



Proteomics of reproductive systems: Towards a molecular understanding of postmating, prezygotic reproductive barriers



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ARTICLE INFO

Article history:

Received 17 August 2015

Received in revised form 28 September 2015

Accepted 11 October 2015

Available online 23 October 2015

Keywords:

Speciation

Fertility

Sperm

Seminal fluid

Sexual selection

ABSTRACT

Following mating and insemination, fertility is dependent on the successful execution of a complex array of morphological, physiological and molecular interactions between male and female proteins, cells and tissues. Many of these interacting components bear hallmarks of co-evolving systems and are suspected to contribute to postmating, prezygotic (PMPZ) reproductive barriers involved in the formation of new species. Although PMPZ reproductive isolation has historically been more difficult to study than precopulatory and postzygotic barriers, recent research has highlighted its potential role in speciation and revealed the impact of molecular investigation utilizing proteomic approaches. Proteomics, in conjunction with transcriptomic and evolutionary genomic studies, has been widely used to identify rapidly evolving male and female reproductive proteins. Increased access to high-throughput and quantitative proteomic techniques, as well as the ease of generating genomic and transcriptomic resources necessary for protein identification, can facilitate the extension of proteomics from traditional model species to systems of relevance to PMPZ phenotypes and hence greatly expand our understanding of how rapidly diverging molecular systems may contribute to PMPZ barriers. Here we review the influence proteomic analyses can have on our understanding of the function and evolution of the complex cellular and molecular processes governing postcopulatory male–female interactions and the study of PMPZ reproductive isolation, with the goal of expanding our understanding of the contribution of PMPZ processes to speciation.

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1. Introduction

Identifying traits that restrict gene flow, or “reproductively isolate” genetically divergent populations, sub-species or species is a central goal of evolutionary biology [1]. Most studies of reproductive isolation have focused on premating mechanisms (e.g., geographical, phenological, courtship and mate preference traits, and mechanical obstacles to copulation) or postzygotic mechanisms (e.g., genetic incompatibility resulting in offspring inviability or infertility). In contrast, mechanisms of postmating, prezygotic (PMPZ) isolation, resulting from reproductive incompatibilities or fertilization biases that occur between the start of copulation and successful karyogamy (the formation of a diploid zygote following fertilization), have received less attention [2]. This neglect is largely attributable to the challenge of discerning events occurring within the female reproductive tract. However, recent insights have been made into the mechanistic basis of PMPZ isolation [3–8], and these suggest that the expanded application of proteomic analyses to investigations of this difficult to study process will prove especially fruitful.

Sexual selection is credited with driving rapid diversification of reproductive characters amongst isolated populations and, consequently, is postulated to play an important role in formation and maintenance of species boundaries [1,8–13]. Natural selection may act on female and male traits that enhance the probability that viable sperm reach the oocyte to ensure the highest level of fertilization efficiency and zygote viability. In addition particular, postcopulatory sexual selection, resulting from female remating and the temporal overlap of ejaculates from different males within the female reproductive tract, can generate conflict between the sexes over paternity and thus drive the evolution of male traits that enhance competitive fertilization success and female traits that mediate cryptic female choice, such as biases favoring particular ejaculate traits [10,14–21]. As our knowledge of postcopulatory sexual selection, including sexual conflict [20], and its underlying reproductive biology [22] have grown over the past few decades, so has the interest in PMPZ reproductive isolation.

Three general themes of rapidly evolving reproductive systems can help us to understand the potential for the taxonomically-widespread occurrence of PMPZ reproductive isolation: (1) internal fertilization is a complex process involving many moving parts, (2) ejaculate–female interactions (EFIs) mediate a diverse array of male and female reproductive behaviors and processes, and (3) interacting male and female characters tend to rapidly co-diversify. Proteomic investigations of

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reproduction have increased markedly and provided novel means to investigate tissues, cells and ultimately proteins involved in critical post-copulatory events. High-throughput protein identification, sensitive quantitative techniques and seamless bioinformatics pipelines have alleviated challenges posed by the proteomic complexity of reproductive systems and limitations associated with low-throughput, protein-by-protein approaches (reviewed by [23–25]). Although too vast a subject to cover exhaustively, we utilize the aforementioned themes to review the application of proteomics to the study of reproductive system evolution and then to propose ways to apply proteomic analyses to probe the molecular mechanisms of PMPZ reproductive barriers. We suggest that proteomic investigations offer uniquely powerful and, as of yet, underutilized opportunities to advance our understanding of speciation biology across diverse taxa.

2. A primer in male–female interactions relevant to postmating, prezygotic (PMPZ) reproductive isolation

PMPZ reproductive isolation, also known as “gametic isolation” [26], is implicated whenever mating between males and females from genetically differentiated populations, strains or species appear normal, yet fertilization or zygote formation is compromised. Reproductive failure may be observed following a single heterospecific (or heteropopulation) insemination (“noncompetitive gametic isolation”), or it may only be evident when ‘foreign’ sperm compete for fertilization with sperm from a conspecific (or native) male [27]. In the latter circumstance, “competitive gametic isolation”, the widely observed pattern is for sperm of the conspecific male to fertilize the majority of eggs irrespective of mating order (a phenomenon known as “conspecific sperm precedence”). There are many opportunities for PMPZ reproductive isolation, particularly in internal fertilizers where fertility is dependent on a complex array of processes occurring within the female reproductive environment. Understanding the precise mechanisms underlying PMPZ isolation is currently a topic of great interest amongst evolutionary biologists [3–8].

2.1. External fertilization

Although externally-fertilizing species do not “mate”, by definition, we begin by considering mechanisms of reproductive isolation in these taxa as it is heuristic to the study of PMPZ reproductive barriers in internal fertilizing species. Some of the events central to an understanding of PMPZ isolation are shared between external and internal fertilizing species, and aspects of reproductive isolation research have proven more tractable in externally-fertilizing species. As these systems have been the subject of excellent reviews [28–30], we will only highlight some hallmark features that are especially relevant to PMPZ barriers. First, sperm–egg interactions exhibit remarkable specificity, and eggs are fertilized more efficiently by conspecific than heterospecific sperm, even amongst closely related (i.e., geographically or phylogenetically) populations/species [31–33]. Second, the rapid co-diversification of molecules governing sperm–egg binding in broadcast spawners, including sea urchins and abalone, presents an elegant scenario for the establishment of reproductive isolation via gametic incompatibilities without jeopardizing the fidelity of sperm–egg interactions within populations [34–36]. Finally, influential interactions have been identified in studies of congeneric fish that are mediated by ovarian fluid released with eggs during spawning [37]. These three-way interactions (sperm x ovarian fluid x egg) exemplify the potentially complex nature of conspecific sperm precedence and, in turn, illustrate how such systems might contribute to reproductive incompatibilities [38]. Although the proteins governing these interactions have yet to be characterized, rapidly evolving sperm–female interactions may be widespread amongst external fertilizers and make substantial contributions to both competitive and noncompetitive reproductive isolation.

2.2. Internal fertilization

Between the initiation of copulation and zygote formation, a series of events must progress correctly for fertilization and karyogamy to occur. Although reproductive systems display extraordinary diversity, even distantly related taxa (e.g., animal phyla) tend to share a general motif of events, as can be seen in the depiction of the common and divergent aspects of internal fertilization for the fruit fly and mouse in Fig. 1. In brief, these events include, (1) insemination, (2) female postmating responses stimulated by copulation and/or the ejaculate, including changes in gene expression, secretory activity and female reproductive tract (FRT) characteristics necessary to support gamete movement, survival and in some cases oogenesis and oviposition [39–41], (3) sperm migration from the site of insemination to storage and, eventually, to the site of fertilization [16,42,43], (4) maintenance of sperm viability while in storage, (5) gamete modification to complete maturation, undergo activation or otherwise become fertilization competent [40], (6) fertilization, including sperm interaction with extracellular egg matrixes and membranes facilitating sperm–egg fusion and, finally, (7) contributions of the egg and the sperm (i.e. centrosome and other chromatin proteins) interact to execute events critical to karyogamy and zygote formation [44–48].

In species where females mate with multiple males, there are also opportunities for postcopulatory sexual selection, including events associated with sperm competition and cryptic female choice [14,17]. These may include the removal, relocation or displacement of resident sperm by the mating male or his ejaculate [49], the formation of a copulatory plug, sperm ejection from the reproductive tract by the female [50] and female immunity responses [51–55]. Despite intense interest in the evolutionary ramifications of sexual selection, a consensus has yet to be reached regarding the importance of conspecific sperm precedence to the establishment of competitive gametic isolation or speciation processes more generally [2,56,57].

3. Proteomics of reproductive systems – There are many moving parts

The application of ‘omic technologies has rapidly advanced the molecular characterization of reproductive systems and established a foundation for the identification of genes and networks potentially contributing to PMPZ isolating barriers. The greatest progress has been made in relation to reproductive gene expression within and between the sexes, initially using array-based approaches and more recently with next-generation sequencing [58–60]. Detailed gene expression atlases are now available for a variety of reproductive tissues in several model species and are becoming readily available for a range of taxa that were not traditionally considered experimental models. Proteomic approaches have been especially informative when applied in conjunction with transcriptomic studies of reproductive systems [61]. Although gross morphological structures, for example male genitalia, may not lend themselves to informative proteomic analysis outside of a developmental context, investigations of spermatozoa and seminal fluid have blossomed with the advent of high-throughput proteomic techniques. Such studies have propagated entirely new avenues of research. Here we provide an overview of the reproductive and evolutionary biology of the “many moving parts” that contribute to successful fertilization with an emphasis on the contribution of proteomic studies to our understanding of the molecular biology of these sex-specific traits, including (1) male genitalia, (2) sperm, (3) seminal plasma, (4) FRT morphology and neurophysiology, (5) the FRT epithelium and secretome and (6) oocytes.

3.1. Male genitalia

Penises are notorious for their phenomenal shape variation and rapidly divergent nature [62]. Unfortunately, there has been a dearth

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