

PREFACE

Following papers are the result of a small German-Czechoslovak working session, the aim of which was to consider together the questions of common interest concerning the evolution of man and human society in multidisciplinary approach.

The research of the descent of man, as it has been started by Charles Darwin more than one hundred years ago, has reached a stage now, when many further disciplines of both natural and social sciences start to be deeply concerned with this set of problems.

To enable an active participation to our specialists it has been decided to leave the theme of the meeting sufficiently broad. Papers on general or even philosophical questions of anthropogenesis have been included besides specific problems of anthropological, archaeological and several other aspects. To give the meeting a truly working character, the number of participants has been limited.

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EVOLUTIONARY MODEL OF SPECIES AND THE SYSTEMATICS OF THE FAMILY HOMINIDAE I — GENERAL CONSIDERATIONS

ABSTRACT. — *An evolutionary definition of species has been suggested and an evolutionary model of it is outlined. The biological species is viewed as an assemblage of genetically related individuals which are for many generations reproductively isolated and are in a temporary evolutionary ballance with the conditions of environment. The dialectical unity between the continuity on the level of individual organisms and the qualitative discontinuity of separate species is emphasized. The relation between species and subspecific and superspecific units is discussed.*

KEY WORDS: *Biological species — Evolution — Qualitative changes — Evolutionary model — Evolutionary balance — Espèces naissantes — Dialectical unity — Predecessors of man — Family Hominidae.*

One of the most discussed questions in biology is nowadays the problem of the biological species. Since the times of K. Linnaeus (1758) who was the first to define the concept of species and to introduce it consistently into the study of all organisms — both plants and animals — many diversified and often quite contradictory opinions con-

cerning objective existence, variability, durability, mutual relations and the most realistic definition of species were professed. Since the time of publication of Darwin's (1859) principal work "On the Origin of Species" more and more specialists came gradually to understanding and acceptance of the concept of evolution, so that nowadays one cannot find

a competent biologist who would deny the fact of the historical evolution of organisms. However, among taxonomists of the most various groups of organisms, there are still many who have not drawn all the conclusions following from this fact for their own work and for the general conception of species. This is obvious among other things from the lack of uniformity and considerable obscurity in the general comprehension of the concept of species. The ideas about species differ considerably between specialists in the individual biological sciences, e.g., morphologists, physiologists, geneticists, biochemists, ecologists, palaeobiologists, etc., equally as between taxonomists of different groups of animals, plants and microorganisms. Until now there is a lack of consistent evolutionary concept of species, which would be at the same time a consistent synthesis of all the existing opinions. In the present paper I wish to attempt such a synthesis on the basis of our previous studies (cf. Novák, 1969) using the experience from a number of groups of organisms. I shall then try to apply the conclusions on the special case of the contemporary data about the predecessors of man. In the case of the evolution of man, the above mentioned obscurities have been especially considerable until now in view of the fact that in this group a new, the highest form of the motion of matter originated historically: the psychosocial motion which has surpassed the biological level.

If we take into consideration the most basic characteristics common to all known species from all different viewpoints, together with the knowledge of dialectical materialism, we can pronounce the following preliminary evolutionary definition:

Biological species is an assemblage of genetically related individuals of many generations, forming a specific quality with specific space and time distribution and isolated as a rule reproductionally from related species including that from which it originated and those which developed from it — a group of individuals which is in a temporary evolutionary balance with the conditions of the given environment.

Qualitative distinctiveness of the whole does not mean, of course, as it is sometimes incorrectly assumed, that there are no transitions between related species on the level of individuals. Qualitative delimitation is testified by a quantitative delimitation in the form of separated peaks of the Gaussian curve of frequencies for individual characters. Discontinuity at the level of species (as groups of individuals) is thus connected with a continuity at the level of individuals (a continuous sequence of generations). The quality of a given species is ordinarily a complex of properties, signifying some substantial advantage from the viewpoint of natural selection in the given environment. In this way an evolutionary equilibrium has been established between the individual hereditary variability (mutagenity) and the variability of the living conditions. This equilibrium is ordinarily disturbed either by more substantial changes in the environment or by the origin of new qualities on the basis of the process of the mutagenesis or by a combination of

mutations advantageous for survival, possessing a certain selective value in the given environment. This takes place usually in a part of the area of the maternal species only by which the possibility is given for a simultaneous existence of maternal and daughter species. Palaeontology estimates the average duration of a species as 10 millions of years. There exist, however, as far as one can judge it on the basis of fossil finds (identity of solid parts of bodies, e.g., shells, chitinous cuticles or bones) much older species (e.g., *Ligula*, *Nautilus*, *Hateria*, many species of insects, etc.) and, on the other hand, much younger species of considerably shorter duration, e.g. individual species of the family *Hominidae*, which were probably differentiated during a period not much longer than one million years. It was not before this paper had been submitted to print that I succeeded to read the Gould's and Eldridge's paper (1977) on the punctuated equilibria, the conception which seems to be rather near to that discussed in this paper (cf. Novák et al., 1969).

As it corresponds to the hierarchical distribution of individual qualities and their relativity, there are qualities corresponding to the subspecific and to supraspecific levels. Changes in *subspecies qualities* which are mutually also in a hierarchical relation (individual mutations, populations, varieties, nations, races, subspecies, etc.) have the character of quantitative changes in relation to the differences between species. At the same time they all differ from qualities of the species by the fact that they are not mutually isolated in reproduction; which, of course, does not rule out in most cases their space and time delimitation in the limits of the area and in the duration of the given species. *Supraspecies qualities* (genus, family, order, class, phylum and a series of transitions, as used in different groups by various taxonomists, e.g., the range of species, subgenus, supergenus, tribus, subfamily, etc.) include mostly greater or smaller number of species and are also delimited in space and time. In relation to them the differences between individual species are of a quantitative nature. In contradistinction from the qualities of species the supraspecific qualities lack, of course, the criterion of mutual mixing and by this their greater delimitation is given. It can be thus said that species is the highest taxonomic unit of individuals which interbreed and, at the same time, it is the smallest unit of individuals isolated in reproduction from related species. By this is given a certain exceptional character of species, which justified the term basic taxonomic unit.

By mutual mixing and isolation in reproduction in the case of a species we do not, of course, understand the corresponding physiological abilities of individuals forming the species (there are known cases of interbreeding and obtaining of fertile offspring even between individuals of different genera), but rather the real state, existing in the given assemblage of individuals — there is a biochemical isolation (incompatibility of the sex cells), physiological (impossibility of fertilization), etological (no attraction between sexes of different species), ecolo-

gical (differences in the way of life, different annual period of sex maturity, etc.), but also geographical (various natural barriers preventing interbreeding — mountains, water basins, etc.) and others. From the evolutionary point of view it is necessary to observe that it is just the isolation of the most diversified sort which results in the origin of species.

Of course, neither the relativity of species and of all other taxonomic units, nor the dispersed occurrence of their individuals among various other organisms, nor the continuity at the level of individuals do affect their objective existence. If some authors understand Darwin's statement that "species is what a competent taxonomist (a specialist in a given group) considers as a species" to be a denying of the objective existence of species, it is a complete misunderstanding. From Darwin's complete work and among other things also from the title of his principal work ("On the origin of species") it is clear that he considered species an objective reality and the same is true about an overwhelming majority of taxonomists who would hardly agree that they describe only their subjective ideas. Moreover all the mentioned properties of species as a biological category or quality are characteristic for any material qualities, both natural and social ones. Qualities of any objects, processes and phenomena in general possess a relative character, they are links of an immensely complex hierarchy of material phenomena from elementary particles over atoms and molecules up to cosmic bodies on one hand and to organisms and human society on the other hand. If we realize that any objects are built from molecules, atoms or even elementary particles, we can see that none of them is a compact body, but rather that they are formed, although they have limits in space and time, by very dispersed units of a lower level. And even if they are endlessly variable, they are formed by continuous series of equal individuals of the lower level.

On the basis of what was said, we can now start to outline a space model of a biological species, which would represent its most important properties in their mutual relations. Individual species in this model are represented by spindle-like formations, any of which grows by its basis from another similar body — the maternal species — and from it itself originate analogously one or more daughter species. A simplified planary drawing of the model can be seen in Fig. 1. The lower hierarchical level, being in the given case the level of individuals, i.e. of individual organisms or individual hereditary lines, is represented by a customary dichotomic scheme. The region of a qualitative change, i.e. of the transition from maternal species to the daughter one, is represented by a lattice zone or, in newly formed not yet separated species, by dotting. The height of the spindle body shows the duration of the given species in time, its breadth the number of individuals constituting it. Hence rare but long-living species are represented by narrow and long spindle bodies; species changing quickly but which are "common", i.e. rich in individuals are shown as spherical or broader than longer forms (Fig. 2).

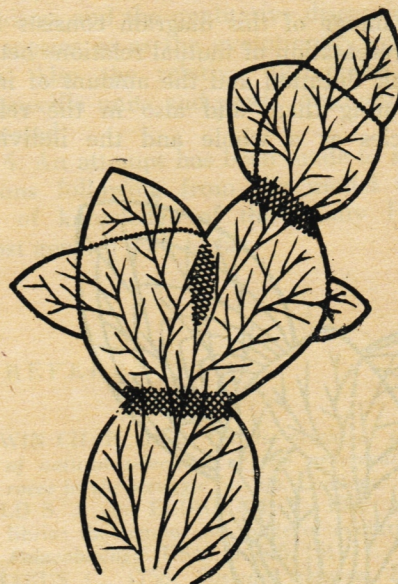


FIGURE 1. Diagram of the evolutionary model of the biological species
Four species with four newly originating species (*espèces naissantes*). The transition between species are demonstrated by the lattice zones, the separation of the originating species by the dotted lines. Individuals and subspecies units within a species are illustrated schematically by the dichotomic lines.

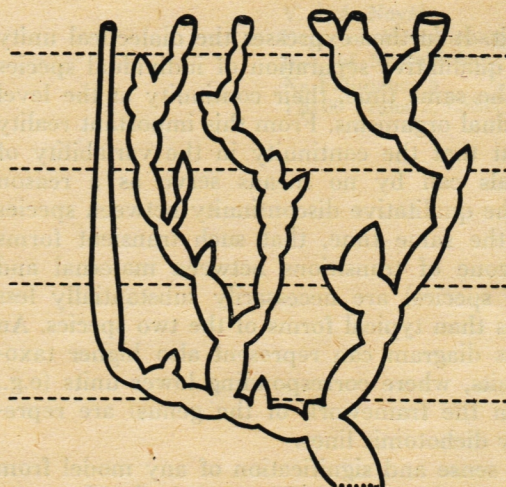


FIGURE 2. Scheme of the phylogenetic relations in a group of species.
The length of each spindle-like structure shows the duration of the species in time, its breadth demonstrates the number of individuals forming it. The long shape on the left is a case of a "living fossil".

Gradual evolution and separation of a new species is shown in Fig. 3. On this basis we can well recognize changes and properties of subspecies, i.e., divisions inside the given quality and starting new species (*espèces naissantes* = semispecies) overpassing the quality of the species even if they are not yet differentiated as new species, i.e. they do not overpass the still existing species in a sufficient extent and do not yet form the narrowed zone of transitions.

The advantage of this diagram consists in its adequate representation of mutual relations between species in their duration and the amount of individuals constituting them and also in the relation between species as a whole and the individuals



FIGURE 3. Two newly originating species evolving from a parental species. Intraspecific units in the parental species are separated by the dotted lines. Several subsequent stages in the evolution of newly originating species are shown.

forming it. It further expresses the dialectical unity between qualitative separation of individual species and, at the same time, their continuity at the level of individual organisms. From this important reality is evident that the continuity in the variability of individuals can by no means serve as a reason against the qualitative discontinuity between species and, at the same time, that such transient forms (in the zone of transitions between maternal and daughter species) are necessarily substantially less numerous than typical forms of the two species. An analogous diagram can represent also higher taxonomic units, where corresponding lower units (e.g., species in the framework of the genus) are represented by dichotomic lines.

The sense and significance of any model from the point of view of scientific work is that it means in a way a definite working hypothesis expressed in a vivid manner and concerning interrelations between the given phenomena as well as their evolutionary or functional relations which are of assistance for further and deeper understanding. Of course, it can prove as fully useful only when it is really used as a working hypothesis, i.e. if it is continuously tested and complemented by newly established facts. On the other hand, if it is taken as a definite piece of knowledge, which is not necessary to verify or change, it could influence the knowledge in a negative way.

Let us have a closer look how the model can be useful when applied to the above mentioned very complex situation in the Hominidae family.

To determine and represent the relations between species on the basis of this evolutionary model

is comparatively simple wherever there is at hand rich material concerning the given species not only from the contemporary period but also sufficiently numerous fossil finds from a longer period in the past. Such finds are preserved wherever there are suitable conditions for fossilization, as it is e.g. on the bottom of sea and with such species or parts of the bodies, which can be well conserved, e.g. shells of various molluscs, or bones of the family Equidae in dry steppes. In botany (palynology) the same is true for pollen grains with their solid exina. In most cases it is of course not the case and the material available is very incomplete and fragmentary, both as individual parts of the bodies are concerned and as the spatial and temporal relations of the found individuals. This is just the situation with our data about the predecessors of man. However, just there can be an analogous model of the greatest utility, since, on one hand, it makes possible at least a hypothetical classification of available information, and, on the other, it draws attention to the existing gaps and hence to that what should be in the centre of further research. It also makes possible to evaluate the plausibility and significance of present conclusions.

Let us consider first which of the main properties of the contemporary man were of the decisive importance in the evolution of his animal and later prehuman and human ancestors the evolution from the origin of anthropoids, the superfamily Hominoidea to the first genera of the family Hominidae and finally to individual species of the genus Homo. Among the most important belong without doubt the following: the erection of the stature (orthostasis) and by this the liberation of upper limbs from the locomotion function and the origin of hands capable of the most various work, the development of human language and related to this the fast evolution of the brain, and in connection with all this the rapidly developing working activity, differentiating and perfecting itself, etc. (cf. Novák, 1981). About all these and especially about the language, which was the most important precondition for the transition from the biological to the psychosocial form of the motion of matter, we can judge only indirectly or only on the basis of incomplete, dispersed and casual findings. There is also no doubt that in all these cases the evolution was long and gradual. Even so we have the right to assume that from the qualitative point of view the evolution was not a continual one but rather that it occurred as a sequence of mutually separated qualitative changes, as it corresponds to our model and to the contemporary anthropological taxonomy. At this evolution, of course, we can assume, apart of the changes of species, also a series of beginning but undeveloped species and of changes resulting in subspecies and lower subspecific units.

SUMMARY

1. The following evolutionary definition of species has been suggested: The biological species is an assemblage of genetically related individuals

of many generations, forming a specific quality, with specific space and time distribution, reproductively isolated as a rule from the related species, i.e. from the one from which it originated and from those which developed from it: a group of individuals being in a temporary evolutionary balance with the given conditions of environment.

2. An evolutionary model of the biological species has been outlined on the following principle: The individual species are represented by spindle-like formations each of them growing by its basis from another similar body, giving rise, in a similar way, to one or more daughter species (Fig. 1). Their composition of individual organisms is represented schematically by customary dichotomic lines within the spindle. The height of the structure shows the duration of the given species in time, its breadth the number of individuals constituting it. Longliving species are thus represented by long and narrow spindle bodies, whereas those changing quickly but rich in individuals are shown as spherical or broader than the longer forms (Fig. 2). The gradual evolution of a new species is shown in the Fig. 3.

3. The model illustrates well the mutual relations between species, their relative delimitation in space and time and it expresses the dialectical unity

between the continuity on the level of individual organisms and the qualitative discontinuity of separate species so as the evolutionary relations among them. Also the relative differences between the intraspecific units and newly originating species are expressed.

4. An attempt has been made to apply the conclusions following from the model to the recent state of knowledge of the family Hominidae, in a most general way so far.

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