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BRIEF COMMUNICATION

Conventional and fundamental problems in the delimitation of genera from a phylogenetic point of view

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INTRODUCTION

What will be considered as problems in the delimitation of genera and what as their solutions depends upon one's views. The same holds for qualifying a particular problem as conventional or fundamental. Thus, choices have to be made. If a scientific status is claimed for systematics, theory should be involved since one cannot speak of science if explanatory theories are lacking. I opt, for the time being, for evolutionary theory as the most relevant theory for systematics, and, in my opinion, the phylogenetic school (Hennig, 1966; Wiley, 1981) offers the best evolutionary interpretation of classifications. Of course, other views are possible, but I would like to remind those who are perhaps irritated by my choice for these 'fashionable' and disturbing views that they are by no means new. In his book *Systematics and the Origin of Species* (first printed in 1942) Mayr wrote:

> "The theory of evolution solved the puzzle of the high degree of perfection of the natural system in a manner that was as simple as it was satisfactory: The organisms of a 'natural' systematic category agree with one another in so many characteristics because they are descendants of one common ancestor! The natural system became a 'phylogenetic' system." (Mayr, 1964: 276),
> "a phylogenetic system has two advantages: first, it is the only system that has a sound theoretical basis (something the natural philosophers of the early nineteenth century looked for in vain) . . ." (Mayr, 1964: 276).

Unfortunately, Mayr wavered between morphological gaps and phylogenetic relations and thus he made 'evolutionary systematics', internally inconsistent.

THE DEFINITION OF GENERA

Before discussing problems of their delimitation we need to know what genera are supposed to be according to phylogenetics. What is the definition of the class of all genera? What properties do all genera share? Pheneticists consider taxa as piles of similar organisms. Species are piles of first order, genera of second order and so on. But in phylogenetics taxon-concepts are employed which allow an evolutionary interpretation. The genus-category is defined in terms of the following criteria:

(1) *Genera do not overlap* (a species never belongs to more than one genus) and *genera are exhaustive* (each species belongs to a genus). These criteria have been used at least since Linneaus. The next two criteria are more specific for phylogenetic systematics:

(2) *Genera are monophyletic groups, embracing one or more species.* I will give a very condensed and simplified explanation of this criterion. Species are supposed to be lineages which, at each time-slice, consist of interbreeding organisms and which have continuity through time as the result of reproduction. A lineage (A) splits up if at a particular time-scale no interbreeding takes place between two parts (B and C) of the (now ancestral) lineage A. The relationships between the ancestor-species A and the two sister-species B and C are the demanded phylogenetic relations. A monophyletic group is an ancestor-species with *all* its descendant-species (in this case A + B, C).

Organisms of a lineage can acquire new properties (so-called evolutionary novelties) via mutations which survive selection and spread, in time, over all organisms of the lineage. Such a novelty is inherited by the (organisms of the) daughter-species and becomes an apomorphy for the monophyletic group A + B, C. Shared apomorphies are the indicators of phylogenetic relations.

(3) *Genera are the first supra-specific monophyletic groups of the phylogenetic tree receiving a rank and a name.* Suppose sister-species B and C (descendants of ancestor-species A) split themselves into species D, E and F, G, respectively; now there are monophyletic groups at two levels: group A + B, C, D, E, F, G at one level, and groups B + D, E and C + F, G at a lower (younger) level, all with their own apomorphies. According to phylogeneticists it is not obligatory to give the very first monophyletic group above the species-level the rank of genus and a name. One can do so, but one can also take one of the next monophyletic groups (including the younger ones), leaving the younger monophyletic groups unranked and unnamed. This criterion apparently contains an arbitrary element.

Finally, a remark about the question whether individual genera exist objectively, independent from human minds. They only do in as far as *all* monophyletic groups are supposed to exist in reality. Usually species are considered to be real entities which can split. Monophyletic groups are the passive products of species-splitting; historical groups with a more abstract reality. In this respect, genera do not differ from (monophyletic) higher taxa.

THE DISTINCTION BETWEEN CONVENTIONAL AND FUNDAMENTAL PROBLEMS

For a better understanding of the problems in the delimitation of genera, one should look at their source. A distinction between conventional and fundamental problems then becomes important.

(a) Fundamental problems are associated with theoretical considerations (accepted hypotheses about biological reality). The solution to such a problem can be true or false depending on its consistency with the supported theory (hypothesized reality). Suppose we ask: which of the higher taxa now distinguished are monophyletic? The truth of any answer obviously depends on biological reality.

(b) Conventional problems have to do with man-made rules. In systematics such rules are meant to promote the utility of classifications. The solution to such a problem cannot be true or false, but it does or does not obey the rules, and thus will affect the usefulness of ensuing classifications. Often, various solutions are possible which are neutral with regard to the (hypothesized) state of affairs in reality. One might say that conventional problems are arbitrary from Nature's point of view. This does not mean that these problems are unimportant. Since classifications have to serve many purposes it is very important to pay attention to stability and nomenclature, but conventions are not allowed to over-rule hypotheses about the state of affairs in reality. If one does not

care about consistency with the supported theory the scientific status of the whole undertaking is at stake.

Let us finally consider some common problems. Which are, from the phylogenetic point of view, conventional and which are fundamental?

(1) All problems concerning the monophyly of a genus are fundamental problems overruling utility considerations. If (after reconstruction of its phylogeny) a genus under revision appears to consist of a monophyletic group and some residual species, those species have to be removed. If it appears to contain only part of a monophyletic group, more groups should be examined.

(2) The relative arbitrariness of the choice of the level in the phylogenetic tree, which is to achieve the genus rank, leaves room for practical considerations. This makes several problems conventional. For practical reasons the genus rank of a too voluminous (monophyletic) group can be given to the smaller monophyletic groups it contains. Shifts in opposite direction are allowed as well. Such practical moves are neutral with regard to theory. Other practical considerations to shift the genus rank concern the relative ease to key out, to recognize and to memorize groups. A single phylogenetic tree allows several classifications. (See Wiley's *Conventions*(!) for translating phylogenies into classifications; Wiley, 1981: Chapter 6).

(3) Problems concerning the number and type of characters needed to identify a monophyletic genus are fundamental problems. According to phylogenetics, apomorphic characters are the indicators (not the defining properties) for monophyly of a group. At least one apomorphy must be found for each monophyletic group. Any stable inheritable property can represent an apomorphy of a particular group. The properties of flowers or seeds are not *a priori* more important than the properties of leaves or wood. If those properties seem to conflict (seem to indicate incompatible phylogenetic relations) it is homoplasy that spoils the picture.

(4) All nomenclatural problems are of the conventional kind. All laws and rules of the Code are man-made rules developed in order to guarantee the reference of taxonomic names to identical natural entities. Though arbitrary, from the point of view of Nature, nomenclature is very important for scientific research. Without a reliable reference of taxon names many disciplines of biology would become chaotic. Nomenclature should not be an end in itself. It only serves to make biological classifications useful and is not allowed to lead to inconsistencies with the accepted theory.

There is a tendency to underestimate the importance of systematics as a scientific discipline. Systematics is not just pure description; explanatory theories are involved. Biology is unfortunate, compared to chemistry for instance, because it has to deal with an enormous diversity and sometimes it is impossible to move beyond the stage of a first global inventarization. In such cases it is only possible to delimitate prescientific taxa and to describe the unexplained phenomena. As explained above, however, systematics does not stop there. To improve their image it might help if systematists became explicit about the theoretical and practical criteria they use to delimitate their taxa.

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