

Possible links between embryology, lack of innervation, and the evolution of male genitalia in spiders

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Summary

The male genitalia of spiders apparently lack innervation, probably because they are derived embryologically from structures that secrete the tarsal claw, a structure which lacks nerves. The resultant lack of both sensation and fine muscular control in male genitalia may be responsible for the fact that male genitalia in spiders tend to have a more complex internal bracing when in use, and to be less often used to seize or pull open the female, than the genitalia of insects. Apparent difficulties with this proposal are discussed, and previous theories regarding the evolution of spider genitalia are shown to be unable to explain several types of data.

Introduction

The male genitalia of many animals with internal fertilisation are elaborate and species-specific in form (summaries in Eberhard, 1985; Shapiro & Porter, 1989). They are relatively well-studied in many groups, because taxonomists have often used genitalic form to distinguish closely related species. In many species a male's genitalia are morphologically, and perhaps sometimes also behaviourally (West-Eberhard, 1984), his most complex structures.

In this context of diversity and complexity, the genitalia of spiders appear to be unusual compared with those of insects. Genitalic mechanisms in spiders that brace the various parts of the male's genitalia internally against each other and allow them to lock against the female are both widespread and often extraordinarily elaborate (e.g. Gering, 1953; van Helsdingen, 1965, 1969; Grasshoff, 1968, 1973a; Blest & Pomeroy, 1978; Huber, 1993a, 1994a, 1995a,b). The genitalia of female spiders are usually relatively rigid, both on her body surface and also deep within her body.

In contrast, the male genitalic structures of insects generally seize, push into or pull open female structures, rather than simply locking against them, and male genitalia generally lack elaborate internal mechanical locking and self-bracing structures. The female structures contacted by male genitalia are often at least partially soft and flexible. This is true in several groups, including Orthoptera (Gregory, 1965; Sakai *et al.*, 1991), Diptera (Spielman, 1964; Lachmann, 1996; Eberhard

& Pereira, 1995; Eberhard & Huber, in press a), Coleoptera (Peschke, 1978; Eberhard, 1993a,b; Krell, 1996; Eberhard & Kariko, 1996), Homoptera (Kunze, 1957), Hemiptera (Bonhag & Wick, 1953; Heming-Battum & Heming, 1986, 1989), and Hymenoptera (Roig-Alsina, 1993) (see also Snodgrass, 1935 on insects in general, and Tadler, 1993, 1996 on millipedes).

It is of course difficult to present quantitative data on these points, and there are obviously exceptions to these general statements. For example, in spiders although male pholcid genitalia have elaborate internal locking and bracing devices (partly in relation to the chelicerae), most or all of the genital structures of the female that are contacted by the male genitalia are membranous (Uhl *et al.*, 1995; Huber, 1994a, 1995c; Huber & Eberhard, 1997). Some portions of the female sperm-receiving organs are also soft in the tetragnathids *Nephila* and *Leucauge* (Higgins, 1989; Eberhard & Huber, in press b), as are the female genital structures that guide the male's embolus in *Histopona torpida* (C. L. Koch) (Huber, 1994b). Many (perhaps all?) mygalomorph as well as some labidognath spiders such as filistatids have no locking or bracing structures in the male palpal bulb, and secondary reduction in the complexity of palpal morphology has also occurred in various groups (Kraus, 1978; Schult & Sollenschlo, 1983; Loerbroks, 1984).

What follows is an attempt to relate what we perceive to be the unusual morphological traits of spider genitalia to the lack of neurons in the palpal bulb, which may in turn be a consequence of its embryological derivation. The presentation is speculative in parts, and some explanations are admittedly tentative. The usefulness of this note probably lies more in introducing a new set of data to discussions of genitalic evolution in spiders than in providing final answers.

Lack of neurons in the palpal bulb

Histological studies using stains capable of differentiating nerve cells have consistently failed to reveal any neurons in the bulbs of the palps of mature males (Osterloh, 1922 on four species in the families Araneidae, Linyphiidae, Agelenidae, and Lycosidae; Harm, 1931 on Segestriidae; and Lamoral, 1973 on Heteropodidae). In addition, sections of the palp of the linyphiid *Neriene montana* (Clerck) showed that the thin basal neck which connects the tegulum with several portions of the bulb that contact the female during copulation (radix, embolus, terminal apophysis, and lamella) is made of solid cuticle, with only the sperm duct inside and no space for nerves (B. Huber, unpubl. data). Studies using ultrathin sections also failed to reveal nerves in the palpal bulb in yet another family (M. Suhm, pers. comm. on the amaurobiid *Amaurobius*).

Additional, less direct data from numerous other species also suggest that palpal bulbs are not innervated. Glands in the bulb of *Amaurobius* spp. lack both muscles and neurons to control the release of their products (Suhm *et al.*, 1995). There are muscles that originate from the cymbium or more proximal portions of the

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palp and insert at the base of the bulb in some spiders; but, as Levi (1961) noted, no muscles have ever been observed within the palpal bulb. Sectioning studies showed that there were no muscles of any kind within the palpal bulb of spiders in 76 genera in 56 different families, including *Liphistius*, six mygalomorph families, *Gradungula*, ten haplogyne families, and 38 entelegyne families (Huber, in prep.) in all major taxonomic groups (Coddington & Levi, 1991). Muscles, of course, would require innervation to function. In addition, external cuticular structures such as slit sensilla and setae (socketed epidermal bristles) that are normally associated with sense organs appear to be completely lacking on palpal bulbs (J. Coddington, pers. comm.). 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 variety of groups (e.g. Kraus, 1978; Opell, 1979; Coddington, 1986; Kraus & Kraus, 1988; Griswold, 1987, 1990, 1991, 1994; Hormiga, 1994).

Presumably the structures of the bulb lack sensory neurons as a result of their embryological origin from the claw, a structure that lacks neurons. The structures of the bulbs of male pedipalps are derived embryologically from the hypodermal cells (the "claw fundament") that secrete the palpal claw and its tendons in females and immatures (Harm, 1931; see summary in Coddington, 1990).

The portion of the palp just basal to the bulb, the cymbium, is derived from the tarsus. In contrast with the bulb, the palpal cymbium is generally richly innervated in spiders, and typically bears many setae, even in groups in which cymbium morphology is very complex (e.g. Pimoidae — Hormiga, 1994) and in which the cymbium is inserted into the female (e.g. Pholcidae — Uhl *et al.*, 1995; Huber & Eberhard, 1997). Presumably there are sensors in the cymbium and/or the muscles and membranes uniting the cymbium with the bulb that give the male at least crude information regarding the position of the bulb with respect to the cymbium. Such sensors have apparently never been searched for. Behavioural evidence for an ability to sense events at the tip comes from male *Leucauge mariana* (Taczanowski). The male can apparently sense whether or not the tips of the embolus and conductor have entered the sperm droplet during sperm induction (Eberhard & Huber, in press b), presumably from the force that results when the tip of the palp is pulled out of the droplet.

In contrast with spiders, the external genitalia of both male and female insects appear to be generally innervated. Sense organs or sensory responses have been confirmed in a butterfly (Arikawa *et al.*, 1980, 1996), a beetle (Peschke, 1979), a cricket (Sakai *et al.*, 1991) and a mosquito (Gwadz *et al.*, 1971; Gwadz, 1972). Both the intromittent phallic organs and the associated genitalic structures arising nearby are provided with muscles in many insects (Snodgrass, 1935). Many grasping and clasping structures of insect genitalia are derived from abdominal appendages (Snodgrass, 1935).

Consequences of lack of innervation for genitalic evolution

Lack of innervation within the palpal bulb implies both a lack of direct sensory feedback to male spiders from the important genitalic structures that engage the female, and a lack of direct motor control. In an important sense, a male spider is more or less "sensorily blind" when he attempts to perform the selectively all-important act of inseminating a female. Lack of sensory feedback from the portion of his genitalia that the male is attempting to insert into the female is likely to result in difficulty in achieving proper alignment with the female's gonopores and her internal ducts. In addition, lack of innervation and the consequent lack of muscles will tend to make it more difficult for the male to make fine adjustments in the positions of structures of the palpal bulb. These problems may have had important consequences for the evolution of spider genitalia.

One solution for the male would be to develop "preliminary locking" structures, whose engagement with the female would require less precise alignment of the palp. Such structures could provide stable points of support to facilitate the final alignment of the male's intromittent structures. They might also enable the male to sense that such alignment had occurred, via sensations from the connections of these structures with more basal, innervated portions of his pedipalp.

These last points can be illustrated using an analogy with humans. It is as if the male spider's palpal bulb were an elongate and elaborate fingernail divided into different sections capable of independent movements, and the fingernail had to perform a mechanically delicate and difficult adjustment inside a machine in the dark. If the fingernail had one or more preliminary locking devices that brought it into progressively finer and finer alignment with the machine, fine alignments and movements could be achieved, even without especially precise motor control at any given stage. A person could sense the proper engagement of the fingernail with the machine, and the alignment of the portions of the fingernail introduced into the machine, by using sensations from the area at the tip of the finger where the fingernail is attached. Another possible source of information for the male spider is the hydraulic system used to move the pedipalp sclerites (J. Coddington, pers. comm.). Variations in pressure associated with the movements and the mesh of the sclerites with the female might give the male useful information on how his genitalia are deployed.

Particular alignments and movements of the bulb could come to depend on complex mechanical bracing of different portions of the male genitalia against each other and against the female (e.g. Grasshoff, 1968, 1973a; Huber, 1993a). This is the kind of elaborate bracing that is generally absent in insects. Males with superior orienting, locking and bracing design features might more often deposit their sperm at appropriate sites in the female, or less often be deterred from transferring normal quantities of sperm by marginally receptive females or females with deviant genitalic

morphology or behaviour that would make genitalic alignment more difficult (see below).

Seen from the evolutionary perspective of females, the mechanical problems experienced by males lacking sense organs in their genitalia could lead to selection on females. Females able to discriminate against those males least able to achieve effective genitalic alignment could gain via the production of sons with superior genitalic designs. Such selection to discriminate could result in changes in female morphology that would make her genitalia selective, facilitating a male's chances of getting his sperm into her spermathecae only if his genitalia had certain mechanical properties. Selection of this sort could favour rigid female genitalic structures with complex forms (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 genital morphology. In entelegyne spiders, such female morphological complexity would be predicted to occur in structures associated with the copulatory or insemination duct (the duct traversed by the male genitalia and his semen on their way to the spermatheca), rather than with the fertilisation duct (the duct from the spermatheca to the site where eggs are fertilised): the insemination duct is indeed the portion of greatest complexity (Eberhard, 1996).

A possible example of such a selective female genitalic trait is the hood of *Anyphaena accentuata* (Walckenaer). The male scrapes his pedipalp repeatedly against the female's epigynum until his retrolateral tibial apophysis (RTA) engages the hood-like prolongation of the epigynum. When the RTA engages this otherwise functionless female structure, the more distal portions of the palp are brought into proper opposition and alignment for intromission of the embolus (Huber, 1995b). Possible female "guiding structures" have been noted in other groups (Gering, 1953; Grasshoff, 1973a,b, 1974a,b).

Apparent problems with this hypothesis

Lack of female sense organs

One apparent problem with our proposed explanation of the association between the morphology of male spider palpal bulbs and their lack of innervation is that the genitalia of female spiders apparently lack sense organs, at least on their outer surfaces (Huber, 1993a, 1995b). If females select among males on the basis of the male's genitalic fit, then one might expect to find sense organs on those portions of the female genitalia with which males must mesh (such as those on the prothorax of female Zygotera where she is grasped by the species-specific clasping organs of males — Robertson & Paterson, 1982; Battin, 1993). It is possible, however, that such female sensory structures are lacking in spiders because selection has favoured mechanical rather than stimulatory properties of male genitalia.

In addition, if females screen males on the basis of sensory stimulation, a female which sensed that a male had engaged his sclerite x with the appropriate cavity in her external genitalia, might obtain only an incomplete

indication of whether or not the entire mechanical mesh of the male's genitalia was appropriate for intromission and sperm transfer. More reliable information on the complete mesh would come from whether the male was able to successfully complete engagement and intromission, and deliver sperm to the appropriate site in the female (Huber, 1993b).

More reliable stimulatory information regarding complete engagement could thus come from structures deeper within the female. Membranous internal structures might be stretched by male intromittent organs, as occurs as the result of energetic pushing by the male in agelenids (Gering, 1953) and in nesticids (Huber, 1993a) (see discussion in Eberhard, 1996). Structures in the spermathecal ducts or the spermathecae themselves may sense the presence of male seminal products. Additionally, successful palpal engagement could apply forces to the female's entire abdomen (Eberhard & Huber, in press b, on *Leucauge mariana*; see also Eberhard, 1985), whose surface has numerous stress receptors (Barth, 1985). Sensory receptors at sites deep in the female body have apparently never been searched for in spiders.

Disadvantage of variant morphology

Spider genitalia, in both males and females, often diverge rapidly compared with other body parts, and hence they are often especially useful characters to distinguish closely related species. Given that species isolation is an unlikely function for spider genitalia (Gering, 1953; Eberhard, 1985; Shapiro & Porter, 1989; Ware & Opell, 1989), it would seem that once the males of a species have evolved a genitalic design that fits the corresponding structures of conspecific females, further changes in either males or females would be disadvantageous. Males with variant genitalia would seem to be at a disadvantage because they would couple more poorly with females. Females with variant morphology that favoured non-standard male designs would also seem to stand to lose; they might run greater risks of not receiving adequate numbers of sperm to fertilise their eggs; and their offspring would tend to be sired by males with less typical genitalic morphology, so their sons might tend to have genitalia that were less well-designed for inseminating females with the most common genitalic forms.

This description of the disadvantages of changes in males and females, however, is a serious oversimplification. In the first place, neither male nor female genitalia are invariant. On the one hand, male and female genitalic forms often vary intraspecifically (see, for example, Levi, 1968, 1971, 1974, 1977, 1981; Grasshoff, 1968; Coyle, 1969, 1971, 1974, 1981, 1985a; Hippa & Oksala, 1983; Kraus & Kraus, 1988; Ware & Opell, 1989). In addition, there is intraspecific variation in the absolute size of male and female genitalia. In six different spider species in five different families this variation in males was of approximately the same order as that in other body parts of the same species (Coyle, 1985b; Eberhard *et al.*, in press). There is thus no single genital morphology in a species. The allometric values of spider

genitalia (the slopes of intraspecific log–log regressions of genitalic size on an indicator of overall body size) were relatively low, compared with the allometric values of non-genitalic body parts of the same species (Eberhard *et al.*, in press). These low allometric values probably represent evolutionary adjustments to reduce difference in genitalic size (Eberhard *et al.*, in press), and thus emphasise the evolutionary importance of such variation. An additional consideration is that there is a certain degree of mechanical flexibility in some male (and perhaps female) genitalic structures that will permit some variation in morphology without loss of function (Grasshoff, 1974b; Loerbroeks, 1984).

In addition to being overly typological with respect to morphology, this description of disadvantages ignores the fact that variations in both male and female behaviour can affect the success of coupling. The repeated failures of insertion attempts (“flubs” of Watson, 1991) that occur in a variety of spiders are a classic demonstration of this problem. Flubs often occur erratically during a given copulation: the same male sometimes succeeds, and sometimes fails in intromission attempts with the same palp applied to the genitalia of the same female, thus confirming the importance of behaviour *per se* in addition to morphology, assuming that the morphological traits of male and female remain constant. A summary of data from the extensive publications of U. Gerhardt showed that flubs occurred in 40% of 151 species from 38 families (Huber, in press) (see also Gering, 1953; van Helsdingen, 1965; Watson, 1991; Stratton *et al.*, 1996). In *Neriene litigiosa* (Keyserling), more frequent flubs are associated with reduced sperm precedence in copulations with non-virgin females (Watson, 1991). In some araneoids and lycosids flubs may have become ritualised as courtship (the beating movements of the palps of *Nephila maculata* (Fabricius) in Robinson & Robinson, 1973; the scrabbling movements of *Argiope* spp. in Robinson & Robinson, 1980; the scraping movements of *Schizocosa* males in Stratton *et al.*, 1996).

Some flubs are probably due to inappropriate male behaviour, but it is likely that some result from female behaviour. For instance, female *Leucauge mariana* flex the opisthosoma ventrally at a variable angle to facilitate intromission, and lack of sufficient flexion sometimes results in repeated flubs (Eberhard & Huber, in press b). Female *Nesticus cellulanus* (Clerck) vary the amount they tilt the opisthosoma dorsally, and they sometimes thereby prevent intromission (B. Huber, unpubl.). A variety of other female movements that can facilitate copulation may not always be executed fully. In many spiders in the secondary hunting-spider group of von Helversen (1976), the female must twist her opisthosoma to allow intromission (Gering, 1953). Movements of the female epigynum itself also probably sometimes affect male access to internal sperm deposition sites. The epigynum of the nephiline *Herennia ornatissima* (Doleschall) protrudes conspicuously during copulation (Robinson & Robinson, 1980); the membranous components of the genitalia of the pholcid *Physocyclus globosus* (Taczanowski) swell markedly just before

intromission (Huber & Eberhard, 1997); and the epigynal plate of the theridiosomatid *Wendilgarda clara* Keyserling is substantially displaced (apparently reflected by special muscles) during copulation (Coddington, 1986). The descriptions of U. Gerhardt include still further female co-operative behaviour patterns in spiders: female lifts or lowers prosoma to facilitate intromission; female becomes catatonic; female opens her chelicerae to grasp the male or presents her chelicerae to be grasped; female uses her legs, palps or chelicerae to help the male bulb find her genital opening; and female positions male correctly (Huber, in press).

These intraspecific variations in male and female morphology, and the crucial and probably often variable effects of male and female behaviour on successful coupling, could make compensatory modifications of both male and female genitalia advantageous. As both the variations and the male and female compensations change, they could give rise to rapid evolution under sexual selection.

Previous hypotheses

The two major previous discussions of the relative complexity of male genitalia in spiders (Grasshoff, 1974a,b; 1975; Kraus, 1984) do not mention sexual selection or embryology. Grasshoff's most concrete ideas regarding the evolution of spider genitalia are part of an explanation for why the morphological complexity of the male genitalia in the araneid genus *Mangora* apparently increased (Grasshoff, 1974a). The explanation has potentially wider applicability (Grasshoff, 1975). He proposed that variations arose in the male design of an *Araneus*-like ancestor that were not disadvantageous, because of the mechanical flexibility of the palp, and that these selectively neutral changes permitted one part of the palp to perform a new, advantageous function (grasp the female genitalia). This new function changed the selective pressures on other portions of the palp, and resulted in their subsequent modification. The general conclusion was that male genitalia evolve to improve and perfect sperm transfer (Grasshoff, 1975).

This idea is similar to the ideas presented above in its focus on the mechanical properties of male genitalia. It lacks, however, an explanation for why female structures should also have changed. This question is crucial, because such changes undoubtedly occurred in this particular case (Grasshoff, 1968, 1973b; Levi, 1971, 1975), and are indeed very widespread in spiders (hence the frequent use of female genitalia in taxonomic descriptions). Discussions of male mechanical functionality cannot ignore female morphology, as Grasshoff himself emphasised (1975). Particular changes in male design will only function in conjunction with certain changes in female designs. Thus while Grasshoff's proposal may have important implications for the evolution of new mechanical abilities in male genitalia, it is not capable of explaining changes in both male and female genitalia.

Grasshoff published several other ideas regarding genitalic evolution in spiders. He noted (1975), as we have above, that male genitalia are relatively “free” to evolve in different evolutionary directions because their only function is to transfer sperm, and this can be accomplished in a variety of ways. He argued, as we will below, that there is no correlation between web building and the complexity of male genitalia. He did claim, however, that spiders which hang from webs have relatively *larger* male genitalia (Grasshoff, 1974a). However, all but two of the hanging species that he used to illustrate this point were from a single taxonomic group, the araneoids; and one of the two others, *Uloborus*, was an exception to his rule. He attributed the difference in genitalic size to the web-hangers’ supposed (but not demonstrated) better ability to balance the extra genitalic weight in their webs, but failed to explain why such weight would be favoured.

Kraus (1984) emphasised the possible mechanical problems when spiders mate on the unstable, highly mobile substrate of a web. Greater morphological complexity, with presumed concomitant greater bracing and stabilising abilities, was proposed to facilitate mating on unstable substrates. There are data that argue, however, against this link with genitalic complexity. Leaving aside the debatable question of whether greater complexity necessarily results in greater stability, there are several groups which show evolutionary changes opposite to those predicted by the substrate stability hypothesis.

Araneine males typically embrace the female’s opisthosoma tightly with their front legs, thus holding their palps stably very near the area on the female where the palps are inserted (e.g. Gerhardt, 1923, 1924a,b, 1925, 1927, 1928). Comparison with mating postures in other araneoid groups (e.g. von Helversen, 1976) suggests that this posture is derived. Yet araneine palps are in general extremely complex, and at least some aspects of this complexity are apparently also derived (e.g. the araneine radix — Hormiga *et al.*, 1995). A similar association between derived, relatively complex palp morphology and an especially solid anchoring of the palps very near the entrance of the female genital tract occurs in pholcids. In this case the male clamps the female’s epigynal area between his chelicerae and the distal portions of his palp. The idea that pholcids are likely to have a relatively unstable coupling with females because they mate in webs (Kraus, 1984) fails to take this cheliceral coupling near the female genital opening into account. Uloborid males also combine a tight grasp on the female’s opisthosoma with their anterior legs that brings their palps near the epigynum (Patel & Bradoo, 1986; W. Eberhard, unpublished observations of *Philoponella* sp.) with relatively complex male genitalia. *Agelenopsis* species show the same combination of complex palpal morphology and a tight male hold on the female (in this case the male chelicerae hold the female patellae II and his legs hold her body and legs) (Gering, 1953). The theridiid genus *Argyrodes* is yet another group combining relatively complex palp morphology (Levi, 1961) with a relatively stable link between male and female, which in this case results from the female

grasping the male’s prosoma with her chelicerae (Lopez & Emerit, 1981; Whitehouse & Jackson, 1994). The derivations of these mating postures and of the palpal complexity are not clear. Males use their legs to grasp the female opisthosoma in species scattered in a variety of other families, including Oonopidae, Dysderidae, Eresidae, Thomisidae, and Linyphiidae (Gerhardt, 1923, 1924a, 1928, 1933).

In contrast, in *Leucauge* (and some other tetragnathids) the male does not grasp the female with his legs, but his chelicerae are clasped by the female’s chelicerae. This clasp keeps the male’s prosoma relatively distant from the female’s copulatory openings, and males have relatively elongate palps that must be extended to reach the female’s epigynum. This, and the fact that the female must bend her opisthosoma ventrally if the male is to reach her, makes the male’s mechanical purchase on her genitalia quite tenuous (contrary to both Levi, 1981, and Kraus, 1984). The exact site on the female’s opisthosoma that is contacted by the male’s palp varies substantially, and flubs in insertion attempts are especially frequent (Eberhard & Huber, in press b). Instead of being complex, however, the palps of *Leucauge* are relatively simple. Cheliceral clasping is a derived feature of tetragnathines (Eberhard & Huber, in press b), and if uloborids are used as an outgroup, so is simplicity of palp morphology, as also indicated by vestigial structures on the palps of the related *Tetragnatha* and *Pachygnatha* (Levi, 1961). At least some aspects of simplified palp design (e.g. loss of the median apophysis) are shared with the related nephilines (Hormiga *et al.*, 1995), which do not perform cheliceral clasps, and thus constitute further evidence against the idea (Kraus, 1984) that genitalic simplicity in tetragnathines resulted from changes in substrate stability resulting from cheliceral clasps.

It is important to note that the substrate stability hypothesis can be modified to accommodate data of this sort. For instance, genitalic complexity might be retained in secondarily webless groups because it was not damaging (O. Kraus, pers. comm.); but this results in a concomitant loss in explanatory power. The species-specific differences typical of complex spider genitalia are also not readily explained by the substrate stability hypothesis without inclusion of additional considerations. It does not seem reasonable to explain species-specific differences by postulating a different kind of substrate instability for each species.

Conclusions and directions for future study

We must emphasise that the link we have proposed between the lack of innervation of the male palpal bulb and complex genitalic designs in spiders does not offer a simple explanation of genitalic evolution in all spiders. Unanswered is the question, for instance, of why mygalomorph spiders failed to develop either complex male palpal bulbs or strongly sclerotised female genitalia. Why have the male genitalia of most haplogyne groups, as well as those of some entelegyne groups, such as Thomisidae and Salticidae, apparently become

simplified secondarily (Kraus, 1978, 1984)? Even within the araneoids with relatively complex palps, there may have been secondary simplification (e.g. Tetragnathidae) and then a subsequent increase in complexity (e.g. in *Meta* and associated genera) (Hormiga *et al.*, 1995). Secondary simplifications are not necessarily contradictory to the sexual selection by cryptic female choice hypothesis, since the evolution of male signalling devices and female choice criteria are very unpredictable (see Eberhard, 1996: 350–351). We are proposing that the lack of innervation of the palpal bulb may have predisposed sexual selection in one or more evolutionary lines of spiders to focus on elaborate mechanical properties in male genitalia, not that such an emphasis will necessarily occur in all spiders whose palpal bulbs lack neurons. Female criteria in some spiders may have evolved to emphasise male genitalic traits other than strict mechanical mesh (e.g. powerful movements, chemicals added to the semen), or non-genitalic traits that come into play before or during copulation. It is not clear, however, why simplification should occur in some particular groups of spiders but not others. Perhaps this question is no more readily answered than, for instance, the question of why flies but not wasps lost their second pair of wings, or why some members of given bird families like Dendrocolaptidae and Furnariidae have complex songs while others do not (Stiles & Skutch, 1989).

There are several types of data that could serve to test or refine the ideas just presented. Many are related to the presence or absence of neurons and sense organs. Will modern techniques confirm the total absence of neurons in palpal bulbs? Are there structures deep in female genitalia that can act as stretch receptors which could sense stimuli from the presence or movements of the male genitalia or their products? Are there receptors in the cymbium that can sense displacements of the bulb? Will experimental denervation of male and female structures produce important alterations in copulatory behaviour, as occurs in mosquitoes (Gwadz *et al.*, 1971; Gwadz, 1972)? Will genera in which females mate only once (and in which sexual selection by cryptic female choice is thus not expected to occur) prove to have relatively simple, invariable male palps?

Further tests of the substrate stability hypothesis are also needed. Will a more complete survey of the changes in the mating positions and clasping devices of spiders (Yoward & Oxford, 1997), and their probable effects on a male's need to brace his palps mechanically during copulation reveal that increased palp complexity is significantly associated with changes in mechanical instability? Is there a correlation between relative palp size and complexity, and is there a correlation between either of these and moving upside-down in webs as proposed by Grasshoff (1974a)? We have noted some cases that do not fit the predictions above, but many other comparisons are also possible, and when information regarding their derivations becomes available, at least some may follow trends predicted by the substrate stability hypothesis. For example, the relatively small nephiline and *Gasteracantha* males that walk on the

female's abdomen (Robinson & Robinson, 1980) both also have relatively simple palp morphology (Hormiga *et al.*, 1995; Levi, 1996). The correlation noted by Levi (1961) in the family Theridiidae between greater palpal complexity and heavier palpal sclerotisation remains unexplained. Given the possibility that heavier sclerotisation is associated with greater forces applied to palps, this possible association deserves further exploration in this and other groups.

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