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Why do velvet worm spermatozoa swim for years?

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ABSTRACT: The sperm of many onychophorans must cross body walls and swim for years before fertilizing an egg. We propose that the cause for such obstacles is the high cost of reproduction in these animals, which leads females to select eggs early in their development; and to invest heavily in their atypically large Golgi apparatus and in the production of glycogen. Velvet worm spermatozoa are subjected to a marathon that selects the most resistant.

KEYWORDS: female and male gametes, high reproductive investment of onychophorans, environmental pressure, female selection.

An impressive characteristic of onychophorans is that the females of some species can keep alive, within their bodies, the spermatozoa they received when they mated 5 years earlier, and that sperm cells are actively swimming during all that time (Lavallard & Campiglia 1975; Walker 1998, Sunnucks, 2000).

Why do not spermatozoa enter a quiescent period until fertilization? Why do they keep swimming after so many months?



FIGURE 1. **Onychophoran female with her offspring; photograph H. Ruhberg.**

A possible cause for the sperm marathon is that reproduction has a **very high** cost for onychophorans: females can use up to a third of their biomass in reproduction, and they take from 5 to 12 months of gestation to give birth to their eight or more offspring each year (Figure 1.). Despite being small worms, female onychophorans need between 15 months and 3 years to reach **reproductive maturity** (Morera-Brenes, Monge-Nájera, & Sáenz, 1988; Havel et al., 1989; Sherbon & Walker, 2004).

In addition to their physiology and high **maternal investment** in offspring, onychophorans are under a lot of environmental pressure, to the point that in places with low humidity, females take longer to mature; can only reproduce in a limited season of the year, and are forced to concentrate their **reproductive effort**, being more fertile but also suffering from greater physiological stress (Monge-Nájera, 1994). It is even possible that the male has to provide **nourishing material** in his spermatophore to help the female with the heavy reproductive effort (Manton, 1938).

A high investment imposes on the female a greater pressure when **selecting the gametes**, both her own and the male's. The formation of female gametes is special in onychophorans due to their extraordinary accumulation of glycogen as a rapid source of energy in oocytes (Huebner & Lococo, 1994). In addition, the ooplasm has a giant Golgi apparatus that produces proteins and lipids at an uncommon rate (Huebner & Lococo, 1994).

No one has studied the evolutionary reason for this glycogen abundance and large Golgi apparatuses, but both indicate a strong pressure to **rapidly produce highly energetic molecules that are insoluble in water, for use in the ovules.**

Therefore, we propose that, in onychophorans, the large reproductive investment has favored the selection of a **strong early competition** between the ovules (topic for further studies) and also among the spermatozoa. Competition is enhanced by the fact that they usually have to cross walls because there are no openings communicating sperm and ovules (Manton, 1938). Additionally, spermatozoa are exposed, within the female body, to a resistance race that eliminates the weak. This allows the mother to **select**, months or even years after mating, which spermatozoa, among many others coming from several males, will have the opportunity to fertilize her eggs.

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EDITED BY: Carolina Seas and Priscilla Redondo.

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