



Research paper

Intra-male sperm variability: Is there heteromorphism in scorpions (Arachnida, Scorpiones)?



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ARTICLE INFO

Article history:

Received 27 April 2015

Received in revised form 4 November 2015

Accepted 28 November 2015

Available online 10 December 2015

Corresponding Editor: Peter Michalik.

Keywords:

Bothriuridae
Reproductive strategies
Sperm bundles
Sperm competition
Sperm count
Sexual selection

ABSTRACT

There is a natural range of variation in sperm morphology inside males. This variation may be adaptive or a result of poor quality control of sperm production. Sperm aggregates can also show different morphologies inside ejaculates. Preliminary analyses in scorpions suggest the existence of a sperm package morphological variation. It is unclear if this is a true polymorphism. The main purpose of this analysis is to evaluate polymorphism in sperm packages of scorpions. Some species from the order showed width variation or spatial variation that was associated to the number of folds. Some ejaculates of *Bothriurus bonariensis* and *Brachistosternus ferrugineus* males showed width dimorphism, but may be related to the natural variation of sperm width. However, sperm packages in *B. ferrugineus* showed lower counts of spermatozoa and the apparition of these sperm packages seemed to increase at the beginning of the reproductive season in one of the species. A marked width dimorphism of sperm packages appeared inside ejaculates of *Caraboctonus keyserlingi*. The adaptive significance of sperm package differences is not well understood. Differences in width may be a consequence of sperm package production errors, resulting in sperm packages with fewer spermatozoa. Sperm package polymorphism in *C. keyserlingi* may be linked to sperm competition risk and may be associated to other characters and strategies. Alternative hypotheses to the pattern found are further analyzed and discussed within a sexual selection framework.

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1. Introduction

Under sexual selection, sperm competition can shape diverse characters such as genitalia, testes mass, sperm size and morphology, (Simmons, 2001). In many groups, sperm competition commonly influences certain traits of reproductive cells (Birkhead and Møller, 1998). For example, different organisms may show a wide variation in three different traits, spermatozoa length (Hosken, 2003; Birkhead et al., 2009), heteromorphism, that is the production of multiple sperm types within each ejaculate (Snook, 1998; Pitnick et al., 2009; Araújo et al., 2011; Dallai, 2014), and aggregation (Jamieson, 1987; Simmons and Siva-Jothy, 1998; Birkhead et al., 2009; Dallai, 2014). Variations in size and morphology of spermatozoa have been widely studied (Simmons, 2001; Birkhead et al., 2009). Studies have demonstrated that a natural range of variation in sperm morphology exists within males (reviewed in Simmons, 2001 and Calhim et al., 2007). This variation may have an adaptive function or just appear as a result

of a poor quality control of spermiogenesis errors (Cohen, 1967, 1973; Simmons, 2001; Hunter and Birkhead, 2002; Birkhead et al., 2009). Heteromorphism is an example of morphological diversification, where two or more different types of sperm may appear in a single ejaculate (Swallow and Wilkinson, 2002; Pitnick et al., 2009). In fact, different types of spermatozoa can have diverse abilities that can serve various functions when fertilizing the female gamete (Pitnick et al., 2009; Higginson and Pitnick, 2011). Among arthropods, insects show many examples of heteromorphism in spermatozoa (reviewed in Dallai, 2014). Lepidoptera shows a classic example in the form of spermatozoa dimorphism, with morphs called eupyrene and apyrene. The first is a nucleated cell and the second lacks the nucleus and is highly motile (Gage and Cook, 1994; He et al., 1995). For example, eupyrene participates in fertilization whereas apyrene may aid their transport, fertilization, and maintenance, or simply serve as “cheap filler” (Cook and Gage, 1995; Simmons, 2001). Variation in spermatozoa is not only morphological, and can also refer to differences in conjugation, a phenomenon where two or more spermatozoa unite for motility and/or transport (Pitnick et al., 2009). Two types of sperm conjugation exist among arthropods (Higginson and Pitnick, 2011). Primary sperm conjugates originated from a single spermatogonium, where

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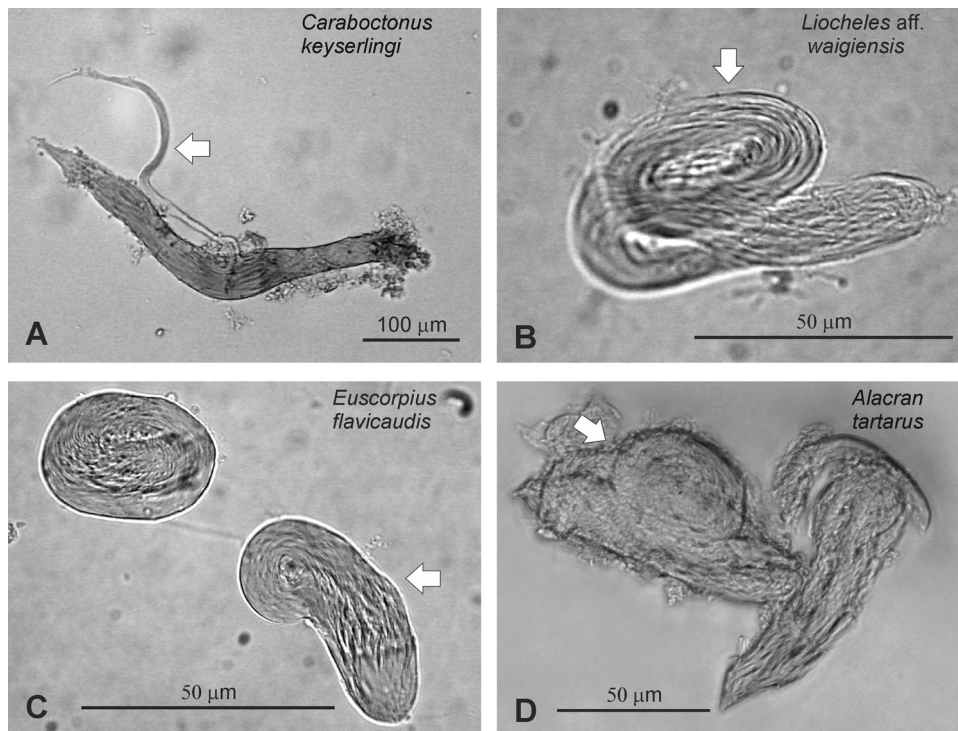


Fig. 1. Sperm packages morphological variation in different scorpion families. (A) *Caraboctonus keyserlingi* (Luridae) showing average thick sperm package together with a thin sperm package (white arrow). (B) *Liocheles aff. waigiensis* (Hormuridae), regular folded sperm package in the background together with a ring-like package (white arrow). (C) *Euscorpis flavicaudis* (Euscorpidae), average folded sperm package and its morphological variant, a spherical sperm package (white arrow). (D) *Alacran tartarus* (Typhlochactidae), two folded sperm packages appear with one ring like sperm package (white arrow). Arrows indicate morphological variants.

spermatozoa remain grouped, and secondary sperm conjugates originated after separation when spermatozoa are fully individualized during spermiogenesis. The resulting sperm aggregates may also show morphological diversity similar to single sperm cells. For example, Takami and Sota (2007) found size heteromorphism in sperm bundles within ground beetles from the genus *Ohomopterus*, with bigger bundles migrating faster to the spermatheca, but with no clear function for small sperm bundles, despite their rapid diversification.

Both types of conjugates appear among spiders, where spermatozoa are coiled and transferred inside a secretion sheath (Michalik and Huber, 2006; Lipke and Michalik, 2012; Michalik and Ramírez, 2014). Scorpions generally show sperm conjugates in dense aggregates called “bundles” (Jespersen and Hartwick, 1973; Alberti, 1983) or, more precisely, sperm packages (Peretti and Battán-Horenstein, 2003; Michalik and Mercati, 2010; Vrech et al., 2011, 2014), the term we will use in the present study. In scorpions, a sperm package contains a range of 70–400 spermatozoa, depending on the species. For example, Jespersen and Hartwick (1973) found 200–400 spermatozoa in several species of Vaejovidae. Similarly, Peretti and Battán-Horenstein (2003) found between 70 and 100 spermatozoa in eight species of Bothriuridae. Recently, various species from different families have shown nearly 250 spermatozoa per sperm package (e.g., Superfamily Scorpionoidea, which includes Bothriuridae, Scorpionidae and Hormuridae, Michalik and Mercati, 2010; Vrech et al., 2011; Troglotayosicidae, Vignoli et al., 2008).

Preliminary analyses in scorpions suggest that sperm package variation could exist within a male's pre-insemination ejaculate (Vrech et al., 2011). However, it is uncertain if such observations correspond to a true heteromorphism, where two or more distinctive types of sperm packages appear systematically within a single pre-insemination ejaculate, or merely to the natural morphological variation. Besides, the distribution of sperm package

heteromorphism among species from different families of scorpions is still unknown. In addition, we lack studies on dissimilarities in sperm packages width, which may be a result of differences in number or width of spermatozoa contained inside each sperm package. Here, we report and evaluate the presence of sperm package heteromorphism in scorpions, including a descriptive comparison among selected scorpion families. First, the morphological variability of sperm packages will be characterized. Second, we will address sperm packages variation in Bothriuridae and Luridae. Finally, the effects of reproductive season and body condition on sperm package morphology will be evaluated for the bothriurid *Brachistosternus ferrugineus* (Thorell, 1876).

2. Material and methods

2.1. Descriptive analysis of sperm package variants

We used species belonging to groups where previous observations suggested the occurrence of sperm package variability (see Vrech et al., 2011). We have increased the taxon sampling on the family Bothriuridae because this is a diverse family in the Neotropical region that shows a wide variation in sperm package morphology (Vrech et al., 2011). Samples from other families were included as examples of variability in the order. We used representatives of following families: Bothriuridae Simon, 1880, Euscorpidae Laurie, 1896, Luridae Thorell, 1876, Hormuridae Laurie, 1896, Scorpionidae Latreille, 1802, and Typhlochactidae Mitchell, 1971. For detailed information of the observed specimen (see Supplementary material A). Voucher specimens are deposited in the scorpion collection of the Laboratorio de Biología Reproductiva y Evolución de la Universidad Nacional de Córdoba (IDEA, UNC-CONICET). Since our approach is merely descriptive we number of samples differ often due to difficulties in obtaining specimen of certain species (see Takami and Sota, 2007; Vrech et al., 2011 for

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