive purposes, but for studies involving dynamic processes (ecology, evolution etc.) a dynamic species concept (i.e. the biological species concept) is required. For most practical purposes (e.g. studies of ecology) the inadequacies of the static species concepts may be amended by indicating the literature used for identification, supplemented with additional description if necessary and a deposition of specimens in a reference collection.

Jorgen Hylleberg: What are the rules for a published species description to be valid?
Answer: According to the International Code of Zoological Nomenclature (Ride et al. (1985), articles 7-9) the essential criteria for publication are: 
(1) it must be issued publicly for the purpose of providing a permanent scientific record; 
(2) it must be obtainable, when first issued, free of charge or by purchase, and 
(3) it must have been produced in an edition containing simultaneously obtainable copies by a method that assures numerous identical copies" (Ride et al. (1985), p. 13). There are no specific requirements for circulation, review or type of journal, but it is emphasized that "authors have a responsibility to ensure that new scientific names, nomenclatural acts, and information likely to affect nomenclature are made widely known. This responsibility is most easily dis-
charged by publication in appropriate scientific journals or well-known monographic series." (Ride et al. (1985), p. 13, recommendation 7A).

There is evidently a strong pressure for only publishing in "appropriate scientific journals", but a description is not necessarily invalid, if it is published in an "inappropriate scientific journal" and the term "appropriate" is certainly open to interpretation!

Some of the modes of publication which may explicitly render a description invalid include: handwritten documents, photocopies, acoustic recordings, distribution of description only to colleagues or students, presentation at a meeting and deposition of a document (e.g. a thesis) in a library.

Jorgen Hylleberg: Please comment on the sterility and biological species concepts, concerning fitness of offspring.
Answer: To the extent it is possible to produce viable, fertile hybrids, there is a problem with the sterility concept. According to the definition, the two original "species" as well as the hybrids are one "species", even if the fitness is reduced.

A slightly different observation applies to the biological species, where the key word is "interbreeding". Individuals which are crossable, but which do not produce offspring in Nature (even if physically capable to do so in captivity), belong to different biological species. If the conditions in Nature change and hybrids are formed, the boundary between the original biological species has disintegrated, even if offspring has a reduced fitness. Figure 1 is a hypothetical example of the dynamic nature of the biological species concept. The biological species A is split by a natural boundary into two new biological species 1 and 2 (these are evidently crossable - they may produce viable, fully fertile offspring - but in Nature they will not interbreed due to the boundary). Following the division, 1 and 2 are subjected to different evolutionary paths. If the natural boundary disappears and if evolution has not produced absolute sterility between 1 and 2, a new biological species, B, will be formed by individuals from the populations 1.3 and 2.2. Hybrids of these may have a
reduced fitness, but they will, as will their parents, belong to the same biological species, B.

From a taxonomic point of view, this is a mess! You have one species A, evolving into two new species, 1 and 2, which later merge into one, B, which is not significantly different from A. Though a mess, this is a possible natural process, and it is relevant in the contexts of ecology and evolution. The biological species concept should be seen as a theoretical entity, made as an attempt of describing Nature the way it is and reacts, not as yet another artificial creation. If an example as this is a mess, it is because Nature (at least potentially) is a mess! If describing this mess in a "reasonable and sound taxonomic manner" is difficult, it should be seen rather as a problem (which may be solved!) of taxonomy and taxonomic techniques, than as a nuisance.

For references to the questions/answer, see page 17.

**Jorgen Hyleberg:** Do you think calcite-aragonite ratios will have any application with tropical molluscs?

**Answer:** Particularly in bivalves from temperate areas, with calcite as well as aragonite it seems established that there is a correlation between the calcite-aragonite ratio and the mean locality temperature (Lowenstam (1954), Kennedy et al. (1969), Carter (1980)). The relationship presumably also holds for tropical species, though it is probably is less pronounced due to less variation in ambient temperatures.

A similar relationship between the calcite-aragonite ratio and the salinity has been proposed by Lowenstam (1954) but the impact may be more complicated, involving more factors. If the relationship is genuine, it may evidently be applied for tropical species as well.

Gastropods with calcite as well as aragonite are quite sparse. Boggild (1930) and Hedegaard (1990) mention several families living in the tropics, where calcite and aragonite occur in the same species (Neritidae, Neritopsidae, Patellidae, "Purpuridae" (=Thaididae, currently included in Muricidae), Trochidae), but in general calcite is rare in gastropods.

**Jorgen Hyleberg:** How many classes of shell structures do we have in mollusc shells? You gave examples from four major shell structures.

**Answer:** The answer will depend very much on the amount of variation you allow within each structure type, but my experience is that there are at least 20 different, easily discernible structures.

**Anuwat Nateewathana:** Is it possible to characterize, e.g., a subfamily by means of shell structures?

**Answer:** To a certain extent yes. Subfamilies are (as are families, genera etc.) normally characterized by some characters, which all show variation at that particular taxonomic level. Shell structures have not been used traditionally for this purpose and may consequently often show variation at another taxonomic level. At least in archaeogastropods, shell structure groups (groups of species, having the same shell structures) show variation at a level approximately equivalent to subfamily, though not necessarily coinciding with the traditional boundaries of subfamilies (Hedegaard, 1990).
REFERENCES


