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ON SOME THEORETICAL AND PRACTICAL ASPECTS OF POPULATION VARIABILITY IN HELMINTHS

J. K. MACKO

Helminthological Institute of the Slovak Academy of Sciences, Košice

Abstract. Possibilities of studies of some microevolutionary processes in helminths on the basis of knowledge of their variability are presented. The practical aspects of the study of helminth variability are also referred to. In conclusion the author states that the investigation of non-morphological characters of helminths, in relation to various morphological structures of phenotypes in the populations of parasite and host, represents a sphere in which the interests of theoretical and practical helminthology meet with one another.

There are great tasks to be fulfilled by the research of population in helmithology. First of all it is necessary to unite the ideas of the population so that it corresponds to the criteria established by biologists engaged in the study of species and intraspecific units. At the same time it is necessary to extend the studies of the population variability of species, since the knowledge of this variability is a basis of various theoretical and practical problems in the contemporary helminthology. General data on the variability of helminths have been published by Gagarin (1972) and Shults and Gvozdev (1972).

The study of population variability in helminths allows 1) to determine more objectively the species and some intraspecific units, 2) to assess the variability of the gene pool of helminth populations, 3) to exclude conservative characters, some of which may be important for the evaluation of phylogenetic relations, 4) to make the classification of taxons of lower rank more exact and easier etc.

The present paper suggests the possibilities of studies of some microevolutionary processes in helminths on the basis of knowledge of the variability. The practical aspects resulting from this variability are also referred to.

The evolutionary processes in helminths at specific and intraspecific level can be best studied in little movable hosts of various endemic, lake and insular species, as well as in progressive, expanding or retreating, dying out and relict animals. Of the birds examined by us, the Gruidae and Ciconiidae belong to this group. The number of their representatives has considerably decreased in the regions of our country during the last decades and therefore the helminths specialized to these hosts seem to be suitable for our studies. For example, according to Skryabin (1947), *Orchipedum formosum* (Sonsino, 1890) parasitizes only *Grus cinerea* (= *Grus grus*). If the variability of body measurements is not considered, the variability in configuration of internal organs of this species is approximately the same (Macko 1970) as in *Cathaemasia hians* (Rud., 1809), which was recovered from the hosts *Ciconia ciconia* and *C. nigra* in Eastern Slovakia in the form of two subspecies (Macko 1960a). The variability of these trematodes, however, is much smaller than the morphological variability of some polyxenic plagiorchids, dicrocoelids, and cyclocoelids, which parasitize rather frequently occurring hosts. Although the morphological variability cannot be identified with the general biological variability,*) it suggests — in relation to the host-specificity of *O. formosum* and *C. hians* to a single host or a small range of non-progressive definite hosts — that these parasites have a smaller general biological variability than those helminths which have also a small morphological variability but parasitize a wider range of hosts. This concerns, e.g., the members of the genus *Trichinella* (Britov 1975). The evolutionary studies reveal that the small biological variability of the parasite often indicates its narrow specialization to a certain host or a small range of host species, which is usually a symptom of its feeble evolutionary potencies.**) Similar results were obtained also by other authors. For example, Osmanov (1975) found that the number of populations of narrowly specialized parasite species, *Neodiplostomum perlatum*, *Cystoopsis acipenseris* and others, is rapidly decreasing in the Aral Sea.

However, the variability of some morphological features of species may vary to a different degree without regard to whether their carriers parasitize a larger or smaller range of hosts. For example, in the polyxenic species *Echinoparyphium recurvatum* (Linstow, 1873) 45 head spines have been reported. Another polyxenic species, *Echinostoma revolutum* (Fröhlich, 1802) has 35—39 head spines (Skryabin and Bashkirova 1956), whereas in the oligoxenic species *Echinostoma bancrofti* Johnston, 1928 their number varies from (43?) 45 to 51 (Macko 1968 c).

If the variability of size of body and organs in helminths is not considered, though it may be rather large in the "large" species, it may be said that the variability of the configuration and structure of individual organs (qualitative variability) is not large in Echinostomatidae and Notocotylidae. In my opinion, compared to the variability of other trematode groups, it is smaller than in a majority of examined species of cyclocoelids (Bykhovskaya-Pavlovskaya 1949, Macko 1960b, 1964, 1965a, b, 1969a, Macko and Feige 1960, Macko and Garrido 1968), dicrocoelids (Skryabin and Evranova 1952, Macko 1968 a, b, 1969 b), and plagiorchids (Krasnolobova 1975). In spite of this, many echinostomatids and notocotylids belong to polyxenic species. These data indicate that the single relatively small qualitative variability of morphological characters cannot be considered an indicator of small biological variability of the parasite.

In relation with the division of trematodes into "more primitive — lower" and "higher" (Ginetsinskaya 1968) a question arises whether there is a difference between the variability of species belonging to these groups. On the basis of our results achieved so far, it may be assumed that in birds, the qualitative variability of "primitive" species of adult trematodes is smaller than that of "higher" species. But Strigeata, Schistosomatata and others are relatively little or less variable, though they are considered to be "higher" trematodes. These facts indicate that much more comprehensive material of adult and larval forms should be studied in relation to the variability of abiophenotes, parthenofenotes (clonophenotes) and organophenotes in order to answer this question.

The present knowledge of the variability of trematodes also indicates that the variability of organophenotes of individual species to some extent depends on whether their cercariae are dispersed in free nature 1) separately like in fasciolids, notocotylids, echinostomatids and schistosomatids, 2) in groups like *Dicrocoelium lanceatum*, or 3) the cercariae remain in the intermediate hosts like *Cyclocoelum microstomum*,

*) "Biological variability" is the general variability of the examined community consisting of morphological, genetical, physiological and other characters and properties.

**) From the viewpoint of surviving and potential possibility of specialization of the monoxenic parasite of great importance is the fact whether it has or has not adapted itself to a progressive species of host (intermediate host, definitive host).

Tamerlania bragai and others. In the second and third case, however, from a single miracidium may originate a clone which may partly (*Dicrocoelium*) or totally (mentioned *Cyclocoelum* and *Tamerlania*, as well as *Echinococcus*, *Alveococcus*, *Coenurus* etc.) get into the definitive host and appear as a specific organophenote. This may differ from the other organophenotes not only in the morphology, but also in the physiology. The mentioned way of propagation is of advantage not only for the survival of the parasite, but also for its further evolutionary potencies, because a suitable mutant may thus rapidly multiply and get in a large number into the definitive host. Under favourable ecological conditions, also various more or less virulent strains of helminths may thus rapidly arise.

In species whose cercariae are dispersed in nature separately, also genetical peculiarities of the clone originating from the snail are "dispersed". The organophenotes of these species may therefore resemble one another more than those of species whose cercariae encyst in the first intermediate host. The variability of Digenea conditioned by genetic factors and way of propagation of cercariae may be considerably changed by ecological selection factors as it was observed in plagiorchids (Krasnolobova 1975). In spite of this it may be supposed that with hermaphroditic trematodes whose cercariae propagate by dissemination the conditions for the formation of a strain are much harder. It is indirectly (from a different view) confirmed by Coles*) who writes in his letter of 1976 in relation with his experience gained during cultivation of *Fasciola hepatica:* "As there is only low level of immunity to fluke in rats and very little, if any, in sheep, there is not a strong immunological pressure for selection of a new strain as there would be, for example, with nematodes or blood flukes (*Schistosoma*) in rodents".

The morphological variability of helminths may be helpful not only for the evaluation of the progression abilities of a certain species, but also for the study of initial processes of speciation. This involves investigations when (in which years) and under which conditions the selection pressure on a certain helmith population is greater or smaller in a certain environment. It may be also studied which environment (e. g., geographical environment or host species etc.) produces a strong or feeble selection pressure on certain communities of parasites. These possibilities of investigations result from the relationship between the variability of a certain character or characters and natural selection affecting these characters. It may be concluded from the papers of evolutionists that higher selection pressure in a certain environment (usually on the edge of a species area) results in an increased selection of phenotypes, i.e., it must lead to a decrease in variability and vice versa. There are no special examples with helminths for the time being. But Belopolskaya (1953) found that the cestodes *Proterogynotaenia variabilis* from birds *Squatarola squatarola* have a variable number of hooks (12, 20, 24 and 28) in East Murman, whereas in the Primorye territory their number is stable (12). Daskalov (1955, ex Shults and Gvozdev 1972) observed that the females of *Ostertagia* have much higher number of morphological variants in adult sheep than in lambs. Another record was published by Voronina (1971).

The data on the evolution further indicate that if the population of a certain species is unable to create a sufficient number of genetic "novelties", it could not assert itself under the relatively rapidly changing conditions of its living environment. Since the helminths with a great biological variability of populations are most adaptable, many of them may be potentially able to adapt themselves under changing ecological conditions also to "new" species or races of host plants and animals.

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*) Dr. G. C. Coles, Mereside Alderley Park, Macclesfield Cheshire, England.

During the civilization process, which radically changes our living environment, the knowledge of helminths with strong evolutionary potency is of both theoretical and practical significance. For example, *Dispharynx nasuta* (Rud., 1819) occurs in both domestic and free-living birds in Cuba. As long as there were only private bastard breeds of poultry, the dispharyngosis was not so frequent as in the large-scale breeding of White Leghorn in 1971 (Birová et al. 1973). Similar results were obtained also by Rumyantsev (1975) who found that under new living conditions, the parasite fauna was formed from polyxenic species.

The results of studies of ecological genetics (Ford 1964) suggest that the population variability changes in different seasons and also prior to and after the expansion of the population. Should this be confirmed also with helminths, then findings of unusual phenotypes may signalize an increase in the infestation wave (in spring in autumn, in enzooties etc.). This phenomenon might become more marked at more frequent findings of helminths on subnormally or abnormally located places, in strongly infected hosts or at their increased occurrence in secondary hosts, as well as more frequent occurrence of immature forms in nonspecific hosts.

Further studies of helminth variability indicate that some morphologically differentiated phenotypes may also have different requirements, properties and ecological, physiological, genetical and other features. For example, investigations of the intrapopulation structure of *Heterakis gallinarum* revealed that the ontogenetic development (including the prepatent period) and viability of short-tailed forms differ from those of specimens with normal tail (Birová and Macko 1976). This suggests, among others, that worms at different levels of development in the host need not originate from superinfections.

The phenotypes which develop more slowly may be sometimes more advantageous from the viewpoint of survival of helminth communities under various unfavourable influences of the living environment. For example, during dehelminthization of ascarids with Santonin, only imaginal stages are eliminated (Pavlovsky and Gnezdilov 1953), whereas the larval and preimaginal stages enable the organophenote to survive.

The phenotypes with preadaptational potencies to changed influences of the environment have a similar function. For example, Drudge et al. (1957) found that the nematodes *Haemonchus contortus* developed, apparently by natural selection, a drug-resistant strain (also Otto 1958, Le Jambre et al. 1976). Also long-termed application of Helmirazine against *Ascaris galli* resulted in a decreasing effect of the drug (Birová and Biro 1970). It is supposed that also in this case nematode populations resistant to this drug have developed. Similar results were recorded also by Katz et al. (1973).

During biparental reproduction, however, arise not only lethal, semilethal and more or less viable phenotypes, but by crossing of representatives of various helminth populations (e.g., during migration of the host) may arise also forms (e.g., biotypes or pathotypes — Decker 1969) with considerably higher viability of virulence. The knowledge of their origin may be of great epizootological significance.

The papers by Shults and Gvozdev (1972) show that the knowledge of helminth variability is not sufficient for the time being. This is also stressed by Gagarin (1972) who recommends to study the helminth variability according to the scheme proposed by Mayr et al. (1953) and Mayr (1963)

In general it may be concluded that the variability of helminths is much greater than it has been supposed till now and that it may serve as a basis for the solution of many theoretical and practical problems. Of the factors causing helminth variability, the genetic variability is the least known one. A certain idea offer the papers published by Schiller (1959, 1974), Daskalov (1971, 1972a, b), Gagarin (1972), Shults and Gvozdev (1972), Drożdż (1974), Macko and Birová (1976), Birová and Macko (1976) and others. From the view of practice, however, it is important that many genes are of pleiotropic character so that a great morphological variability may be, to a certain extent, an indicator of greater non-morphological variability. In general, it is the biological variability that conditions different adaptability, virulence, survival etc. under various conditions of living environment of helminths. The above-mentioned data indicate that the study of non-morphologica, variability of helminths, in relation to different morphological variability of helminths, in relation to different morphological structure of phenotypes in the population of the parasite and host, represents a sphere where the interests of theoretical and practical helminthology are meeting.

О НЕКОТОРЫХ ТЕОРЕТИЧЕСКИХ И ПРАКТИЧЕСКИХ АСПЕКТАХ ПОПУЛЯЦИОННОЙ ИЗМЕНЧИВОСТИ ГЕЛЬМИНТОВ

Й. К. Мацко

Резюме. В работе приведены возможности исследования некоторых микроэволюционных процессов на основе знания изменчивости гельминтов. Кроме того также указаны практические аспекты изучения этой изменчивости. В заключении автор приводит, что изучение неморфологических свойств гельминтов, в зависимости от разной морфологической структуры фенотипов в популяции паразита и хозяина, представляет сферу, в которой встречаются интересы теоретической и практической гельминтологии.

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J. K. M., Helmintologický ústav SAV,
ul. Dukelských hrdinov 11,
040 01 Košice, ČSSR