

We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,900

Open access books available

186,000

International authors and editors

200M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com



An Essentialistic View of the Species Problem

Larissa N. Vasilyeva and Steven L. Stephenson

Additional information is available at the end of the chapter

<http://dx.doi.org/10.5772/52625>

1. Introduction

In this paper, we support the critical attitude expressed by some biologists [1-4] of the failure of any *species concept* proposed in the biological literature. Nonetheless, we still believe that species themselves are "entities that [are] actually discovered" in nature and not "merely invented" [5, p. 4]. We don't want a situation of 'questioning species reality' [2] to exist and also don't want a "species-free taxonomy" [1], but to fulfill these two desires we should discard most of the modern and popular ideas about species.

During the history of species debates, there have been different reasons for believing the concept of species to be faulty, but most serious of these were two general points that have surfaced from time to time. Quite recently, Vrana & Wheeler [6, p. 67, *italics added*] suggested that, rather than species, "*individual organisms... should be used as the terminal entities in phylogenetic analysis*". This view returns us to times of Buffon, who wrote that "in reality individuals alone exist in nature" [7, p. 75], and some authors after Buffon also stated that nothing except a living individual possesses "an indisputable ontological significance" [8, p. 344]. Nevertheless, since "a coherent knowledge of the living world is possible only with the aid of a hierarchic classification" (l.c.), and "*there can be no science about individuals*" [7, p. 37, *italics added*], the ontology of individual organisms should not exclude the ontology of species, at least as the participants in the *natural hierarchy*, if we can prove that the *taxonomic hierarchy* corresponds to the latter.

Even more frequently, the existence of species, similar to that of higher taxa, has been questioned from the whole perspective of the theory of evolution representing 'life' as a dynamic world that is supposedly devoid of any static elements. "An analysis of the situation shows where the difficulty lies. The concepts of the taxonomic categories, as all the taxonomic concepts, are essentially static" and leave "out of consideration the dynamism which is one of the most essential, if not the most essential attribute of life" [8, p. 353]. It has been concluded

from the general perspective of evolution that "the taxonomic categories in general, and species in particular, are not static but dynamic units" (l.c.). In such a statement, one can see the poor discrimination between 'categories' and 'units', and this is the most obvious example of a confused view of species that was developed in Mayr's "replacement" of 'typological thinking' by 'populational thinking' [9]. The false contradiction between 'typological thinking' and 'populational thinking' which should be referred to static and dynamic aspects of taxa, respectively, and which characterize each taxon *simultaneously*, has dominated biological literature for a long time, although these aspects correspond to such notions as *intension* and *extension* of taxa [10]. The failure at developing an understanding of intensional and extensional nature of taxa was the main omission from the history of the 'idea of species' [7], and precisely this failure led to a large number of useless arguments [5, p. 21]. Although the attempt to make the "crucial distinction between the species category and species taxa" [5, p. 18] is related to the distinction between intension and extension, this insight has had little impact, since the primary attention was directed toward the vain search for the vague 'intension' of a general 'species category', whereas *each species* (genus, family, etc.) *has its own intension*. (Of course, this diversity of intensions is akin to the diversity of individuals, and, as such, also demands to be placed in the context of a proper science to be naturally ordered.)

In this paper, we expose one more *general* reason for the failure of almost all species concepts, and, paradoxically, this is rooted in the continuous endeavor to introduce a biological sense into 'species' which has constituted an older problem of ancient metaphysics [5, 7]. The incorporation of biology into the species problem was the emphasis on the relationships *within* species, and those relationships involved, for example, a gene flow between populations (in the so-called 'biological species concepts') or lineages from ancestors to descendants (in many phylogenetic species concepts). However, this incorporation of biology was apparently misplaced, since *none of inner interactions within taxa* are of any consequence for the *discovery* of natural entities that make up "a natural system, a system that carves nature at its joints" [5, p. 16]. It might seem that the exclusion of internal interactions as the basis of a species reality throws the species problem back to pure "metaphysics" with its indiscrimination between living and non-living objects, but this is not the case. First, *organisms* remain in the focus of taxonomy and provide unique patterns of relationships that could not be found outside the organic world. Second, the evolutionary perspective keeps its primary importance, although all of the major aspects of this should be re-emphasized. Thus, we don't believe that 'descent' plays an unnecessary role [6, p. 67] in the understanding of nature of taxa and their monophyly, but, in our view, the 'descent' should not be conceived in terms of ancestors and descendants as suggested by some phylogeneticists who wants to reorganize "the very core of biological taxonomy" [11, p. 309], using an inappropriate approach.

We are sympathetic with the statement that "the species problem is not something that needs to be solved, but rather something that... needs to be *gotten over*" [12, p. 232, *italics added*]. We want to get over species but in a way that is different from the one taken by O'Hara [12] and the like-minded persons whom he mentioned [13-14]. In contrast to opinions that the 'species concept' is "most fundamental in biology" [8, p. 344], and "a central problem to that science" [5, p. 2], we think that species play a rather modest role in the natu-

ral world. They are considered unduly important only by being more numerous than genera or families. Artificially inflated, the 'species problem' is extremely narrow from the perspective of the hierarchy of life. This problem often has overshadowed the 'Natural System', and Mayr [15] even indicated that there is no such thing as the Natural System. Here we are more in line with Darwin, who believed in that it does exist and thought that "descent [was] always used in classification" [16, p. 394]. However, what we should do is to be more specific about what is meant by 'descent', since the *only* kind of 'descent', or the only evolutionary sequence, that can be expressed in the system of organic beings is the successive appearance of new differences during the history of the biota, and precisely this sequence gives rise to the *hierarchical structure* of the system.

2. Species problem and evolutionary models

The quest for a correct hierarchy of *equally natural taxa of an individual nature* at different levels was partly blocked by some of the ideas derived from one or more aspects of the narrow 'species problem', as well as from accepting certain general evolutionary models.

One of the most unfortunate—for the construction of a natural system—evolutionary models was the Great Chain of Being (ancient *scala naturae*). As Wilkins [7, p. 53] wrote, "The Great Chain does imply that there is no real distinction between species, as all intermediate gaps are filled." This implication threatened the reality of species, so many old 'species concepts' have required 'gaps' between groups for the latter to be clearly outlined. "To Darwin, species form vague, human-defined, and difficult to discern way stations in evolution. *They are detectable only by means of gaps in variation...*, as contrasted to continuous variation normally found among varieties within species" [17, p. 499, italics added], and "Darwin's view of species as clusters of similar individuals separated by gaps remains relevant today" [17, p. 502].

The idea that gaps should exist and that there are larger gaps between higher taxa than between species [15] is highly popular, and "the size and nature of gaps" [18, p. 118] are thought to be identifiable, although few notions in taxonomy are as senseless as 'gaps'. (Having described numerous new species and genera, we don't recall the necessity to measure any 'distance' from a new taxon to any other already described one. Moreover, if two fungal phyla such as the Ascomycota and the Basidiomycota differ in endogenic or exogenic spore production, two orders within the Ascomycota differ in the presence or absence of paraphyses between asci, two genera differ in the number of septa present in their spores, and two species differ in the presence or absence of ornamentation on spore walls, then who is to say which 'gap' is larger, given that a single character is involved in the delimitation at each level?).

The idea of 'gap' has stemmed from the old transformist thesis, shared by some later philosophers of biology, that species 'transform *into each other*' [19-21]. Biologists have imagined a flow of 'species' with no place for genera and families, and only the breaks in that continuum provided some scraps called 'good species' that were arbitrarily united into genera and

families by taxonomists. (For example, supraspecific groupings are "arbitrarily delimited sections of phylogenetically *continuous chains of species*" [22, p. 219, italics added]). Although idea of species transformation 'into each other' was seemingly dropped [23] and "the Great Chain of Being had been broken" [24, p. 476], this concept of world development did not die altogether and has only transformed into seemingly different schemes.

A much more promising model is the "Tree of Life", which is currently predominate among biologists, although this model has its own difficulties with the representation of reality. Two main difficulties relate to (1) the incorporation of the above mentioned 'chain-thinking' into 'tree-thinking' (the latter term was used by O'Hara [25]) and (2) the dichotomous branching of 'Tree of Life'.

The fact of preserving a 'chain-thinking' approach within a tree-thinking approach is well illustrated by the discussions about the *trees at the "species level"* [12, p. 244] and the *natural system at "the species level"* [12, p. 243]. However, a tree as a metaphor for the whole of life and for the entire natural system—in Haeckel's sense [26]—cannot be crammed into the flat plane of a single level. If the poetic mind can think of species as green or withered 'leaves' on a 'tree', it also can conceive that leaves by themselves are disconnected and only united by twigs and branches that are 'larger taxa'. Separate 'leaves' can comprise a disordered heap but not a tree or a system. The most important issue to be considered here is the unpleasant fact, that—similar to the linear sequence of 'species' in the Chain of Being—"trees at the species level" rule out the consideration of natural higher taxa. The description of the modern 'processual system' of speciation as a "hierarchy" of species-lineages splitting [27] implies that only single-level relationships are involved, so the *natural system* is out of question.

Additional problem with single-level "trees", or cladograms, is their construction as *dichotomous* branching patterns. In this respect, they are similar to the keys for identification used in taxonomy, and it already has been recognized that keys, stemming from "Plato's method of classification" and "Porphyry's comb of tree", are topologically the same as cladograms [7]. There is a belief that "a major distinction between a phylogenetic tree and Porphyry's comb is that the former is derived from history, while the latter is derived from diagnosis" [7, p. 29], but this distinction is really an illusory one. Both cladograms and keys are mostly constructed on the same information about character distribution, and *no character weighting* (see below) is usually involved in this process, so the results are highly subjective. Moreover, the cladograms do not convey a history, not only because of the chaotic choice of characters, but because they are dichotomous.

Interestingly enough, cladists themselves have begun to argue against the tree-like representation of relationships *because of the dichotomy of trees*. The pioneer of cladistics is acknowledged to be Sinai Tschulok [28], who saw systematics as "a tool that allows the investigating mind to master the biological multidimensional multiplicity" and recognized that "every attempt to group plants on the basis of as many characters as possible... had to result in reticulated relationships" [24, p. 490]. On this basis, there was a conclusion that "the dichotomous Tree of Life cannot be a universal metaphor"; instead, "it is an illegitimate metaphor", as also is the case for "Hennig's description of speciation as a universally dichotomous process of cleavages" [24, p. 488].

We agree that the Tree of Life is hardly dichotomous, but a number of unnecessary opposing points are involved in the above critique. First, although the employment of as many characters as possible actually leads to reticulate representation of relationships, these same relationships also could be expressed in an artificial dichotomous key (and a single-level cladogram), so *taxonomic reticulations* (which are different from hybridization processes) are not enough to reject Hennig's description of speciation as a universally dichotomous process of cleavage. Actually, and secondly, we think that Hennig was right in his understanding of speciation, but he wrongly inferred a dichotomous tree from that understanding. Thus, even in clear cases of fan-like or radial speciation on different islands of some archipelago, when different characters of an ancestor change in several descendants, *each particular event of speciation involves a dichotomy* (divergence) of some character into two states—one is possessed by an ancestor and another one by a descendant. In other words, although there is an opinion that "there is nothing in speciation theory that mandated dichotomous speciation" [24, p. 483], speciation *is* a dichotomous splitting, whereas the Tree of Life is not dichotomous: "The appropriate image for the post-Darwinian system is a much-branched tree" [29, p. 5].

Recently, the Tree of Life as an evolutionary model for the development of organic world was strongly attacked from the perspective of a "rampant lateral gene transfer, sometimes across vast phylogenetic distances" [24, p. 488]. The same line of thought could be traced to various theories of endosymbiosis: "In representations of standard evolutionary theory, branches of 'family trees' (phylogenies) are allowed only to bifurcate. Yet symbiosis analysis reveals that branches on evolutionary trees are bushy and most anastomose...; indeed, every eucaryote, like every lichen, has more than a single type of ancestor..." [30, p. 10]. However, the entire matter relating to the opposition of the Tree of Life and lateral gene transfer or hybridization is a confusion of representations. It is well known that there are "many slight differences which appear in the offspring from the same parents" [16, p. 60], i.e. in the progeny *from two 'ancestors'*. The differences can even be not so slight (as is often the case with hybridization), but what is more important is that 'children' *diverge* from each other and from parents in some features. It is exactly *these differences and the estimation of their hierarchical level* that are the main concern of taxonomists, so a divergence is the focus of all efforts to convey relationships in the taxonomic system, hence the representation as a tree. Even with extensive gene transfer leading to novelties, we should, first of all, find out how different the new organisms are from those that existed previously, and on which taxonomic level the resultant differences deserve to be placed.

With due consideration to all of the merits of the Tree of Life as an illustration of a natural system, it is unsatisfactory not only because of the endeavors by biologists to make it strictly dichotomous but also because of the confusion that exists between single-level cladograms (lacking *hierarchical*—in a taxonomic sense—relationships) and the tree representing structure with many levels. It is correctly noted that more work is required "to structure a classification in terms of a *nested hierarchy* that corresponds to a branching tree of life" [24, p. 490, italics added], but the image of a tree does not convey a *nested hierarchy*, since its branches are not included within each other.

Stamos [5, p. 29, italics added], when indicating that taxonomists "either take the metaphor of the Tree of Life seriously or they eschew it altogether, providing nothing in its place", stated that "real history reconstruction, combined with a truly viable species concept, requires a *completely new metaphor for best capturing the nature of the history of life*". He was right but did not provide a new metaphor or, in O'Hara's words [12], a new "generalized representation of the single natural system", and, actually, could not do that, because his focus was only on the 'species problem' which cannot be solved outside the context of a *natural* hierarchy of taxa. He purposefully avoided the discussion of the relationship of higher taxa to the species problem [12, p. 28], and that had a limiting influence on his conclusions.

3. Hierarchical model of evolution and its implications for the 'species problem'

We began to discuss the hierarchical model of evolution about 15 years ago [31] and paid greater attention to it later [32-36]. There is nothing new about that model, since it is "the traditional *inclusion hierarchy* set out by the ancient Greeks" or "the Linnaean hierarchy, which is an *inclusive system* of groups within groups" [27, p. 311, italics added].

The main problem with the traditional hierarchical model is that it was proposed without any reference to evolution. Although the idea of such a hierarchy was rather productive for the construction of *taxonomic system*, it was described as an "atemporal hierarchy of sets within sets" [27, p. 312] which is "just rather boring ways of arranging things" [37, p. 9]. To overcome this difficulty and to devise a *natural system* from a rather subjective Linnaean hierarchy, we should identify the points of contiguity of the taxonomic model with evolution. The first step in this direction was made by Darwin [16, p. 73, italics added], who described the evolutionary process by which "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*". He also associated the *due subordination* of groups with the word 'genealogy' [16, p. 400], but that led to a great confusion afterwards because of the existence for two kinds of 'genealogies'.

These two 'genealogies' ('phylogenies') correspond to two 'hierarchies' as the latter are discussed by David Hull [27, p. 311; 34]. One of them implies the sequence of ancestors and descendants, whereas the other—the sequence of new characters accompanying the division into "groups subordinate to groups". Unfortunately, the first kind of genealogy (ancestral-descendant lineages) was acknowledged as the true basis for taxonomy [38-39], but, contrarily, the *natural system* can only reflect the second kind of genealogy, or the character sequence in time. The 'entities' in this evolutionary sequence cannot be 'ancestors' and 'descendants' to each other, and the presence of a nucleus as marking a highest level of hierarchy is not more 'primitive' with respect to the presence of a dorsal chord, which is later in appearance and lower in level.

After Darwin, Spencer [40, p. 471] considered the arguments from classification in favor of evolution and wrote that "organisms fall into groups within groups; and this is the ar-

rangement which we see results from evolution". Later, "Tschulok also found the enkaptic [inclusive - L.V. & S.S.] nature of the biological system to provide the strongest evidence for the theory of evolution" [27, p. 313], and Hennig's phylonenetic system was recognized as an encaptic one. It was correctly noted that "Hennig's phylogenetic system can easily be read as a Linnaean hierarchy of sets within sets" and "many of the same sorts of inferences can be made with respect to both" [27, p. 315], so this favorable comparison can allow us to recognize a phylogenetic system in the *properly* constructed Linnaean hierarchy. It is not correct that "the Linnaean system... makes no reference to evolution" [3, 39], and it is only necessary to find ways to construct a taxonomic evolutionary model. Extensionally, the taxonomic hierarchy is an inclusive system of groups within groups, and this structure reflects the evolution of groups by differentiation. However, intensionally, the taxonomic hierarchy is the system of levels marked by different sets of characters appearing successively during evolution.

With respect to general schemes, the hierarchical model overcomes the difficulties of the Great Chain of Beings and allows for the *equal naturalness of all taxa* that are characterized by the same differences, from their very origin up to the present day. It does not require the notion of 'gaps', but, instead, it is based upon the *proper subordination of characters*. It does not require "a strictly dichotomous system of encapsulation" [27, p. 314] or "a logical dichotomization of the world" [24, p. 479] either, since the older groups can split into many subgroups simultaneously (cf. 'Cambrian explosion' [41] or 'Ordovician radiation' [42]). The hierarchical model conflates micro- and macroevolution, which often have been divorced in the biological literature [43], since lower and higher taxa could originate *simultaneously* in the same process of splitting.

The hierarchical model turns the Darwin's scheme of evolution upside-down, because the image of "lesser difference between varieties becoming augmented into the greater difference between species" [16, p. 112] is hardly correct, since varieties originate *within* already existing species and differ in their own characters, which are lower in level. The differences between taxa at higher levels—for example, between the animal and plant kingdoms (such as the main types of nutrition [i.e. heterotrophic or phototrophic], food reserve substances in the form of glycogen or starch, the presence or absence of cellulose in the cell walls, etc.)—seemed to separate them at the dawn of their existence and have not been 'augmented' during the millions of years since. These groups were *only differentiating into subgroups* during their further evolution and retain the differences that exist between them as the *same phylogenetic relationship*.

Notably, there are two kinds of innovations, namely *new states* of previously existing characters (as in the sequence of primitive and advanced states in ancestors and descendants), and completely *new characters* (in their own diversity of states) within existing groups. The appearance of new states is accompanied by an increase in diversity at some hierarchical level, but the appearance of new characters makes the organic world hierarchically structured. The increase of species diversity due to evolution of characters does not mean the evolution of species themselves, whereas the differentiation is almost the synonym of the evolution of all taxa. Therefore, the *evolution of species* could be described in similar terms and should be

based on their further *disintegration* into numerous populations. Of course, such a view of *species as an evolving entity* would likely conflict with some of the concepts that describe species as the "most integrated" units when compared with higher taxa. Moreover, such terms as 'reality' and 'individuality' of species are mostly discussed in association with their 'integrity', provided by some inner processes, so it might seem that exactly the '*evolutionary species concept*', representing species as a disintegrating unit, threatens other species concepts that seem to be 'non-evolutionary' ones. To overcome this possible conflict, the whole issue relating to 'reality', 'individuality' and 'integrity' of taxa might be modified by examining the hierarchical model of evolution more closely.

It already has been noted that the *increase of inner diversity* is accompanied by strong tendencies towards disintegration in time and space [44] and that "species cohesion is often guaranteed by non-reproductive factors" [45, p. 186]. Through time, species should gradually lose "one kind of cohesiveness" [46, p. 262] but keep another kind of cohesiveness, and the "*character continuity* is sufficient and testable evidence of such cohesion" [47, p. 220, italics added]. From the hierarchical model of evolution it follows that there is a *persistence of differences*, or *phylogenetic relationships*, between earlier originated groups. That was exactly Darwin's [16] understanding of *the same 'genealogical arrangement'* that exists between groups at each successive period of their modification. The groups themselves could change drastically, and one can compare the world of dinosaurs or the forest of the Carboniferous Period with modern organisms belonging to animal and plant kingdoms, respectively. From their very origin, these groups have become highly differentiated, but they remain the same. In other words, they continue as the same evolutionary units, and the *integrity* of such units is *provided by those sets of characters* that distinguish them from closely related taxa. The set of features distinguishing each taxon from its relatives at the same hierarchical level is called *intension*. Another aspect of a taxon is related to its changeable content and is called *extension* [10]. Because of the incessant changes of extensions that cause the same taxa to look so different during evolution, the *cohesiveness, reality, and individuality of historical taxa can be associated only with intensions*.

Moreover, the considerations mentioned above may destroy the *extensional* definition of monophyly in phylogenetic systematics. There is a belief that a monophyletic genus should include an ancestral species and *all* of its descendants [13, 48-49], but even if the genus at the time of its origin was represented by a single species (an ancestor of other species in that genus), it already should have been characterized by intensional monophyly (hidden in characters marking a genus appearance) and had to retain this monophyletic nature during the increase of inner diversity. In addition, the descendants of an initial species may be taxa of different levels in accordance with changes in different characters distinguishing groups of the previously originated hierarchical diversity. Just this case was described by Darwin [16, p. 401] as follows: "Nor can the existing species, descended from A, be ranked in the same genus with the parent A." The unification of all descendants into a single genus would result in an unnatural classification. Therefore, the only acceptable definition of monophyly may be associated with intensions, or defining characters that also show the common descent of members. Moreover, the intensional monophyly causes the notion of paraphyletic

taxa completely to be both useless and superfluous. In taxonomy, the phrase "Much of life's history consists of *non monophyletic ancestral taxa*" [50, p. 413, italics added] would mean that the *proper* intensions of 'ancestral taxa' providing their monophyly are not to be found.

Now, what about the debates that surround the species problem and exhaust the energy of biologists? There is no place here to discuss all of them, and we only refer to "a sterile debate about whether species are individuals or classes" [51, p. 191]. We can admit that species are individuals with respect to evolutionary theory [52] and this is in agreement with the hierarchical model of evolution. However the narrow form of "the individuality thesis" as advocated by Ghiselin [53-54] is so inadequate for biological systematics that Ruse [55] believed Ghiselin to be 'dead wrong' in this matter, while Kitcher [56, p. 649] wrote that the 'species-as-individuals' thesis is "one of the least-promising suggestions in recent philosophy of science". It was even suggested [57: p. 456] that modern evolutionary theory does not require species to be individuals and "does not require species at all, only lineages". However, the hierarchical model of evolution requires 'species' as one of lower levels in the genesis of a nested hierarchy of groups, while all evolving taxa are necessarily individuals (with the promising aspect of individuality associated with intensions).

The opposition of individuals and classes usually has been described from the perspective of spatiotemporal location. It is said that biological species have been treated traditionally as spatiotemporally unrestricted classes, but they must be spatiotemporally localized individuals [58]. However this opposition can appear in a different light from the perspective of intension and extension. Intension (as a set of features) makes a class of a species, but intension has its origin in time (at the point of speciation) and keeps together organisms scattered in space, so the class-forming aspect of species is deeply related to spatiotemporal localization of a species. On the contrary, individuality and spatiotemporal restriction would be expected from extensional relationships, but precisely indefinite extensional changes in the number, structure and relations of populations (with the increase of inner polymorphism) make 'rivers' of species flowing through time and space within the 'banks' of the same differences. Thus, *species evolution* is completely extensional (internal), and species cannot be "spatiotemporally restricted" in this aspect (cf. also '*spatiotemporally unrestricted [nature] of evolutionary theory*' [58, p. 354, italics added]).

The popular belief that "classes cannot evolve" [5, 59] is not pertinent to biological taxa, since they are classes of a special kind—they are the constituents of the hierarchically evolving organic world. Their intensions comprise an evolutionary sequence themselves and, simultaneously, *direct* the internal (extensional) evolution of taxa, *defining their internal diversity*. (Surely the main kinds of nutrition—photosynthetic, osmotic, digestive—which early separated such groups as plants, fungi, and animals did not allow the members of those higher taxa to have the same features at lower levels. By analogy with this influence, the internal or external skeleton of animals defines a completely different diversity of forms, say, within the phyla Chordata and Arthropoda). From this perspective, the opposition of single-level relationships (the so-called "hierarchy" of species lineages) and the Linnaean hierarchy (which should be properly constructed to embody the *natural hierarchy of intensions*) as having "directional and temporal dimension" and being "atemporal and non-directional" [27, p.

311], respectively, should be read inversely. The dichotomies connecting species in cladograms look much more atemporal and non-directional (often simply appearing meaningless) than the "phylogenetic hierarchy of groups within groups" (l.c.) characterizing the true taxonomic hierarchy. At least the latter allows us to understand the *directional and temporal* influence of older characters (which are higher in level) on the appearance of later ones during evolution. Moreover, the dichotomous trees constructed for a particular group of species could be numerous, whereas the phylogenetic hierarchy should be a single one.

4. Concept of a character and character-based concepts of species

The practice of taxonomy is surely at odds with the suggestions to reject, abandon, or replace the Linnaean system [38-39, 60-63]. One of the reasons of rejecting the latter is an observation that there is no clear distinction between species and higher taxa, and that species are *non-comparable* entities [64]. Indeed, there is no distinction between species and higher taxa, since the former can evolve (differentiate) into the latter while the organic world develops [16, 23], but, for taxonomists, the deep distinction between categories of the Linnaean system is different characters marking different levels. Moreover, taxonomists can make species (and other taxa) *comparable* entities, and this, again, depends upon dealing with characters. In fact, characters are *all* that matters most to taxonomists, despite what we have been told about "the poverty of taxonomic characters" [65]. Of course, characters by themselves can be miserable, and only their correct distribution among hierarchical levels can help us to develop a natural classification. The *characters* are the main "building bricks" in taxonomy, not 'species', although the latter were assigned such an important role [66].

Long ago Darwin supposed that simply being a competent taxonomist was enough to have 'good species', but competent taxonomists often disagree about their species or genera to a greater extent than incompetent ones, since the latter simply follow, often unquestionably so, the concepts proposed by the former. What would be most attractive to a taxonomist in Darwin's views is "his character-based view of species" [17, p. 503], although Darwin himself was hopeless in dealing with characters. Moreover, the *Origin of Species* contains a number of phrases about species that are not based on characters. Thus, he wrote 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" [16, p. 68]. However, the number of individuals (extensional characteristics of a group) is not a basis for recognizing a group as 'species' or 'variety'.

"What was required to sort out the... multiplicity of characters was a *theory of taxonomic characters*" [24, p. 480, italics added], but exactly such a theory is wanting in the science of taxonomy. We do not have a claim here as to the full development of the character theory, but we can think of two concepts that require the consideration as a first step. These two concepts are (1) the character concept and (2) character weighting (= ranking). Although "characters are among the most fundamental units we use to systematize the things in our world, together with ideas about species" [67, p. 2], there are many notions about characters which

are unsuitable for taxonomic theory. "A preliminary definition of a character that could temporarily serve as a guide through the jungle of ideas and observations around the character concept" suggests that "a *biological character* can be thought of as a part of an organism" [67, p. 3. italics added], but this is not the definition of a taxonomic character. The definition given above is considered to be "broader" than "the narrow definition of a character in systematics" (l.c.), but, actually, that "broader" sense, when associated with systematics, was always the source of confusion, since *taxonomic characters are not parts* of organisms. As in the case of the species problem, the biological "burden" in the character problem prevents the construction of a natural system.

The *taxonomic* character concept also has narrow and broad meanings, and the first of these tends to dominate. In its narrow meaning, a 'character' is merely a feature or any attribute of a member of a taxon [15, 68-69], and many biologists have expressed its inadequacy for taxonomy. They have tried to make a shift from 'organismal traits' to 'phylogenetic relationships' [11], but the wider character concept also was proposed long ago, and it even covers 'phylogenetic relationships' as a particular case. In a wider meaning, a character is an independent variable consisting of mutually exclusive character states [59, 70-71]. These states may be displayed simultaneously, as in Mendelian inheritance, or, being apomorphic and plesiomorphic [72], they may follow each other in time. The main consequence of the broader character concept is that it is a *partial basis* for making taxa *comparable* in their hierarchical levels: *Taxa of equal rank should be characterized by different states of the same characters*. [When we say "a species differs", this means "from other species", since a species cannot "differ" from a genus (being a subordinate unit) or a variety (being a super-taxon). This rule excludes the distribution of plesiomorphic and apomorphic states of the *same* characters among different hierarchical levels [24, p. 482].

The character in a broader sense means a *discriminative relation between* taxa and represents a "unity in diversity", whereas the narrow sense of a "character" is related only to similarity *within* taxonomic groups. The broader concept is always of greater importance for any theory, and the broader character concept removes, for example, the opposition between the Linnaean hierarchy supposedly based on 'intrinsic' properties and Hennig's hierarchy based on 'relational' properties [27]. The Linnaean hierarchy is based on the ranking of *characters in all the diversity of their states*, so it is also based on relational properties. If only the narrow character concept is the focus, rather limited species concepts appear, and one of them is a "biosimilarity species concept". We believe the discussion of this concept to be highly productive [5], especially because it admits the *ontology of similarity relations* (contrary to the dismissive attitude to 'organismal traits'). However, this concept is not very helpful for dealing with species diversity in nature. Apart from the fact that it fits a taxon of any level, this concept does not make an important discrimination between intensional and extensional similarity.

The main problem with the extensional similarity of characters comprising an *internal* polymorphism in closely related taxa, for example in genera within the same family, is that it greatly overweighs few differences between those taxa. The most famous examples are Vavilov's studies of variation within genera of several families of vascular plants [73]. Thus, he has counted more than *hundred* of the same features repeating themselves *within* such gen-

era as *Secale*, *Triticum*, *Hordeum*, *Avena* (and others), which differ in very few characters. Vavilov's law tells us that species and genera that are genetically closely related are characterized by similar series of heritable variations with such regularity that by knowing the series of forms within the limits of one species, we can predict the occurrence of parallel forms in other species and genera. The more closely related the species in the general system, the more resemblance there will be in the series of variations. However, despite the fact that extensional similarity can serve as an indicator of close relationships, the employment of similar internal polymorphisms for the unification of organisms would entail the use of artificial groups instead of natural taxa. Exactly such an unfavorable situation exists in many current molecular studies, since the extensional similarity in molecules should be even higher than for morphological features [74]. The discrimination of intensional and extensional similarity of taxa requires the distribution of characters among hierarchical levels, but this is impossible when the focus is on the 'species problem'.

Another character-based concept, rather popular today, represents species (and higher taxa) as natural kinds. In a wider sense, this concept seems to be the familiar class-concept, judging from discussions that have appeared in the biological literature. Thus, classes and individuals have been opposed in the 'species problem' before, but now natural kinds take the place of classes in this opposition. Also, in an analogous way, natural kinds, similar to classes, are thought to be supposedly incapable of undergoing evolutionary change, and it has been noted rather clearly that "species had originally been considered as *classes or natural kinds*" [59, p. 78, italics added]. Here, we want to emphasize that the traditional opposition of 'classes' and 'individuals' was based upon the false opposition of intension and extension; it was false because two different aspects of taxa do not constitute a polarity. As pointed out in the discussion given above, the *intension of each evolving taxon* is the *class-forming and individual-forming* aspect of such a biological unit *simultaneously*, so the intensional consideration does not contain any opposition between classes or individuals. In this respect, our attitude deviates from some older one-sided views of biological taxa and, moreover, represents the traditional concept of species as natural kinds in a different light.

What is wrong with an interpretation of biological taxa as natural kinds? The main features of the latter were described as follows [59, p. 79, italic in the original]: "(1) All members of a natural kind have the same characteristic properties... (2) The identity and boundary of a natural kind is *metaphysically* determined by an essence... The first condition does not apply to species as there is substantial variation across the members of a species, and even a feature shared by all conspecifics at a time may be modified in evolution." Let us look more closely at the first objection to natural kinds as it is applied to species. This objection does not seem to be valid, because it does not consider intensional and extensional changes during the evolution of species. The fact that each taxon can possess a substantial internal variation in its extension does not exclude the presence of some characteristic properties in its intension, and when intensional features are modified in evolution, new taxa of the same level appear. Now, what about the second of the two "wrong" characteristics of natural kinds? "In the case of the second condition,... an essence has typically been taken to be an *intrinsic* property of a kind member, as in the case of chemical structure. But no intrinsic

property (= internal feature) of an organism — be it genotypic or phenotypic — can serve as the definition of its species..., as other species members have or may evolve different features" (l.c., *italic in the original*).

As indicated, different features in the members of a particular species are observed in an extensional aspect (species content), so this is not the reason for the failure of 'intrinsic' properties in intension. What is more important here is the fact that *all* of the available *properties* of organisms may define taxa at different levels (and be 'essential' at some level), so there is no need to look for special 'intrinsic' properties. The intensions do really define the *identity and boundary* of taxa since the differences between earlier appearing taxa are not disturbed by either their differentiation into subgroups or the appearance of new taxa of the same level. The position in which some features determine a taxon's identity was considered to be a version of essentialism [75-76], and this might have a negative taste for many biologists, but the *science of taxonomy* was born in the framework of essentialism. More productive than the struggle with essentialism is the search for points for its compatibility with the evolutionary development of a biota.

From the considerations outlined above, it follows that the old concept of natural kinds could be—with some reservations (about intensional and extensional aspects)—applied to taxa, but its alleged failure has stimulated the appearance of a new concept of natural kinds, describing them as "homeostatic property clusters" [59, 77-78] and directed towards the biologically meaningful units. At first inspection, the new concept also might seem to remove the old opposition of classes and individuals based on an opposition between intension and extension and to make the shift of individuality to intension, which was discussed earlier. Thus, the *cluster of properties* should determine "the identity and boundary" of a taxon across time and make it a "cohesive entity" [59, p. 80]. However, the discussion of proponents of the new concept have repeatedly slipped back into extensional considerations of cohesiveness. For example, "gene flow" is mentioned as "one of the several features determining a taxon's identity" [59, p. 82], although such processes as gene flow or interbreeding occur in the extensional space of taxa and should have nothing to do with the concept of intension as a cluster of properties. In addition, the "new philosophical notion of a natural kind" has been said to attempt "to reconcile the fact that such kinds are *cannot be defined by necessary or sufficient conditions...*" [59, p. 79, *italics added*]. However, this is exactly the old objection against natural kinds (or classes) altogether, so the "new" concept does not have any advantages.

There is even an impression that the proponents of the new natural kinds look only for extensional 'cluster of properties (= processes)' and this does not distinguish them from the advocates of the extensional 'individuality thesis'. In other words, they admit the notions of "individuals" and "classes" to encounter *metaphysically* (in Brigandt's [59] words) within extension, whereas we associate both these notions with intension. That's why we agree with Brigandt's view [59] that both approaches to taxa (as individuals and classes) are compatible but on the different grounds. There is also a trend in phylogenetic taxonomy that involves *extensional considerations* when taxa are thought to be defined "*intensionally*". Thus, De Quieroz [11, p. 304] wrote that "intensional phylogenetic definitions" have a focus "on the parts [of taxa - L.V. & S.L.] and the relationships that unite them to form the whole", and the relevant

process responsible for the unification of populations to form a whole of a particular species is indicated as *interbreeding* (l.c.), whereas higher taxa are supposedly united by the relationships between ancestral and descendant species. However, such relationships cannot "form the whole", since the "whole" is earlier in origin and might exist in an undifferentiated state similar to an egg prior to embryogenesis. That was really a trick to consider the extensional relationships *within* taxa as their "defining properties" [11, p. 305], and that, once again, reconciled the opponents in the debate whether species are classes or individuals. Such a 'phylogenetic' approach [11] to taxonomy coincides with the "new concept of natural kinds", and we have already emphasized the dominance of extensional thinking in biology [35], especially in the 'species problem'.

5. Character weighting and ranking

The problem of character weighting in taxonomy is much more important than the species problem, but it is not so popular among biologists. At present, this problem is complicated by an unfounded belief that "molecular techniques have provided a powerful new tool to independently *evaluate the validity* of taxonomic designations" [2, p. 67, italics added], although molecular characters still need to be evaluated themselves. It is really interesting that same authors [2, p. 74] suggest that "abandoning the concept of species" and replacing "the current artificial views of life with a system that describes groups of organisms based on the amount that they differ from other groups" would be an appropriate course of action. Unfortunately, using the 'amount' of difference as the delimitative basis for classifying taxa strongly reminds one of a 'gap' and thus has no meaning in taxonomy. It is not the 'amount' of difference but rather the weight assigned to the differences that matters.

It has been correctly understood that "weighting was, in fact, at the heart of taxonomy" [79], although practical taxonomists were doing weighting rather intuitively, and the theoretical basis for this process was not properly developed. Moreover, the earlier suggestion by Adanson to assign an *equal* weight to characters [29]—which is incompatible with the taxonomic hierarchy that is based on admitting the higher or lower position of characters instead of their equality—was appreciated as the anticipation of the advent of evolutionary theory [19]. This situation, again, shows that biologists failed to perceive the character hierarchy as the *only* evolutionary sequence reflected by a taxonomic system.

Apart from the complete denial of character weighting, which is surely most unproductive, there has been an array of opinions about character values. For example, there was an observation that "any character that varies in a particular case cannot have general value" [29, p. 33]. In Darwin's notebooks, one can find the following sentence: "Definition of species: one that remains at large with constant characters..." [7, p. 131]. The constant characters were always highly evaluated, but we should keep in mind that a character in a broader sense might be always changeable in its states and *always the same as the discriminative relation* between groups, so all characters are variable and constant simultaneously. As for particular character states marking particular taxa, they might be variable or non-variable at different

levels, but this does not influence their usefulness. Variable states can be very valuable, because they characterize taxa on the basis of *certain ranges of variability*, which sometimes repeat themselves in different species of the same or different genera within a particular family with a remarkable regularity. So, the constancy or variability of characters (and their states) does not influence their comparative importance for taxonomy.

Further, there is a belief that "unique characters have a real taxonomic weight" and that "we can attach some importance to shared rarity" [80, p. 350, 354]. This conviction was a key to the development of the cladistic notion of 'autapomorphy' (as a unique trait characterizing a given taxon), and even the 'autapomorphic species concept' was suggested [81-82]. However, a unique state of some character can be of weight at the species or genus levels only in those instances in which other states of that character have the same relative importance (see below). Otherwise, unique states lead to the haphazard segregation of taxa that are non-comparable in level. Exactly this chaotic practice is recommended in current molecular taxonomy, and people think that such phrase as "This species is *distinguished by this gene from all others* in the species complex..." [83, p. 325, italics added] is a good discriminative basis. Some biologists are anxious about situations in which there is "the move away from providing character evidence with phylogenies" [84, p. 26], and they state that it is "time to show *some* character". However, "some character" might be of no importance at the level in question. As such, we need numerous characters that should be properly distributed in the taxonomic hierarchy.

"A connection between the taxonomic importance of a character and its function" also has been considered by some biologists [29, p. 82], and very often the fundamental importance of characters to the life of organisms was confused with their taxonomic importance. In taxonomy, the *function of all characters* is to discriminate groups at different hierarchical levels, and the importance of some trait for the functioning of some organism is not relevant. Besides, in this matter, there is some misunderstanding about the nature of taxonomic characters. For example, the fruits of flowering plants are functionally important as the protectors of seeds, but when taxonomists use fruits for comparisons, they use such characters as *the presence or absence* of fruits (in the rough division of seed-bearing plants), *simple vs. compound* (i.e. formed from a single or several ovaries or carpels) fruits, *fleshy vs. dry* fruits, *dehiscent vs. indehiscent* fruits—at lower (and different) taxonomic levels. On one hand, taxonomists use characters that are mostly irrelevant for the functioning of plants, and organisms with dehiscent or indehiscent fruits are likely to be doing equally as well. But even if, on the other hand, the character is as important as the presence or absence of the protection provided for seeds, one can understand that a *taxonomic character* is not a trait of an organism, it is *something* that exists only in opposite qualities and quantities.

The most valuable characters are considered to be those which are indicating relationships [29, p. 122], but exactly *all characters indicate relationships, although at different hierarchical levels*. So, the weight of a character has nothing to do with the description of a character itself (its constancy, uniqueness, importance for an organism, etc.). Instead, *the weight of a character reflects its position in the taxonomic hierarchy*, and the weighting should come to *ranking*. That is the gist of the whole subject of taxonomy, but the problem of character ranking has never

been solved completely: "The establishment of *principles* that would allow a proper subordination of characters remained a desideratum" [29, p. 123, italic added]. Strangely enough, a ranking has been considered by some biologists as something that is "simple" and "must be gone beyond" [84]. Hierarchies that fulfill the desideratum are believed to be "hierarchies of embedment in which the components of each level interact in such a way that novel properties are expressed at higher levels" [85, p. 121]. However, this statement cannot be applied to the taxonomic hierarchy as a hierarchical *model of evolution*. Not a single interaction between components of lower level (e.g., species) can define the expression of novel properties at a higher level; on the contrary, properties of higher levels appear earlier in evolution and define the appearance of properties at lower levels, including some of their interactions.

There has been at least one general principle consistently used by biologists in their classifications, namely the 'principle of generality': "the more general characters marking out more inclusive groups, less general characters marking out subordinated, less inclusive groups" [24, p. 479]. Exactly this principle reflects the evolutionary sequence of characters, since groups of lower level with their less general characters appear within groups that appeared earlier. As a result, biologists can have a kind of 'rough' hierarchy reflecting the stepwise development of the organic world. However, really "heavy" characters marking certain steps or levels of evolution did not originate frequently, and after the initial great evolutionary events there was an increase of diversity at lower hierarchical levels along with the development of characters into states and a combination of character states. Even with few characters possessing several states, the combinatorial variation might lead to large numbers of species and genera. This combinatorial variation is the cause of reticulate relationships between taxa at the same level and has nothing to do with "reticulations" caused by hybridization, simply because the combinations appear as the result of an usual divergence of characters [36].

Now, if the evolutionary sequence of characters can help us to construct the axis of a taxonomic hierarchy, the combinatorial variation of states at each level can provide the "principle" of finding numerous *taxa of equal rank*. The problem inherent in all taxonomy is the chaotic employment of the differences that exist between groups, especially between species and genera, and this does not allow them to be comparable in rank. To overcome this difficulty, we have suggested a special method for the weighting of differences that can be considered as a *posteriori weighting* or *test for rank equality* [32]. The analysis begins with the available diversity of *tentative* species or genera segregated by taxonomists chaotically, so that some of them might represent 'good' taxa at their appropriate level, whereas others need to be united or separated. All of the tentatively described groups represent *taxonomic hypotheses* for us. These hypotheses might be deduced from very different *a priori* considerations, including morphological, ecological, biogeographical, even those that are associated with reproduction in case of 'species'. The groups could be *very unequal extensionally* (i.e. they could be small and large), but they should be *equal intensionally* if we call taxa of the same level 'species' or 'genera'.

What is most important is the *estimation of differences* between already segregated groups, and since this estimation is carried out *after* group formation, the testing or weighting is of a

posteriori nature. In this process, the most "heavy" differences are those that most frequently participate in the delimitation of species within a genus or genera within a family. In our experience, it appears that very few characters are sufficient to outline the majority of already established species and genera, and not many of the previous taxonomic hypotheses need to be re-considered. As a result, *taxa at each level came to be defined by state combinations of the same character set*, and the characters of each level produce the multidimensional combinatorial space of states. This procedure of testing for rank equality can be used for an evaluation of different taxonomic schemes. Each particular classification before *a posteriori* weighting could contain 'good' and 'bad' elements, but in comparing some of them, the approach used can be either eclectic and based on subjective choosing of 'good' elements from all schemes or be synthetic and based on objective *self-coordination* of taxa defined by a *single character set*. Linneaus was completely right when he wrote that "every genus is natural...; it is not to be capriciously split or stuck [to another], for pleasure,... especially *a posteriori*" [86, p. 114, italics added].

One could regard these considerations as 'operational' and not 'ontological', but they have a number of implications for taxonomic and evolutionary theories. First of all, the resulting combinatorial arrangement at each level (after weighting) might possess a very high prognostic power and thus allow us to predict taxa with certain combinations of features. Such predicted combinations are often found to occur in nature, and we have never described a new species or a new genus without checking the existence of an 'empty' place for it in the network of combinatorial space. It should be noted that a prognostic value was required from a *natural* system [87], and this might impart the necessary ontological sense to single-level combinatorial arrangements. At the same time, the employment of a single character set for delimitation of taxa at each level allows us to have a 'fundamentum divisionis' that is *necessary for the logic used in classification* [88]. In the case of small genera where species are not numerous and sometimes cannot be arranged within a combinatorial space, a taxonomist can make a comparison with a large genus within the same family (or order) and evaluate equally the same differences between species within small and large genera. Such an approach will conform to Vavilov's law of homologous variation occurring within closely related genera.

The combinatorial arrangements might help resolve several useless debates encountered in the taxonomic literature. For example, the opposition known as "a single difference vs. many differences" for outlining particular groups is hardly adequate, but even today reviewers may reject some manuscripts because a species or a genus is described on the basis of a single difference. However, the whole set of characters is used to distinguish groups at each level, and the combinatorial space of their states is constructed on the basis of many differences, whereas *each taxon* within that space *differs from a neighboring one* (along the line of character states) *in a single difference*. So, it's quite permissible to indicate only one difference between a new species or genus and its nearest taxon, if the states of a delimitative character belong to a weighted discriminative complex. Thus, characters are of highest value at some level if they are most frequent, and their *unique* states characterizing particular groups also are of great importance. On the contrary, if we encounter some character that

occurs very rarely in group delimitation, its unique states are mostly of no value at all. Therefore, one cannot apply thoughtlessly the "autapomorphic species concept" to the analysis of species diversity.

There is also an unfounded appraisal of apomorphic states to the prejudice of plesiomorphic ones. We have explained the origin of combinatorial (reticulate) relationships as the result of the initial divergence of characters into states in different descendants of the same ancestor and the subsequent combination of primitive and advanced states during further evolution [36]. We also have emphasized that the resulting combinations can include only one combination of exclusively apomorphic states and only one combination of exclusively plesiomorphic states (an ancestor), but all other ones are mixtures of apomorphic and plesiomorphic features. Therefore, any unification of these entities into a higher taxon on the basis of 'shared similarity' (apomorphy) will lead to artificial groups.

It has been supposed that the obligate reticulation in relationships "effectively invalidates hierarchical classification" [89, p. 583], but this is not the case. Reticulate relationships are observed at each level of the hierarchical classification and cannot be incompatible with the latter. On the other hand, taxa of the same level also can be connected by a key-like structure, or cladogram. In this respect, reticulations could be considered to be in opposition with *single-level* 'trees', although these arrangements do not exclude each other. The main problem here is that the combinatorial space contains repetitive character states in all directions, and the different ways of folding that space into tree-like structures along any delimitative character might divide very closely related taxa and separate them by some distance in the cladogram, or those taxa that possess the repetitive state appear to be neighbors in the 'tree', and taxonomists think they represent a 'natural clade'. In any case, the construction of cladograms strongly distorts the multiple relationships that exist between taxa on the same level.

6. Some words about essentialism

Essentialism as a "philosophical idealism" [90, p. 217] was associated with the typological theory that "stems from Plato and his sources" [91, p. 46] and implies the existence of static 'patterns' shared by all members of a particular group. These 'patterns' or 'types' correspond to Plato's 'ideas' (or 'forms') and those examples of Aristotle's 'essences' that were identified with 'differences' (cf. "the *definition* is the formula of the *essence*" and "the *definition* is the formula which comprises the *differentiae*": *Metaphysics* 7, 1031a, 10-15 & 1038a, 5-10, italics added [92]). Hence, the 'essences' of taxa were designated as sets of *distinguishing* or *defining* characters.

Two problems have arisen with respect to such 'essences' and the consequence of both is the conviction that any classification is completely arbitrary. The first problem related to the uncertainty about 'defining' or 'essential' characters; and such an uncertainty led to the creation of numerous artificial groups of organisms chaotically segregated on the basis of subjectively chosen characters that seemed to be 'essential'. This problem could not be resolved without evolutionary ideas, but the advent of the latter did not help and only created the second

problem. Instead of an elaboration of a program with the purpose of searching for essential characters, the very existence of 'essences' was rejected. It was noted that evolutionary theory "necessarily challenged the ontological assertion that species as Forms existed" [19, p. 318]. Consequently, taxonomists were forced "to abandon Aristotelian definitions of taxa names" [19, p. 317] in terms of essential characters that are shared by all members of a given taxon. In fact, the solution to essentialistic "mysteries" could be found in the "practice of weighting some properties more heavily than others because of their varying phylogenetic significance" [19, p. 316], but all the practice and theory went in wrong direction.

It has been supposed that "the concept of distinct and static patterns cannot meaningfully be applied to real groups of organisms, which are parts of an evolutionary continuum and which are always highly variable", and that "typological theory... should have no part in modern taxonomy" [91, p. 50]. Contemporary generations of biologists have been trained to believe that "*typological thinking* is the other major misconception that had to be eliminated before a sound theory of evolution could be proposed" [93, p. 4, italics in original]. In a real sense, this statement has proposed to eliminate systematic foundations for the sake of evolution theory. Later, Mayr [94, p. 145, 156] wrote in an assertive tone that "biological species... have no essence", because "the outstanding characteristic of an essence is its unchanging permanence". Therefore, "it was precisely the variability of species populations that led to population thinking, a dramatic departure from essentialism." [94, p. 156].

Terms such as 'essentialist' or 'typologist' rapidly became disgraceful and abusive, so that systematists are completely intimidated to remain silent. Some scientists have ventured to vote for essentialism [20, 95-100], but their opponents simply ascertained their effort as an "unfortunate attempt to reintroduce essences into systematics" [101, p. 110-111]. The latter were partially right because, very often, non-*classificatory* 'essences' were reintroduce (for example, the 'genetic code' [97]). Such 'essences' were correctly thought to be quite different from "Platonic or Aristotelian essences"; and the main advantage of the former was seen in the fact that they contain "nothing metaphysical about them" (l.c.). This fear of metaphysics seems to be the most striking characteristic of contemporary theorists, but systematics actually needs precisely '*metaphysical* essences' for the ordering of natural diversity.

Sometimes, the defenders of 'essences' are forced to make various reservations to convince readers that their attitude has nothing to do with what Mayr calls 'essentialism', and they do not ignore variation and evolution [102, p. 52]. Others [103, p. 446] have distinguished 'good' essentialism with the fruitful idea that species taxa are classes and 'bad' essentialism, a "virulent version of essentialism" or "typological essentialism". Curiously, 'good' essentialism is associated with the class concept (i.e., with 'types' as sets of properties), while 'bad' essentialism is what has been referred to as 'organismic' essentialism [104] dealing with 'types' as particular things or organisms. The latter 'typology' which considers only type specimens (valuable exclusively for the purposes of nomenclature) sometimes becomes a 'virulent version' of essentialism indeed, because it obscures the advantages of Plato's typology. Lidén and Oxelman [105, p. 183, italics added] wrote that «nomenclatural types allow us to free systematics from *typology*»; thereby, the good practice of the 'type method' is placed in opposition to the very core of classification and becomes an 'enemy'.

Caplan and Bock [103, p. 446] agreed with Mayr that "typology has hindered the development of evolutionary and other theories in biology and that it has no conceptual role in modern biology". Such a criticism is only relevant to the set of ideas surrounding 'typical organisms' but is directed against Plato's typology. Moreover, Caplan and Bock believed that "quite possibly typology as advocated by Plato has no role in any area of science" and that Plato's philosophy is merely "a ghost, long since dead, buried and forgotten". They [103, p. 453] announced "the funeral of Plato's ghost", but one can only be surprised at such a low estimation of Plato's ideas that have been, are, and always will be the one of the most fertile and vital components of the theory of knowledge, which includes the classification of objects in the world. Precisely typology as advocated by Plato has role in any area of science; it cannot be dead, buried and forgotten at all. Biologists have been appreciated for their struggling with older philosophical traditions [106, p. 185], but such an arrogant orientation is most fruitless and disastrous for the development of science.

Plato was a philosopher of primarily universal thinking; his 'ideas' or 'forms' make sense only in the world of estimations, and classification is precisely such a world. *Plato's 'ideas' are 'characters' in the diversity of their particular states* (cf. *Parmenides*, 132c-d [107]) of many levels that determine the place of a particular thing among others. This place is not the place of a thing (an organism) in the 'economic of nature' (for example, a tree in the nearest forest); instead, it is the place of a thing (an organism) in the *whole world of existing differences*. Beyond comparison and reasoning, one cannot see the 'idea' (or 'essence') of a 'thing' (cf. *Theaetetus*, 186d-e: "knowledge does not consist in impressions, but in reasoning about them" [107]). Aristotle's essentialism was more complicated; he preferred particular things but *could not* avoid universals in discussions of *species and genera*. In the latter context, Plato's 'forms' repeatedly appeared in Aristotle's metaphysics, and Aristotle even wrote that "nothing... which is not a species of a genus will have an *essence*—only species will have it" (*Metaphysics* 7, 1030a, 10-15, italics in original [92]).

Although Aristotle "dissected fishes with Plato's thoughts in his head" [108, p. 136], biological systematics assimilated mainly the part of his metaphysics relating to the equation of 'thing' and 'essence' ("Each thing... and its essence are one and the same"; *Metaphysics* 7, 1031b15-20 [92]). Since taxa became to be perceived as 'individuals' (i.e. 'things' of a kind), the equation cited above led to the shift from relationships between taxa to the search for 'essences' *within* isolated taxa, and naturalists tried to figure out what is represented by a 'typical organism'. However, the enterprise was completely hopeless: there were no typical organisms to be found, and when the high diversity of members within a group was observed, a most fantastic 'type' was invented. It was either an 'average' caricature (schematic figure of a plant or an animal) or a chimera combining all the variability of organs in different individual organisms [109]. In both cases, 'types' were unreal, and this kind of 'typology' was justifiably criticized because, being merely an exercise in imagination, it could not help in the construction of the natural system. More than that, those unreal 'types' led to the conviction that the only real 'type' is a type specimen [15]. This created a second variety of 'organismal' typology (although with the same equation of 'essence' and 'thing') that has nothing to do with classificatory typology.

As a result of inventing such an image of 'typology', biologists and philosophers began to criticize their own fantastic notions and, what is worse, the imaginative 'ideal organism' became to be associated with Plato's 'ideas' [110, p. 501]. In addition, some authors accused Plato's essentialists of requiring that "type specimens represent the 'typical' species member" [111, p. 465]. Others, on the contrary, separated the platonic line of thought (or 'class interpretation') and the practice of 'type' specimens and wrote that "on the class interpretation, the role of particular organisms as type specimens is anomalous" [58, p. 353]. It is true that specimens cannot be 'types' of taxa, and—to continue Hull's statement—one can read that, on the class interpretation, "the role of lower taxa as types for higher taxa is even more anomalous" (l.c.). Here, a typologist of the platonic line would even more emphatically agree, because lower taxa *cannot* be 'types' for higher taxa indeed. Taxa of all levels have their own types (different sets of characters). Furthermore, Hull (l.c.) put in opposition "class interpretation" and "historical entity interpretation", but, as was emphasized above, the class interpretation allows historical entity interpretation because 'essences' (as sharing traits) are often the only indicators of such entities (how to find 'essences' is another matter).

In fact, all 'pitfalls' of essentialism originate from misunderstood 'essentialism'. Grantham [111, p. 464] wrote that, in his critique of 'essences', he followed Sober's "important insight", but the reading of Sober's papers [112-113] does not leave a negative impression. Sober [112, p. 355] even noted that "the mere fact of evolution does not show that species lack essences" [112, p. 356], and that "if essentialism is simply the view that species have essential properties..., then the doctrine remains untouched (by Hull and Ghiselin)" [112, p. 359]. Nevertheless, Sober [112, p. 370, italics added] believed that "far from ignoring individuals, the typologist... focuses on individual organisms as the entities which possess invariant properties". In our opinion, this is a quite untenable view of the typologist. The 'invariance' of the *organisms* belonging to a species was not maintained by platonic typologists, since things are "almost always changing and hardly ever the same, either with themselves or with one another...; they are always in a state of change" (*Phaedo*, 78e-79, italics added [107]). The 'essentialist theories' about 'essences' have treated the latter as something more than merely properties that are common to some group of objects because 'essences' were supposed to cover the opposite properties, too. Plato's theory of 'forms' repeatedly represented an 'essence' as the 'unity of opposites'.

Thus, 'essences' are not 'invariant properties' in particular individuals; they are 'invariant' (the same) units (unity of opposite properties) and, in addition, they are 'themes' with variations. 'Essences' consist of evolving characters and also could be called 'individuals', taking into account Ghiselin's [114, p. 303] statement that "if something can evolve, it must be an individual". Therefore, nothing supports Sober's [112] view that 'the essentialist's method of explaining variability' failed. Interestingly, Sober [112, p. 381, italics added] believed that "essentialism pursued an *individualistic (organismic) methodology*, which population thinking supplants by specifying laws governing objects at a higher level of organization". This only demonstrates how deeply Aristotle's 'organismic' essentialism is rooted in modern biology and how carelessly it is deduced from Plato's essentialism which could be called 'classificatory essentialism'.

7. Conclusions

It has been said that the treatment of the species problem is seriously unbalanced because the biological aspects of the problem are quite strong, but the philosophical aspects are very weak [5, p. 4]. When trying to show that the interactions *within* species (i.e. the very "biological aspect" that was always the primary focus) are of no consequence for the construction of a natural system and for the segregation of natural species themselves, we seem to make a shift to the philosophical aspects. Moreover, trying to show that only the weighting of *differences* between groups matters, and taking into account that 'differences' (or delimitative characters) are *ontological relations* between groups, we return the biological 'species problem' to the 'theory of universals' [52] and the wider field of metaphysics [5]. Ghiselin [114, p. 304] stated that "we are still being metaphysical, albeit opting for a better metaphysics". He is right in that bad 'metaphysical' beliefs that "have no heuristic value" [91, p. 49] dominated biological systematics for a long time, but we may hope for a better metaphysics.

In the light of the discussions outlined herein we can answer some questions in a peculiar way. "(1) Should taxonomic classification proceed in terms of descent alone or on the basis of similarity (cladism versus gradism)? (2) If classification rests on clades, are homologies (apomorphies) indicators of history, or are they patterns that are evidence in favor of a historical reconstruction but not themselves a model of evolution? Briefly, this is the distinction between ontological and epistemological notions of classification" [7, p. 208].

First, our classification proceeds in terms that are neither 'cladism' nor 'gradism', and both 'descent' and 'similarity' are represented in intensions distributed among different hierarchical levels along the evolutionary sequence of novelties. Second, classification can be based on 'clades', if 'clades' are defined by combinations of character states at different hierarchical level. Apomorphies, of course, should not be considered "themselves as *model of evolution*", since the latter term is applied only to the whole taxonomic system, whereas apomorphic and plesiomorphic states of the same character are of equal weight (equal rank). Lastly, we believe that our epistemological notions of classification are not divorced from ontological ones.

There has been an opinion expressed that "a species concept is the description of the role a species plays in the household of nature" [115, p. 99], and we have tried to show that the only role of species is to represent the biological diversity at one of the lower levels of the biological hierarchy. The theory of evolution was "invented" to *explain* taxonomic relationships, and the proper formulation of an evolutionary theory requires a good taxonomic theory as a starting point. Therefore, we wish to attract more attention to notions that are important for the development of taxonomic theory, mostly those dealing with characters and their ranking. We also wish to emphasize that the taxonomic hierarchy is *not* "a fictitious grid we place on nature" [50, p. 422]; it is the model of evolutionary differentiation of the organic world, and that evolution proceeds within the framework of differences that originated earlier in time. The notions of extension and intension can help us to trace the development of taxa and also to understand their changeable and unchangeable aspects. Some authors [116, p. 444] wrote that "the world may appear static or dynamic, discontinuous or

continuous, hierarchical or linear, as revealed by the taxic versus transformational approach". However, the taxic (taxonomic) approach does not exclude transformation, while the world is simultaneously 'static' (in intensions) and dynamic (both in extensions and intensions because the latter display variation in character states), discontinuous (in characters of different levels) and continuous (in states of characters at the same level), hierarchical (multileveled) and linear (at each level).

When discussing the failure of species concepts, we are not opposed to species in taxonomy and we do advocate their *objective* segregation or their *discovery* in the nature. Before coming up with a definition of the term 'species', biologists should check out whether or not all of their particular 'species' are described properly (i.e. they should test the tentative species hypotheses for a rank equality). After dealing with all natural diversity and testing all taxa in the hierarchy, it may appear that species represent the first level where self-coordination of taxa is possible.

Author details

Larissa N. Vasilyeva^{1*} and Steven L. Stephenson²

*Address all correspondence to: vasilyeva@biosoil.ru

1 Institute of Biology and Soil Science, Far East Branch of the Russian Academy of Sciences, Vladivostok, Russia

2 Department of Biological Sciences, University of Arkansas, Fayetteville, USA

References

- [1] Pleijel F. Phylogenetic taxonomy, a farewell to species, and a revision of Heteropodidae (Hesionidae, Polychaeta, Annelida). *Systematic Biology* 1999;48(4): 755-789.
- [2] Hendry AP, Vamosi SM, Latham SL, Heilbut JC, Day T. Questioning species realities. *Conservation Genetics* 2000;1(1): 67-76.
- [3] Pleijel F, Rouse GW. Least-inclusive taxonomic unit: a new taxonomic concept for biology. *Proceedings of the Royal Society London, B*, 2000;267(1443): 627-630.
- [4] Hey J. On the failure of modern species concepts. *TRENDS in Ecology and Evolution* 2006;21(8): 447-450.
- [5] Stamos DN. *The species problem*. Lanham: Lexington Books; 2003.
- [6] Vrana P, Wheeler W. Individual organisms as terminal entities: laying the species problem to rest. *Cladistics* 1992;8(1): 62-72.

- [7] Wilkins JP. *Species. A history of the idea*. Berkeley: University of California Press; 2009.
- [8] Dobzhansky T. A critique of the species concept in biology. *Philosophy of Science* 1935;2(3): 344-355
- [9] Mayr E. Species concepts and definitions. In: Mayr E. (ed.) *The species problem*. Washington: AAAS; 1957. p1-22.
- [10] Vasilyeva LN. Does the clash between instinct and science exist in naming nature? *Cladistics* 2012;28(3): 330-332.
- [11] De Queiroz K. Phylogenetic definitions and taxonomic philosophy. *Biology and Philosophy* 1992;7(3): 295-313.
- [12] O'Hara R. Systematic generalization, historical fate, and the species problem. *Systematic Biology* 1993;42(3): 231-246.
- [13] De Queiroz K, Donoghue MJ. Phylogenetic systematics and the species problem. *Cladistics* 1988;4(4): 317-338.
- [14] De Queiroz K, Donoghue MJ. Phylogenetic systematics and species revisited. *Cladistics* 1990;6(1): 83-90.
- [15] Mayr E. *Principles of systematic zoology*. New York: McGraw-Hill; 1969.
- [16] Darwin C. *The origin of species*. A Mentor Book; 1958.
- [17] Mallet J. Why was Darwin's view of species rejected by twentieth century biologists? *Biology and Philosophy* 2010;25(4): 497-527.
- [18] Stevens PF. An end to all things? Plants and their names. *Australian Systematic Botany* 2006;19(2): 115-133.
- [19] Hull DL. The effect of essentialism on taxonomy - two thousand years of stasis. *British Journal for Philosophy of Science* 1965;15: 314-326.
- [20] Kitts DB, Kitts DJ. Biological species as natural kinds. *Philosophy of Science* 1979;46(4): 613-622.
- [21] Loevtrup S. On species and other taxa. *Cladistics* 1987;3(2): 157-177.
- [22] Kinsey AC. Supra-specific variation in nature and classification from the view point of zoology. *American Naturalist* 1937;71(734): 206-222.
- [23] Gayon J. The individuality of the species: a Darwinian theory? - From Buffon to Ghiselin, and back to Darwin. *Biology and Philosophy* 1996;11(2): 215-244.
- [24] Rieppel O. The series, the network, and the tree: changing metaphors of order in nature. *Biology and Philosophy* 2010;25(4): 475-496.
- [25] O'Hara RJ. Population thinking and tree thinking in systematics. *Zoologica Scripta* 1997;26(4): 323-329.

- [26] Haeckel E. *Anthropogenie oder Entwicklungsgeschichte des Menschen*. Leipzig: W. Engelmann; 1874.
- [27] Rieppel O. Hennig's enkapitic system. *Cladistics* 2009;25(3): 311-317.
- [28] Rieppel O. Sinai Tschulok (1875-1945) - a pioneer of cladistics. *Cladistics* 2010;26(1): 103-111.
- [29] Stevens PF. *The development of biological systematics*. New York: Columbia University Press; 1994.
- [30] Margulis L (1991) Symbiogenesis and symbiogenesis. In: Margulis L, Fester R. (eds.) *Symbiosis as a source of evolutionary innovation*. Cambridge: MIT Press; 1991. p1-14.
- [31] Vasilyeva LN. The hierarchical model of evolution. *Zhurnal Obzschey Biologii* [Journal of General Biology] 1998;59(1): 5-23. (in Russian with English Summary).
- [32] Vasilyeva LN. Systematics in mycology. *Bibliotheca Mycologica* 1999;178: 1-253.
- [33] Vasilyeva LN. Evolutionary and classificatory meanings of the Linnaean Hierarchy. In: Kryukov AP, Yakimenko LV. (eds.) *Problems of evolution*. Vol. 5. Vladivostok: Dalnauka; 2003. p9-17 (in Russian).
- [34] Vasilyeva LN. The hierarchy and combinatorial space of characters in evolutionary systematics. *Proceedings of Zoological Institute of Russian Academy of Sciences*, 2009;Supplement 1: 235-249 (in Russian).
- [35] Vasilyeva LN, Stephenson SL. The Linnaean hierarchy and 'extensional thinking'. *The Open Evolution Journal* 2008;2: 55-65
- [36] Vasilyeva LN, Stephenson SL. The problems of traditional and phylogenetic taxonomy of fungi. *Mycosphere* 2010;1(1): 45-51
- [37] Grene M. Hierarchies and behavior. In: Greenberg G, Tobach E. (eds.) *Evolution of Social Behavior and Integrative Levels*. Lawrence: Erlbaum Associates; 1988. p3-17.
- [38] De Queiroz K, Gauthier J. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* 1992;23: 449-480.
- [39] De Queiroz K, Gauthier J. Toward a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution* 1994;9(1): 27-31.
- [40] Spencer H. *The principles of biology*. Vol. I. New York, D. Appleton and Company; 1868.
- [41] Marshall CR. Explaining the Cambrian "explosion" of animals. *Annual Review of Earth and Planetary Sciences* 2006;34: 355-384
- [42] Droser ML, Finnegan S. The Ordovician radiation: a follow-up to the Cambrian explosion? *Integrative and Comparative Biology* 2003;43(1): 178-184.
- [43] Gould SJ. *The structure of evolutionary theory*. Cambridge: Belknap Press; 2002.

- [44] Corning PA. Rethinking categories and life. *The Behavioral and Brain Sciences* 1981;4(2): 286-288.
- [45] Stamos DN. Popper, falsifiability, and evolutionary biology. *Biology and Philosophy* 1996;11(2): 161-191.
- [46] Frost DR, Kluge AG. A consideration of epistemology in systematic biology, with special reference to species. *Cladistics* 1994;10(3): 259-294.
- [47] Nixon KC, Wheeler QD. An amplification of the phylogenetic species concept. *Cladistics* 1990;6(3): 211-223.
- [48] Mishler, BD, Brandon RN. Individuality, pluralism, and the phylogenetic species concept. *Biology and Philosophy* 1987;2(4): 397-414.
- [49] Ridley M. The cladistic solution to the species problem. *Biology and Philosophy* 1989;4(1): 1-16.
- [50] Ereshefsky M. Darwin's solution to the species problem. *Synthese* 2010;175(3): 405-425.
- [51] Kitcher P. Ghostly whispers: Mayr, Ghiselin, and the 'philosophers' on the ontological status of species. *Biology and Philosophy* 1987;2(2): 184-192.
- [52] Williams MB. Species are individuals: theoretical foundations for the claim. *Philosophy of Science* 1985;52(4): 578-590.
- [53] Ghiselin MT. A radical solution to the species problem. *Systematic Zoology* 1974;23(4): 536-554.
- [54] Ghiselin MT. Species concepts, individuality, and objectivity. *Biology and Philosophy* 1987;2(2): 127-143.
- [55] Ruse M. Species as individuals: logical, biological, and philosophical problems. *The Behavioral and Brain Sciences* 1981;4(2): 299-300.
- [56] Kitcher P. Bewitchment of the biologist. *Nature* 1986;320(6063): 649-650.
- [57] Stamos DN. Buffon, Darwin, and the non-individuality of species – A reply to Jean Gayon. *Biology and Philosophy* 1998;13(3): 443-470.
- [58] Hull DL. A matter of individuality. *Philosophy of Science* 1978;45(3): 335-360.
- [59] Brigandt I. Natural kinds in evolution and systematics: metaphysical and epistemological considerations. *Acta Biotheoretica* 2009;57(1-2): 77-97.
- [60] Hull D. Phylogenetic nomenclature. *Systematic Zoology* 1966;15(1): 14-17.
- [61] Griffiths G. On the foundation of biological systematics. *Acta Biotheoretica* 1974;23(3-4): 85-131.
- [62] Griffiths G. The future of Linnaean nomenclature. *Systematic Zoology* 1976;25(2): 168-173.

- [63] Ereshefsky M. Some problems with the Linnaean hierarchy. *Philosophy of Science* 1994;61(2): 186-205.
- [64] Ereshefsky M. Species and the Linnaean Hierarchy. In: Wilson RA. (ed.) *Species: new interdisciplinary essays*. Cambridge: MIT Press; 1999. p285-305.
- [65] Rieppel O, Kearney M. The poverty of taxonomic characters. *Biology and Philosophy* 2007;22(1): 95-113.
- [66] Stuessy T. *Plant taxonomy*. 2nd ed. New York: Columbia University Press; 2009.
- [67] Wagner GP. Characters, units and natural kinds: an introduction. In: Wagner GP. (ed.) *The character concept in evolutionary biology*. San Diego: Academic Press; 2001. p1-10.
- [68] Ghiselin MT. 'Definition', 'characters' and other equivocal terms. *Systematic Zoology* 1984;33(1): 104-110.
- [69] Rodrigues PD. On the term character. *Systematic Zoology* 1986;35(1): 140-141.
- [70] Sneath PHA, Sokal RR. Numerical taxonomy. *Nature* 1962;193(4818): 855-860.
- [71] Colless DH. On 'character' and related terms. *Systematic Zoology* 1985;34(2): 229-233.
- [72] Hennig W. *Phylogenetic systematics*. Urbana: University of Illinois Press; 1966.
- [73] Vavilov NI. The law of homological series in variation. *Journal of Genetics* 1922;12(1): 47-89.
- [74] Sanderson MJ, Donoghue MJ. Patterns of variation in levels of homoplasy. *Evolution* 1989;43(8):1781-1795.
- [75] Keller RA, Boyd RN, Wheeler QD. The illogical basis of phylogenetic nomenclature. *Botanical Review* 2003;69(1): 93-110.
- [76] Rieppel O. The PhyloCode: a critical discussion of its theoretical foundation. *Cladistics* 2006;22(2): 186-197.
- [77] Boyd R. Homeostasis, species, and higher taxa. In: Wilson RA. (ed.) *Species: new interdisciplinary essays*. Cambridge: MIT Press; 1999. p141-185.
- [78] Griffiths PE. Squaring the circle: natural kinds with historical essences. In: Wilson RA. (ed.) *Species: new interdisciplinary essays*. Cambridge: MIT Press; 1999. p209-228.
- [79] Yoon CK. *Naming nature: The clash between instinct and science*. New York: W.W. Norton; 2009.
- [80] Kendrick B. The generic concept in Hyphomycetes - a reappraisal. *Mycotaxon* 1980;11(1): 339-364.

- [81] Rosen DE. Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative biogeography. *Bulletin of the American Museum of Natural History* 1979;162: 267-376.
- [82] Nelson GJ, Platnick NI. *Systematics and biogeography: cladistics and vicariance*. New York: Columbia University Press; 1981.
- [83] Cook LG, Edwards RD, Crisp MD, Hardy NB. Need morphology always be required for new species description? *Invertebrate Systematics* 2010;24(3): 322-326.
- [84] Mooi RD, Gill AC. Phylogenies without synapomorphies – A crisis in fish systematics: Time to show some character. *Zootaxa* 2010;2450: 26-40
- [85] Zylstra U. Living things as hierarchically organized structures. *Synthese* 1992;91(1-2): 111-133.
- [86] Freer S. *Linnaeus' Philosophia Botanica*. Oxford: Oxford University Press; 2003.
- [87] De Hoog GS. Methodology of taxonomy. *Taxon* 1981;30(4): 779-783.
- [88] Stafleu FA. *Linnaeus and the Linnaeans*. Utrecht: A Oosthoek's Uitgeversm; 1971.
- [89] Lawrence JG, Retchless AC. The myth of bacterial species and speciation. *Biology and Philosophy* 2010;25(4): 569-588.
- [90] Johnson LAS. 'Rainbow's end: the quest for an optimal taxonomy. *Systematic Zoology* 1970;19(3): 203-239.
- [91] Simpson GG. *Principles of animal taxonomy*. New York: Columbia University Press; 1961.
- [92] Aristotle (1984) *Metaphysics*. In: Barnes J. (ed.) *The Complete works of Aristotle*. Princeton: University Press; 1984. p1552-1728.
- [93] Mayr E. *Populations, species, and evolution*. Cambridge: University Press; 1970.
- [94] Mayr E. The ontological status of species: scientific progress and philosophical terminology. *Biology and Philosophy* 1987;2(2): 145-166.
- [95] Caplan AL. Back to class: a note on the ontology of species. *Philosophy of Science* 1981;48(1): 130-140.
- [96] Schwartz SP. Natural kinds. *The Behavioral and Brain Science* 1981;4(2): 301-302.
- [97] Kitts DB. Can baptism alone save a species? *Systematic Zoology* 1983;32(1): 27-33.
- [98] Kitts DB. The Names of species: a reply to Hull. *Systematic Zoology* 1984;33(1): 112-115.
- [99] Bernier R. The species as an individual: facing essentialism. *Systematic Zoology* 1984;33(4): 460-469.
- [100] Grene M. A defense of David Kitts. *Biology and Philosophy* 1989;4(1): 69-72.

- [101] Hull DL. Can Kripke alone save essentialism? A reply to Kitts. *Systematic Zoology* 1984;33(1): 110-112
- [102] Van Valen LM. Species, sets, and the derivative nature of philosophy. *Biology and Philosophy* 1988;3(1): 49-66.
- [103] Caplan A, Bock WJ. Haunt me no longer. *Biology and Philosophy* 1988;3(4): 443-454.
- [104] Vasilyeva LN. [Essentialism and typological thinking in biological systematics]. *Zhurnal Obshchey Biologii* [Journal of General Biology] 2003;64(2): 99-111. (in Russian, with English summary)
- [105] Liden M, Oxelman B. Do we need phylogenetic taxonomy? *Zoologica Scripta* 1996;25(2): 183-185.
- [106] Kitcher P. Ghostly whispers: Mayr, Ghiselin, and the 'philosophers' on the ontological status of species. *Biology and Philosophy* 1987;2(2): 184-192.
- [107] The collected dialogues of Plato including letters. Princeton: University Press; 2005.
- [108] Whitehead AN. *Adventures of ideas*. New York: Free Press; 1933.
- [109] Hammen L. Type-concept, higher classification and evolution. *Acta Biotheoretica* 1981;30(1): 3-48.
- [110] De Queiroz K. Replacement of an essentialistic perspective on taxonomic definitions as exemplified by the definition of "Mammalia". *Systematic Biology* 1994;43(4): 497-510.
- [111] Grantham TA. Beyond 'individuality' and 'pluralism': a review of Ereshefsky's *Units of Evolution: Essays on the Nature of Species*. *Biology and Philosophy* 1993;8(4): 457-468.
- [112] Sober E. Evolution, population thinking, and essentialism. *Philosophy of Science* 1980;47(3): 350-383.
- [113] Sober E. Sets, species, and evolution: comments on Philip Kitcher's "Species". *Philosophy of Science* 1984;51(2): 334-341.
- [114] Ghiselin MT. Taxa, life, and thinking. *The Behavioral and Brain Science* 1981;4(2): 303-310.
- [115] Mayr E. Comments by Ernst Mayr. *Theory in Bioscience* 2002;121(1): 99-100.
- [116] Christoffersen ML. Cladistic taxonomy, phylogenetic systematics, and evolutionary ranking. *Systematic Biology* 1995;44(3): 440-454.

