

Spider Genitalia

Precise Maneuvers with a Numb Structure in a Complex Lock

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INTRODUCTION

The structures with which male spiders transfer sperm to females are unique among all animals in several respects. From the ancestral arachnid sperm transfer mechanism via an external spermatophore (Thomas & Zeh 1984), male spiders have evolved to transfer sperm to the female by using their pedipalps, a portion of the male's body that is not associated directly with his primary genitalia. Similar but independent evolution of "secondary" genitalia involving different male structures that subsequently come under sexual selection has occurred in several other arachnid orders (solifugids, ricinuleids, some pseudoscorpions, and mites—Kaestner 1968; Thomas & Zeh 1984; Alberti & Michalik 2004), as well as in other groups, such as odonate insects. The use of the pedipalps as secondary male intromittent genitalia is a unique synapomorphy of spiders, without convergence in any other arachnid, and without a single known reversal.

More important, however, is the fact that the portion of the male spider's pedipalp that has become specialized to receive and transfer sperm, the palpal "bulb", is apparently unique among all animal genitalia in that it lacks nerves, and thus also lacks sense organs and muscles (Eberhard & Huber 1998b). Much of this chapter will be

dedicated to exploring the consequences of this lack of nerves for the evolution of spider genitalia. We will concentrate first on males because we believe that this lack of nerves in males has probably been largely responsible for many peculiarities of genitalic evolution in spiders, and then turn to females.

Despite the profound differences associated with a lack of nerves, spider genitalia clearly share the overall evolutionary trend seen in the male genitalia of many other groups, in being relatively distinct morphologically even among closely related species. This pattern of sustained, relatively rapid divergent evolution in genitalia was discovered long ago by spider taxonomists (summary, Comstock 1967), and their accumulated work constitutes a treasure chest of information on how spider genitalia have evolved. Although it is possible that the generality of this trend may be somewhat overestimated due to the possible bias of some taxonomists to recognize species mostly on the basis of genitalic differences (Huber 2003a; Song 2006) (see chapter 04 in this book), there is an independent indication that sustained rapid divergence has characterized genitalia in spiders. Male spider genitalia have such a diverse array of different sclerites that it has been very difficult to homologize them (e.g., Gering 1953: 33; Merrett 1963; Platnick 1975; Coddington 1990; Griswold et al. 1998, 2005; Agnarsson et al.

2007; Kuntner et al. 2008). Spider genitalia may even have a greater tendency toward qualitative rather than just quantitative changes than other traits (Huber 2003a).

Spider genitalia are an interesting “test” case for the various hypotheses that attempt to explain genitalic diversity, both in the sense of the same trend occurring in a different structure (the palpal bulb), and also because this structure has such strange characteristics (lacking nerves, muscles and sense organs).

MALE SPIDER GENITALIA

Spider Sperm and Sperm Transfer—the Male Perspective

Spiders and their closest relatives all transfer sperm in an inactive state, with the flagellum rolled up around the nucleus (Alberti 1990; Alberti & Michalik 2004). Within spiders, apparent vestiges of ancestral spermatophores still occur. Sperm are packaged in small transfer units (coenospermia) in the Mesothelae and Mygalomorphae (Alberti 1990; Alberti & Michalik 2004; Michalik et al. 2004), taxa that are characterized by many plesiomorphic characters (figure 12.1). The more derived Araneomorphae mostly transfer sperm cells individually, and each sperm is surrounded by its own secretion sheath (cleistospermia).

In its simplest form, the genital bulb is a bulbous (pyriform) organ with no further subdivisions, as in many Mygalomorphae and Haplogynae (figures 12.1 and 12.2). Many other groups have evolved highly complex bulbs, however, consisting of a variety of sclerites that are connected by membranes (hematodochae) that can be inflated by hydraulic pressure and thus move the sclerites (most Entelegynae; figures 12.2–12.4). Inflation of hematodochal membranes that are twisted, folded irregularly, or composed of fibers of different elasticity can produce complex movements of sclerites (Osterloh 1922; Lamoral 1973; Grasshoff 1968; Loerbroks 1984; Huber 1993a, 2004b). The ‘primitive’ Mesothelae have moderately complex bulbs, suggesting that, after an early elaboration when palps evolved to transfer sperm, evolution has proceeded in both directions, towards simplification and towards higher complexity (Kraus 1978, 1984; Haupt 1979; Coddington 1990). The aberrant family Pholcidae, in which the male inserts a unique,

elaborate extension of the palpal segment just basal to the bulb deep into the female, and in which the female genitalia are also unusual in being largely membranous and lacking spermathecae, will be omitted from most of the discussions here.

Before sperm transfer, a male spider must charge his palps with sperm. The male constructs a small sperm web (which ranges from a single thread to an elaborate structure of silk lines), deposits a drop of sperm from his gonopore on the ventral surface of his abdomen, and takes the sperm up into his palpal bulb. The bulb contains a blind-ended, tube-like invagination (the sperm duct) that is formed by highly specialized cuticle; in most species the sperm duct is relatively rigid, is porous, and is surrounded by a glandular epithelium (Cooke 1970; Lopez & Juberthie-Jupeau 1985; Lopez 1987). During sperm uptake (induction), sperm is probably sucked into the sperm duct by pulling the fluid that fills this duct out through its rigid walls (presumably the epithelium imbibes the liquid); ejaculation is probably effected by the inverse mechanism of moving fluid into the lumen of the sperm duct through its walls (Cooke 1966; Juberthie-Jupeau & Lopez 1981; Lopez & Juberthie-Jupeau 1982, 1985; Lopez 1987). Other mechanisms must exist, however, because in some spiders the wall of the sperm duct lacks pores (Cooke 1970; Lopez 1987). Insertion and ejaculation can be surprisingly rapid in some species (< 5 s in *Argiope*—Schneider et al. 2005b; see Huber 1998), also leading one to wonder if secretion of these gland cells is the complete explanation. In mesothelid spiders the wall may be more flexible, and collapse under hemolymph

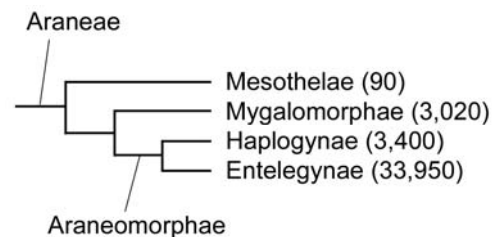


FIGURE 12.1 Simplified relationships among the major groups of spiders, with approximate numbers of known species (from Coddington and Levi 1991; Platnick 2007). By far the greatest number of species are in the more derived group Entelegynae, in which both male and female genitalia are also the most complex and diverse.

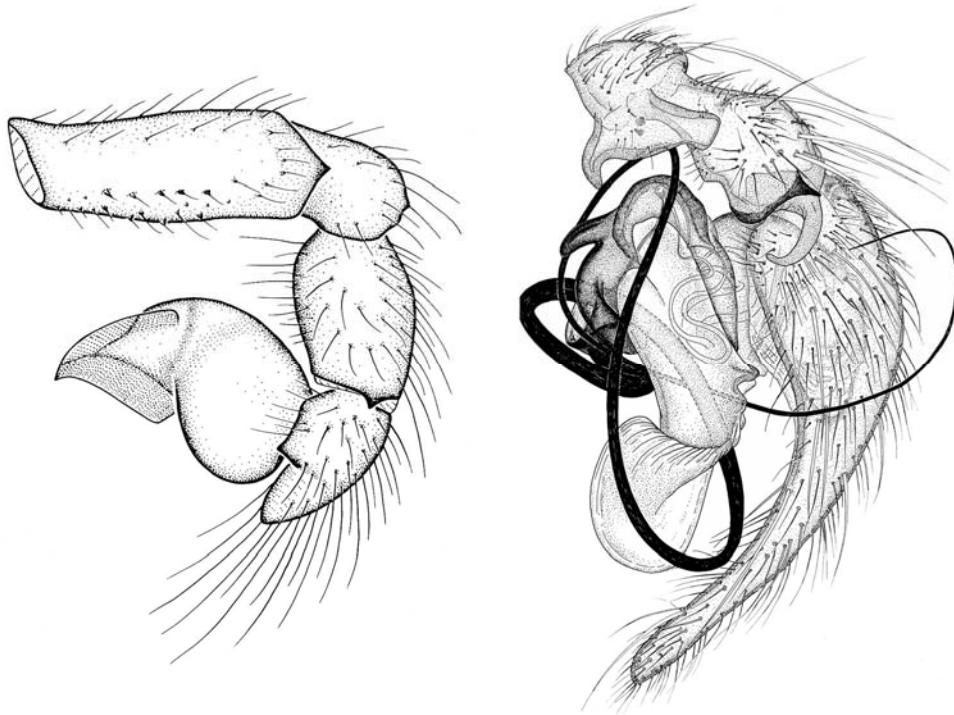


FIGURE 12.2 Male spider genitalia range from simple to extremely complex, but mapping of genital bulb complexity on cladograms suggests that medium complex bulbs are plesiomorphic, while very simple bulbs like that of *Segestrioides tofo* (left) and highly complex bulbs like that of *Histopona torpida* (right) are derived (from Platnick 1989; Huber 1994; with permission from AMNH and Blackwell).

pressure during ejaculation (Kraus 1984; Haupt 2003, 2004).

In a virgin male, the fluid that is pulled out of the duct would presumably have been produced when the bulb developed during the penultimate instar; in a nonvirgin, it could be the secretions that pushed sperm out during a previous ejaculation. The extraordinary complexity of the internal sperm ducts of the palps of some spiders (Coddington 1986; Sierwald 1990; Huber 1995b; Agnarsson 2004; Agnarsson et al. 2007; Kuntner 2007) suggests that this account is seriously incomplete; but to date no hypotheses to explain the function of this complex morphology are available. In theridiids, sperm duct trajectories vary greatly between genera, but are often constant within species and genera (Agnarsson et al. 2007). The fact that copulation does not always result in sperm transfer (Bukowski & Christenson 1997a; Schneider et al.

2005a, b) also suggests that additional, still unappreciated processes may occur.

Movements of sperm once they have been deposited within the female have seldom been studied. Soon after a female's second copulation in the lycosid *Schizocosa malitiosa*, the ejaculates of the two males, which can be distinguished because the second male's sperm are still encapsulated while those of the first male are decapsulated, are already largely mixed in most parts of the spermatheca (Useta et al. 2007). The female of the tetragnathid *Leucauge mariana* has compound spermathecae, with one soft-walled chamber in which sperm are deposited and decapsulated, and two other rigid chambers to which decapsulated sperm then move (or are moved) (Eberhard & Huber 1998a). Similarly, the dysderid *Dysdera erythrina* has compound spermathecae with different glands hypothesized to function for short-term and

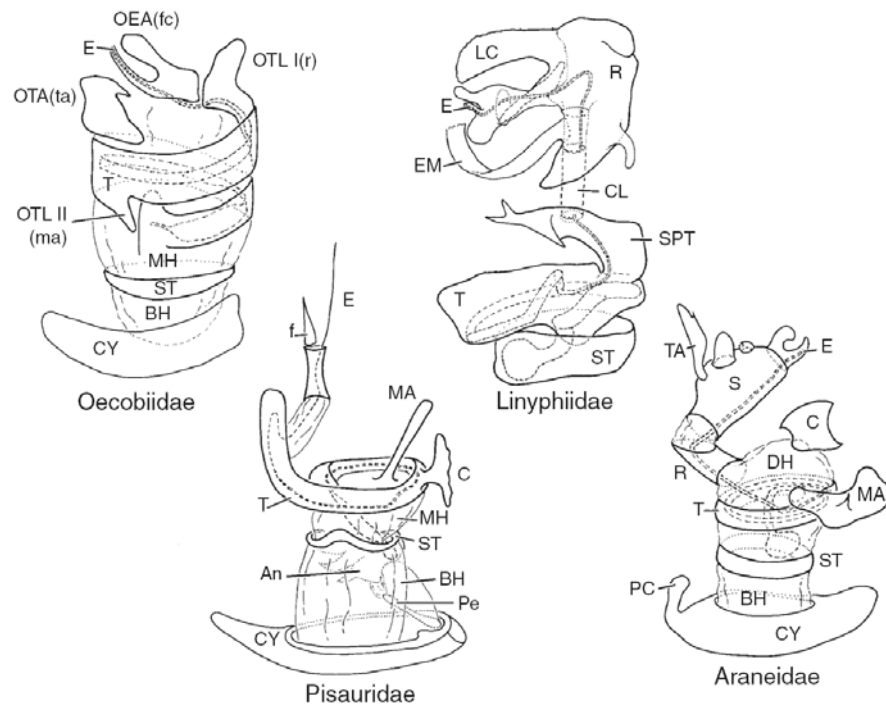


FIGURE 12.3 Schematic illustrations of palpal bulb designs in different groups of spiders, in which putatively homologous sclerites are labeled (from Coddington 1990) illustrating the diversity of sclerites and their arrangements. E indicates the embolus, the structure through whose tip sperm are transferred to the female, CY is the cymbium, the most distal segment of the palp that carries the genital bulb (with permission).

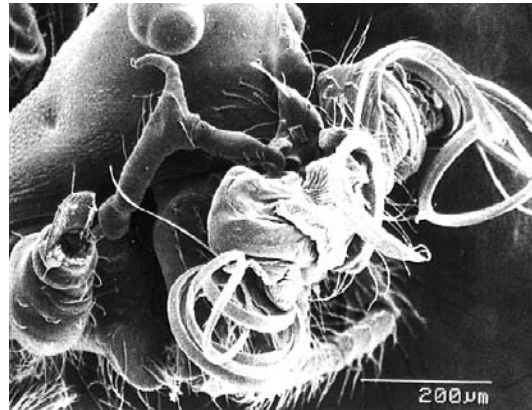


FIGURE 12.4 A male *Anapisona simoni* is partially hidden behind his elaborate, partially expanded genitalia, illustrating both the elaborate complexity often found in spider male genitalia and the appreciable material investment that they sometimes represent.

long-term storage (Uhl 2000). The second of two intromissions (one on each side) in the araneid *Micrathena gracilis* is twice as long as the first, and experimental manipulations showed that the prolongation of the second intromission did not influence the amount of sperm transferred, but did increase the amount of sperm stored from the first intromission (Bukowski & Christenson 1997a), suggesting that active female participation in sperm storage is induced by the male palp.

Evidence that Palpal Bulbs Lack Neurons

Histological studies using stains capable of differentiating nerve cells have failed to reveal any neurons in the bulbs of mature males (Osterloh 1922; Harm 1931; and Lamoral 1973 on six different families). Sections of the palp in a member of a seventh family (Linyphiidae) showed that a thin basal neck (“column”) that connects more distal portions of the bulb with the rest of the bulb is made of solid cuticle, with only the sperm duct inside and no space for nerves (B. Huber, unpublished on *Neriene montana*). Ultrathin sections also failed to reveal nerves in the palpal bulb in yet another family (M. Suhm unpublished on *Amaurobius*, cited in Eberhard and Huber 1998b).

Additional, less direct histological data from many other species also suggest that palpal bulbs are not innervated. Glands in the bulb of *Amaurobius* lack both muscles and neurons to control the release of their products (Suhm et al. 1995). There are muscles that originate from the more proximal portions of the palp and insert at the base of the bulb in some spiders, but as Levi (1961) noted, no muscles have ever been seen within any palpal bulb. Sectioning studies showed that there were no muscles of any kind in the palpal bulbs in 76 genera of 56 different families in all major taxonomic groups (Huber 2004b).

In addition, external cuticular sense organs such as slit sensilla and setae (socketed epidermal bristles) appear to be completely lacking on palpal bulbs (figure 12.5; Eberhard & Huber 1998b; Berendonck & Greven 2005). The setae that are present on large areas of a spider’s body, and that are innervated and function as tactile organs (Foelix 1985), are conspicuous by their absence in SEM micrographs of the bulbs of a large variety of groups (e.g., Kraus 1978; Opell 1979; Coddington 1986; Kraus & Kraus 1988; Griswold 1987, 1990, 1991,

1994, 1997; Hormiga 1994; Haupt 2003; Griswold et al. 2005; Bond & Platnick 2007; Miller 2007a).

Our earlier speculation (Eberhard & Huber 1998b) that the reason for the lack of nerves in the bulb is due to its developmental derivation from the palpal claw (e.g., Harm 1931) (the claw lacks neurons) is contradicted by the finding that both rudimentary claws and bulbs occur during bulb development in some spiders (Coddington 1990). The reason nerves are missing from palpal bulbs is not known. Perhaps both the bulb and the claw are derived from the same anlagen. Muscles attached to the base of the bulb are thought to be homologous with the levator and depressor muscles of the claw (Cooke 1970).

The portion of the palp just basal to the bulb, the cymbium, is not involved directly in sperm transfer, although it sometimes makes direct contact with the female during copulation. In contrast with the bulb, the cymbium is generally richly innervated and usually bears many setae (figure 12.2). Presumably there are sensors in the cymbium and/or the membranes and muscle (if present) that unite the cymbium with the bulb, but they have apparently never been searched for. A male spider may thus have at least some information regarding the position of his bulb with respect to his cymbium during copulation. There is behavioral evidence of at least a crude sensitivity, as a male *Leucauge mariana* can apparently sense whether or not the

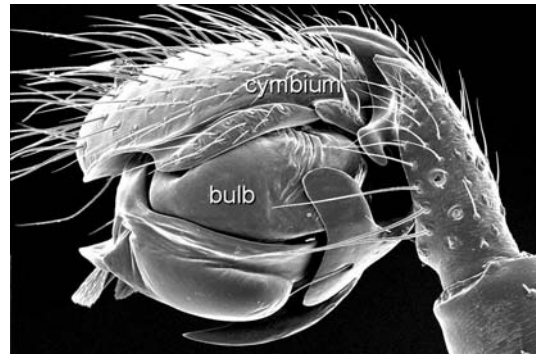


FIGURE 12.5 Distal palpal segments and genital bulb of a male linyphiid (*Triplogyna major*), showing the total absence of hairs on the bulb while hairs cover most of the cymbium and other palpal segments (from Miller 2007a; with permission from Blackwell).

structures at the tip of his bulb (the embolus and conductor) have entered the sperm droplet when he is taking up sperm into the bulb (Eberhard & Huber 1998a).

SEM photographs of palps (Silva 2003 on Ctenidae; Griswold et al. 2005 on several families; Miller 2007 on Linyphiidae) show that the cymbium, paracymbium, and tibial apophyses also sometimes have small regions lacking setae; apparently these areas contact the female epigynum during copulation. In contrast, there are abundant setae on the portion of the cymbium of *Leucauge mariana* that rests loosely on a featureless portion of the surface of the female abdomen away from the epigynum (the exact site varies) (Eberhard & Huber 1998a). Perhaps this loss of setae is an adaptation to fit more tightly with the female, or to avoid damage that would otherwise result from friction with the female during copulation. Additional groups need to be checked to see whether similar bald spots occur in other taxa, and whether areas lacking setae consistently contact the female. This pattern has a major implication. Males do not seem to be in urgent need of sensory information from the sites specialized to contact particular sites on the female.

The lack of innervation in the male intromittent genitalia of spiders is in clear contrast with other groups like mammals and insects. For instance the intromittent phallic organs and the associated genitalic structures arising nearby are provided with sense organs and muscles in many insects (Snodgrass 1935; Peschke 1978, 1979; Chapman 1998; Sakai et al. 1991; Schulmeister 2001).

Consequences for Males of Lack of Genitalic Innervation

Because of the lack of nerves in the palpal bulb, the challenges faced by a male spider attempting to copulate can be likened to those of a person attempting to adjust a complex, delicate mechanism in the dark, using an elongate, elaborately formed fingernail. A male spider is more or less “sensorily blind” when he attempts to perform the selectively all-important act of inseminating a female. Spider males are likely to have difficulty in achieving the proper alignment with both the external and internal portions of the female (which are often quite complex—see below). The only sensations it is reasonable to expect to be available to the male would be from more basal portions of his palp such

as the cymbium, the connections between the bulb and the cymbium, and from the hydraulic system (pressure changes, perhaps flow of fluid into the bulb?) that is involved in inflating the palpal hematodochae.

Apparent confirmation that male spiders have difficulty positioning their palps precisely with respect to the female comes from behavioral observations of possibly exploratory movements of the male’s palp in the close vicinity of the female’s copulatory openings, variously called “scraping” (Rovner 1971; Blest & Pomeroy 1978; Huber 1995b; Eberhard and Huber 1998a; Stratton et al. 1996), “stroking” (Bristowe 1926; Melchers 1963), “rubbing” (Montgomery 1903; Bristowe 1929), “scrabbling” (Robinson & Robinson 1980), “beating” (Robinson & Robinson 1973), “poking” (Whitehouse & Jackson 1984; Fromhage & Schneider 2006), “slapping” (Gering 1953) “fumbling” (Snow et al. 2006), “flubs” (Watson 1991), and “brushing” (Senglet 2004). Flubs are very widespread: they were reported in 40% of 151 species in 38 families in a survey study (Huber 1998). Some authors have concluded that these movements represent failed intromission attempts (Watson 1991); other non-exclusive hypotheses are that these movements represent exploration, or courtship stimulation of the female (Robinson 1982; Stratton et al. 1996; Eberhard 1996). The fact that male *Portia labiata* and *P. schultzi* scrape on one side, then scrape and insert on the other side (Jackson & Hallas 1986) implies that scraping in this species has a stimulatory function rather than being just a searching movement. Salticid and lycosid males trying to mate with females whose genitalia were experimentally sealed, scraped for prolonged periods (Rovner 1971), suggesting a searching function and at least crude sensory feedback. Fragmentary observations of male *Nephila edulis* withdrawing their palps from the already inseminated side of female epigyna to shift to the other, non-inseminated side (Jones & Elgar 2008) also hints at sensitivity of some sort.

One solution to possible orientation problems would be to develop “preliminary locking” structures, either on the bulb or on the more basal, innervated palpal segments (cymbium, tibia, etc.), whose engagement with the female would require less precise alignment with her, but would provide a stable point of support to facilitate more precise alignment during subsequent stages of intromission that demand more precision. They might even

enable the male to sense that such preliminary alignment had occurred, via sensations from the cymbium or its articulation with the palp. Preliminary locks, and sclerites specialized to produce locking of this sort between male and female are widespread in spiders (figure 12.6; van Helsdingen 1965 on the paracymbium of *Lepthyphantes*; Eberhard & Huber 1998a on the conductor of *Leucauge*; Melchers 1963 on the “retinaculum II” of *Cupiennius*; Loerbroks 1983, 1984 and Huber 1995a, b on the rta of various families; Stratton et al. 1996 on the median apophysis of *Schizocosa*). As the different positions of these structures and their widely separate taxa suggest, preliminary locking has probably evolved several times independently. Coupling is sometimes a multi-stage process. In *Agelenopsis*, the embolus engages the female, the hematodocha expands and couples the conductor to the female, and the embolus then enters the female (Gering 1953). For reasons that are not clear, some groups have lost palpal locking structures (e.g., some linyphiids lack a paracymbium, G. Hormiga personal communication; some lycosids lack a rta, Griswold 1993).

A second important consequence relates to the difficulty of fine motor control over a structure that lacks muscles. The male genitalia of spiders are

moved only by more proximal muscles in the palp, and by internal pressure changes that result in inflation of the membranes between sclerites (hematodochae) within the bulb. Although there are very few studies concerning the degree of variability in the genitalic movements in spiders (or other animals for that matter; most studies of the functional anatomy of genitalia are unfortunately extremely typological), it seems likely that this type of movement mechanism results in less ability to make fine adjustments in movements compared with structures controlled by individual muscles, as in the genitalia of other groups. Spiders probably have some general control of movements during intromission, for instance of whether some hematodochae inflate while others do not, but there is probably little fine control; for instance, the sequence with which the one to three hematodochae of a bulb inflate seems to be fixed. In the tetragnathid *Leucauge mariana*, the movements of the palpal bulb prior to and following removal of a copulatory plug in the female showed no perceptible qualitative differences (Méndez & Eberhard, unpublished data).

The anatomical lack of nerves precludes direct sensory feedback from palpal bulbs, and some experimental manipulations of males (Rovner 1966,

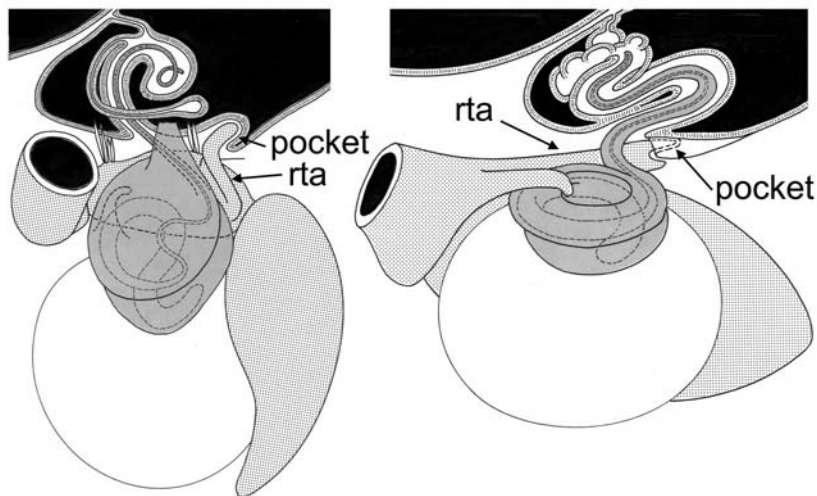


FIGURE 12.6 Females of the rta clade often provide the male with cooperative structures that facilitate coupling of his genitalia. In the cases shown here (left: *Anyphaena accentuata*; right: *Philodromus aureolus*), the females (black) provide pockets for the male retrolateral tibial apophyses (rta); palps in light gray, bulbs in dark gray (from Huber 1995a, b; with permission from Blackwell).

1967, 1971) and female *Rabidosia* (= *Lycosa*) *rabida* (Rovner 1971) reveal lack of proprioceptive feedback from the palps. Nevertheless, some species show surprising discriminations. Male *Latrodectus hasselti* spiders tended to use the palp containing the greater amount of sperm first when they copulate (Snow & Andrade 2004). Proper positioning of the male of *L. rabida* on the female depended on feedback from the male palps, and when one side of the female's epigynum was artificially sealed, the male gradually decreased his attempts to insert his palp on that side (although males did perform some "pseudoinsertions" on the plugged side) (Rovner 1971). Removal of the bulb in this species reduced the usual male attempts to moisten the bulb in his mouth. Male *Argiope bruennichi* never attempted to copulate using the stump of an ablated palp (Nessler et al. 2007a). The mechanism(s) responsible for selective hematochoal inflations and the differences in their patterns (e.g., pulsating rather than sudden inflations in *Agelenopsis*) presumably involve differences in hydraulic pressure (Gering 1953). The extensive "cleaning" or "lubricating" of the palps by the male that is often associated with copulation (van Helsdingen 1965; Costa 1979; Lopez 1987) might result in softening of the membranes of the palp, causing them to become more flexible and thus to move palpal sclerites in particular ways (Gering 1953).

A further function in spiders, which appears to be much more common than in insects, is the use of some palpal sclerites to brace or push others, both during the process of preliminary locking and during subsequent orientation and deeper intromission. This bracing function appears to be widespread in spiders (Gering 1953; van Helsdingen 1971; Grasshoff 1973; Loerbroks 1983; Huber 1993a, 1995a; Costa & Pérez-Miles 1998; Eberhard & Huber 1998a; Knoflach & Pfaller 2004; Agnarsson et al. 2007). It is much less common in insects, and was not even included in the review of genital functions by Scudder (1971), or in a survey of functions documented in 43 species of Diptera (Eberhard 2004a). Still another related function not mentioned for insects but present in spiders is that of the "tethering membrane" of *Agelenopsis* which guides the movements of other sclerites (Gering 1953). Presumably these differences occur because the lack of muscles makes independent adjustments of the positions of different structures more difficult in spiders, and also because of their lack of sensory feedback during coupling.

There is a wealth of morphological variation with as yet unknown functions and even apparently paradoxical (e.g., the longitudinally split embolus in the theridiid *Anelosimus*, the extremely long coiled embolus that does not contain a sperm duct in the theridiid *Stemmops*—Agnarsson et al. 2007) that lies below the level of this necessarily superficial review.

FEMALE SPIDER GENITALIA

Sperm Storage and Fertilization

The female spider copulatory organ is closely associated with the gonopore on the ventral surface of the abdomen. Sperm are usually stored in separate internal receptacles ("spermathecae"). In the plesiomorphic "haplogyne" condition, sperm are introduced through the same opening that is used for oviposition (figure 12.7). The spermathecae of haplogyne spiders have only a single duct, through which sperm both enter and exit the receptacle (the "cul-de-sac morphology" of Austad 1984). In the derived, entelegyne condition, an "insemination" (or copulatory) duct which connects each spermatheca with the outside is used to introduce sperm into the spermatheca; and a separate "fertilization" duct, running from the receptacle to the uterus, is used to transfer sperm to the eggs (Wiehle 1967a; Cooke 1970). Austad (1984) called this two duct arrangement a "conduit" morphology, and proposed that haplogyne and entelegyne female morphology may influence sperm precedence patterns. In some entelegynes, however, both ducts enter the same end of the spermatheca, resulting in an effectively cul-de-sac design; in addition, there is no clear relationship between these designs and sperm use patterns (Uhl & Vollrath 1998; Uhl 2002). The conduit morphology could also affect sperm usage by promoting the evolution of copulatory plugs by males (see below). Cul-de-sac designs have evolved secondarily from conduits in two and perhaps four families (Dimitrov et al. 2007). Hypodermic insemination, which circumvents female ducts, has recently been discovered in one species (Rezác 2007).

The standard belief is that eggs are fertilized as they reach the portion of the oviduct near the mouth of the fertilization duct, but the discovery of fertilized eggs in the ovarian cavity of the theridiid *Chaeearanea tepidariorum* (Suzuki 1995) indicates

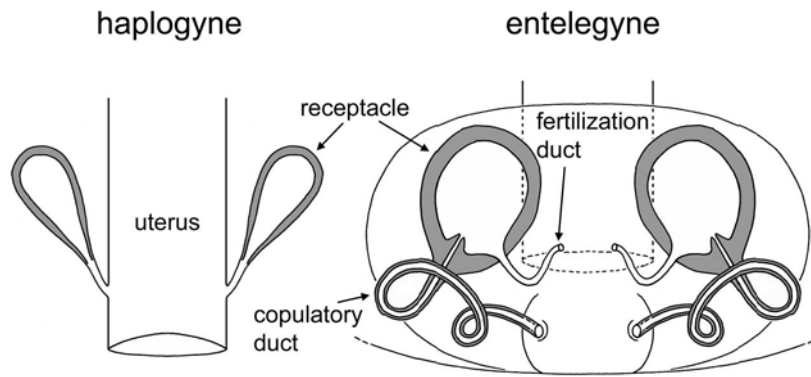


FIGURE 12.7 Female spider genitalia, schematic. In the haplogyne design, sperm enters and exits the receptacle (gray) through the same duct. In the entelegyne design, sperm enters through a copulatory (insemination) duct and exits through a fertilization duct (after Wiehle 1967b; with permission from Senckenberg Gesellschaft).

that sperm sometimes range more widely within the female (see also Burger et al. 2006a). The presence of a flap covering the opening of the fertilization duct into the oviduct in the nephilid *Nephila edulis* (Uhl & Vollrath 1998) also hints that sperm may move into the oviduct at times other than oviposition. The function of this flap is uncertain; it lacks muscles (G. Uhl, personal communication). It is not known whether similar flaps occur in other species.

While male spider genitalia are universally paired, the female genitalia vary. A few Mesothelae have a single spermatheca, and in some other “primitive” species the female has a pair of receptacles but the male can fill both with a single palp (Haupt 1979, 2003; Costa et al. 2000). Kraus (1978) suggested that the unpaired vulva of *Liphistius* is plesiomorphic, and that paired receptacles are derived; Forster (1980) and Forster et al. (1987) suggested that a bursal storage is plesiomorphic and that receptacles evolved several times independently. In at least one group (some tetragnathids) an unpaired sperm storage organ or area in the oviduct has been secondarily derived from paired spermathecae (Dimitrov et al. 2007). The finding of sperm in the ovarian cavity of other spiders suggests one possible, but untested explanation for the loss of spermathecae: males under sexual selection may have “short-circuited” female storage organs and introduced sperm directly into the oviduct. Perhaps this change was facultative at

first, as some unpaired sacs that might store sperm are present in other tetragnathids that still have spermathecae (Dimitrov et al. 2007).

In most araneomorphs (the majority of spiders—figure 12.1) the spermathecae are paired, and each must be inseminated separately. Almost universally each spermatheca is inseminated by the insertion of a different palp (von Helversen 1976). This makes it possible for females to influence insemination by interrupting copulation after a male has inseminated only one side (“hemiscopulation”) (e.g., Bukowski & Christenson 1997b). Detailed proof that such behavior can alter sperm precedence patterns was obtained in the theridiid *Latrodectus hasselti*. When two males were forced to inseminate a single spermatheca, there was strong first male precedence (mean 78.9% of the offspring). When, in contrast, males inseminated opposite spermathecae, the first male had no advantage (49.3% of the offspring). Because females control whether the first male inseminates one or both spermathecae, and because females often remate, a female can thus alter a first male’s chances of obtaining paternity advantage (Snow & Andrade 2005).

It is theoretically possible that the female further influences paternity by favoring the use of sperm in one spermatheca over that in the other in fertilizing her eggs. Such a bias has never to our knowledge been demonstrated, and there is evidence that it does not occur in *Nephila* (e.g., Jones & Elgar 2008).

None of the male traits that Snow and Andrade (2005) measured in *L. hasselti* correlated with paternity success when each male inseminated a different spermatheca, but (as they note) their small sample size and the limited number of traits they measured mitigates against confident conclusions (Snow & Andrade 2005). A few species have many more spermathecae (up to about 100) (Forster & Platnick 1984); their significance (and even whether they all store sperm) is not known.

External Rigidity and Internal Complexity

The more external portions of entelegyne female genitalia are often strongly sclerotized and rigid. Associated with this trend to female rigidity is the fact that, in strong contrast to many other animal groups, the morphology of the female genitalia is very often species-specific in form. All of the rigid portions, including the epigynum, the ducts, and to a lesser extent the spermathecae themselves, show diverse forms. This tendency toward rigid species-specific female genitalia has been exploited by taxonomists for many years, and taxonomic descriptions of spider species usually include descriptions of both male and female genital morphology. There is thus a huge (and to date largely unexploited) accumulation of data on female genital morphology which can be used to check for evolutionary trends.

The more internal portions of the female genitalia are less well known; in at least some species they are very complex. Recent studies of haplogyne spiders revealed several moveable sclerites attached to muscles (Burger et al. 2003, 2006b; Burger 2007, 2008) (figure 12.8). Proposed functions include locking of one area of the female's reproductive tract closed, packaging a male's ejaculate in a secretion that prevents sperm mixing, and ejecting it from her body as a single mass (Burger et al. 2006b; Burger 2007, 2008). There are also muscles attached to female internal genitalia in other groups such as Antrodiaetidae (Michalik et al. 2005), Dysderidae (Cooke 1966; Burger & Kropf 2007), Pholcidae (Uhl 1994; Huber 2004a), Pisauridae (Carico & Holt 1964), and Theridiidae (Berendonck & Greven 2005) whose functions are poorly understood.

One generalization about female genital morphology is that the insemination and fertilization ducts of entelegyne spiders show quite different patterns of evolution (figure 12.9). The insemination

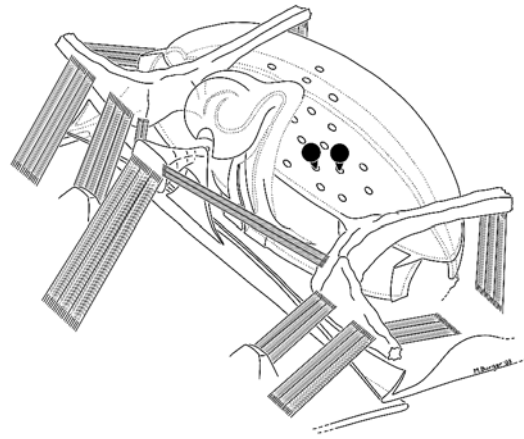


FIGURE 12.8 The complex array of muscles (shaded) and sclerites in the internal genitalia of the female haplogyne oonopid *Silhouettella loricatula* imply that the female plays an active role in sperm management in her body (from Burger et al. 2006b; with permission from Wiley).

duct, through which sperm enter the spermatheca, is usually much longer and more tortuously coiled than the fertilization duct, through which sperm leave the spermatheca to enter the oviduct and fertilize the eggs. In extreme cases insemination ducts are coiled in >15 loops. Fertilization ducts, in contrast, are generally simpler and shorter, usually running directly from the spermatheca to the oviduct (Eberhard 1996). The selection responsible for the elaboration of these two types of duct thus seems to be related not to the sperm themselves, but to the access that the sperm (or the male genitalia) have to the spermathecae. In some groups of Linyphiidae with long coiled insemination ducts or furrows, the male has a long thread-like embolus that is inserted into the coiled female tube and reaches the spermatheca (van Helsdingen 1969; Hormiga & Scharff 2005). Long emboli are also known to traverse long coiled insemination ducts in other families (Wiehle 1961; Abalos & Baez 1963; Uhl & Vollrath 1998; Jocqué 1991; Snow et al. 2006; Jäger 2005), in one extreme case, the theridiid *Kochiura aulica*, the embolus is three times the length of the male's entire body (Agnarsson et al. 2007). In some other species of Linyphiidae, in contrast, the insemination duct is very thin and the male genitalia do not enter the duct (Wiehle's "Anschluss-Embolus" group). In the

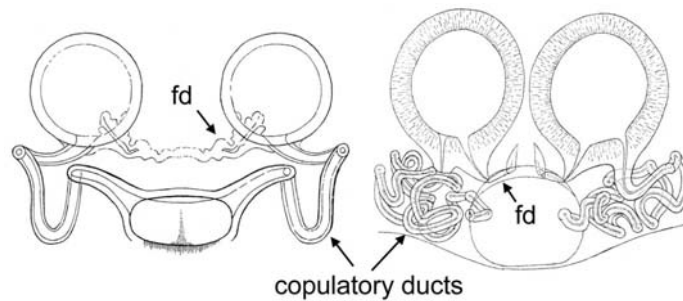


FIGURE 12.9 Female internal genitalia of two representatives of *Theridion* (Theridiidae) illustrate the longer, more tortuous ducts sperm need to traverse to enter storage sites. The species on the left has short copulatory and fertilization ducts (fd). The species on the right has highly elongated copulatory ducts, but the fertilizations ducts have remained short (from Wiehle 1967a; with permission from Senckenberg Gesellschaft).

linyphiid *Neriere* the embolus falls far short of reaching the spermatheca, and the long duct is actually an open groove. Prior to sperm transfer, this groove is filled with a substance (presumably produced by the female; B. Huber, unpublished data) through which the sperm are then pushed or sucked; a long duct that is inaccessible for the male could test his ability to push the sperm (or induce the female to push/suck) rather than to insert his embolus deeply. Experimental manipulations of male palps in the theridiid *Latrodectus hasselti* showed that males obtained more paternity when they penetrated deep enough to ejaculate sperm directly into the spermatheca rather than in the insemination duct (Snow et al. 2006).

The insemination ducts and (especially) the spermathecal walls are often riddled with pores that connect the lumen with glandular ductules (e.g., Coyle et al. 1983; Uhl & Vollrath 1998). In some cases in which the insemination ducts are longer than the emboli, the part of the duct that is not traversed by the embolus is glandular and has been hypothesized to aid in sperm transport (Baum 1972). Glandular ducts also occur, however, in at least one species in which the embolus reaches the spermatheca (Uhl & Vollrath 1998 on *Nephila*). At present, we are nearly completely ignorant of the functions of the glands associated with spermathecae and their ducts. Products of these glands have been hypothesized to induce sperm to emerge from their membranous capsules (“decapsulate”) (Eberhard & Huber 1998a), or nourish or otherwise maintain sperm. In addition, they could be responsible for sperm transport, causing the

spermathecae to take up sperm by absorbing the liquid contents of the spermatheca, and/or to expel sperm by secreting into the lumen and thus displacing the sperm (Foelix 1996; but see Berendonck & Greven 2005). The usually rigid walls of entelegyne spermathecae and their ducts seem to rule out sperm transport by female muscular contractions.

Sensory Blindness of Contact Structures

A third, more surprising possible generalization about female spider genitalia is based on the large number of SEM micrographs in the taxonomic literature. Female genitalia (in particular the epigynum) generally lack setae, at least on the externally visible portions that are contacted by the male bulb during copulation, and thus lack possible tactile sense organs (Huber 1993a; Berendonck & Greven 2005) (figure 12.10). The abdominal cuticle of spiders is typically densely covered with setae, so the lack of setae on the epigynum, which may reduce damage due to abrasion with the male’s genitalia, is a derived feature. It is less clear (because close-up SEM photos are needed, and taxonomic works generally do not provide such photos) whether epigyna also lack slit-sense organs that could sense stress in the cuticle. Epigyna are typically very dark and heavily sclerotized, however, and thus seem unlikely to be bent by the forces applied by male palps. Clearly there are exceptions (e.g., the atrium of *Linyphia triangularis* stretches during copulation—van Helsdingen 1969; the scape of many araneids is deflected during copulation—Grasshoff

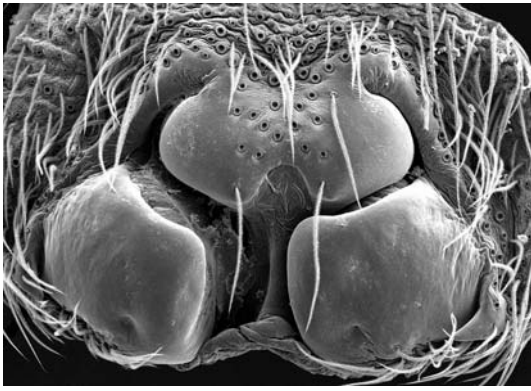


FIGURE 12.10 Mechanoreceptive hairs are conspicuously absent in large parts of external female spider genitalia. (*Griswoldia acaenata*, from Silva 2003; with permission from AMNH).

1968, 1973). But the relative rigidity of most external areas of most epigyna seems undeniable. Our tentative conclusion is that female spiders have also evolved an extraordinary absence of mechanical sensitivity in their genitalia (at least on the outer surface) that matches the insensitivity of males! It is not known whether internal portions of the female genitalia such as insemination ducts and spermathecae possess sense organs (such as those described by Foelix & Choms 1979 in walking legs).

Male–Female Fit and Coevolution

A final generalization is that the often complex sculpturing of the external surface of the epigynum fits very precisely with male genitalic structures during copulation. This generalization is based on a much more limited sample of species in which pairs have been killed instantaneously during copulation by freezing or by hot fixatives (van Helsdingen 1965, 1969, 1971; Grasshoff 1968, 1973; Huber 1993a, 1994, 1995a, b; Eberhard & Huber 1998a; Knoflach 1998; Senglet 2004; Uhl et al. 2007). A previous technique, which depended on artificially expanding male palpal bulbs not in contact with the female and attempting to deduce how they fit with females, is likely to lead to erroneous conclusions (Huber 1993a). All available studies document consistent, precise male–female fits: male and female morphology is clearly coevolved, and species-specific male traits are often reflected

in species-specific female traits with which the male structures fit (table 12.1). This coevolutionary interaction may have imposed limits on sexual size dimorphism in some spiders (Ramos et al. 2005).

Summarizing, the external genitalia of female spiders generally have rigid, complex designs that are at least sometimes “selectively cooperative” (see below); they are associated with tortuous ducts through which sperm arrive for storage in the spermatheca, but simple direct ducts through which they leave storage when they fertilize eggs. They fit physically complementary structures of the male genitalia, and are largely devoid of sensation. Why would this unusual set of male and female traits evolve? We will discuss the three most commonly cited hypotheses for genital evolution (for additional reasons to discard two additional hypotheses, see Eberhard & Huber 1998b).

WHY THESE STRANGE MALE AND FEMALE GENITALIA?

Lock and Key

At first, the descriptions just given seem to fit perfectly with expectations of male and female morphology that have evolved under selection for species isolation by mechanical “lock and key”. This hypothesis supposes that female genital structures evolved to exclude the genitalia of males of other species, to thus enable the female to avoid cross-specific inseminations; males could also benefit (though to a lesser extent because of their cheaper gametes). But there are reasons to doubt the species isolation part of this hypothesis in spiders. Spider species that have evolved in isolation from other close relatives, and that should thus have been free of selection to avoid cross-specific fertilizations, nevertheless have elaborate, species-specific genitalia. Examples include species endemic to particular isolated islands with no other congeners present (figure 12.11; Platnick & Shadab 1980; Peck & Shear 1987; Gertsch & Peck 1992; Hormiga 2002; Hormiga et al. 2003). Multiple congeneric species endemic to different isolated caves that have probably also been isolated and nevertheless have species-specific genitalia are further examples (Gertsch 1974; Deeleman-Reinhold and Deeleman 1980; Hedin 1997), though in these cases strict isolation is less certain. In addition, the genitalic

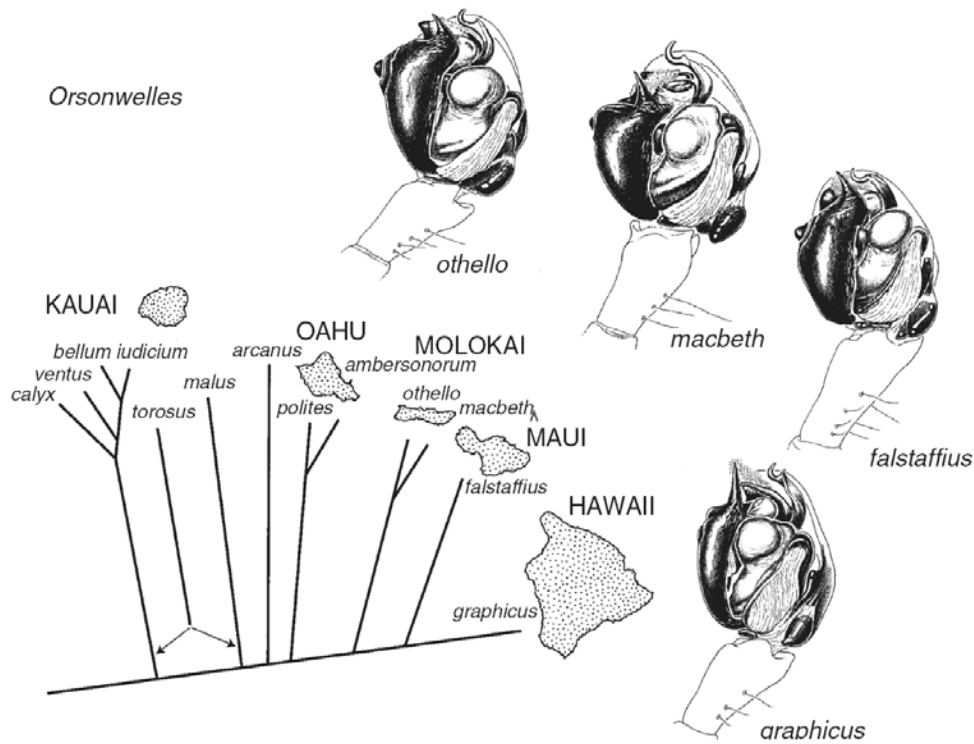


FIGURE 12.11 Male palps (above and at right) of four species of *Orsonwelles* spiders fail to fit the predictions of the hypothesis that species isolation by lock-and-key is responsible for the rapid divergent evolution of these spider genitalia. All of the 13 species are single-island endemics, and most have very small, non-overlapping distributions, usually in high, wet areas and often limited to a single mountain top (Hormiga 2002; Hormiga et al. 2003). A biogeographic pattern of progressive colonization from older to newer islands in the archipelago is consistent with a phylogeny of the spiders based on both morphological and molecular traits (Hormiga et al. 2003). Although there has been substantial intra-island speciation (where strict isolation from congeners is less certain), 4 of 12 cladogenic events occurred between islands (and thus in apparent strict allopatry). Contrary to expectations of lock and key, genitalia are complex and especially useful in distinguishing species throughout the genus (Hormiga et al. 2003), and constituted 53 of 71 phylogenetically informative morphological traits. The islands farther to the right are younger, as are the species endemic to them (phylogeny below). There is only one *Orsonwelles* species on Maui and one on Hawaii, but despite this isolation, neither their female nor their male genitalia are simpler. In addition, the female genitalia of the two species sympatric on Molokai (*othello* and *macbethi*) are, contrary to predictions especially similar rather than especially different from each other (after Hormiga et al. 2003; Hormiga 2002; with permission).

character displacement in zones of overlap that is predicted by selection for species isolation did not occur in one pair of species that was carefully chosen to maximize the likelihood that it would occur (Ware & Opell 1989). Character displacement, which should be widespread, seems in fact to be quite rare; we know of only one case (the genitalia

of *Argiope trifasciata* are smaller in areas of sympatry with *A. florida*; Levi 1968) (and of course random variation is expected to produce a certain number of apparent confirmations). Detailed study of morphology has showed that cross-specific pairing is not precluded by the female's genitalic design in some spiders (Gering 1953).

Table 12.1 Examples of “selectively cooperative” female genital structures and the corresponding male structures

Taxa	Female structures	Male structures	References
Haplogynae			
Pholcidae, various genera	Epigynal and abdominal pits	Cheliceral and bulbal apophyses	Huber 2002, 2003b, 2005b
RTA clade			
Many families	Various folds and pits	RTA	Bristowe 1958; Loerbroks 1983, 1984; Huber 1995a, b
Agelenidae, <i>Agelenopsis</i>	Coupling cavity	Conductor	Gering 1953
Oxyopidae, <i>Peucetia</i>	Epigynal depression	Ventral paracymbium prong	Exline & Whitcomb 1965
Lycosidae	Epigynal pockets	Bulbal apophyses	Osterloh 1922; Sadana 1972
Miturgidae, <i>Cheiracanthium</i>	Epigynal pit	Processes of tibia and paracymbium	Gering 1953
Orbiculariae			
Uloboridae, <i>Hyptiotes cavatus</i>	Vaginal invagination	Median apophysis spur	Opell 1983
Linyphiidae, Araneidae	Pits, grooves, and bulges near tip of scape	Projecting point of male suprategular apophysis (= median apophysis), or paracymbium	van Helsdingen 1965, 1969; Blest & Pomeroy 1978; Grasshoff 1968, 1973; Uhl et al. 2007
Linyphiidae, <i>Neriene</i> and <i>Linyphia</i>	Spiral-shaped atrium	Spiral-shaped bulbal terminal apophysis	Osterloh 1922; van Helsdingen 1969

Sexually Antagonistic Coevolution (“SAC”)

One currently popular explanation for rapid divergent evolution in sexual traits like genitalia is sexually antagonistic coevolution (“SAC”) of males and females. Briefly (see Chapter 4 of this book for a more detailed discussion), SAC supposes that because male and female interests are not synonymous, conflict between the sexes over control of copulation will lead to coevolutionary races between “aggressive” male traits that enhance the male’s control over copulation, and “defensive” female traits that enhance the female’s control and thus reduce the damage done to her reproductive output by the male.

One SAC prediction is that female morphology should tend to coevolve with male morphology. As noted above, this prediction is clearly supported in spiders. A second aspect of this predicted coevolution, however, is clearly not confirmed in spiders. If genitalic diversification were due to an arms race between males and females for control of copulation, female genitalia should often have recognizably “defensive” designs, appropriate for excluding male genitalia. We know of no case, however, in the

huge array of female spider genitalia illustrated in taxonomic descriptions, in which the female has an erectable spine, or a hood that can be pulled down over the epigynum, and that would thus represent a facultatively imposed female barrier to which males might then be expected to evolve countermeasures under the SAC hypothesis. Such optional barriers (as opposed to fixed barriers which could also be used to filter males under cryptic female choice) would be expected under SAC to defend non-selectively against all male attempts to copulate; if they existed, they would constitute strong evidence in favor of SAC. Instead, many of the traits of female spider genitalia are most easily understood as being “selectively cooperative” structures, such as pits or grooves whose only apparent function is to receive and provide purchase for male structures that have particular forms, aiding the male whose structures fit adequately to perform functions such as to physically couple genitalia together. Examples of selectively cooperative female structures abound in spider genitalia (table 12.1; figures 12.6 and 12.12).

A third prediction of SAC is that rapid divergent genitalic evolution should be associated with certain types of male–female pre-copulatory interactions

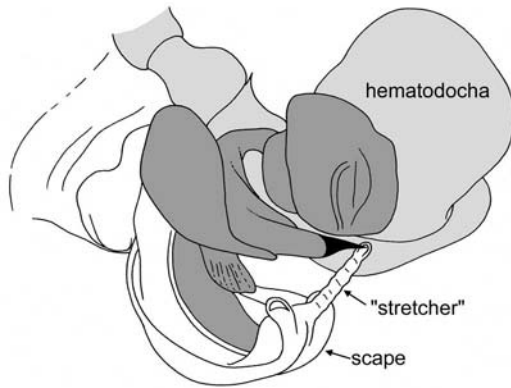


FIGURE 12.12 Female genitalia of *Lepthyphantes leprosus* (white) with male palp coupled (palp and hematochocha light gray, bulb dark gray). The tip of the male median apophysis (black) sits in a small “selectively cooperative” depression near the tip of the “stretcher” (the depression has no other known function); pressure from the median apophysis extends the scape, and allows intromission when the hematochocha is expanded (after van Helsdingen 1965).

but not others (Alexander et al. 1997). Coevolutionary races are most likely in groups in which males are more able to physically coerce or sexually harass unreceptive females (“coercive” interactions—Alexander et al. 1997). In contrast, male–female conflict and coevolutionary races are less likely in groups in which males are, for one reason or another, not able to physically coerce females into copulating, and only interact with females that are receptive (for instance, females which have been lured into the male’s vicinity and are thus presumably receptive) (“luring” interactions) (Alexander et al. 1997). A major review of spider mating behavior in more than 150 species (Huber 1998) showed that interactions preceding copulation are typically of the luring type; nevertheless, in contradiction to the SAC prediction, spider genitalia very typically show sustained rapid divergent evolution.

This contradiction of SAC predictions extends to the fine details of the physical coupling between male and female genitalia. It is clear in a number of groups that tiny movements of the female can easily disrupt the difficult process of alignment of the male, arguing against the likelihood that adjustments

of the morphology of the female genitalia are needed as defenses against males, and thus against the idea that such morphological differences in females function in this context. For instance, Gering (1953) noted that “Even relatively slight movements of the female ... could effectively preclude the possibility of mating” (p. 53), and concluded that “The cataleptic state of the female is an essential feature in copulation in the genus *Agelenopsis*” (p. 76). The females of *Faiditus* (= *Argyrodes*) *antipodiana*, *Leucauge mariana* and *Nesticus* must flex their abdomens ventrally for the males to be able to couple; the angle of flexion varies, and sometimes it is insufficient for the male to achieve coupling (Whitehouse & Jackson 1994; Eberhard & Huber 1998a, unpublished). In a number of species other female movements are crucial to permit coupling, and sometimes are not executed fully: protrusion of the epigynal area in *Tenuiphantes* (= *Lithyphantes*) (van Helsdingen 1965), the nephilid *Herennia* (Robinson & Robinson 1980), and the theridiosomatid *Wendilgarda* (Coddington 1986); lateral inclination of the abdomen to facilitate intromission in the agelenid *Agelenopsis* (Gering 1953), several lycosids (Rovner 1971; Costa 1979; Stratton et al. 1996) and the ctenid *Cupiennius salei* (Melchers 1963); inflation of the genital area in the mecicobothriid *Mecicobothrium* (Costa & Pérez-Miles 1998); and erection of the scape in araneids (Grasshoff 1968, 1973). Similar examples of female cooperative behavior patterns abound in the papers of U. Gerhardt (Huber 1998). In sum, the idea that female spiders are generally physically coerced via male genitalic structures into copulation is simply not correct.

Cryptic Female Choice

We have proposed (Eberhard & Huber 1998b) an hypothesis that depends on a lock-and-key type of mechanical fit between the male and the female, but in which rapid evolutionary divergence is due to sexual selection by cryptic female choice (“CFC”), rather than natural selection to avoid cross-specific fertilization. Seen from the male’s evolutionary perspective, variations in genital morphology that enable him to solve the difficult mechanical challenges of copulation (e.g., more rapid, more reliable, deeper intromission) could confer advantages over other males. Seen from the evolutionary perspective of females, the mechanical problems

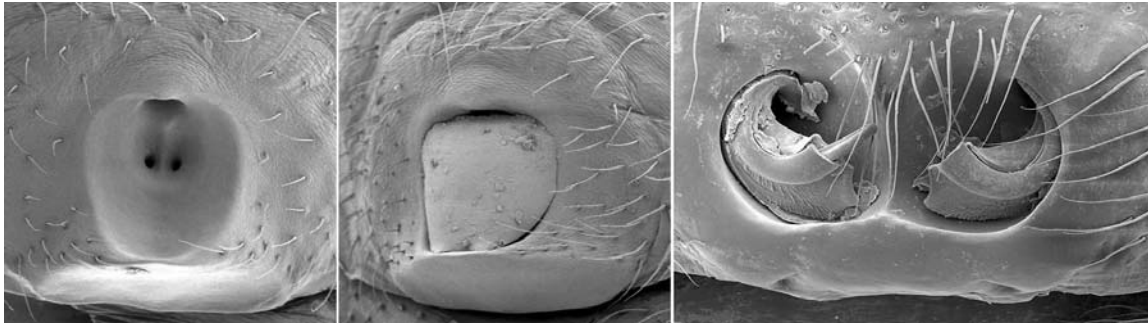


FIGURE 12.13 Mating plugs are common in spiders and vary in many respects. On the left and center unplugged and plugged female specimens of *Theridion varians* (from Knoflach 2004; with permission from Oberösterreichisches Landesmuseum), showing a secretory mating plug. On the right broken portions of male genitalia plug both openings to insemination ducts on the epigynum of a female *Herennia multipuncta* (from Kuntner 2005; with permission from CSIRO).

experienced by males that lack sense organs in their genitalia could lead to selection on females to discriminate against those males least able to achieve effective genitalic alignment, either through the stimuli received or via changes in morphology that bias male abilities to fit mechanically. The female could gain via the production of sons with superior genitalic designs. Such selection to discriminate among male designs could favor changes in female morphology that would make her genitalia more selective, facilitating a male's chances of getting his sperm into her spermathecae only if his genitalia have certain mechanical properties. Selection of this sort could favor rigid female genitalic structures with complex forms that would act as filtering devices (Huber 1993b). The female would thus be exercising sexual selection by cryptic female choice with respect to the male's ability to adjust mechanically to her complex genitalic morphology.

CFC could explain the prevalence of "selective cooperative" female designs that was mentioned above as evidence against the SAC hypothesis. But CFC might seem unable to explain why either male or female genitalia would change, much less change rapidly. Once the males of a species evolved a genitalic design that fits with the corresponding structures of conspecific females, further changes in either males or females would seem to be disadvantageous. A male with variant genitalia should be at a disadvantage because he would couple more poorly with females. And a female with variant morphology that favored non-standard male designs would also stand to lose: she might run

greater risks of not receiving adequate numbers of sperm, and her male offspring might be more likely to have deviant genital morphology because their fathers were atypical.

This description of the disadvantages of changes is based, however, on typological oversimplifications. In the first place, despite the impression given from the usual descriptions in taxonomic papers, neither the genital form of the male nor that of the female is invariant in spiders (figure 12.13; Gering 1953; Lucas & Bücherl 1965; Levi 1968, 1971, 1974, 1977a, b, 1981; Grasshoff 1968; Coyle 1968, 1971, 1974, 1981, 1984, 1986, 1988; Hippa & Oksala 1983; Kraus & Kraus 1988; Ware & Opell 1989; Pérez-Miles 1989; Milasowszky et al. 1999; Azarkina & Logunov 2006). There is also a certain degree of mechanical flexibility in some male genital structures (and perhaps in those of the females of some species) so that morphological variation does not necessarily imply loss of function (Grasshoff 1974, 1975; Loerbroks 1984). In addition, the absolute sizes of male and female genitalia in most if not all species also vary. In six different species measured in five families, the coefficients of variation in the size of male genitalia was of approximately the same order as that of other body parts (Coyle 1985; Eberhard et al. 1998). In sum, there is generally no single genital morphology for a given species. If the pattern of geographic variation in spider genitalia resembles that of some other traits (Mayr 1963), intra-specific differences in genital form could be especially great in small, geographically peripheral populations, where speciation is likely to occur.

An empirical indication that there is indeed a certain amount of imprecision or flexibility in male–female fits (and thus “room” for functional male innovations) is that the males of several groups have changed the side of the female epigynum that they inseminate. A tetragnathid and two distantly related theridiid groups have changed from inserting each palp into the ipsi-lateral insemination duct opening on the female epigynum, and now insert into the contra-lateral side (Huber & Senglet 1997; Agnarsson 2004, 2006). The early stages of such a change must have involved less than perfect male–female fits.

Intraspecific variations in male and female morphology and behavior may often influence the possibility of successful coupling, but their effects are almost completely unstudied, due to the unfortunate typological emphases in studies of the functional morphology of spider genitalia to date (including our own). The problems a male faces are surely not uniform, and a male variant that improves his ability to solve these problems could be favored. These problems could include the need to fit mechanically with the female, to stimulate her effectively, or both. Changes in males could in turn favor changes in females that further bias paternity in favor of certain males, perhaps including

morphological adjustments of females that guide these males’ sensorily deprived palps. The combination of male variations and compensatory changes in females could result in rapid evolution under sexual selection by cryptic female choice.

OTHER UNUSUAL TRAITS IN SPIDERS

Lack of a Forceful Grasp on the Female

In insects, the female’s reproductive opening is near the tip of her abdomen, and male genitalia often include powerful clasping structures that are capable of largely restraining the movements of the female’s abdomen (Snodgrass 1935; Robson and Richards 1936; Tuxen 1970; Wood 1991). In spiders, probably due to the position of the female’s epigynum on the anterior portion of her abdomen and the lack of muscles in the palpal bulb, male genitalia are only seldom (Uhl et al., in press) powerful clasping devices (except in Pholcidae—Huber 1999). More delicate clasps, which serve more to hold the palp in contact with the female, rather than restrain her abdomen, are common, however.

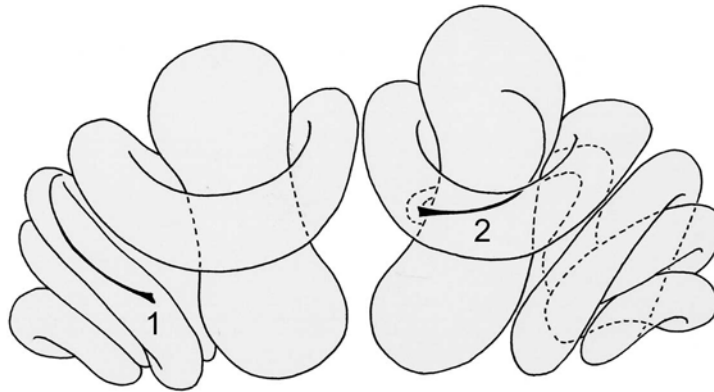


FIGURE 12.14 Broken tips of the male embolus (black) of the redback spider *Latrodectus hasselti* lodged in the female’s insemination ducts and spermatheca. When placed at the entrance to the spermatheca (2), the thin, hair-like embolus tip effectively blocks the access of subsequent males to the spermatheca; but when the embolus tip is positioned elsewhere (1), it does not constitute an effective block. The poor morphological design of the tip for blocking is probably due to the tortuous coiling of the female’s insemination ducts, which makes it necessary for the embolus to be thin and flexible to arrive at the entrance of the spermatheca (after Snow et al. 2006; with permission from Blackwell).

TABLE 12.2 Genital plugs in spiders. Note that several of the statements about origin and function are not based on detailed observation and need reexamination. Mating plugs consisting of ectomized male body parts are covered in Table 12.3 (largely from Suhm et al. 1995 and Huber 2005a)

	Origin	Barrier for further males	References
Agelenidae:	Female secretions	Possibly	Chyzer & Kulczynski 1897 and Strand 1906 in Suhm et al. 1995; Engelhardt 1910
<i>Agelena labyrinthica</i>			
<i>Agelena limbata</i>	Male palpal glands	Yes (when complete)	Masumoto 1993
Amaurobiidae:	Male bulbal gland	Yes (when complete)	Gerhardt 1923; Wiehle 1953; Suhm et al. 1995
<i>Amaurobius</i>			
<i>Tasmarubrius</i>	?	?	Davies 1998
Anyphaenidae	?	?	Ramírez 1999, 2003
Araneidae:	?	Possibly * ¹	Levi 1995a
<i>Metazygia</i>			
Ctenidae	?	?	Silva 2007
Desidae (sub Toxopidae)	?	?	Forster 1967
Dictynidae	Male?	?	Bertkau 1889
Gnaphosidae	?	?	Grimm 1985; Suhm et al. 1995
Linyphiidae	?	?	Millidge 1991; Stumpf 1990 in Suhm et al. 1995 and Eberhard 1996: 153
<i>Oedothorax</i>	Male?	Yes (depends on copulation duration)	Uhl & Busch personal communication
Lycosidae	?	?	Suhm et al. 1995
Nesticidae:	?	?	Weiss 1981; B. Huber unpublished data
<i>Nesticus</i>			
Oxyopidae:	?	?	Brady 1964; Exline & Whitcomb 1965; Whitcomb & Eason 1965 in Jackson 1980
<i>Peucetia</i>			
Philodromidae:	Sperm and (male?) secretions	?	Huber 1995a
<i>Philodromus</i>			
Pholcidae:	?	?	Huber 2005b (Figures 292-294, 394); common also in other genera, B. A. Huber, unpublished data
<i>Belisana</i>			
Salticidae			
<i>Heliophanus</i>	Sperm plug* ²	?	Harm 1971; K. Thaler in Harm 1971
<i>Phidippus</i>	Male secretions?	At least in 30%	Jackson 1980
<i>Portia</i>	Sperm plug* ²	?	Jackson & Hallas 1986
Tetragnathidae:	Male and female secretions	Depending on plug composition	Eberhard & Huber 1998a; Mendez 2002
<i>Leucauge</i>			
Theridiidae			
<i>Argyrodes</i>	?	?	Exline & Levi 1962
<i>Argyrodes argyrodes</i>	Male bulbal secretions	Not necessarily	Knoflach 2004
<i>Argyrodes antipodiana</i>	sperm plug* ²	?	Whitehouse & Jackson 1994
<i>Argyrodes</i> and <i>Rhomphaea</i>	?	?	Gertsch 1979: 88
<i>Steatoda bipunctata</i>	Male bulbal secretions	Not necessarily	Knoflach 2004
<i>Steatoda castanea</i>	Male bulbal or oral secretions?	No	Gerhardt 1926
<i>Steatoda triangulosa</i>	Male oral secretions	Possibly	Braun 1956; Knoflach 2004
<i>Theridion</i>	Male genital tract and female vulval secretions	Yes	Gerhardt 1924; Levi 1959; Knoflach 1997, 1998, 2004
Thomisidae:	?	Probably	Muniappan & Chada 1970
<i>Misumenops</i>			
Uloboridae:	Male palpal (and oral?) secretions	Possibly	Patel & Bradoo 1986
<i>Uloborus</i>			
Zodariidae	Male cymbial glands?	?	Jocqué 1991

*¹ The amorphous black secretion was difficult to remove for the observer (Levi 1995a)

*² No evidence presented

Blest and Pomeroy (1978) describe a calliper-like clasp of the female genitalia by two male structures; Grasshoff's (1968, 1973) schemes show male structures clasping female structures; Knoflach and van Harten (2006) describe the *Echinotheridion* palp as functioning like a forceps; and Stratton et al. (1996) describe a palpal process of some lycosids that pinches the sides of the epigynum (further examples in Huber 1993a, 1994, 1995a, b; Uhl et al. 2007).

A second type of forceful activity common in the genitalia of male insects, pulling portions of the female's reproductive tract apart to allow male entry or deeper penetration (Sakai et al. 1991 on a cricket; Byers 1961 on a tipulid fly; Whitman & Loher 1984 on a grasshopper), seems to be absent in spiders. In this case the apparent reason lies with the female, not the male; the genitalia of most female spiders form a single, rigid unit, with few or no moving parts so prying apart female sclerites is often not an option for the male. This description of female rigidity must be tempered, however, by the recent description of muscles that move portions of internal female genitalia in one species (figure 12.8) (Burger et al. 2006b), and our current ignorance of internal female musculature.

Mating Plugs are Common

Solid material is often deposited on the genital openings of female spiders (and sometimes the entire epigynum) (figure 12.14). This material or "mating plug" varies with respect to its composition, origin, hardness, and the degree to which it covers the epigynum. The material is generally amorphous. Mating plugs have been described in many spiders (reviewed in Suhm et al. 1995; Huber 2005a; table 12.2), and the taxonomists' practice of 'cleaning' the female genitalia in order to study their morphology almost certainly results in an underestimate of their frequency in the literature. Few studies have gone beyond the traditional assumption that these plugs are produced by the male to impede access of rival males to the female, and other potential functions like preventing sperm leakage, backflow, desiccation, or genitalic infection generally remain to be tested. Alternative explanations are surely important, because some "plugs", such as the sparse blobs of waxy substance in the salticid *Phidippus johnsoni* (Jackson 1980) and the thin and easily broken plugs in some females of the tetragnathid *Leucauge mariana* (Méndez & Eberhard, unpublished data), surely do not impede

the access of subsequent males. Plugs constituted by broken pieces of the male's own genitalia inside the female are also common in spiders (figures 12.13 and 12.14).

Several studies suggest that sperm competition is a major factor driving the evolution of spider mating plugs. The clearest evidence comes from a combination of several types of observations: that males more often fail in attempts to insert their palps when a female bears a mating plug; that when a male succeeds in removing a plug he is then able to achieve intromission more frequently; and that males sometimes fail in attempts to remove plugs (Masumoto 1993; Méndez 2002) (both of these studies were incomplete, however, in that they did not demonstrate that subsequent offspring were sired by the male that had removed the plug). The fact that eggs in entelegynes exit via a different opening from the opening used for intromission means that especially tenacious, durable plugs are less damaging to the female than they would be in other groups in which such a plug might interfere with oviposition, and thus help explain the commonness of plugs in spiders. Plugs utilizing portions of the male's own genitalia may be advantageous in some species due to the possibly low probability that the male will live to encounter another female (Snow et al. 2006). On a more mechanical level, the rigid sclerotized nature of most female external genitalia and copulatory ducts (see above) probably makes physical plugging more feasible than it would be if the female tracts were highly flexible.

Some male plug secretions originate in glands, including bulbal glands, glands in the mouth area, and glands in the genital tract (table 12.2). Other plugs apparently consist mainly of sperm (Huber 1995a; Whitehouse & Jackson 1994). Female production of plugs or at least of components of plugs, has also been known for a long time (e.g., Strand 1906 in Suhm et al. 1995; Engelhardt 1910; Gerhardt 1924), and recent observations have confirmed important female roles in plugging their own genitalia. Females of several species of theridiids and the tetragnathid *Leucauge mariana* contribute a liquid that combines with male products and is crucial if the plug is to form a barrier against further intromissions (Knoflach 1998; Méndez 2002; Méndez & Eberhard, unpublished data). Females of the latter species are more likely to add liquid when the male performs more of certain copulatory courtship behavior patterns (Aisenberg & Eberhard, 2009). Evidence for a less direct female role in plug

TABLE 12.3 Male ectomized genital structures in spiders. Only those cases are listed in which a male structure commonly or obligatorily breaks during or at the end of mating. Occasional breaking is probably much more widespread (e.g., Wiehle 1961, 1967b; Harm 1981)

	Structure	Barrier for further males	Males sterile after mating	References	
Araneidae					
	<i>Argiope</i>	Embolus tip	Yes, if placed properly	Males die during or shortly after mating	Abalos & Baez 1963; Levi 1965, 1968; Foellmer & Fairbairn 2003; Nessler et al. 2007a, b; Uhl et al. 2007
	<i>Larinia</i> (incl. <i>Drexelia</i>), <i>Aculepeira</i> , <i>Araneus</i> , <i>Metepeira</i>	Embolus cap	?	Yes	Abalos & Baez 1963; Grasshoff 1968: 43, 1971; Levi 1970, 1973, 1975a, b, 1977b, 1991; Scharff & Coddington 1997; Piel 2001
	<i>Acacesia</i> , <i>Hyposinga</i>	Embolus scale	?	?	Levi 1972a, b, 1976
	<i>Cyclosa</i>	Tooth of conductor	?	?	Levi 1999
	<i>Metazygia</i>	Part of embolus	?	?	Levi 1995a
	<i>Madrepeira</i>	Appendage of embolus	?	?	Levi 1995b
	<i>Singafrotypa</i>	Embolus	?	?	Kuntner & Hormiga 2002
Cybaeidae					
	<i>Cybaeus</i>	Conductor	?	?	Ihara 2006, 2007
Nephilidae					
		Palp broken or only disfigured	Variable* ¹	Yes	Wiehle 1967b; Robinson & Robinson 1978; Schult & Sellenschlo 1983; Fromhage & Schneider 2006; Schneider et al. 2001, 2005a, b; Kuntner 2005, 2007
Oxyopidae					
	<i>Peucetia</i>	Paracymbium	?	No	Brady 1964, Exline & Whitcomb 1965, Santos & Brescovit 2003, Ramirez et al. in press
Theridiidae					
	<i>Achaearanea</i>	Embolus tip	No	No	Abalos & Baez 1963; Lockett & Luczak 1974 in Miller 2007b; Knoflach 2004
	<i>Latrodectus</i>	Embolus (part or entire), flagelliform	In some species probably yes* ²	Variable* ³	Bhatnager & Rempel 1962; Abalos & Baez 1963; Kaston 1970; Wiehle 1967b; Breene & Sweet 1985; Müller 1985; Berendonck & Greven 2002, 2005; Knoflach & van Harten 2002; Andrade & Banta 2002; Knoflach 2004; Snow et al. 2006
	<i>Tidarren</i> / <i>Echinotheridion</i>	Part of palp, (some species no mutilation)	No (maybe short-term)	Males die during mating	Knoflach & van Harten 2000, 2001, 2006; Knoflach 2002, 2004

*¹ Effective barrier in *Nephila fenestrata* (Fromhage & Schneider 2006), no barrier in *N. plumipes* (Schneider et al. 2001).

*² Probably effective barrier in *L. renivulvatus* (Knoflach 2004), *L. revivensis* (Berendonck & Greven 2002, 2005), *L. hasselti* (Snow et al. 2006).

*³ Male sterility after mating (Abalos & Baez 1963; Andrade & Banta 2002; but: Breene & Sweet 1985) may be due to sperm depletion rather than organ breakage (Snow et al. 2006).

production comes from the behavioral cooperation of the female with the male. For instance, the male of the theridiid *Argyrodes argyroides* interrupts copulation after sperm transfer and leaves the female, then returns to deposit the plug, with the female continuing to cooperate (Knoflach 2004). Direct female participation in producing a plug is apparently very unusual in other animal groups; the only example that we know of in which females may play a similar role is *Drosophila* (the so-called “insemination reaction”, whose significance seems not to have been established) (Markow & Ankney 1988).

One hypothesis that could explain why females sometimes play active roles in forming plugs is related to the fact that most entelegyne spider females have sclerotized external genitalia, and cannot close the openings of their insemination ducts. This might result in possible problems of sperm leakage, backflow during oviposition, and microbial infections (Simmons 2001). This explanation would suggest, however, that some sort of flimsy, self-made plug would also be advantageous *before* copulation, and such plugs are not known (though if they were internal, they could be difficult to discover).

Male genital structures that break off (are “ectomized”) and remain in the female can also function as mating plugs (figures 12.13 and 12.14). In entelegyne spiders, routine or obligatory genital ectomization has evolved independently in several groups (Miller 2007b; table 12.3). In some species, males invariably die during copulation and the pedipalp or even the entire male body remains attached to the female for at least a short while, and may function as a short-term mating plug (Knoflach & van Harten 2001; Foellmer & Fairbairn 2003; Knoflach & Benjamin 2003). Genital breakage that leaves pieces inside the female occurs in few other groups of animals (Eberhard 1985).

In some spider species there is a line of weakness at the point where the male genital structure breaks (Bhatnager & Rempel 1962), leaving no doubt that breakage is not accidental, and is advantageous for males. One species has a process that apparently functions only as a plug, and is not involved in insemination (Nessler et al. 2007b). In one and perhaps two species of the theridiid genus *Latrodectus*, genital breakage does not prevent the mutilated male from inseminating subsequent females (Breene & Sweet 1985; Snow et al. 2006), but in others such as the araneid *Argiope bruennichi*,

male breakage leaves the male unable to inseminate additional females (Nessler et al. 2007a). The alternative possibility that “break-away” sclerites function to facilitate male escape from female attempts to cannibalize the male has been ruled out in two species (Snow et al. 2006; Nessler et al. 2007a).

Some of these pieces of male genitalia seem to seal the external opening of the female insemination ducts, as with the plugs just discussed (Levi 1972a; Kuntner 2005) (figure 12.13), while other ectomized structures obstruct internal portions of this duct, permitting intromission by subsequent males but preventing them from reaching more internal portions of the female (Nessler et al. 2007a). In other species, however, there are sometimes pieces from several males inside a single female spermatheca (Abalos & Baez 1963; Müller 1985), suggesting that male ectomized structures are not always effective as plugs (Schneider et al. 2001; Snow et al. 2006). Of course, such plugs could be favored as paternity assurance mechanisms even if they only partially reduce the success of subsequent males.

Recent data indicate even more dynamic, exciting possibilities. In the orb weaver *Argiope bruennichi*, there is variation in whether or not the male’s palpal sclerites break off (in 15% of copulations they failed to break), in whether the fragments that broke off remained lodged in the female (3% failure), and in which of two predetermined breakage lines is used (Nessler et al. 2007a; Uhl et al. 2007). Different sized pieces break off in different populations, with the more drastic type of mutilation in only one population (Uhl et al. 2007). Both plugs and ectomized male processes were more common in the epigyna of females of the oxyopid *Peucetia viridans* at drier sites in California (Ramirez et al. 2007), leading the authors to speculate that they serve to resist desiccation; this function seems more likely for the plug (which may come from the female) than for the male process. The form of the process that breaks off in the distantly related *Cybaeus* varies among species (Ihara 2006, 2007), and even varies over the geographic range of *C. kuramotoi* in western Japan (Ihara 2007), again suggesting rapid divergence.

In still another family, broken fragments of the male block access of subsequent males of *Latrodectus hasselti* (Theridiidae) when they lie at the entrance to the female spermatheca (where the insemination duct is narrow and heavily sclerotized (Berendonck & Greven 2005), but for unknown

reasons they are sometimes found instead more proximally in the insemination duct, where the lumen is wide; here they do not impede the access of subsequent males (Snow et al. 2006) (figure 12.14). Some male ectomized structures left deep in the female are thin and hairlike, and poorly designed to function as physical plugs (figure 12.14). Probably the reason for this sub-optimal design is the little discussed fact that the female morphology constitutes the “playing field” on which the males must compete to deposit or remove plugs; her morphology imposes limitations on the functional designs that are available to males when they attempt to plug females. Possible coevolutionary male-female interactions remain to be explored.

Perhaps spider males are prone to use such drastic techniques to prevent female remating because males have relatively small expectations of finding and inseminating additional females (Andrade & Banta 2002; Andrade 2003; Fromhage et al. 2005; Kasumovic et al. 2006). A reduced ability to find and inseminate a second female could increase the net advantage of self-sacrifice, which could in turn lead to further reduction in the ability to inseminate other females. Snow and colleagues (2006) speculated that ectomized plugs originated with more costly “accidental” organ breakage, for instance when females attempted to interrupt copulations that males were attempting to prolong. Such “accidental” breakage may be widespread (Wiehle 1961 1967b; Harm 1971).

If plugs do in fact often serve to impede the access of rival males, then males should be under selection to remove plugs. The most obvious male structures for plug removal are sclerites of the male’s palp. A partial confirmation of this hypothesis comes from a recent study of *Leucauge mariana*: a hook-shaped process of the conductor is used to snag and remove plugs but does not seem to be crucial for the insertion of the embolus (Eberhard & Méndez, unpublished data). Males of *Agelena limbata* and *Dubiaranea* sp. also remove plugs with their palps (Masumoto 1993; Eberhard 1996), but the particular structures that they use remain to be determined.

The durability of plugs has also been little studied. Lifelong plugs are feasible in entelegyne spiders, because they do not occlude the duct for oviposition (above). Durable plugs may occur in *Amaurobius* (Suhm et al. 1995), and also in *Nesticus cellulanus*, in which a male apophysis ruptures the cuticular cover of the female’s vulval pocket and is

lodged in this pocket during copulation (Huber 1993a). When a second male copulated immediately after the first copulation, he was able to insert his apophysis, but if two days elapsed before the second copulation, the second male was unable to insert his bulb in the mated side of a half-virgin female, presumably as a result of the hardening of substances in the ruptured female vulval pocket (Huber 1993a). A more extreme case of female mutilation occurs in *Metazygia* orb-weavers, in which the male apparently tears off a portion of the female’s epigynum (the scape) during or after mating (Levi 1995a). This mutilation may prevent subsequent males from inseminating the female, because the female scape is crucial in araneid genital mechanics (Grasshoff 1968, 1973a; Uhl et al. 2007).

First Male Sperm Precedence and the “Suitor” Phenomenon

Direct measurements of sperm precedence in doubly-mated female spiders are not common, and have given mixed results (summary, Elgar 1998). Indirect evidence suggests, however, that strong first male sperm precedence is common. Many male spiders associate with immature, penultimate instar females rather than with mature females (the “suitor” phenomenon) (Jackson 1986; Robinson 1982; see also Eberhard et al. 1993; Bukowski & Christenson 1997b). Males associated with penultimate females typically mate with the female soon after she moults to maturity, and then leave. Thus the likely reason for the suitor phenomenon is that the first male achieves appreciable sperm precedence.

Variation and Exaggeration in Female Genitalia

The attention paid by taxonomists to female genitalia in spiders allows a more detailed look at female genital evolution than is possible in many other groups of animals. It may be that female genitalia are more variable intra-specifically than those of the males (Kraus & Kraus 1988 on *Stegodyphus*, especially *S. dufouri*; Baehr & Baehr 1993 on Hersiliidae; Heimer 1989 on Filistatidae; Pérez-Miles 1989 on Theraphosidae; Sierwald 1983 on *Thalassius*; Levi 1997 on *Mecynogea*; Crews & Hedin 2006 and Crews in preparation on Homalonychidae; Bennett 2006 on Amaurobiidae

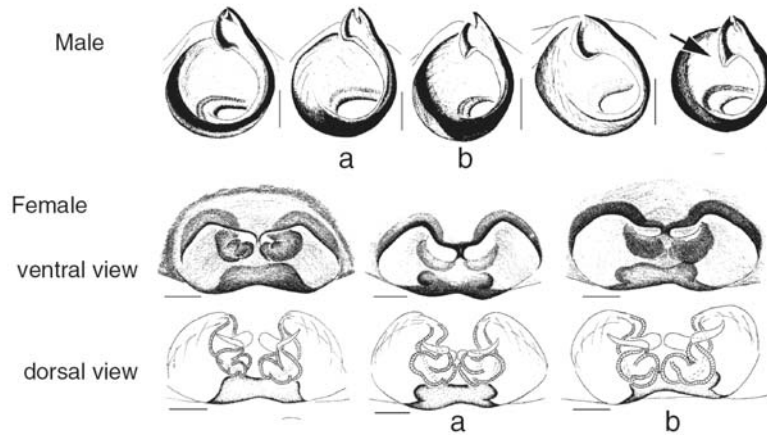
Aelurillus luctuosus

FIGURE 12.15 Intraspecific variation in the genitalia of both males (above) and females (below) of the salticid spider *Aelurillus luctuosus*; the female genitalia are shown in both ventral (external) and dorsal (internal) view. Pronounced intraspecific variation in genitalia is common in this family (from Azarkina & Logunov 2006; with permission).

and Cybaeidae). Another possible intra-specific trend is that both male and female genitalia are especially variable intra-specifically in some groups, such as certain genera of salticids (Azarkina & Logunov 2006) (figure 12.15) (also Crews, unpublished data). The reasons for greater variation in some taxonomic groups than others, or in one sex as opposed to the other are not clear. Further data to evaluate these trends would be welcome.

Not only is it clear that intraspecific variation in genitalia exists in spiders, there is also evidence that such variation has been selectively important. The genitalia of both male and female spiders resemble those of insects in showing negative static allometry (relatively large genitalia in smaller individuals, and relatively small genitalia in large individuals of the same species) (Eberhard et al. 1998; Eberhard 2008). These low allometric values probably represent special evolutionary adjustments to reduce the amount of difference in genital size between males and females (Eberhard et al. 1998), allowing the male to fit effectively with the most common (intermediate) size of female. The negative allometric pattern in females is surely not just a pleiotropic effect of the male pattern, because completely different structures are involved. Relatively invariant genital size in females could enable them to evaluate more precisely the male's degree of allometric adjustment,

or the genitalic form of the most common (intermediate) sized males (Eberhard, 2009).

In the context of female choice by mechanical fit, the need to evaluate male exaggerations may select for other types of exaggeration (Huber 2006). Females of some species of the pholcid genus *Mesabolivar* have exaggerated external genitalia, and these exaggerations are functionally correlated with extravagant male cheliceral morphology (Huber et al. 2005). In *Mesabolivar* (originally *Kaliana*) *yuruani*, males have unique genitalia, with one specific structure (the 'procurus') about six times as long as usual in the family, and this exaggeration is paralleled in the female internal genitalia (Huber 2006; cf. Jäger 2005 on delenine sparassids). Similar coevolutionary pressures may have obliged the males of some groups with extreme sexual size dimorphisms to evolve such disproportionately large genitalia that they seriously reduce the male's agility, and favor self mutilation behavior in which the male tears off one of his palps shortly after the penultimate molt (Ramos et al. 2004).

CONCLUSION

As we have argued elsewhere (Eberhard 2004b), spiders have several traits that make them well-designed for

studies of genitalic function. Despite their unique attributes, they seem to conform to the general evolutionary patterns of genital evolution seen in other groups. They should play an important role in the next generation of studies of genital evolution and function.

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