Sharpilo V. P., Salamatin R. V. Paratenic Parasitism: Origins and Development of the Concept. Historical Essay, Bibliography. (In Russian).

Parasitologists encountered the paratenic parasitism phenomenon since a long time. However, its ecological essence, the differences among paratenic and intermediate hosts as well as the role of paratenic hosts in the parasites' life cycles and their role in the transmission of parasitic organisms invasive stages have been generally understood only in the early 20th century. Besides, for a long time the paratenic parasitism has been associated only with helminths — trematodes, cestodes, acanthocephales and nematodes. Now, it is quite clear that the phenomenon is also characteristic of the nematomorphs (horsehair worms), parasitic arthropods (Pentastomida), Apicomplexa (Coccidia) and, probably some other groups of parasites.

The fundamentals of the concept of paratenic parasitism were laid down by *Ch. Joeyux and J. Baer* (1934). They based their concept on the studies of *L. Seurat* (1910, 1920 etc.) who was the first to understand the real meaning of this phenomenon, as well as on their own field and experimental studies. Shortly afterwards and most likely independently, K. I. Skrjabin and R. S. Schulz (*Скрябин, Шульц*, 1937, 1940) have also come up with a concept of paratenic (reservoir) parasitism.

Later on, the paratenic parasitism has been investigated by many researchers from different countries and scientific schools. Among them, most important contributions into theory of paratenic parasitism have been made by *G. Witenberg* (1928—1932), K. Ryzhikov (*Рыжиков*, 1941—1954 etc.), R. Schulz and E. Davtyan (*Шульц, Давтян*, 1955), V. Savinov (*Савинов*, 1955—1975), V. Sudarikov (*Судариков*, 1959—1971 etc.), V. Ivashkin (*Ивашкин*, 1961—1976 etc.), *R. Anderson* (1962—2000 etc.), *B. Czapliński* (1963), Y. Berezantsev (*Березанцев*, 1963—1982 etc.), A. Mozgovoy (*Мозговой*, 1963—1975 etc.), B. Ryshavi, V. Baruš (*Рышави, Баруш,* 1965 etc.), *K. Odening* (1965—1978 etc.), *D. Bozhkov* (Божков, 1969—1972 etc.); V. Kontrimavičius (*Контримавичус*, 1969—1978), *F. Moravec* (1970—1994 etc.), I. Vasilev (*Василев*, 1976).

From the modern viewpoint, the paratenic parasitism can be defined as the ability of infective stages of several groups of parasitic organisms to settle and persist in organs and tissues of animals which are not suitable as definitive hosts for these parasites. The larvae of parasites persisting in these hosts, usually do not show obvious morphological changes, although sometimes may grow and advance in their development. Such hosts harbouring infective stages of parasites— paratenic hosts — usually play a role of an alternate source of infection for definitive hosts, alongside intermediate hosts. In some cases, however, due to environmental constraints, paratenic hosts may become important, main or even almost the only source of infection of definitive hosts. The role of intermediate hosts in these cases becomes insignificant or even decreases completely. On the other hand, there are paratenic hosts, whose role in the transmission is limited and entirely unimportant for purely environmental reasons.

Beginning from 1960's, it becomes more and more evident that transmission potential of paratenic host may increase considerably due to the ability of the parasite larvae to pass along the food chains from one paratenic host (prey) to

another (predator). Such a passage may be repeated ones or multiple times (phenomenon of paratenesis according *Beaver*, 1969). The larvae settled in new paratenic hosts do not lose their infectivity and can persist in them for a long time. It should be also pointed out that larvae of some helminths, mainly trematodes and nematodes persisting in the mammal paratenic hosts, are capable of transplacentary (in pregnant females) and, more often, of transmammary (in lactating females) transmission to the offspring (*Stoye*, 1970, 1976 *a, b*; *Sharpilo*, *Tkach*, 1989 etc.). The larvae may persist in the offspring and retain their infectivity.

Transmammary infection has been found not only in paratenic hosts, but also in amphixenous, in particular amphiparatenic, hosts. Such hosts serve at the same time as both definitive and paratenic hosts. After reaching the amphiparatenic host through peroral infection, larvae either settle in the intestine where they continue their development, or migrate into different organs and tissues where they persist like in paratenic hosts. In pregnant or lactating females — amphiparatenic mammal hosts — persisting larvae may reactivate, migrate into the mammary glands, from where they have a direct access to organisms of the offspring (*Olsen, Lyons,* 1965; *Stoye,* 1973; *G. Miller*, 1981; *Prociv*, 1983; *Shoop*, *Corcum*, 1983 *a*, *b* etc.). However, larvae may reactivate not only in case of pregnancy or lactation of female amphiparatenic host. It may also happen when the number of adult parasites in the intestine decreases; in this case larvae may migrate into intestine and attain maturity as in any definitive host.

Transmammay infestation of progeny by paratenic and amphiparatenic hosts, as well as the phenomenon of paratenesis, increase number of possible sources of infection of definitive hosts. A resulting **"duplicating" system is increases stabil**ity and sustainability of the host-parasite system as a whole.

The efficiency of the duplicate systems is quite evident. For instance, a shrew species, Sorex cinereus, introduced to Newfoundland, was incorporated in the life cycle of the nematode *Skrjabingylus nasicola* (fam. Skrjabingylidae) as a paratenic host (*Jennings et al*., 1982).). As a result, the main pathway of the circulation was switched and the shrews became a main source of infection of definitive hosts — mustelid carnivores whose infestation rate increased from 10% to 100% (*Jennings et al*., 1982). The development of a duplicate system in the life cycle of the nematode *Dioctophyme renale* (fam. Dioctophymatidae) has enabled passage of this parasite to new definitive hosts — canid carnivores. The main source of the definitive hosts' infection are paratenic hosts (fishes) instead of intermediate hosts (aquatic oligochaetes) (*Шарпило*, 1979).

Among a huge number of paratenic hosts represented by invertebrate and vertebrate animals there may occur species which have no trophic connection with potential definitive hosts. The parasite larvae persisting in such hosts, do not have a chance to reach definitive or other potential hosts. Paratenic hosts in such cases become peculiar ecological traps or "trap hosts" according to *Шарпило и др.* (1996). In spite of the fact that trap hosts occur in any aquatic or terrestrial ecosystem, they cannot substantially decrease the transmission role of the most paratenic hosts.

A range of the potential paratenic hosts is rather wide — from coelenterates to mammals, including humans who on most occasions may be considered a trap

host. Humans are parasitized by larvae of different helminth groups causing such serious diseases as toxocarosis, gnathostomosis, angiostrongylosis, paragonimosis, alariosis, spirometrosis and other larval helminthoses. Among non-helminth diseases of man (as paratenic host) should be noted toxoplasmosis. Unlike most helminthoses, this disease is widely distributed and represents one of the most important epidemiological problems, particularly because it is one of the major opportunistic diseases associated with AIDS and other diseases accompanied by immune deficiency.

The infective helminth larvae may persist in the paratenic hosts for a long time. The duration of persistence varies in different paratenic host. It was reflected in the division of paratenic hosts into optimal and pessimal (*Савинов*, 1970, 1973) or suitable and less suitable (*Szekely et al.*, 1996). In long-living hosts this persistence often extends for years (*Sharpilo*, 2004). It derives from the fact that in vertebrate paratenic hosts the larvae can inhibit the leukocyte reaction and this way escape the immune defence of the host. It is also important to mention the capsules formed by the host around parasites (not without inducing influence on the part of larvae), as well as the cysts formed by the parasites themselves (*Березанцев*, 1968, 1978 etc).

It is well known that the capsules are physiologically active. They do not only protect the larvae from host's antibodies, but also provide the transportation of nutrients to the parasite (*Березанцев*, 1963 etc). Prolonged existence of the larvae in paratenic host results in their accumulation and often leads to the high intensity of infection sometimes reaching dozens, hundreds and even thousand larvae. Sometimes it is explained by the ability of some larvae, particularly in cestodes of the genus *Mesocestoides*, to asexual reproduction in paratenic hosts (*Speacht*, *Vogel*, 1965; *Mueller*, 1972; *Novak*, 1975).

There are, however, larvae lacking both capsules or cysts. Among them are. for instance, plerocercoids of *Spirometra* spp. and L_3 larvae of *Gnathostoma* spp. They larvae can freely migrate in the subcutaneous tissue of their paratenic hosts including humans.

The ability of infective larvae to long-term persistence in paratenic hosts opened an opportunity to use these hosts to accumulate larvae for research purposes through experimental infection. We successfully used laboratory cultures of this kinds on several occasions (*Шарпило*, 1971).

The larvae of some helminth species, once settled in the paratenic hosts, do not grow nor develop, remaining morphologically unchanged. However, it is now clear that larvae of many helminth species persisting in paratenic hosts, not only grow, but also advance in their development which normally occurs in a definitive host. In these cases we can speak about precocity growth and/or development (*Anderson*, 1988). Precocity development was found, among others, in fish paratenic hosts in cases of the nematode *Eustrongylides* spp. (see: *Anderson*, 1992), *Cystidicoloides ephemeridarum* (see: *Moravec*, 1994) and many other nematodes. Moreover, some spirurids and ascaridids demonstrate an extreme precocity, when in a parasite may reach maturity in a paratenic (and some intermediate), hosts (*Chabaud*, 1971). Precocity and also extreme precocity is also known in trematodes.

Fully mature specimens of *Derogenes varicus* and *Hemiurus* sp. (superfam. Hemiuroidea) have been found in *Sagitta* spp. — paratenic hosts of these species (*Myer*, 1956; *Кулачкова*, 1972 *а, б*), on numerous occasions.

In our opinion, paratenic hosts, may be considered evolutionarily as might-have-been intermediate or definitive hosts of heteroxenous parasitic organisms. Available data provide some grounds to suggest that during evolutionary process paratenic hosts might transform into definitive ones (*Контримавичус*, 1978). This statement is supported by the by the findings of mature (containing eggs) nematodes of the genus *Eustrongylides* (fam. Dioctophymatidae) in fishes (*Микаилов и др.*, 1992). We still have no strong evidence for paratenic hosts transformation into intermediate host (second intermediate host).

One of the most important ecological prerequisites of the origin of paratenic parasitism is represented by interconnections of organisms in ecosystems. Their spatial overlap and ramified trophic connections create conditions for the larvae of parasites to penetrate or reach in a different way, organisms of different animal species. Among them can be not only obligate intermediate and definitive hosts, but also those in which the larvae do not find necessary conditions to develop into an adult stage, but, at the same time, they can survive for some period of time and retain their infectivity. These hosts, as mentioned above, are called paratenic.

Discovery of the ability to paratenic parasitism in representatives of different, including systematically remote groups of the parasites, is an evidence of its multiple and independent origins. Widespread occurrence of this phenomenon is determined by the important role of paratenic hosts in the transmission of infective stages of parasites. It is clear today, that without taking into account the role of paratenic hosts it is impossible to control all pathways of parasite circulation. It determines the high epidemiological and epizootological importance of the paratenic parasitism.