Charles Darwin *In Memoriam*

Evolutionary looks at the why of biological and cultural phenomena.

[LEER EN ESPAÑOL]

Why do some Australian onychophorans have fantastic heads?

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ABSTRACT: **Males of some Australian onychophorans transfer their spermatophores with spectacular structures in their head, such as pits with palps and spines. No one has explained why these structures allow this species to be identified. Here we propose that, when its head is the genital apparatus, natural selection treats it as a genital apparatus. Probably these fantastic heads of Australian onychophorans are just another case of divergent sexual evolution by sexual selection.**

KEYWORDS: male onychophoran, modified papillae, palps and spines, male genital apparatus, spermatophore, sexual selection.

Males of some Australian onychophorans manipulate and transfer their **spermatophores** to the females with spectacular head structures (Monge-Nájera, Barquero-González, & Morera-Brenes, 2019). These structures, described in detail by Tait and Norman two decades ago (2001), can be divided into **four stages** of complexity (Figure 1):

1. A zone of the head develops enlarged **papillae**.
2. A pit develops behind the antennae.
3. Papillae merge into a single volcano-shaped structure, and one or several **spikes** form inside it (these spikes might be enlarged and hardened papillae).
4. The pit develops concentric rings of palps and sensors, and four spikes, to manipulate the spermatophore, as well as a lipped rim to hold it in place.

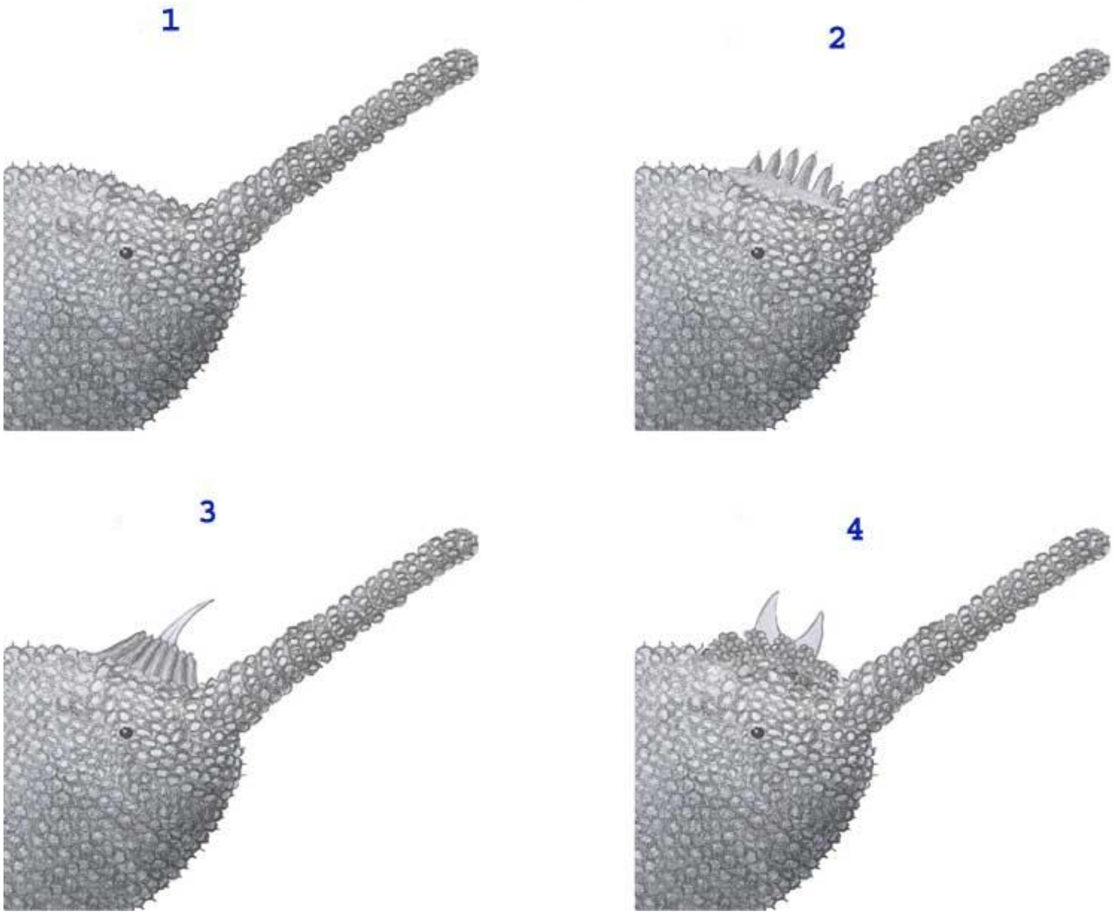

FIGURE 1. **Theoretical stages in the evolution of head structures in male Australian onychophorans; graphite pencil drawing by Julián Monge based on photographs by Tait and Norman (2001). For clarity, the adhesive organ is omitted.**

The fact that there are currently examples of all this stages can be interpreted, in Darwinian style, as **gradual evolution:** in each generation, males with longer and stronger papillae, which better support their spermatophore, dominate DNA passing to the next generation.

Regarding the **function of the spikes**, Tait and Norman (2001) suggested that they break the spermatophore to release sperm, or that they prick the skin of the female for sperm to enter into her lumen. However, in better known invertebrates, the skin and the spermatophore are broken by physiological mechanisms, without any need for spikes. It is more likely that, as has been documented in many other invertebrates (Schaller, 1971), **the spikes and palps serve to manipulate the spermatophore.**

It is possible to identify each of these Australian species just by looking at their cephalic structure. They are that specific, but, why?

Here we propose the hypothesis that, **when the head begins to perform functions of the male genital apparatus**, **natural selection treats the head itself as a genital apparatus**. We know that, both in invertebrates and in vertebrates, male genitalia are extremely varied and specific, to the point that they can be used to identify species. In fact, genital organs can change evolutionarily at twice the speed of other parts of the body (Klaczko, Ingram, & Losos, 2015).

There is **evolutionary race** in the world of reproduction (Eberhard, et al., 2018). Both sexes compete for greater control of the gametes, leading to long and contorted vaginas, and to penises that adapt to them, and this has been recorded in many groups, from water bugs to ducks. The idea that vaginas are all more or less the same, is widespread, but this could be a myth: we have not looked with enough attention (e.g. Puniamoorthy, Kotrba, & Meier, 2010).

Several hypotheses try to explain the evolution of species-specific genitalia: **key and lock, pleiotropism,** and **sexual selection**. The idea that the vagina must be different, so that the penis of the wrong species cannot enter it, is unlikely, because animals normally distinguish their own species before mating. The idea of pleiotropism, that is, that sexual evolution is a collateral effect of other factors, does not have much evidence in its favor. The hypothesis of sexual selection is the strongest according to previous work in many animals. In this case, our idea is that the fantastic heads of Australian male onychophorans result from their interaction with females (Monge-Nájera et al., 2019). **Females make insemination difficult to achieve a more stringent selection of their males.**

If our hypothesis of sexual selection is correct, it explains the existence of sensory hairs, thorns, spikes, and even manipulative palps in the male heads: these structures allow them to manipulate the spermatophore and to place it properly into the female. This occurs in the sexual organs of insects full of sensors, which have a variety of structures and adhesives to hold and manipulate the spermatophore (Schaller, 1971). If the spermatophore simply remained on the ground, as in some springtails, there would be no guarantee that the female would be fertilized; by attaching or inserting it with these cephalic structures, the male has a much better chance of fathering her offspring. Actually, spermatophore-supporting structures, resembling pads with spikes or fingers, have evolved repeatedly in invertebrates (e.g. Weygoldt, 1999) and probably the fantastic heads of Australian onychophorans are another case of divergent sexual evolution by sexual selection.

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