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The Hierarchy and Combinatorial Space of Characters in Evolutionary Systematics**

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ABSTRACT

The Linnaean hierarchy is discussed as the taxonomic model for the evolutionary differentiation of the earth's biota. Careful examination of this model allows us to understand a number of ideas relating to evolutionary theory. The arguments about species constancy *vs* species variability, natural species *vs* 'artificial' higher taxa, the connection *vs* disconnection of microevolution and macroevolution are meaningless. Two kinds of phylogeny are considered. The first reflects the appearance of new *characters* in the course of evolution, and their sequence provides a basis for the nesting hierarchy of groups. The second reflects the appearance of new *character states* and provides a basis for the diversity of taxa that may exist at each hierarchical level. The method of character ranking and the improvement of a tentative taxonomic hierarchy with the help of *a posteriori* weighting of differences are also discussed.

Keywords:

characters, hierarchy, phylogeny, ranks, system of organisms, taxa

Васильева Л.Н., Стефенсон С.Л. Иерархия и комбинаторика признаков в эволюционной систематике

В статье обсуждается "иерархия Линнея" в качестве таксономической модели эволюционной дифференциации земной биоты. Данная модель позволяет объяснить ряд идей, связанных с теорией эволюции, и показывает бесплодность споров о постоянстве или изменчивости видов, о единстве или разобщенности микроэволюции и макроэволюции, а также исключает противопоставление естественных видов "искусственным" высшим таксонам. Рассматриваются различные аспекты филогении в применении к появлению новых признаков в эволюции, что обеспечивает иерархию групп, и к смене состояний признаков, что увеличивает разнообразие таксонов одного уровня. Обсуждается возможность ранжирования признаков и коррекции таксономической иерархии, построенной на основании предварительного распределения общих признаков по уровням, с помощью апостериорного взвешивания отличий и построения комбинативных прогностических таблиц.

Ключевые слова:

иерархия, признаки, ранги, система организмов, таксоны, филогения

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THE HIERARCHICAL MODEL OF EVOLUTION

One of the commemorative books devoted to the celebration of the Linnaean tercentenary is titled "A Passion for Systems. Linnaeus and the Dream of Order in Nature" (Schmitz & Uddenberg 2007). The title of the book is rather ironic, since many modern taxonomists denounce the great systematist for imposing an artificial system on nature. Linnaeus himself acknowledged "that he had sacrificed natural principles to some extent in order to devise a useful sorting principle" (http://go.hrw.com/resources/go_sc/bpe/HM9PE340), but he believed that such a state of things is temporal, and "artificial classes are substitutes for natural ones, until the discovery is made of all the natural classes" (*Philosophia Botanica* § 160, Freer 2003).

Biologists could ask themselves a question about how the *discovery* of natural classes is possible, but instead they often have transferred their views of the artificial and tem-

poral aspects of the Linnaean system to the fundamental idea of hierarchical structure in biological diversity. As a result, the 'Linnaean Hierarchy' has begun to be considered as inconsistent with the real natural order, an evolutionary world view and 'the principle of descent' (De Queiroz 1997). An earlier book with the abusive title "The Poverty of the Linnaean Hierarchy" (Ereshefsky 2001) had a subtitle indicating an intention to carry out 'a philosophical study of biological taxonomy'; however, this effort failed since both the Linnaean contribution to the classification of living organisms and its deep connection with a philosophy of taxonomy were misunderstood.

The entire Linnaean hierarchy of categorical ranks is believed to have "dubious theoretical underpinnings" (Ereshefsky 2001: ix), and serious considerations are supposed to be given to "a *rankless* system based on phylogenetic taxonomy" (Hibbett & Donoghue 1998: 347, *italics added*). The latter is a rather careless requirement, since the *system* of

living organisms *cannot* be 'rankless'. The notion of a 'rankless' system seems to be the consequence of a world view referred to as the 'great chain of being'. It held a central place in Western thought for centuries and its proponents viewed the organic world as ordered in a *linear sequence* (Nee 2005). Such a sequence does not entail the appearance of ranks, but modern evolutionary views suggest a hierarchical development of the biota. "When we depict evolutionary relationships in the form of a tree, we acknowledge that *genealogical relationships are hierarchical by nature*" (Spatafora & Blackwell 1994: 233, italics added).

However, it should be emphasized that the two world views do not necessarily exclude one another. Living or extinct *beings* do comprise a sequence, while *relationships* among organisms might be hierarchical. It is currently known that the original gene pool that once existed on the Earth split into smaller pools, and these constitute the groups now recognized as Bacteria, Archaea and Eucarya (Woese 2000). This event might be illustrated as three cones originating from a single point of common descent (Vasilyeva & Stephenson 2010: Fig. 1). The expansion of these cones is a reflection of the increase in the numbers of living beings within them through time. Each 'pool' or domain has evolved in its own way, limited by the innate potential of the genes present, whereas the differences among them have persisted from their very appearance to the present day. These differences are the oldest fundamental ones that can be recognized for living organisms.

Later, the domain Eucarya gave rise to a number of kingdoms (Leontjev & Akulov 2002) and their differences – once again – remained the same during the further differentiation of the Eucarya into even smaller groups. While almost all animal phyla were established during the 'Cambrian explosion' (Marshall 2006), the appearance of new groups during the 'Ordovician radiation' was manifested at lower taxonomic levels (Droser & Finnegan 2003). As a result, the organic world represents a *nested hierarchy* of groups, and the Linnaean hierarchy conveys both the nesting of small groups within the larger ones and the distribution of characters among levels in accordance with their appearance in time. In other words, the 'Linnaean hierarchy' could be considered as a *taxonomic model of hierarchical evolution*. The successive appearance of novelties marks certain *steps in evolution* that are conveyed by the 'ranks' in the system of organisms: "Ranks represent fundamentally different levels of reality, not convenience" (Atran 1998: 549).

When systematists attempt to *rank differences* (special kinds of relationships) among groups of organisms, they make their greatest contribution to the historical understanding of the organic world. As such, the calls for a 'rankless system' depreciate the work of systematists and the value of biological systematics as the most fundamental field in biology. It is relevant here to recall the arguments from classification in favor of evolution as they were discussed by Spencer (1868). These are simple and claim that "organisms fall into groups within groups; and this is the arrangement which we see results from evolution" (l.c.: 471). Interestingly, a linear arrangement of organic beings is described as one of the early ideas put forth by a certain

'school' of naturalists (who strongly remind one of some modern phylogeneticists): "The watchword of their school was '*Natura non facit saltum*'. They called their system *la chaîne des êtres*" (l.c.: 299, italics in the original). They "persisted in thrusting organic forms into a quite *unnatural order*" (l.c.: 300, italics added), but in successively later attempts "a gradual abandonment of a linear arrangement for an arrangement in divergent groups and re-divergent sub-groups" (l.c.: 295) was observed. Thereby, "the classifications of botanists and zoologists have become more and more natural" (l.c.: 304).

The evolutionary differentiation of the organic world reminds one of the development of an organism from an egg. Although the ontogeny of an individual is not considered evolution and individual organisms are not supposed to evolve (Futuyma 1998), there are contradictory claims about 'evolution of the organism' (Rose & Mueller 2005). However much these terms might be uncertain, the parallels between the developments of the organic world and an organism are evident, and this corresponds to the views held by some early philosophers that "world and organism are one in kind" (Oken 1808). The very idea of a phylogenetic *tree* for all organisms implies a *super-organism*, and Spencer (1868: 366), once again, observed the parallelism between an embryo and "the *embryological tree*, expressing the developmental *relations of organisms*".

The *hierarchical model of evolution* – as represented in the *system of organisms* – could be used to explain many of the arguments that have arisen related to the theory of evolution. For example, it offers an explanation as to why the idea of 'scala naturae' as a linear development from lower forms to higher ones is unfortunate. Von Baer rejected this idea as it was applied to embryogenesis, whereas Cuvier doubted its relevance to the whole of Nature long ago (Kanaev 1963: 242). A man does not tread all other organisms underfoot, as is the case at the top of Aristotle's 'scala naturae' or famous genealogical tree, as depicted by Haeckel (1874). Similar to any other organism, a man is enclosed *within* a many-layered 'cocoon' of differentiated groups (family *Hominidae*, order *Primates*, class *Mammalia*, etc.)

Every hierarchical level in the model under consideration is marked by its own characters, which then represent so-called *hierarchical types* (Vasilyeva 2003). In this context, the famous public debate between Geoffroy Saint-Hilaire and Cuvier can be elucidated. There have been different interpretations of that classic confrontation, but "French contemporaries were more likely to interpret the debate as a contest between one plan of nature and four" (Appel 1987: 6). Geoffroy believed all animals to share the same plan of organization, whereas Cuvier postulated four basic plans of organization and insisted that there were no transitions between plans. Although accounts of the debate usually declare Cuvier the victor, it was admitted that both contestants had supposedly taken "extreme positions, and it was left for the next generation of naturalists to reconcile them" (l.c.: 144). However, these 'extreme positions' were simply located at different hierarchical levels. Geoffroy Saint-Hilaire could not prove his point of view (it was impossible to make a quadruped similar to a cuttlefish merely by bending it over backwards), but he looked at animals from the 'level

of kingdoms' where *all* animals possess a *single plan (type) of organization* or a certain set of features which differentiate them from other kingdoms. Cuvier's attention was directed not only at characters of another hierarchical level where the animal kingdom is divided into several subgroups but also to partial states of those characters (Cuvier's '*embranchements*' or 'types').

The debates between transformists (Lamarck 1809, Geoffroy Saint-Hilaire 1830) and systematists (Linnaeus 1751, Cuvier 1825) on the variability or constancy of species were also all for naught. However, in these debates, attention was not focused upon different hierarchical levels; instead, the rivals turned to a consideration of different aspects of species, namely to what have been referred to as *extension* and *intension*, the two terms designating the inner *content* and the *differences* of a species from other species, respectively (cf Vasilyeva & Stephenson 2008). Strangely enough, these aspects that characterize a species *simultaneously* were counter-opposed to each other as underlying different *views* of species, and the one-sided view from the perspective of *extension* (content) was always acknowledged as more fruitful and 'natural'. The title of the paper "From logical universals to historical individuals" by Sloan (1987) exemplifies the old debate in which the 'logical universals' of Aristotle and Linnaeus are seen as opposed to Buffon's 'historical individuals'. However, judging from the hierarchical model of evolution, all groups, if they do not become extinct, are always changeable inside (extensionally), but systematists are engaged in differences among them (in intensions) which persist from their very appearance. Moreover, precisely intensions, being also 'universals' or 'essences' (see below), provide the individuality of taxonomic groups through evolutionary changes and keep the increasing inner diversity in a unity: "species arise (in geological time) with their differences established at the start" and "play the same role in an evolutionary trend that individual organisms" (Gould 1982: 139–140).

Beyond the hierarchical model of evolution, transformism has been understood to suggest the idea of species transformation '*into each other*'. That idea was taken seriously by philosophers of biology and even used as proof of the imaginary impossibility of constructing a natural system of organisms: "The only basis for a natural classification is evolutionary theory, but according to evolutionary theory, species developed gradually, *changing one into another*. If species evolved so gradually, they cannot be delimited by means of a single property or set of properties. If species can't be so delineated, then... species can't be real. If species aren't real, then 'species' has no reference and classification is completely arbitrary" (Hull 1965: 320, italics added).

However, one species *never transforms into another*, since "the problem of the multiplication of species... is to explain how a natural population is *divided* into several that are reproductively isolated" (Mayr 1970: 250, italic added). Each new species *originally* separated from all other species and continues to evolve in this isolation. Such a view of speciation allows us to admit the existence of *natural higher taxa*, since the inner evolution of an isolated group can take place only through its differentiation into subgroups. Therefore,

such natural groups as species cannot be transformed into 'unnatural' genera and families. The dominant idea of species transformation '*into each other*' did not entail natural genera and families for a long time. The appearance of higher taxa was impossible to insert in the continuous 'species flow'. As such, higher taxa were considered to be artificially made up of the scraps of 'transformation ribbon'. Even species themselves appeared to be unnatural (cf above – Hull 1965: 320), and only the extinction of intermediate forms has supposedly provided the definite boundaries between groups. In this connection, the notion of 'gaps' was formulated, and the gaps between genera and families were postulated to be greater than any found between species (Ashlock 1979: 446). Even very recently, the 'size' and 'nature' of gaps were discussed (Stevens 2006: 118), although these are of no use to the classification of living beings. The hierarchical model of evolution represents all groups (extinct and extant) as 'fans of cones' at each level. The boundaries among those groups are always the same, and the 'gaps' between species, genera and families might be lacking, but this does not influence the rank of groups. Only the *sequence* of character appearance matters in the problem of ranking.

The tradition of an absolute separation of microevolution and macroevolution was stated to have been a contentious issue within evolutionary theory from the very beginning (Gould 1982: 141), but the hierarchical model of evolution does not separate the two processes. Higher and lower taxa appear *simultaneously* during the same process of differentiation. The inner *disintegration* of species into isolated populations leads to a hierarchical pattern in 'geological scaling' (Gould 1982). This deprives species of their privilege status as the "largest cohesive population" (Mayr 1987: 165), since internal splitting of species prevails over internal (extensional) integration in evolution, whereas taxa of all levels are equally cohesive (integrated) in their intensions. The hierarchical model of evolution answers the expectations that "when a proper *hierarchical theory* is fully elaborated, it will not be entirely Darwinian in the strict sense of reduction of natural selection", yet "it will embody the essence of the Darwinian argument in a more general form" (Gould 1982: 141, italics added).

TWO PHYLOGENIES

Darwin (1958: 73, italics added) wrote that "the larger genera... tend to *break up* into smaller genera, and thus, the forms of life throughout the universe become divided into groups subordinate to groups". The spirit of a hierarchical system contained in these words is also in accordance with the description of "Darwin's ideas of classification as being a group-in-group arrangement of organisms" (Stevens 1994: 245). The *hierarchical relationships* of groups at different levels were called '*genealogical*' by Darwin (1958: 395): "The grand fact of the natural subordination of organic beings in groups under groups" is related to a "genealogical succession". However, the fact is that "Darwin regarded the lack of intermediate forms in both the living world and the fossil record as the main impediment to achieving a fully genealogical classification" (Padian 1999: 355) and this

redirects genealogical relationships to the plane of a single (and also every) level.

The 'intermediate forms' can exist only between states of some characters at a certain hierarchical level. Unfortunately, the employment of the same term – 'genealogy' or 'phylogeny' – for relationships of different quality (hierarchical and one-leveled) led to a considerable confusion in the biological literature. Darwin himself made *taxonomically erroneous* statements when he discussed 'species' and 'varieties'. Thus, he wrote: "Certainly no clear line of demarcation has as yet been drawn between species and sub-species... or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These *differences blend into each other by an insensible series*; and a series impresses the mind with the idea of an actual passage" (Darwin 1958: 67, italics added). However, there *cannot* be a clear *line of demarcation* between 'species' and 'subspecies'; this sounds as if such a 'line of demarcation' could exist between 'organism' and 'organ'. There *cannot* be an *insensible series* of differences between species and subspecies. Subspecies are parts of species, and the differences between them delimit groups within species: these differences are not the same as those that work at the species level. The characters delimiting subspecies comprise their own insensible series of states, and those series appear later in the hierarchical differentiation of biota.

Darwin also wrote (l.c.: 68, italics added) that "if a variety were to flourish so as to exceed in numbers the *parent species*, it would then *rank* as the species, and the species as the variety". He did not seem to understand that if a variety is a new isolate of a species, the remaining part of that species could be considered as a *parent variety*. The increase or decrease of members does not make a 'species' or a 'variety' of a group; only the special *weighting* of differences that appear at *different times* can help in the problem of ranking. Much later, Hennig (1966: 193) tried to connect *rank* with *time* or *age*, but he thought that the rank of a group depends upon the age of the particular group in question, which is totally unacceptable in the framework of hierarchical classification as reflecting hierarchical evolution. The species *Homo sapiens* appeared rather late in the history of the earth's biota, but it is a 'species' all the same (within its genus, family, etc.), as is the case for any species in the Paleozoic Era.

Hennig (l.c.) wrote that sister groups are of equal rank *because of their equal age*, and this makes them 'coordinate and completely equivalent'. However, sister groups are of equal rank and completely equivalent in the taxonomic system *because they are described by states of the same characters*. States might be primitive or advanced, and the groups possessing them might appear at different times and have a different age, but the character(s) distinguishing them should have a certain level in the system, whereas groups represent a system of genealogical relationships at the plane of that level.

Thus, there are two types of phylogeny with different meanings for the classification of living beings. "*Vertical-historically* (or we might say *phylogenetically*)" (Sirks 1952: 12, italics added) the *sequence of characters* marking different levels

is of greatest importance. This is the *only evolutionary evidence* ('natural scale') in the hierarchical system, and if one could establish the sequence of characters (not their states) correctly, one would identify the only structure that retains stability in the continuing process of change. There is no need to arrange genealogically the groups themselves at each level of hierarchy, and the construction of a system does not require the tracing of ancestors and descendants. Unfortunately, this '*horizontal genealogy*', or '*horizontal phylogeny*', is not only the main focus of 'phylogenetic systematics' but also the starting point of the severe opposition to the 'Linnaean hierarchy' that conforms to 'vertical phylogeny'. Modern phylogenetic systematists try to reorganize "the very core of biological taxonomy", taking "the concept of evolution seriously" (De Queiroz 1992: 309), but they merely emphasize one aspect of evolution, namely the evolution of characters in sequence or the simultaneous divergence of states.

Linnaeus' description of the evolutionary process that occurred in the plant kingdom is found in the 12th edition of his "Systema Naturae" (Linnaeus 1772: 10, italics in the original, our translation, but see the similar passage in: Sirks 1952: 13): "... from simple progressively to complex; from few to numerous! At the very beginning of plant kingdom, as many different plants as *natural orders* were created. Then, ordinal plants productively mingle with each other, so that as many plants as distinctive *genera* existing today have appeared. Then, naturally, generic plants – by two ways of reproduction (which did not change flower structures) – mingle with each other and multiply into as many existing species as possible, except for a number of species producing *hybrid*, and therefore, sterile plants. Thus, every genus is natural, and this confirms that the nature does not make leaps".

Many critics have seen only the word 'created' in these phrases and thus have gone on to blame Linnaeus for anti-evolutionism, but the whole discussion actually contains a number of fruitful ideas. Although the language used was not very good and Linnaeus did not distinguish between characters and groups, one can deduce the hierarchical development marked by the first appearance of characters distinguishing orders of plants. Later in evolution, characters defining the present genera originated, whereas existing species appear on the scene more recently. The most embarrassing connotation here is the reference to the origination of lower taxa by an *intermingling of higher* ones which have simultaneously been multiplied.

Multiplication can be explained as the natural differentiation of original groups, but the vague ideas about 'hybridization' as the source of new diversity were probably based upon the similarity of *network relationships* produced by both hybridization and combinatorial spaces of characters that are the result of adaptive *radiation*, or *divergence* (see below). Linnaeus was a very good observer to note that many features in plants represent combinations. With the empirical knowledge that a calyx can be represented by seven kinds of expressions (a 'character' with seven states), a corolla has two expressions (presumably, he was referring to the actinomorphic and zygomorphic conditions), stamens and pistils might be of three kinds (as per his statement), and so on for other floral structures such as pericarps and seeds,

Linnaeus tried to count how many genera characterized by those combinations could exist (cf *Philosophia Botanica* § 167). Since the same kinds of calyx, corolla or other flower structures could be encountered in different orders, this situation might have given him the impression of a 'mixture' of orders.

It should be emphasized that Linnaeus did not oppose the combinatorial arrangement of groups at the same level (genera in the above case) to the hierarchical structure of the whole classification. He even shared the slogan 'nature does not make leaps' with transformists, but that did not influence his hierarchical vision of nature. Later, many biologists were inclined to express false oppositions. Thus, "a purely combinative system" that "has not the form of a tree, but instead forms a lattice of many dimensions" (Lubischew 1963: 418) was acknowledged as a better 'form of a system' in comparison with a "concept of Darwinian systematists" who believe that "*classification should be hierarchical, formed by repeated subdivisions of groups*" (l.c., italics in the original). As noted above, combinatorial arrangements at each level of the hierarchy do not eliminate the hierarchical subdivisions of groups, but the taxa from combinatorial space can also be arranged in the form of a one-leveled and plane tree that is so often the result of phylogenetic studies. In the latter case one has two 'contradictory' pictures of relationships among the *same taxa*, but they might merely express different purposes of studies.

The opposition between combinatorial (horizontal) and hierarchical (vertical) relationships as different 'shapes of nature' was postulated rather long ago, and the different interpretations of 'hierarchy' played their role in how the two points of view developed. Thus, "discussions of the linear 'scala naturae' emphasized the relative highness and lowness and the relative perfection and imperfection of organisms; all organisms could be arranged on a *chainlike, hierarchical scale*" (Stevens 1994: 164, italics added). However, since "all combinations of characters occurred", there was a conclusion that "the scala did not exist" (l.c.: 195). That is correct – the 'scala' might not exist even with respect to *organisms* (in the sense of a 'chain of beings') since 'imperfect' and 'perfect' organisms exist simultaneously *within* weakly or strongly differentiated groups. Unfortunately, the mistaken reference to 'scala' as a 'hierarchy' led to the rejection of the concepts of taxonomic hierarchy and hierarchical evolution altogether: "If relationships really were multidimensional, what could the taxonomic hierarchy mean?" (l.c.: 196). This question already contains a partial answer, since the discussion is about *relationships*, not about organisms or groups, whereas the relationships involved might be both hierarchical and combinatorial (cf: "partly hierarchic, partly reticulate, order" – Bremer & Wanntorp 1979: 625).

As noted above, the only point at which the terms 'chain' and 'hierarchy' are equivalent is the *hierarchy of characters* that appear successively in time. However, characters do not appear *one by one* as depicted in cladistic dichotomous schemes; the latter presentation is the source of the mistaken conclusion that "a large number of ranks are necessary to classify complex phylogenetic trees" (Hibbett & Donoghue 1998: 347). This also represents an additional

'ground' upon which to attack the relatively few ranks in the Linnaean hierarchy. However, there could not be many ranks, since the radical novelties in vertical evolution were rare, whereas horizontal evolution most often took place.

One can remember the well known – Darwinian – 'indefinite' variation meaning that any character of an organism can change in a good or bad direction. Moreover, the changes of different features could proceed simultaneously. If one designates some features of an ancestor by capital letters (ABCD), one can find several descendant combinations such as aBCD, AbCD, ABcD, ABCd. Then, if only one character changes in each case, any descendant shares with an ancestor almost the same genetic program and even the ability to change in the same directions. Therefore, already the third generation of descendants might represent more diverse combinations (i.e., abCD, abcD, aBcD, AbcD, AbCd, AbCd, ABcd, etc.). After all, a combination consisting of completely advanced, or apomorphic, states (abcd) might originate, and the combinatorial space constructed with the help of four changing characters will be completed with groups of the same level. Thus, all groups in the combinatorial space appeared in a *genealogical* way, but the depiction of their origin is irrelevant to classification.

One should take into account that every such diversification includes one group that is characterized only by plesiomorphies and one group that possesses exclusively apomorphies. Character states of all other groups are mixtures of apomorphies and plesiomorphies in different proportions. This causes the cladistic 'principle of synapomorphy' demanding the unification of organisms into groups on the basis of shared apomorphic features to be invalid to the same degree as the 'principle of dichotomy'. If we admit that the combinations under consideration are 'species' or 'genera', the 'principle of synapomorphy' does not work at all when apomorphies and plesiomorphies represent *distinguishing* characters (i.e., when they constitute *intensions*). In such cases, it is impossible to create a natural genus or a natural family using any apomorphic feature.

There are also other situations when the 'principle of synapomorphy' can work, but it merely creates heterogeneous groups and increases the artificiality of systems. Those situations are associated with the remarkable parallelism of features (representing *extensions*) within *closely related* genera and families. This parallelism is the *direct consequence of divergence*. When some difference(s) among organisms or groups appear, they often stand out against the background of the almost similar genetic programs found in their descendants. As such, similar heredity might be realized in divergent groups in a similar way, and the similarity of internal polymorphism in many *closely related* genera and families could be much higher than the few differences between them. Such regularity is described by the law of homologous variation (Vavilov 1922). For example, *hundreds* of the same features are repetitive in such genera as *Secale*, *Triticum*, *Hordeum*, and *Avena*, whereas they differ in very few characters.

The same type of internal polymorphism found in several genera within a family consists of characters distinguishing species, and the repetitive features – *at the species level* – might be apomorphic and plesiomorphic. Now,

what is it that phylogeneticists do when they use the 'principle of synapomorphy'? They take species from different genera and unite those with the same apomorphic features into new heterogeneous groups. Thereby, a parallel *species* feature becomes – artificially – a uniting *generic* feature. It also should be emphasized that characters of internal polymorphism *always outnumber* the few differences that exist between closely related genera and families. In molecular taxonomy, which provides many more characters than morphology, the characters of internal polymorphism become an overwhelming majority, and the number of erroneous taxonomic arrangements increases.

Thus, cladistic *methodology* is completely alien to taxonomy; curiously, at present "cladistics (phylogenetics) and taxonomy" are considered to be "two main rival schools" (Grant 2003: 1263). From this opposition one can conclude that cladistics is not taxonomy at all, although it "was invented for the purpose of improving on taxonomy" (i.e.: 1268). This invention appeared to be both unworkable and popular, whereas the pages of biological journals are filled with whimsical 'phylogenetic' trees that are merely graphic reflections of dichotomous *keys for identification* based upon chaotically chosen differences of uncertain rank. It was correctly admitted that cladogram nodes "may have nothing to say about the *hierarchy of taxonomic ranks*" (Niklas 2001: 2250, italics added). Then, what is this to say about hierarchy?

THE EMPLOYMENT OF COMBINATORIAL ARRANGEMENTS IN THE RELATIVE CHARACTER RANKING

The first step in the elaboration of a '*hierarchical theory of systematics*' (Wood 1994) is to redirect attention from horizontal phylogenetic relationships between 'ancestors' and 'descendants' to the vertical phylogeny of character (not their states) sequences and to consider the taxonomic system of organisms as the *hierarchical model of the evolutionary differentiation* of the organic world. The point of view that 'phylogeny' is real while classification is only utilitarian (Benton 2000) denies any possibility of understanding the world's biodiversity properly. The pattern of *taxonomic diversity* should become "the basis for *causal inference* in systematics" (Atran 1998: 564, italic added).

It is not true that the Linnaean hierarchy lacks the "ability to represent the organic world" (Ereshefsky 2001: ix), but the difficulties of character ranking make the task almost impractical. One more problem – in addition to the one-sided view of phylogeny as reflecting relationships between ancestors and descendants – is a so-called *absolute ranking* that supposedly implies the equality of 'families' and 'orders' in all kinds of organisms. As already emphasized above – in the discussion of sister groups (i.e., groups of the same rank) – *rank equality* is provided when groups possess features that are *states of the same characters*. With this in mind, we cannot say that a 'family' of flowering plants and a 'family' of insects are equivalent since they do not share any characters at all. However, it is not an absolute ranking that matters in the construction of the natural system. One can make an existing (imperfect) system more natural if one finds the correct "*relative* rather than absolute hierarchy of

characters" (Stevens 1994: 90), but one should remember that *many characters are of equal rank*, so the task is to find such *sets of characters* at every level.

The most vulnerable practice of systematists is the chaotic employment of differences for the delineation of groups ('species', 'genera' or 'families') at the same level. As a result, we have 'classifications' as described by the great Argentine writer Jorge Luis Borges in an essay titled "El idioma analítico de John Wilkins" ("The analytical language of John Wilkins": <http://www.crockford.com/wrrrld/wilkins.html>). Borges reproduced a classification of animals purportedly found in 'a certain Chinese encyclopedia', where animals were divided into the following groups: (1) those belonging to the emperor, (2) embalmed, (3) sucking pigs, (4) sirens, (5) fabulous, (6) stray dogs, (7) looking like flies from a long distance, etc. Modern 'phylogeneticists' could even arrange these groups in a 'phylogenetic' tree, but ancient philosophers would say that such a 'classification' lacks a *single basis for division* or '*fundamentum divisionis*' in terms of ancient times (Stafleu 1971). Unfortunately, Linnaeus' language with respect to the discussion of this problem appeared to be completely alien to many later taxonomists. He wrote that "the essential character as a *unique idea* distinguishes a genus from those of the same kind included in the same natural order" ("Essentialis character *unica idea* distinguit Genus a congeneribus sub eodem ordine naturali" – *Philosophia Botanica* § 187, italics added). The 'unique idea' refers to *all genera* that are distinguished simultaneously and somehow serves as a *cohesive* agent at the generic level. However, the very term 'idea' was and is disgusting for biologists who grew up with a negative attitude towards any form of 'idealism' (cf Hull 1965, Caplan & Bock 1988, De Queiroz 1994). The English version of "*Philosophia Botanica*" by Freer (2003: 141) translates 'unica idea' as 'unique pattern', but Linnaeus' statement merely means that taxa (genera, for example) are comparable in level only when they are distinguished by states of the *same character set*, and this character set is 'essential' for genera delimitation.

Sometimes, the Linnaean hierarchy is described as an 'artificial' one '*because*' its divisions are supposedly based upon few characters, sometimes with only a single character being used at each level. That is not the whole truth, and the example given above of the segregation of genera based upon the combinations of different kinds of calyx, corolla, stamens, pistils, fruits and seeds shows the employment of many characters at the same level. However, these characters as a *single set* compose the necessary '*fundamentum divisionis*' that allows us to divide genera non-chaotically. The problem here is that Linnaeus admitted *a priori* that all these characters played their role just at the generic level, and this was a mistake. He could not improve upon the situation with the imperfect knowledge of his time, but with our current knowledge we can distribute characters among levels using a *posteriori* analysis. What does this mean?

Today, biologists have a kind of 'rough' hierarchy where characters are distributed in accordance with some 'degree of commonness': thus, common features of the Magnoliophyta are higher in level than common features of the Magnoliopsida or Liliopsida, whereas the common

features of the latter are higher than those in Rosidae or Liliidae (Takhtajan 1997). Nevertheless, when taxonomists deal with groups at the same level, especially 'species' and 'genera', they are often passionate to divide and subdivide groups, as well as to describe new ones, by using chaotic differences. Therefore, such groups actually might not be of equal rank and should be *tested* for rank equality *after* their segregation (i.e., *a posteriori*). For such testing, the *method of estimation of distinguishing characters* based upon the frequency of their participation in delimitation has been suggested (Vasilyeva 1999).

As a mycologist, the first author of this paper provides an example involving the analysis of supposedly generic characters in the family Gnomoniaceae (Diaporthales, Ascomycota). The most frequently used distinguishing character has been the kind of spores, which may be non-septate (amerspores), septate with a septum in the middle (didymospores), septate with a septum near one end (apiospores), and elongated to thread-like (scoleospores). This character distinguishes *Gnomoniella*, *Gnomonia*, *Apiognomonina*, and *Ophiognomonina* (Vasilyeva & Stephenson 2010: Fig. 2). A second character often used for distinguishing genera in this family is the position of the elongated neck of the fruit body (perithecium), which may be central (*Gnomonia*, *Apiognomonina*, *Ophiognomonina*) or lateral (*Plagiostoma*, *Apioplagiostoma*, *Pleuroceras*). A third character that has been used most frequently to describe new genera in the Gnomoniaceae is the kind of fruit body. The latter can be simple without any stromatic development (and thus consisting of a compact mass of vegetative hyphae) or such a stromatic development is present and referred to as a clypeus. The presence or absence of a clypeus distinguishes *Gnomoniella* and *Mazgiantia*, *Gnomonia* and *Melanopelta*, *Apioplagiostoma* and *Hypospilina*, *Pleuroceras* and *Linospora*. The further development of stromatic tissue leads to the appearance of a stromatic capsule that surrounds the fruit body, and this kind of fruit body can occur in combination with different kinds of spores, as is the case for *Mamianiella* (amerspores) and *Mamiania* (apiospores).

The Gnomoniaceae in two monographs (Barr 1978, Monod 1983) also includes the genus *Plagiosphaera*, which shares the same position in the matrix with *Pleuroceras* as a result of having the same combination of the characters in question. These two genera differ from *Ophiognomonina* by having the same differences for these characters, and the most important question relates to what character distinguishes *Pleuroceras* and *Plagiosphaera*. One treatment (Barr 1978) separates these genera on the basis that members of *Pleuroceras* occur on the dead leaves of deciduous trees, whereas members of *Plagiosphaera* occur on herbaceous stalks. Such a difference does not allow us to consider these two taxa as separate genera, since many closely related genera, such as *Plagiostoma*, *Gnomonia* or *Gnomoniella* include members that occur on both the leaves of trees and herbaceous stalks. As such, this character displays variability within genera (an element of the internal polymorphism) in the Gnomoniaceae and cannot be used to divide some other genera. Therefore, in Barr's system, *Pleuroceras* and *Plagiosphaera* should be united. The difference between them actually appears to be 'accidental' in comparison with other differences that are repetitive.

In another treatment (Monod 1983), one can see that *Ophiognomonina* and *Pleuroceras* are distinguished from *Plagiosphaera* because the first two genera lack paraphyses (sterile hyphae that occur among asci containing spores), as do all other members of the Gnomoniaceae. In such a case, *Plagiosphaera* should belong to a different family, since the presence or absence of paraphyses is of taxonomic value at that higher level. In both systems, the removal of *Plagiosphaera* (either by reducing its name to synonymy or by finding another place for it) would increase both the *naturalness of the family composition* and the *naturalness of character hierarchy*, since one false 'generic' character (occurrence on the leaves of deciduous trees or herbaceous stalks) appears to be at a lower level, whereas another character (presence or absence of paraphyses) that is wrongly used for genera delimitation appears to be at higher level.

Moreover, the increase in system naturalness is supported by its high prognostic capacity, and this fully conforms with Linnaeus' statement that "a system by itself indicates even plants that are omitted; which enumeration in a catalogue never does" (*Philosophia Botanica* § 156). Evidently, the empty places at each level can predict the possible – living, fossil, forthcoming, or not yet found – organisms with certain character state combinations. Some expected combinations in the family Gnomoniaceae really do exist, but – without the method of *a posteriori* estimation of delimitative characters – these combinations are buried in the wrong places. Thus, the genus *Chalcosphaeria* (didymospores + clypeus + lateral perithecial necks) was described almost a century ago, but its name was reduced to a synonym of either *Plagiostoma* (Barr 1978) or *Hypospilina* (Monod 1983). One author underestimated the character "presence or absence of a clypeus" and another underestimated the difference in ascospores, but both views are *inconsistent*, taking into account that precisely the same differences are involved in the delimitation of so many genera. The species *Mamiania alni* (didymospores + central necks + stromatic capsule) might deserve segregation from the otherwise apiosporous genus into its own genus, which is not yet described. This would be not unlike the situation that already exists for the genus *Apioplagiostoma*, which was established as an "apiosporous counterpart" of the didymosporous *Plagiostoma* (Barr 1978: 102).

The recent treatment of the Gnomoniaceae by Lumbsch & Huhndorf (2007) is rather heterogeneous and generally follows Barr's views (1978), thus excluding a number of genera with lateral necks from this family. That was the consequence of the *arbitrary overestimation* of this character (central or lateral position of perithecial necks) as being of sufficient importance to be used for delimiting families. However, not a single family was established based upon just this character, it was employed only for segregation of genera in all families with perithecioid fruit bodies. When families are considered in *a posteriori* comparative analysis, one should estimate the frequency of differences between them.

It might seem surprising that the improvement of a character hierarchy is carried out with the help of combinatorial arrangements. As noted above, some authors consider the latter to represent a special kind of a system that has a

reticulate structure (De Hoog 1979) as opposed to a hierarchical system. However, the opposition is imaginary, since reticulations are particular phenomena at different levels of the hierarchy. In such a way one can make the *existing system* more natural without eliminating the Linnaean ranks that are so severely attacked today.

An *a posteriori* method of genera comparison is exactly "the method by which every generic character *is to be determined*" (*Philosophia Botanica* § 167, italics added), although some botanists could not understand the need for a search of generic characters even *after* 'genera' were established. We can only repeat here that 'genera' established *a priori* are only *taxonomic hypotheses* and not all of them would be assigned to the same level. Linnaeus also wrote that "every genus is natural...; it is not to be capriciously split or stuck [to another], for pleasure, ... especially *a posteriori*" (*Philosophia Botanica* § 159, italics in the original). Indeed, our suggestion to unite or divide genera as outlined in the practical example given above was not influenced capriciously; a comparison of genera with one another revealed a set of characters that *coordinates* them by itself at the same level. Therefore, some taxonomic hypotheses are verified, since they stand the *test for rank equality*, whereas other groups disappear. The coordinating set of characters does not allow us to split or lump genera "according to each man's theory" (l.c.), but one can find valuable ideas in different systems. Indeed, it should be possible to develop a *synthesis* of best views based on a *posteriori weighting* of delimitative characters in contrast to eclectic joining of personal preferences in each man's system.

Mayr (1969: 218) wrote that "all existing good classifications are the result of... a posteriori weighting", but confessed that "the scientific basis of a posteriori weighting is not entirely clear" (l.c.). Actually, he could not identify the basis of such weighting, since that basis is rooted in the ancient and Linnaean essentialism that was the main point of Mayr's criticism. Mayr (1957) began a crusade against essentialism and 'typological thinking', and the 'hordes of crusaders' literally trampled down the roots of taxonomy that had their origin in the original hierarchy of 'species' and 'genus' in treatises of ancient philosophers (cf Sloan 1987). Thereby, Mayr essentially eradicated the most fruitful taxonomic ideas. The opposition between 'populations' and 'types' (which are not the 'type' specimens that serve for the priority of names) is imaginary, since populations are located *within* taxa, whereas 'types' – *hierarchical types* – at every level of the system of organisms. The *set of characters revealed by a posteriori weighting at a certain level* is an 'essence' of that level, whereas the state combinations of those characters are 'essences' or 'types' of separate taxa assigned to that level. Consequently, if one takes into account that the terms 'essence' and 'idea' are identical in Plato's 'theory of ideas', one can better understand Linnaeus' statement that "the essential character as a *unique idea* distinguishes a genus from those of the same kind included in the same natural order" (see above). Here, a 'unique idea' is a set of characters at the generic level, whereas 'essential character of a genus' is a certain combination of states characterizing a separate genus.

Since many biologists dislike the term 'essential character', they think Linnaeus' term 'natural character' would be more suitable for the theory of *natural* classification. However, Linnaeus wrote that "the natural character will rehearse all the different and peculiar features of the fruit-body that agree throughout its individual species" (*Philosophia Botanica* § 192). In other words, the *natural* character is a character in the diversity of its states proceeding through individual taxa at the same level. Therefore, *any* character might be natural, but the character that is 'essential' at a certain hierarchical level could be found only by a *posteriori* comparison of taxa.

CONCLUSIONS

Even if one leaves essentialism alone, the *method* suggested for taxonomic hypotheses to *test* them for *rank equality* might be difficult to accept, since it demands a huge body of comparative material for a posteriori weighting. If one analyzes differences among genera in a family, one should know *all* of its genera and even all genera in closely related families or orders. If one studies a small group (of species or genera), one cannot estimate differences properly within that group; therefore, one should carry out the analysis in the larger *related* group and then use Vavilov's law of homologous variation to assign the same rank to repetitive differences in both groups. Of course, the collective work of many taxonomists can be helpful in overcoming the difficulties of character rank estimation when particular genera or families are studied. One of the idiosyncratic aspects of such an approach is that it depreciates many of the theoretical debates in biology, especially those centered on the 'species problem'.

Despite the enormous body of literature that exists on the species problem (cf Wilson 1999, Wheeler & Meier 2000, Stamos 2003) and of the numerous concepts that have been suggested, *not a single species concept* is important for the construction of a natural system of organisms. At the present stage of evolution, there are groups with different degrees of differentiation and a huge number of groups that are called 'species' (which are also differentiated into populations with different degrees of isolation). The only thing that might be done to increase system naturalness is an analysis of the differences that exist among them so as to determine whether or not those groups really belong to the same level. After this analysis, some 'species' become 'subspecies', others deserve their own genera, still others are transferred to different families, and the naturalness of a whole system increases considerably.

The debates that surround the 'species problem' are also useless because they leave groups at other hierarchical levels without any natural basis, although all higher groups could be natural if the character hierarchy is constructed correctly. Although phylogenetic systematists often refer to 'genealogical relationships' between ancestors and descendants *within* a group when its characteristics are regarded as those of a natural group, this does not work in taxonomy, since, as noted above, those relationships are irrelevant for the construction of a hierarchical system.

It was correctly stated that in the *character-based phylogenetic Linnaean classification* "taxa should be both ranked and monophyletic" (Potter & Freudenstein 2005: 1033), but 'phylogeny' should be 'vertical' (a sequence of the characters themselves)

in contrast to the horizontal phylogenies that are observed in character *state sequences* as they proceed in ancestors and descendants. Also, monophyletic taxa should be defined in terms of *weighted intensions*, whereas an *extensional* definition of a monophyletic group through its *content* as including an ancestor and *all* of its descendants (De Queiroz & Donoghue 1988, Ridley 1989) is, once again, of no use to classification. Hierarchical evolution through differentiation continuously *separates* ancestors and descendants in different groups. Both ancestral and descendant species could become genera through further differentiation and isolation of their populations, but the species in those new genera cannot be assigned to a single 'natural' genus even though *all* of the descendants have the same ancestor.

More than thirty years ago the paper "Hierarchy and reticulations in systematics" (Bremer & Wanntorp 1979) was published, and its title is similar to that of the current text, but it was directed towards the critics of hierarchical order. It was supposed that "the principle of hierarchy prohibits speciation by hybridization (since this implies a reticulate and not a hierarchic distribution of characters)" (l.c.: 624). However, there are two aspects of this criticism that warrant comment. First, as might be emphasized again, the principle of hierarchy does not prohibit reticulate relationships in the combinatorial space of characters at each level. These reticulate relationships can appear as the result of adaptive radiation or *divergent* evolution. Second, the principle of hierarchy does not prohibit speciation by hybridization. Moreover, it is well known that genera, especially in higher plants, can be of hybrid origin (e.g., *Sorbotoneaster*) and a number of higher groups (lichens, eukaryotes) appeared as a result of a 'fusion' of already existing groups. Actually, we have the same confusion here as in the case of a single 'chain of *beings*'. In the framework of taxonomy,

living beings are connected by *many-leveled relationships* with each other, and this reflects the step-wise multiplication of diversity in the organic world. When the hybridization of some *beings* takes place, the *differences* between ancestors and descendants are observed (i.e., there is a *divergence* in some characters). The work of a taxonomist is to assign a *weight* to those differences or to find their correct place on the hierarchical scale. The result of a hybridization event can be a species, a genus, a variety, or merely a monster, and only a taxonomist – by a *posteriori* comparative analysis – can estimate the level of such an event.

Curiously, the criticism of a 'hierarchy' by Bremer & Wanntorp (1979) strikes a blow to the 'hierarchical' constructions of cladists. As noted above, cladistic dichotomous trees do not often convey hierarchical relationships, since they involve only species (or genera). The relationships among taxa at the same level *cannot be* hierarchical, but exactly this kind of 'hierarchical' relationship was attacked: "... we may specifically ask, what is the hierarchic order *among species* of organisms?.. A hierarchic description of a fishing net... would certainly be a poor one" (l.c.: 624–625, italics added). This is a good point, and the criticism is not outdated, since the nonsensical word combination "hierarchy of species" (Cowan 1962) is repeated at the present time. One of the titles of a recent paper indicates that it is about "classification of *nested diversity at the species level*" (Kizirian & Donnelly 2004, italics added), although there should not be 'nested' diversity at a single level. Such cladistic 'classifications' could be constructed only by the chaotic employment of differences of uncertain levels (otherwise relationships are combinatorial or network-like) and the testing of groups for rank equality is not even envisioned. Ironically, these absurd dichotomies are considered to be 'phylogenetic' ones and are opposed to the Linnaean system as "more in line with the current understanding of evolution" (Pennisi 2001: 2304).

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