ON THE PECULIARITY OF MOST COMMON INTRASPECIFIC COMMUNITIES IN ANIMALS IN GENERAL AND WITH SPECIAL REGARD TO HELMINTHS

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Abstract. The public acceptance of the proposed species concept in helminths is analyzed along with considerations on the peculiarity of intraspecific communities. Reasons are given for the author’s opinion that the population and various intrapopulation communities are not universal intraspecific units in all types of species and it is explained why the author did not use terms derived from the word “deme” for the classification of specific intrapopulation communities of helminths. The differences between the lowest intraspecific hierarchic levels in helminths are stressed in relation with the studied problems.

While constructing the species concept it is necessary to take into consideration numerous points at issue. One of them is the question whether the population is really a universal intraspecific unit. This has a bearing on the problems of universality or non-universality of other intraspecific communities, as well as on their universal or differentiated nomenclature. Since these questions are fundamental and concern also the classification of intrapopulation communities in helminths (e.g. Zavadsky 1961: 61, Lebedev 1979 and others) they should be dealt with separately.

I.

During the 20th century there appeared numerous species concepts with specific classification of intraspecific communities. From the viewpoint of population they can be divided into two main groups. The first one includes concepts which do not consider the population to be a legitimate unit in asexual and exclusively uniparental species (e.g., Mayr’s biological concept). The other group comprises the concepts regarding the population as a universal unit in all types of species (e.g., evolution concept of Simpson 1961, or Zavadsky’s concept 1961, 1968). This dissension in opinions on the universality of populations is due to the existence of two basic types of organisms with different way of reproduction and with a very different intraspecific structure. These are 1) sexually reproducing species, and 2) species reproducing exclusively asexually, obligatorily parthenogenetically and equivalently to them.

In animals belonging to the first type of organisms (with sexual reproduction), the population is a part of an objective criterion of species which is the reproductive isolation of natural populations*. If one of the attributes of this criterion is determined subjectively, then also the resulting taxon-biospecies “can be imaginary. A wrong determination of species may occur particularly” in less studied animals if the presumption on reproductive isolation is deduced from the existence of (e.g. morphological) hiatuses (gaps) in the communities which are not populations. For instance, the material for

* In asexual and equivalent species no adequate objective criterion has been found.
helminth determination are usually not "samples" of populations, but intrapopulation 
communities, as, e.g., preorganophenotes, organophenotes, idiohost populations etc. 
Their morphology is influenced by concrete helminth-host relationships in each host 
specimen separately. Consequently, individual helminth communities can also be pecu-
liar; if the systematian has only two or three organophenotes of a certain taxon (or 
"samples" of them) it may happen that he finds some morphological hiatuses between 
them. If he is convinced at the same time that each organ or each host is parasitized 
by a single helminth population, this is a justification for regarding the studied forms 
as two different species. However, if he is aware of the fact that only intrapopulation 
units are involved, he will probably try to examine a whole series of larvophenotes and 
organophenotes from various host species and from various seasons in order to make 
a picture of possible variability of populations. Even morphological hiatuses between 
sympatric and parapatric helminth populations, in correlation with other non-morpho-
logical criteria, can be used as a basis of "morphospecies" or "taxospecies" determi-
nation. These facts indicate that if our aim is the determination of species, as objective 
as possible, the population cannot be understood either subjectively or freely as it is 
commonly understood.

The populations are determined on the basis of many definitions. In principle these 
definitions can be divided into two groups. The first group includes the definitions allow-
ing to a great extent a subjective determination of populations. Among them are 
definitions considering the population a set of organisms in a certain space or territory. 
The following population definition is often cited: "The organisms, collectively, inhab-
it ing an area or region" (Webster's Collegiate Dictionary, Mayr 1964, Allee et al. 
1961, Zavadsky 1968: 233). Also the definitions regarding as populations the organisms of 
the same species in a certain ecotope (biotope) enable an objective determination of 
populations only in a certain part of animals in the given ecosystem (cfr. Stugren 1972, 
Macko 1979a).

The second group includes the definitions according to which the population has a 
single hierarchic level which can be objectively determined. The most progressive is 
now considered that defining the population as an elementary evolutionary unit of 
species*. This concept of population is adopted not only by many biologists, but also 
philosophers engaged in the problems of species (Borzenkov 1977, Sershtanow 
1978, Sucker 1978 and others). A great "disadvantage" of this "objective" definition is 
the fact that it excludes the possibility of existence of population in exclusively asexual 
species and those equivalent to them, since their elementary evolutionary unit is each 
specimen separately. This conclusion follows, e.g., from the context of papers by Mayr 
(1963: 587), Zavadsky (1961: 145) and others. If the population is determined after 
the definition 1, according to which it is any complex of organisms of the given species 
inhabiting a certain area (region), whether it reproduces sexually or asexually (Severtsov 
1951 ex Zavadsky 1968) or definition 2 "the organisms, collectively, inhabiting 
an area or region", then also asexual types of species may form a population. However, 
as it was mentioned above, these and similar definitions admit subjective decision which 
communities should be regarded as a population and therefore they are unsuitable for 
an unbiased determination and objective criterion of species.

Those who consider the population a universal intraspecific unit and support the 
objective determination of communities (being aware of the discrepancy in the "object-
ive" definition of population) regard this community as a basic evolutionary or demo-
graphic unit (of species), or an elementary biochorologic unit of species (cfr. Zavadsky

* Its objective determination is enabled by many criteria (Macko 1974). Alternative definitions: 
Population is a basic evolutionary unit etc.
Theoretically, the definitions formulated in this way do not ensure sufficiently objective determination of the population. For example, the basic unit of evolution is not only the population, but also other communities, e.g., species (Simpson 1961, Čižek 1977). In some cases, the elementary bioclorologic units of species can be also the micropopulations, subpopulations and other communities. The population sensu Shvarts et al. (1972) has the character of a typical elementary evolutionary unit of species.

Some biologists aim at separating from the Mayr's biological concept the criterion of reproductive isolation of populations and at applying it in the conceptions considering the population-species organization a universal form of existence of living organisms. This is not quite suitable particularly in case that the population is considered an elementary evolutionary unit or a certain panmictic community. Each funded concept of species is the system of mutually related conclusions and therefore a “new” conception cannot be created by choosing and more or less mechanically connecting most attractive criteria and definitions.

The studies of these problems indicate that at present it is possible to choose either the concepts which are still more aiming at determining the species on the basis of objective criteria, or those which do not consider objective criteria and are based on more or less subjective opinions in the determinations of populations and species. Since there is a trend in the systematics to avoid the criteria based on “subjective opinion of a competent specialist”, it is logical that also in the problems of species the characteristics enabling objective determination of communities will be preferred. At present, there is no more objective definition available than that defining the population as “elementary evolutionary unit of species”. It should be therefore accepted particularly by those who prefer the most objective possible determination of populations and species. However, to avoid ambiguities in the question which species exist in form of populations, the definition of natural population or simply population should read as follows: “The natural population is an elementary evolutionary unit of species with biparental way of reproduction and with such a way of reproduction when the exchange of genetic information between members of the reproducing community occurs at least in some of the consequent generations” (Macko 1978b). The fact that asexual and equivalent species do not form populations has been mentioned, besides Mayr (1963) and his school, also by Timofeev-Ressovsky (1965 ex Starobogatov 1968), Timofeev-Ressovsky et al. (1973: 42), Starobogatov (1968: 884), Hull (1976: 183) and others. I assume that this opinion is more correct than those which, in order to keep the idea on the universality of population-species structure of organisms, must recognize also the definitions allowing to a great extent a subjective determination of population.

II.

Before the lowest intraspecific levels of helminths are dealt with, it is necessary to note that there is a strong tendency in biology to use the term population or its modifications as subpopulation, micropopulation etc. (Macko 1977) for heterogeneous communities. Obviously it is due to the euphony of this word, as well as to the reaction to a great number of various terms introduced in the literature (see Zavadsky 1961, Yablokov-Khnzoryan 1968 and others). For instance, Zavadsky (1961: 61) writes that the systematists-specialists, among them also helminthologists, introduced hundreds of “own” terms, a majority of which are synonyms or half-synonyms. Lebedev (1979) also assumes that it is more suitable to use known terms, as those derived from the term “dem”, for the intrapopulation communities of helminths than new terms originating from the word “phenote”.

321
In order to unite the existing diversity in the terminology of intraspecific units, several authors published schemes for the classification of intraspecific communities. For example, Zavadsky (1961: 136) gives this hierarchic structure of species: 1. species, 2. subspecies, 3. ecotype, 4. local population, 5. ecoelement, 6. morpho-biological group or isoreagent, 7. biotype and mixobiotype. Dubinin (1966): 1. semispecies, 2. subspecies, 3. race, 4. microtopographic race, 5. line, 6. individual. Shkorbatov (1968: 924) in biological species: 1. geographical race, 2. ecological race., 3. population, 4. local population, 5. elementary population, 6. herd, 7. stable, 8. family. Shvarts et al. (1972): 3. proposes to term all intrapopulation units “micropopulations” etc.

Nothing can be objected against unification of terms and abolition of synonyms. It should be stressed, however, that opposite cases are often connived, at, if the same term is used for heterogeneous communities at various hierarchic levels. Most important is to differentiate population communities, to which belong also races and subspecies, from intrapopulation communities as micropopulations, hemipopulations, organophenotes and others. The intrapopulation communities are ephemeral, unstable aggregations. Many of them exist only in the detriment of the influx of new specimens “from outside”. Others are formed only from certain developmental stages or certain age groups of animals (Beklemishev 1959, Zavadsky 1968, Shvarts et al. 1972). In the classification of intrapopulation units it should be taken into consideration 1. genetic heterogeneity of intrapopulation communities (caused, among others, by different ways of reproduction), 2. diversity of the life cycles of organisms (particularly their homotopy and heterotopy), 3. diversity of the ways of propagation and aggregation of animals.

In the studies of species structure of parasites, the communities inhabiting hosts are particularly stressed. According to Pavlovsky (1961), the individual host organism represents a whole microcosmos for the parasites. Various tissues, organs, body cavities, as well as blood and lymphatic system represent various living environments for the helminth. In individual organs arise more or less isolated communities of parasites. This follows not only from the studies on parasitocenoses (Pavlovsky 1961), but it is documented also by the speciation of conjugate species—“sopryazhennye vidy” (Dogel 1962, Kontrimavichus 1978) and speciation of “cogeneric simultaneous doublets” (Lebedev 1978). For these reasons, and from the viewpoint of different ways of realization of (a part of) life cycles of helminths in the organisms, it is necessary to distinguish in individual hosts usually one (“organ”) or two (“organ” and “organism”) hierarchic levels. Since these levels are rarely differentiated, I am giving their characteristics as follows:

1. Only one, “organ” intrapopulation hierarchic level is formed on individual hosts by the helminth species parasitizing only the organ or tissue of the organ in which they are established and where originated the helminth-host relationship between their infective stages and the host. These parasites do not migrate from the organ in which they are established. This type of migration could be termed according to Shults and Gvozdev (1972): a) small retrograded or small prograded migration (in this way migrate many trematode and cestode species in the small intestine of the host; b) small tissue migration (as with Haemonchus contortus and others). Both these types of migration (1a, b) could be termed small migration of helminths in hosts.

On the basis of the above way of parasitization and movement of helminths, exclusively “organ” communities are formed in individual definitive hosts (s.l.). Macko (1961, 1979b) recommends to term them organophenote.

2. Two intrapopulation hierarchic levels, “organ” and “organism”, are formed in individual hosts by helminths migrating in such a way that they actively or passively leave a) the organ of the digestive tract in which they were established, i.e., where the parasite-host relationship occurred between their infective stages and the host, b) the
organ into which they penetrated or were inoculated through body surface. These migrations (2a, b) can be more or less widespread (Schistosomatidae, *Ascaris*, *Parascaris*, *Fasciola hepatica* and others, see Shulits and Gvozdev 1972).

At the “organ” hierarchic level, the helminths with such “large” migration form several types of communities. Most frequent types were recommended by Macko (1979b) to be termed preorganophenotes or parthenomicropopulations in the intermediate hosts and preorganophenotes and organophenotes in the definitive hosts (s.l.).

The communities formed at “organism” level are recommended to be termed biophenotes, parthenophenotes (Macko 1961, 1979b) and idiohost populations (Kisielewska 1970, 1974). The communities of migrating helminths (described sub. 2) existing at “organ” hierarchic level (preorganophenotes, organophenotes and others) are a component of communities at higher “organism” hierarchic level. These “two-level” hierarchic communities of migrating helminths in individual definitive hosts are proposed to be termed idiohost population (Macko 1979b).

It is of interest that the retarded larvae (preorganophenotes) or some migrating nematode species survive in various parts of definitive hosts (s.l.) for the same long time as adults in the “target” organ. For example, *Ancylostoma caninum* can survive in the subcutaneous tissue of older dogs as long as for five years (Stoye 1973).

Nevertheless, studies carried out in the last years suggest that in some cases it will be necessary to differentiate, even within a host organ, further suborgan, “niche” levels, as it is pointed out by Lebedev (1978) in Monogenea. It is possible that a special term will have to be created for helminth communities differentiating at the level of “niches” in a single organ.

### III.

Hoare (1956 ex Dogel’ 1962) published a classification of intraspecific communities of based on the nomenclature consisting of words derived from “deme”. This nomenclature was not used for the classification of specific intrapopulation helminth communities for the following reasons: The term “deme” was introduced into the literature by the botanists Gillmour and Gregor in 1939 without any exact definition (Mayr 1963, 1978, Jonckers 1973). Probably for this reason some authors use this term for the communities at various hierarchic levels. For instance, serodeme for a strain differing in immunological properties, clinodeme for geographical differences (cfr. Dogel 1962). According to Yablokov—Khinzoryan (1968), gamodeme are “more or less well isolated micro-populations”. On the other hand, Jonckers (1973) defines gamodeme as follows: “A population belongs to the type “gamodeme”, if the individuals of that population are capable of interbreeding in nature and are distributed in space in such a way that they are not reproductively isolated”. Krassilov (1976) recommends to use various modifications of the word “deme” for communities at species level (species of systematics—eiodeme), at level of population and below this level (e.g., small colonies—neodeme). Most frequently the term deme and its compounds are used as a synonym of (local) population (Mayr 1963, 1978, Zavadsky 1968, Jonckers 1973 and others).

If the deme nomenclature (eiodeme, xenodeme and others) should be used for specific intrapopulation communities of helminths, these terms would have to be understood in a wider sense than is that ascribed to them by a majority of authors. This would not be correct, as in the original publication by Gillmour and Gregor from 1939 the term deme represents a population (Mayr 1963, 1978) and according to Bertalanffy (1964) the terms should be used in the sense given them originally by their authors. For these reasons, while characterizing the deme communities, the homotopic and heterotopic realization of life cycles, which is a basis of the classification of intrapopulation parasite communities (Beklemishev 1959) could not be taken into con-
consideration. The specificity of these intrapopulation communities is stressed also by the fact that all developmental stages of (according to Henning 1966 they may be regarded as semaphoronts) homotopic parasites develop in consequent generations within the parasitocoenosis of a single host specimen, whereas semaphoronts of heterotopic species enter various coenoses during their ontogenetic life. For example, in a certain larval stage, many of the heterotopic helminth species exist as nonparasitizing groups (abiophenotes) in the biocoenosis, whereas in the adult stage these parasites are usually members of host parasitocoenoses as organophenotes, idiohost populations etc. For this reason the homotopic and heterotopic way of development of the parasite must be included among the most important criteria of classification of their intrapopulation communities.

All "phenotes" of helminths, e.i., organophenotes, biophenotes, hostophenotes and others, have exclusively intrapopulation character. They exist at qualitatively lower hierarchic level than demes (populations) and therefore the deme nomenclature would not express their specificity.

However, the application of the term "deme" in helminthology is justified in the sense of Dogel's (1962) report. He writes that the "deme" of Hoare is close to the term population. In this sense, which agrees also with the opinion of Timofeev-Ressovsky et al. (1973), the term deme could be used for relatively short-living communities ("populations") of worms which die in the ecosystems after a certain small number of consequent life-cycles (Macko 1978a).

Due to the ambiguities associated with the term "deme", it has been lately ascribed rather neutral* than exclusively population character.

CONCLUSION

The studies of the species structure indicate that if its communities are regarded from the viewpoint of their specific characters and their hierarchic subordination (Macko 1968, 1975, 1978b), then only the species has a universal character. The lower the intraspecific hierarchic level of the certain type of community the lower the number of species types in which it occurs. For example, sexually reproducing organisms can form the following hierarchic structure of intraspecific non-taxonomic communities.

Species, population (populations): Ursus arctos in Slovakia (deduced from data of Feriancová 1955 and others).

Species, populations, micropopulations (various homotopic animals: protozoans, ectoparasites—Phthiraptera (Beklemishev 1959), endoparasites with endocycles, e.g., Probstmayria (Oxyurata) and other nematodes** (Odening 1974), various small vertebrates (Shvarts 1960, Shvarts et al. 1972).

Species, populations, hemipopulations: e.g., Anopheles maculipennis and other insect species (Beklemishev 1959).

Species, populations, hemipopulations, abiophenotes and organophenotes (various species of homoxenic helminths—geohelminths, e.g., Trichocephalus).

Species, populations, hemipopulations, abiophenotes, idiohost populations, preorganophenotes, organophenotes (various species of homoxenic helminths migrating out of the host organ in which they were established, e.g., Parascaris).

The heteroxenic helminths (biohelminths) form, beside the above communities, also some intrapopulation communities parasitizing the intermediate hosts.

* Of neutral character are, e.g., the terms community, form, aggregation and others.
** Nematodes with endocycles were reported by Ivashkin and Babaeva (1973).
Exclusively asexual and equivalent organisms can have the following hierarchic structure of intraspecific non-taxonomic communities: species, ecotype complex of clones—apomixodeem* (Bdelloidea, exclusively parthenogenetic species of Archaeolacerta and others—Mayer 1963, Shimansky 1969), clone.

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* Apomictic deme sensu Krassilov (1976).


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