

The Problem of Species Revisited

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Abstract—Hypothetical-deductive analysis is an alternative to both induction and deduction, the difference between which is considered less important. The hypothetical-deductive approach requires a scientist to abandon the synthetic theory of evolution in favor of the epigenetic theory. This latter treats species as a discrete level of biodiversity and, particularly, the one where sympatric biparental groups show reproductive independence. In the case of uniparental (asexual and parthenogenetic groups), as well as in bisexual allopatric groups, the species level of divergence is identifiable by analogy to sympatric biparental relatives. The biological and evolutionary species concepts are disproved: the former contradicts observation, and the latter is non-operational.

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INTRODUCTION

For a long time, species concepts were among the most important and most actively disputed problems of taxonomic and evolutionary biology. For example, in Russia/Soviet Union from the 1940s to the early 1980s about a dozen original books and translations appeared that were directly devoted to this problem (Mayr, 1947, 1968, 1974; Sinskaya, 1948; Poljansky, 1956; Kein, 1958; Zavadsky, 1961, 1968; Gritsenko et al., 1983). Since the 1980s, the discussion has gradually ceased, at least in Russia, in part because of the common illusion that the biological species concept, which became generally accepted, mostly solved the problem. However, I believe that the main reason was the rapid, universal switch of the majority of the scientific community to the American way of thinking, aggressive and tending to the extreme simplification and pragmatism. In our scientific area, this process was expressed by a lack of interest in many significant problems, including the problem of species, and by focusing attention on technical means of phylogeny reconstruction; phylogeny was simplified to genealogy and without profound analysis declared to be the only conceivable basis for biodiversity sciences, such as taxonomy, evolutionary questions, etc. [see Rasnitsyn (2002, 2006) for an extended discussion].

To continue the discussion, I need to formulate in the simplest way several general ideas related to scientific methodology. Two main approaches, deductive and inductive, were long differentiated. Relatively recently, less than a century ago, one more approach (hypothetical-deductive) appeared, associated with the

name of Karl Popper. To simplify significantly, it can be said that a scientist who uses the deductive approach relies on a certain system of postulates that he/she considers to be true, and that is said to derive strictly logically from inferences that are also considered to be true. Using the inductive approach, a scientist does not draw conclusions from postulates, but from observations (“facts”), and being convinced of the verity of these facts, he/she also considers the conclusions to be true, i.e., describing the real state of things (that “does exist”). In my opinion, these two approaches are not fundamentally different, as far as the postulates do not appear from nothing: they are formulated, even if subconsciously, in agreement with the human experience. Consequently, deduction is also an observation-oriented approach that is based on induction to a greater or lesser extent. On the other hand, using the inductive approach, results of observations are generalized in the form of conclusions concerning the nature of things, which are further used as postulates. This is the similarity that allows one to use deduction and induction as an entire method, an alternative to the hypothetical-deductive method.

Unlike induction and deduction, any conclusions of the hypothetical-deductive method, regardless of their origin (i.e., drawn from either observations, or postulates, or any other generalizations) remain hypotheses, i.e., conclusions that demand obligatory examination. The hypothetical-deductive approach proposes methods for such examination. A hypothesis is impossible to verify, i.e., to show its correctness once and for all. Instead, it is claimed that we can falsify it: can prove its incorrectness by comparison between predictions that

come from the hypothesis and observations. Although the real situation is much more complicated [see Rasnitsyn, (1996, 2006) for more details], it is not important for the present discussion. The core is that within the framework of hypothetical-deductive method, no generalization can be considered as a final, once and for all established (verified) generalization, but merely better (or worse) than others consistent with currently available data. In other words, any generalization is always opened to further examination.

A typical example of a deductive construction is cladism, a method that is very fashionable these days. As a postulate, a very plausible statement is used: a common phylogenetic past predetermines the similarity between related groups. A conclusion is made, which is not tested further, that the system of organisms should be strictly isomorphic to their genealogy, expressed in the cladogram. At the same time, no evidence is seriously taken into consideration showing that at least some of the major postulates of cladism lack biological justification, and results of their consecutive application often contradict both common sense and the results obtained by other methods, including paleontology and molecular biology. In fact, there is no biological reason why divergence should take place only as a strict dichotomy with obligatory disappearance of the ancestral species at the moment of dichotomy. On the contrary, there are reliable observations on fossil organisms that, during millions of years, an ancestral species can produce more and more new species (e.g., Nevesskaja et al., 1986, 2001). Similarly, genealogical closeness can adequately reflect relations of other characteristics of organisms only if evolution is considerably gradual and even; however, paleontology provides plenty of very convincing observations of an extremely uneven evolutionary process (see an extended discussion in Rasnitsyn, 1996, 2006).

The biological species concept ("species are groups of interbreeding natural populations that are reproductively isolated from other such groups" Mayr, 1974, p. 21) is one more example of deduction. It is generally agreed that a species usually consists of populations within and between which a more or less intensive exchange of genetic information takes place, which levels the genetic and adaptive characteristics of populations. However, this observation was seen in absolute terms and transformed into a postulate. A conclusion was drawn that it is gene exchange that is the main cause of the integrity, relative uniformity, and discreteness of species. The next logical step of this chain of inferences was the statement that the level of species is unique in the system of taxa and, at the same time, specific for groups with bisexual (biparental) reproduction. There should be no true species (i.e., discrete and with more or less uniform characteristics) in groups with uniparental (asexual or parthenogenetic) reproduction. Consequently, the most promising area of the study is

the population level of life organization, population genetics, and exchange of genes and their interactions with natural selection, which is only understood as a factor changing the frequency of alleles in populations.

This is the essence of population thinking, reasoning in terms of the dynamics of allele frequencies, mutation frequencies, selection coefficients, parameters of differential reproduction, mortality, and migration. Supported by the high prestige of Ernst Mayr, population thinking was declared to be the only scientific approach to the study of evolution and opposed to the typological approach, which was vigorously criticized as outdated and almost unscientific. However, typology is an area of methodology focused on the analysis of similarities and dissimilarities between objects of scientific study, and a progenitor of the highly respectable comparative method.

Creators and users of the biological species concept, like present-day cladists, ignored numerous observations that did not fit their scheme. Indeed, if their concept is true, if the only or at least the main mechanism of unification of individuals and their genotypes within the population and populations within the species is gene exchange resulting from bisexual reproduction and migration, then the degree of this unification should be correlated with the presence of bisexual reproduction and efficiency of migration. It was repeatedly shown that this correlation is very low, and uniparental (parthenogenetic and asexually reproducing) species often differ very little from their biparental relatives living in similar conditions, and isolated populations of biparental species often retain their specific identity for a long time (including geological periods of time), in spite of the absence of gene exchange (Rasnitsyn, 2006, and references therein).

The contradiction between observations and predictions of the biological species concept is quite explainable, but only within another evolutionary theory, the epigenetic theory, as an alternative to the synthetic theory of evolution, which still holds much favor (see below). Although this explanation appeared relatively late (Rasnitsyn, 1987), problems with predictions based on the biological species concept were known much earlier (Poljansky, 1956, 1957, 1977), but they attracted no attention at all from the authors of this concept.

The above-mentioned explanation of common but not universal occurrence of uniformity and discreteness of species (and other taxa) is given in detail by Rasnitsyn (1987, 2002, 2006). I summarize below. According to the epigenetic hypothesis of Schmalhausen-Waddington-Shishkin, the organization of living things is not as much determined by genotype, that is traditionally understood as an assemblage of discrete genetic factors, which define particular characters, as by epigenotype (Shishkin, 1987, 2006). Epigenotype is a totality of more or less stable ontogenetic pathways

(creods, that is, stabilized routes and mechanisms of ontogenesis). Obviously, these mechanisms are also affected by genetic factors, but the activity of the latter is extremely complex and usually virtually unpredictable in real circumstances in nature. One way or the other, effects characterizing this level are invisible at the level of macroevolution. By contrast, the influence of epigenetic factors is obvious: first of all, this concerns discrete changes in the organization of living things (Rasnitsyn, 2006).

The discreteness of evolution is a natural result of stability or even evolutionary rigidity (buffered state) of a well-balanced epigenotype, i.e., all mechanisms of normal development of the organism. Indeed, in the complex system of interactions and interdependencies between the developmental factors of different subsystems of organisms (different creods) a change in any element would affect the function of more than one, and eventually all, morphogenetic systems. The most likely result for the epigenotype will be negative, but only if this change was not tested during previous evolution and included in the morphogenetic repertoire of the developmental system. This is why evolutionary novelties occur rarely but tend to touch upon different aspects of organization. To put it differently, normally, evolution has a more or less distinctly stepwise and saltatory character, and groups (taxa) that originate as a result of evolution are more or less discrete in their characters.

Therefore, in terms of the epigenetic hypothesis of evolution, discreteness and uniformity are not universal, but characteristic features of all natural groups of organisms, not only species. The species level of organization of biological diversity appears less different from other taxonomic levels, but more versatile than in the biological species concept. It is merely one of many levels of discreteness in biodiversity, reflecting different degrees (depths) of stabilization of the epigenotype. Species does not have any fundamental differences from subspecies and (sub)genera. Following the tradition, I can define the species as a level of morphogenetic discreteness that in biparental species corresponds (closest) to the level of divergence at which reproductive independence (under natural conditions) appears between the closest interbreeding totalities of individuals. If it is impossible to reveal the level at which populations show reproductive independence, as is the case with uniparental organisms and allopatric (not contacting in nature) biparental populations, then the species level of divergence is defined only by analogy with the closest sympatric biparental forms, if any exist. The reservation mostly concerns prokaryotes, in which the search of biparental analogues is problematic, to say the least.

Although the epigenetic hypothesis of evolution is in better agreement with observations than the biological species concept, it also has some difficulties (prob-

lems of the interpretation of the observed distribution in evolutionary rates of taxa are reviewed by Rasnitsyn, 2006). However, no hypothesis has so far been proposed that would more adequately explain the contradictions revealed. On the other hand, the situation with the biological species concept is not as simple as that.

In fact, already the founders of the biological species concept clearly saw the discreteness of species in uniparental groups. Mayr (1970, p. 367) even provided a remarkably precise and laconic explanation of this phenomenon, in the spirit of the epigenetic concept: "Almost any change, but particularly a major change, of the phenotype in such a well-balanced system will be deleterious. Although minor gene substitution may be frequent, the well-buffered system of developmental canalizations shields the phenotype from major changes. There is opportunity for speciation, but a major alteration of the morphotype is impossible as long as the epigenotype is intact." However, his resoluteness to defend the biological species concept was not shaken (Kolchinskii, 2006), which allows me to classify the concept as a deductive one. It should be stressed that this example shows a certain ambiguity in opposing hypothetical-deductive and deductive/inductive approaches. This dichotomy does not concern inferences per se: the difference is not limited to the point that in one case we deal with a supposition demanding an obligatory testing, and in the other, with a supposition pretending to be the truth. The alternative of hypothetical-deductive vs. deductive/inductive methods does not lie in the field of conclusions, but concerns scientists who treat the same idea either as the truth or merely a hypothesis.

The biological species concept was discussed above in its classical definition, as proposed by Mayr (1942, 1963). Later, Simpson (1961, p. 153; 2006, p. 178) made modifications and named it the evolutionary species concept: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." This change was approved by the scientific community, but it was not developed further, as it was completely non-operational. The evolutionary role of a population can be estimated only a posteriori, as far as populations that produced or did not produce new species apparently do not possess any reproducible differences, related to their evolutionary role. This is mostly (but not entirely) predetermined by the conditions under which a given species lives. The long-living species referred to above exemplify this conclusion particularly clearly. Such species have repeatedly and at different time points produced new phyletic lines, if they entered a relatively unoccupied ecological site with deviating environmental parameters (mollusks from the Oligocene and up to the present day in seas of the Paratethys in southern Europe and eastwards up to Turkmenistan; Nevesskaja et al.,

1986, 2001). However, even under such conditions the species behaved in a different and currently unpredictable manner: some regularly produced new pools of forms, others diversified in some basins but did not diversify in apparently similar basins, others perished, and others persisted without producing new forms.

Simpson (1961, p. 160; 2006, p. 186) transformed the biological species concept into the evolutionary species concept because of the same discrepancy between the observed discreteness of taxa and boundaries of reproductive communities, which was already mentioned: "Different genetic species [which formed reproductive entities, i.e., biological species in the terms of Mayr, A.R.] that lack any determinable anatomical or ecological distinction [i.e., sibling species, as the context implies, A.R.] are single species under the evolutionary definition: they do not have definably separate evolutionary roles. The collective evolutionary species so defined is analogous to a uniparental species, in which unity of role is maintained without interbreeding." Nonetheless, he proposed no mechanism responsible for the discreteness of taxa at the species level, and reproductive entity remained an important criterion of species. Therefore, it is hard to believe that Simpson's proposition significantly improved the definition of species in the synthetic theory of evolution, within the frameworks of which both Simpson and Mayr worked.

Summarizing, first of all I should point out that I do not discuss the species as a unit of taxonomic nomenclature: the existing codes do not leave much space for alternative readings. When the species is considered as an object of population, ecological, and evolutionary processes, we find no clear indication of significant distinctness of this level of organization of living things; it is no more distinct or specific than, for example, a subspecies or a group of related species, particularly sibling species. The species is merely one of many levels of discreteness of biodiversity. It is the very level where biparental organisms are closest to the level of divergence at which reproductive independence is revealed in natural sympatry. In asexual and parthenogenetic groups, as well as in allopatric populations of bisexually reproducing organisms, the species level of divergence is identifiable only by analogy: the species level is a level at which reproductive independence appears in the closest sympatric biparental relatives.

In a broader aspect, this example has shown that many hard scientific problems are unsolved because of inappropriate methodology. The inductive-deductive approach to the concept of species and, in particular, overestimation of gene exchange in the biological species concept led to the result that the essence of the notion of species was not revealed, and scientists simply lost interest in the problem, and mostly switched their attention to other areas that seemed more promising. We are now witnesses to the same situation occur-

ring with cladism: although in outward appearance it still dominates, the feeling of a cul-de-sac is increasing. The increase in the number of characters that serve as the basis of an analysis does not lead to the convergence of results obtained by different analyses and does not smooth contradictions between morphological and molecular cladograms and, especially, between cladograms and paleontological records (Rasnitsyn, 2000, 2006a, 2006b). A trend toward the consumption and extirpation of morphological cladistics by molecular phylogenetics is already apparent. However, even this will not allow the methodological crisis to be overcome, until scientists finally abandon inductive-deductive theorization and add the hypothetical-deductive method, which is readily praised but difficult to implement, to their armory.

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