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ON THE PROBLEM OF RETARDING DEFINITIVE HOST (s. l.)

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Abstract. The significance of the species and individual level in determining the hosts as a category of helminth life cycles is pointed out. From the viewpoint of species level, the categories of intermediate host and definitive host are ascribed to certain organisms as representatives of a certain species on the basis of the fact that a respective stage of helminth life cycle can take place inside them. From the viewpoint of individual level, these types of hosts are determined on the basis of associations between the helminth individual and host individual. In order to avoid discrepancies, which might occur in determining the host type in these ways, it is proposed that the organism, which was determined as intermediate or definitive host at the species level, should be regarded identically also at the individual level. In addition, the existence of retarding definitive host (s. l.) is substantiated on the example of helminths which survived the interorgan migrations and passed to the offsprings through the intrauterine or transmammary route.

From time to time, the host categories are dealt with in relation with various opinions on their validity or with new information on unusual life cycles of helminths (Ryzhikov 1954, Savinov 1964, Odening 1968, 1969, 1974a, b, c, 1976, Bozhkov 1969, 1970, 1971a, b, 1976a, b, Bozhkov and Odening 1979, Baruš and Ryšavý 1977, Sudarikov 1971, Macko 1980, 1981a, b and others). Among others, also the problems of paratenic and definitive host (s.l.)[1], metaparatenic, retarding definitive host (s.l.), and non-permanent intermediate host are discussed (Bozhkov and Odening 1979, Macko 1981b, Shoop and Corcum 1983 and others).

The retarding definitive host (s.l.) was mentioned in the papers by Macko (l.c.) only in relation with other host categories and therefore its function was underestimated. This seems to be the reason why the validity of this term has been discussed (in personal communications as well as in the literature). The discussions concerned also the necessity to consider the level of community and to determine the definitive host and retarding definitive host (s.l.) from this point of view. For these reasons the above problems are dealt with in the present paper.

ON THE RELATIVITY OF HELMINTH HOST CATEGORIES

At the present time, it has been reported in more and more papers that the ontogenic development of members of a certain helminth species can be different in different strains and races of hosts, as well as in well fed animal hosts compared to those weakened by a disease or lack of vitamins. The development of worms within a certain host species can be different in juvenile, adult or resistant hosts, as well as in mixed infections with antagonic parasite species etc. It is therefore quite natural that there exist different conceptions as to the determination of the host, if a certain stage of ontogenetic development of the helminth is realized in a different way than it is commonly known. The discrepancies can be caused also by the fact that the character of the host can change if it is regarded from the viewpoint of the 1) species or 2) individual level.

1. The obligatory hosts[2] of helminths (host of homoxenous helminths, intermediate host and definitive host) were originally established on the basis of associations between organisms of two species or two organisms with different names (Shults and Gvozdev 1970, Whitfield 1979 and others). The interspecific aspect is manifested also in the "ontogenetic" specificity of invasive stages of heteroxenous helminths. In most cases, these parasites[3] need for their cyclic development a successive intermediate host and a definitive host, which belong to different species or to different groups of species.

As the species level, the character of intermediate or definitive host is ascribed to individual hosts on the basis of the fact that a certain helminth species can develop into a higher invasive or adult reproductive stage within these hosts as representatives of a certain species. The obligatory host is regarded as the definitive host (s.l.) even if it performs the function of the intermediate host. For example, the definitive hosts of *Alaria alata* are the Canidae etc.

In the sense of "species" determination of the character of the host it can be concluded that, e.g., individual species of the genera *Ascaris*, *Parascaris*, *Toxocara*, *Strongylus*, *Alfortia* and others are secondary geohelminths or secondary homoxenous helminths.

As it will be shown in further text, the specification of hosts from the viewpoint of species level is the least ambiguous.

2. As it is known, not all of the helminth specimens must develop into the higher invasive or adult reproductive stage within each intermediate or definitive host. Some of the invasive larvae may be retarded in their postinvasive development inside the definitive host so that they require two successive definitive hosts for the completion of their ontogenesis. The life cycle of some helminths at the stage of larvae can be prolongated by their stay within the paratenic hosts or it can be shortened inside the polyvalent hosts. In this case, the intermediate and definitive hosts are often determined from the viewpoint of individual level, i.e., the respective host categories are ascribed only to the organisms in which the invasive or reproductive stage of helminth specimen really develops, without regard to the hosts serving as intermediate host and definitive host at the species level. It may happen that the same host, which has the character of the definitive host at the species level, has the character of "only" intermediate host from the viewpoint of individual development of the parasite. This is due to the fact that the definitions on the life cycle of helminths concern "only" the development of individuals (Dogel' 1951, Bykhovsky 1957, Khotenovsky 1976).

The data on the development of *Rodentolepis straminea* f. *nana* (= *Hymenolepis nana*) can be used as an example of determination of the host type at the species and individual levels. After an infection of mouse ("A") with *H. nana* eggs the course of the parasite development can be as follows: 1) Some of the eggs can pass through the whole digestive tract of the mouse into the outer environment (Hunninen 1935) where they can be swallowed by the intermediate host *Tribolium confusum* or they passively infect another mouse ("B"). In both cases, the oncospheres released from the transit eggs can continue to develop.

2. A part of eggs infecting the mouse ("A") can perform their function immediately: the oncospheres are released, the cysticercoids develop from them inside the intestinal villi and the adult worms develop inside the lumen of intestines.

3. Some of the oncospheres or developing larvocysts can pass with the lymph from the intestinal villi of mouse ("A") to the mesenteric and lymphatic nodes where cysticercoids develop from them (Astafyev and Fedyanina 1975). Then a successive definitive host is necessary for their further development.

From the viewpoint of species level, the mice (as species community) are definitive hosts to *H. nana*, regardless of the fact that some of the eggs pass through the whole

alimentary tract of some mice or that some of the larvae remain at the stage of cysticercoids within the mesenteric and lymphatic nodes of mice.

It can be said, however, that the mouse is a polyvalent host. In this case the definitive host (mouse) took on also the function of the intermediate host, like other species of mammals in case of *Alaria alata*, *Trichinella spiralis*, *Taenia solium* and others (Bozhkov 1976b).

From the viewpoint of individual level, the mouse ("A") is 1. the paratenic host to transit eggs of *H. nana*, 2. the intermediate host and definitive host to the adult cestodes in the intestine, and 3. the intermediate host to the cysticercoids in the lymphatic and mesenteric nodes. It is quite logical that a consequence of this way of host type determination is the opinion that a) for example, the mammals as polyvalent hosts of *Trichinella spiralis* are its definitive hosts and at the same time also intermediate hosts, or that the polyvalent hosts, dog and fox, can become not only definitive hosts (s.l.) of *Toxocara canis*, but also its paratenic hosts etc., b) that the members of the genera *Ascaris*, *Parascaris*, *Toxocara*, *Strongylus*, *Alfortia* and others are biohelminths, since they have alternative cycles with the intermediate host. Sudarikov (1971) recommends to term them "semibiohelminths".

The determination of the intermediate host and definitive host from the viewpoint of individual level is generally used and formally correct. However, from the viewpoint of the species level it is less suitable. In the case of some helminth species (*Toxocara canis*, *Neoascaris vitulorum*, *Alaria marcianae* and others) it leads to regarding the old hosts of a certain species as paratenic hosts or intermediate hosts, and juvenile hosts as the definitive hosts (see Petrov, cit. Mozgovoy 1953). Moreover, Shoop and Corcum (1983) even established a term "amphiparatenic host" for those species that are paratenic hosts as adults, but that can serve as definitive hosts as juveniles. According to this opinion, for example, the cattle (*Bos taurus*) would not be the definitive host (s.l.) to *Neoascaris vitulorum* (Goeze, 1782), but amphiparatenic host (see below *Alaria marcianae*). From the viewpoint of individual level, the old cattle could be regarded as abortive hosts to *N. vitulorum* (cfr. Shults and Gvozdev 1972).

If the host categories are ascribed to the animals only at the individual level, as it follows from the definitions on the helminth life cycles, the members of a certain species of definitive host (s.l.) could serve as intermediate, definitive or paratenic hosts etc. to the respective and other species of helminths, in relation to the fact whether the host specimens would be old, young, well fed, weakened by a disease or lack of vitamins, genetically resistant, affected by immunosuppressors etc. Therefore the category "retarding definitive host (s.l.)" was proposed at the individual level.

The retarding definitive host (s.l.), from the viewpoint of encapsulated and retarded larval forms of helminths, is represented by single individuals of a definitive host (s.l.) within which a part of the penetrated invasive stages of a certain helminth species are able to complete their life cycle, whereas the other (invasive) individuals of this helminth species can be encapsulated within these hosts or retarded at a certain developmental phase (Macko 1981b). It should be emphasized that the retarding definitive host (s.l.) is not determined if the associations between the parasites and their hosts are regarded from the viewpoint of species level. In such a case these types of hosts are termed only definitive, solitary or standard hosts, in which a part of the invasive stages can be retarded, encapsulated etc.

Odening (1974c, 1976) terms the obligatory host of homoxenous helminths "solitary host of adult helminths". A disadvantage of this term is that it requires an accumulation of words if other host types are to be established or derived from it. For example, the solitary host of adult helminths often retards the larvae. From the viewpoint of ontogenesis of these retarded larvae, this host should be termed "retarding solitary host

of adult helminths". Such a term would be not only too long, but it would not even accord with the associations it should express, as it does not retard the adult helminths, but their larvae. Therefore Macko (1980, 1981a, b) established the term "standard host". It should be used, if necessary, as an alternative term of "solitary host of adult helminths". An example is the case of *Ancylostomum caninum* Ercolani, 1859 in dogs.

Stoye (1973) found that after an invasion of dog (1 ♀) with 20 000 L_3 of *A. caninum* some of the larvae matured to the reproductive stage within the intestine after migration[4], whereas the others were immobilized in the striped muscles. These immobilized larvae became active during the lactation, leaved the host together with the milk and infected the filial generation of pups, within which they developed up to the adult stage.

Some of the L_3 larvae were released from the dog even after the third lactation, i.e. after 486 days. If the L_3 larvae completed their development up to the adult reproductive stage inside both the old dog and puppies, there is no doubt that, at the species level, the dog is a solitary (= standard) host for *A. caninum*. If we regard the hosts of *A. caninum* from the individual level, it can be concluded that to the larvae partly retarded and immobilized at the L_3 stage in the adult dog (♀), this dog represents the retarding standard host (= retarding definitive host s.l.) and not the paratenic host. The paratenic hosts of *A. caninum* are, for example, the rodents.

Another example is *Toxocara canis* Werner, 1782 in dogs. As it is known, the representatives of this species at the postinvasive period before maturity migrate within the body of puppies and adult dogs. Some of them reach maturity inside the digestive tract of the host, others can penetrate with the blood into different organs and tissues where they encapsulate (Fülleborn 1921, Mozgovoy 1953, Stone and Smith 1973, Uhlíková and Hübner 1983 and others). Moreover, Dunsmore et al. (1983) found that *T. canis* larvae did not encapsulate inside the mouse brain and they noted that "it needs to be established whether or not the brain forms the major, or even a significant part of the reservoir from which *T. canis* larvae invading puppies are derived".

According to Fülleborn (1921), the dog can be infected either a) directly by ingesting the invasive eggs, or b) by the change of hosts. Consequently, from the viewpoint of species level, the dog is the standard host for *T. canis*, though the adult dogs get the infection more hardly than the puppies (Schanz and Biagi 1968, Jakubovich 1982). As it follows from the data published by these authors, the site of *T. canis* larvae maturation shifts from the adult hosts to puppies. However, if the adult dogs lack vitamin A or if they are weakened by insufficient nutrition, they can be rather easily infected with *T. canis* (Mozgovoy 1953). Stone and Smith (1973) found that even inside the puppies the larvae of this species can pass through the large blood circulation into different organs and become retarded in their development.

From the viewpoint of individual level, the adult dogs and their puppies are the retarding standard hosts (or retarding definitive hosts s.l.) to the retarded and encapsulated larvae of *T. canis*.

A "worse" reproductive host of *T. canis* is the fox. Petrov (cit. Mozgovoy 1953) found that foxes older than 3.5 years were not directly infected. In sexually immature foxes, the adults of *Toxocara* developed within 29 days. However, at another place Petrov (cit. Mozgovoy 1953) writes that rather strong *T. canis* infections may occur even in adult foxes if they are poorly fed. On the basis of his experiments Petrov came to the conclusion that rats and foxes are paratenic hosts to *T. canis*. According to other authors, dogs and foxes are at the same time paratenic and definitive hosts of *T. canis*.

From the viewpoint of species level, fox is a standard host to *T. canis*. From the viewpoint of individual level, older foxes are retarded standard hosts to encapsulated larvae of *T. canis*. The relation is apparent in the case of a maturing fox (♀), in which

after a single invasion with *T. canis* larvae some of the larvae completed their development, whereas the others encapsulated inside different organs. If this fox reached maturity and became pregnant, the parasite larvae could invade the fox embrya by the intrauterine route. In the postnatal period, the retarded larvae of *T. canis* could infect the puppies during the lactation.

These results clearly show the shift of *T. canis* development from the adult fox to the offsprings. This indicates that the fox should be regarded rather as a "bad" definitive host (s.l.) than paratenic host[5]. On the other hand, the parasite even under these bad conditions can gain an advantage, since after invasion of the adult host (female) it can penetrate with the milk into other hosts, the filial generation. It is problematic whether an "escape" from the bad host or a certain type of adaptation is involved. Anyhow, bovine ascaridosis caused by *Neoascaris vitulorum* (Goeze, 1782) occurred only in calves at the age of 22 days to 4 months. No infections with adult worms were detected in adult animals (Mozgovoy 1953). It was found on the basis of experiments that *N. vitulorum* infection probably passes from gravid cows to the calves by the intrauterine route (Mozgovoy and Shakhmatova 1969, Mozgovoy et al. 1973) and in the postnatal period via mammary glands (Stone and Smith 1973). Direct infections of calves were unsuccessful in most cases (Mozgovoy 1953, Mozgovoy and Shakhmatova 1969, Mozgovoy et al. 1973).

From the viewpoint of the species level, cattle is the definitive host (s.l.) or standard host to *N. vitulorum*, regardless of the fact that the development of postinvasive larvae into adult stage was shifted from the cows to the calves. From the individual viewpoint, the cows are retarding standard hosts and the calves successive standard hosts.

An example of helminth (mesocercariae) retardation inside the body of the definitive host was recorded by Miller (1981). The author bred for more than 11 years a female of raccoon (*Procyon lotor*), which was invaded with *Pharyngostomoides procyonis* Harkema, 1942 in the laboratory, without any possibility of reinvasion. The female produced 25 offsprings, most of which were invaded with *P. procyonis*, through the 6th litter. After nearly 12 years she continued to pass a few trematode ova. Rather than to assume that she has retained the same adult worms for 12 years, it is reasonable to conclude that mesocercariae moved through her body and eventually matured in the intestine. Another "bad" definitive host to *P. procyonis* is cat, within which the parasites mature inside the small intestine only in the case that the cat has eaten infected lungs of the raccoon. Since, according to Miller (1981), this trematode species has no paratenic host, the transmitted developing mesocercariae utilized two definitive hosts of different species for the completion of their ontogenesis. One of them was the retarding definitive host (raccoon) and the other the successive laboratory definitive host (cat). Other ways of cat infection were unsuccessful.

The existence of the retarding definitive host was indirectly confirmed also by Savinov (1953). The author observed that the metacercariae[6] of *Alaria alata*, which moved aside the normal migration path inside the definitive host and penetrated, e.g., into the muscles or subcutaneous layer in dog, do not continue to develop, but encyst at these sites and survive for a long time like in the paratenic hosts. Consequently, in Savinov's (l.c.) opinion, the marten, rodents, chicken, hedgehog and other animals can be regarded as paratenic hosts, but the dog cannot.

The helminths utilize also the hosts which cannot be determined either as paratenic or as definitive hosts. For example, Shoop and Corcum (1983), in relation with a transmammary passage of *Alaria marcianae*, writes that if the mesocercariae are introduced into an amphiparatenic host (terminology after Shoop and Corcum l.c.), such as raccoon, some of the larvae remain undifferentiated in the female, but others are transmitted to the offspring where they mature to adults.

Similar associations exist also in *Neodiplostomum spathoides* Dubois, 1937. Odening (1965) found that some of the metacercariae of this species behave inside the hosts *Buteo buteo* and *Milvus milvus* like inside the paratenic hosts, whereas others try to reach maturity. However, he observed also other combinations. For example, an experimental infection of one young (?) specimen of *Buteo buteo* resulted in only slight invasion of adults (with prolonged development of metacercariae to adult stage), without any finding of refixed metacercariae.

Most probably, extreme cases of invasion with *A. marcianae* and *N. spathoides* were involved in these host species. From the species viewpoint, it is first necessary to decide what is the host character of *Procyon lotor* or *Buteo buteo* and *Milvus milvus* in relation to the respective helminths in the nature. Odening (1965) reported that spontaneous invasions of *B. buteo* with adults of *N. spathoides* occur only exceptionally, whereas spontaneous invasions of *M. milvus* have not been recorded at all. Therefore it may be assumed that these animals are rather paratenic hosts, in which, under laboratory conditions, the worms can reach the adult stage inside the young birds.

CONCLUSION

As it follows from the studies of the host problems, the intermediate, definitive and paratenic hosts should be determined on the basis of associations occurring in nature.

The retarding definitive host (s.l.) can be determined only from the viewpoint of individual level. A typical form of this host can exist only in those species of helminths which migrate between the organs inside the host body.

The studied associations suggest that the "worse" definitive host (s.l.) is the warm-blooded host, the greater are the differences between the number of maturing helminth specimens in old and young hosts of the same species. These differences can be diminished if the adult hosts are weakened by a bad nutrition, disease or lack of vitamins. In extreme cases, the maturation of postinvasive larvae into adult stage is shifted from adult hosts to juvenile ones (*Neoascaris vitulorum*).

The decreased ability or unability of migrating helminths to reach the reproductive stage within old (retarding) definitive hosts (s.l.) is to some extent compensated by the fact that they can invade the filial host generation by the intrauterine route or during the lactation. Miller (1981) writes that there are at least 13 helminth species (nematodes, trematodes and cestodes) which may be transmitted as prenatal invasions and at least 17 species are transmitted via the mammary glands. This number is in fact much higher and therefore one can agree with the opinion that the transmammary transmission of larvae is a viable alternative in the life cycles of a number of helminths and in some instances it is probably the major route of invasion.

Retarded preadults (adults) of members of the genus *Fasciola* occur in the definitive host. These forms are transmitted also to the successive definitive host. According to Odening (1974c), a so-called paradefinitive host is involved in this case. In other mentioned migrating species, the larval forms are retarded in the definitive host (s.l.) and transmitted to successive definitive hosts. No special term has been established for these hosts (Macko 1980, 1981b).

If a certain host species is recognized in the taxonomy as a definitive host (s.l.) of a certain helminth, then the host can also perform the function of the intermediate host. From the viewpoint of species level, however, the status of paratenic (metaparatenic) host, characterized by Baruš and Ryšavý (1977) as reservoir habitationism, should not be ascribed to the representatives of the definitive host. However, this does not concern the "extreme" hosts like *Buteo buteo* and *Milvus milvus* for *Neodiplostomum spathoides* and other cases in the laboratory (see above).

EXPLANATIONS

1. If it is necessary to term the host in which the helminths complete their life cycle, regardless of the fact whether homoxenous or heteroxenous helminths are involved, the terms "definitive host" (s. l.) and "retarding definitive host" (s. l.) will be used. The latter concept includes the terms "retarding definitive host" s. str. (for biohelminths — heteroxenous helminths) and "retarding standard host" (for geohelminths — homoxenous helminths).

2. The term "obligatory host" here is applied to host categories of the life cycle. The obligatory hosts represent the "inevitable minimum of stadiogenous hosts" (Savinov 1964).

3. The stadiogenous development of some helminth species can take place even in two specimens of the same host species or in a single host specimen, namely: 1. heterochronously, i.e. in a regular sequence — like *Hymenolepis nana* in mice. In this case the definitive host (s. l.) takes on the function of the intermediate host. 2. Isochronously, i.e. potentially at the same time, like *Taenia solium* in man. Even in this case the definitive host takes on the function of the intermediate host.

4. Migrating helminths are those which survive the migration between organs inside the host body after infection.

5. If the adult fox is regarded as a paratenic host, it would be necessary to admit that the maturing fox — definitive host — grows within a short time into a paratenic host — adult gravid fox.

6. On the basis of the present knowledge the mesocercariae are involved.

О ПРОБЛЕМАТИКЕ РЕТАРДНОГО ОКОНЧАТЕЛЬНОГО ХОЗЯИНА (s. l.)

Й. К. Манко

Резюме. В работе обсуждается значение видового и индивидуального уровня при определении хозяев как категории жизненных циклов гельминтов. С точки зрения видового уровня, определенный организм называется промежуточным хозяином или окончательным хозяином из-за того, что в нем, как представителе определенного вида, может осуществляться часть жизненного цикла гельминта. С точки зрения индивидуального уровня, эти типы хозяев определяются на основе ассоциаций между гельминтом и хозяином. Чтобы уклониться от противоречий, возникающих при определении типа хозяина этими способами, предлагается оставить эту функцию организму, у которого характер промежуточного или окончательного хозяина на уровне вид, также на индивидуальном уровне. Кроме того обосновывается существование ретардного окончательного хозяина (s. l.) на примере тех гельминтов, которые осуществляют миграции между органами хозяина и переходят на потомство через матку или с молоком во время лактации.

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