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## MORPHOGENESIS AND THE PROBLEM OF MORPHOSPECIES

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*An analysis of the morphospecies concept is presented. The concept as such is rejected, and it is suggested that it retains its validity only as a historical opposite of the biospecies concept, and as an operational concept in some groups of organisms. On the other hand, the necessity of the inclusion of morphological criteria in the species concept is stressed. We believe, however, that their inclusion will be possible only after a virtual solution of the relation between genotype and phenotype.*

Key words: morphospecies concept, morphological description, morphogenesis

### INTRODUCTION

Classical neo-Darwinism assumes (following Johannsen 1909) that each organism is characterised by a *genotype* and a *phenotype*. The phenotype has been conceived by neo-Darwinists as a sum of all morphological characters of an (adult) individual, while genotype has been considered by them as a sum of genes present in an individual. The *ontogeny*, i.e. the way from an individual's genotype to its phenotype has been considered by neo-Darwinists as a process determined solely by the information beared by (or coded in, as they used to say) the genotype. Neo-Darwinists admitted that genes materialize their information in the interaction with their (non-specified and non-structured) environment, but allowed it to cause

only non-hereditary modifications, i.e. to cause variations of the phenotype within the limits of the so-called *reaction norm* (Baldwin 1896; cf. Simpson 1953, White and Smith 1956, Mayr 1963, Dobzhansky 1970, Severcov 1982).

Prior to the neo-Darwinian synthesis, species had been defined purely on the basis of morphological criteria, i.e. on the basis of the phenotype of individuals. It is now common to call species defined in this way *morphological species*, or shortly *morphospecies*. Neo-Darwinists transformed the species notion in the following way: They supposed that species do not consist of phenotypically similar individuals, but of genotypically similar ones. At the same time they suggested the gene flow as the mechanism of maintenance of genotypic similarity as well as of generation of the combinatory variability. By this action they believed to have substituted morphological criteria by biological ones, especially by the reproductive isolation and common *genepool* ("genofond", Serebrovskij 1928), where genepool (GP) is defined as

$$GP = \sum_{i=1}^i GT_i \quad (1)$$

where  $GT_i$  = genotype of the  $i$ -th individual of the given species. They called then species defined in this way *biological species*, or shortly *biospecies* (Mayr 1942).

Neo-Darwinists believed that biospecies are identical with real species. Thus, a necessity arose for them to study the relations between the morphospecies and biospecies concept and between sets of individuals belonging to a species defined on the basis of morphological, or biological (genetic) criteria, respectively. For a long time this problem had been studied solely by practical systematists, especially paleontologists, who often could still work with morphological characters only, but, being influenced by the neo-Darwinian paradigm, they attempted to infer from these findings biospecies, i.e. real species as they believed. Only since late 1960s the problem has been approached also at the philosophical level (Ruse 1969, 1971, 1973, Hull 1970, Giray 1976, Bělka 1984, in press a,b).

We are aware of two important shortcomings of this neo-Darwinian approach: (1) that it has not been justified that biospecies are identical with real species, and (2) that it is not possible to compare directly two concepts, one of which was erected as an opposite of the other one. The single correct way is to compare both of them independently with the reality, i.e. to investigate whether sets of individuals defined on the basis of certain criteria meet all intuitive demands made on respective sets of individuals which are supposed to really occur in nature as species.

At the general level, the problem under study, i.e. the morphospecies problem, has three possible solutions: (1) the morphospecies are identical with real species, (2) the morphospecies differ from real ones, but a finite set of transformation rules exists which makes it possible to relate them, and (3) there is no relation between real species and morphospecies. Leaving the phenomenological level of description we can see that the case (1) assumes an unequivocal relation between genotype and phenotype, the case (2) assumes a certain (but not necessarily unequivocal) relation between genotype and phenotype, while the case (3) assumes no relation between genotype and phenotype, this being non-sense, of course. The case (2) propounds thus the problem of the control of the morphogenetic process. The present paper aims to contribute to the search for the correct one of these alternative solutions.

### THE MORPHOLOGY NOTION

Before we now directly approach the morphospecies problem, which is in the focus of this paper, it is necessary to clarify what is *morphology*.

In classical descriptive biology, morphology was considered as a description of the so-called macromorphological characters (characters understood as operational units of recognition). With the progressive development of biology this description was extended on histological, cytological, karyological, etc., characters, too, i.e. on the description of the whole *structure* of organisms (structure in the biological sense). Moreover, recent applications of the systems approach in biology caused the shift in the understanding of the term structure from its bio-

logical meaning to a general scientific one, i.e. to structure understand as a certain invariant of organization in its dynamic sense (Novotný 1981). We use the term structure in the latter sense throughout this paper. Note, that contrary to Hennig (1966), Ruse (1973), Giray (1976) and others, we do not include non-structural characters, such as behavior, in the morphology notion. We do this for the sake of lucidity of this paper, although we are aware of the fact that some of behavioral characters could also be included in the morphology notion, especially those which influence the morphogenetic process (cf. Zemek et al. 1985).

### MORPHOLOGICAL DESCRIPTION OF INDIVIDUALS

After this more or less terminological excursion, we can now directly approach the morphospecies problem. The starting point is here the morphological description of organisms. We are, of course, not able to describe the organism's structure directly, but only via *characters* (auctorum), called in more specified sense also *phenes*\* (Johannsen 1909), or *biocharacters* (Osborn 1917).

From this point of view, any organism may be understood as a set of characters (phenes) termed *semaphoront* (sensu Hennig 1966). On each semaphoront there is an actual infinity (sensu Vopěnka 1979) of characters, the sum of which Johannsen (1909) termed *phenotype*, Hennig (1966) *holomorphy*, and Wiley (1979) *epiphenotype*. All these notions include not only morphological, but also non-morphological, such as behavioral, characters. On the other hand, Hennig (1966) explicitly reduced the semaphoront notion to but one moment, or short time span, respectively, of the organism's ontogeny. Nevertheless, Hennig, as an entomologist, was aware of the fact

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\* Note, that Johannsen (1909) erected the phene concept in belief, that some (hypothetical) hereditary units exist in each zygote, each of which determines one phenotypical character. He termed then the mentioned determinant units genes, and the resulting (ontologized!!) characters phenes. Contrary to the gene term and concept, the phene term and concept became later forgotten and has been rediscovered only recently by Serebrovskij (1973), Jablokov (1980), and few others. However, supposing that the "one gene - one character" concept is incorrect, these authors use the term phene in the sense of morphological character.

that ontogenetically related semaphoronts differ in their holomorphies, and termed the process of their change during ontogeny *metamorphism* of holomorphies.

Wiley (1979), the most important recent continuator of Hennig, wholly confused Hennig's terminology. He cites Hennig (1966) as an author of the holomorphology (of individuals) notion in the sense of a sum of characters of an individual during its whole ontogeny. This is clearly incorrect, because (1) Hennig (1966) explicitly restricted his holomorphy (not holomorphology!!) notion to any one of the stages of the individual's ontogeny, and (2) Hennig erected and used his term holomorphology in the sense of a scientific discipline studying holomorphies.

The above mentioned notions can be also expressed formally in mathematical terms. Considering that

$$C = \{cm_{ijk}\} \cup \{cr_{ijk}\} = \{c_{ijk}\} \quad (2)$$

and

$$cm \cap cr = \emptyset \quad (3)$$

where  $C$  = sum of all characters of an individual,  $c_{ijk}$  =  $i$ -th character on the  $j$ -th individual at its  $k$ -th stage of ontogeny,  $cm$  = morphological characters, and  $cr$  = non-morphological characters, we become:

$$PT_{jk} = H_{jk} = E_{jk} = \sum_i c_{ijk} = \sum_i cm_{ijk} \cup \sum_i cr_{ijk} \quad (4)$$

and

$$HI_j = \sum_k PT_{jk} = \sum_k H_{jk} = \sum_k E_{jk} = \sum_{ik} c_{ijk} = \sum_{ik} cm_{ijk} \cup \sum_{ik} cr_{ijk} \quad (5)$$

where further  $PT$  = phenotype,  $H$  = holomorphy,  $E$  = epihenotype, and  $HI$  = holomorphology of individuals (sensu Wiley 1979).

## MORPHOLOGICAL DESCRIPTION OF SPECIES

Now, when we characterized organisms by their morphological characters, we can proceed to the morphological description of species. This description may be derived from any of the notions. A species may be considered as a sum of organisms in this case, although it is not but that, of course (cf., e.g., Mlíkovský and Zemek 1983). Then, starting from the holomorphy notion we become by summarizing holomorphies over organisms what is termed *morphological pool* (Ruse 1973), and starting from the holomorphology-of-individuals notion (sensu Wiley 1979) we become by summarizing these holomorphologies over organisms what Wiley (1979) termed *holomorphology of species*. Terms applicable to the sum of all morphological characters of all organisms belonging in a species during their whole ontogenies are *phenotypical pool* (sensu Bělka 1984, in press a,b), and *phenofond* ("fenofond" in Russian). According to remenberings of N.V. Timofeev-Resovskij (see Jablokov 1980), the latter term was coined somewhen during 1920s in Soviet genetic schools led in Leningrad by Ju.A. Filipčenko and in Moskva by N.K. Kol'cov (see Dobzhansky 1980 for a review of these schools).

Again, these notions can be expressed in mathematical terms. Using the symbolics introduced in the previous chapter we become:

$$MP_k = \sum_j PT_{jk} = H_{jk} = E_{jk} = \sum_{ij} c_{ijk} = \sum_{ij} cm_{ijk} \cup \sum_{ij} cr_{ijk} \quad (6)$$

$$\begin{aligned} HS &= \sum_k MP_k = \sum_{jk} PT_{jk} = \sum_{jk} H_{jk} = \sum_{jk} E_{jk} = \sum_j HI_j = \sum_{ijk} c_{ijk} = \\ &= \sum_{ijk} cm_{ijk} \cup \sum_{ijk} cr_{ijk} \end{aligned} \quad (7)$$

$$PP = PF = \sum_{ijk} cm_{ijk} \quad (8)$$

where further MP = morphological pool, HS = holomorphology of species, PP = phenotypical pool, and PF = phenofond.

## THE PHENON NOTION

From the statistical point of view, a phenotypical pool (or a phenon) is a cluster of character points in a multidimensional space and has, consequently, a multidimensional statistical distribution. This distribution can be either unimodal or multimodal. Any such group of conspecific organisms which exhibits the unimodal distribution of the phenotypical pool was termed *phenon* by Camp and Gilly (1943). It means that a phenon cannot be composed of more than one species, but that it can represent a complete species, or its part (1/2, 1/3, etc.) only.

Mayr (1969) believed that the neo-Darwinian phenon concept is identical with the pre-neo-Darwinian morphospecies concept. This seems to be incorrect because what appears to be a morphospecies can be composed of one, two, or more species, or, on the other hand, to represent a complete species, or only its part (1/2, 1/3, etc.). This can be graphically expressed (see Fig. 1). In this figure we assume (1) that the organisms involved are described by two characters only (abscissa, ordinate), (2) that we have found two clusters of individuals only (see the left column in the figure 1), (3) that a species consists maximally of two phenons, and (4) that we have maximally two species in the sample.

In figure 1, the case (A) represents the so-called *polymorphic species* (auctorum) or *biomorphospecies* (sensu Macko 1983), i.e. species which consists of more than one (here two) phenons. These phenons may be related with sex, stage of ontogeny, or with various other intra-specific groups. In our case, a species consists of two "morphospecies" which are here identified with phenons. The case (b) represents two species which are at the same time phenons (these being the *typomorphospecies* of Macko 1983). Only if this would be the only natural case, species could be recognized on the basis of morphological characters, and the morphospecies concept would be correct. These are also the so-called "good" *species* (sensu Darwin 1859), which served as a basis for the development of most of contemporary ideas. The case (C) represents two species, each of which consists of two phenons. This case was de-

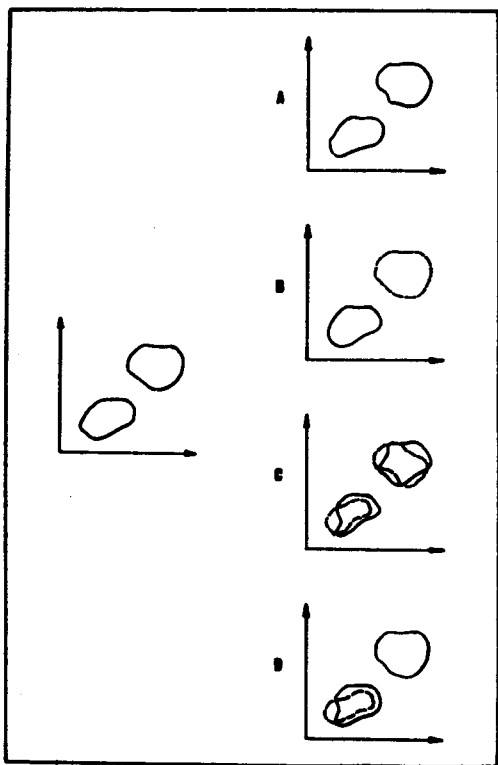


Fig. 1.

noted in evolutionary systematics with various terms as, e.g., *cryptic species* (auctorum), *Geschwister-Arten* (Ramme 1930), *espèces jumelles* (Cuénot 1936), *sibling species* (Mayr 1942), *ex-conspecies* (Stepanjan 1970), etc. The case (D) represents a complementary combination of the cases (A), (B) and (C).

All these cases (A, B, C, D) are well known from nature and exemplified in most various groups of organisms (cf., e.g., Mayr et al.



1953, Mayr 1963, 1969, Ross 1974). It means, that it cannot be deduced on real species purely on the basis of morphological criteria, i.e. that the expectations of the proponents of the morphospecies concept are not fulfilled. Thus, the morphospecies concept as such loses its supposed validity, and retains its importance as a historical opposite of the biospecies concept only. This does not mean, of course, that the rejection of the morphospecies concept implies the validity of the biospecies concept, or of any other species concept developed in biology. On the other hand, the rejection of the morphospecies concept does not necessitate the rejection of morphological criteria as such from the species concept. We believe, however, that the inclusion of morphological criteria in the species concept will be possible only after a solution of the problem of the relation between genotype and phenotype, i.e. after the elaboration of morphogenetical criteria. This problem has not been adequately taken into account neither in any of the contemporary species concepts, nor in the analysis of the evolution of species.

#### THE AGAMOSPECIES CONCEPT

Cain (1954) developed the *agamospecies* concept for asexually reproducing animals. If these organisms would be organized at the population level (cf. Mlíkovský and Zemek 1983), then the agamospecies notion would be identical with the pre-neo-Darwinian morphospecies notion. However, because asexually reproducing organisms are not organized at the population level (see, e.g., Mayr 1963, Dobzhansky 1970, Mlíkovský and Zemek 1983), the agamospecies concept is a contradictory theoretical construct with no real meaning, which has only pragmatic value for applied systematics.

#### IMPLICATIONS FOR APPLIED SYSTEMATICS

Because, as outlined above, there is no unequivocal relation between morphospecies and real species on the contemporary theoretical basis, it is evident, that those systematists (e.g., paleontologists, various

invertebratologists, etc.) can identify only clusters of phenotypically similar individuals, but cannot deduce from them on either biospecies, or even real species. Unfortunately, the latter seems to be a common praxis among these systematists. Many paleontologists have been aware of this difficulty (e.g., Sylvester-Bradley 1956, Simpson 1961, Tintant 1980), and their inability to solve it (being substantiated in the present paper) led even to a proposal to exclude the species notion from paleontology (Shaw 1969).

#### REFERENCES

- Baldwin J.M. (1896) A new factor in evolution. *Amer. Nat.* 30: 441-451, 536-553.
- Bělka L. (1984) Některé filozofické aspekty teorie biologického druhu (Some philosophical aspects of the theory of biological species). Thesis, J.E.Purkyně University, Brno, 125 pp.
- (in press a) K diskusi o biologickém druhu I. (To the discussion of biological species I.). *Stud. minora Fac. phil. Univ. brunensis* (B)32: in press.
- (in press b) K diskusi o biologickém druhu II. (To the discussion of biological species II.). *Stud. minora Fac. phil. Univ. brunensis* (B), in press.
- Cain A.J. (1954) *Animal species and their evolution*. London: Hutchinson University Library.
- Camp W.H., C.L.Gilly (1943) The structure and origin of species. *Brittonia* 4: 323-385.
- Cuénot L. (1936) *L'espèce*. Paris: Dion, 310 pp.
- Darwin C. (1859) *On the origin of species*. London, Murray, 502 pp.
- Dobzhansky T. (1970) *Genetics of the evolutionary process*. New York: Columbia University Press, 505 pp.
- (1980) The birth of the genetic theory of evolution in the Soviet Union in the 1920s. In: E. Mayr, W.B.Provine: *Evolutionary synthesis*: 229-242. Cambridge: Harvard University Press.
- Giray E.F. (1976) An integrated biological approach to the species problem. *Brit. J. Phil. Sci.* 27: 317-328.
- Hennig W. (1966) *Phylogenetic systematics*. Urbana: University of Illinois Press, 263 pp.
- Hull D.L. (1970) Morphospecies and biospecies. A reply to Ruse. *Brit. J. Phil. Sci.* 21: 280-282.
- Jablokov A.V. (1980) *Fenetika (Phenetics)*. Moskva: Nauka, 136 pp.
- Johannsen W. (1909) *Elemente der exakten Erblichkeitslehre*. Jena: Fischer, 516 pp.
- Macko J.K. (1983) To the problem of morphospecies, taxospecies and biospecies. I. The establishment of species of the biomorphospecies and biotaxospecies types. *Helminthologia* 20: 13-20.
- Mayr E. (1942) *Systematics and the origin of species*. New York: Columbia University Press, 334 pp.

- (1963) Animal species and evolution. Cambridge: Harvard University Press, 797 pp.
- (1969) Principles of systematic zoology. New York: McGraw-Hill, 428 pp.
- , E.G.Linsley, R.L.Usinger (1953) Methods and principles of systematic zoology. New York: McGraw-Hill, 336 pp.
- Mlíkovský J., K.Zemek (1983) On the history and present state of the species concept. In: V.J.A.Novák, K.Zemek: General questions of evolution: 281-304. Praha: Czechoslovak Academy of Sciences.
- Novotný V. (1981) Dialekticko-materialistické pojetí úlohy systémového přístupu v přírodních vědách (Dialectic and materialistic concept of the problem of the systems approach in natural sciences). Acta Fac. med. Univ. brunensis 73: 209-252.
- Osborn H.F. (1917) Biocharacters as separable units of organic structure. Amer. Nat. 51: 449-456.
- Ramme W. (1930) Revisionen und Neubeschreibungen in der Gattung Pholidoptera Wesm. (Orth., Tettigon.). Mitt. zool. Mus. Berlin 16: 798-821.
- Ross H.H. (1974) Biological systematics. Reading: Addison-Wesley, 345 pp.
- Ruse M. (1969) Definitions of species in biology. Brit. J. Phil. Sci. 20: 97-119.
- (1971) The species problem: a reply to Hull. Brit. J. Phil. Sci. 22: 369-371.
- (1973) The philosophy of biology. London: Hutchinson University Library.
- Serebrovskij A.S. (1928) Genogeografija i genofond sel'skochozjajstvennych životnych SSSR (Genogeography and genepool of farm animals of the U.S.S.R.). Nauč. Slovo 1928(9): 3-22.
- (1973) Nekotorye problemy organičeskoj evoljucii (Some problems of the organic evolution). Moskva: Nauka, 168 pp.
- Severcov A.S. (1982) Selection towards the increase in reaction norm. In: V.J.A.Novák, J.Mlíkovský: Evolution and environment: 165-173. Praha: Czechoslovak Academy of Sciences.
- Shaw A.B. (1969) Adam, Eve, paleontology, and the non-objective arts. J. Paleont. 43: 1085-1089.
- Simpson G.G. (1953) The Baldwin effect. Evolution 7: 110-117.
- (1961) Principles of animal taxonomy. New York: Columbia University Press, 237 pp.
- Stepanjan L.S. (1970) Konceptcija nadvida (superspecies) i predeli eš pri-loženija (The superspecies concept and the limits of its applications). Zool. Ž. 49: 653-659.
- Sylvester-Bradley P.C. (ed., 1956) The species concept in paleontology. London: Systematists Association, 145 pp.
- Tintant H. (1980) Problématique de l'espèce en paléozoologie. In: C. Bocquet, J.Génermont, M.Lamotte: Les problèmes de l'espèce dans le règne animal III: 321-372. Paris: Société Zoologique de France.
- Vopěnka P. (1979) Mathematics in the alternative set theory. Stuttgart: Teubner.
- White F.N., H.M.Smith (1956) Some basic concepts pertaining to the Baldwin effect. Turtox News 34: 51-53.
- Wiley E.O. (1979) Phylogenetics. New York: Wiley, 439 pp.
- Zemek K., J.Mlíkovský, R.Socha (1985) Multilevel system of heredity and its ontogenetic and phylogenetic consequences. In: J.Mlíkovský, V.J.A. Novák: Evolution and morphogenesis: this volume. Praha: Academia.