

# The evolutionary origin of *signa* in female Lepidoptera: natural and sexual selection hypotheses

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## Abstract

*Signa* are structures of the inner wall of the female *corpus bursae* (structure where males deposit a spermatophore during copulation) of many Lepidoptera that assist in tearing open spermatophores. In this paper, three hypotheses on the evolutionary origin of *signa* are proposed. The first hypothesis considers natural selection pressures arising from ecological changes that favor an increase in oviposition rate as the force behind the evolution of *signa*. The other two hypotheses involve sexual selection. The second hypothesis proposes that sexually antagonistic coevolution is responsible of the evolution of *signa*: According to this hypothesis, the inverse relation between the length of the female's refractory period and the amount of ejaculate remaining in her corpus bursae, observed in most Lepidoptera studied, selects in males a decreased rate of spermatophore digestion (e.g. a thicker spermatophore envelope or a higher chitin content) that increases the length of the refractory period beyond the female's optimum; in response, females evolved *signa* as a counteradaptation to restore the female's optimum by increasing the rate of spermatophore digestion. The last hypothesis considers that *signa* may have evolved as a female device for cryptic choice of males based on the ability of these to influence the length of post-copulatory female refractory period. The different hypotheses make different predictions of the sequence of appearance of specific ecological factors and novel phenotypic traits through evolutionary time. Therefore, testing the relative importance of the hypotheses requires a formal comparative analysis.

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## 1. Introduction

The *corpus bursae* of female Lepidoptera is a sac-like structure in which males deposit a spermatophore during copulation (Drummond, 1984; Scoble, 1992). Sperm cells leave the spermatophore through an aperture located in the collum (the elongated part of the spermatophore) and travel, by means of peristaltic contractions of the genital tract of females and sperm motility, to a different receptacle called spermatheca, whereas the spermatophore is gradually digested within the *corpus bursae* (Drummond, 1984) and its elements

incorporated into the female's soma and immature eggs (Boggs, 1990, 1995). The cuticle of the inner wall of the *corpus bursae* varies between taxa: in some groups it is smooth, whereas in others it has one or more sclerotized structures in form of bands, patches, teeth, spines or plates—plates can be plain, spined or toothed—known as *signa* (Hinton, 1964; Drummond, 1984; Scoble, 1992) (Fig. 1). The number, size, form and location of *signa* vary between taxa, and it is sometimes of taxonomic value (e.g. Penz, 1999; Rubinoff and Powell, 1999; Sánchez, 2004).

According to Hinton (1964), four hypotheses on the function of *signa* have been proposed: (a) *signa* are titillating organs that stimulate ejaculation; (b) *signa* are filters that permit the passage of spermatozoa and prevent the seminal duct (the duct through which sperm

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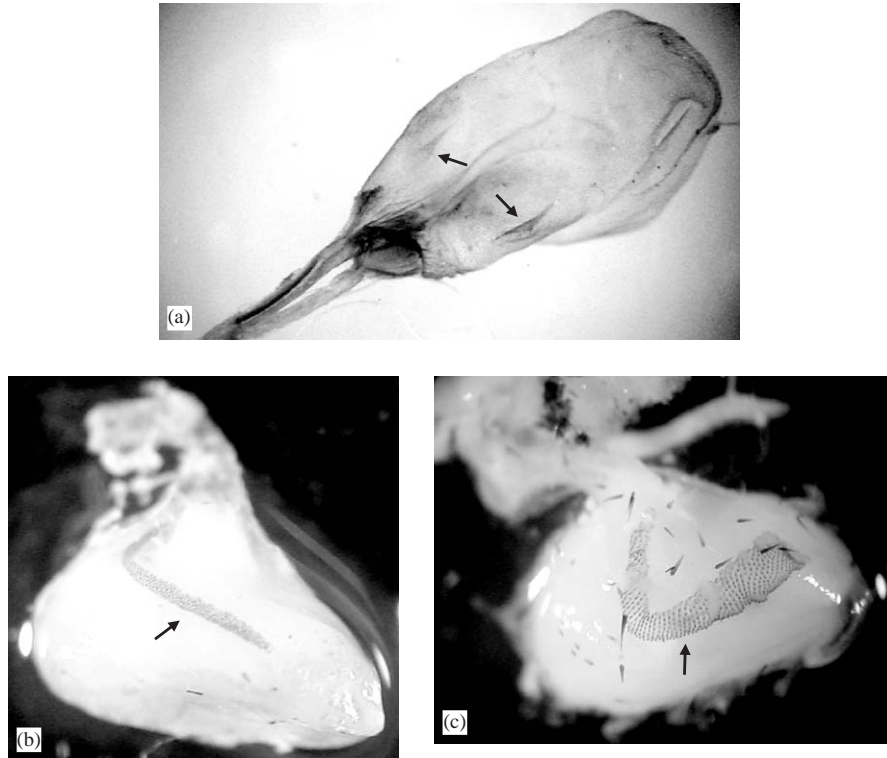


Fig. 1. Examples of *signa* in three butterfly species: (a) *Callophrys xami* (Lycaenidae), (b) *Eueides lybia* (Nymphalidae) and (c) *Heliconius ismenius* (Nymphalidae). Photos courtesy of Ivette Galicia (a), and Víctor Sánchez (b and c). In each panel a complete *corpus bursae* is shown and the *signum* (b and c) or *signa* (a) are indicated with arrows.

cells move from the *corpus bursae* to the spermatheca) from becoming blocked with larger particles; (c) *signa* are organs for holding the spermatophore in position (for example, when the aedeagus is removed from the female tract; Ferro and Akre, 1975); and (d) *signa* are organs for tearing open or piercing the spermatophore. Hinton (1964) evaluated these hypotheses and concluded that *signa* assist in tearing open spermatophores. Subsequent investigations support Hinton's conclusion (Rogers and Welles, 1984; Tschudi-Rein and Benz, 1990; I. Galicia, N. Caballero and C. Cordero, in preparation). Two clarifications are pertinent here. First, since sperm leave the spermatophore through an special aperture located in the collum and travel to the spermatheca by means of peristaltic contractions of the genital tract of females and its own motility (Drummond, 1984), the spermatophore, in principle, does not need to be ruptured by the *signa* to allow the sperm to escape (as claimed by Klowden, 2003); however, more work is needed on this issue. Second, it should be noted that function (c) does not necessarily excludes function (d) and both could be performed by *signa* in some species.

Why *signa* first arose during evolution and why they are not present in all lepidopterans, are questions that remain to be addressed. In this paper, three hypotheses to explain the evolutionary origin of *signa* are advanced.

In the three hypotheses it is assumed that females obtain resources (such as ovogenesis and oviposition stimulants, nutrients, and defensive compounds) from the spermatophores transferred by males and that at least part of such resources are used for egg production; this assumption is supported by experimental studies in several lepidopterans (reviews in Boggs, 1990, 1995; Karlsson, 1995; Vahed, 1998; Wiklund, 2003; Torres-Vila et al., 2004). The first hypothesis considers natural selection pressures arising from ecological changes that favor an increase in oviposition rate, while the other two hypotheses involve sexual selection.

## 2. Hypothesis 1: *Signa* are adaptations to increase oviposition rate

According to the first hypothesis, ecological pressures selecting for an increase in the rate of oviposition favor the evolution of traits, like *signa*, that increase the rate of spermatophore digestion. An increase in the rate of spermatophore digestion is favored in order to increase the rate at which ovogenesis/oviposition stimulants are released from spermatophore, and/or to increase the rate at which nutrients and defensive substances are made available to females for egg provisioning. Two situations that could favor an increase in oviposition

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