c0070

7 Ejaculate– and sperm–female interactions

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sp0130 *in every order of creation there are two sorts of creators, contrary yet complementary*

sp0140 *(John Barth 1968)*

s0010 ## 7.1 Introduction

s0020 ### *7.1.1 Ejaculate–female interactions are predicted to be complex and evolutionarily dynamic*

p0020 Sexual reproduction is complicated business. A review of sperm–egg interactions in externally fertilizing species referred to fertilization as one of the least understood of fundamental biological processes (Vacquier 1998). Moreover, one of the most striking evolutionary trends to emerge in the last decade is the rapid diversification of proteins involved in reproduction. This pattern has been demonstrated for protein pheromones that control mating (i.e., conjugation) in the marine ciliate *Euplotes* (Luporini et al. 1995; Kuhlmann et al. 1997), the gene coding for a cell surface protein necessary for the fusion of '+' and '−' mating types in the green alga *Chlamydomonas* (Ferris et al. 1997), and the proteins mediating sperm–egg recognition and binding in externally fertilizing marine invertebrates (Swanson & Vacquier 2002; Clark et al. 2006; see Chapter 8 of this volume).

p0030 It is reasonable, therefore, to expect the mechanisms of reproduction to be complex and evolutionarily dynamic in internally fertilizing species, where numerous biochemical, physiological, morphological and behavioral mechanisms mediate insemination, sperm migration, sperm storage, the maintenance of sperm viability and sperm modification, all of which must be properly executed before fertilization can begin. In addition, in most species, females mate with more than one male within a breeding cycle, and sperm can remain viable for a considerable time within females (Birkhead & Møller 1993; Neubaum & Wolfner 1999b). This situation provides the opportunity for postcopulatory

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sexual selection, which is predicted to further enhance complexity and diversification in genes contributing to differential male fertilization success and female control over paternity (Birkhead & Møller 1998a; Clark 2002; Arnqvist & Rowe 2005; see Chapter 6 of this volume). It is becoming increasingly clear that sperm and ejaculate constituents evolve in response to selection pressures imposed by the female reproductive tract (Parker 1984; Sivinski 1984; Eberhard 1996; Pitnick et al. 1999). Ejaculate–female interactions (EFIs) can determine whether or not a reproductive attempt is successful and can influence the outcome of sperm competition within populations (Wilson et al. 1997; Clark et al. 1999; Miller & Pitnick 2002; Bjork et al. 2007; Pattarini et al. 2006). Evolutionary diversification of EFIs may further determine the extent of reproductive isolation and gene introgression between closely related species (see Chapter 9 of this volume).

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7.1.2 A love–hate relationship?

p0040 Sexually reproducing females need viable sperm to reproduce. During ejaculation and some phases of sperm transport through the female reproductive tract, sperm are subjected to physical stresses and may sustain oxidative damage to their plasma membrane lipids. Because sperm generally are terminally differentiated cells without an active nucleus and transcription apparatus, they lack the full repertoire of repair mechanisms available to somatic cells or oocytes. Thus, and given that there may be a lengthy interval between insemination and fertilization, the female must protect sperm against degenerative changes. Indeed, females exhibit a variety of adaptations for sustaining sperm viability.

p0050 It is thus initially paradoxical to recognize that the female reproductive tract may also present an environment that is somewhat unfavorable to, and thus selective on, sperm. Conditions precluding some sperm reaching eggs may include (i) active sperm ejection by females (e.g., Pizzari & Birkhead 2000), (ii) physical barriers (e.g., cervix, long ducts), (iii) chemical barriers (e.g., low pH and viscous mucus), and (iv) leukocytic/phagocytotic responses within the female (Suarez 2006). Consequently, in many species only a small proportion of the inseminated sperm ever have the opportunity to encounter an egg. For example, of the 189 million sperm in a typical human ejaculate (Handelsman et al. 1984), only a few thousand ever reach the oviduct (Suarez & Pacey 2006). In birds, typically fewer than 2% of inseminated sperm even reach a female's sperm-storage tubules (Birkhead 1998b). However, this is not universal, as in some species females can be highly efficient in their sperm use (Snook & Markow 2002).

p0060 Four non-mutually exclusive hypotheses have been proposed to explain the evolution of a female reproductive tract that is selective on sperm (Birkhead et al. 1993); these in turn may explain the complex and evolutionarily dynamic nature of EFIs. First, an environment that is selective on sperm may be a by-product of safeguards against parasites, bacterial infections and other pathogens that may enter the female reproductive tract, particularly at the time of mating. Second, 'challenges' to sperm may be adaptations to discriminate against sperm that have abnormal morphology, weak motility or are otherwise unfit for fertilization.

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Third, high sperm mortality and the consequent presence of few sperm at the site of fertilization may benefit females by reducing the risk of polyspermy. Fourth, conditions of the female tract may be sexually selected in two ways. (i) By posing challenges to sperm, females may ensure that their eggs are fertilized by the 'best' sperm, or by sperm from the 'best' males (or are not fertilized by 'poor' sperm) (see also Eberhard 1996; Birkhead 1998a; Section 7.5). (ii) Alternatively, sexual conflict over paternity will favor male adaptations (e.g., seminal protein and sperm traits) that increase the probability of a given male's sperm being used over those from other males. To the extent that male adaptations to bias paternity are harmful to females, there will be selection for female adaptations that provide resistance to them (Parker 1979; Holland & Rice, 1998; Chapman et al. 2003; Arnqvist & Rowe 2005). The first and fourth hypotheses are especially likely to drive rapid and pervasive diversification of EFIs, as both pathogen/host interactions and sexual conflict traits can enter into arms races or perpetual coevolutionary cycles.

p0070 Rapid evolutionary diversification of reproductive traits has largely been attributed to sexually antagonistic coevolution (e.g., Arnqvist et al. 2000; Swanson et al. 2001b). In practice, however, it is extremely difficult to discriminate this process from more traditional, 'cooperative' models (e.g., good genes and runaway sexual selection) for the evolution of reproductive traits (Pizzari & Snook 2003; Rowe et al. 2003; Arnqvist & Rowe 2005; Kokko et al. 2006). These different selection pressures can be acting simultaneously to varying degrees and differentially over time (Arnqvist & Rowe 2005). Conflict between the sexes is expected to be ubiquitous among species that are not strictly monogamous (Rice 1998), but so is cooperation between the sexes. For example, it may be advantageous to females to use males as 'hormone-delivery systems' for controlling some aspects of their postmating physiology. The evolution in *Drosophila melanogaster* of male seminal prteins ('Acps'; see below) that stimulate oogenesis and ovulation in females, for instance, may mean that females only produce large numbers of eggs after mating when there will be sperm to fertilize them and/or that males manipulate female reproductive physiology to their own benefit and at a cost to females. Thus, cooperation and conflict are both likely to be potent forces shaping the evolution of EFI traits.

s0040 ### 7.1.3 Chapter goals

p0080 We have two goals: (1) to illustrate the pervasiveness of EFIs by discussing different types and what is known about their underlying mechanisms and (2) to consider the evolutionary significance of EFIs. We review evidence for (i) rapid evolutionary diversification of EFI genes, (ii) correlated evolution of sex-specific EFI traits ('evolutionary EFIs') and (iii) the relationship between genetic compatibility, male–female interactions and patterns of sperm precedence. We have highlighted some of the interesting variation observed across animal taxa, but rather than be exhaustive in our review, we have focused on providing detailed descriptions of selected examples.

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p0090 We use the term 'EFI' for any modifications to ejaculate (or an ejaculate subcomponent) form or function that are induced by the female reproductive tract, and vice versa. 'Evolutionary EFIs' include genetic differentiation between populations or species in ejaculate traits resulting from selection generated by the female reproductive tract, and vice versa. Whenever sperm per se are known to interact directly with the female reproductive tract, we use the term sperm–female interactions ('SFIs'). For the majority of phenomena, however, we prefer the term EFI because the specific agent(s) of interaction are unknown. For example, some seminal components can bind to sperm and in some cases can later be cleaved off within the female to influence reproduction (e.g., Peng et al. 2005a). Such complex (and not widely investigated) sperm × seminal plasma × female interactions frequently preclude discrimination of the more narrowly defined SFIs from EFIs. It is important to note that these definitions exclude many interesting interactions between the sexes, as well as sex-specific mediation, that impact fertilization success.

s0050 7.2 Types and mechanisms of ejaculate–female interaction

s0060 *7.2.1 Ejaculate-induced modification of female gene expression*

p0100 Components of the ejaculate can affect the molecular composition of the female. By inducing or repressing particular gene expression or by modifying proteins and other macromolecules, ejaculate components can convert a female from an 'unmated' to a 'mated' physiological, immunological and behavioral state. To identify these effects, studies have been carried out to compare the transcriptomes or proteomes of mated and unmated females.

p0110 In the fruit fly *D. melanogaster*, by 1–3 h postmating, physiological changes are already apparent between mated and unmated females and sperm have been stored. In one study, postmating changes in transcript level were detected in about 13% of the transcriptome at this time, but almost all those changes (1737/1783) were very small (i.e., less than twofold) (McGraw et al. 2004). Members of many classes of genes showed such very small transcript level changes upon mating. These classes represented a broad range of biological functions: immune response (these were most of the genes with more than twofold changes, and most were induced), energy metabolism (mostly repressed), detoxification, proteolysis and odorant/pheromone binding. Mutant and transgenic fly strains were used to tease apart the contribution of sperm, seminal proteins and of other aspects of mating to the transcriptome changes (McGraw et al. 2004). Of the 1783 genes whose transcript level differed between mated and unmated females, 160 were modulated in response to Acps. Particularly enriched among the latter were genes involved in immune response (see Section 7.2.3). Another 540 genes were modulated in response to receipt of sperm; these included metabolic genes (usually repressed), and genes involved in detoxification and in proteolytic cascades. Sperm, Acps and, especially, non-sperm non-Acp cues also induced expression of ~50 transcription factors that

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could potentially mediate a later transcriptome-level response to mating. The remaining mating-responsive genes were regulated by other aspects of mating that could not be tested in those experiments (such as mechanical stimuli, contact pheromones, energy expenditure, and non-Acp components of seminal fluid). In another study, the transcriptomes of courted but unmated females were compared to those of mated females (Lawniczak & Begun 2004). This study reported fewer genes with changes, and the mating-regulated genes they found overlapped significantly with those of the larger study (some differences were likely due to use of different microarray platforms and statistical analyses.)

p0120 These microarray experiments used whole females. Thus, they could have missed changes in transcript levels that occurred in small groups of cells or only in particular tissues, or genes regulated in opposite directions in different tissues. Consistent with this prediction, a subsequent proteome- and transcriptome-level study of the lower reproductive tract of female *Drosophila* (Mack et al. 2006) detected genes that had been found in the whole-body analysis as well as genes that were not detected in that analysis and might thus be regulated in the reproductive tract only. That study also confirmed that gene expression changes are small shortly (<3 h) after mating, despite the physiological changes that occur during this time, but showed that at later postmating times (>6 h) there were larger fold changes in the transcriptome.

p0130 Collectively, all of these studies suggest that initial changes in the physiology of the mated female derive from posttranscriptional or posttranslational effects on RNAs or proteins already present in the mature female. Later, large-scale transcriptome/proteome changes extend or carry out subsequent steps in the female's response. This hypothesis still needs to be tested, by determining the functions of some of the mating-regulated genes.

p0140 Consistent with these findings, coculturing of bovine oviductal epithelial cells with sperm is reported to alter the profile of proteins secreted into the oviductal fluid (Ellington et al. 1993b; see also Fazeli et al. 2004 for related mouse study). Interestingly, proteins in some of the same classes are found in seminal fluid in *Drosophila* (Mueller et al. 2004), consistent with the idea that the male provides proteins that can modulate female reproductive processes in addition to inducing the female to synthesize proteins in these classes.

s0070 7.2.2 Ejaculate-induced modification of female reproductive physiology

p0150 Dramatic changes in female physiology and behavior that are induced by mating are likely universal. Nevertheless, there is tremendous variation across taxa in the sex-specific factors that interact to trigger these changes. For example, the reduction in female receptivity to remating in the fowl *Gallus gallus domesticus* has been experimentally demonstrated to be entirely due to mounting by the male and independent of insemination (Lovlie et al. 2005). In contrast, mating-induced changes appear solely attributable to the action of Acps in one species of mosquito, *Aedes aegypti* (Craig 1967; Fuchs et al. 1968), and have been attributed to the act of the spermathecae filling with sperm in another species,

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Anopheles gambiae (Klowden 2001, 2006). Finally, in *D. melanogaster* (as detailed above and below) both Acps and sperm are responsible for the changes females undergo.

p0160 Males provide the female with a suite of proteins and other molecules in the seminal fluid (Poiani 2006). For example, in *D. melanogaster*, 112 seminal proteins expressed in the male's accessory glands have been identified to date (Swanson et al. 2001a; Ravi Ram & Wolfner 2007). Other reproductive tract tissues and glands (the ejaculatory duct, ejaculatory bulb) also make seminal proteins (Gilbert et al. 1981; Cavener & MacIntyre 1983; Ludwig et al. 1991; Samakovlis et al. 1991; Lung & Wolfner 2001). A comprehensive EST screen and other screens identified ~80% of the Acps (DiBenedetto et al. 1987; Monsma & Wolfner 1988; Simmerl et al. 1995; Wolfner et al. 1997; Swanson et al. 2001a; Walker et al. 2006). Annotation and comparative structural modeling of their predicted proteins identified potential functional families to which Acps belong (e.g., Mueller et al. 2004, 2005). Approximately 40% of *D. melanogaster* Acps appear to be peptide hormones or their prohormonal precursors (Mueller et al. 2004, 2005). The other ~60% of Acps fall into predicted functional classes: proteolysis regulators (proteases and their inhibitors), lipases, cysteine-rich secretory proteins (CRISPs), antioxidants, and antimicrobial peptides (Mueller et al. 2004). In addition, *D. melanogaster* ejaculate contains two enzymes from the ejaculatory duct (esterase 6 and glucose dehydrogenase) that assist in sperm storage (Gilbert et al. 1981; Cavener & MacIntyre 1983; Iida & Cavener 2004) and an abundant ejaculatory bulb protein, PEB-me, which is a constituent of the mating plug (Ludwig et al. 1991; Lung & Wolfner 2001). Insect males also transfer other small molecules to females in the ejaculate: *Drosophila* males transfer lipids (e.g., Butterworth 1969; Brieger & Butterworth 1970) and phosphorus (Markow et al. 2001), and *Aedes* mosquito and male moths transfer juvenile hormone (Shirk et al. 1976; Shirk et al. 1980; Klowden & Chambers 1991; Borovsky et al. 1994).

p0170 Tissue targets for 16 Acps have been determined by immunostaining or by incubating sectioned females with labeled Acp (Monsma et al. 1990; Bertram et al. 1996; Lung & Wolfner 1999; Heifetz et al. 2000; Ottiger et al. 2000; Ding et al. 2003; Ravi Ram et al. 2005). Interestingly, each Acp has a unique set of target tissues: for example, the sperm-storage organs (Bertram et al. 1996; Bloch Qazi et al. 2003; Ravi Ram et al. 2005) and the ovary base (Heifetz et al. 2000; Ravi Ram et al. 2005). In addition, about half of Acps leave the female's reproductive tract to enter the circulatory system (Monsma et al. 1990; Lung & Wolfner 1999; Ravi Ram et al. 2005), and one of those has been shown to be capable of binding to the female's brain cells (Ottiger et al. 2000; Ding et al. 2003).

p0180 Genetic experiments in *D. melanogaster* have shown that Acps affect the female's physiology and behavior. Relative to normal matings, female mated to males lacking Acps fail to (i) increase their production, ovulation and laying of eggs (Kalb et al. 1993), (ii) store sperm at normal levels, and the few (~10%) sperm they do store are utilized at lower than normal rates (or not at all) for fertilization (Tram & Wolfner 1999; Xue & Noll 2000), (iii) become refractory

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to male courtship (Kalb et al. 1993; Xue & Noll 2000) and (iv) increase food intake (Carvalho et al. 2006). Sperm competition also is influenced by receipt of Acps by females (Harshman & Prout, 1994). Finally, Acps shorten female lifespan (Chapman et al. 1995; Wigby & Chapman 2005). Typically, Acps are only detectable within the female for several hours after mating, and their effects are transient, lasting for only 1 day (Monsma et al. 1990; Bertram et al. 1996; Ravi Ram et al. 2005). Some effects do persist longer, however (e.g., egg-laying and receptivity changes can persist for up to 2 weeks; Manning 1962). It is believed that stored sperm either trigger the continuation of these changes on their own through neural channels, as in *Anopheles* or in some Lepidoptera (Sugawara 1979; Klowden 2006) or by carrying and slowly releasing an Acp over time (shown for at least one *Drosophila* Acp; Peng et al. 2005a).

p0190 In some cases, specific insect seminal proteins have been shown to mediate particular postmating effects in females. For example, in *D. melanogaster*, experiments in which Acps are knocked out by mutation or knocked down by RNAi (Hannon 2002) in males or ectopically expressed in, or injected into, unmated females, have begun to elucidate Acp functions. Three examples are:

p0200 (i) *The sex peptide (Acp70A)* is a peptide hormone that appears to act from the circulatory system to induce oogenesis (Chen et al. 1988; Soller et al. 1997, 1999), stimulate postcopulatory feeding (Carvalho et al. 2006), decrease receptivity (Chen et al. 1988) and induce the transcription of some immune-response genes (Peng et al. 2005a). It has been implicated in the cost-of-mating (Wigby & Chapman 2005). In vitro, sex peptide can increase the production of a form of juvenile hormone (JHB3) by corpora allata (Moshitzky et al. 1996; Kubli 2003; Swanson 2003).

p0210 (ii) *The prohormone ovulin (Acp26Aa)* targets to the base of the ovaries and causes increased ovulation (Herndon & Wolfner 1995; Heifetz et al. 2000, 2005). Some ovulin also enters the female's circulatory system to go to sites as yet unidentified (Monsma et al. 1990; Lung & Wolfner 1999). Ovulin is cleaved three times within the reproductive tract (Monsma et al. 1990; Park & Wolfner 1995). Two of the resulting forms, including one with a short region of sequence similarity to a mollusk egg-laying hormone, can each independently induce female *Drosophila* to ovulate (Heifetz et al. 2005).

p0220 (iii) *Acp36DE* is a large glycoprotein that is essential for sperm entry into the sperm-storage organs (Bertram et al. 1996; Neubaum & Wolfner 1999a). Acp36DE binds to sperm and enters storage with them (Bertram et al. 1996; Bloch Qazi & Wolfner 2003), but the nature and function of this binding, as well as the means by which it influences sperm storage, are unknown.

s0080 ### 7.2.3 EFI and female immune response

p0230 Any female response to invasion by microbes during mating must be carefully regulated to avoid prematurely attacking non-self proteins (e.g., seminal proteins) and cells (e.g., sperm) that are essential for fertility. Evidence suggests that seminal proteins modulate the female's immune response, both positively and negatively (e.g., Robertson et al. 2003; Fedorka et al. 2004, 2007; Fedorka & Zuk 2005; Lawniczak et al. 2007; but see Schwarzenbach et al. 2005).

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Male reproductive tracts of diverse taxa (e.g., rats, humans, *Drosophila*) synthesize peptides thought, or known, to have antimicrobial activity (Samakovlis et al. 1991; Li et al. 2001; Lung et al. 2001; Yamaguchi et al. 2002). These peptides could protect the female's reproductive tract and/or the male's sperm from microbes introduced during mating or from resident microbes whose growth was stimulated by sugars or other molecules in the ejaculate. They could also protect laid eggs or young from infection (Marchini et al. 1991, 1997). In addition, Acps and sperm have each been shown in *Drosophila* to induce the expression of eleven antimicrobial peptide genes in females (and to repress two others) (McGraw et al. 2004; Peng et al. 2005b). Finally, several ejaculate proteins, identified in diverse taxa (e.g., hamster, mouse, rat, *Drosophila*), may be protective against redox damage to the female tract or to the sperm (Perry et al. 1993; Vernet et al. 1996; Chen et al. 2002; Mueller et al. 2004).

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7.2.4 Ejaculate-induced modification of female reproductive tract conformation

p0240 The female reproductive tract in many organisms undergoes changes in conformation after mating. These changes have the potential to facilitate the movement of sperm, or their storage, and the movement of eggs. In a few cases, ejaculate components have been shown to play a role in these changes.

p0250 In *Drosophila*, mating induces a series of stereotyped changes in the shape of the female's reproductive tract (Adams & Wolfner 2007; Figure 7.1). Prior to mating, the lumen of the reproductive tract is tightly closed and a flap of tissue covers the openings to the sperm-storage organs. After mating, the lumen opens and straightens and the flap of tissue is moved away from the openings to the storage organs. Induced muscle contractions may also push the mass of sperm toward the sites of storage. Acps trigger these changes, whereas sperm do not.

p0260 An analogous reproductive process occurs when an hermaphroditic snail stabs its sexual partner with a calcareous 'love dart'. The dart is fired toward the end of courtship, prior to copulation. It has no impact on either the decision to copulate or the size of the ensuing sperm donation (Adamo & Chase 1988; Chase & Vaga 2006). However, snails with good aim more than double the average number of donated sperm stored by the recipient (Rogers & Chase 2001; Chase & Blanchard 2006) and correspondingly increase their paternity when competing against an unsuccessful shooter (Landolfa et al. 2001; Rogers & Chase 2002). These effects are mediated by an allohormone (likely a peptide) transferred in mucus coating the dart (Koene & ter Maat 2001). In the brown garden snail, *Cantareus aspersus*, 99.98% of sperm transferred is digested by enzymes within the bursa copulatrix of the recipient (Rogers & Chase 2001). In vitro experiments revealed that the dart's mucus induces muscle contractions that reconfigure the copulatory canal by closing off the tract leading to the bursa and making the spermathecal sacs more accessible to sperm (Koene & Chase 1998). A similar use of allohormones may take place when the hermaphroditic earthworm *Lumbricus terrestris* uses its numerous copulatory setae to pierce its partner's

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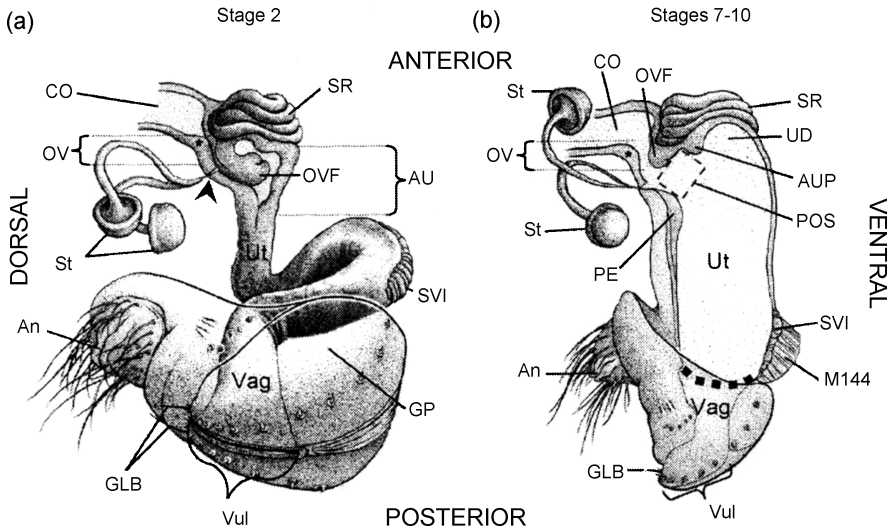

f0010 **Figure 7.1** Seminal proteins can trigger dramatic changes in the conformation of the lower reproductive tract of wild type (Oregon R) *Drosophila melanogaster* females. (a) At the start of ejaculate transfer, the uterus (Ut) is contracted and forms a loop at the specialized vaginal intima (Miller 1950; SVI). In addition, the uterus is bent laterally above the SVI such that, in the drawing, the SVI and vagina (Vag) appear to project toward the reader at a 45° angle to the plane of the page. Within the anterior uterus (AU), the oviduct valve flap (OVF) is curled posterio-ventrally, covering the openings to the spermathecal ducts (filled arrowhead; note that only the AU and common oviduct (CO) are shown in cross section in this drawing, the rest of the reproductive tract is shown only from the exterior). (b) During the later stages of sperm storage, the uterus is fully expanded and turgid. In the anterior uterus, the pre-oviduct space (POS) forms between the anterior portion of the papillate elevation (Miller 1950; PE), the anterior uterus projection (AUP), and the oviduct valve flap, which has uncurled. In this drawing, for clarity, the oviduct valve (OV) is shown open, although in most instances the OVF contacts a ridge in the dorsal oviduct wall (*) just above the openings to the spermathecal ducts, closing the OV. The dashed line denotes the margin between the uterus and Vagina. An, anus; GLB, gonopod long bristle(s); GP, gonopod plate; M144, muscle 144 (Miller 1950) attached to the SVI; St, spermatheca; SR, seminal receptacle; UD, uterine dome; Vul, vulva. (The female accessory glands, or parovaria, have been omitted from these drawings. Drawings by Anthony Yori.) Reproduced with permission from Adams and Wolfner (2007).

skin and inject a substance from its setal glands (Koene et al. 2005). This manner of delivery may have been favored as an alternative to the delivery of seminal fluid in order to access critical anatomical structures that semen cannot contact (Chase & Blanchard 2006) or because there are advantages of inducing the physiological responses prior to the transfer of ejaculate.

p0270 Ejaculate components can also produce more extreme conformational changes via the formation of mating plugs. These plugs can occlude the

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reproductive tract or change its shape in ways that prevent subsequent mating or sperm entry/storage (insects: Thornhill & Alcock 1983; mammals: Dewsbury 1988). Interesting in this regard are the semenogelins, which are abundant seminal proteins of primates (Lilja et al. 1989). Semenogelins initially form a coagulum in the ejaculate, and are the major components of the mating plug (Roussel & Austin 1967; Peter et al. 1998). Subsequently, they are cleaved by kallikrein-3 (also called prostate specific antigen, PSA) in the ejaculate (Lilja 1985). Semenogelin I has also been shown to inhibit sperm motility and capacitation (Robert & Gagnon 1999; de Lamirande et al. 2001). Mating plugs may also facilitate the movement of sperm into storage by serving as a scaffold along which sperm can migrate (Bairati & Perotti 1970; Polak et al. 2001). Mechanisms underlying mating plug formation have not been well studied, but may frequently include an interaction between conditions or molecules in the female and ejaculate molecules from the male.

s0100

7.2.5 EFIs mediating sperm transport

p0280 Even in externally fertilizing species, SFIs may mediate the ability of sperm to reach eggs. For example, the sperm of salmonids swim faster and live significantly longer in the presence of ovarian fluid, which is present in a spawn (Lahnsteiner 2002; Turner & Montgomerie 2002). It seems likely that structural complexity of the female tract and the protracted survival of sperm, relative to the aqueous environment of external fertilization, will enhance the scope for complex EFIs and SFIs impacting sperm motility and transport. Three relevant interactions have been demonstrated: (1) seminal plasma can alter the penetrability of mucus within the female tract in mammals; (2) seminal plasma can induce contraction of reproductive tract muscles that facilitate sperm transport; and (3) sperm surface proteins (or other components) may interact with the female tract to influence sperm transport.

p0290 In the case of vaginally inseminating mammals (e.g., humans, cattle), sperm rapidly enter the cervical canal, where they encounter large volumes of cervical mucus. There is evidence from humans that components of seminal plasma facilitate penetration of sperm into cervical mucus (Overstreet et al. 1980). Despite this facilitation, however, sperm that cannot swim properly are less successful at penetrating the mucus and thus the mucus may serve to select for vigorously motile sperm (Hanson & Overstreet 1981; Barros et al. 1984; Katz et al. 1990, 1997).

p0300 Once past the cervix, mammal sperm must traverse the uterus. There is evidence for some species that seminal plasma components, including prostaglandins, stimulate uterine contractions capable of transporting sperm rapidly through the uterus (e.g., Claus 1990; Crane & Martin 1991; Fouchecourt et al. 2002; Langendijk et al. 2005; similarly, for insects see Loher et al. 1981; Stanley 2006). Because coitus induces infiltration of the uterine cavity by leukocytes, which have been observed phagocytizing uterine sperm in mice, rats and rabbits (Austin 1957; Bedford 1965), rapid transport of sperm through the uterus is advantageous.

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p0310 In *Drosophila*, Acps also regulate muscle contraction of the female reproductive tract during sperm storage (Adams & Wolfner 2007) and ovulation (Heifetz & Wolfner 2004). The insect female tract is rich in vesicles that can contain neuromodulators (Heifetz & Wolfner 2004), and at least one such neuromodulator (i.e., octopamine) can modify muscle contraction in oviducts of cockroaches, grasshoppers and *Drosophila* (Orchard & Lange 1985; Bamji & Orchard 1995; Lee et al. 2003; Monastirioti 2003; Cole et al. 2005; Middleton et al. 2006). Receipt of Acps regulates the release of the contents of vesicles at nerve termini that innervate the reproductive tract (Heifetz & Wolfner 2004), stimulating release of their contents in some regions and inhibiting their release in others. This interaction may underlie the muscle contractions that lead to conformational changes (Adams & Wolfner 2007). Receipt of sperm also can, independently, modulate release of some vesicles (Heifetz & Wolfner 2004), although sperm do not trigger the large-scale muscular contractions (Adams & Wolfner 2007).

p0320 Biochemical SFIs can also be critical for successful sperm transport. For example, despite having sperm with normal morphology and motility, male mice that lack fertilin β (Cho et al. 1998), testis-specific angiotensin-converting enzyme (ACE) (Krege et al. 1995; Hagaman et al. 1998) or calmegin (Ikawa et al. 1997; Yamagata et al. 2002) are infertile because their sperm cannot pass through the uterotubal junction. Fertilin β is normally localized on the plasma membrane overlying the acrosome on mature sperm from wild-type males (Cho et al. 1998). There is evidence that ACE has an enzymatic effect on the surface of maturing sperm in the testis that somehow enables them to pass through the uterotubal junction (Metayer et al. 2002). Similarly, there is evidence that calmegin is a chaperone protein that operates during spermatogenesis in the testis to ensure the proper folding and transport of proteins to the sperm plasma membrane. The inability of the sperm of all three mutant mice to pass through the uterotubal junction indicates that specific sperm surface proteins are required to gain access to the oviduct. The role of calmegin in enabling sperm to pass into the oviduct was examined using chimeric males that produced an equal mixture of sperm with wild-type and disrupted calmegin genes. When these males were mated with wild-type females, the presence of wild-type sperm did not 'rescue' the null mutant sperm, as only wild-type sperm could be found within the oviduct (Nakanishi et al. 2004). Thus, proteins on the sperm surface do not appear to assist passage by signaling the uterotubal junction to open; rather, it is likely that a particular (set of) surface protein(s) is required by each sperm in order to pass through the junction (Nakanishi et al. 2004).

p0330 SFIs of the kind described above may be widespread. For example, the removal of surface-associated proteins from chicken sperm brought about no detectable change in their viability or motility, but impeded the ability of the sperm to migrate through the chicken vagina (Steele & Wishart 1996a, 1996b). Various experimental treatments to remove surface proteins severely limited the ability of sperm to reach the infundibulum or the sperm-storage tubules (SSTs) located in the uterovaginal junction following intravaginal insemination. However, the treated sperm performed these functions as well as untreated control sperm

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following insemination directly into the uterovaginal region (Steele & Wishart 1996a, 1996b). Additionally, in the compound ascidian, *Diplosoma listerianum*, the female oviduct has been shown to 'assess' sperm surface proteins and block passage of genetically incompatible sperm to the ovary (Bishop 1996; Bishop et al. 1996). At a localized region of the oviduct, those sperm sharing self-recognition markers with the maternal tissue are removed via immune-like phagocytotic processes (Bishop 1996; Bishop et al. 1996). It is noteworthy that this system also serves to bias fertilization against sperm of unrelated males presumably sharing the recognition markers (Bishop et al. 1996) and, remarkably, in favor of sperm of genotypes that are underrepresented in the population (a 'rare male effect'; Pemberton et al. 2003). Finally, Watnick et al. (2003) postulate SFI as the reason why *D. melanogaster* males bearing a null mutation for the polycystin-2 homologue PKD2 (*amo*) gene exhibit nearly complete sterility. The *amo* males transferred normal amounts of motile sperm to females, but mutant sperm failed either to enter or to remain stored within the females' sperm-storage organs (Gao et al. 2003; Watnick et al. 2003).

s0110

7.2.6 EFIs mediating sperm storage and utilization

p0340 Females of most species possess one or more specialized organs for storing sperm, typically referred to as a spermatheca (general reviews: Walker 1980; Birkhead & Møller 1993; Eberhard 1996; Neubaum & Wolfner 1999b). As a consequence of storage within these specialized organs, sperm may survive within females for as long as 10 weeks in some birds (typically about 10 days; (Birkhead & Møller 1992a, 1993), for months and perhaps as long as a year in internally fertilizing frogs (Sever et al. 2001, 2003), for several years in reptiles (Olsson & Madsen 1998), for months to years in some sharks (Pratt 1993), and typically for weeks or months in many insects (Parker 1970), though some ants hold the record of approximately 30 years (Pamilo 1991).

p0350 Marsupial mammals (and some insectivores) have distinct sperm-storage structures in the form of tubules or saccules in the oviduct (sperm in these taxa do not bind to the female epithelium; see below). Eutherian mammals present an exception to the general rule of specialized female sperm-storage organs, with females lacking a spermatheca and sperm usually surviving within the female for only a few days (Gomendio et al. 1998; note that bats are an exception, with sperm surviving up to 198 days in some species: Racey & Entwistle 2000).

p0360 Because prolonged sperm storage uncouples copulation and fertilization, variation among species in female sperm-storage attributes bears an integral relationship with variation in numerous other aspects of breeding biology and ecology. Prolonged survival of sperm, combined with multiple mating by females, facilitates postcopulatory sexual selection (Parker 1970; Smith 1984; Birkhead & Møller 1998b; Simmons 2001; Arnqvist 2004; see Chapter 6 of this volume). Prolonged sperm storage also necessitates EFIs, as the female must provide protection and nutrition to sperm. The spermathecae of virtually all taxa have associated specialized secretory glands or cells (e.g., Fritz & Turner

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2002). Although not yet well understood, spermathecal secretions have been demonstrated to contain various sugars, glycoproteins and antioxidants that interact with sperm membranes and likely contribute to sperm maturation and survival (e.g., Davey & Webster 1967; Alumot et al. 1969; Giuffrida et al. 1996; Uhl 1996; Weirich et al. 2002; Collins et al. 2004; Klenk et al. 2004). Non-sperm components of the ejaculate can also be critical for complete or efficient sperm survival while stored within the female (e.g., Tram & Wolfner 1999; Xue & Noll 2000).

p0370 In numerous cases, sperm are found to interact intimately with epithelial cells lining the female's reproductive tract. One of the more spectacular examples is found in scale insects. Despite females having a specialized spermatheca in which sperm may be stored for several days, the sperm eventually migrate up the oviducts and then are again stored within specialized 'vestibule cells' until oocytes have completed meiosis. Mated females possess one vestibule cell per mature ovariole, and each vestibule cell may contain more than one spermatozoon. Within the cell, the sperm are wrapped around, and can be observed swimming around, the cell's nucleus (Figure 7.2d; Robison 1970; see Chapter 13 of this volume for discussion of possible evolutionary significance). Similarly, Pijnacker and Drenth-Dephuis (1973, as cited in Thomas & Zeh 1984) present evidence that, in a spider mite, the sperm enter cells lining the wall of the seminal receptacle and then are transported to the hemolymph, from which they arrive at the ovaries.

p0380 Whereas sperm entry into female somatic cells appears to be a rare phenomenon, there are numerous examples of sperm either binding to or becoming embedded within female epithelial cells. Examples include the polychaete worm *Spirorbis spirorbis* (Figure 7.2c; Daly & Golding 1977; Picard 1980), the gastropod snail *Cochlostoma montanum* (Giusti & Selmi 1985), the brooding clam *Mysella tumida* (Figure 7.2e and f; Ó Foighil 1985), the isopod crustacean *Porcellio laevis* (Longo et al. 1998), the hard tick *Dermacentor andersoni* (Brinton et al. 1974), the tailed frog *Ascaphus truei* (Sever et al. 2001), the garter snake *Thamnophis sirtalis* (Hoffman & Wimsatt 1972) and a variety of eutherian mammals (below). In the case of the clam *M. tumida*, fertilization and brooding of young takes place within the suprabranchial chamber. After entering a female clam, sperm adhere to the gill lamellae by interdigitation of sperm acrosomal microvilli with gill epithelium microvilli (Figure 7.2e and f; Foighil 1985).

p0390 The physiological details of sperm–female binding have been the subject of intense study in eutherian mammals, for which sperm collect in the uterus, uterotubal junction and/or caudal isthmus of the oviduct (the 'sperm reservoir'; Figure 7.2a and b; Yanagimachi & Chang 1963; Racey et al. 1987; Suarez 2003). Sperm are held in the reservoir by binding to the epithelium lining the lumen. Motile sperm have been observed to bind by their heads to the apical surface of the oviductal epithelium in cattle (Figure 7.2a; Suarez et al. 1990), mice (Suarez 1987), hamsters (Smith & Yanagimachi 1991), pigs (Suarez et al. 1991), horses (Thomas et al. 1994), and dogs (Petrunkina et al. 2004) and in the uterus and uterotubal junction in bats (Figure 7.2b; Racey & Potts 1970; Racey 1979;

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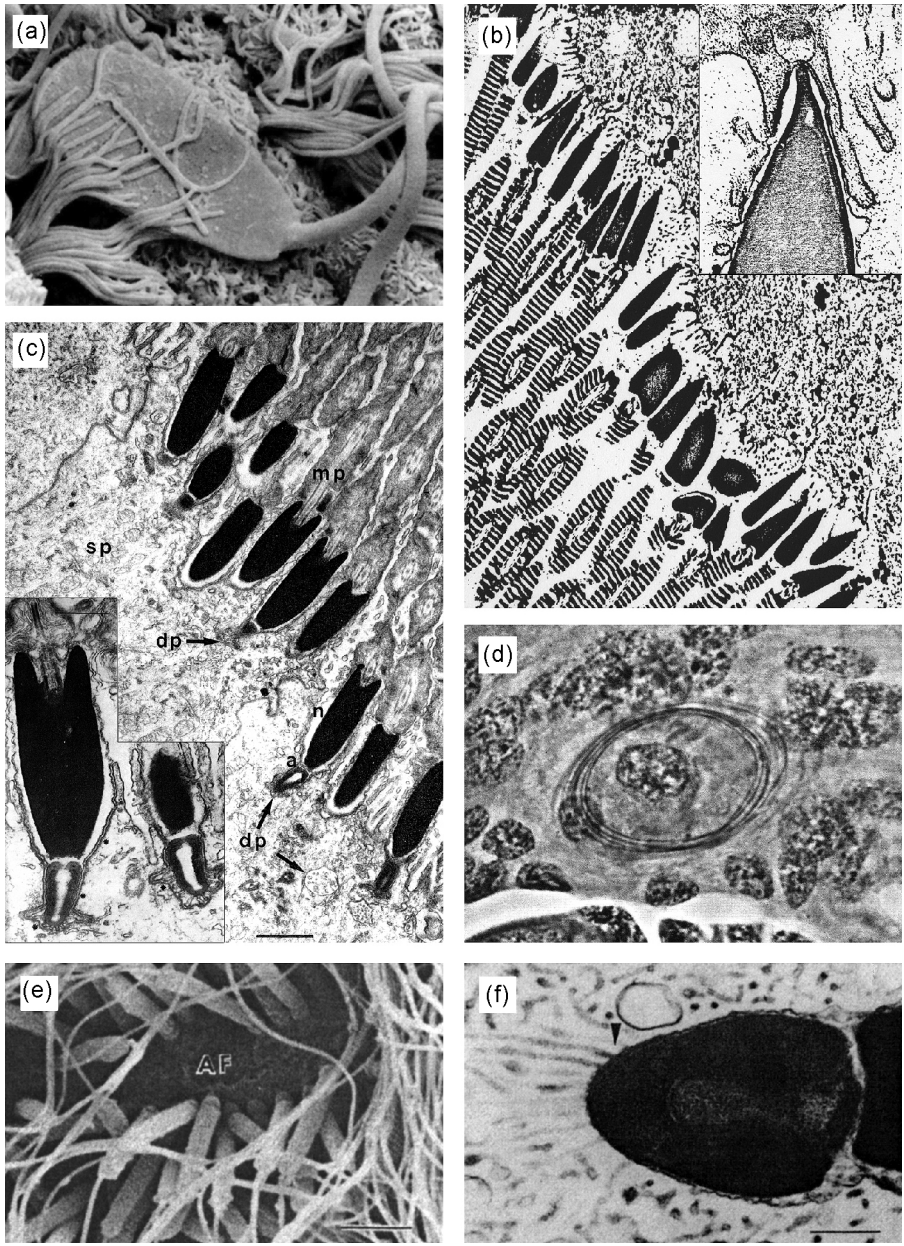

f0020 **Figure 7.2** Sperm can interact intimately with the epithelia of the female reproductive tract while in storage across diverse taxa.
(a) Scanning electron micrograph (SEM) of bovine sperm cell associated with the cilia of the mucosal epithelium of the oviductal isthmus (bar = 1 μm). (b) Transmission electron micrograph (TEM) of sperm embedded by their heads to the uterine epithelium from a

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Andreuccetti et al. 1984; Racey et al. 1987). Binding involves carbohydrate recognition; that is, proteins coating the sperm head recognize carbohydrate moieties on the surface of the oviductal epithelium (DeMott et al. 1995; Lefebvre et al. 1997; Green et al. 2001). Sperm fertility and motility are maintained longer in vitro if the sperm are incubated with oviductal epithelium (cattle: Pollard et al. 1991; Chian & Sirard 1994; pig: Suarez et al. 1990; horse: Chian & Sirard 1994; human: Kervancioglu et al. 1994; and dog: Kawakami et al. 2001), suggesting that the female reproductive tract provides substances that maintain sperm viability.

s0120

7.2.7 Female reproductive tract-induced modification of the ejaculate

p0400

Across a diversity of taxa, it is common for sperm to undergo biochemical, structural and/or behavioral modification within females. These changes may represent the completion of sperm maturation, activation of motility and/or modifications necessary to become fertilization competent. It is likely that conditions encountered by sperm within the female or, more commonly, specific female-derived molecules are the agent of change. However, the molecular mechanisms responsible for the modifications have been not been explored in most cases, and are universally unknown.

p0410

Among arthropods, sperm modification (sometimes referred to as 'capacitation', but see definition below for mammals) within the female is commonplace. Here we describe only a few of myriad interesting examples. In spiders and most other chelicerates, the sperm at insemination are quiescent and rolled into balls, with each sperm (or synspermia) surrounded by a secreted sheath (Figure 7.3b; Alberti 1990; Baccetti 1970; Michalik et al. 2004). After a variable number of days, the sperm capsule is lysed and the sperm flagellum unravels and becomes motile (Brown 1985). Although the activational triggers have not been identified, they are believed to be secretions from the female's spermathecal glands (Brown 1985; Eberhard & Huber 1998; Uhl 2002; Berendonck & Greven 2004).

hibernating *Pipistrellus kuhli* bat. Inset: longitudinal section of sperm head interacting with uterine cell. The tip is included in a plica of the cell surface, and plasma membrane at tip appears fused with membrane of uterine cell granule. (c) TEM of sperm heads embedded in cells at the base of the spermatheca in the polychaete worm *Spirorbis spirorbis* (bar = 1 μm); a, sperm acrosome; d.p., digitate processes from sperm head; m.p., sperm midpiece with flagellum and mitochondria; s.p., spermathecal cell cytoplasm. Inset: TEM showing areas of specialized contacts between sperm and spermathecal cell membrane with scalariform junctions (*) (bar = 0.5 μm). (d) Phase contrast micrograph of single sperm cell coiled around the nucleus of a specialized cell (vestibule cell) in the female reproductive tract of the scale insect, *Parlatoria oleae*. (e) SEM of sperm heads attached by acrosomal end to abfrontal gill epithelium (AF) in the brooding clam *Mysella tumida* (bar = 5 μm) and (f) TEM of median longitudinal section through acrosomal vesicle. Sperm cell microvilli are apparent as extensions of the plasmalemma (arrow) where it comes into proximity with underlying acrosomal vesicle (bar = 0.4 μm). Adopted with permission from (a) Lefebvre et al. (1995); (b) Andreuccetti et al. (1984); (c) Daly and Golding (1977); (d) Robison (1970); (e and f) Foighil (1985).

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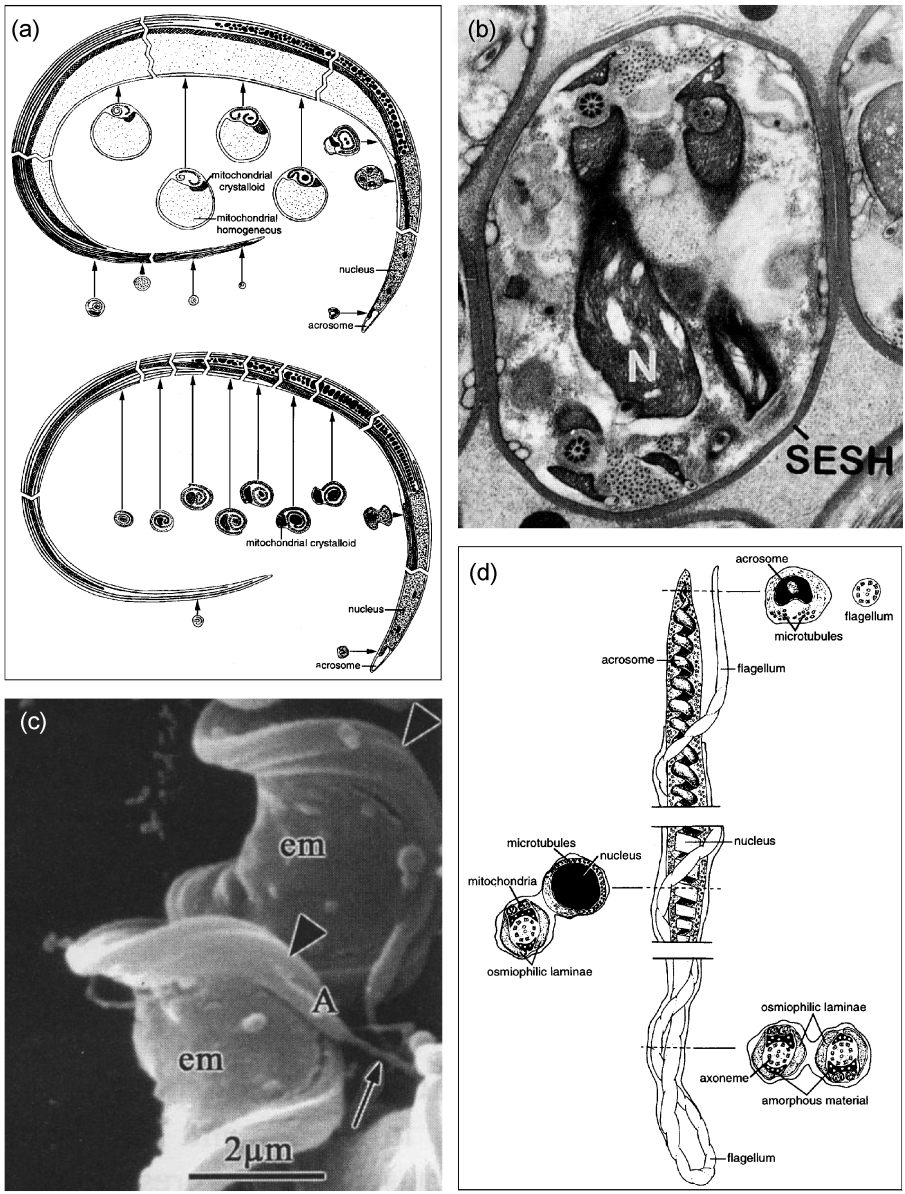

f0030 **Figure 7.3** Sperm frequently undergo modification within the female reproductive tract. (a) Illustration of sperm of the fungus gnat, *Sciara coprophila*, from the testis (top) and following 2 days of storage within the female spermatheca (bottom). (b) A synspermium (sperm capsule containing syncytial spermatozoa) of the spider *Segestria senoculata*. Note bases of three (of four) axonemes. Within the female's spermatheca, the secretion sheath (SESH) is digested, the sperm unravel and become motile; N, nucleus. (c) SEM of the discoidal sperm structures from the deferent ducts of males of the collembolan *Allacma*

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In a primitively wingless insect – the jumping bristletail *Machilis distincta* (order Archeognatha), sperm enter the female in an immotile state with the flagellum bent like a hairpin within a common plasma membrane (Figure 7.3d). It is only within the spermatheca that the sperm unfold and become motile (Dallai 1972 as cited in Jamieson et al. 1999). In another group of primitively wingless insects (order Collembola), sperm within spermatophores are coiled into flattened ellipsoids that surround a central extracellular cavity filled with a dense material (Dallai et al. 2003). During transformation within the female's spermatheca, the extracellular material is released as the sperm are transformed into filiform, motile cells (Figure 7.3c). Dallai et al. (2004) postulate that the membrane surrounding the central extracellular cavity is specialized for receiving and transmuting the signal from the female that induces transformation. In ticks, spermatid development is arrested in males. Within the female, the sperm essentially turn inside out, resulting in a doubling of length in some species, and development of the capacity for motility and penetration (Feldman-Muhsam & Filshie 1979; Oliver 1982).

p0420 One of the more remarkable examples of sperm capacitation within females takes place in the fungus gnat *Sciara coprophila*, which also exhibits one of the most bizarre forms of sperm ultrastructure (Phillips 1966, 1970). Whereas the flagellum of most insect sperm have a 9 + 9 + 2 axonemal structure (i.e., nine accessory tubules, nine doublets and two central microtubules; Jamieson et al. 1999), the axoneme of *S. coprophila* consists of approximately 70 doublet microtubules, each with an associated singlet tubule, arranged in a spiral. In addition, there is only a single mitochondrial derivative, which extends most of the length of the sperm. The largest portion of the derivative (and indeed of the entire cell) is a large homogenous mass of proteinacious material (Figure 7.3a, top). After arriving in the female's spermatheca, the sperm slough off this homogeneous material, along with the mitochondrial cristae (Figure 7.3a, bottom), so that this material occupies most of the volume of the spermatheca (Makielski 1966; Phillips 1966). The function and fate of this material inside the female is unknown. In addition, the crystalloid component of the mitochondrial derivative that is retained by the sperm is repositioned, and the axoneme uncoils and subsequently recoils into a spiral that is the mirror image of the arrangement observed in sperm from the testes (Figure 7.3a). Finally, the transformed sperm remain in an inactive state within the spermatheca until (it is presumed) the female activates them immediately prior to oviposition (Phillips 1966).

fusca. The flagellum forms almost three complete loops around the periphery (arrowheads) that surrounds an extracellular cavity filled with dense material (em). A long, slender peduncle emerges from the acrosome of each sperm. Within the female, the peduncle is lost and the sperm unrolls, releasing the extracellular material. (d) Sperm of jumping bristletail, *Machilis distincta*, from female spermatheca but prior to transformation. Adopted with permission from (a) Phillips (1966); (b) Alberti (2000); (c) Dallai et al. (2003); (d) Dallai (1972).

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p0430 Sperm capacitation and hyperactivation within females is apparently universal among mammals (Suarez 2003). Capacitation involves changes in the plasma membrane, such as loss of proteins and cholesterol, which prepare sperm to undergo the acrosome reaction and fertilize oocytes. Hyperactivation is a change in the pattern of flagellar beating that involves increased flagellar bend amplitude and, usually, increased asymmetry of the beat (Ho & Suarez 2001; Suarez & Ho 2003; see Chapter 5 of this volume). It has been postulated that both of these modifications are interrelated with sperm binding to, and release from, the oviductal epithelium (Suarez 2006). Specifically, observations indicate that capacitation-induced changes in the sperm head surface are responsible for reduction of binding affinity with the epithelium, and hyperactivation provides the force necessary for the bound sperm to detach from the epithelium (Smith & Yanagimachi 1991; DeMott & Suarez 1992; Lefebvre & Suarez 1996; Suarez & Ho 2003).

p0440 Although the specific mechanisms triggering capacitation and hyperactivation are unknown, SFIs involving factors secreted by the female epithelium are likely candidates. Oviduct-specific proteins and glycoproteins have been demonstrated to bind to sperm in brushtail possum (Sidhu et al. 1999a), hamster (Boatman & Magnoni 1995), sheep (Sutton et al. 1984), horse (Ellington et al. 1993b), bull (McNutt et al. 1992; King & Killian 1994; Lapointe & Sirard 1996; Lapointe et al. 1998) and humans (Lippes & Wagh 1989). Moreover, factors in oviductal fluid enhance capacitation of sperm in vitro in the brushtail possum (Sidhu et al. 1999a, 1999b), the tammar wallaby (Sidhu et al. 1998), bull (Chian et al. 1995; Mahmoud & Parrish 1996), horse (Ellington et al. 1993a) and humans (Zhu et al. 1994).

p0450 Sperm are not the only ejaculatory component to undergo modification within the female. In *Drosophila*, at least three Acps (ovulin, Acp36DE and the sex peptide (Acp70A); Monsma & Wolfner 1988; Park & Wolfner 1995; Bertram et al. 1996; Peng et al. 2005a) are modified within the female, in this case by proteolytic cleavage. This modification requires contributions from both female and male (in addition to the Acp that is the target of the modification). Processing of ovulin and Acp36DE requires an Acp that is a predicted protease in the astacin family (Ravi Ram et al. 2006). Although this protease is made in the same tissue as both of its target Acps, it does not cleave these Acps until they have reached the female (Ravi Ram et al. 2006). Cleavage of Acps within a female could serve to activate an otherwise inactive molecule, or could be degradational, perhaps to limit the time that the Acp is present. For ovulin, some data suggest an activational role for the cleavage: ovulin's primary structure resembles that of a known prohormone (ELH: Scheller et al. 1982; Kaldany et al. 1985) to which it also has a very short region of sequence similarity (Monsma & Wolfner 1988; Heifetz et al. 2000). The two fragments of ovulin that are released by its cleavage each can stimulate ovulation (Heifetz et al. 2005).

p0460 *Drosophila* sex peptide also appears to undergo cleavage within the mated female. Sex peptide's C terminal half has been shown to be the active portion inducing changes in female egg productivity and receptivity (Schmidt et al. 1993). Peng et al. (2005a) showed that upon entry into the female, some sex

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peptide is bound to the sperm. Over several days, the C terminal region of the peptide gradually disappears from the sperm (Peng et al. 2005a). This observation and the observation that stored sperm are needed for the persistence of several postmating changes in females (Manning 1962, 1967), are consistent with a hypothesis that the C terminal region of sex peptide is released intact from sperm and can then enter the circulatory system of the female. Such 'slow release' of sex peptide from a protected storage would allow the effect of sex peptide to persist for several days after mating (free Acps are usually degraded in the female's reproductive tract within hours; Monsma et al. 1990; Bertram et al. 1996; Ravi Ram et al. 2005). Mutation to prevent cleavage releasing the C-terminal piece of sex peptide from the sperm eliminates the long-term persistence of sex peptide effects on egg production and remating (Peng et al. 2005a).

s0130

7.3 Rapid evolutionary diversification of ejaculate–female interaction traits

p0470

It is intuitive that sperm biochemistry, physiology and morphology correlate with the biology of fertilization (Franzén 1956; see Chapter 3 of this volume). For internally fertilizing species, the female reproductive tract is the principal selective environment for mature sperm. Were this environment evolutionarily static, sperm and other ejaculatory components would be expected to achieve some optimal design that maximizes fertilization efficiency and success. However, if the female reproductive tract is evolutionarily dynamic, then sperm and seminal proteins may be as well. Likewise, postcopulatory sexual selection, which may derive in part from antagonistic interactions with other males (or their sperm) and/or the female, may place a selective premium on evolutionary innovation of ejaculate characteristics (Arnqvist & Rowe 2005). Here we review evidence that ejaculate and female tract traits likely to participate in EFIs are rapidly divergent.

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7.3.1 Ejaculatory proteins

p0480

Seminal proteins as a class exhibit remarkable evolutionary dynamics. Although functional classes of seminal proteins appear to be conserved across organisms, the primary sequences of a surprisingly high number of seminal proteins show rapid evolutionary change (e.g., Wyckoff et al. 2000; Swanson et al. 2001a; Swanson & Vacquier 2002; Jensen-Seaman & Li 2003; Dorus et al. 2004). For example in *Drosophila*, gene sequences of ~17% of Acps show characteristics of positive selection (regions with $dn/ds > 1$ see Chapters 8 and 11) when compared between the closely related species *D. melanogaster* and *D. simulans* (2–3 My apart) (Swanson et al. 2001a; Mueller et al. 2005), a percentage far higher than that of nonreproductive genes between these species (Swanson et al. 2001a). There is also evidence that there are a few Acps found in *D. simulans* that are not in *D. melanogaster* (Swanson et al. 2001a; Begun & Lindfors 2005;

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Mueller et al. 2005). Analogous rapid evolution of Acps has been shown for sister *Drosophila* species in the repleta group (Wagstaff & Begun 2005). Moving yet further away in evolutionary time, 42% of *D. melanogaster* Acps have no apparent ortholog in *D. pseudoobscura* (~30 My from *D. melanogaster*) (Mueller et al. 2005) and orthologs in the honeybee, *Apis mellifera*, are extremely rare (Collins et al. 2006). Consistent with rapid between-species evolution, there is also evidence that several Acps have experienced recent directional, or balancing, selection within species (Aguadé et al. 1992; Cirera & Aguadé 1997, 1998a, 1998b; Tsaur & Wu 1997; Tsaur et al. 1998; Aguadé 1999; Begun et al. 2000; Swanson et al. 2001a; Holloway & Begun 2004; Kern et al. 2004; Stevison et al. 2004; Begun & Lindfors 2005; Mueller et al. 2005; Schully & Hellberg 2006). Signs of positive selection are also seen for some Acps in the field cricket (Andrés et al. 2006).

p0490 Although an unusually high proportion of Acps show signs of rapid evolution, this is not characteristic of all Acps. For example, the sex peptide, which was discussed earlier as eliciting several postmating responses in *Drosophila* females, appears to be conserved both at the sequence level and in bioassays, although in one *Drosophila* lineage there is evidence of adaptive divergence following gene duplication (Cirera & Aguadé 1997, 1998a, 1998b). For example, injecting *Drosophila melanogaster* sex peptide into female *Helicoverpa armigera* moths suppresses sex pheromone production (Fan et al. 1999, 2000) and can stimulate juvenile hormone synthesis by those moths (Fan et al. 1999) (analogous to the stimulation of JHB3 synthesis in corpora allata of *D. melanogaster*, by sex peptide in vitro; Moshitzky et al. 1996). Moreover, molecules with immunoreactivity to sex peptide are found in male accessory glands of *H. armigera* (Nagalakshmi et al. 2004).

p0500 Rapid evolution of some seminal proteins is also seen in mammals. For example, the sequence of semenogelin genes in primates shows unusual evolutionary characteristics (e.g., Wyckoff et al. 2000; Jensen-Seaman & Li 2003; Kingan et al. 2003; Dorus et al. 2004). First, there is evidence of selective sweeps at semenogelin in some lineages, suggesting that certain alleles of semenogelins were advantageous. Second, the SEMG2 gene of primates (which encodes semenogelin II) evolves rapidly in some lineages, particularly so in lineages with the highest levels of promiscuity or polyandry (e.g., chimpanzees). This pattern suggests semenogelin function may be important in sperm competition – consistent with the biochemical role of the semenogelin in mating plugs (see Section 7.2.4).

s0150 ### 7.3.2 Sperm proteins

p0510 Sperm proteins include a relatively large fraction that appears rapidly divergent (see Chapter 11 of this volume). For example, comparison between mouse and human tissue-specific orthologs found that sperm-specific proteins evolve more rapidly, with larger changes in protein size, than genes expressed in most other tissue types (Torgerson et al. 2002). In addition, X-linked sperm proteins were found to have an average nonsynonomous mutation rate almost twice as high as

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autosomal sperm genes, a pattern not found for genes expressed specifically in somatic cells types (Torgerson & Singh 2003). A study of positively selected genes in the genomes of human and chimpanzees reports 'the group of genes that show the strongest evidence for positive selection also includes a surprising number of genes . . . involved in spermatogenesis . . . [and] . . . genes with maximal expression in the testis tend to be enriched with positively selected genes' (Nielsen et al. 2005). Examination of sperm-specific protamine genes in primates has found further evidence of positive Darwinian selection (Rooney & Zhang 1999; Wyckoff et al. 2000). Studies of *Drosophila* also reveal a number of examples of rapid sperm protein evolution (see Chapter 11 of this volume). However, our understanding of EFIs and in particular their underlying mechanisms, in most cases, is insufficiently resolved to know whether any of these studies just described address EFI-relevant proteins.

p0520 One interesting study does however specifically implicate divergence of sperm proteins that interact with the female reproductive tract. As discussed above (see Section 7.2.5), the removal of surface-associated proteins from chicken sperm impeded their ability to migrate through the chicken vagina (Steele & Wishart 1996a, 1996b). Evidence that these sperm-associated proteins are rapidly divergent comes from a similar analysis of heterospecific SFI. Turkey sperm exhibit similar morphological features and motility characteristics to chicken sperm, yet have a distinct surface antigenicity (Steele & Wishart 1992). When untreated turkey sperm were artificially inseminated into the vagina of chicken hens, they failed to reach infundibulum and were only occasionally found within the SSTs. By contrast, when inseminated directly into the uterovaginal junction, turkey sperm were able to populate the SSTs as well as chicken sperm (Steele & Wishart 1992).

s0160 ### 7.3.3 Other EFI mediators

p0530 Rapid evolution has also been found in carbohydrate binding groups. As described above for eutherian mammals (see Section 7.2.6), sperm binding to oviductal epithelium involves carbohydrate recognition. Although carbohydrate involvement in sperm binding appears widespread, the particular carbohydrate moiety involved varies among species (Dobrinski et al. 1996; Lefebvre et al. 1997; Green et al. 2001; Wagner et al. 2002).

p0540 The proteins responsible for binding bull sperm to oviductal epithelium have been identified as three closely related members of the bovine seminal plasma protein family (BSP). The three BSPs are secreted by the seminal vesicles and coat the heads of sperm during ejaculation. Each alone can bind sperm to the epithelium and extend the lifespan of sperm incubated with epithelial membranes in vitro (Gwathmey et al. 2006). Homologues have been identified in several eutherian mammals, although in some cases BSPs are synthesized by the epididymis rather than the seminal vesicles (Fan et al. 2006; Lefebvre et al. 2007). The divergence of carbohydrate binding specificities of sperm as well as the divergence of the BSP homologues implies divergence of sperm proteins that interact with the oviduct (Fan et al. 2006; Lefebvre et al. 2007).

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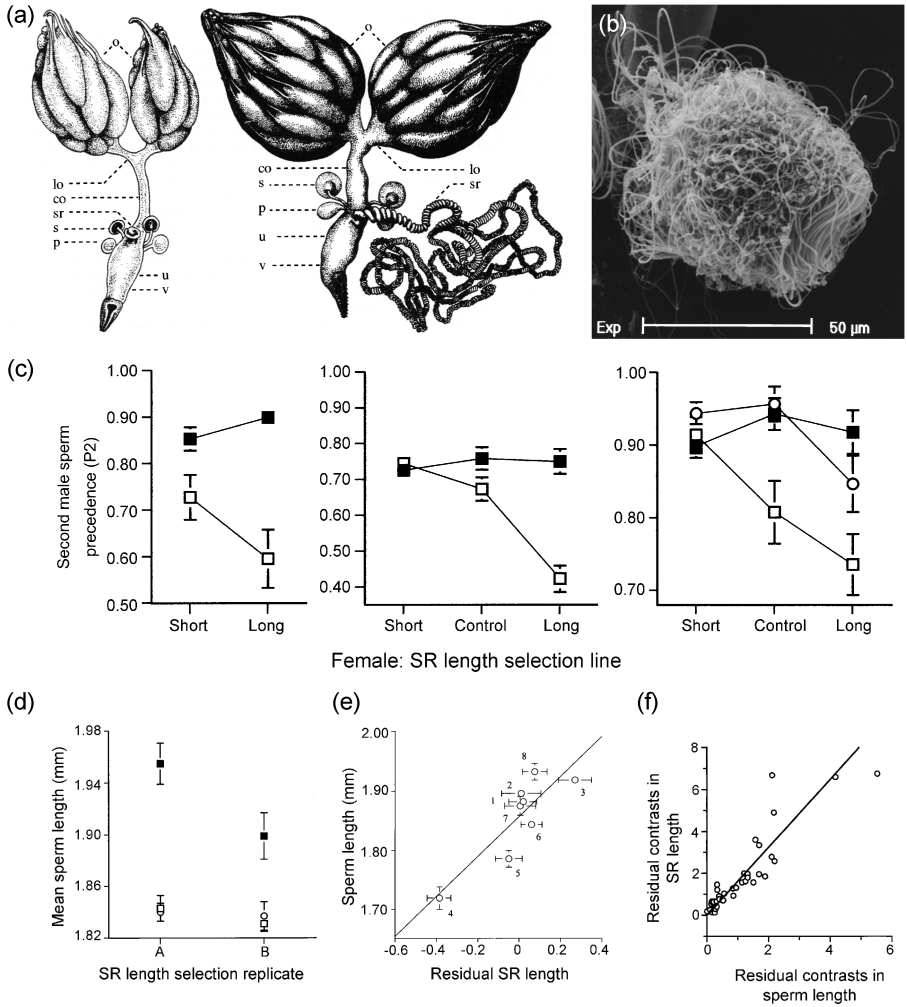

f0040 **Figure 7.4** There is a widespread pattern of coevolution between sperm morphology and female reproductive anatomy, illustrated here for sperm length and female seminal receptacle (SR) length among *Drosophila* species.
(a) Female reproductive tracts of *D. pseudoobscura* (left), which has a short seminal receptacle (SR; 0.41 mm) and short sperm (0.36 mm), and *D. bifurca*, which has the longest known SR (81.67 mm) and sperm (58.29 mm). (b) SEM of single *D. bifurca* spermatozoon dissected from a male's seminal vesicle, where sperm are individually rolled into compact balls; photo by R. Dallai. (c) An experimental evolution study with *D. melanogaster* reveals that the advantage to males of producing relatively long sperm (i.e. higher P_2) increases with female SR length (results of three experimental replicates shown; open squares, short-sperm selection line males; open circles, control-sperm selection line males; solid squares, long-sperm selection line males). (d) Experimental evolution for increased SR length consistently drives evolution of sperm length across two experimental replicates (a and b) in *D. melanogaster* (open squares, short-SR selection line; open

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s0170 ### 7.3.4 Sperm morphology

p0550 Spermatozoa are the most diverse cell type known, exhibiting dramatic evolutionary divergence in form in nearly all taxa. Because sperm diversity and diversification is covered in depth in Chapters 3 and 6 of this volume, we here only briefly address sperm length evolution in the genus *Drosophila*, because it has been the subject of a detailed investigation of the coevolution of sex-specific EFI traits (Figure 7.4; see Section 7.4). The sperm flagellum is more variable among *Drosophila* species than it is in the remainder of the animal kingdom. The sperm of *D. bifurca* are 58,290 ± 670 μm long (see Figure 7.4b; Pitnick et al. 1995b), which is over 400 times longer than those of *D. obscura* (long sperm morph are 139 ± 19 μm; (Joly & Bressac 1994). Comparative/phylogenetic analysis reveals that gigantic sperm have evolved independently numerous times (Pitnick et al. 1995a). In addition, sperm length divergence in nature can be sufficiently rapid to be diagnostic of different geographic populations within *Drosophila* species (Figure 7.4e; Snook 2001; Miller et al. 2003; Pitnick et al. 2003). Finally, evidence for the evolutionary liability of sperm length in *Drosophila* comes from an experimental evolution study that showed that this trait responds quickly and dramatically to selection (Miller & Pitnick 2002).

s0180 ### 7.3.5 Female reproductive tract morphology

p0560 Female reproductive tract morphology also appears to be rapidly divergent. This is particularly true for spermathecae and their ducts and glands, which can vary among species in virtually every attribute, including size, number, shape and structure (as well as in the biochemical environment within the spermathecae; e.g., Sever & Brizzi 1998). In some cases, females may even have more than one kind of sperm-storage organ (e.g., Pitnick et al. 1999; Presgraves et al. 1999). Within sperm-storage organs, there can be considerable substructure (e.g., Eberhard & Huber 1998; Beese & Baur 2006; Pattarini et al. 2006). As a result, sperm are frequently found to be highly organized in their distribution and orientation within the female organ(s) (e.g., Burger et al. 2006a, 2006b; Pattarini et al. 2006). Sperm of different males may further be differentially stored within different spermathecae (Otronen et al. 1997; Snow & Andrade 2005). Here we first describe some of the broadscale variation among a few taxa, and then discuss the few detailed studies of diversification in female spermathecal morphology among closely related species.

p0570 Baur (1998) describes the enormous variation observed among terrestrial pulmonate snails in the structure and morphology of the spermatheca,

circles, control-SR selection line; solid squares, long-SR selection line; bars = 1S.E.). (e) Sperm-SR coevolution occurs rapidly in nature, as indicated by variation among eight geographic populations of *D. mojavensis* (bars = 1S.E.). (f) This same pattern is found at the macroevolutionary level, illustrated here for 46 species, after controlling for allometry and phylogeny. Adopted with permission from (a and f) Pitnick et al. (1999); (b) Bjork and Pitnick (2006); (c and d) Miller and Pitnick (2002); (e) Pitnick et al. (2003).

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fertilization chamber and sperm-digesting organ. In female *Trigonephrus gypsinus*, sperm are stored within a 'fertilization pouch' that has no compartmentalization. In contrast, the pouch is divided into a separate spermatheca and fertilization chamber in other species. Further, the number of separate compartments or 'spermathecal tubules' within the spermatheca varies among species, with *Oxychilus draparnaudi* having one, *Succinea putris* having two, and *Drymaeus papyraceus* having 34.

p0580 Most spiders have a pair of one- or two-chambered spermathecae that have been characterized as having one of two generalized morphologies (Austad 1984). Haplogyne spiders are characterized as having 'cul-de-sac' spermathecae, with a single duct connecting the sperm-storage organ to the vagina. Entelegyne spiders are characterized as having 'conduit' spermathecae bearing two separate ducts, one for sperm entry into the spermatheca and a separate duct by which sperm leave for fertilization. Spider female reproductive tracts are notorious for their complexity and between-species variability, however, and comparative analyses indicate that female spider reproductive tract anatomy deviates markedly from any generalized expectation (Uhl 2002; Huber 2005; Burger et al. 2006b). There can also be great variation in spermathecae number. For example, female *Liphistius* spiders can have up to 40 spermathecae, and females in some mecysmaucheniid spider species have been found with up to 100 spermathecae (Eberhard 1985). In addition, other spider species possess an additional kind of sperm-storage organ having distinctly different glandular tissue (Uhl 2000).

p0590 Female birds store sperm within numerous long, thin blind-ended tubules found in the epithelium lining the junction of the uterus and the vagina. These sperm-storage tubules can be as short as 130 μm in the cedar waxwing and as long as 1000 μm in the turkey *Meleagris gallopavo*. There are also distinct species differences in the number of SSTs (from 500 to 20 000), the extent of tubule branching and in general shape (SSTs can be straight-walled, 'bud' shaped, or a series of sequential, interconnected buds) (Bakst 1987; Shugart 1988; Birkhead & Møller 1992b).

p0600 Some of the most comprehensive studies to date of variation among closely related species in their sperm-storage organ morphology has been in insects, particularly with robber flies (Asilidae; Figure 7.5a–f), carabid beetles (Liebherr & Kipling 1998), predaceous diving beetles (Dytiscidae; Figure 7.5g–k) and fruit flies (Drosophilidae; Figure 7.4). All *Drosophila* have a pair of spheroid spermathecae surrounded by a secretory, cellular envelope, each with a separate, slender and relatively short duct arising from the anterodorsal uterine wall. In addition, all *Drosophila* and certain other families of acalyptrate flies have evolved a second kind of organ specialized for sperm storage, the seminal receptacle (SR), which is a slender, blinded-ended tubule arising from the anteroventral uterine wall (Figure 7.4a; Nonidez 1920; Sturtevant 1925, 1926). Among *Drosophila* species, SR length varies from 0.23 to 81.67 mm (Joly & Bressac 1994; Pitnick et al. 1999). Like sperm length, SR length in *Drosophila* responds dramatically to selection (Miller et al. 2001; Miller & Pitnick 2003) and evolves so rapidly in nature that length of this organ is diagnostic of different geographic

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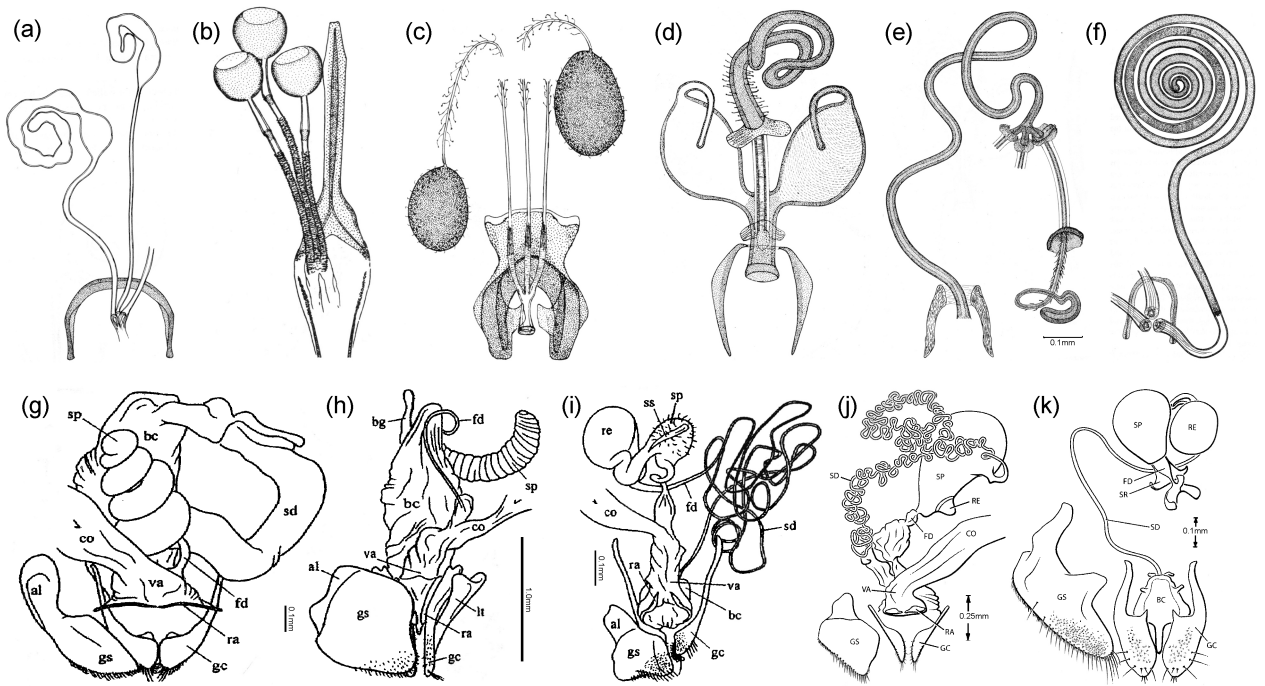

Figure 7.5 Female reproductive tract morphology can be evolutionarily rapidly divergent.
(a–f) illustrations of spermathecae of robber flies (Asilidae); note only one (e–f), two (a and c) or all three (b and d) of the three spermathecae are shown. (g–k) illustrations of female reproductive tracts and genitalia (less lateral oviducts and ovaries) of predaceous diving beetles (Dytiscidae). (a) *Ctenota molitrix*; (b) new genus A; (c) *Habropogon* species no. 1; (d) *Leptogaster* species no. 2, note: difference between center and lateral spermathecae; (e) *Leptogaster* species no. 1; (f) *Trichardis leucocoma*; (g) *Herophydrus* sp.; (h) *Hybius hypomelas*; (i) *Hemibidessus bifasciatus*; (j) *Hydroporus melsheimeri*; (k) *Macrovatellus mexicanus*. See Miller (2001; Table 1) for abbreviations. Adopted with permission (a–f) Theodor (1976); (g–i) Miller (2001); (j and k) Miller et al. (2006).

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f0050

populations within a species (Figure 7.4e; Miller et al. 2003; Pitnick et al. 2003). In addition, a study including 113 species found the paired spermathecae to be structurally vestigial with loss of sperm-storage function in 34% of species, the consequence of an estimated 13 independent evolutionary events. By contrast, only a single evolutionary loss of SR use was found (Pitnick et al. 1999).

p0610 Whereas females of nearly all robber flies have three spermathecae (some have only two), with all three typically of the same form (but see, e.g., Figure 7.5d), there is extraordinary among-species variation in nearly all aspects of spermathecal form (Figure 7.5a–f). In his beautifully illustrated monograph describing the spermathecal morphology of approximately 260 species from 85 genera, Theodor (1976) concludes: 'the differences are so marked in most cases that they are apparently of specific rank'.

p0620 An astonishing level of variation in female reproductive tracts, with substantive species-level differences indicative of rapid diversification, has also been found among dytiscid beetles and their relatives. Hundreds of species have been examined in detail, along with numerous outgroups (Mazzoldi 1996; DeMarzo 1997; Miller 2001; Miller et al. 2006). Across the family, there are very different states of overall configuration of the female reproductive tract, and numerous structures were found to discriminate among closely related species. There were extensive and complicated differences in shape and size of the bursa (including its absence) and the spermatheca, in addition to the spermathecal and fertilization ducts (Figure 7.5g–k). Staggering variation among species was also found for the presence, absence, number and size of secretory glands occurring on the spermatheca, receptacle, spermathecal duct and/or fertilization duct (Miller 2001; Miller et al. 2006). As described in Chapter 3 of this volume, it is noteworthy that dytiscid beetles also display some of the greatest within-family variation in sperm form and function ever identified (D. M. Higginson and S. Pitnick, unpublished data).

p0630 A variety of selection pressures likely contribute to diversification of sperm-storage organ morphology (Pitnick et al. 1999). Primary among these are sexual selection on females to control paternity, alternative responses to such selection and coevolution with interacting male traits (see Section 7.4; Walker 1980; Austad 1984; Eberhard 1985, 1996; Siva-Jothy 1987; Birkhead et al. 1993; Keller & Reeve 1995; Hellriegel & Ward 1998; Pitnick et al. 1999; but see Thomas & Zeh 1984, p. 209 for discussion of macrochelid mites). Postulating that the complexity and apparent selectivity of the female reproductive tract has arisen to challenge males (or more accurately, their ejaculates) as a form of cryptic female choice, Eberhard (1996, pp. 338–342) predicted that insemination ducts should be longer than fertilization ducts, when separate ducts are present, and tested this prediction with entelegyne spiders. He found insemination ducts to be longer in 314 species, shorter in 40 and of equal length in 6. Unfortunately, with few exceptions (e.g., Siva-Jothy 1987; Gack & Peschke 1994; Miller & Pitnick 2002; Pattarini et al. 2006), the functional relationship between female reproductive morphology and sperm precedence pattern is unknown for any species.

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7.4 Correlated evolution of ejaculate–female interaction traits

p0640 As described above, numerous (but not all) sperm, seminal fluid and female reproductive tract traits believed to participate in EFIs have been shown to evolve rapidly. Confirmation of EFIs, and evidence of their evolutionary significance, would come from demonstration that the interacting male and female traits exhibit correlated evolution across species. Such a pattern could result from selection acting on one sex only, followed by compensatory evolution by the other sex. For example, females could evolve changes in their reproductive tracts due to life history selection and ejaculates would evolutionarily track such changes. Alternatively, interacting ejaculate and female traits could mutually generate selective pressure on one another, resulting in a coevolutionary process (Andersson 1994; Arnqvist & Rowe 2005).

p0650 In most cases, only one of the participating traits (typically the male) in an EFI has been identified. For example, the *Drosophila* seminal fluid protein ovulin (see Section 7.2.2) might act directly on targets in the reproductive tract, as it binds to sites at the base of the ovaries (Heifetz et al. 2000). However, the female receptor for ovulin, or any other male-derived molecule, has not yet been identified. Hence, it is not yet possible to perform molecular evolutionary analyses to ascertain whether these EFI traits exhibit correlated evolution in the manner of a signal-receiver system. The only putative EFI traits for which we currently can conduct such analyses involve interacting morphologies of female sperm-storage organs and either sperm or spermatophores. In addition to these studies, we describe experimental evidence of reproductive failure in crosses between divergent populations or species, which provide indirect evidence for evolutionary EFIs.

p0660 An evolutionary EFI has been beautifully illustrated for the sperm-storage system of the rove beetle, *Aleochara curtula* (Gack & Peschke 1994; Förster et al. 1998). As for the majority of species, the phallus of male *A. curtula* cannot directly access the female's spermatheca (Eberhard 1985). However, males of this species have evolved a novel mechanism to displace resident sperm from within the spermatheca (Figure 7.6). Within the female, the ejaculate forms a spermatophore consisting of a rigid sperm sac and at least seven different layers of secretions (Förster et al. 1998). While still in copula, a dramatic transformation of the spermatophore begins, probably driven by osmotic processes. From the sperm sac, a primary tube emerges, which the male guides up the female's spermathecal duct using his endophallus (Gack & Peschke 1994). After mating concludes, the tube continues to grow. At the distal end of the spermathecal duct, the tube encounters and pushes through a narrow valve. Once inside the spermatheca, the end of the tube bursts and a secondary tube emerges through the rupture. The secondary tube continues to elongate, doubles back on itself after reaching the end of the spermatheca, and then inflates until it fills most or all of the organ. Suddenly, liquid containing densely packed spermatozoa rushes up through the tube and fills the swelling balloon. The female then actively contracts her

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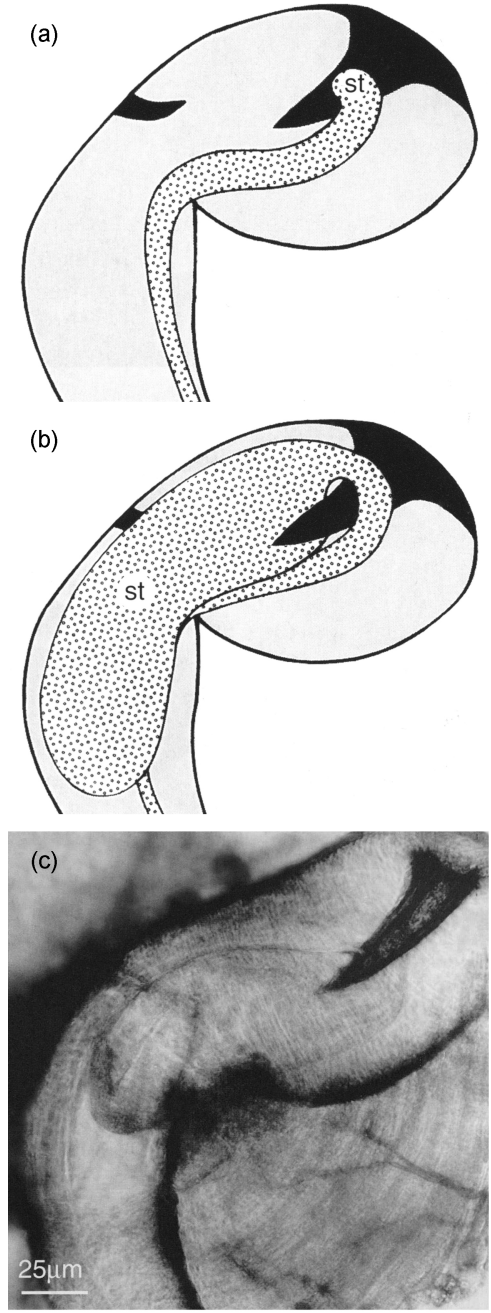

f0060 **Figure 7.6** Coevolution of spermatophore physiology and spermathecal morphology in the rove beetle, *Aleochara curtula*.

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spermathecal muscle causing two sharp, opposing, sclerotized spermathecal 'teeth' to shear though the wall of the balloon. Expansion and subsequent rupture of the balloon cause any sperm from previous matings to be backflushed through the valve and down the spermathecal duct (Gack & Peschke 1994; Förster et al. 1998).

p0670 A very different kind of evolutionary EFI involves the coevolution of sperm length and female sperm-storage organ morphology. Across diverse taxa, the total length of sperm exhibits correlated evolution with the dimension of the female sperm-storage organs and/or their ducts. Sperm length positively covaries with the length of the spermatheca in featherwing beetles (Dybas & Dybas 1981), with SR length in fruit flies (Figure 7.4e and f; Pitnick et al. 1999, 2003), with SR and spermathecal duct length in stalk-eyed flies (Presgraves et al. 1999), with spermathecal duct length in dungflies (Minder et al. 2005) and in moths (Morrow & Gage 2000), and with SST length in birds (Briskie and Montgomerie 1992; Briskie et al. 1997). The extreme example of the evolutionary consequences of such correlated evolution is found in the fruitfly *D. bifurca*, in which males produce nearly 6 cm long sperm (Pitnick et al. 1995b) and females have 8 cm long SRs (Pitnick et al. 1999; see Figure 7.4a and b).

p0680 The interpretation that sperm length and sperm-storage organ length coevolve is supported by an experimental evolution study with *D. melanogaster*, in which males with relatively short or long sperm were competed within females with relatively long or short SRs. Differential male fertilization success was largely determined by an interaction between sperm and SR length, such that the fitness advantage to males of producing relatively long sperm increased with increasing SR length (Figure 7.4c). Consistent with this result, evolutionary increases SR length were independently found to drive the evolution of sperm length (Figure 7.4d; Miller & Pitnick 2002). Subsequent experiments established that the length of competing sperm interact with the female tract to determine the probability of occupying a unique region of the organ from which sperm for fertilization are likely to come (Pattarini et al. 2006). Examination of geographic populations of *D. mojavensis*, thought to represent incipient species (Markow & Hocutt 1998), suggests similar coevolution is occurring in natural populations (Figure 7.4e; Pitnick et al. 2003). The experimental evolution studies further demonstrated substantive development time and longevity costs to females of having a relatively long SR (Miller & Pitnick 2003); the selective benefits to females underlying the evolution of long sperm-storage organs remains a mystery.

p0690 Indirect evidence of the correlated evolution of sex-specific EFI traits comes from experimental demonstration that normal EFI-controlled reproductive processes become dysfunctional in crosses between divergent populations. For example, in some *Drosophila* species, non-sperm components of the ejaculate trigger rapid secretion by the vaginal epithelium, resulting in an opaque mass that

(a) The elongating secondary tube (st) of the spermatophore reaches the blind end of the spermatheca and doubles back on itself; (b) the tube then balloons between the two spermathecal spines; (c) micrograph taken just prior to balloon popping and releasing sperm into the female organ. Adopted with permission from Gack and Peschke (1994).

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fills the uterus for several hours. Whether this mass is comprised of female- or male-derived molecules, or a combination is not known, nor is the function of the mass. Females do not oviposit or remate until this 'insemination reaction' subsides (Patterson 1946; Wheeler 1947; Lee 1950; Patterson & Stone 1952; Alonso-Pimentel et al. 1994). Early experiments by Patterson (1947) and Baker (1947) revealed that the insemination reaction, which usually persists 8–9 h in intraspecific matings, was larger and lasted longer in interspecific matings, sometimes remaining for several days. Recent experiments with both *D. mojavensis* and *D. arizonae* found insemination reactions to be consistently larger and/or of longer duration in interpopulation relative to intrapopulation matings. This pattern suggests rapid biochemical coevolution between the sexes in this EFI, with independent trajectories in isolated populations (Knowles & Markow 2001). Crosses between male and female *D. mojavensis* from different geographic populations also implicates evolutionary EFIs influencing egg volume (Pitnick et al. 2003).

p0700 Further evidence for evolutionary EFIs comes from studies of postmating/prezygotic reproductive isolating mechanisms. Despite apparently normal mating and insemination between males and females of different species, or those from genetically divergent populations, successful reproduction can be compromised to varying degrees. Such 'gametic isolation' (Dobzhansky 1951) may occur following a single heterospecific (or heteropopulation) insemination, or it may only be evident when the 'foreign' sperm are competing for fertilization with sperm from a conspecific (or native) male (e.g., Chang 2004). In the latter circumstance – known as competitive gametic isolation or conspecific sperm precedence – the widely observed pattern is for the sperm of the conspecific male to fertilize the majority of eggs, irrespective of mating order (see Chapter 9 of this volume). Demonstrations of competitive gametic isolation between geographic populations within species indicate that putative EFI traits diverge and coevolve rapidly (Brown & Eady 2001; Hosken et al. 2002; Pitnick et al. 2003; Fricke & Arnqvist 2004; Ludlow & Magurran 2006).

p0710 The mechanisms underlying gametic isolation are poorly known in most cases, but are likely attributable to ejaculate–female incompatibilities arising as a consequence of populations or species evolving independently of one another (see Chapter 9 of this volume). For example, when queens of the honeybee, *Apis mellifera*, were each inseminated with an equal number of sperm from drones of either *A. mellifera*, *A cerana*, *A. dorsata* or *A. florae*, there were significant differences among crosses in the number of sperm reaching the spermatheca, the motility of sperm at 3 days and at 4 weeks after insemination and egg fertilization rate. These differences were in accordance with the degree of species relatedness (Phiancharoen et al. 2004). Similarly, in the ground crickets *Allonemobius socius* and *A. fasciatus*, heterospecific sperm appear less motile than do conspecific sperm within the female sperm-storage organs (Gregory & Howard 1994). In the bruchid beetles *Callosobruchus subinnotatus* and *C. maculatus*, conspecific sperm are better at displacing heterospecific sperm from the female's spermatheca (Rugman-Jones & Eady 2007). Finally, conspecific sperm precedence between

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D. simulans and *D. mauritiana* appears to involve complex sperm × Acp × female interactions (Price et al. 2000). The mechanisms of gametic isolation are expected to be heterogeneous across study systems, given that any compromise in the biochemical, physiological, morphological and/or behavioral basis of insemination, sperm migration, sperm storage, sperm viability and/or fertilization may render foreign sperm less competitive (see Chapter 9 of this volume).

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7.5 Genetic compatibility, male–female interactions and sperm precedence

p0720 Investigations of two separate yet possibly related phenomena are contributing to an emerging realization that discerning EFIs will enhance our understanding of the mechanisms underlying the maintenance of genetic variation and directional sexual selection in a diversity of taxa. These phenomena are (1) the selective benefit of polyandry arising through male–female genetic compatibility, (2) the extent to which complex genotypic interactions between the sexes mediates differential male fertilization success.

p0730 Indirect selection can favor multiple mating by females if, as a consequence of ejaculates from more than one male mixing within the female's reproductive tract, the ensuing mechanisms of postcopulatory sexual selection (see Chapter 6 of this volume) result in the best sperm fertilizing the female's eggs. In fact, numerous experimental studies have demonstrated that postcopulatory sexual selection can enhance offspring viability (reviewed by Jennions & Petrie 2000; Tregenza & Wedell 2000; Neff & Pitcher 2005; but see Brown et al. 2004). Several alternative models have been proposed to explain how such an adaptive process might work, with the difference among them being the definition of 'best sperm'.

p0740 According to the 'sexually selected sperm hypothesis', by creating a competitive fertilization environment, females enhance the probability of fertilizing their eggs with sperm from males who are good at sperm competition, and hence benefit by producing sons who are superior sperm competitors (Sivinski 1984; Harvey & Bennett 1985; Curtsinger 1991; Keller & Reeve 1995).

p0750 Alternatively, according to the 'good sperm hypothesis', females accrue indirect genetic benefits through positive covariation of sperm competitive ability and male genetic condition (Sivinski 1984; Madsen et al. 1992; Yasui 1997). In support of this hypothesis, studies have found (i) a positive relationship between males' sperm competitive ability and the viability (i.e., development time, survival) of their offspring in the yellow dung fly (Hosken et al. 2003) and the marsupial *Antechinus stuartii* (Fisher et al. 2006), (ii) positive relationships between male attractiveness or condition and sperm competitiveness in red deer (Malo et al. 2005), guppies (Matthews et al. 1997; Evans et al. 2003; Locatello et al. 2006) and Atlantic cod (Rakitin et al. 1999) and (iii) condition dependence of ejaculate characteristics in a dung beetle (Simmons & Kotiaho 2002) and of sperm offense ability in *D. melanogaster* (Amitin & Pitnick 2007; McGraw et al. 2007).

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p0760 A third explanation for the positive relationship between polyandry and female reproductive success, however, has received much greater attention. According to the 'genetic compatibility hypothesis', the best sperm are those bearing haplotypes most compatible with the female genome (or those that minimize genetic incompatibility) (Zeh & Zeh 1996, 1997; Jennions 1997; Jennions & Petrie 2000; Tregenza & Wedell 2000; Neff & Pitcher 2005; Oh & Badyaev 2006). Because this criterion will be female-specific, the relevant genetic variation in fitness will be nonadditive (Neff & Pitcher 2005; Bjork et al. 2007). Some of the strongest evidence in favor of the genetic compatibility hypothesis comes from experiments examining the relationship between inbreeding, an obvious source of genetic incompatibility, and male competitive fertilization success. Fertilization bias to minimize inbreeding (or selfing) has been convincingly shown to occur in mice (Wedekind et al. 1996), the sand lizard *Lacerta agilis* (Olsson et al. 1996), the field cricket *Gryllus bimaculatus* (Bretman et al. 2004; Tregenza & Wedell 2002), the fruitfly *D. melanogaster* (Mack et al. 2002), the soil nematode *Caenorhabditis elegans* (LaMunyon & Ward 1995, 1997) and the compound ascidian *Diplosoma listerianum* (Bishop 1996; Bishop et al. 1996). The mechanism(s) underlying this effect are unknown for *L. agilis*, *G. bimaculatus* and *D. melanogaster*. In the sequentially hermaphroditic (i.e., sperm are produced prior to irrevocably switching to egg production) and typically self-fertilizing *C. elegans*, the sperm of males outcompete self-sperm (males are XO, the result of a rare nondisjunction event, and hermaphrodites will mate with males). This effect is attributable to male sperm being larger, faster and hence superior to 'self-sperm' in occupying the anterior end of the spermatheca, rather than to EFIs (LaMunyon & Ward 1995, 1997). In the mouse, nonrandom fertilization has been demonstrated with respect to the MHC (major histocompatibility complex) genotype of males, but appears to be mediated by sperm–egg interactions (Wedekind et al. 1996; EFIs not examined; see Chapter 8 of this volume). Finally, in *D. listerianum*, biased fertilization has definitively been demonstrated to involve EFI (see Section 7.2.5).

p0770 An alternative approach to examine the influence of genotypic interactions between the sexes on fertilization bias has been to use factorial crossing designs to partition variation among sources contributing to competitive male fertilization success. In an early study, Zimmering and Fowler (1968) compared the efficiency of sperm use by females after *D. melanogaster* males from an Oregon-R strain had mated either to Oregon-R or *yellow* strain females. They concluded: '... the proportion of non-functional sperm [is] determined in the female and results from an interaction between the genotype of the female and the genotype of the sperm'. More recently, Wilson et al. (1997) took advantage of familial relatedness to partition sources of variation in the proportion of progeny sired by the second of two males following remating by the female (P_2) in the cowpea weevil, *Callosobruchus maculatus*. Successive episodes of sperm competition between the same two males resulted in a consistent outcome only when the successive females were genetically similar (i.e., full sisters). Likewise, P_2 was only consistent among full sisters when they were both mated to genetically

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similar male pairings. Another study of sperm precedence used *D. melanogaster* lines rendered homozygous for X, second and third chromosomes to demonstrate the presence of polymorphic female genes affecting P_2 (Clark & Begun 1998). The authors recognized that 'genetic variation of this type is completely neutral in the absence of pleiotropy or interaction between variation in the two sexes'. Clark et al. (1999) followed up with an analysis of pairwise P_2 experiments among six different isogenic lines, which demonstrated significant male–female interactions on P_2. A similar result was obtained using different wild-type strains of the flour beetle, *Tribolium castaneum* (Nilsson et al. 2003). Recently, Bjork et al. (2007) used an outbred *D. melanogaster* population with natural genotypic variation to quantify the extent of male–female and male–male interactions on both P_2 and P_1 (the proportion progeny sired by the first of two males following remating by the female). They found the pattern of sperm precedence to be statistically repeatable only when each male competed against the same rival male and within the same female. Repeatability of P_1 and P_2 declined significantly when the rival male stayed the same but the female changed, and they disappeared when males competed each time against different rival males within different females.

p0780 These male–female interactions have been interpreted to be a consequence of complex EFIs (and male–male interactions). Such interactions are predicted to generate a pattern of nontransitivity among males in their sperm competitive ability (Clark et al. 2000), in a manner comparable to the 'rock-paper-scissors' game (Maynard Smith 1982). This prediction has been supported by a study using chromosome-extracted lines of *Drosophila* (Clark et al. 2000) and by an assay of fertilization success following artificial insemination of mixed male ejaculates in domestic fowl (Birkhead et al. 2004). Nontransitivity of sperm competition success should theoretically increase the opportunity for polymorphism in genes that influence the EFIs (Prout & Bunndgaard 1977; Clark et al. 1999, 2000).

s0210 7.6 Conclusions and future directions

p0790 In this chapter, our goal was to bring together evidence for mechanistic and taxonomic diversity of EFIs in order to encourage investigators to expand the arena in which they consider reproductive biology. It was not our goal to *test* the extent to which EFIs are important or pervasive, because EFIs have not been sufficiently studied to permit such evaluation. Thus, we made no attempt to determine the contribution of EFIs to reproductive success relative to the contribution of, say, among-male variation in traits that do not involve interaction with the female (e.g., Pattarini et al. 2006).

p0800 In contrast to processes contributing to differential male mating success (Wiley & Poston 1996), there is still debate over the relative contributions of male–male competition (i.e., sperm competition) and (cryptic) female choice, in determining differential male fertilization success (Gowaty 1994; Eberhard 1996; Birkhead

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1998a; Pitnick & Brown 2000; Simmons 2001). However, evidence reviewed here indicates that EFIs can be complex and females can influence everything from the number of sperm transferred to sperm motility, storage and survival. Variation among males in the ability of their ejaculates to interact with the female is likely to be a ubiquitous determinant of competitive fertilization success in internally fertilizing species. We therefore agree with Eberhard (1996, 1998, 2000) that distinguishing between sperm competition and cryptic female choice presents a false dichotomy in most cases, and we equate any distinction made between them to that applied to passive versus active female choice (Parker 1983; Sullivan 1988). When referring to both process and mechanisms, we encourage usage of the more comprehensive expression 'postcopulatory sexual selection' over the more ambiguous terms 'sperm competition' and 'cryptic female choice'.

p0810 Distinguishing between alternative models for the evolution of female preferences is notoriously difficult (Bradbury & Andersson 1987; Rowe et al. 2003; Arnqvist & Rowe 2005; Kokko et al. 2006). Detailed knowledge of the mechanisms by which males and females interact may be pivotal to any empirical exploration of alternative scenarios for the evolution of sexual traits (Rowe & Day 2006). Experimental evolution and phenotypic engineering approaches applied to traits known to mediate interactions between the sexes can then be used to perturb the system while examining sex-specific fitness consequences. EFIs provide good candidates for such analyses (e.g., Chapman et al. 1995; Rice 1996; Hosken et al. 2001; Miller & Pitnick 2002; Bjork & Pitnick 2006).

p0820 Increased knowledge of EFIs will also have direct, applied applications. Approximately 25–30% of human couples exhibit 'unexplained infertility' (see Chapter 15 of this volume; also Garcia-Gonzalez 2004). Because some of these cases are likely to involve some incompatibility in terms of EFI, a more comprehensive understanding of EFIs might lead to better diagnostics and novel treatments for human infertility. In addition, intracytoplasmic sperm injection (ICSI), in which a single sperm (often aspirated from the male's testis) is injected into an egg, is now widely practiced. This technique circumvents any 'selection' among sperm imposed by the female tract and any female-induced modification of sperm (Cummins & Jequier 1995; see Chapters 5 and 15 of this volume). Knowledge of both proximate and ultimate aspects of EFIs should be part of any comprehensive medical and ethical evaluation of such techniques. Similarly, assisted reproduction technologies are increasingly being employed in comprehensive plans to rescue threatened and endangered species (see Chapter 14 of this volume). Comparative knowledge of EFIs may improve the success of these endeavors.

p0830 We are excited about recent genomic and proteomic approaches to investigate EFIs (Fazeli et al. 2004; McGraw et al. 2004; Lawniczak & Begun 2004; Georgiou et al. 2005; Mack et al. 2006). Great advances are likely to come from comparative analyses across closely related species, particularly if coupled with assays involving hybrid (particularly artificial) inseminations. Recent advances in whole-cell proteomics, exemplified by the recent publication of the *D. melanogaster* sperm proteome (Dorus et al. 2006; see Chapter 11 of this

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volume), are also likely to dramatically improve our understanding of EFIs. An example of an approach that may be fruitful in this regard would be to compare proteomes among purified samples of sperm: (i) isolated from male seminal vesicles (thus not exposed to most seminal fluid proteins); (ii) isolated from seminal vesicles and then mixed, in vitro, with secretions of male reproductive tract glands; and (iii) isolated from female sperm-storage organs (thus exposed to male seminal fluid proteins and subsequent opportunity for modification within the female reproductive tract). There would be much to learn from including among-species experiments of treatments (ii) and (iii) (i.e., hybrid mixing of sperm and Acps and hybrid inseminations) in such an endeavor. These comparisons would identify proteins from male glands and from the female reproductive tract that become associated with sperm, and modifications to sperm proteins that result from exposure to seminal fluid and/or female reproductive tract proteins. Identification of the female receptors or female-derived proteins that target or serve as targets of specific male-derived proteins, coupled with evolutionary analyses to determine whether the sex-specific interactants coevolve, would also present a great advance. Another promising endeavor would be to quantify within-population variation in both male and female EFI traits, particularly if such knowledge could be applied to discerning the mechanisms by which male–female interactions impact sperm precedence. Finally progress will also come from comparative studies of sperm behavior across species differing in design of the female reproductive tract. Although sperm motility has been widely investigated in vitro, relatively little is known about sperm flagellar motion and other sperm behavior within females (see Chapter 5 of this volume).

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