

FROM A MONO TO A DIGENETIC LIFE-CYCLE: HOW WAS THE JUMP FOR FLAGELLATES OF THE FAMILY TRYPANOSOMATIDAE?

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It has been found that species of the digenetic genus Trypanosoma as well as species of monogenetic trypanosomatids of insects can grow in the lumen of the scent glands of opossums reproducing the cycle they perform in the intestinal tract of their insect hosts. Based on these findings, speculations are made on the incompletely known cycles of many mammalian trypanosomes and on the evolution of the family Trypanosomatidae.

Key words: *Trypanosoma* – monogenetic insect trypanosomatids – opossum – scent glands

Sustained multiplication of monogenetic insect flagellates of three different genera in the lumen of the scent glands of opossums was observed (Jansen et al., 1987). These results together with the previous findings for two species of two subgenera of the genus *Trypanosoma* (Deane et al., 1984, 1986; Lenzi et al., 1984; Deane & Jansen, 1986a, b) indicate that these glands offer a suitable environment for the maintenance of trypanosomatids that spend their whole life-cycle or part of it in the intestinal tract of insects. It should be stressed that the flagellates that undergo transformation in the invertebrate host, such as *Herpetomonas* and *Trypanosoma*, also transform in the opossum scent glands.

Besides an obviously adequate supply of nutrients, the suitability of this environment for the type of development of the flagellates is probably related to temperature, as discussed elsewhere (Deane et al., 1984, 1986). Most striking is the fact that in the lumen of the glands the parasites seem to be perfectly protected from the innate and immune defences of the vertebrate host.

The complete life-history of many mammalian trypanosomes is very little known and species-naming has been based mostly on host specificity (proven or presumed) and on the morphology of rare bloodstream trypomastigotes (Hoare, 1972). It is quite interesting, for

instance, that 76 years after the species was named, a redescription of the common cosmopolitan *T. melophagium* has been deemed necessary (Büscher & Friedhoff, 1984).

Mammalian trypanosomes have developed different mechanisms which permit their reproduction in the tissues of the immune host. There are many species, however, that seem to have been unable to develop such mechanisms and in Hoare's words, "are still essentially insect-parasites" (Hoare, 1972). For these species, such as *T. melophagium* and others, chiefly of sub-genus *Megatrypanum*, multiplication forms in the vertebrate are unknown – as they were until recently for *T. (M.) freitasi*.

Since "insect-parasites" can thrive so well in the lumen of the opossum scent glands, and since glands of this type are so common among mammals, we are here suggesting that other trypanosomes might perform, in their vertebrate host, a cycle similar to that found for *T. freitasi*. The glands could function as a sort of reservoir from where infective metatrypomastigotes would periodically invade host tissues. Even for those species that can maintain themselves in the immune host, the possibility of a parallel cycle such as is has been seen for *T. cruzi* in the opossum, should not be overlooked. A cryptic cycle in scent glands could account perhaps for the cryptic infections so common among wild reservoirs of trypanosomes, including those of subgenus *Trypanozoon*.

Going further on this line of speculation we suggest that scent glands could have offered a convenient stepping-stone for the passage of kinetoplastid flagellates from a monogenetic

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to a digenetic life-cycle. It seems to us that in their way to adaptation to the tissues of the vertebrate, the non-specific and immune defences of the latter were one of the great obstacles, possibly the major one, that the flagellates had to come across. Originating either directly from free-living ancestors, or, as we think more probable, with an intermediate passage through the intestinal tract of arthropods, chiefly insects, and ingested by the vertebrate, some flagellates could have gained the glands; once here they would have all the time to develop phases such as the metatrypomastigotes, capable of surviving the first confrontation with the host defences and get a foothold in its tissues.

In this connection it should be remembered that insects made and still make an important contribution to mammalian diets. The omnivorous didelphid opossums, for instance, are quite fond of insects (Hunsacker, 1977; Deane et al., 1986).

The passage from the vertebrate intestinal tract to cutaneous (scent) glands should offer much less difficulty than a direct adaptation involving multiplication in the tissues.

Spreading of the flagellates among their vertebrate hosts could have been guaranteed, at first, through food contamination by the glandular material as it has been demonstrated for *T. cruzi* (Deane et al., 1986). Following the acquisition of bloodsucking habits by some groups of insects, the host-range of the trypanosomes was enormously amplified through mechanical or cyclical transmission. In the latter case a true digenetic life-cycle was established. An atavistic "memory" should make easier the secondary adaptation to the intestinal tract of hematophagous insects which, in many cases, can harbour both mono and digenetic trypanosomatids.

For those trypanosomes that, like *T. cruzi*, are already fully adapted to a digenetic life-cycle and have spread their host-range much beyond the primitive limits, the cycle in the glands is obviously unnecessary and may be envisaged as an evolutionary reliquat, occurring only, and perhaps occasionally, in the primordial host.

Our suggestions have, at least, the merit of conciliating conflicting views on the evolution of the family Trypanosomatidae, such as those expressed in the following statements, made, respectively, by Wallace (1966) and Hoare (1972): 1) "Experimental infection, even transitory, of a vertebrate by an insect flagellate, other than those which normally alternate between the two hosts, has never been accomplished", and, 2) "One of the strongest arguments against the descent of insect flagellates from parasites of vertebrates is the complete absence of evidence of any Trypanosomatid flagellates inhabiting the alimentary tract of these animals, with the possible exception of some reptilian *Leishmania* . . .".

In relation to the first statement, it should be pointed out that insect flagellates can maintain themselves through multiplication (i. e., can produce infection) in a vertebrate, as we have demonstrated. As for the second statement, we might consider the opossum scent glands as an appendix of the intestinal tract since their contents are discharged into the terminal portion of the rectum where sometimes large numbers of metacyclic trypomastigotes may be found in the case of *T. cruzi* infections (Barrett, personal communication).

RESUMO

De ciclos monogenéticos para ciclos digenéticos: como foi o salto para os flagelados da família Trypanosomatidae? — Foi verificado que tanto espécies digenéticas do gênero *Trypanosoma* como espécies de tripanosomatídeos monogenéticos de insetos, podem desenvolver-se no lúmen das glândulas de cheiro do gambá, reproduzindo o ciclo que fazem no tubo digestivo dos insetos que lhes servem de hospedeiros e/ou transmissores. Com base nesses achados especula-se sobre o ciclo incompletamente conhecido de muitos tripanosomas de mamíferos e sobre a evolução da família Trypanosomatidae.

Palavras-chave: *Trypanosoma* — tripanosomatídeos monogenéticos de insetos — gambá — glândulas de cheiro

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