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Retro fashion: did onychophorans abandon ovoviviparity and revert to laying eggs?

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ABSTRACT: Viviparity is so advantageous that it has evolved at least 140 times in the invertebrates, but some Australian and New Zealand onychophorans have gone back, abandoning ovoviviparity to return to laying eggs. Why? Here we propose that it is an adaptation to climatically inhospitable habitats and low food availability.

KEYWORDS: evolution of reproductive modes, viviparity, ovoviviparity, velvet worms, climate and reproduction.

From their marine origins in the Cambrian, to their current terrestrial life, onychophorans have undergone selective pressures that have led to five main reproductive types (Monge-Nájera, 1995). These types have five levels, from the simple egg to the complex placenta:

1. **Normal egg**, with abundant yolk and thick shell, laid on the soil (Level I: oviparous).
2. **Egg, rich in yolk**, stays inside the mother and she lays it when the baby is going to be born (Level II: [lecithotrophic viviparity](#)).
3. **The embryo** continues to receive additional food in a thick shelled egg that has abundant yolk (Level III: [combined viviparity](#)).
4. **Egg** not only stays inside the mother, but the shell becomes thin and facilitates food intake (Level IV: [matrotrophic viviparity](#)).
5. **Instead of egg**, a placenta feeds the embryo (Level V: [placental viviparity](#)).



FIGURE 1. **Onychophoran hunting prey; watercolor by Gerardo Ávalos.**

The direct feeding of the embryo by the mother is so advantageous that it has evolved independently at least 140 times in invertebrates (Ostrovsky et al., 2016). The words viviparity and ovoviviparity are over-simplifications that include varied forms of nutrition of the embryo (Reid, 1996). Although this series from Level I to Level V is the logical sequence of progress, DNA suggests that some onychophorans have reverted; abandoning ovoviviparity to return to eggs (Reid, 1996). So far no one has analyzed **the reason for this return to the past.**

Monge-Nájera (1994, 1995) proposed that, in order to survive the climate (very dry or very cold) and to be able to hunt, there is a "**minimum obligatory size**" for newborn onychophorans. In the viviparous and ovoviviparous species, keeping the young inside the body also requires a certain minimum size for the mother, and that she gets enough food during the entire gestation period. Therefore, in cold or dry environments with little food, a return to oviparity could be favored: the cause is that producing eggs and leaving them to complete their cycle under environmental conditions is less demanding for the mother. Oviparous mothers can survive and reproduce with less food and under more adverse climatic conditions.

Does the evidence support this hypothesis? Are the oviparous species typical of environments, that are cold dry or with little food, and smaller than those that invest more in reproduction?

In fact, a look at the environmental conditions of the species with each type of reproduction shows that the species that lay eggs inhabit New Zealand and the south of Australia, **climatically more hostile zones** (with an exception in the north of Australia, perhaps a recent colonization).

On the other hand, the benign climate throughout the year and the abundant food of the Neotropics, corresponds with the placental species, which are also larger, around 6 cm long, against the 1-2 cm of the oviparous genera of Australia such as *Ooperipatus* and *Ooperipatellus*. An **apparent exception** is *Ooperipatellus nickmayeri*, whose females reach 6 cm, but this species matches our hypothesis because it lives in a humid habitat rich in vegetation from western Tasmania (Oliveira & Mayer, 2017).

In summary, the current distribution of the oviparous species of Australia and New Zealand are consistent with our hypothesis that returning to **oviparity is an adaptation to climatically inhospitable and food-poor habitats**.

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