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TAXONOMY AND THE DANGERS OF SEX WITH SPECIAL REFERENCE TO PSEUDOSCORPIONS

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Abstract — Most arachnid reproduction is a hazardous affair, particularly for the male who could easily be taken for a meal rather than a mate. Elaborate behavioral and morphological adaptations have evolved in the different orders to minimize the risks involved in sex. Selective pressure has led to these adaptations frequently becoming species-specific. Consequently, as well as isolating the species, the adaptations can also be used as tools to define taxa. Within the Aranea, the epigyne of the female and the complex pedipalps of the male form a 'lock and key' of fundamental importance in the taxonomy of the order. An equivalent system occurs in the Ricinulei, where the male's tarsi of the third legs are elaborated for mating. The use of pedipalps or legs involves semi-direct contact. Other orders, including the Pseudoscorpiones, have opted for a more remote method of sperm transfer – the deployment of spermatophores. These products of the complex male genitalia are deposited on the substratum for the female to find or be guided to by the male. Her elaborate genitalia then pick up the sperm. Both male and female genitalia, particularly the former, are variable to the extent that they too can be important taxonomic characters, but are infrequently considered in species descriptions.

Key words: Pseudoscorpion, arachnid, spermatophore, sperm transfer, sex, genitalia, taxonomy

As Cloudsley-Thomson (1958) observed, "reproduction in most arachnids is a hazardous affair." As predators prospective mates must be careful that they do not end up as their partner's meal, so consequently various behavioral and morphological adaptations have evolved. In the arachnids two, or possibly three, methods of copulation can be recognized: direct transfer (copulation), which involves the greatest and most intimate contact; and indirect or dissociated sperm transfer, which involves the least intimacy. Within the latter, some authors recognize an intermediate condition, paired-indirect sperm transfer (Proctor, 1998).

With the exception of the Opiliones, the dominant feature of arachnid mating (excluding the Acari), consists of the process of indirect sperm transfer. Should the mating relationship break down, partners need to be either apart from one another so one or other of them can flee, or, if united, positioned so that contact can be broken off easily and in such a way that reduces the likelihood of things going wrong.

Direct genital contact and the use of a penis could be fatal as such an intimate union 'face to face' could be difficult to disengage should one or either of the partners decide that the other is more a meal than a mate. Of course, sexual cannibalism does occur in the arachnids (as well as in insects and amphipods) and has aroused a fervent debate. Cannibalism could occur through accident or the female may benefit from eating the male by gaining nutrients that can aid egg production.

Indirect sperm transfer, involving the use of spermatophores or 'alternative' appendages (modified legs or palps), avoids or reduces intimate contact. Pre-copulatory behaviors have also been developed as strategies to reduce the hazards of sex. These involve, among others (especially the spiders), appeasement, signalling, caressing, 'dancing', stupefying, giving food, restraining, and even being below the female's prey threshold size, i.e., the male is too small for the female to consider him as a meal. Within the scorpions and pseudoscorpions, there are techniques that help nullify the predatory instinct or neutralize the pedipalps and the aggressive tendencies of the female – they physically grasp each other's palps to effectively put them out of action.

Table 1. summarizes the techniques used by various arachnids.

Thus arachnid sperm transfer methods include:

• Solifugae: the male applies sperm directly to female's genital area using chelicerae.

• Scorpions, Pseudoscorpions, Schizomida, Amblypygi: a more or less complex spermatophore is deposited on the substratum ready for the female to pick up the sperm; these may be deposited randomly by males with or without the presence of a female, or she may be guided over one with or without contact with the male

• Aranea: the male ejaculates sperm onto a special web and then sucks it into his modified pedipalps, which are then used to inject it into female's genital atrium.

• Ricinulei: similar to Aranea, sperm is ejaculated via penis and taken into complex appendage on leg III, from which it is injected into the female.

With the development of complex morphological adaptations, it is not surprising that selective pressure has led to the evolution of male and female structures intimately and specifically designed to work together: the lock and key mechanisms of reproductive isolation. In spiders and other arachnids, the complex male and female genitalia are specifically designed to match and so only conspecifics can mate (Mayr 1963). Similarly, in the Amblypygi and Pseudoscorpiones, there has been co-evolution of spermatophores, their organs of production, and those parts of the female genitalia which are used to pick up and store the spermatozoa (Weygoldt, 1999). Consequently, these structures have been exploited in defining species. This is most noticeable in the Aranea, where the male's palps and female's epigyne are consistently used as key taxonomic characters.

In pseudoscorpions the genitalia vary considerably between genera, and in many cases species, preventing interbreeding and providing useful taxonomic characters

Table 1. Summary of techniques used by various arachnids

Group	Secondary Sexual differences	Pre-mating Behavior	Method
Scorpiones	male and female with slight differences in body proportions	'dance' – promenade à deux	spermatophore; female guided over it by male
Solpugida	male smaller than female; legs longer	male strokes female to calm her; seizes and carries her a short distance and lays her on her side	male massages female genital area, opens aperture, ejaculates on substrate and gathers sperm mass with chelicerae and forces it into female; runs away quickly
Pseudoscorpiones	some with size differences and some males with special erectile organs	variable behavior including none, male aroused in presence of female; pheromones deployed by many	male deposits spermatophore on substratum; female may or may not be present; if present, male may guide her over it and pair may 'dance'
Palpigrada/ Microthelyphonida	slight	pheromones used	not known, but appear to react in the presence of each other
Thylyphonida	virtually identical	simple 'dance'	male grips antenniform first leg of female with his palps; walks backward; female raises her opisthosoma; male strokes female's genital area; complex spermatophore produced and held against female's genital aperture
Schizomida	similar; males rare	little known; in *Trithyreus sturmi*, female grips last segment of male's opisthosoma and the pair walk forward	male deposits spermatophore and guides female in tow over it
Amblypygi	slight differences	prolonged courtship dance	male deposits spermatophore in front of female, turns away, then turns back and lures her over it
Aranea	variable; differences in male and female	complex and very varied pre-copulatory behavior	male ejaculates sperm onto special web and then draws it up into modified pedipalpal 'syringe', which is used to 'inject' it into the female's matching genitalia
Ricinulei	male with modified tarsus on leg III	little	male unclips prosoma/opisthosoma and collects sperm in modified tarsus from penis and transfers it to female's genital area (Cooke, 1967)
Opiliones	slight differences	casual sex; some involve contact maneuvers	male inserts penis directly into female's genitalia

Plate 1. Modified male tarsus IV of *Ricinoides hanseni* used in sperm transfer (modified from Legg, 1976).

for the separation of species. However, unlike spiders (where the use of male pedipalp and female epigyne morphology are key to defining species and higher taxa), the use of their equivalents in pseudoscorpions is rare. Other characters (setation, the position of trichobothria, form of pedipalps, galea, etc.) appear to over-shadow the reproductive structures in their apparent greater significance. However, the bias away from using genitalia features may give rise to misplaced taxa (Legg, 1987) or can resolve disputes over the validity of species (Legg, 1975b). At the very least, the morphology of the genitalia helps to reinforce relationships. An examination of the literature shows that relatively few taxonomists even mention genital characters (e.g., Harvey, Muchmore, Ducháč, Legg) and these may be in a very simple way or, rarely, shown in more detail.

PSEUDOSCORPION MALE GENITALIA

The genitalia of the male pseudoscorpion are designed to produce and store sperm, produce seminal fluid, secrete (and in many cases mold) the spermatophore, and produce a pheromone. Consequently the genitalia and associated glands form a complex arrangement of reproductive organs (Vachon, 1938; Legg, 1973). The testis is the source of sperm and also nutritive fluid for the sperm. These two products are conveyed by the vasa deferentia to the seminal vesicles, which act as temporary sperm stores. Prior to the release of sperm, the large posterior dorsal gland secretes

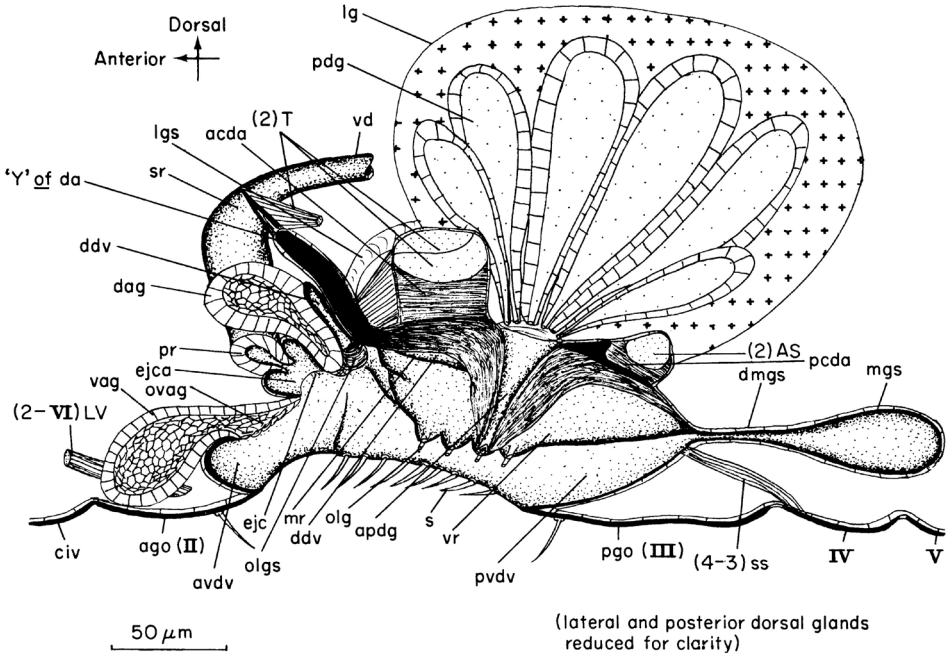

Fig. 1. Diagrammatic half lateral view of the male genitalia of *Chthonius ischnocheles* (Hermann) (modified from Legg, 1973). Abbreviations: ago(II) - anterior genital operculum, avdv - anterior ventral diverticulum, apdg - atrium of the posterior dorsal gland, civ - coxa of leg four, ddv - dorsal diverticulum, dmgs - duct of the median genital sac, ejc - ejaculatory canal, ejca - ejaculatory canal atrium, lg - lateral gland, lgs - lateral genital sac, mgs - median genital sac, mr - median ridge, olg - opening of the lateral gland, olgs - opening of the lateral genital sac, ovag - opening of the ventral anterior gland, pcda - posterior crest of the dorsal apodeme, pdg - posterior dorsal gland, pgo(III) - posterior genital operculum, pr - prostatic reservoir, pvdv - posterior ventral diverticulum, s - seta, vag - ventral anterior gland, vd - vas deferentia, Y-da - Y of dorsal apodeme.

the spermatophore stalk and, if present, its apical modifications. Following the spermatophore stalk's secretion, the sperm and seminal fluid (possibly slightly augmented by that of the prostatic reservoir) are ejaculated via the ejaculatory canal atrium into the genital atrium and encapsulated by secretions from the anterior glands. The encapsulated sperm and fluid are then deposited on the apex of the spermatophore stalk. Where lateral glands occur, as in the Chthoniidae, these appear to secrete a pheromone that is deposited on the spermatophore stalk as a droplet.

Being designed for the production of spermatophores, the genital atrium is complex and varied. It consists basically of a cuticular invagination between sternites 2 and 3 of the opisthosoma, associated with which are accessory glands, a number of thickenings of cuticle (some forming distinct apodemes), and a number of muscles that operate the system (Vachon). Anteriorly the vasa deferentia are modified into seminal vesicles, which open into a prostatic reservoir. This in turn is surrounded by a cup-shaped antero-dorsal evagination from the genital atrium, the ejaculatory

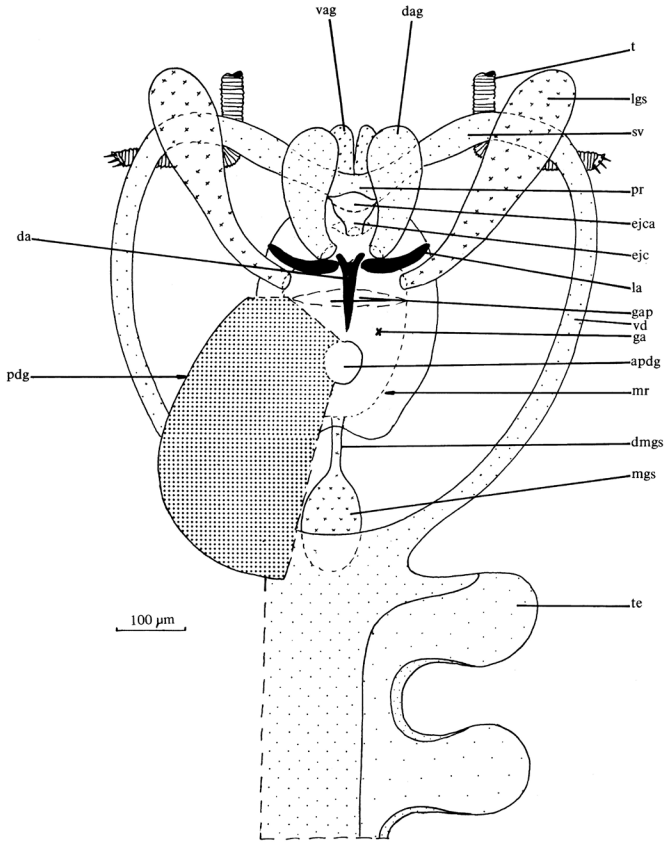

Fig. 2. Dorsal view of the generalized male genitalia and associated glands (modified after Vachon, 1938; from Legg, 1975a). Abbreviations: apdg - atrium of the posterior dorsal gland, da - dorsal apodeme, dag - dorsal anterior gland, dmgs - duct of the median genital sac, ejc - ejaculatory canal, ejca - ejaculatory canal atrium, ga - genital atrium, lgs - lateral genital sac, la - lateral apodeme, mgs - median genital sac, mr - median ridge, pdg - posterior dorsal gland, pr - prostatic reservoir, t - tracheole, te - testis, vag - ventral anterior gland, vd - vas deferentia

canal atrium. The ejaculatory canal atrium opens into the anterior region of the genital atrium via an ejaculatory canal. Paired cuticular evaginations, the lateral genital sacs, are also associated with this anterior region. These gas-filled sacs open lateral to the ejaculatory canal. Two sets of accessory glands are associated with the genitalia. Opening into the anterior region are the anterior glands. Associated with the posterior region of the genital atrium is the posterior dorsal gland, which opens via a dorsal cuticular invagination in the mid-line of the atrium. Also associated with the posterior region is the cuticle-lined median genital sac. The genital aperture, which can vary in shape in relation to form of the spermatophore produced within the genital chamber, is bordered anteriorly by the anterior genital operculum

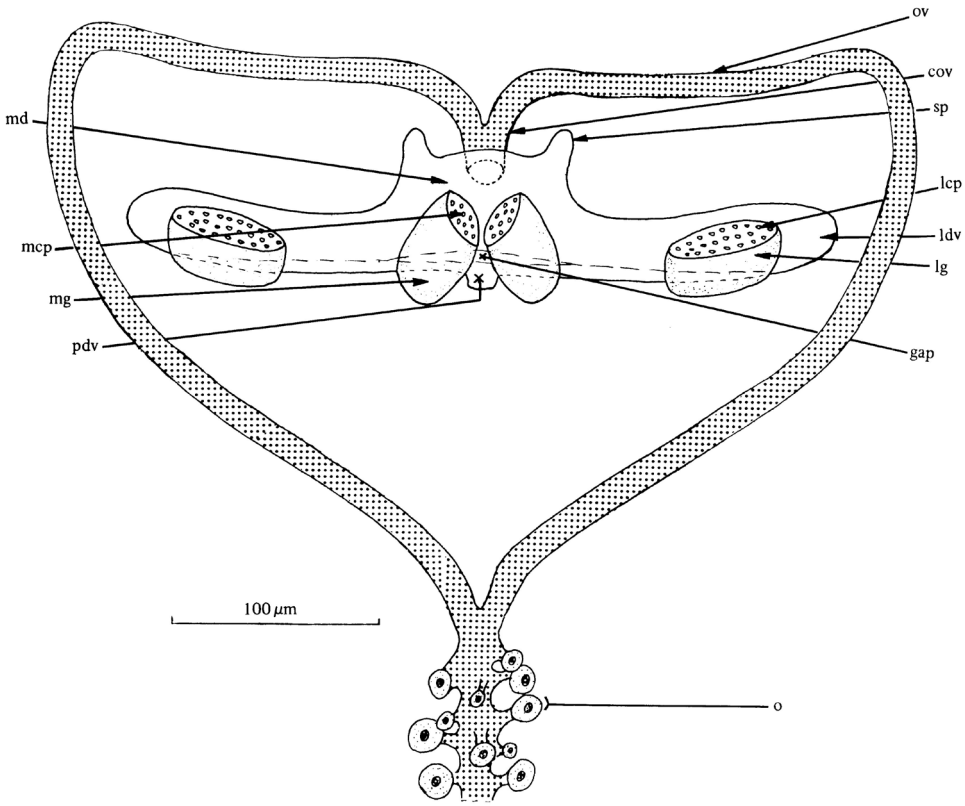

Fig. 3. Dorsal view of generalized female genitalia and associated glands (modified after Vachon, 1938; from Legg, 1974b).

(sternite 2) and posteriorly or postero-laterally by the posterior genital operculum (sternite 3). These plates are covered by variously placed setae, some of which protect the otherwise exposed genital aperture.

FEMALE GENITALIA

These are designed to receive sperm, produce eggs, carry the brood sac containing developing young, and nourish eggs/young (Wood and Gabbutt, 1971). The genital atrium is complex but less variable than that of the male. It consists of an invagination between sternites 2 and 3 of the opisthosoma that is divided into four regions: a median, two lateral, and a posterior diverticulum. The median diverticulum opens to the exterior via the genital aperture, while antero-dorsally the oviduct opens into it. Two sets of accessory glands, median and lateral glands, are present which open into the median and lateral diverticula via median and lateral cribriform plates, respectively. A number of muscles are also present. The genital aperture is bordered by plates in a form similar to, but usually simpler than that of the male.

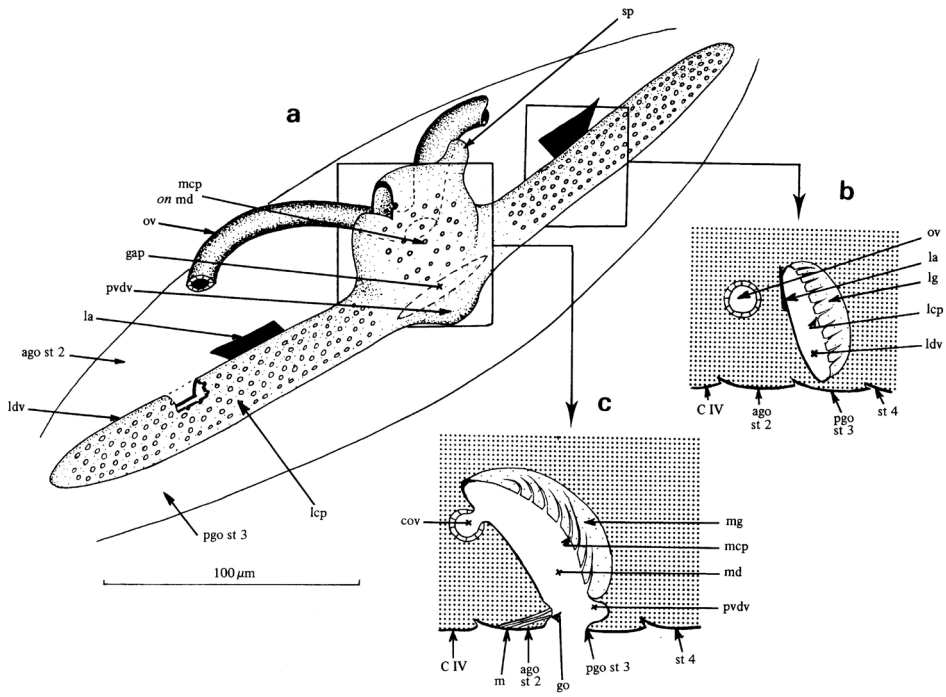

Fig. 4. Views of the generalized female genitalia: a) antero-lateral view of the genitalia after clearing in potassium hydroxide (the oviducts have been included); b) transverse section through the lateral diverticulum; c) transverse section through the median diverticulum (modified from Legg, 1974b).

Female genital characters that can be useful in defining a group include setation of the genital opercula, size and form of the genital diverticula, and size and form of the cribriform plates and distribution of their pores.

(a) antero-lateral view of the genitalia after clearing in potassium hydroxide (the oviducts have been included)

(b) Transverse section through the lateral diverticulum

(c) Transverse section through the median diverticulum (modified from Legg, 1974b)

The spermatophore's complexity is correlated with the type of mating behavior involved. Weygoldt (1969) classifies pseudoscorpions into four groups depending on the type of mating behavior they exhibit:

1. Sperm transfer without mating, males and females acting independently in both space and time (Chthoniidae, Neobisiidae, and Cheiridiidae).

2. Sperm transfer without mating; one mate acts only in the presence of the other (Olpiidae).

3. Sperm transfer with mating; both sexes active:

a. Without firm body contact throughout the nuptual dance (Chernetidae).

b. With firm body contact throughout the nuptual dance (Cheliferidae).

This is correlated with increasing complexity of the type of spermatophore produced and form of the male genitalia, the former being a function of the latter (Legg, 1971). Associated with these developments is the trend towards an increase in complexity of the female genitalia, namely in the development of spermathecae. These morphological and behavioral characteristics, together with other, non-genitalial characters, have led to the conclusion that the least specialized families include the Neobisiidae, Chthoniidae, and Cheiridiidae, while the Chernetidae and Cheliferidae are regarded as being more specialized.

As far as complexity of the spermatophore is concerned, there is also an environmental input. Species belonging to the least specialized families frequently live in habitats that have a high humidity. Their spermatophores consist of a stalk upon which a simple packet of sperm is deposited that is potentially prone to desiccation. The spermatophores may be left unattended for some time, making them extremely vulnerable. High losses may occur and so, at least in the Chthoniidae and Neobisiidae (Legg, pers. obs.), a male will deposit a number of spermatophores over a few hours. Those with more complex spermatophores have a tougher complex membrane surrounding the sperm mass protecting it from desiccation. In addition, these species indulge in mating rituals which ensure that the spermatophores are not left around indefinitely, being picked up by the females relatively soon after deposition by the male. Simple spermatophores are also produced in the Cheiridiidae. *Cheiridium museorum* is a species built to tolerate dry conditions of hay barns and buildings with an opisthosomal cuticle thickness totalling nearly a third of the thickness of the entire animal. Their spermatophores are likely to be prone to desiccation but it is not known how long they are left before a female finds them or if the structure of the envelope surrounding the sperm mass differs from that found in species of Chthoniidae and Neobisiidae.

Much more needs to be done. Future studies will hopefully unravel the form and function of the genitalia in other pseudoscorpions and furthermore the genitalia themselves will provide additional characters that will enhance the definition of species, genera and families.

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