

## An evolutionary interpretation of fertilization patterns in the Onychophora

J. Monge Nájera (Museo de Zoología, Universidad de Costa Rica, Costa Rica)

## Introduction

The onychophora are gonochoristic and the general organization of the reproductive organs is similar in both sexes, which have gonopores (Brusca and Brusca 1990). Although there are no reliable reports of real copulation, males of the South African *Peripatopsis* deposit spermatophores on the female body surface.

*Cephalofovea tomahmontis*, representing a new genus and species from Australia, has cephalic cavities in both sexes. The cavity is much bigger in the male, which during the mating season everts a rossete-like structure contained in it. Two captive males have been seen with spermatophores in the "rossete", but the function of these structures is unknown (Ruhberg et al. 1988).

In the Onychophora, there has been a strong selection for increased parental investment, in the "progression" from the less derived oviparous species (Australia) to the viviparous taxa (Neotropics) (Morera et al. 1988). Recent quantitative data agree with that suggestion (Havel et al. 1989).

This note (a preview of a forthcoming paper by J. Monge-Nájera and Bernal Morera on the evolution of Onychophora) applies current evolutionary thought to onychophoran reproduction (particularly fertilization) and shows that it fits the predictions of the Local Mate Competition model of Hamilton ("LMC"), as developed by Ramirez (1987). A hypothesis on the fertilization sequence of *Cephalofovea tomahmontis* is also presented.

Organisms from very restricted habitats have evolved several distinctive characteristics. For example, Ramirez (1987) has shown that fig wasps and *Varroa* Acari (restricted to the secluded environments of fig fruits and bee cells, respectively) have -among several others- the following common tendencies: (1) males copulate early in life; (2) females are inseminated once at early age, even before eclosion; (3) males have only one set of chromosomes; (4) in some cases males are eliminated and females reproduce by parthenogenesis; (5) genetic variability is generally low. To check how this model fits the Onychophora, it will be useful to review very recent information on the evolution of the group. A cladistic analysis of onychophorans (Brusca and Brusca 1990) shows that they had a common ancestor with the Annelida. Since the Clitellata are derived forms adapted to terrestrial life (Brusca and Brusca 1990), comparisons with the Polychaeta appear to me more appropriate for an evolutionary analysis. Cladistically, the ancestral proto-Onychophora was a marine form without slime glands (they would have been ineffective in water) which probably reproduced through external fertilization (Brusca and Brusca 1990).

On that basis, the following sequence for their evolutionary history is proposed:

As the onychophores colonized the land, they already had clawed lobopods. Feeding and defense required a new system, and the evolution of slime glands (probably from nephridia (Brusca and Brusca 1990) allowed entangling prey and potential predators in adhesive. Slime glands function with the help of a pair of eyes of the direct type, with a large chitinous lens and a developed retinal layer.

Gas exchange also posed a problem, solved through the development of tracheae. Nevertheless, there was no tendency towards protection from desiccation, other than their nocturnal and photonegative behavior. As a result, the group is highly restricted to moist habitats and populations are easily isolated in small patches (Morera and Monge-Nájera 1990). Precisely, this habitat restriction is necessary for the development of the local mate competition system (Ramirez 1987).

The above predictions of the model fit the Onychophora, as far as data are available: (1) very young males inseminate females (Havel et al. 1989); (2) females are inseminated at a young age and must store sperm until they reach a size fit for reproduction (Havel et al. 1989). It is ignored if females copulate only once in nature and if (3) males have only one set of chromosomes; but (4) parthenogenesis has indeed been reported in *Epiperipatus imthurni* (Reed 1988) although it does not appear to be common in the group. Issues (3) and (5) require genetic studies. Pedro León and his team (University of Costa Rica) are doing pioneer research in this field. One empirical test does not require complex equipment: experimental crosses between taxonomically distant species should be possible (they probably have similar chromosome numbers, according to the model).

Another basic question on onychophoran reproduction is the origin of atypical systems for insemination in *Peripatopsis* and *Cephalofovea*. The evolution of insemination through the body surface, starting from

normal copulation, would be difficult to explain. The argument presented here is that the original condition was external fertilization, as known in most Polychaeta, which are postulated here as the optimal cladistic outgroup of the Onychophora. From that condition, the independent development of various inseminating systems becomes intellectually acceptable. Furthermore, analogous developments are known in other organisms. In some Hemiptera-Homoptera, insemination is similar to that known in *Peripatopsis*, and in the Odonata, the gamete transfer is very similar to the hypothesis presented here for *Cephalofovea*. I suggest this sequence for the Australian onychophore *Cephalofovea tomahmontis*: a) the male bends to transfer spermatophores from the genital pore to his rosette; b) mating occurs when male inserts spermatophores into open female cephalic cavity; c) blood amebocytes bring about a breakdown of the cephalic cavity integument, allowing sperm to reach the female reproductive tract through the hemocoelic fluid.

If this hypothesis is correct, as suggested to me by the ultrastructural observations of Ruhberg et al. (1988), another novel aspect which requires special study is the function of distinctly colored areas around the cephalic cavities of *C. tomahmontis*. It is hard to imagine why onychophores, being nocturnal, would have colored structures related to mating. If they, for example, are sensible to infrared emissions, it would be useful to obtain IR photographs of living specimens: possibly the colored areas are greatly conspicuous under such light, as occurs for ultraviolet light in butterflies (Silberglie 1979). Yet their gregarious tendency in terraria strongly suggest the existence of a pheromone which also helps individuals to find each other at close range.

Other subjects to be treated in detail in the forthcoming paper are (1) the vicariant biogeography of onychophorans, (2) the meaning of the resemblance of their jaws to certain conodonts and (3) the discovery of bacteria (short and long bacilli) specifically associated to a mid-dorsal line pit in *Epiperipatus*, a finding made by Francisco Hernández (Universidad de Costa Rica).

#### Acknowledgements

This paper benefited from the assistance of several colleagues, who kindly shared their information and ideas, particularly William Ramirez, Jose Vargas and Alvaro Wile.

#### References

- Brusca, R.C. & G.J. Brusca. 1990. Invertebrates. Sinauer, Massachusetts. 922 p.
- Havel, J.E., C.C. Wilson & P.D.N. Hebert. 1989. Parental investment and sex allocation in a viviparous onychophoran. *Oikos* 56: 224-232.
- Morera B., B. & J. Monge-Nájera. 1990. *Epiperipatus hilkae*, n. sp. from Costa Rica. *Rev. Biol. Trop.* 38-2B.
- Morera, B., J. Monge-Nájera. & R. Sáenz. 1988. Parturition in onychophorans: new record and a review. *Brenesia* 29: 15-20.
- Ramirez B., W. 1987. Biological Analogies Between Some Fig-wasps (Hymenoptera: Agaonidae and Torymidae: Sycophaginae) and *Varroa jacobsoni* (Acari: Varroidae). *Rev. Biol. Trop.* 35: 209-214.
- Reed, V.M.S.J. 1988. The Onychophora of Trinidad, Tobago and the Lesser Antilles. *Zool. J. Linn. Soc.* 93: 225-257.
- Reed, V.M.S.J. & R.N. Hughes. 1987. Feeding behaviour and prey choice in *Macroperipatus torquatus* (Onychophora). *Proc. B. Soc. Lond.* B 230: 483-506.
- Ruhberg, H., N.N. Tait, D.A. Briscoe & V. Storch. 1988. *Cephalofovea tomahmontis* n.gen., n.sp., an Australian Peripatopsid (Onychophora) with a Unique Cephalic Pit. *Zool. Anz.* 221: 117-133.
- Silberglie, R.E. 1979. Communication in the ultraviolet. *Ann. Rev. Ecol. Syst.* 10: 373-398.