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Silk gene expression of theridiid spiders: implications for male-specific silk use

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ABSTRACT

Spiders (order Araneae) rely on their silks for essential tasks, such as dispersal, prey capture, and reproduction. Spider silks are largely composed of spidroins, members of a protein family that are synthesized in silk glands. As needed, silk stored in silk glands is extruded through spigots on the spinnerets. Nearly all studies of spider silks have been conducted on females; thus, little is known about male silk biology. To shed light on silk use by males, we compared silk gene expression profiles of mature males to those of females from three cob-web weaving species (Theridiidae). We de novo assembled species-specific male transcriptomes from *Latrodectus hesperus*, *Latrodectus geometricus*, and *Steatoda grossa* followed by differential gene expression analyses. Consistent with their complement of silk spigots, male theridiid spiders express appreciable amounts of aciniform, major ampullate, minor ampullate, and pyriform spidroin genes but not tubuliform spidroin genes. The relative expression levels of particular spidroin genes varied between sexes and species. Because mature males desert their prey-capture webs and become cursorial in their search for mates, we anticipated that major ampullate (dragline) spidroin genes would be the silk genes most highly expressed by males. Indeed, major ampullate spidroin genes had the highest expression in *S. grossa* males. However, minor ampullate spidroin genes were the most highly expressed spidroin genes in *L. geometricus* and *L. hesperus* males. Our expression profiling results suggest species-specific adaptive divergence of silk use by male theridiids.

1. Introduction

Sexual dimorphism is a phenomenon resulting in significant differences in how males and females interact with their environment. In spiders, males and females show extraordinary sexual size dimorphism, with some males being dwarfs in comparison to females (Vollrath and Parker, 1992; Vollrath, 1998; Hormiga et al., 2000; Schütz and Taborsky, 2003, 2005). Often, this dwarfism in male spiders is associated with a nearly parasitic relationship between males and females, with males feeding on prey captured by females and living on female spider webs (Vollrath, 1998).

Differences between the sexes in spiders have been recognized regarding size, venom, and behavior, but differences in silk use remain largely unknown (Atkinson, 1981; Vollrath and Parker, 1992; de Oliveira et al., 1999; Binford, 2001; Binford et al., 2016). While there have been many studies that characterize spider silk genes, they have been based almost entirely on female spiders (Tian and Lewis, 2005; Zhao et al., 2006; Perry et al., 2010; Correa-Garhwal and Garb, 2014). For many species, including cob-web weavers (Theridiidae), this is because males mature at smaller body sizes than females, and males tend to have shorter lifespans (Fig. 1A; Kaston, 1970; Andrade, 2003). Furthermore, female spiders have more types of silk glands than males (Kovoor and Peters, 1988; Peters, 1992; Park and Moon, 2002; Moon and An, 2006; Moon, 2008). Thus, virtually nothing is known regarding silk use and silk gene expression in male spiders.

Silk spinning in spiders involves a highly specialized system of genes, proteins, glands, and behaviors. An individual spider can have multiple types of silk glands that can be categorized according

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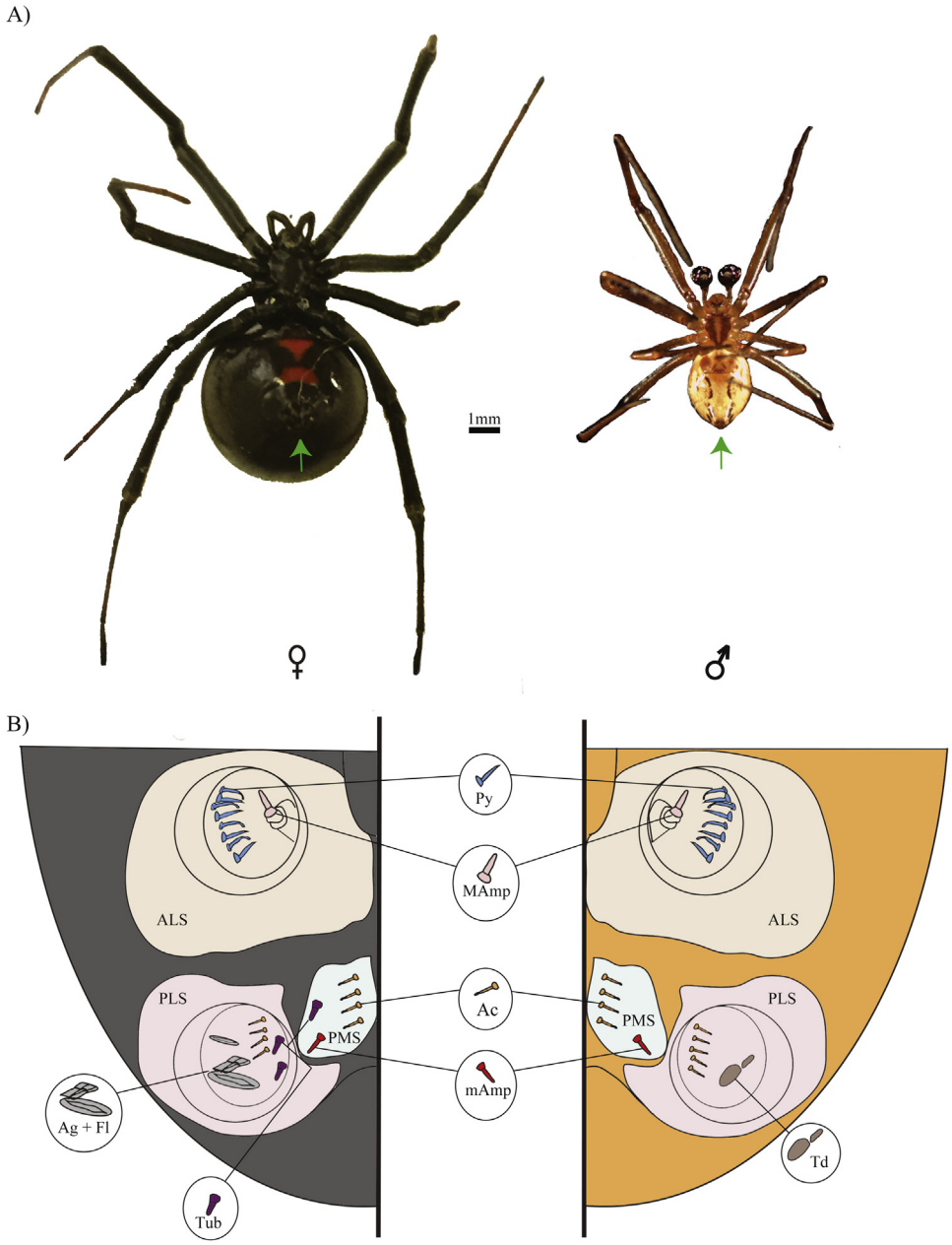

Fig. 1. Spinnerets and spigots of female and male *Latrodectus hesperus*. (A) *L. hesperus* female (left) and male (right). Ventral view, anterior to the top. Spinnerets indicated by green arrows. Scale bar = 1 mm. (B) Spigots associated with the spinnerets in female (left) and male (right) spiders after Moon and An (2006). Diagrams not to scale. Vertical line indicates sagittal midline, only one side of the spinneret region is shown. Anterior lateral spinnerets (ALS) in beige, posterior median spinnerets (PMS) in light blue, and posterior lateral spinnerets (PLS) in pale pink. Spigots abbreviated as follows: Ac, aciniform gland spigots (orange); Ag, aggregate gland spigots (grey); Fl, flagelliform gland spigots (grey); Py – pyriform gland spigots (blue); Td, non-functional remnants of aggregate and flagelliform gland spigots (light brown). "Am" and "Cy" of Moon and An (2006) are shown here as: Am = MAmp, major ampullate gland spigot (pink) and mAmp, minor ampullate gland spigot (red); Cy = Tub, tubuliform gland spigots (purple).

to their morphology (e.g., aciniform, aggregate, flagelliform, major ampullate, minor ampullate, pyriform, and tubuliform silk glands; Vollrath, 1992). Each gland type produces a unique, gland-specific proteinaceous silk spinning dope. As needed, silk dope exits the glands through ducts, and then is extruded from external spigots on the spider's spinnerets (Gosline et al., 1986; Coddington, 1989). Silk spigots vary in size and shape and each spigot is associated with a single silk gland. Spider silk spigots are identified based on morphological characteristics such as relative size, number, and position on the spinnerets. Spigots are named according to the silk gland connected to them. For example, major ampullate spigots, which are located on the anterior lateral spinnerets, are attached to the major ampullate silk glands (Coddington, 1989).

From spider silk gland cDNA studies, it has been established that silk gland types differ in their expression of silk structural protein encoding genes. The predominant silk proteins are spidroins (a contraction of "spider fibroins"; Hinman and Lewis, 1992), which are encoded by a gene family (Guerette et al., 1996). Each silk gland type can express a particular set of spidroins. For example, major ampullate silk glands predominately express major ampullate spidroins, whereas silk protein expression in aciniform silk glands is dominated by aciniform spidroins. Each spidroin type forms task-specific silk fibers. Major ampullate spidroins are the main constituent of draglines, and aciniform spidroins form the silk used in prey wrapping.

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