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ON THE HISTORY AND PRESENT STATE OF THE SPECIES CONCEPT

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Abstract

In the present paper, the history of the species concept in biology is briefly outlined. According to its analysis as presented here the species concept evolved through two basic paradigms, as follows:

(1) A species is a discontinuity at the lowest level of the taxonomical hierarchy.

(2) A species is a discontinuity at a special, from all other levels of the taxonomical hierarchy qualitatively different level.

After analysing the present state of the species concept we suggested then a new definition of species:

(3) A species is an evolutionary whole unit at the population level, the evolution of which is realized in a particular, ecological time through its particular forms, i.e. populations.

The species notion belongs to basic biological notions. It is, then, quite natural that a remarkable attention of biologists (e.g. Zavadskij 1961, 1968, Mayr 1963, Grant 1971, Vent 1974, Škorbatov 1976, Endler 1977, White 1978, Bocquet et al. 1977-1980) as well as philosophers (e.g. Čížek 1963, Nowiński and Kuźnicki 1965, Abdyldaev 1966, 1971, Volkova and Filjukov 1966, Volkova 1972, Sucker 1978) has been paid to the species problem in last decades. In biology, the species notion denotes not only a basic evolutionary unit, but reflects also a unity of the systemic

and historical in biology, since it reflects, in a certain respect, the relation between the evolution and environment at the population level. In spite of much efforts aimed at the special (biological) as well as general (philosophical) analysis of the species notion, the history of both the concept and notion of species is still little elaborated.

The history of the species notion in biology has many aspects identical with the development of most notions which reflect the existence and specifity of a certain part of the objective reality. It proceeds from a simply realistic or ontological approach to the apprehension of reality, through continuous realization of cognitive difficulties and problems resulting from both the specifity of the given object and the process of recognition itself, up to a conscious reflection of ontological, gnoseological as well as methodological aspects of the investigation of that given object. In the whole history of the development of the species concept, it is possible to trace the way from the original understanding, identification and description of the given object on the basis of a still undifferentiated unity of all those aspects (where just this undifferentiated unity of ontological, gnoseological, logical and methodological aspects prevents deeper understanding), through their more or less conscious reflection (and, hence, also their more or less unconscious confusion, or, on the other hand, their separation and overestimation), up to attempts to synthesize particular positive but onesidedly considered and interpreted knowledge. For the purposes of the most general classification of various alternative approaches in the history of the species concept we attempted to separate questions regarding primarily the species concept from those regarding primarily the species notion. Note,

that in connection with the species notion also the term species underwent remarkable shifts in its meaning (from the linguistical point of view).

By the "species concept" we mean a certain, especially biologically-ontological image of natural scientists which, on a more or less extensive theoretical basis, summarizes or synthesizes the actual knowledge about a certain part of reality.

The "species notion" contains not only the above image of the reality which belongs to its constituting elements, but also other levels of the reflection of the objective reality as well as the self-reflection of man during the process of recognition of this reality. Hence, the species notion contains explicitely aspects of the gnoseological and generally methodological characters, too.

Note, however, that the distinction between the species notion and species concept is rather of a methodical character, while there is no sharp dividing line between them in biological practice. It is, then, not surprising that both the concept and notion of species have been confused during their whole history, but their historical beginnings were as independent that they may be analyzed separately.

The species concept originated apparently long before the origin of science as such. It is supported by the respective studies of non-civilized tribes (e.g. Žitkov 1934, Dennler 1939, Concklin 1962, Diamond 1965, Mayr 1969, Berlin 1973, Berlin et al. 1974, Majnep and Bulmer 1977, Gould 1979; cf. also Berlin et al. 1966), the members of which recognize in their territories species almost as precisely as modern taxonomists. But even a number of higher non-human vertebrates are able to distinguish very precisely biological entities which in many

cases, though not always, correspond to the current species concept (cf., e.g., Spurway 1955, Tinbergen 1960, Gibb 1962, Inozemcev 1963, Croze 1970, Murton 1971, and many others). Generally speaking, perceiving and distinguishing discontinuities of a certain level of taxonomical hierarchy is under discussion in both cases. These discontinuities are rather distinctive from the spatially (geographically) and time-local point of view. In many primitive human tribes, understanding of the hierarchical arrangement of taxonomic entities has been even formed in which the species correspond to entities of the lowest of these levels (cf. Žitkov 1934, Gould 1979).

Now, let us turn to the origin of the species notion. The species notion was, in its Greek form (eidos) proposed by Plato as a general philosophical term which, in relation to the genus notion (Greek genos) designated discontinuities at two neighboring levels of a hierarchy (Nowiński and Kuźnicki 1965, Lõther 1972). Both these notions have been introduced into biology by Aristotle who considered quite properly the multilevel hierarchy of taxa to be a special case of Plato's hierarchy, and used both the notions eidos and genos similarly relatively as Plato himself (Rádl 1909, Uhlmann 1923, cf. also Balme 1962). Hence, at the end of the Ancient era, it is still not possible to speak about the species concept in the complete meaning of the word; only pre-conditions for the creation of the taxon concept and notion appeared and the species notion occured only in its general philosophical form.

We know essentially nothing about the development of the species concept and notion in biology in the Middle Ages (cf. Zirkle 1959). In spite of this, a significant event happened at that time, namely the shift (contraction) of the species notion in biology. It started here

to be explicitly used for entities at the lowest level of the taxonomical hierarchy only, i.e. for the species infima of the general philosophical hierarchy. The biological species concept itself (now, this term can be used literally) remained, however, unaltered. At this stage, the species concept was adopted by all biological encyclopedists of the 16th century, so that we can conclude that the first paradigm in the development of the species concept was formed which can be, in general, expressed as follows:

The species is a discontinuity at the lowest level of the taxonomical hierarchy.

This approach was maintained without any larger problems up to the 18th century when the point of view of taxonomists ceased to be spatially local (note that biologists essentially had no knowledge of the idea of evolution at that time), and, in addition, they disposed about much more comparative material. This progress resulted in the discovery of anomalies of the 1st paradigm: (1) occurence of geographical variability and of transitional forms between species, and (2) occurence of the so-called varieties, i.e. of intrapopulation variability in modern terminology. Consequently, it was no more clear what actually is the species infima in the sense of both the extent and the content of that notion.

The discoveries of these anomalies evoked naturally attempts to solve them. At the most general level, the former anomaly could be solved essentially in three ways: (1) by stating that the species evolve, (2) by refusing the reality of species, and (3) by interpreting species as fuzzy-sets, not as classical ones. The variant of fuzzy-sets was, however, not developed at that time, while in the competition between the first and the second

variant, i.e. between the evolutionism and nominalism (sensu, e.g., Bloch 1956 or Mayr 1969, 1982) the first variant clearly won. Its victory led subsequently to the formation of a new paradigm in the development of the species concept (see bellow).

On the contrary, the problem of an unambiguous attribution of the species notion to a certain level of the taxonomical hierarchy has not been solved satisfactorilly up to this time. Three basic variants of its solution were elaborated, as follows: (1) the species level is qualitatively different from other taxonomical levels (note, that this does not imply its automatical recognizability), (2) the species level is not qualitatively different from other taxonomic levels, but it can be defined by a convetion, and (3) as in the latter variant, but the species level cannot be defined. In the competition between these three variants, the variant (1) clearly won, i.e. the opinion that the species level is qualitatively different from all other taxonomical levels.

It is, then, possible to summarize that during the 2nd half of the 19th century a second paradigm in the development of the species concept was formed which can be formulated as follows:

The species is a discontinuity at a special, from all other levels of the taxonomical hierarchy qualitatively different level.

One fundamental problem remained, however, unsolved in this paradigm, namely what is the difference between the species level and other levels of taxonomical hierarchy and how to recognize it. In addition, doubts about the discontinuous character of species in space

appeared again and, since the penetration of the idea of evolution into the biology, new anomalies were discovered related to the postulate of the continuity of species in time. Each of these problems could be solved in a limited number of ways only, which were soon proposed.

The problem of the continuity vs. discontinuity of species in space could be solved again by the same three variants as in the 1st paradigm. The first variant, i.e. the suggestion that continuities occur as a result of the evolution of species, was developed at this stage particularly in direction of the terminological denotation of species at different stages of differentiation (see, e.g., concepts and notions of subspecies, superspecies, semispecies, Rassenkreis, Formenkreis, Artenkreis, aggregate species, species collectiva, ex-species, etc.).

In the second variant of the solution of the problem of the continuity of species in space which appeared only recently, the species are interpreted as fuzzy-sets. The theory of fuzzy-sets was developed few years ago only (Zadeh 1965), and its applications to the species problem are still very rare although the species as well as other taxa can be meaningfully considered fuzzy-sets only (cf. Mlíkovský 1982, in prep.). The opinion that species are classical sets is clearly an expression of the typological thinking which is still quite common in entire biology and particularly in biosystematics.

Also at this, actually current stage of the development of the species concept, many authors, while solving the problem of the continuity of species in space, tended to sceptic standpoints and refused the reality of species.

The competition between the above three solutions did not proceed sufficiently for creating a new paradigm so far. In our opinion, the true solution should result from the combination of former two variants. As a matter of fact, when the species are considered evolving fuzzy-sets, problems connected with the opinion that species are evolving classical sets are avoided, and the concept of evolution remains saved.

Now, let us turn back to the second anomaly of the paradigm under discussion, i.e., to the problem of the continuity of species in time. This anomaly has three possible solutions, as follows: (1) the evolution of species is continuous, hence, it is principally impossible to delimit species in time and, consequently, they are non-real; (2) species evolve by jumps, so that they are discontinuous in time, and (3) species do not evolve gradually but are limited by zones of rapid evolutionary changes. The latter variant is a fundamental notion of the so-called punctuated equilibria theory (Eldredge and Gould 1972, Gould and Eldredge 1977). We consider it the only one which is compatible with both the data available and the contemporary theory of evolution.

Now, we can consider the problem which remained unsolved within the framework of the 2nd paradigm, i.e. what is the difference between the species level and other levels of the taxonomical hierarchy and how it can be recognized. In spite of the fact that most authors searched (at various levels) for the true criterion of the species level, both alternative, negative variants of the solution of this problem appeared again, namely the refusal of the unique character of the species level with either a possibility of a conventional definition

of this level or even an impossibility of such a definition. Even at this stage of the development of the species concept these variants brought no remarkable success.

Let us, then, consider now in more detail the further development and the fate of the positive variant of the solution, i.e. of the opinion that the species level is qualitatively different from all other levels of the taxonomical hierarchy. After the theory of evolution became in contact with ecology in the beginnings of the 20th century (probably via population genetics), and the notion of population (which was developed quite separately in ecology, i.e. within another thinking tradition and for different purposes) has been introduced into evolutionary biology, most authors compared the species level with the population one. In result, the species has been usually defined as a set of populations. We agree that the population and species level should be compared with one another, but we do not believe that species are sets of populations. On the contrary, we believe that species and populations are two sides of the same notion. We consider a population to be a particular, in time and space restricted mode of existence of a species in a particular, ecological time. On the other hand, the species is, in our opinion, a historical, evolutionary unit, the evolution of which is realised in a particular, ecological time through its particular forms, i.e. populations. It can be, then, defined, as follows:

The species is an evolutionary whole unit at the population level, the evolution of which is realised in a particular, ecological time through its particular forms, i.e. populations.

We may, then, conclude, as follows:

(1) In spite of the fact that the speciation proceeds in the functional (ecological) time, the species can be defined in the historical (evolutionary) time, only. (See, e.g., Blauberg and Judin 1973, Blauberg et al. 1978, and Mamzin 1978 for a mutual relation between the functional and the historical time.) This distinction has not been considered in the literature dealing with the species problem till now, perhaps with the exception of Šmal'gauzen (1974) who, in another context, approached this opinion while attempting to point out differences between the macro- and microevolution.

(2) The basic characteristics of the species is its evolutionary wholeness, not its morpho-functional uniformity or even its difference from other species. It should be noted in this context that the wholeness does not imply uniformity, i.e. that the species may be polymorphic, polyphenic, and/or polymodic (sensu Mlíkovský 1976). The requirement for the uniformity which has been often repeated in the history of the species concept (cf., e.g., the concepts and notions of ecads, isoreagents, ecoelements, ecotypes, biotypes, morphobiological groups, etc.) always led to strong narrowing of the species notion and, consequently, to splitting the species into small units which have been later necessarily again combined into various summary units, as, e.g., superspecies, Rassenkreis, Formenkreis, Rotte, etc.

(3) The species notion is not universal in biology. It may be applied to sexually reproducing organisms only, which are organized in populations.

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