GENERAL QUESTIONS OF EVOLUTION, 1983
Proc. Int. Colloq., V.J.A. Novák and
K. Zemek /eds./, 305-317 Praha: ČSAV

ON THE FOUNDATIONS OF BIOLOGICAL SYSTEMATICS: A HISTORICAL APPROACH

Jiří Mlíkovský

Abstract

In the present paper, the history of biological systematics is briefly outlined. It is suggested that the originally uniform biological systematics splitted gradually into taxonomical and ecomorphological ones, the latter being still much less elaborated than the former one. An attempt is made to synthesize these approaches and to create foundations to a new theory of biological systematics.

Biological systematics, or biosystematics, is a scientific discipline dealing with the study of natural groupings of organisms and their classification. Three alternative approaches to this problem are possible: the **ecological, the ecomorphological, and the taxonomical one.** In the former one, the classified units are the biocenoses, in the second one the life forms, and in the latter one the taxa. Among them, the ecological classifications are largely independent of the latter two ones, and will not be treated in this paper (see, e.g., Pielou 1977: 312--331 for this problem). On the other hand, a close relation exists between taxa and life forms (Mlíkovský 1982), but this relation remained largely unrecognized by biosystematists, and the development of ecomorphological and taxonomical classifications was, in principle, independent of each other for long periods.

Both these approaches, however, have much in common in their methodology: they produce sets of systematic propositions about the classified units (i.e. taxa or life forms, respectively), and consider them scientifically meaningfull, having, unfortunately, usually no knowledge of the respective criteria elaborated in the general methodology of science, which should be fulfilled by that propositions.

According to that criteria, all biosystematic propositions should be based on (1) a certain data basis, (2) a set of decision algorhythms, and (3) an underlying theory in the frame of which the decision algorhythms are valid and meaningfull. In addition, the conclusions reached during the classificatory process should be testable, namely at both the empirical and theoretical levels.

An attempt will now be made to trace briefly the use and the fate of these criteria during the history of biological systematics in order to show the historical roots of the contemporary biosystematics and its problems, and to analyze the possibilities of their solving.

The Beginnings

First classifications of organisms presented by Ancient Greek scholars (e.g. Aristotle, Theophrastos, and others) were based largely on the theory of creation, while the only decision algorhythm used during that period was the degree of similarity of classified organisms inter se (cf., e.g., Lloyd 1961, Mayr 1982). The data basis was unsufficient, although morphological (sensu lato), ethological, and ecological data were used. The result of such a classificatory process were essentially ecomorphological classifications which did not substantially differ from pre-scientific people's classifications. As far as it is known to me, no attempts to test these classifications have been ever performed.

This situation remained principally unaltered during the entire Medieval Ages till the 17th and especially the 18th century. Here, the underlying theory was still the theory of creation, but the only formerly recognized algorhythm (the similarity) became broadly discussed, because it turned out that using different data sets different classifications of the same entities may be constructed (Adanson 1763 - cf. Stafleu 1963, Burtt 1966, Mayr 1982). In addition, although the data were usually weighted, no clear criteria have been established for how their weight should be estimated. This led naturally to great confusions in biosystematics, because no test of classifications constructed in such a manner have been possible.

Furthermore, it is worthwhile to mention here that the data basis became gradually restricted to morphological data during this period (of museum systematics), and no behavioral and ecological data were used more, although this restriction was, to my best knowledge, never codified in any algorhythm. Such an a priori selection of data led soon to a hitherto non-mentioned (and perhaps unrecognized) but a very important result. While before this event no distinction was made between the ecomorphological and the taxonomical classifications, only the taxonomical one has been now regarded to be the classification, whereas the ecomorphological component diminished wholly from the biological classifications during the 18th century. Ecomorphological classifications did not appear before the 20th century again, and their development became more vivid during the last few decades only.

Such a duality in the development of biosystematics makes it necessary to consider now the development of the ecomorphological and the taxonomical biosystematics separately.

Taxonomical Biosystematics

In the taxonomical biosystematics, an important change happened during the 19th century: the theory of creation has gradually been replaced by the theory of evolution (see, e.g., Guyénot 1941, Nowiński and Kuźnicki 1965, Mayr 1982). The decision algorhythms remained, however, unaltered, and, moreover, although the theory of evolution made taxonomical classifications testable, no attempts to make such tests have, at least to my best knowledge, ever appeared. Otherwise, only slight progress in the theory of taxonomical biosystematics can be detected till 1950/1960ies (see, e.g., Plate 1914, Rensch 1934, Schilder 1952, Mayr et al. 1953, Simpson 1961, Blackwelder 1967, Mayr 1969, Smirnov 1969, Bărănescu 1973, Ross 1974). In those decades, a large and thorough debate about the validity of respective decision algorhythms originated, and alternative sets of decision algorhythms were proposed, including that of cladistic ("phylogenetic") systematics (e.g. Hennig 1950, 1965, 1966, Crowson 1970, Schlee 1971, Dupuis 1979, Wiley 1981), and numerical ("phenetic") systematics (e.g. Sokal and Sneath 1963, Jardine and Sibson 1971, Sneath and Sokal 1973, Leuschner 1974, Clifford and Stephenson 1975).

Much attention has been also paid to the theory of evolution during this period, but all the efforts resulted in only one novelty important for the biosystematics, namely in the formulation of the so-called punctuated equilibria theory as an alternative to the formerly generally accepted (though usually not clearly formulated) gradualistic theory of the evolutionary process (Eldredge and Gould 1972, Gould and Eldredge 1977). Although Eldredge and Gould who originally described this concept discussed it at the species level (of taxonomical hierarchy) only, I will suggest here that the punctuated equilibria theory seems be valid also at certain higher taxonomic levels, particularly at the genus, family, and phyllum ones (see bellow).

Ecomorphological Biosystematics

Unlike the taxonomical biosystematics, the ecomorphological biosystematics has only scarcely been discussed till now, and its development is still in its very beginnings although the roots of it may be traced back to Raunkiaer (1905, 1934) who formulated the concept of life forms, which are the units of ecomorphological classifications. However, it seems more suitable to summarize here, with historical comments, the present state of the ecomorphological biosystematics than to describe its history which still lacks any marked steps, because (1) no algorhythms for the recognition of life forms have yet been elaborated, (2) the same is true for the levels of ecomorphological hierarchy, and (3) also the respective underlying theory remains still markedly underdeveloped.

It became recently known in ecology that niches inhabited by individual species are not distributed stochastically within any ecosystem (cf., e.g., Root 1967, Cody 1974, MacMahon 1976, Herrera and Hiraldo 1976, Ulfstrand 1977, Pianka 1978, Wiens and Rotenberry 1980), but that they build clusters called guilds (Root 1967), a term which I consider synonymous to the term adaptive zone (Simpson 1944). As every organism is characterized by its adaptive suite (Bartholomew 1972), called sometimes also optimal design (Rosen 1967), which approximately correspons to the niche which the given organism inhabits, it follows from the non-stochastical distribution of niches within ecosystems that also organismic designs are distributed non-stochastically therein. This has been actually observed in the nature, and clusters of organisms with similar adaptive suites have been termed life forms (Raunkiaer 1905). Although the concepts of life forms and adaptive zones developed independently of each other, I suggested quite recently (Mlíkovský 1982) that a close relation exists between life forms and adaptive zones, namely that adaptive zones are inhabited by life forms, similarly as niches are inhabited by species.

The Synthesis

No synthesis of taxonomical and ecomorphological biosystematics appeared till now, although Bock (1965), Wahlert (1965, 1973), and Illies (1970) (cf. also Lack 1947, and Mayr 1969) made first steps toward it. I will, then, outline here briefly one possible way how to reach it. I guess that such a synthesis, which is now a rather common phenomenon in biological sciences (cf., e.g., Čepikov 1975, Novák 1979, Fedorov 1979, Mayr 1982) will help to both taxonomical as well as ecomorphological biosystematics to overcome their own difficulties and problems.

The basic prerequisite for a synthesis of taxonomical and ecomorphological biosystematics is to find a relation between the units classified by them, i.e. between taxa and life forms. There was no search for this relation in biology till now, but it does, indeed, exist (Mlíkovský 1982). Generally speaking, a taxon is a part of a phyletic line boredered by the limits of an adaptive zone, or, in other words, a taxon is a monophyletic part of a life form. From the point of view of phylogeny, I believe, adaptive zones may be considered punctuated equilibria for phyletic lines at several supraspecific levels, while the process of subsequent transitions between adaptive zones is already known as adaptive radiation (Osborn 1899, 1900, 1902).

From the relation between taxa and adaptive zones, a relation between the hierarchy of taxa and the hierarchy of adaptive zones, i.e. between the taxonomical and the ecomorphological hierarchies may be easily inferred. It is, however, necessary to note that the taxonomical hierarchy has evidently more levels than the ecomorphological one. After comparing these hierarchies in birds and mammals, and in organisms in general, I will suggest that the levels of the taxonomical hierarchy which correspond to the levels of the ecomorphological one are the genus, family, and phyllum levels. Note, that the agreement between an ecomorphological classification which may be constructed for every group of organisms and their present taxonomical classification will not be perfect. This is caused by the individual development of every particular classification, which proceeds from an initial state in which it is constructed as a more or less pure ecomorphological classification, through intermediate states in which it is constructed as a more or less pure taxonomical classification, and it should tend to a classification constructed on the basis of a synthesis of ecomorphological and taxonomical approaches to the biosystematics in the sense as outlined in this paper. Unfortunately, the classifications of all known groups of organisms are presently in the intermediate state of their development. The degree of agreement between the ecomorphological and the taxonomical classifications seems to be correlated with the exact state of the development of the taxonomical classification. This was also the main reason for my selection of birds and mammals for the study of the relation between the levels in the ecomorphological and taxonomical hierarchies, because their taxonomical classifications seem to be the most advanced among the classifications of individual groups of organisms. The less advanced the taxonomical classification of a group of organisms will be, the less agreement between the ecomorphological and the observed taxonomical classification of that group will be found by respective specialists. Such a disagreement cannot be, then, used as a disprove of the theory presented in this paper.

Also the remaining basic levels of the taxonomical hierarchy, i.e. ordo and classis levels, seem to have an ecological basis. I will suggest here that they should be conceived as units of adaptive radiation, but because their closer analysis would exceed the frame of the present paper, I will leave it for a next one. The species, i.e. the taxa at the species level of taxonomical hierarchy, are units of a quite another character, and are, hence, treated in a separate paper (Mlíkovský and Zemek 1983).

A number of implications for both the taxonomical as well as the ecomorphological biosystematics follow from the synthesis outlined above, but they remain to be more closely studied in the future. Among the most important ones are the possibilities:

(1) to define concrete taxa more exactly than previously;
(2) to correlate the ecomorphological and the taxonomical classifications of particular groups of organisms;
(3) to distinguish between analogy and homology, and, consequently, between the so-called morphological series and true phylogenetic lines (see Mlíkovský 1982);
(4) to test (partly) monophyly of proposed taxonomical groups (see Mlíkovský 1982);
(5) to define exactly monophyly, polyphyly, and allied terms (Mlíkovský in prep.);
(6) to distinguish between identification diagnoses and phylogenetic diagnoses (see Mlíkovský 1983);
(7) to elaborate the theory of evolution at supraspecific levels (i.e. the phylogeny). This field has been largely neglected during the whole era of the so-called synthetic theory of evolution due to the neo-Darwinian reduction of evolutionary processes to the population-genetic ones.
(8) to elaborate new sets of decision algorhythms in both the taxonomical and the ecomorphological biosystematics on the basis of newly elaborated underlying theory of phylogeny; and
(9) to extend the data basis in the taxonomical biosystematics on ecological data.

References

Adanson, M. (1763) Familles des plantes I. Paris: Vincent.

Băranescu, P. (1973) Principiiles şi metodele zoologiei sistematice. (Principles and methods of zoological systematics). Bucuresti: Acad. Republ. Soc. Romania, 219 pp.

Bartholomew, G.A. (1972) Body temperature and energy metabolism. In: M.S.Gordon (ed.): Animal physiology: principles and adaptations: 298-368. New York: Macmillan.

Blackwelder, R.E. (1967) Taxonomy. New York: Wiley, 698 pp.

Bock, W.J. (1965) The role of adaptive mechanisms in the evolution of higher levels of organization. Syst. Zool. 14: 272-287.

Burtt, B.L. (1966) Adanson and modern taxonomy. Notes roy. bot. Garden Edinburgh 26: 427-431.

Čepikov, M.G. (1975) Integracija nauki. (Integration of sciences). Moskva: Mysl', 244 pp.

Clifford, H.T. and W.Stephenson (1975) An introduction to numerical classification. New York: Academic Press, 229 pp.

Cody, M.L. (1974) Competition and the structure of bird communities. Princeton: Princeton University Press, ix + 318 pp.

Crowson, R.A. (1970) Classification and biology. London: Heinemann, vii + 350 pp.

Dupuis, C. (1979) La "systematique phylogénetique" de W.Hennig (historique, discussion, choix des references). Cah. nat. 34: 1-69.

Eldredge, N. and S.J.Gould (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: T.J.M. Schopf (ed.): Models in paleobiology: 82-115. San Francisco: Freeman and Co.

Fedorov, V.M. (1972) Sintetičeskie tendencii v sovremennom estestvoznanii. (Synthetical tendencies in contemporary science). Moskva: Izd. Moskovskogo Gosudarstvennogo Universiteta, 117 pp.

Gould, S.J. and N.Eldredge (1977) Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology 3: 115-151.

Guyénot, E. (1941) Les sciences de la vie aux XVII[e] et XVIII[e] siecles: l'idée d'évolution. Paris: Michel.

Hennig, W. (1950) Grundzüge einer Theorie der phylogenetischen Systematik. Berlin: Deutscher Zentralverlag, 370 pp.

Hennig, W. (1965) Phylogenetic systematics. Annu. Rev. Entomol. 10: 96-116.

Hennig, W. (1966) Phylogenetic systematics. Urbana: University of Illinois Press, 263 pp. (reedition: ibidem, 1979).

Herrera, C.M. and F.Hiraldo (1976) Food-niche and trophic relationships among European owls. Ornis scand. 7: 29-41.

Illies, J. (1970) Die Gattung als ökologische Grundeinheit. Faun.-ökol. Mitt. 3: 369-372.

Jardine, N. and R.Sibson (1971) Mathematical taxonomy. New York: Wiley, 286 pp.

Lack, D. (1947) Darwin's finches. Cambridge: Cambridge University Press, 204 pp.

Leuschner, D. (1974) Einführung in die numerische Taxonomie. Jena: Fischer.

Lloyd, G.E.R. (1961) The development of Aristotle's theory of the classification of animals. Phronesis 6: 59-81.

MacMahon, J.A. (1976) Species and guild similarity of North American desert mammal faunas: a functional analysis of communities. In: D.W.Goodal (ed.): Evolution of desert biotas: 133-148. Austin: University of Texas Press.

Mayr, E. (1969) Principles of systematic zoology. New York: McGraw-Hill, 428 pp.

Mayr, E. (1982) The growth of biological thought. Diversity, evolution, and inheritance. Cambridge: Harvard University Press, xiii + 974 pp.

Mayr, E., E.G.Linsley and R.L.Usinger (1953) Methods and principles of systematic zoology. New York: McGraw-Hill, 336 pp.

Mlíkovský, J. (1982) Zur Methodologie phylogenetischer Rekonstruktionen in der Paläontologie. Wiss. Z. Humboldt-Univ. Berlin (Math.-nat. R.) 31: 143-146.

Mlíkovský, J. (1983) Methodological problems of the contemporary systematics of the family Hominidae. Anthropologie 21: 33-36.

Mlíkovský, J. and K.Zemek (1983) On the history and present state of the species concept in biology. In: V.J.A.Novák and K.Zemek (eds.): General questions of evolution: this volume. Praha: ČSAV.

Novák, V.J.A. (1979) Vývoj vědy jako formy společenského vědomí a přirozená soustava věd. (Development of sciences as a form of social consciousness, and a natural classification of sciences). Filoz. Čas. 27: 824-836.

Nowiński, C. and L.Kuźnicki (1965) O rozwoju pojecia gatunku. (On the development of the species notion). Warszawa: PWN, 293 pp.

Osborn, H.F. (1899) The origin of mammals. Amer. J. Sci. 6: 92-96.

Osborn, H.F. (1900) The geological and faunal relation of Europe and America during the Tertiary period and the theory of the successive of an African fauna. Science 11: 561-574.

Osborn, H.F. (1902) The law of adaptive radiation. Amer. Nat. 34: 353-363.

Pianka, E.R. (1978) Evolutionary ecology. 2nd ed., New York: Harper and Row, 397 pp.

Pielou, E.C. (1977) Mathematical ecology. New York: Wiley, x + 385 pp.

Plate, L. (1914) Prinzipien der Systematik mit besonderer Berücksichtigung des Systems der Tiere. In: P.Hinneberg (ed.): Kultur der Gegenwart III (4/4): 92-164.

Raunkiaer, C. (1905) Types biologiques pour la géographie botanique. Overs. danske Vidensk. Selsk. Forhandl. 5: 347-437.

Raunkiaer, C. (1934) The life forms of plants and statistical plant geography. Oxford: Clarendon Press, 632 pp.

Rensch, B. (1934) Kurze Anweisung für zoologisch-systematische Studien. Leipzig: Akademischer Verlag, 116 pp.

Root, R.B. (1967) The niche exploitation patterns of the blue-grey gnatcatcher. Ecol. Monogr. 37: 317--350.

Rosen, R. (1967) Optimality principles in biology. New York: Plenum Press, 198 pp.

Ross, H.H. (1974) Biological systematics. Reading: Addison-Wesley, 345 pp.

Schilder, F.A. (1952) Einführung in die Biotaxonomie. Jena: Fischer, 162 pp.

Schlee, D. (1971) Die Rekonstruktionen der Phylogenese mit Hennigs Prinzip. Aufs. Red. senckenberg. naturforsch. Ges. 20: 1-62.

Simpson, G.G. (1944) Tempo and mode in evolution. New York: Columbia University Press. xviii + 237 pp.

Simpson, G.G. (1961) Principles of animal taxonomy. New York: Columbia University Press, xiii + 247 pp.

Smirnov, E.S. (1969) Taksonomičeskij analiz. (Taxonomical analysis). Moskva: Izd. Moskovskogo Gosudarstvennogo Universiteta, 187 pp.

Sneath, P.H.A. and R.R.Sokal (1973) Numerical taxonomy. San Francisco: Freeman and Co., 573 pp.

Sokal, R.R. and P.H.A.Sneath (1963) Principles of numerical taxonomy. San Francisco: Freeman, 359 pp.

Stafleu, F.A. (1963) Adanson and his "Familles des plantes". Carnegie Inst. Technol., Monogr. Ser. 1: 123-264.

Ulfstrand, S. (1977) Foraging niche dynamics and overlap in a guild of passerine birds in a south Swedish coniferous woodland. Oecologia 27: 23-45.

Wahlert, G. von (1965) The role of ecological factors in the origin of higher levels of organization. Syst. Zool. 14: 288-300.

Wahlert, G. von (1973) Phylogenie als ökologischer Prozess. Naturwiss. Rdsch. 26: 247-254.

Wiens, J.A. and J.T.Rotenberry (1980) Patterns of morphology and ecology in grassland and shrubsteppe bird populations. Ecol. Monogr. 50: 287-308.

Wiley, E.O. (1981) Phylogenetics. The theory and practice of phylogenetic systematics. New York: Wiley and Sons, 439 pp.

Jiří Mlíkovský

Department of Evolutionary Biology, MBÚ ČSAV

Na Folimance 5
120 00 Praha 2

Czechoslovakia