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The male genital system of spiders (Arachnida: Araneae) with notes on the fine structure of seminal secretions

Peter Michalik

ABSTRACT

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The general organization of the male genital system of Araneae is poorly studied and a comparative investigation including taxa of all main groups is still lacking. The present paper reports on the male genital system of selected taxa of Mesothelae, Mygalomorphae and Araneomorphae in order to give a first overview of its general organization. As already described by former authors, the genital system consists of paired distinct testes, which lead into thin deferent ducts. Near the genital opening the deferent ducts fuse to form an ejaculatory duct, which opens into the genital opening. The shape of the different parts is very diverse between the taxa and bears a potential for phylogenetic studies. Exceptions from this organization, e.g., fusion of testes, were found in the observed species of Liphistiidae, Dysderidae and Scytodidae.

The high structural diversity of seminal secretions, shown in the present study for the first time, is most remarkable. Besides the secretion matrix, different kinds of secretion droplets are present in most of the observed species. The ultrastructure of these secretions differs between all species and ranges from homogenous, electron-dense roundish secretion droplets to secretions composed of different compounds. The possible functions of seminal secretions, e.g. their role in sexual selection processes are discussed.

Keywords: Male reproductive system, spermatozoa, testis, phylogeny.

Introduction

First descriptions of the morphology of the male genital system of spiders are already known from the 19th century. Bertkau (1875) briefly described the genital system of several spider taxa, but depicted only the organization of *Tegenaria domestica*. He recognized that male spiders possess a pair of long testes, which each lead into thinner deferent ducts. These finally fuse near the genital opening forming a short ejaculatory duct. Furthermore, he described a different organization for a few taxa (*Segestria* and *Atypus*) in which testes and deferent ducts are not clearly distinguishable. Since then, only few further descriptions of isolated taxa were published (e.g., Bösenberg 1905, Melchers 1964, Juberthie & al. 1981, Kim & al. 1993, Knoflach 1998, Costa-Ayub & Faraco 2007). The only comparative study was presented by Crome (1951) who compared in detail the genital system of species from Araneidae, Cybaidae, Pisauridae and Philodromidae, which show the general organization with distinct testes and deferent ducts (he also presented the first figures of the spider male genital system since the first observations of Bertkau in 1875!). On the other hand, Melchers (1964) described a completely different organization for theraphosid spiders, which possess very long and convoluted tubes, which are fused near the genital opening – an organization that has not been shown for other spider taxa yet.

The internal organization of the male genital system of spiders was already described by early authors based on light microscopical observations (e.g., Bertkau 1878, Bösenberg 1905, Warren 1928, 1931). These studies showed that spermatogenesis usually occurs in cysts, which are of different developmental stage. The spermatozoa are accumulated in the lumen of the testes, transferred into the deferent ducts and finally taken up into the palpal organ. Recent observations on the haplogyne spider *Pholcus phalangioides* revealed that the seminal fluid contains different types of secretion products consisting of proteinaceous substances, which are produced in the testes and deferent ducts (Michalik & Uhl 2005). The functions of these secretion products are still unknown.

Due to the inadequate knowledge, the present study shall give a first overview of the diversity of the general organization of the male genital system in spiders, including representatives of all main spider groups. Furthermore, the secretion products in the seminal fluid of selected species are investigated ultrastructurally, in order to show their astonishing structural diversity in the different spider taxa for the first time.

Material and Methods

Males of the following species were dissected in phosphate buffer (0.1 M, pH 7.2) to isolate their genital system: Mesothelae – *Liphistius* cf. *phuketensis* (Liphistiidae); Mygalomorphae – *Lasiodorides striatus* (SCHMIDT & ANTONELLI, 1996) (Theraphosidae); Haplogynae – *Kukulcania hibernalis* (HENTZ, 1842) (Filistatidae); *Dasumia taeniifera* THORELL, 1875 (Dysderidae); *Harpactea pili-gera* (THORELL, 1875) (Dysderidae); *Tedia abdominalis* DEELEMEN-REINHOLD, 1988 (Dysderidae); *Psilochorus simoni* (BERLAND, 1911) (Pholcidae); *Loxosceles hirsuta* MELLO-LEITÃO, 1931 (Sicariidae); *Scytodes globula* NICOLET, 1849 (Scytodidae); Entelegynae – *Stegodyphus dumicola* Pocock, 1898 (Eresidae); *Scolecurea* sp. (Linyphiidae); *Steatoda grossa* (C.L. KOCH, 1838) (Theridiidae); *Steatoda bipunctata* (LINNAEUS, 1758) (Theridiidae); *Nigma flavescens* (WALCKENAER, 1830) (Dictynidae); *Anyphaena accentuata* (WALCKENAER, 1802) (Anyphaenidae); *Creugas* sp. nov. (undescribed species of the *bellator* group) (Corinnidae); *Hogna gumia* (PETRUNKEVITCH, 1911) (Lycosidae); *Philodromus dispar* WALCKENAER, 1826 (Philodromidae). Vouchers are deposited in the Zoological Institute and Museum Greifswald (ZIMG) and the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Buenos Aires (MACN).

Light Microscopy (LM): Male specimens of *Psilochorus simoni* were fixed in Bouin solution, rinsed in graded ethanols and embedded in Paraffin wax. Sections (7 µm) were made with a Leica microtome and stained according to Gollner (1938). Finally, the sections were mounted with Eukitt medium. Examination was performed with an Olympus BX 60 and pictures were taken with an Olympus DP 10 digital camera.

Scanning Electron Microscopy (SEM): The isolated male genital system of *Psilochorus simoni* (BERLAND, 1911) was split open in a droplet of phosphate buffer (see above) by thin needles onto glass coverslips covered with 1% poly-L-lysine. After 10 min sedimentation the adhering material was fixed with 2.5% glutaraldehyde in buffer for 1h at 4°C. Samples were then rinsed in buffer and post-fixed in buffered 1% osmium tetroxide, dehydrated in graded ethanols, dried in a BAL-TEC CPD 030 critical point dryer using amylacetate as intermediate, coated with gold-palladium in a Quorum Technologies SC7620 sputtering device and examined in a Leo DSM 940A scanning electron microscope.

Transmission Electron Microscopy (TEM): For the observation of the ultrastructure of secretion in the genital system, males of the following species were dissected in phosphate buffer (0.1 M, pH 7.2): Haplogynae – *Theotima* sp. (Ochyroceratidae); *Protoleoneta italica* (SIMON, 1907) (Leptonetidae); *Scytodes globula* NICOLET, 1849 (Scytodidae); Entelegynae – *Ero aphana* (WALCKENAER, 1802) (Mimetidae); *Micrathena gracilis* (WALCKENAER, 1805)

(Araneidae); *Comaroma simoni* BERTKAU, 1889 (Anapidae); *Nesticus cellulanus* (CLERCK, 1757) (Nesticidae); *Achaearanea tabulata* LEVI, 1980 (Theridiidae); *Crustulina guttata* (WIDER, 1834) (Theridiidae); *Nesticodes rufipes* (LUCAS, 1846) (Theridiidae); *Textrix denticulata* (OLIVIER, 1789) (Agelenidae); *Nigma flavescens* (WALCKENAER, 1830) (Dictynidae); *Oxysoma longiventre* (NICOLET, 1849) (Anyphaenidae); *Hogna gumia* (PETRUNKEVITCH, 1911) (Lycosidae); *Zodarion jozefienae* BOSMANS, 1994 (Zodariidae). The genital systems were fixed in 2.5% glutaraldehyde in the same buffer followed by postfixation in buffered 2% osmium tetroxide. After washing, the tissue pieces were dehydrated in graded ethanols and embedded in Spurr's resin (Spurr 1969). Ultrathin sections were made with a Leica UCT ultramicrotome and stained with uranyl acetate and lead citrate. Examination was performed with a Zeiss EM 10A electron microscope.

Results

The male genital system of spiders is generally organized in three different parts – paired testes leading into paired deferent ducts (vasa deferentia), which finally open into an unpaired ejaculatory duct (ductus ejaculatorius).

The testes are mostly tube-like and extend deeply into the body cavity. Usually, they are ventrally bordered by the silk glands and surrounded by parts of the midgut gland (Fig. 1). Within the testes the developing spermatids are organized in cysts (Figs. 1c, d). In the lumen of the testes secretion droplets and coiled spermatozoa are present. The deferent ducts and the ejaculatory duct only contain the encysted spermatozoa (transfer forms) and seminal secretion, i.e., secretion droplets (Figs. 1a, b). Accessory glands are not present.

The gross morphology of the genital system can differ remarkably (Figs. 2). In the mesothele spider *Liphistius cf. phuketensis* the long testes are distally fused and convoluted due to the very compact shape of the opisthosoma. The thin deferent ducts are fused near the genital opening, but without extending into a prominent ejaculatory duct (Fig. 2a). The observed theraphosid spider *Lasiodorides striatus* possesses a genital system consisting of two long tubes, which are fused near the genital opening. In contrast to all other observed spider species, an external differentiation of testes and deferent ducts is not visible (not shown, but in accord with Melchers 1964).

The highest morphological diversity of the male genital system is present in the observed Haplogynae. The males of the filistatid *Kukulcania hibernalis* possess long convoluted testes, which lead into small deferent ducts. The

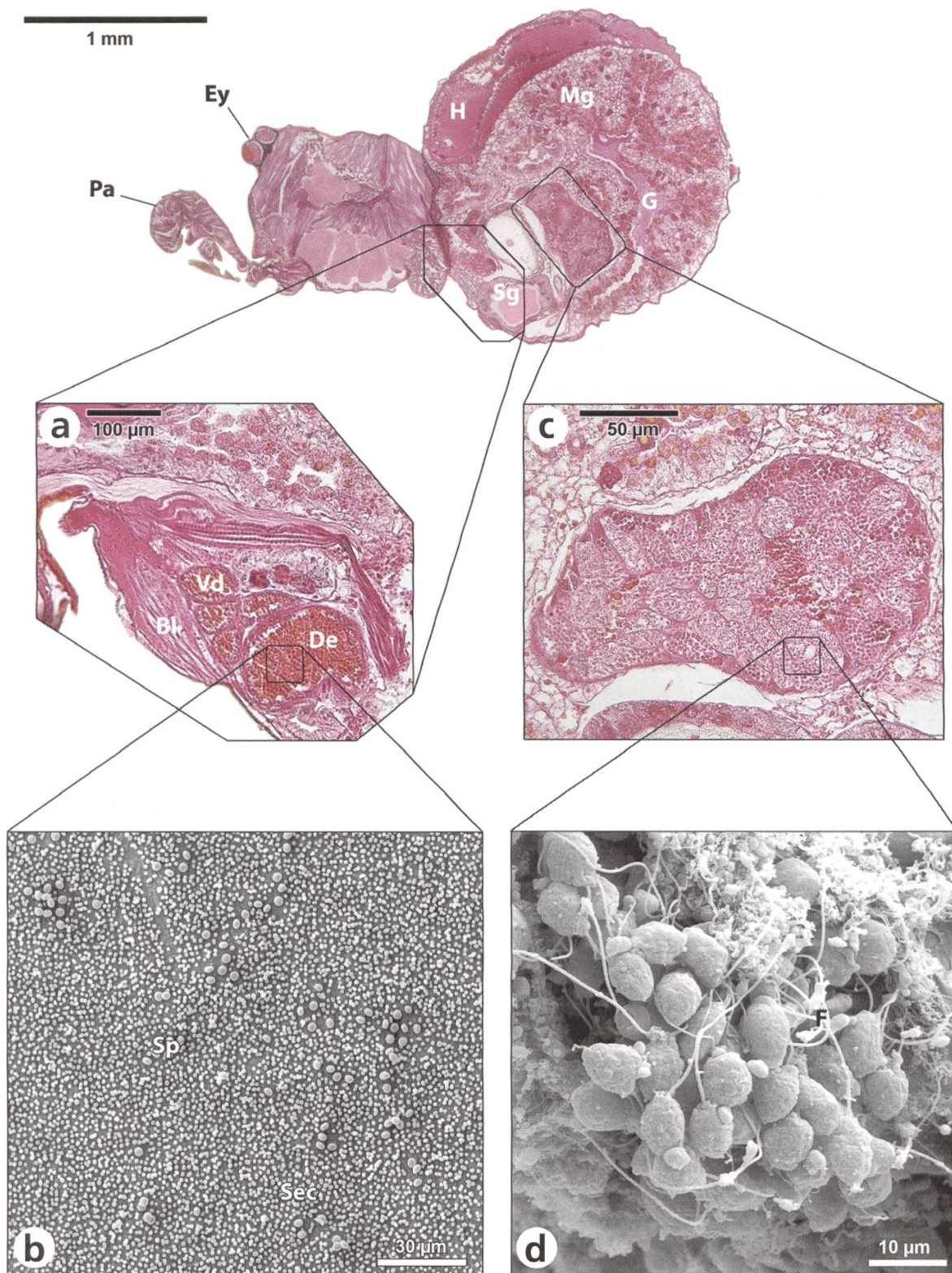


Fig. 1. The male genital system of *Psilochorus simoni*. – a: Detail of the region of booklungs and genital opening. The deferent ducts have a thin lumen in contrast to the wide ejaculatory duct. Both parts are filled with seminal fluid. LM. – b: The seminal fluid consists of spermatozoa, which are clustered in small groups, and large amounts of secretion droplets. SEM. – c: Within the testis all stages of spermatogenesis are present resulting in a heterogeneous character. LM. – d: Early spermatids of the same developmental stage, which are clustered together in the testis. SEM. Abbreviations: Bl = book lung; De = ejaculatory duct; Ey = eyes; G = gut; H = heart; Mg = midgut gland; Pa = palp; Sg = silk glands; Vd = deferent duct.

ejaculatory duct of this species has a square shape (Fig. 2b). In contrast, the testes of the sicariid *Loxosceles hibernalis* are oval-shaped and continue into long, but uncoiled deferent ducts (Fig. 2c). A similar organisation is also present in all observed pholcid species. In contrast, the genital system of the observed *Harpactea*, *Dasumia* and *Tedia* species is characterized by proximally fused testes, which lead into short and uncoiled deferent ducts (Fig. 2d). Highly remarkable is the genital system of the observed *Scytodes globula* specimens, which is characterized by large proximally fused testes and asymmetrically organized deferent ducts, i.e., the length of the left vas deferens was more than twice that of the right duct (Fig. 2e). This peculiar arrangement should be confirmed by further observations on more specimens.

In Entelegynae a fusion of testes was not observed. There are always two clearly divided testes leading into thin deferent ducts. The shape of the testes can differ remarkably, as seen in Figs. 2f–n. For example, the eresid *Stegodyphus dumicola* possesses long slightly convoluted testes leading into highly coiled deferent ducts (Fig. 2g). On the other hand, the testes of *Anyphaena accentuata* are very small and possess an oval shape (Fig. 2k). Conspicuously, several entelegyne families seem to have distinctive characteristics. For example, the observed dictynid *Nigma flavenscens* is characterized by seminal vesicles present at the most distal part of the deferent ducts (Fig. 2j). The observed philodromid *Philodromus dispar* shows a large arrow-shaped ejaculatory duct not found in any of the other studied species (Fig. 2n). In some observed Theridiidae, i.e., *Steatoda grossa*, a large, roundish ejaculatory duct (=Vesicula seminalis in Knoflach 1998) is present (Fig. 2h).

Most remarkable is the enormous structural diversity of secretions in the seminal fluid. In all species investigated so far, different kinds of secretion are present (Fig. 3). The secretion matrix can be electron-lucent as, e.g., in *Ero aphana* (Fig. 3d) or electron-dense as present in *Zodarion jozefienae* (Fig. 3o). The secretion droplets, which are mostly present in the matrix, differ in shape and electron density, as seen in Fig. 3. For example, in *Scytodes globula* the droplets are very dense in comparison to *Theotima* sp. or *Protoleoneta italica*. In *Ero aphana* they possess a needle-like shape (Figs. 3a–d). Furthermore, in some species composed secretion droplets are present, e.g., in *Achaearanea tabulata* or *Textrix denticulata* (Figs. 3e, i). In some species several different kinds of secretion can occur, as present, e.g., in *Nesticus cellulanus*, *Nesticodes rufipes* or *Crustulina guttata* (Figs. 3h, j, k).

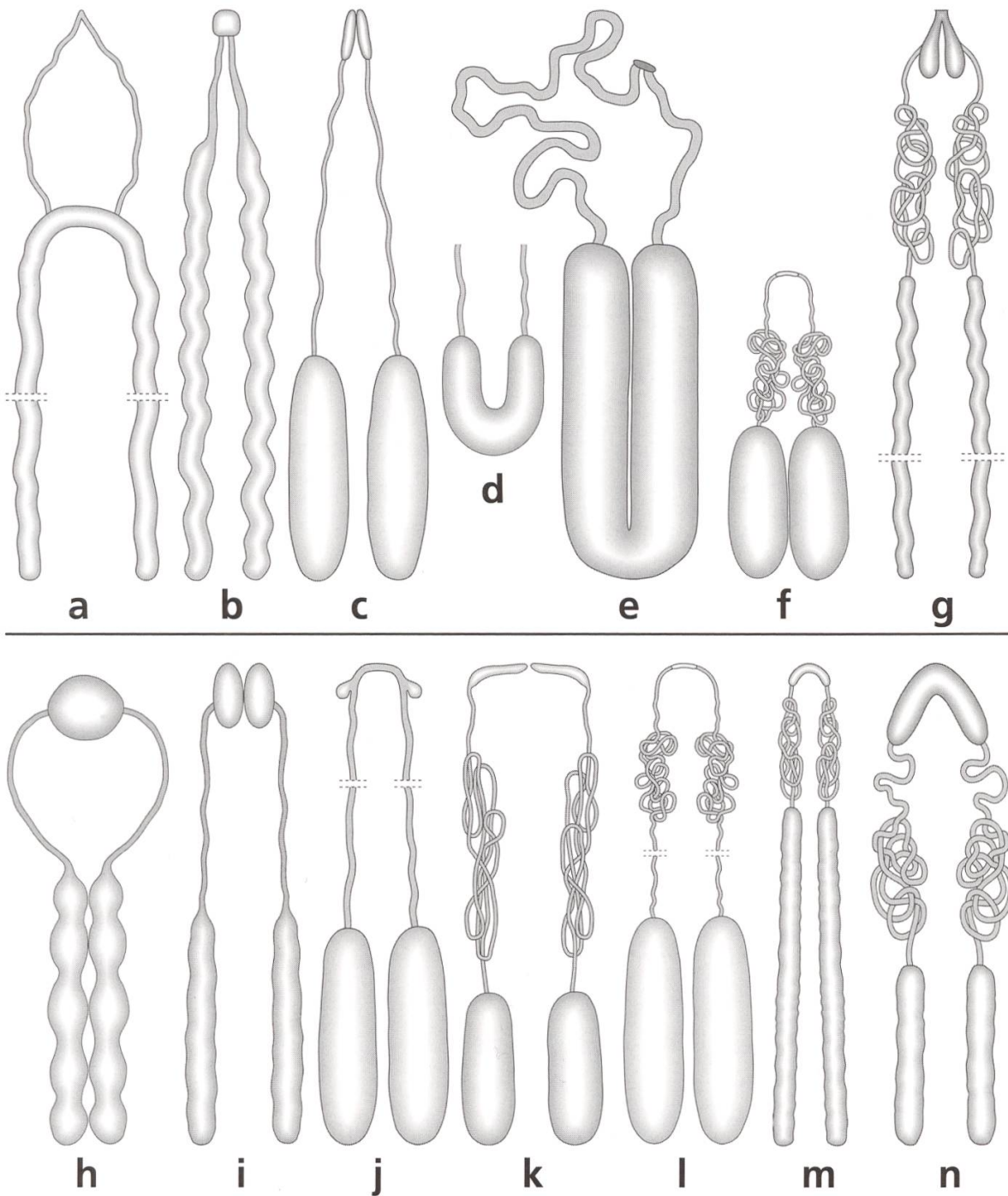


Fig. 2. Drawings of the male genital system of the observed species. – a: *Liphistius* cf. *phuketensis* (Liphistiidae); – b: *Kukulcania hibernalis* (Filistatidae); – c: *Loxosceles hirsuta* (Sicariidae); – d: *Dasumia taeniifera* and *Harpactea piligera* (Dysderidae); – e: *Scytodes globula* (Scytodidae); – f: *Scolecuroa* sp. (Linyphiidae); – g: *Stegodyphus dumicola* (Eresidae); – h: *Steatoda grossa* (Theridiidae); – i: *Steatoda bipunctata* (Theridiidae); – j: *Nigma flavescens* (Dictynidae); – k: *Anyphaena accentuata* (Anyphaenidae); – l: *Creugas* sp. nov. (*bellator* group) (Corinnidae); – m: *Hogna gumia* (Lycosidae); – n: *Philodromus dispar* (Philodromidae).

Discussion

The two possible general organizations of the male genital system already described by Bertkau (1875, 1878) could be confirmed with this first comparative study. Except for the studied theraphosid *Lasiodorides striatus*, all observed species showed clearly distinct testes and deferent ducts, which are fused near the genital opening (a distinct ejaculatory duct is present in most species). This general organization was also described for a few other araneomorph species by subsequent authors (Bösenberg 1905, Gerhardt & Kaestner 1938, Crome 1951, Juberthie & al. 1981, Lopez 1984, Kim & al. 1993, Knoflach 1998). In contrast, in *Lasiodorides striatus* the extremely convoluted testes and deferent ducts are nearly identical in their external morphology (i.e. diameter) – an organization only known for other Theraphosidae (Melchers 1964), Atypidae and Segestriidae (Bertkau 1875, 1878). Thus, it is misleading that Foelix (1996) and Felgenhauer (1999) consider this organization as general for spiders. Furthermore, Bertkau (1878) described a ring-shaped genital system, i.e., proximally fused testes, for species of the genera *Atypus* (Atypidae), *Segestria* (Segestriidae) and *Dysdera* (Dysderidae). In the present study, this peculiar organization was also found in the observed *Harpactea*, *Dasumia*, *Tedia* (Dysderidae) and *Scytodes* (Scytodidae) species. On the other hand, the dysderid *Rhode scutiventris* possesses two clearly distinct and unfused testes (personal observation). Hence, it seems likely that the conspicuous ring-shape, which is formed by fusion of the proximal ends of the testes, evolved convergently within spiders. In contrast, the observed species of the most primitive spider family Liphistiidae possesses distally fused testes, which was not found in any other spider taxa yet. Further observation on more species of Mesothelae will show whether this organization is a general trait of this primitive spider group.

In several of the observed species peculiar modifications are present, which might be species, genus or family specific (further observation on more taxa are needed). For example, the dictynid *Nigma flavescens* possesses conspicuous seminal vesicles in the most distal region of the deferent ducts and a large arrow-shaped ejaculatory duct characterizes the genital system of the philodromid *Philodromus dispar*. Relatively short, uncoiled deferent ducts and a remarkable ejaculatory duct characterize the theridiid species investigated so far. The ejaculatory duct in, e.g., the observed *Theridion* or some *Steatoda* species is an enlarged seminal vesicle (= Vesicula seminalis according to Knoflach 1998), which might be evolved from a normal fused duct still present in *Latrodectus* species (personal observation). Interestingly, these findings are in accord with present phylogenetic hypotheses, which revealed a basal position of the Latrodectinae (Agnarsson 2004).

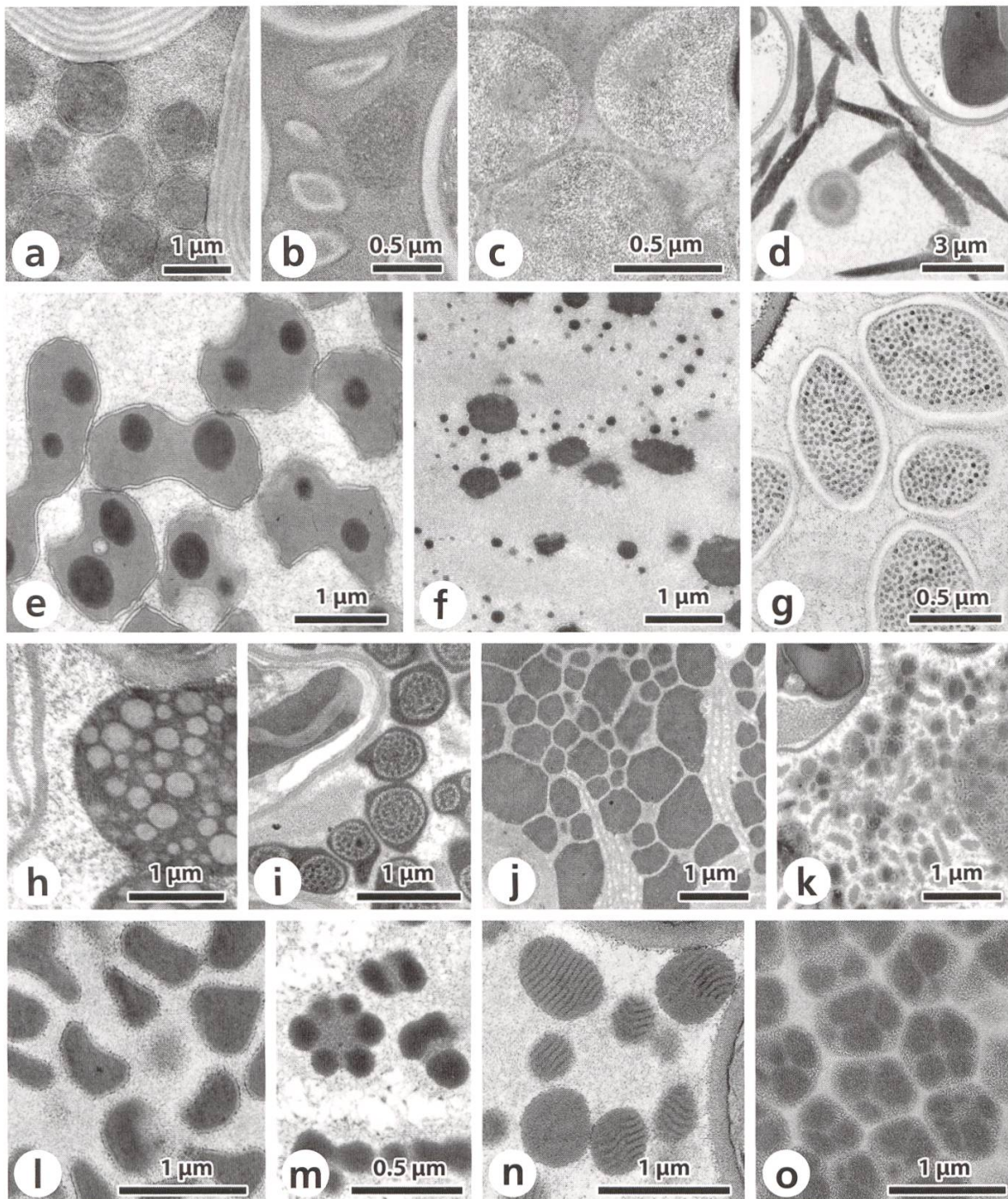


Fig. 3. Secretions within the seminal fluid of the observed species. TEM. – a: *Scytodes globula* (Scytodidae); – b: *Theotima* sp. (Ochyroceratidae); – c: *Protoleptoneta italica* (Leptonetidae); – d: *Ero aphana* (Mimetidae); – e: *Textrix denticulata* (Agelenidae); – f: *Hogna gumia* (Lycosidae); – g: *Micrathena gracilis* (Araneidae); – h: *Nesticus cellulanus* (Nesticidae); – i: *Achaearanea tabulata* (Theridiidae); – j: *Nesticodes rufipes* (Theridiidae); – k: *Crustulina guttata* (Theridiidae); – l: *Comaroma simoni* (Anapidae); – m: *Oxysoma longiventre* (Anyphaenidae); – n: *Zodarion jozefienae* (Zodariidae); – o: *Nigma flavescens* (Dictynidae).

To conclude, the male genital system of spiders shows a much higher diversity in its general organization than expected. A recent study on the male genital system of goblin spiders (Oonopidae) showed a completely fused testes, which supports the monophyly of this highly diverse family (Burger & Michalik

in press). Thus and in contrast to Petrunkevitch (1933), a potential for phylogenetic analyses is obvious (see above) and should be considered in future studies on spider systematics.

A novel and unexpected result of this study was the enormous diversity of secretion products present in the different parts of the male genital system. The secretions are produced by the somatic (testes) and epithelial cells (deferent ducts) (e.g. Alberti & Weinmann 1985, Alberti & al. 1986) since accessory glands as known, e.g. from insects are absent in male spiders (see also Alberti 2005). The reason for the loss/absence of accessory glands is still unknown. It can be assumed that due to the evolution from indirect (via spermatophores as present in the related taxa Amblypygi and Uropygi) to direct sperm transfer (via palpal organs), accessory glands lost their main function – producing spermatophores – as it still occurs, e.g., in Amblypygi (see, e.g., Weygoldt 1972, 1975, 1978, Alberti 2005).

What are the functions of the secretions present in the male genital system of spiders? Since spider males produce transfer forms (sperm aggregates) at the end of spermiogenesis, which are surrounded by a secretion sheath in the deferent ducts (see e.g., Alberti 2000, Alberti & Michalik 2004, Michalik & al. 2004), it seems likely that part of the secretions are used for the production of the sheath. For example, in the pholcid spider *Psilochorus simoni* transfer forms are already formed within the lumen of the testes, where two different kinds of secretion droplets are present; in contrast, in the seminal fluid only one type of secretion was observed (Michalik & Huber 2006). A further function could be the nutrition of the spermatozoa, which are usually stored in an inactive state for longer periods (e.g., Bösenberg 1905, Lopez 1987, Michalik & al. 2005a). But these suggestions do not explain the enormous diversity of secretions, which was exemplarily shown in observations on Pholcidae for the first time (Michalik & al. 2005b, Michalik & Uhl 2005, Michalik & Huber 2006). Most likely the evolution of male secretions in spiders is related to processes of sexual selection as already demonstrated for insects (Eberhard & Cordero 1995, Eberhard 1996). For example, secretions of the accessory glands of insect males can influence the receptivity of females and the oviposition (e.g., Wolfner 1997, Jin & Gong 2001, Gillot 2003). Hence, it can be assumed that also in spider males seminal secretions evolved rapidly and, thus, diversify as predicted by the sexual selection hypothesis. Interestingly, Estramil & Costa (2007) concluded from their studies on the mating behaviour of the wolf spider *Schizocosa malitiosa* that sperm-associated substances have an influence on the female reluctance – the first indirect evidence for a possible role of male secretions in the processes of sexual selection in spiders. Future studies should concentrate on this problem to evaluate the influence of sex-

related substances in the reproduction of spiders (see also Eberhard 2004, Huber 2005).

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