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SHORT COMMUNICATION

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Taking more care in using different species concepts – an opinion

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Introduction

Some articles recently published in "Parasitology Research" concern the problem of using morphological or molecular traits to award defined populations of parasites the taxonomic level of being separate species. Differences in or (alternatively) the lack of distinguishing features in oocyst morphology (McAllister 2000) and different ultrastructural or serological data (Frenkel and Dubey 2000; Mehlhorn and Heydorn 2000) in *Toxoplasma* and some related genera have been considered to have a species-specific value. Also, similarities or differences observed in 18S rDNA sequences in dinoflagellates have been used as species-specific traits (Janson et al. 2000); and the magnitude of any difference in the internal transcribed spacer (ITS) of the ribosomal DNA sequence among related *Trichuris* groups (Oliveros et al. 2000) and in the *Contracaecum osculatum* complex (*Ascaridoidea*) has been used to award some taxa the status of species.

Discussion

Interestingly, some of the authors in their above cited publications are aware of the ambiguous situation (Zhu et al. 2000), since they mention the case of three obviously different schistosome species where the ITS sequences are definitely identical (Després et al. 1995) and thus do not reflect any species-level distinction. The controversy among Frenkel and Dubey (2000), McAllister (2000) and Mehlhorn and Heydorn (2000) in a certain sense reflects the regrettable lack of clearly defined species definitions.

In my opinion, one has first of all to be aware that evolution shows us that anagenesis and cladogenesis are not correlated (Huxley 1957). Anagenesis means the alteration of structures over time; and the results are continuing changes in traits and characters during evolution. Cladogenesis means the branching of lineages; and the result is the phylogenetic tree or the genealogical relations of taxa, which today is easily to be observed and quantified by DNA sequence alignments. Most important for the species definition is the problematic fact that in evolution a dense series of branching events linked with only slight anagenetic changes can occur. In other cases, only a few branchings occur during an evolutionary time interval of considerable structural alterations. The lack of correlation between anagenesis and cladogenesis explains why it is not possible to combine anagenetic changes in traits with the genealogy into any single taxonomic system. This simple fact gives rise to the different approaches taken in systematics (Peters 1998).

Taxonomists who prefer to use traits for the discrimination of different species (typologists) have their own system, which enables them to define the species in their preferred sense; and this has been proven in the past to be a useful working system. Taxonomists who prefer to use DNA sequence divergence for species discrimination (cladists) use other parameters for their system. They also define the species in their preferred sense; and this has also been proven to yield a useful working system. What has strictly to be avoided, however, is a combination of both parameters within a single system.

What is common to both the trait-oriented and the cladistic system is the fact that the unit defined as a species is artificially forced into the jacket of the thinking habits of the taxonomists themselves. The species unit reflects the inborn urge of the taxonomist to classify natural diversity into workable categories (Bachmann 1998). No underlying theoretical concept defines how far

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taxonomists can go in awarding a population the rank of species. In the case of the trait-oriented typological system, one can ask: has it to be an entire body plan, a simple colour, or a morphological trait that can only be seen with high-tech instruments; or can it be a single mutation or even a single molecule that an insect uses as a mating signal? In the case of cladistic taxonomy, one can ask: how many base exchanges between two homologous DNA sequences (or in other words: how many years after the branching of two divergent lines) are sufficient to justify the rank of species? It is evident that both the trait-oriented and the cladistic concept use man-made, subjective delimiters to discriminate between two species. This has little bearing on the practical work of taxonomists. In an epistemological sense, however, the question of whether two populations are different species or not cannot be judged in terms of true or false.

In great contrast, the biological species concept (Mayr 1942) considers the species as an entity in nature that really does exist as an objective unit, independent from subjective human classification principles. This species concept is purely empirical, because it is based on the observed criterion of presence or absence of interbreeding. The decision as to which populations have the rank of species is not made on the basis of their degree of difference. Instead, the biospecies concept defines the species by its isolating mechanisms and not by traits or characters. Modern studies indicate that, in some cases, just a few genes may control effective reproductive isolation and hence give rise to a rapid radiation of many new species, whereas in other cases even a rather profound genetic restructuring of populations may not result in reproductive isolation, but instead leads to a highly polymorphic group of individuals all belonging to the same species. A comparison of the multitude of east African cichlid fish species with the polymorphic Trinidadian guppies, which all belong to the same species, provides the best example (Morell 1999a). In extreme cases, two populations that do not differ at all in characters recognised by the human senses are "good" species according to the biological species concept.

The biospecies concept has no problem in answering the "why" of speciation (Mayr 2000): why are there species? Why do we not find in nature simply an unbroken continuum of similar or more widely diverging individuals? The species as the unit of reproductive isolation protects its well balanced, well adapted gene pool from genetic recombination, i.e. from the exchange of its genes with genes from the gene pool of another species. The biospecies is a system which prevents any breakdown of harmonious genotypes, since the production of hybrid offspring between species yields hybrids of reduced fertility and vitality. In a Darwinistic sense, it would be a reduction in fitness for heterospecific parents if they did not hesitate to produce interspecific hybrids. Therefore, there exists a highly selective pressure, called "reinforcement", for the acquisition of isolating mechanisms, that favour breeding with conspecific individuals and inhibit mating with non-conspecific individuals (Wu et al. 1995; Nei and Zhang 1998; Ting et al. 1998; Korol et al. 2000). The genes responsible for the production of the isolating mechanisms, called "speciation genes", constitute a class of genes of increasing importance for the understanding of the biospecies concept.

For most researchers in the past, allopatric isolation was considered to be a *sine qua non* requirement for speciation to occur, at least in animals, because the accumulation of a large number of mutations with little effect was considered to be a prerequisite for the separate evolution of new species. This seemed to contradict the possibility that new species originated as a sympatric branching event, since only the coordinated function of several new characters seemed to warrant the emergence of a new species in competition with any other in the same geographic region. But today, since researchers are beginning to uncover the specific mutations that separate species, their first findings show the opposite pattern: mutations involving only a few genes, but having large phenotypic effects on body shape and function, have been discovered (Morell 1999b). This opens the way to adaptive speciation events in sympatry in different ecological niches, despite the fact that the individuals of emerging new different species meet each other daily in the same geographic region (Korol et al. 2000).

In particular, parasitic organisms that differ in host-choice genes are ideal biological models for sympatric speciation (de Meeus et al. 1998). Sympatric speciation is much more likely in parasitic than in free-living organisms. Therefore, parasites should be the preferred biological objects for studying ecological specialization and speciation. Continuous mutual aggression resulting from the host–parasite relationship has largely shaped their life traits and their evolutionary pathways.

Considering the controversial discussion between Frenkel and Dubey (2000) and Mehlhorn and Heydorn (2000), the point cannot be too strongly emphasized that reproductive isolation is one of the best species-criteria, in the sense of the biological species concept, since heteroxeny warrants reproductive isolation.

However, as seen for the typological and cladistic species concept, the biological species concept also has major disadvantages. The most profound argument against the biological species concept lies in the fact that it is not applicable to populations that are isolated by geographic barriers (allopatries). Allopatry is an isolation mechanism defined by exclusively external separation barriers. Depending on the organism, these can be oceans or highways. The barriers, however, must be geographic, i.e. they are not properties of the organisms themselves. Allopatric distribution is not caused by any trait or character manifested in the organisms. For example, if populations colonize new ecological niches (or, in the case of parasites, new hosts), this is not an allopatry, but a prezygotic separation based on the traits of the organisms themselves.

When populations are not in putative reproductive contact with each other, there is no selective pressure for the development of isolating mechanisms. Instead, among allopatric taxa, pre- and post-zygotic isolation mechanisms arise only slowly, by random genetic events (Coyne and Orr 1999).

It is a serious limitation for the application of the biological species concept that the criterion of interbreeding cannot be applied to populations with allopatric distribution. Since this includes the vast majority of all existing diversely structured organisms worldwide, the biological species concept is not a workable concept for taxonomists who want to classify the multitude of existing biodiversity. It has also been argued that the biological species is basically not a fundamental unit of evolution, but rather a by-product of evolution (Peters 1998). In its theoretical concept, the reproductive isolation of a species is simply the result of selection against unsuccessful interbreeding, an invention of nature to avoid deleterious hybridization. This becomes clearer when one realizes that nature has created in parallel a second, independent mechanism besides the biospecies concept to protect a gene pool from deleterious recombination with other genotypes. This is uniparental reproduction. Obviously, the biological species concept is not applicable to parthenogenetic and asexually reproducing organisms, because in the theory of the biospecies concept, the question cannot be substantiated as to whether parthenogenetic organisms belong to different species or not. In a certain sense, parthenogenesis and asexual reproduction are an invention of nature, separate from species. Because uniparentally reproducing organisms maintain their genotype from generation to generation by not interbreeding with other organisms, they do not need any isolating mechanisms to protect the integrity and harmony of their genotype.

Conclusion

A species concept as a generally accepted unit of biodiversity does not exist. The confrontation of different schools sometimes takes on the character of a religious war. It is one of the most grotesque situations in biology that one and a half centuries after the publication of "The Origin of Species" by Darwin, there is still no general definition on that unit, whose origin the theory of evolution wants to explain (Martin and Salamini 2000).

Different systematists define "species" within the framework of very different concepts. The typological recognition of species on the basis of traits works adequately in practice, provided it is not scrutinized with intensive scientific rigour. The biological species concept does not sufficiently work in practice. My main thesis here is that one approach has to be avoided: the ambiguous mixing of different species concepts with equal weight at the same time. Using different criteria in definitions leads to uninformative concepts, because one can never know which criterion was used in a particular case. For example, delimiting species both by morphology and by reproductive isolation at the same time creates problems and will lead to conflict (Meier and Willmann 2000).

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