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POPULATION AND CLASSIFICATION OF INTRAPOPULATION UNITS OF HELMINTHS

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Dedicated to the memory of Academician K. I. Skryabin on the occasion of the centenary of his birthday

Abstract. The study of the population problems revealed that the population is an elementary evolution unit of a species with biparental way of reproduction. This is a general theoretical definition which the author elaborated in detail for the helminths. With regard to the complicated intraspecific structure of these parasites also the classification of intrapopulation helminth units is proposed.

The population is now considered a most important intraspecific unit and a great attention is paid to this subject. This attention is greater or smaller in individual biological disciplines and therefore also the conceptions of this community are different. For example, many helminthologists regard the population as a community inhabiting a certain organ of the host or a certain host specimen. This idea follows from an earlier conception which did not take into account some essential characters of the population (Macko 1974).

The close relation between helminth population and host population arises from the very substance of the helminth-host relationship, when the phenotype of the parasite and that of the host are in mutual interaction. Each of these phenotypes is contingent on a special genotype which is closely related to the gene pool of the population from which each of the partners originated. The communities of helminths and hosts, as well as their relations, are regulated by a natural selection which tends to keep in the gene pools the genes capable of harmonious cooperation and formation of gene complexes. The "historical experience" of helminths concerning their hosts and vice versa, coded in the genes, is thus accumulating in the gene pools of both helminth and host populations, i.e., above individual level. These relations enable any crossing pair in the helminth (or host) population, including the autogamy of hermaphrodites, to produce a vital progeny[1] more or less adapted to their hosts (or parasites) and to the living environment which forms a certain ecosystem. Consequently, the populations of helminths and the populations of hosts (or, figuratively, gene pools of helminth populations and gene pools of host populations) and their living environments are responsible for their previous (parallel) evolution, for their settled mutual relations, and for further development of their parasite-host relationship. This indicates that the population level may be ascribed only to the intraspecific communities of helminths and hosts capable (under suitable conditions) of development in a certain space potentially for an unlimited period. The mutual genetical and ecological dependence of the helminth and host populations, as well as their (parallel) development, require an identical theoretical definition of their populations. Since the application of most objective methods of investigation has lately been stressed more and more, the population definitions enabling this tendency are of great importance. Considering the information and ideas published by Chetverikov (1926), Shmalgauzen (1958, 1961), Mayr (1963), Jonckers (1973) and Macko (1974), the elementary evolution unit of a species with biparental reproduction, whether parasites or free-living organisms, may be considered a general theoretical definition of natural population. The definitions which regard (in various modifications) the population as a group of specimens in a certain area are unsuitable from the theoretical

view, since the geographical factor cannot be an independent criterion for biparentally reproducing population communities. Moreover, in many cases it is not specified what is the extent of the respective area.

From the viewpoint of an inhabited area of the population these communities may be divided into two pole types. One type is a small population or local population. Its members have such radiuses of individual activity that they comprise potentially (actively or passively, in helminths through their host) the whole habitat of the population. The other type is a large population. Its members have much smaller radius of individual activity compared to the population habitat, so that the members of one part of the population cannot get into contact (cross) with members of the opposite part.

Beklemishev (1959 a, b, 1960, 1970) may be considered the founder of a progressive population concept in parasitology. Although some of his definitions of intraspecific units should be revised from the present point of view, his conception should serve as a basis in the study of the population structure. Following this conception and the general theoretical definitions we are submitting here a detailed definition of population for helminths. The helminth population is an elementary evolutional structural community of one species which has a special integrated gene pool and which has evolved in common symphysiological relations with the host population or more or less sympatric populations of various species of definitive, intermediate, parathenic or other types of hosts in a relatively permanent habitat enabling the members of the population a panmiction and reproduction, which are accomplished either in the hosts or in nature, as well as gradual realization of all developmental stages in successive life-cycles potentially without any time limit.

The size of helminth population depends on the factor allowing the integration of its gene pool. For many helminth groups this factor is the population of their definitive hosts or more or less sympatric range of definitive hosts[2]. This formulation of helminth population was given by Macko (1961).

At the population level, it is necessary to differentiate between population and pseudopopulation which after Beklemishev (1959 a) represents a settlement of animal or plant organisms which cannot reproduce independently, due to unfavourable conditions, and exist only thanks to the influx of other specimens from the outside. As an example of pseudopopulation and pseudofocus Beklemishev (l.c.) quotes Isaev's observations of the inhabitants of Yerevan. They are strongly infected by ascarids introduced to Yerevan with the fruit originating from infested suburb, while in the town the conditions for the survival and development of ascarid eggs are unfavourable. "If this is the case", writes Beklemishev, "then the ascarids in Yerevan represent a pseudopopulation and the inhabitants of this town infected by them are a pseudofocus of ascaridosis."

These conclusions suggest that the pseudopopulations of helminths are formed in the ecosystems with unfavourable conditions for the completion of their life-cycles. For this reason the pseudopopulations exist only in form of some intrapopulation units, e.g., organophenotes only.

INTRAPOPULATION UNITS

Intrapopulation units are an important problem in the study of the intraspecific structure. For some types of species (helminths) the intrapopulation communities are an unseparable form of population existence, whereas in other types of species they may be formed occasionally, according to the size of population and conditions of living environment.

The intrapopulation non-taxonomic units of helminths have been termed as follows: micropopulation (Macko 1961, Eichler 1971 — for parasites in general, Odening 1974), hemipopulation (Beklemishev 1959 b, Odening 1974), subpopulation (group of authors — see Wiad. Parazytol. No. 5, 1974). We have also met with some other terms, as biotype, variety, form, ecotype, deme, strain and others. It should be noted, however, that sometimes it is difficult to recognize whether they were used in the function of an intrapopulation or some other intraspecific unit.

In addition to the above-mentioned terms the following ones have been set by Macko (1961, 1966): 1) larvophenotes, larval communities including abiophenotes, biophenotes and parthenophenotes; 2) organophenotes; and 3) hostophenotes. Hennig (1966) used the term semaphoront which is suitable also for helminths, Ginetsinskaya (1968) mentioned swarms in relation to cercariae, Mozgovoy and Sudarikov (1968) and Mozgovoy et al. (1968) applied the term colonies. Kisielewska (1970, 1974) proposed the terms idiohost, synhost and panhost population; Romashov (1973) imaginal endopopulation, larval endopopulation, larval endomicropopulation and exopopulation. Odening (1974) prefers the terms nonparasitizing larvophenote and parasitizing larvophenote to abio- and biophenote. Freze (1976) introduces the term host eco-form, whereas Ternopolskaya (1976) uses the term adaptive form for the helminth community the varability of which is determined by the species of host.

In this paper, the reproductive host of adult helminths is often named (definitive) host. This is a term ad hoc and should express particularly all obligate reproductive hosts of adult forms of (1) heteroxenous and (2) homoxenous helminths. The names of helminth communities parasitizing (definitive) hosts can usually be applied also to organ communities of helminths in a postcyclic host, paradefinitive host and to the organ communities in polyvalent hosts in which the helminths complete their life-cycles.

CHARACTERISTICS AND DEFINITIONS OF COMMUNITIES WHOSE NAMES ARE ASSOCIATED WITH THE CLASSIFICATION OF INTRAPOPULATION UNITS

Aberration (aberratio). An older taxonomic unit. Der Grosse Brockhaus (1928) gives the following definition of aberration: "In der Tier- und Pflanzensystematik eine seltene, doch meist starke, häufig krankhafte Abänderung einer Art." Příruční slovník naučný (Concise encyclopaedia) (1963): In zoology a subspecific systematical unit. Yablokov-Khnzoryan (1968) according to Semenov Tian-Shansky's paper published in 1910 recommends to use the term aberration for individual variability only. In the same sense it was used for helminths by Macko (1964) and Ladygina and Barabashova (1976). Application of this term in helminthology is possible in accordance with the proposal of Semenov Tian-Shansky, without any claim to a special taxonomic name.

Abiophenote. According to Macko (1961), the abiophenote is an intrapopulation unit of nonreproducing free-living larval forms of gonochoric worms — geohelminths. According to Odening (1974), the abiophenote (nonparasitizing larvophenote) is "im Biotop der Wirtpopulation freilebende Larvenformen." This characterization extends the application of these terms to free-living larval intrapopulation units of biohelminths. Odening (1974) ascribes to abiophenotes also "Parasitenformen in oder auf Transportwirten" (= anadaptive transmitters; a pointer of the absence of parasite-host relation).

The helminth larvae may be more or less evenly distributed in the habitat of small populations and therefore they may exist in form of one abiophenote. In the habitat of greater populations, the

free-living helminth larvae may form several groups. In this case each group represents an abiophenote.Some of the abiophenotes may get the character of a colony (Mozgovoy and Sudarikov 1968, Mozgovoy et al. 1968), others have the character of a swarm (Ginetsinskaya 1968).

On the basis of the present knowledge, the abiophenote may be defined with more precision as an intrapopulation unit of free-living larval forms and eggs of helminths in the habitat of the helminth population.

Abnormitas. An irregular individual deviation from a standard — anomaly (Yablokov-Khnzoryan 1968, Macko 1964).

Adaptive form. According to Ternopolskaya (1976), it is a community of helminths the variability of which is determined by the host species. The author's paper on adaptive forms of *Fasciola hepatica* suggests that hostophenotes are involved.

Biophenote (parasitizing larvophenote). This is an intrapopulation unit of nonreproducing larval forms of helminths in one specimen of intermediate (larvo-intermediate), parathenic or nonreproducing host of homoxenic helminths (e.g., in Mermithidae). According to Odening (1974) "der Begriff Biophänote gilt also... für solche adaptiven Translatoren anderer Parasiten, in denen keine Vermehrung der Parasiten erfolgt".

Biotype. According to Johannsen (1903 ex Der Grosse Brockhaus 1929) the biotype represents a pure line, or according to Stempell (1935), Mayr (1963), Zavadsky (1961) and others a group of genetically identical individuals. Without a genetic examination, the term biotype with helminths might be used for an intrapopulation community, e.g., clone, which arised from a single germ by gemmation, polyembryony or ameiotic parthenogenesis. The term biotype is used for communities of phytohelminths in the sense of race or also in the sense of intrapopulation unit (Decker 1969: 117, 338). The biotypes of phytohelminths expressing themselves as aggressive races are considered to be a pathotype if they are genetically homogeneous. Decker (1969) writes about them: "Der Terminus 'Pathotyp' wurde von Howard (1964) als Ersatz für die Bezeichnung 'Biotyp', welche genetische Homogenität der Population voraussetzt, vorgeschlagen und von Videgard (1967) auf alle Formen der 'pathogenetischen Spezialisation' bei pflanzenparasitären Nematoden ausgedehnt. Videgard schlug ferner vor, zur Kennzeichnung verschiedener Pathotypen einer Art einheitlich arabische Zahlen zu verwenden". The term pathotype seems to be close to the term strain in a certain respect.

Clone. According to Mayr (1963), the clone represents all the individuals derived by asexual reproduction from a single sexually produced individual. Since from the genetical view there is no difference between the reproduction in which new individuals are produced vegetatively and the reproduction by ameiotic parthenogenesis, some biologists (Mayr 1963) take even parthenogenesis for an asexual reproduction. Considering these genetical principles, the clone may be regarded as a community which arised by vegetative reproduction or ameiotic parthenogenesis (Shimansky 1969) from a single organism.

According to Ginetsinskaya (1968), the meiosis of the germ cells of sporocysts and rediae is an atavistic feature and appears only in "primitive" trematodes (Paramphistomatidae, Fasciolidae). In "higher" trematodes (Strigeidae, Schistosomatidae, Plagiorchidae), an ameiotic parthenogenesis occurs (Ginetsinskaya l.c.) in parthenites and the term clone is therefore suitable for these forms. In general, however, the term clone is used in case of a vegetative and uniparental reproduction, during which arise genetically homogeneous genotypes (homozygous or heterozygous).

Clonophenote. The clonophenote represents an intrapopulation unit consisting of various clones of helminths in a single host specimen. The clonophenotes may be formed by larvae of some cestodes in a certain host specimen, e.g., *Coenurus*, *Multiceps*, *Echinococcus*, *Alveococcus;* members of Dicyemida and Orthonectida (*Rhopalura ophiocomae*), Mesozoa (Shults and Gvozdev 1972), as well as the trematode species reproducing

in molluscs by polyembryony, gemmation etc. (Ginetsinskaya 1968, Odening 1974, Clark 1974).

Colony. The term colony is used for a set of numerous individuals living together (Příruční slovník naučný 1963, Allee et al. 1951—61, Vergesellschaftung von Einzell-organismen der gleichen Art, Brockhaus ABC Biologie, 1967). According to Bolshaya sovietskaya entsiklopediya (Great Soviet Encyclopaedia) (1963, Vol. 22), the colonies are organisms which after an asexual (vegetative) reproduction remain connected with daughter organisms and further generations; however, colonies of sexually reproducing organisms are also mentioned.

It is generally admitted that the colonies may consist of representatives of a single species (homotypical colony) or of representatives of several species (heterotypical colony). According to Zmoray (personal communication), the main criterion of colony is a certain suitable place where the organisms find suitable conditions (shelter, climate, food etc.) for their common life.

These facts indicate that not every group of animals is a colony. For example, the bats living together in a cave can be regarded as a colony, but the bats passing the night on a tree cannot. Similarly, an accumulation of eggs and cysts of helminths in nature cannot be regarded as a colony. Also a group of larvae in an unsuitable living environment can be harldy termed colony. According to Mozgovoy and Sudarikov (1968) and Mozgovoy et al. (1968). the larvae of *Contracaecum spiculigerum*, *C. microcephalum* and *C. spasskii* attached to small objects swimming in water or lying on the bottom of a water reservoir may form colonies.

The above-mentioned facts concerning the colonies, as well as the data on parasite communities, indicate that a homotypical colony of helminths represents an intrapopulation group of non-parasitizing forms of helminths living together in a certain characteristic environment in the habitat of the helminth population which offers them particularly suitable conditions for their existence before infecting the host.

The colonies are formed mainly by non-parasitizing forms of helminth species which reach their sexual maturity and cross in nature before infecting the host. The representatives of some species kinds can even reproduce before infecting the host. These groups include, e.g., *Sphaerularia bombi*, *Atractonema gibbosum*, *Heterotylenchus aberrans* (Tylenchida), *Psammomermis korsakowi* (Dorylaimida, Mermithidae) and others in (or on) the soil, in water, in pools and on their bottoms (*Reesimermis nielseni*, *Hexamermis albicans* (Mermithidae), various Gordiacea, and in decaying substances members of Rhabditata, *Parasitaphelenchus papillosus* (Aphelenchoididae) and others (Shults and Gvozdev 1972, Slobodyanyuk 1973). Some colonies are monomorphous, i.e., they consist of specimens of the same type, others are polymorphous, i.e., they consist of various morpho-physiological types. For example, *Strongyloides papillosus* forms colonies comprising in addition to adults also filariform and rhabditiform larvae.

The intraspecific structure of helminths (cestodes) in relation to a solitary and colonial way of living of the hosts was studied by Bona (1975).

If non-parasitizing forms of helminths develop in a certain environment in a very small number or are dispersed in such a manner that the term colony would be unsuitable for them, then we recommend to use the terms abiophenote and topophenote.

The topophenote is a small (not numerous) intrapopulation community of non-parasitizing forms of helminths in the habitat of helminth population. Sexually mature individuals of these helminths can freely cross before infecting the host. It remains to be solved whether it is necessary to differentiate nomenclatorically the colonies and topophenotes on the basis of their demands of a specific living environment. In a positive case we may use the term pedophenote for the topophenote developing and crossing in the soil or on it; hydrophenote for the topophenote developing and crossing in water; saprophenote for the topophenote developing and crossing on or in decaying substances; bentophenote for that developing and crossing on the bottom of water reservoirs etc.

Deme. According to Mayr (1963), this term was introduced into the literature by Gilmour and Gregor in 1939. It was neither rigidly defined nor clearly restricted. Many authors consider it a synonym of local population. Others (e.g., Krassilov 1976) use it as a suffix in various terms, as gamodeme, topodeme, pangamodeme, paleodeme, apodeme, morphodeme, ecodeme, chronodeme, mixodeme etc. Also Hoare (1956 ex Dogel 1962) uses the terms ecodeme, serodeme, xeniodeme, klinodeme, and nosodeme for biological races of parasites.

With regard to the fact that Gilmour and Gregor did not exactly define which com-

munity should be called deme and that various authors use this term for communities at various levels, it gets rather a neutral character than a character of population.

Ecological polymorphism. Ecological polymorphism represents in individual helminth populations a simultaneous occurrence of different phenotypes (morphs) with such a gene arrangement that enables them to occupy different subniches within the general habitat of the species.

Ecotype. This term was first used in the literature by Turesson in 1922 for plant communities which originated as a result of the genotypical response of an ecospecies to a particular habitat. See also Bolshaya sovetskaya entsiklopediya (1957, vol. 48) according to which the ecotype includes a larger or smaller number of biotypes. According to Clausen (1958) and Mayr (1963), the ecotype may represent a population or a complex of populations. The cited authors further state that the biological and evolutionary meaning of the ecotype of botanists counterparts with the term "ecological race" used by animal systematicians.

In parasitology it is usual to use for the representatives of a certain species, which are adapted to a particular habitat (e.g., to a certain host species), the terms host, ecological (Dogel 1962) or biological races (Hoare 1952). Application of another term (ecotype) is therefore disputable for this helminth community.

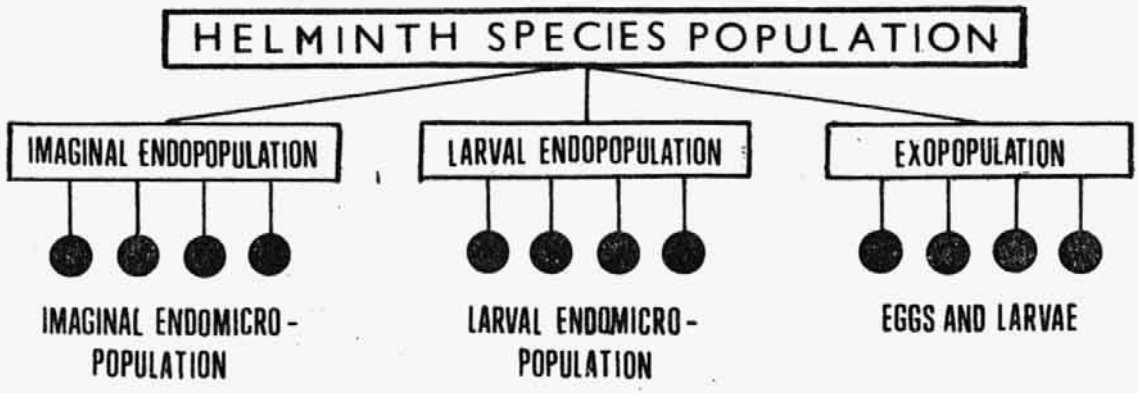

Fig. 1. Hierarchic structure of intrapopulation helminth units after Romashov (III International Symposium in High Tatras, 1976).

Endopopulation and exopopulation. Romashov (1973) divides the helminth population into imaginal endopopulation (consisting of imaginal endomicropopulations), larval endopopulation (consisting of larval endomicropopulations) and exopopulation consisting of eggs and larvae. The hierarchy of these communities is shown in Fig. 1 and in the following original definition: "Imaginal endopopulation is a totality of individuals of various ages and generations of helminths of a single species inhabiting the organism (organ) of host (hosts) of a single population, developing in it up to a sexual maturity and giving sexual products. Imaginal endopopulation consists of imaginal endomicropopulations of helminths.

Imaginal endomicropopulation is a totality of individuals of various ages and generations of a single species inhabiting the organism (organ) of a single host specimen, developing in it to sexual maturity and giving sexual products.

Larval endopopulation is a totality of all larval specimens (also parthenites) of helminths of a single species, inhabiting intermediate, complementary and reservoir hosts and united by a common territory of the habitat. The larval endopopulation consists of larval endomicropopulations.

Larval endomicropopulation is a totality of larval specimens (also parthenites) of

helminths of a single species inhabiting a single specimen of intermediate, complementary or reservoir host.

Exopopulation is a totality of all eggs and larvae of helminths of a single species in the outer environment, united by a common territory (usually with some small variations within the host population range)".

The above definitions show that the term imaginal endomicropopulation is a synonym of organophenote. Also exopopulation and abiophenote are synonyms. The imaginal endopopulation represents the imaginal part of the synhost population. The larval endopopulation is a general term for non-reproducing and reproducing forms of helminths in intermediate, complementary and parathenic hosts. If it is true that parthenites are larval forms of trematodes, as it is supposed by Clark (1974), the term larval endopopulation could be used in helminthology, similarly as the term larval endomicropopulation, which represents a combination of biophenote and parthenophenote, or clonophenote.

The terms of Romashov (1973) which are not synonyms of other names used before 1973 should be kept in reserve, because it may happen that their definitions will make them suitable for some intrapopulation units.

Form. The term form was originally used for a taxonomic unit (Dubinin 1954). According to Semenov Tian-Shansky (1910 ex Yablokov-Khnzoryan 1968), the term form represents identical types of aberrant variations, e.g., f. *microptera*. At the present time it is recommended to consider the term form to be a neutral term (see this entry).

Hemipopulation. The concept of hemipopulation was explained in general by Beklemishev (1959b) as communities of heterotope animals originating by introduction of eggs (germs) into heterogeneous biotopes or microbiotopes. For example, according to Beklemishev (1960) "Each population of heterotope living organisms is divided into hemipopulations. Thus, for instance, a population of the mosquito *A. maculipennis* can consist of an imago hemipopulation occupying the flood plain and the village over it and of a number of pre-imago hemipopulations dwelling in the water pools of the flood plain". The author places to hemipopulations also all phase parasites of Vertebrata (Beklemishev 1959b). He states that a complex of ascarids in the intestine of man forms the same hemipopulation as a complex of mosquito larvae in a pool.

In my opinion, the host (micro) biotopes of parasites represent a quite different living environment than the (micro)biotopes of heterotope, free-living animals. Not only every host species, but also each of its members (host specimen) represents a specific habitat for the helminth community parasitizing it (Dineen 1963 ab, b, Shad 1966 and others). A selection of helminth phenotypes may occur in every host, and different host species often tend to select more or less specific communities. After a selection of "foreign" infective and preimaginal forms of parasites by the host, "its own" helminths start to copulate and the genetic structure of the community is thus "directed" (cfr. Schiller 1959, Smyth 1966, 1969, Rogers 1962). The parasites are at the same time a selecting factor from the viewpoint of the host evolution. It is therefore necessary to differentiate the helminth communities parasitic in individual organs of the host or in individual hosts from hemipopulations. The term hemipopulation, however, may be applied for some types of helminth species (Odening 1974).

In many heterotype helminths the development of some larvae and adults occurs in the same living environment. These helminths form a non-parasitizing hemipopulation and a parasitizing hemipopulation. For example, larval, pre-adult and adult forms of many nematode species develop in (definitive) hosts. Specific free-living non-parasitizing and parasitizing communities — hemipopulations are formed also by Dicyemida and *Rhopalura ophiocomae* (Mesozoa), members of Gordiaca, some nematodes belonging to Dorylaimida, Tylenchida, e.g., *Sphaerularia bombi*.

The problem of the concept of hemipopulation with some biohelminths requires still a solution, because these species occur rather in form of complex populations than in form of hemipopulations, For example, according to many authors the digenetic trematodes have parthenogenetic females — adults (?) in snails and hermaphroditic adults in definitive hosts. Instead of hemipopulation the term endopopulation proposed by Romashov (1977) would be more suitable for them. This would include also the above-mentioned "parasitizing hemipopulations" of Mesozoa, Mermithidae, members of Gordiacea and others. Non-parasitizing larvae and adults of these species could be termed exopopulation. Romashov should express his opinion about these proposals and the respective definitions should be amended.

Host eco-form. This term was proposed by Freze (1976), who writes: "In order to determine the population of the poly-host species of helminths parasitic in a defined phase of the life-cycle parasitizing in the host of one species and in order to characterize both morphological and ecological differentiation it is proposed to apply the term host eco-form". The term host eco-form seems to be close to hostophenote. However, Freze's characteristic does not clearly say what is the criterion of delimitation of population of poly-host helminth species.

Hostophenote. According to Macko (1966), the hostophenote is a complex of organophenotes of a single population of helminths which got specific non-hereditary properties and features in certain host species. According to Mayr et al. (1953) and Gagarin (1972) it is a host-determined variation.

The hostophenote may appear as a specific phenotypic complex(organophenotes) of helminths in a single host species or in a certain range of host species. For example, *Fasciola hepatica* may form in cattle and rabbits a hostophenote which is erroneously regarded as subsp. *oblongata* and in sheep a hostophenote named subsp. *ovata* (Ternopolskaya 1976). These facts indicate that the hostophenote is a synhost population or group of synhost populations differing from other synhost populations in its non-hereditary modified characters. The hostophenotes may be identical in morphology with host pseudoraces and preraces. The existence of these two communities is based mainly on experiments with different organisms and it can be therefore demonstrated only experimentally.

The term hostophenote may be applied also to biophenotes or parthenophenotes forming non-hereditarily modified intrapopulation units in individual species or groups of species of intermediate hosts.

The experiments carried out by Krasnolobova 1975, Colles 1975, Ternopolskaya 1976 suggest that hostophenotes are often formed with adult trematodes with a hermaphroditic way of reproduction. From the genetical viewpoint, the formation of these host non-hereditary modifications seems to be enabled by their wide norm of reaction. The data on host modifications were published also by Dönges (1967, 1970), Eichler (1971) and others.

Idiohost population. This term was proposed for the parasites by Kisielewska (1970 1974) "for a monospecific assemblage in a single host individual". In the sense of the given definition, the term idiohost population should be identical not only with endomicropopulation of adults and larvae reported by Romashov, but also with biophenote and parthenophenote proposed by Macko. Several authors (see Wiadom. Parazitol. 1974, No. 5) name the idiohost population also subpopulation.

With regard to the fact that communities of different function are formed in the intermediate and definitive hosts we recommend to use the term idiohost population only for the community inhabiting one specimen of (definitive) host where usually a biparental reproduction of helminths takes place. A part of the idiohost population is the preorganophenote or organophenote or a complex of these intrapopulation units in a single specimen of the (definitive) host. For example, *Trichinella spiralis* forms in the host an idiohost population consisting of an organophenote in the intestine and preorganophenotes in muscles.

Intrapopulation unit. In the mentioned classification the term intrapopulation unit represents 1) intrapopulation community, 2) group of cysts and capsules which developed together or originated in the same host or in the habitat of the population of the helminth under study, 3) group of eggs in nature.

Larvophenote. This is a general term for a group of larval forms of helminth population developing or existing in free nature and in various types of hosts. Larvophenotes may be divided into 1) non-reproducing larvophenotes, which are further separated in a) abiophenotes (non-parasitizing larvophenotes) which under certain circumstances may get a character of a colony or swarm, and b) biophenotes (parasitizing larvophenotes) (see the respective items for more detailed data); 2) reproducing larvophenotes reproducing in the intermediate hosts (e.g., *Coenurus* = *Multiceps*, *Echinococcus*, *Alveococcus*).

Micropopulation. According to Beklemishev (1959b), the micropopulation is an intrapopulation community of organisms reproducing and developing in an ephemeral

living environment (i.e., on or in a microbiotope) in subsequent generations[3]. The origin and extinction of this community depends on the origin and extinction of the microbiotope inhabited by the micropopulation.

The micropopulation can be formed by various species of phytohelminths on one plant, on its parts or on a group of plants living close to one another, the roots or green parts of which are interlaced. The micropopulations are formed for instance by *Aphelenchoides ritzemabosi*, *A. fragariae*, *Ditylenchus dipsaci* and in the soil by *Heterodera schachti* which often forms "foci" infesting the cultures of sugar beet. This "focality" is characteristic for various species of phytonematodes (Valocká and Sabová 1974). According to Sabová (personal communication), these "foci" may represent already communities of a higher rank than micropopulation. The complex population structure of phytonematodes requires a more wide study.

In animal hosts, the micropopulation can be formed within a single host. It is formed by some oxyurids of the genus *Atractis*, *Probstmayria vivipara*, *Techygonetria vivipara* (Rogers 1962, Shults and Gvozdev 1972, Odening 1974), *Rodentolepis straminea* (syn. *Hymenolepis nana*). These communities may form in individual host organs also combinations between organophenote and micropopulation.

Monstrositas. Monstrosity (teratological phenomena).

Morph. Morph is an older taxonomical unit. According to Semenov Tyan-Shansky (1910 ex Yablokov and Khnzoryan 1968) the morphs are numerous distinct deviations caused by a change of some special living conditions; they need not be of hereditary character and have no isolated area. According to this author, the morphs should be characterized on the basis of their origin, e.g., morpha edaphica, thermica, montana, alpestris, lacustris etc. The legalized morphs in helminth system should be discussed more widely.

Natio. This is an older taxonomic term. According to Semenov Tyan-Shansky (1910 ex Yablokov and Khnzoryan 1968) natio is a subrace, i.e., a small geographical race. The category natio is not used in helminth taxonomy for the time being.

Neutral term. A taxonomic term of convenience, such as form or group, which may be employed without reference to the formal taxonomic hierarchy of categories and which has no significance in the nomenclature (Mayr et al. 1953). In this paper the mentioned terms are used as neutral terms for various intraspecific units of non-taxonomic character, together with other terms as community or assemblage.

Organophenote. According to Macko (1961), the organophenotes are the lowest imaginal intrapopulation units of helminths developing in individual organs of a certain host specimen. They include separated communities of preimaginal and mature parasitic stages within which the fertilization (or self-fertilization) of the members of the organophenote usually occurs.

This characteristic is not quite clear as to the structure of organophenotes, because it mentions both imaginal and preimaginal stages. Somewhat obscure is the term preimaginal stage which is now recommended to be termed preimaginal phase or preadult. These are juvenile forms of helminths in the postlarval stage till the period of reproduction in the definitive host. For example, according to Shults and Gvozdev (1970: 419) the "larvae" of 5th stage are no more "larvae", but "juvenile adult specimens". However, some authors assume that even larval stages of nematodes should be considered juvenile stages. Rogers (1962: 31) writes: "the egg hatches to give the first larval stage (more correctly, the first juvenile stage)". In the opinion of some others, only larvae and adults (imagoes) should be recognized in the ontogenetical development of helminths, among others also due to the fact that it cannot be exactly determined, particularly in males, when a certain form is a preadult or adult. In order to make the definition of organophenote more unambiguous I have amended it as follows: The organophenote is an intrapopulation community of helminths in a certain organ, tissue or cavity of the (definitive) host where the representatives of the organophenote complete their life cycles and reproduce: their propagative elements must get into the outer environment or another host to realize a new life cycle of the helminths.

If the infective helminth elements develop to adult stage at the place of attachment (co-location) in the host, only one organophenote develops in the host organism. If the infective elements migrate

for a shorter or longer distance after the penetration into the (definitive) host, the larval and preadult forms (immature forms) may develop or mature in various organs. Moreover, during their migration they may stay (or be retained) for some time in the organs, tissues, body cavities or blood and lymphatic system of the (definitive) host. In this way the larval preimaginal and imaginal forms can form several preorganophenotes (non-reproducing communities) or organophenotes (reproducing communities) in a single host organism.

The organophenotes in the same host specimen may differ from one another, as the trematodes *Prosotocus confusus* in the stomach and in the intestine of *Rana esculenta* (Dogel 1962). The organophenotes of Prosthogonimidae developing in the oviduct differ in their morphology from those developing in the bursa Fabricii in chickens (Krasnolobova 1967). Great differences may also exist between the organophenotes developing in larval and adult (definitive) hosts. A typical example is *Polystoma integerrimum* (Bykhovsky 1957), various Monogenoidea (Bykhovsky and Nagibina 1967, Gusev and Kulemina 1971) and others.

In some migrant hosts the members of the organophenotes may originate from various populations of parasites. Since the existence of an organophenote is conditioned by a specific life cycle of helminths realized at an intrapopulation level, it is necessary to regard the organophenotes in general as intrapopulation communities. A similar state may occur also in other intrapopulation units.

Panhost population. This term was proposed by Kisielewska (1970, 1974) "for all developmental populations of parasites collectively, that is, for a population corresponding to those of free-living animals".

Parthenoclone. The parthenoclone is a clone reproducing by ameiotic parthenogenesis (Shimansky 1969).

Parthenophenote. The parthenophenote is an intrapopulation unit of helminths developing and reproducing parthenogenetically in a single specimen of (intermediate) host without completing their life cycle in this host. Odening (1974) regards parthenophenote as a micropopulation and partly also organophenote.

I would like to note that the following aspects have been particularly considered at the differentiation of intrapopulation helminth communities: 1) whether the environment in which the intrapopulation unit develops has an ephemeral or permanent character; 2) whether the life cycle of members of the intrapopulation units is realized (or completed) in a certain living environment (host) completely or partly: 3) whether the members of intrapopulation communities reproduce by a biparental or uniparental way and whether a genetic recombination occurs with them.

The life cycle of trematodes terminates by a hermaphroditic generation in the definitive host. Considering that no crossing of reproducing parthenites occurs in snails and that the parthenophenote represents a higher hierarchic unit than the community developing in individual host organs, we assume that the parthenophenote differs from both micropopulations and organophenotes. It is true that the helminthologists are not at one whether or to what extent individual species of digenetic trematodes reproduce parthenogenetically, by polyembryony, gemmation etc. (Dogel 1962, Ginetsinskaya 1968, Odening 1974, Clark 1974 and others). For this reason it is still difficult to state to what extent the term parthenophenote covers the specific characteristics of communities in molluscs. The fact that meiosis occurs in mother sporocysts and rediae of *Fasciola hepatica* and that the number of germ cells in the miracidium corresponds exactly to the number of rediae developing in it is an argument against the hypothesis on general polyembryony of trematodes in molluscs. The polyembryony occurs, however, in strigeids and plagiorchids (Ginetsinskaya 1968). The communities reproducing by ameiotic parthenogenesis, polyembryony and gemmation (Clark 1974) can be considered clones and clonophenotes.

The occurrence of meiosis in sporocysts and rediae of "primitive" trematodes (Paramphistomatidae, Fasciolidae), as well as the polymorphism[4] of parthenites, their phylogenetic development and other characters (Ginetsinskaya 1968) supports the opinions regarding the parthenites as parthenogenetic females[5]. We have therefore excluded the parthenophenote from the larvophenotes in the present classification in contrast to the original one (Macko 1961).

Further studies of trematode communities in molluscs will probably require to separate the parthenophenote in lower hierarchic units developing in individual parts of the host body (organs, tissues and cavities). The terms parthenoclone(s) or clone(s) could be used for these (organ) communities reproducing by ameiotic parthenogenesis, polyembryony, gemmation etc. The term parthenoclone was used by Shimansky (1969) for a clone reproducing parthenogenetically.

The intrapopulation trematode communities reproducing by meiotic parthenogenesis should be differentiated from clones and should be termed, e.g., parthenomicropopulations. According to Clark (1974) the existence of meiotic parthenogenesis in Digenea is uncertain or may not be significant.

The life cycle of Strongyloididae can be completed without participation of a free-living generation (cfr. *S. fulleborni*). From the helminthological viewpoint the life cycle of these nematodes terminates by reproduction of parthenogenetic females in the host intestine, i.e., in organophenotes. If the life cycle of nematodes (with a heterogonic way of reproduction — heterogony) terminates by a gonochoric generation, the parthenogenetic community within the host should be regarded as a parthenophenote.

Parthenomicropopulation. Parthenomicropopulation is an intrapopulation community reproducing by meiotic parthenogenesis on or in an ephemeral microbiotope. Further studies are necessary for a more exact characteristic of this community.

Preorganophenote. Preorganophenote is an intrapopulation unit of larval and preimaginal forms of helminths developing or existing in a certain organ, tissue or cavity of a single host specimen (intermediate host, parathenic host, strange host, definitive host) without sexual relations and without reproduction. In the intermediate or parathenic host, the preorganophenote (or preorganophenotes if there are more of them) is a part of the biophenote. In the definitive and reproduction host of homoxenic helminths the preorganophenotes are a part of the idiohost population. The preorganophenote is formed, e.g., by *Porrocaecum crassum* under the cuticle of gizzard (under the corneous membrane of the ventriculus) of the duck, *Cyclocoelum microstomum* in the liver tissue of the definitive host (Ginetsinskaya 1968). or *Metastrongylus elongatus* in the mesenteric lymphatic node of *Sus scrofa* (Shults and Gvozdev 1972).

Prerace. (Ecological or host prerace). The prerace is an intrapopulation community which keeps, at least for some generations, within its population a partly isolated gene pool by an assortative mating of specific host morphs.

The existence of ecological or host intrapopulation groups has been reported by several authors (Smith 1966, Pimental et al. 1967, Grossman and Evguniev 1969). Kreslavsky et al. (1976) have recently described this phenomenon in leaf beetles *Chrysochloa cacaliae* which form intrapopulation ecological (host) groups on *Senecio nemorensis* and *Petasites albus*. Statistically reliable ($P < 0.05$) differences in the length of elytrons were noted between the beetles feeding on different plants. The mating of beetles by the type "length of elytrons" is of non-random character. A distinct tendency towards homonomic mating was noted. A suggestion is put forward to the effect that the initial stages of the formation of ecological races (according to Macko preraces) are dealt with in this case. Similarly Solomatin et al. (1977).

The data on the population structure of helminths indicate that a homogamy between specific habitat preference morphs may occur in a higher degree within the population of some oligo- and polyxenic helminth species as a result of disruptive selection. This selection may lead up to the elimination of "foreign" infective or preimaginal phenotypes of helminths within a certain range of species, one species, race, strain or sort of hosts. This is supported also by the results of breeding of resistant plant sorts of hosts (Decker 1969: 116). In this relation Decker writes on p. 121: "Als erschwerend muss die Möglichkeit des Auftretens von Bioytypen (Pathotypen) mit resistenzbrechenden Eigenschaften gewertet werden (Riggs und Windstead 1959)". Apparently a selection of "foreign" phenotypes of helminths in animal hosts (e.g., by their elimination, suppression of development etc.) occurred in the experiments carried out by Scott (1928, 1929, 1930), Zelentsov (1972), Wassom et al. (1974), Astafyev and Fedyanina (1975). A disruptive selection thus forms a basic prerequisite for a "mosaic-like" differentiation of the gene pool of helminth population. It is difficult to ascertain without further genetic experiments if this assemblage of phenotypes keeps in nature the "mosaic-like", differentiated gene pool at least for some subsequent generations within a single helminth population, because the structure of the gene pool may be changed by the dispersion of larval forms.

It may be concluded that from the theoretical viewpoint the existence of preraces is possible even with helminths. This is suggested particularly by the experiments with phytonematodes (Ladygina and Barabashova 1976). An experimental verification of preraces is important particularly in terms of the studies of the population structure.

Pseudorace. According to Mayr (1963) distinct phenotypes of a single population are often erroneously designated as races. These morphs differ in the habitat preference utilizing in a higher degree different subniches. They interbreed, usually at random, with other "genotypes" of the same population.

On the basis of these data, as well as of experiments with helminths, the community comprising a higher number of these habitat preference morphs may be termed pseudorace with the following characteristic: The pseudorace of population represents in actively propagating organisms an intrapopulation unit in which an increased number of specific morphs is kept, particularly due to their genetically conditioned tendency to prefer a certain subniche (e.g., a certain host species) which may produce a specific morpho-physiological character of this community. In passively propagating organisms (e.g., in some oligo-and polyxenic helminth species) the increased number of morphs can persist in a certain subniche (e.g., in a certain host species) particularly due to an increased selection of "foreign" phenotypes. The members of the pseudorace usually cross at random and thus participate in the formation of a common gene pool of the population in every generation. For instance, Daskalov (1972) reports that in mountain regions in Bulgaria where goat breeding usually prevails, knobbed forms predominate in *Haemonchus contortus*, whereas in lowland regions where goat breeding is usually poorly developed, linguiform specimens predominate. Similar results were obtained also by Das and Whitlock (1960). LeJambre and Whitlock (1973) write in relation to various phenotypes of *H. contortus* that a genetic polymorphism is involved and that each phenotype has a different maturation rate and each has its own specific temperature at which hatching is most efficient. In combination therefore these phenotypes tend to give a *H. contortus contortus* population at a wide range of temperature tolerance. The results of these authors show, among others, that a random crossing occurs between individual morphs during common infections. Consequently, it may be supposed that pseudoraces, preraces or races may be formed in some regions contingently on the selection press of ecological factors. Also other studies indicate that the adaptation of helminths to different conditions of living environment is realized by means of ecological polymorphism (Bona 1975, Ladygina and Barabashova 1976).

Race. The race is a population or group of populations which, owing to their genetical adaptation to certain specific types of living environments, are characterized by a common phenotypical character differentiating them from other races of the same species existing in other types of habitats.

There are differing opinions on the races in parasitology. According to Gagarin (1972) it is necessary to formulate exactly the concept of race, strain and others or to cease using them.

From a taxonomical viewpoint, the races are often considered to be at the level of subspecies (Mayr 1963, 1970, Mayr et al. 1953). This problem will be dealt with more widely in another paper.

Semaphoront. According to Hennig (1966), the semaphoront is the character bearer which must be regarded as the element of systematics, because, in a system in which the genetic relationships between different things that succeed one another in time are to be represented, we cannot work with elements that change with time. Accordingly the semaphoront corresponds to the individual in a certain theoretically infinitely small time span of its life, during which it can be considered unchangeable. In this sense the individual is to be regarded as the lowest taxonomic group category; it includes those semaphoronts that are connected by genetic relationships. No generally applicable statements can be made about how long a semaphoront exists as a constant systematically useful entity. It depends on the rate at which its different characters change. In the maximum extreme it would be approximately congruent with the duration of the life of the individual. In many other cases, particularly in organisms that undergo metamorphic and cyclomorphoric processes, it would be notably shorter. (See scheme in Fig. 2).

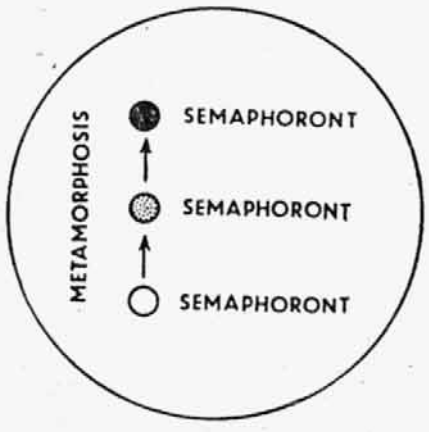

Fig. 2. Semaphoronts of a specimen after Hennig (1966).

For example, the larva of the may beetle assumes an entirely different place in an ecological system, that is, in a system that seeks to present the whole of all living organisms as a community, than the sexually mature beetle does. In this system the larva would be more closely associated with other animals that live in the ground and eat roots than with the imago of may beetle into which it later develops. The imago would be more closely associated with other (flying and leaf-eating) animals.

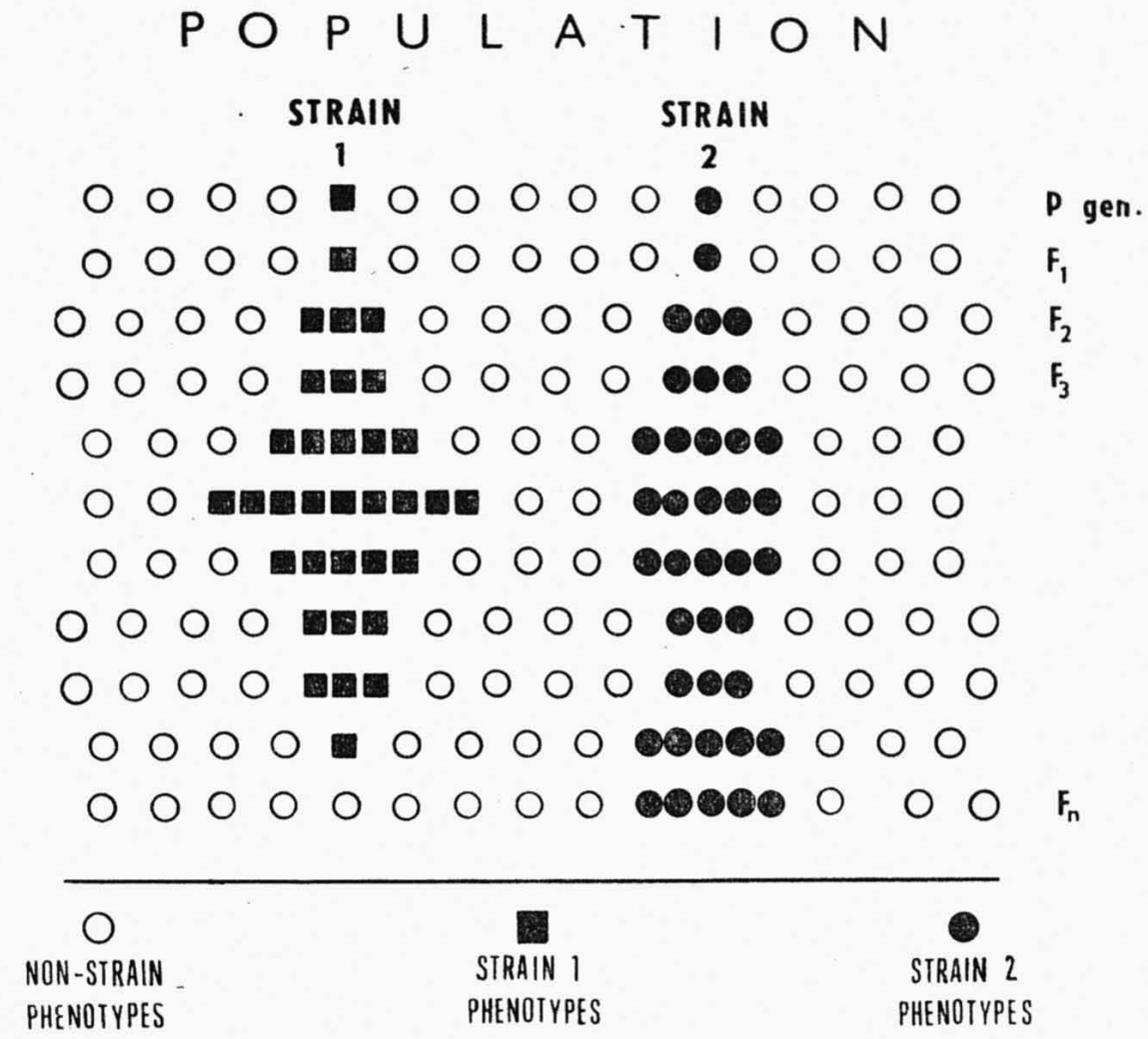

Fig. 3. Phenotypically specific strain in helminth population (orig.).

Strain. According to Mayr (1963: 454) in forms where sexual reproduction is temporarily or permanently abandoned, parthenogenetically reproducing strains that differ in biological characteristics may be distinguishable. Strains of very different virulence may be isolated from the same local population. (Also Odening 1974.) After completing its parthenogenetic phase a strain will return to the common gene pool of the local population and therefore cannot be considered a race, as it is stated in some places (Der Grosse Brockhaus 1934, Dogel 1962, Brockhaus ABC — Biologie 1967, Decker 1969: 337).

As it follows from the study of various sources, from the non-taxonomic viewpoint the term strain in animal organisms represents an intrapopulation community which has usually a common origin and can (but need not) be characterized by certain genetically fixed peculiarities or characteristics differentiating it from other phenotypes of the population.

The term strain seems to have penetrated into helminthology from microbiology. Within a short time it became so widespread and habitual that, according to the opinion expressed at the Third International Symposium in the High Tatra Mountains in 1976, this term is unacceptable in hel-

minthology and does not seem to be justified. In my opinion, the term strain is needful for the helminth community which has usually a common origin in the population and besides population or race properties and features of adaptive character may possess also genetically fixed peculiarities, i.e., properties or characteristics (some of them need not be of adaptive character) differentiating it from other strains of the same helminth species or from the "mass of normal" representatives of a certain larger community — population, race etc. (See schema in Fig. 3.) These facts indicate that various helminth strains can be isolated from a certain host species or a certain geographical region.

However, the often used terms cat strain, dog strain of *Ancylostoma caninum*, geographic strain etc. are insufficient, particularly in case that it is said in the methods that, e.g., the strain *Hymenolepis nana* was obtained from spontaneously infected specimens of *Rattus norvegicus*. It is difficult to ascertain whether a community of a common origin is involved or whether the specific "strain" properties are not in fact the characters of a race. For these reasons it is necessary 1) to designate the strains more exactly, as *A. caninum*, dog strain 1, + locality: 2) to specify the peculiarities of the strain on the basis of a comparison of communities of common origin with those of different origin.

From the theoretical viewpoint it may be supposed that in some instances the strain may be so wide that it reaches the level of a population. For example, when a new niche is occupied or if its members migrate to unoccupied habitats. But in this case it is already a real population or race which cannot be considered a strain.

Subpopulation. According to Beklemishev (1959b) the subpopulation is a concentrated assemblage of organisms in an evenly occupied habitat of a large population ("superpopulation"). Beklemishev (1959 b) writes in this relation that all populations and subpopulations occupy certain limited areas of earth surface, i.e., they are adjusted to certain biotopes or a complex of biotopes.

In the sense of this characteristic, also the subpopulation of helminths manifests itself in a certain area (or areas) of evenly "inhabited" population habitat of the helminth by an increased density of free-living forms in nature and increased intensity and incidence of infection in hosts. The helminth subpopulation can be delimited either by a subpopulation of the (definitive) host or by a complex of other ecological factors (e.g., by a more intensively infected group of intermediate hosts — Ginetsinskaya 1968, 1971, Grabda 1976) in a part or in parts of the habitat of helminth population. The subpopulations of monophagous insect species need not have a geographical character (Pimentel et al. 1967).

Swarm. The term swarm is generally defined as a large number of individuals and things (bodies) in a certain movement. In astronomy, a swarm of meteorites; in biology, a swarm of bees.

It should be noted, however, that swarm is not any quantity of individuals in movement. For example, a number of bees flying out and in the bee-hives are not a swarm under normal circumstances. Not even moving miracidiae or cercariae in water do represent a swarm, but an abiophenote which, under certain conditions, may get a character of the swarm. This state occurs when the moving cercariae, due to a certain factor, gather into a cluster. Ginetsinskaya (1968) termed as swarms the clusters of cercariae in a shadowed or lighted part of water reservoir, near the bottom etc.

These facts indicate that the swarm is an intrapopulation non-parasitizing community of helminths representing a cluster of specimens induced by a certain factor (or factors); the specimens are in a certain movement within the habitat of the helminth population.

Synhost population. This term was proposed for the parasites by Kisielewska (1970, 1974) "for a monospecific assemblage in a host population".

Within the habitat of helminth population there may exist also several host populations of a certain species of intermediate host, parathenic host or other types of hosts. Consequently, in the sense of the above definition, there may exist, e.g., three synhost populations of *Fasciola hepatica* at level of intermediate host (*G. truncatula*) and one synhost population of *F. hepatica* at level of definitive host[6] (*Ovis aries*) etc. within a single natural population of *F. hepatica*.

Topophenote. See colony.

Variety. An ambiguous term of classical (Linnean) taxonomy for a heterogeneous group of phenomena including nongenetic variations of the phenotype, morphs, domestic

breeds, and geographic races. In helminthology, the term variety was used, for example, by Sinitsin (1915 ex Skryabin 1948). According to this author, *Fasciola hepatica* exists in form of three varieties (var. *ovata*, var. *oblongata* and var. *lineata*) differing from one another in the shape of body. This term was used also by Dubinin (1954) in his species concept and, more recently, by Britov (1971 ex Britov 1974). Mayr recommends not to use it.

CLASSIFICATION OF INTRAPOPULATION HELMINTH UNITS

The population structure of individual helminth species is varied and more or less complicated. It is documented by still newer and newer data on the intrapopulation communities, their variability and life cycles. Attention was first paid to the most common of the intrapopulation communities, but later it was found necessary to study also others. Since the classification was made by several authors, individual intrapopulation units were given incongruous names. In spite of this, these terms should be taken into consideration in newer classification, even if new terms would be sometimes more suitable. These principles were considered also in the following classification of intrapopulation helminth units. It should be pointed out, however, that the order in which these units are named does not represent their hierarchic relations in nature. The attached characteristics are mostly of orientation importance only. Complete definitions can be found under the respective items in the previous part. It is necessary to note that all proper definitions of the intrapopulation units are drawn in relation to helminth population. This relation is expressed in individual definitions as follows: "...intrapopulation unit ... of helminths", or "intrapopulation community ... of helminths", in contrast to the definitions of synhost population and imaginal endopopulation which are drawn in relation to host populations (see these items).

I. INDIVIDUAL ELEMENTS OF HELMINTH POPULATION

The present state of studies on individual helminth variability was reported by Shults and Gvozdev (1972). Gagarin (1972) considers and recommends to study the helminth variability according to the scheme proposed by Mayr et al. (1953) and Mayr (1963, 1968). Therefore it need not be dealt with in the present paper.

II. NON-TAXONOMIC INTRAPOPULATION HELMINTH UNITS

α) Units consisting of larval forms

1. Larvophenote — general term for an assemblage of larval forms of helminth population in nature and in hosts. The larvophenote may be divided into:

A. Non-reproducing larvophenotes — abiophenotes, biophenotes, preorganophenotes.

a) Abiophenote (non-parasitizing larvophenote) — general term for an accumulation of eggs, cysts and larvae in free nature and in transport hosts (sensu Odening 1974). Abiophenotes may get a character of colony or swarm.

— Colony (homotypical). Assemblage of non-parasitizing larvae living together in a particularly suitable living environment in the habitat of helminth population.

— Swarm. Accumulation of non-parasitizing helminth forms produced by certain factor (factors); the specimens are in a certain movement in the habitat of helminth population.

— Complex of abiophenotes (in small populations also one abiophenote) may form a larval hemipopulation. Particularly larval forms of some geohelminth species are concerned.

b) Biophenote (parasitizing larvophenote) — larvae in individual specimens of non-reproductive host, intermediate host and paratenic host. Complexes of biophenotes may form (larval) synhost population, hostophenote and other units.

c) Preorganophenote — see below.

B. Reproducing larvophenotes — larval intrapopulation units the members of which reproduce in individual specimens of intermediate host (*Coenurus* = *Multiceps*, *Echinococcus*, *Alveococcus*. In a given case a clone or clonophenote may be involved).

β) Units consisting of various developmental forms

2. Parthenophenote — intrapopulation community reproducing parthenogenetically in individual specimens of (intermediate) host without completing the life cycle of helminths in these hosts.

3. Clone — intrapopulation unit arised by vegetative reproduction or ameiotic parthenogenesis (parthenoclone) from a single organism. Clone may be also regarded as biotype.

4. Biotype — a group of genetically identical individuals.

5. Clonophenote — intrapopulation unit consisting of various clones in a single host specimen.

6. Preorganophenote — larval or preimaginal non-reproducing intrapopulation unit in an organ, tissue or cavity of a single host (intermediate host, parathenic host, strange host and (definitive) host).

7. Organophenote — intrapopulation community reproducing propagatively and completing its life cycle in an organ, tissue or cavity of a single (definitive) host specimen.

8. Idiohost population — a monospecific assemblage in a single (definitive) host individual (emend).

9. Micropopulation — intrapopulation community of helminths reproducing biparentally in the state of imago and developing in subsequent life cycles in a certain ephemeral living environment in the habitat of helminth population.

10. Topophenote — small (not numerous) intrapopulation unit of non-parasitizing larval and adult helminth forms in nature.

11. Homotypical colony — assemblage of non-parasitizing larvae and adults of helminths living together in a particularly suitable living environment in the habitat of helminth population (Mermitidae and others) before infecting the host.

12. Synhost population — monospecific assemblage of helminths in a host population.

13. Hostophenote — a complex of organophenotes of a single helminth population which acquired specific non-hereditary properties or characters in a certain species or group of species of hosts.

14. Pseudorace — intrapopulation community with an increased number of habitat preference morphs reproducing without assortative crossing in a certain relatively permanent living environment (host species, biotope) within the helminth population.

15. Prerace — intrapopulation community which may, for several generations, keep by an assortative crossing a partly isolated gene pool in a certain relatively permanent living environment within the helminth population.

16. Strain — intrapopulation community which has usually a common origin in the helminth population.

17. Hemipopulation (half-population) — a part of population of heterotopic helminths the members of which pass a certain period of their life cycles in other living environment than the remaining part of this population.

18. Subpopulation — a more dense territorial community of helminths occupying certain areas in the habitat of a large helminth population.

In general, the helminth population may be divided into two types, namely large and small populations. The large populations exist in form of subpopulations (sensu Beklemishev), whereas the small ones exist without this intrapopulation structure.

III. TAXONOMIC UNITS OF HELMINTHS

Semaphoront — developmental stage of a certain helminth specimen (e.g., miracidium). According to Hennig (1966) the semaphoront is the character bearer which must be regarded as the element of systematics.

Varietas, aberratio, natio, morph and others are not legalized in the taxonomy (of helminths). As they are not applied uniformly, their significance is questionable for the time being. The above-mentioned categories were dealt with particularly by Semenov Tyan-Shansky in 1910, more recently by Dubinin (1954), Dogel (1962), Yablokov and Khnzoryan (1968).

As these problems are very broad, we have not dealt with the subspecies which should be discussed in more details than it is possible in the present paper.

The mentioned structure of helminth populations with the proposal of their classification is only a draft of the intrapopulation units. Only the most important characters and examples were used in their descriptions and it is therefore possible that some

confusions may occur in the determination of some intrapopulation units. For example, the term hostophenote should be dealt with more widely. This community has most synonyms as it resembles ecomorphose (Cassagnau 1955 ex Bährmann, 1977) which arises on the basis of individual organisms. Attention should be also paid to cyclomorphoses in helminths (e.g., in *H. contortus*) and to communities of progenetic forms of helminths. Some of them form organophenotes (e.g., metacercariae in *Paralepoderma brumpti*) and others do not (cfr. *P. progeneticum* Buttner, 1951). The most recent studies of Bayanov (1977) indicate that further intrapopulation terms are necessary. There are very many problems to be solved and it may be therefore expected that some knowledge will be changed with the progressing studies of helminths and their intraspecific structure. Some of the terms may lose their importance, whereas some new ones will be required. At the present time it is difficult to foresee all these circumstances and therefore only the future and practice will verify the validity of the proposed intrapopulation units.

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EXPLANATIONS

[1] This is valid only in case that the mating specimens are sexually mature, of opposite sex (in heterosexual organisms), and equivalent with respect to sexual selection.

[2] This conclusion is supported by the finding of Bykhovskaya-Pavlovskaya (ex Trofimenko 1975) that the areas of helminths coincide in fact with the areas of their definitive or intermediate hosts (even if the area of the helminth and area of the host are not always identical).

[3] From the view of helminths it would be more unambiguous to say "in subsequently realizing life cycles".

[4] Mayr (1963) proposed the term polyphenism for the occurrence of several phenotypes in a population, the differences between which are not the result of genetic differences. As regards the parthenites, it will be necessary to ascertain in which cases it is suitable to use the term polymorphism or polyphenism as these two different phenomenons should be respected from the viewpoint of the population studies of helminths.

[5] Clark (1974) agrees with the authors who regard parthenites as larval forms of trematodes. The differences in the authors' opinia suggest that this problem should be thoroughly studied by a team of scientists. Genetical data on the variability of organisms might supply some information while looking for the trematodes in which meiosis might occur also besides the hermaphroditic individuals. It may be supposed theoretically that the existence of recombination in parthenites might be confirmed by a simultaneous occurrence of different genetically conditioned phenotypes (cercariae or adults) originating from a single miracidium, with the frequence even of the rarest type higher than can be maintained by recurrent mutation.

[6] In other words, various synhost populations from intermediate and parathenic hosts may participate in the formation of a synhost population in the definitive host. For an uninterested biologists this classification may seem to be contradictory and it is therefore more suitable to use such terms for different types of intrapopulation helminth units which are not a modification of the word population. But the intrapopulation communities of parasitic Scolecida, the existence of which is associated with the host population, are significant from the viewpoint of the knowledge of the species structure.

ПОПУЛЯЦИЯ И КЛАССИФИКАЦИЯ ВНУТРИПОПУЛЯЦИОННЫХ ЕДИНИЦ ГЕЛЬМИНТОВ

Й. К. Мацко

Резюме. Из изучения проблематики популяции вытекает, что популяция является элементарной эволюционной единицей вида с бипарентальным способом размножения. Это общая теоретическая дефиниция, которую автор детализировал для гельминтов. Имея в виду сложную внутривидовую структуру этих паразитов, приводится также предложение классификации внутрипопуляционных единиц гельминтов.

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