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ORIGINAL ARTICLE

Genital morphology of the haplogyne spider *Harpactea lepida* (Arachnida, Araneae, Dysderidae)

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Abstract Female *Harpactea lepida* possess a single genital opening leading into a diverticulum. This diverticulum shows no secretory layer. It continues posteriorly into a receptaculum which is associated with gland cells. In the two already described dysderids, *Dysdera crocata* and *D. erythrina*, the bilobed spermatheca lies anteriorly to the diverticulum. Gland cells are associated with the spermatheca and the diverticulum. In *H. lepida*, the sclerotized genital structures lie dorsally to the diverticulum and consist of a posterior and an anterior part. The posterior part shows a lamella extending laterally to sclerites functioning as muscle attachments. The anterior part has two roundish structures. A hollow stalk-like sclerite functioning as muscle attachment extends towards anterior. The posterior and the anterior part of the sclerotized genital structures fit together. A narrow uterine valve connecting the uterus externus with the diverticulum forms between them. It may be opened by muscles as also suggested for *D. erythrina*. In *H. lepida*, spermatozoa embedded in secretion are found in the diverticulum and the receptaculum. There is no evidence that they are stored under different conditions like in *D. erythrina*. Additional spermatozoa are found in the uterus externus of *H. lepida* which could be an indication for internal fertilization. Spermatogenesis occurs in cysts in the testes of male *H. lepida*. In the vasa deferentia, the ductus ejaculatorius and the palpal bulb, the spermatozoa are embedded in homogenous secretion. The palpal bulb has a distal extension bearing a crown-like structure. The embolus is situated at the base of the extension.

Keywords Genital structures · Spermatozoa · Secretion · Haplogynae · Dysderidae

In memoriam of Konrad Thaler.

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Introduction

In haplogyne spiders, the female reproductive system is characterized by a single copulatory duct serving for insemination and fertilization. Sperm is stored in receptacula which arise directly from the wall of the uterus externus. In entelegynes, separate fertilization ducts lead from the receptacula to the uterus externus (Wiehle 1967; Uhl 2002). However, several studies revealed that the internal genital structures of some haplogynes appear more complex than previously expected (Brignoli 1978; Cooke 1966; Uhl 1994a, b, 2000; Huber 2002; Burger et al. 2003, 2006a, b). The complexity of the female genital tract may be correlated to its use in postcopulatory female choice (Eberhard 1996; Hellriegel and Ward 1998; Uhl 2002; Burger et al. 2003). Detailed investigations of female genital organs by means of serial sections and scanning electron microscopy have only been done for a few haplogynes so far (e.g., Uhl 1994a, 2000; Huber 1994, 1995; Burger et al. 2003, 2006a, b). Such studies allow conclusions on the functional morphology of the genital structures (Huber 2002; Burger et al. 2003,

2006a, b) and contribute to a better understanding of their evolution and their role in the context of sexual selection (Alberti 2000; Eberhard 1996; Galis 1996; Hellriegel and Ward 1998; Uhl 2002; Alberti and Michalik 2004; Michalik et al. 2005; Burger et al. 2006a, b).

According to Coddington and Levi (1991) the haplogyne spider family Dysderidae belongs to the Dysderoidea together with the Segestriidae, Oonopidae and Orsolobidae. Little is known about the biology and ecology of dysderids (Gerhardt 1927, 1933; Wiehle 1953). Certain species of the genus *Harpactea* are relatively common in Europe where they inhabit the leaf layer of woods. Dysderids are also found in moss growing over rocks and under dead wood (Wiehle 1953).

Investigations of dysderid genital structures have only been done for two species so far, *Dysdera crocata* C. L. Koch, 1838 (Cooke 1966) and *Dysdera erythrina* (Walckenaer, 1802) (Cooke 1966; Uhl 2000). The present study gives a detailed description of the female genital system of *Harpactea lepida* by means of serial semi-thin sections and scanning electron microscopy. Furthermore, the male genital organs are briefly described. The study aims at finding differences between the genital structures of *H. lepida* and the genitalia of *D. crocata* and *D. erythrina*.

Materials and methods

Adult specimens of *Harpactea lepida* (C. L. Koch, 1838) were collected in Styria, Austria: one female on the Radlpass near the Slovenian border (23 November 1984, leg. Kropf, Schuster and Haumann), two females and one male in St Josef-Wetzelsdorf (25 November 1984, leg. Kropf), two females in Gleichenberg (7 April 1991, leg. Komposch) and one male in Leibnitz (5 May 1995, leg. Kropf). Two females were collected in Gastein, Austria (10 September–2 October 1993, leg. Relys). The material is deposited in the Natural History Museum of Bern, Switzerland (NMBE) where the study was carried out.

The opisthosomata of four females and the opisthosoma and the prosoma of one male were dehydrated in ethanol, embedded in LR White Resin (Soft Grade Acrylic London Resin) and semi-thin serially sectioned (1 μm) with a microtome (Leica RM 2145) using glass knives. The sections were stained with toluidine blue (1%) in an aqueous borax solution (1%) at 90°C for 18–20 min. One male palp and the vulva of one female were embedded in Hoyers's medium and slide-mounted. Light microscopic studies were performed with a Zeiss Axioplan 2.

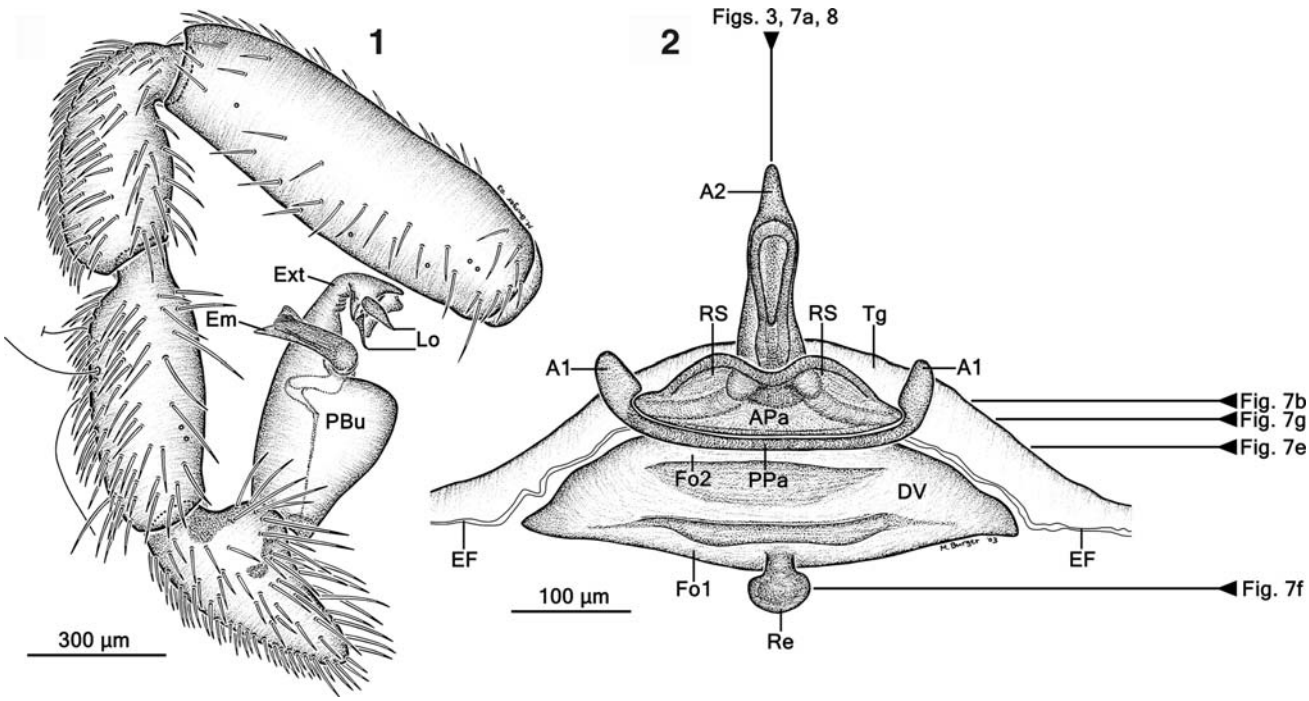
The opisthosoma of one female was serially sectioned until the genital region was longitudinally cut in the middle. The opisthosoma was then kept in ethanol (80%) for several days until the LR White Resin was dissolved. The cut opisthosoma and one vulva, which was isolated and kept in 5% KOH solution for several days until the tissue was dissolved, were dehydrated in graded ethanols, critical-point dried, gold sputtered and examined with a Philips XL30 FEG scanning electron microscope.

Results

Female genital structures

The slit-like genital opening (GO in Figs. 3, 7a) of *Harpactea lepida* lies distally on a tongue-like protrusion (Tg in Figs. 2, 3, 6, 7a, b) on the ventral side of the opisthosoma and leads into a cavity. The cavity expands posteriorly to a chitinized diverticulum (DV in Figs. 2, 3, 6, 7a–c, e) that continues dorsally to a fold (Fo2 in Figs. 2, 3, 6, 7a). The fold extends towards lateral and opens in the epigastric furrow (EF in Figs. 2, 3, 6). The diverticulum has another fold (Fo1 in Figs. 2, 3, 6, 7a) in its posterior wall and it leads into a roundish receptaculum (Re in Figs. 2, 3, 6, 7a, c, f) whose posterior wall is pervaded with pores (Po in Figs. 3, 6, arrowheads in Fig. 8c). Gland cells (Gl in Figs. 3, 6, 7a, c, f) are associated with the receptaculum. The glandular ducts (GD in Figs. 3, 8c) of these gland cells lead into the pores in the posterior wall of the receptaculum. The heavily sclerotized genital structures lie dorsally to the diverticulum. The posterior part of the sclerotized genital structures (PPa in Figs. 2, 3, 4, 7a, d, 8b) is situated anterior to the fold (Fo2) of the diverticulum. It shows a lamella (La in Figs. 3, 4, 6, 7a, 8b) extending towards the anterior. The lamella has an oval gap (OG in Figs. 4, 7d) in the middle and extends laterally to curved sclerites (A1 in Figs. 2, 3, 4, 6, 7b, d) that are directed anteriorly. These sclerites serve as muscle attachments (see "Muscles associated with the female genital structures"). The dorsal extension (Ex1) of the posterior part of the sclerotized genital structures (PPa) appears narrow laterally (Figs. 4, 6) whereas it becomes broader and bifurcated mesially (Figs. 3, 7a).

The anterior part of the sclerotized genital structures (APa in Figs. 2, 3, 4, 7a–c, g, 8b) shows a narrow dorsal extension (Ex2 in Figs. 3, 4, 6, 7a) and a broad furrow (Fu in Fig. 4) posteriorly. A T-shaped sclerite (TS in Figs. 4, 6, 7d) reaches into this furrow posteriorly. Anteriorly, the anterior part of the sclerotized genital structures forms two roundish structures (RS in



Figs. 1, 2 Male and female of *Harpactea lepida*. **1** Left pedipalp of male, retrolateral view. **2** Female genital region, dorsal view. *Arrowheads* indicate positions of the sections seen in Figs. 3, 7 and 8. *A1* sclerite serving as muscle attachment, *A2* stalk-like sclerite serving as muscle attachment, *APa* anterior part of the sclerotized genital structures, *DV* diverticulum, *EF* epigastric furrow, *Em* embolus, *Ext* extension of palpal bulb, *Fo1, 2* folds of diverticulum, *Lo* sclerotized lobe, *PBu* palpal bulb, *PPa* posterior part of the sclerotized genital structures, *Re* receptaculum, *RS* roundish structure of anterior part of sclerotized genital structures, *Tg* tongue-like protrusion

Figs. 2, 3, 4, 6, 7a, d, 8a). A stalk-like sclerite (A2 in Figs. 2, 3, 4, 6, 7a, d, 8a) with a strongly thickened distal part extends from these roundish structures (RS) toward the anterior. The stalk-like sclerite appears hollow (Figs. 3, 7a, 8a). It serves as muscle attachment (see "Muscles associated with the female genital structures"). The lateral edges of the anterior part of the sclerotized genital structures (Ed in Figs. 3, 4, 6, 7b, d) extend towards dorsal.

When the posterior and the anterior part of the sclerotized genital structures are put together (arrow in Fig. 4), a narrow slit forms between them. It is the uterine valve (UV in Figs. 3, 7a, 8b). The lamella (La) proceeds in the furrow (Fu) and the T-shaped sclerite (TS) fits exactly into the oval gap (OG) of the lamella (Figs. 4, 6, 7d). The sclerites (A1) lie beneath the lateral edges (Ed) of the anterior part of the sclerotized genital structures (Figs. 3, 4, 6, 7b, d). The uterus externus (UE in Figs. 5, 7b, g) is connected with the diverticulum (DV) via the uterine valve (UV) (Figs. 3, 7a) and shows lateral extensions (EUE in Figs. 5, 7b).

Spermatozoa inside the female genital structures

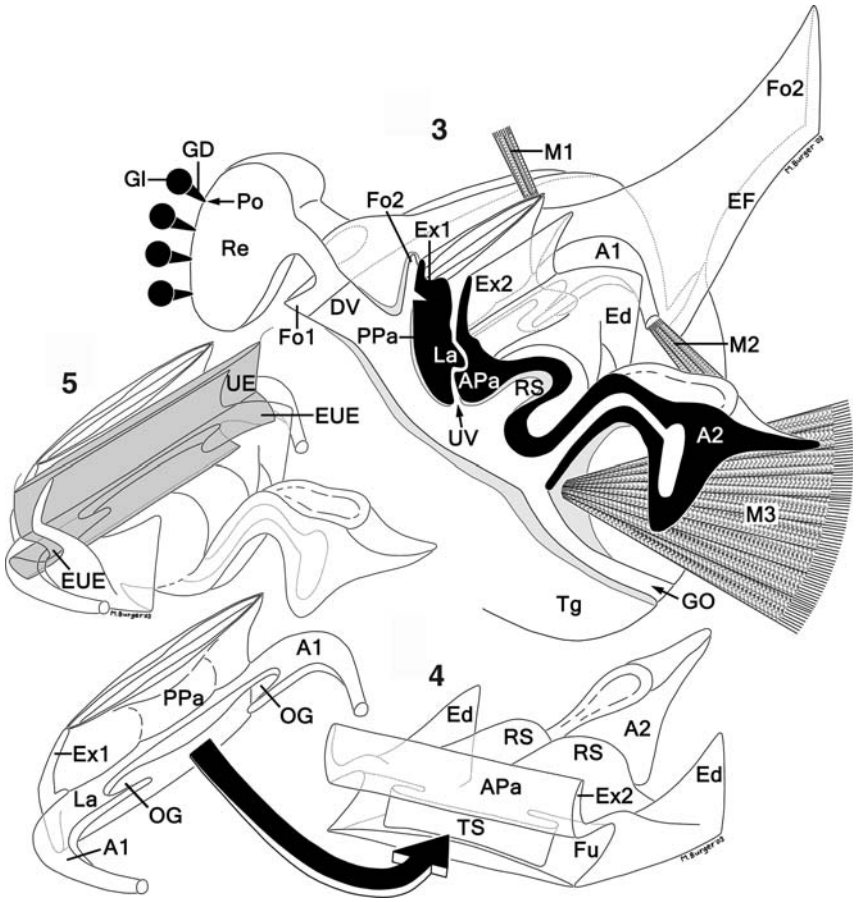
Accumulated spermatozoa are found in the diverticulum (DV) (Fig. 7a, b, e), the roundish structures (RS) (Fig. 7a) and the receptaculum (Re) (Fig. 7a, f). Further masses of spermatozoa (SP) are found in the uterus externus (UE) dorsally to the sclerotized genital structures and in the lateral extensions of the uterus externus (EUE) (Fig. 7b, g). All spermatozoa are embedded in pinkish secretion (stained with toluidine blue) (Sec in Fig. 7b, e, f).

Muscles associated with the female genital structures

The extension (Ex1) of the posterior part of the sclerotized genital structures serves as attachment for a paired set of muscles (M1 in Figs. 3, 6) which run backwards and ventrally, ending on the cuticle of the opisthosoma. The sclerites (A1) and (A2) are connected by the muscles (M2) (Figs. 3, 6, 7a, d). A huge set of muscles (M3 in Figs. 3, 6, 7c) is attached to the base of sclerite (A2). These muscles are arranged fanlike and directed anteriorly, ending on the cuticle of the opisthosoma near the pedicel.

Male genital structures

The palpal bulb of *H. lepida* (PBu in Figs. 1, 9a) is longish and cone-shaped. It narrows distally and continues into a bent extension (Ext in Fig. 1) that is folded on



Figs. 3–5 Schematic drawings of female *Harpactea lepida*. **3** Longitudinally cut genital region. **4** Sclerotized genital structures. *Arrow* indicates position of posterior part *PPa* when put together with anterior part *APa*. **5** Sclerotized genital structures with course of uterus externus *UE* and its extensions *EUE*. *A1* sclerite serving as muscle attachment, *A2* stalk-like sclerite serving as muscle attachment, *DV* diverticulum, *Ed* lateral edge of anterior part of sclerotized genital structures, *EF* epigastric furrow, *Ex1* dorsal extension of posterior part of sclerotized genital structures, *Ex2* dorsal extension of anterior part of sclerotized genital structures, *Fo1, 2* folds of diverticulum, *Fu* furrow of anterior part of sclerotized genital structures, *GD* glandular ducts, *Gl* gland cells, *GO* genital opening, *La* lamella on posterior part of sclerotized genital structures, *M1–M3* muscles 1–3, *OG* oval gap of lamella, *Po* pore on receptaculum, *Re* receptaculum, *RS* roundish structure of anterior part of sclerotized genital structures, *Tg* tongue-like protrusion, *TS* T-shaped sclerite of anterior part of sclerotized genital structures, *UV* uterine valve

the prolateral side. The distal part of the extension forms a crown-like structure with five sclerotized lobes (Lo in Fig. 1). The flat embolus (Em in Figs. 1, 9a) is situated at the base of the extension (Ext). It shows slight furrows and two small lateral horns distally (Fig. 1). The spermatozoa in the palpal bulb are closely packed (Sp in Fig. 9a) and embedded in homogenous secretion.

The male genital system of *H. lepida* consists of large testes (Te in Fig. 9b) and convoluted vasa deferentia (VD in Fig. 9c). The vasa deferentia lead into the ductus ejaculatorius (DE in Fig. 9c, d) that opens in the genital opening (GO in Fig. 9d). Spermatogenesis occurs in cysts. The spermatozoa (Sp in Fig. 9b) are accumulated in the lumen of the testes (LuT in Fig. 9b). In the vasa deferentia and the ductus ejaculatorius where the seminal fluid is gathered, the spermatozoa (Sp in Fig. 9c, d) appear densely packed and surrounded by secretory products (Sec in Fig. 9d).

Discussion

In accordance with the investigations on *D. crocata* and *D. erythrina* by Cooke (1966) and Uhl (2000), the present study on *H. lepida* shows that the genital structures of some dysderids appear rather complex. This is in contrast to the simple type of a haplogyne vulva proposed by Wiehle (1967) and Austad (1984). In *D. crocata* and *D. erythrina*, there are two structures

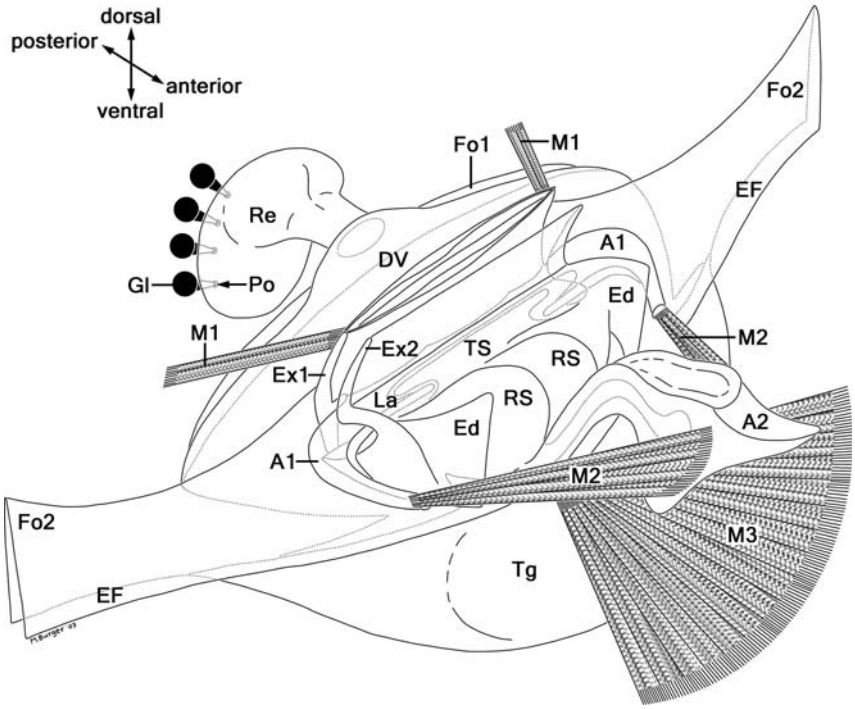


Fig. 6 Schematic drawing of female genital region of *Harpactea lepida*. *A1* sclerite serving as muscle attachment, *A2* stalk-like sclerite serving as muscle attachment, *DV* diverticulum, *Ed* lateral edge of anterior part of sclerotized genital structures, *EF* epigastric furrow, *Ex1* dorsal extension of posterior part of sclerotized genital structures, *Ex2* dorsal extension of anterior part of sclerotized genital structures, *Fo1*, *2* folds of diverticulum, *Gl* gland cells, *La* lamella on posterior part of sclerotized genital structures, *M1–M3* muscles 1–3, *Po* pore on receptaculum, *Re* receptaculum, *RS* roundish structure of anterior part of sclerotized genital structures, *Tg* tongue-like protrusion, *TS* T-shaped sclerite of anterior part of sclerotized genital structures

functioning as sperm storage organs: the anterior bilobed spermatheca and the posterior diverticulum which was considered to represent a synapomorphy for the Dysderoidea (Forster and Platnick 1985). According to the two different glandular equipments associated with the spermatheca and the posterior diverticulum in *D. erythrina*, it was suggested that sperm can be stored under different conditions (Uhl 2000).

In *H. lepida*, there is a single receptaculum lying posteriorly to the diverticulum. The diverticulum shows no secretory layer and gland cells are only associated with the receptaculum. The spermatozoa of some *Harpactea* species were described as synspermia by Alberti and Weinmann (1985) and Michalik et al. (2004). In the investigated *H. lepida*, spermatozoa are found in the diverticulum, the two roundish structures, and the receptaculum. There is no evidence that these spermatozoa are stored under different conditions like in *D. erythrina* (Uhl 2000). The spermatozoa inside the female genital structures of *H. lepida* are embedded in secretion, which may be produced by the gland cells adjoining the receptaculum but it could also partly be transferred by the male together with the spermatozoa. In the male genital system of *H. lepida*, spermatogenesis occurs in cysts and the spermatozoa are found closely packed and together with secretory products in the vasa deferentia which is in accordance with the situation in other dysderid species (Alberti and Weinmann 1985; Michalik et al. 2004). The secretion could afford nutriments to the spermatozoa (Uhl 1996; Berendonck and Greven 2005; Michalik et al. 2005; Burger et al. 2006a) or provide a matrix in order to keep the spermatozoa in the female sperm storage site (Uhl 1994a, b, 1996).

Schult (1980) called the hollow space of the sclerite A2 "frontal sperm space" suggesting that females may store sperm there. In our examined species, we never found sperm inside the sclerite A2. We suggest that the main function of this sclerite is to serve as a muscle attachment and not as a sperm storage organ.

Interestingly, masses of apparently inactive spermatozoa are found in the uterus externus of *H. lepida* which could be an indication for fertilization in the uterus externus or internus. Such internal fertilization was suggested for the tetrablemmid *Indicoblemma lannaianum* Burger 2005 (Burger et al. 2006a).

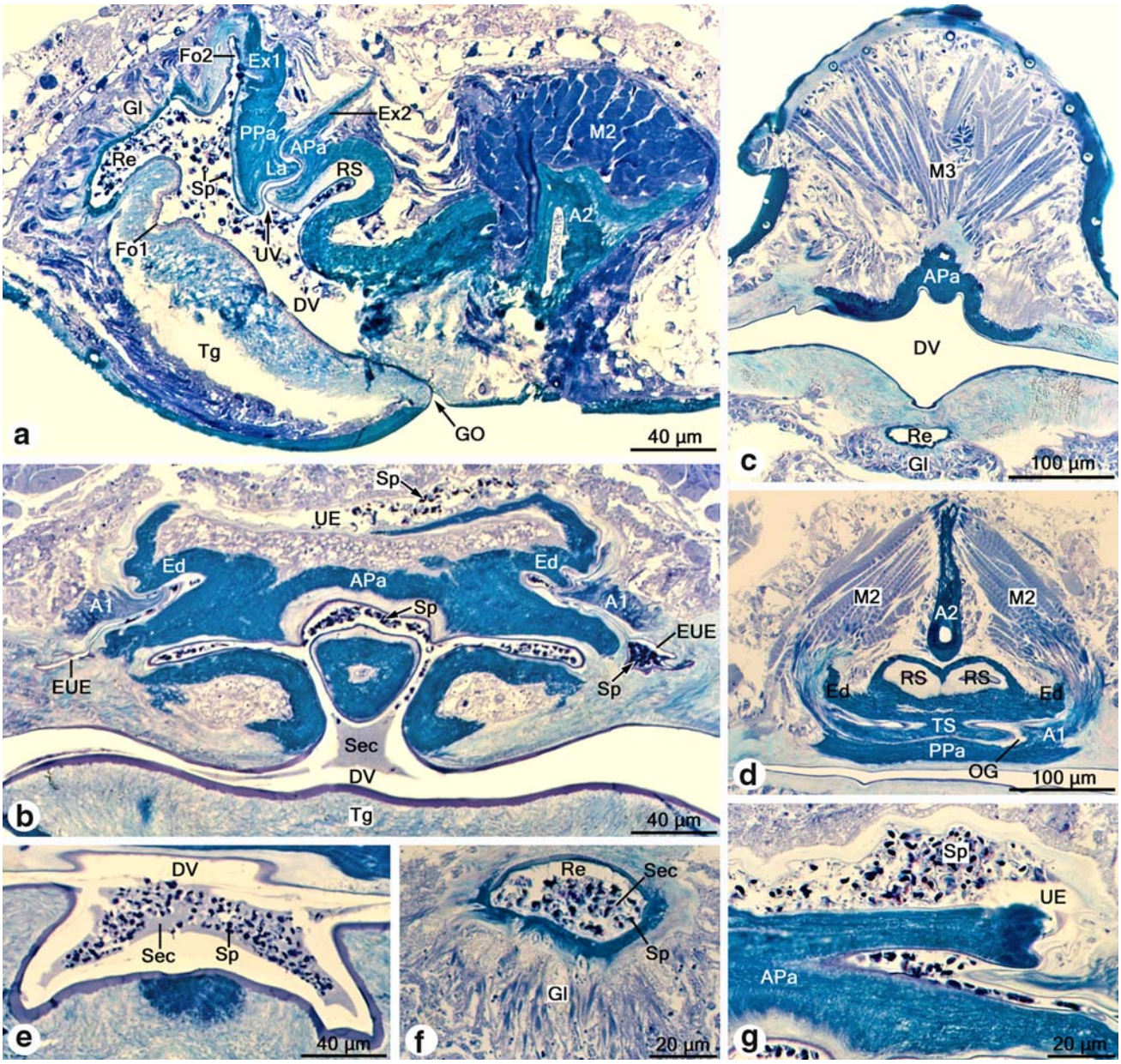


Fig. 7 Female genital region of *Harpactea lepida*. Light microscopy. **a** Longitudinal section. **b, e–g** Cross sections. **c, d** Horizontal sections. *A1* sclerite serving as muscle attachment, *A2* stalk-like sclerite serving as muscle attachment, *APa* anterior part of sclerotized genital structures, *DV* diverticulum, *Ed* lateral edge of anterior part of sclerotized genital structures, *EUE* lateral extension of uterus externus, *Ex1* dorsal extension of posterior part of sclerotized genital structures, *Ex2* dorsal extension of anterior part of sclerotized genital structures, *Fo1*, *2* folds of diverticulum, *Gl* gland cells, *GO* genital opening, *La* lamella on posterior part of sclerotized genital structures, *M2*, *M3* muscles 2, 3, *OG* oval gap of lamella, *PPa* posterior part of sclerotized genital structures, *Re* receptaculum, *RS* roundish structure of anterior part of sclerotized genital structures, *Sec* secretion, *Sp* spermatozoa, *Tg* tongue-like protrusion, *TS* T-shaped sclerite of anterior part of sclerotized genital structures, *UE* uterus externus, *UV* uterine valve

Passing the uterine valve seems to be the only way for the spermatozoa to get from the diverticulum to the uterus externus. The massive muscles M1–M3 in *H. lepida* may be used to open the uterine valve which was also suggested for *D. erythrina* (Uhl 2000). The spermatozoa may either be moved from the diverticulum to the uterus by the female or the male may produce enough pressure during sperm transfer to bring the spermatozoa in the uterus via the uterine valve. The peculiar extension with the crown-like structure could be used to "anchor" the palpal bulb in order to bring the embolus in the right position for insemina-

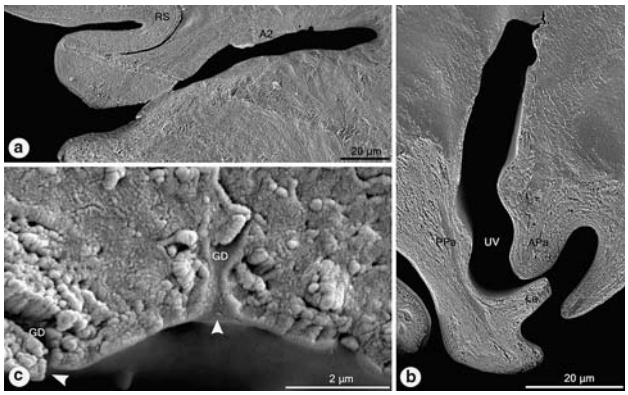


Fig. 8 Longitudinally sectioned female genital region of *Harpactea lepida*. Scanning electron microscopy. **a** Roundish structure *RS* and sclerite *A2* functioning as muscle attachment. **b** Uterine valve *UV* and lamella *La* between sclerotized genital structures *PPa* and *APa*. **c** Glandular ducts *GD* and pores *arrowheads* in posterior wall of receptaculum

tion and sperm transfer. It seems that the valve can hardly be opened due to the T-shaped sclerite (TS) fitting in the oval gap (OG) of the lamella (La). Nevertheless, the uterine valve can be slightly opened in freshly fixed females (personal observation Konrad Thaler). However, it is hardly imaginable how the oocytes pass the narrow uterine valve during oviposition. In certain parthenogenetic insects, i.e., parasitic wasps, the cleavage of the eggs is initiated by mechanical forces, which arise, when the eggs are pressed through a narrow slit during oviposition (Quicke 1997). These forces are necessary because the development of the eggs is normally induced by the fertilization, which does not take place in parthenogenetic species (Quicke 1997). Interestingly, parthenogenesis indeed occurs in a dysderid species: *Dysdera hungarica* Kulczyn'ski, 1897 (Gruber 1990). Similar sclerotized valves to the uterine valve of *H. lepida* are present in other haplogynes, e.g., pholcids (Uhl 1994a, b; Huber 1994, 1995) where valval ridges and grooves match exactly (Uhl 1994a), which seems to restrict the opening of the valve too. However, the valves in pholcids should separate the uterus externus from the uterus internus (Uhl 1994a, b; Huber 1994, 1995). This is clearly not the case in *H. lepida* where the uterus externus is connected with the diverticulum by the uterine valve.

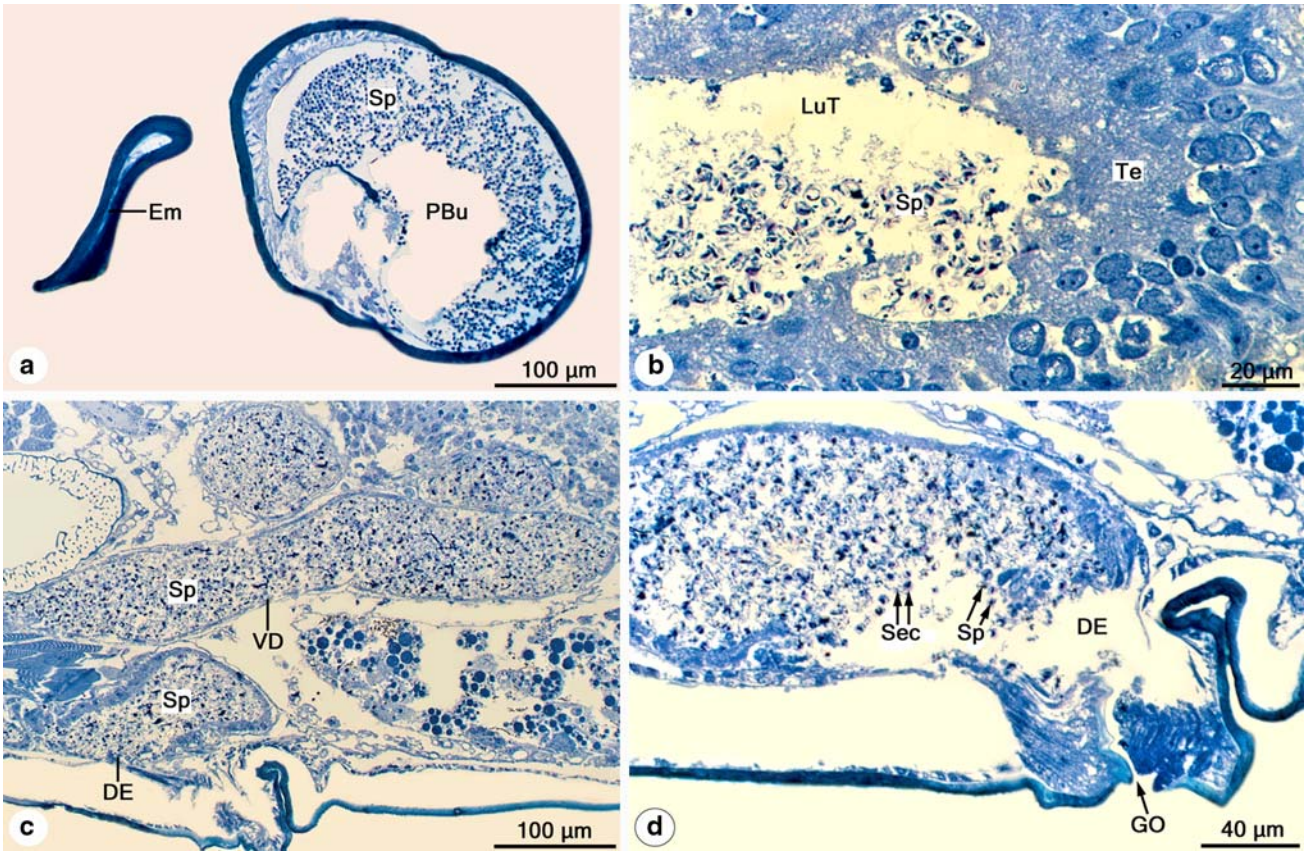


Fig. 9 Longitudinal sections through male of *Harpactea lepida*. Light microscopy **a** Embolus *Em* and palpal bulb *PBu* containing spermatozoa *Sp*. **b** Testes *Te* showing lumen of testes *LuT* with spermatozoa *Sp*. **c, d** Vas deferens *VD* and ductus ejaculatorius *DE* containing spermatozoa *Sp* and secretion *Sec* and genital opening *GO*.

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References

Alberti G (2000) Chelicerata. In: Jamieson BGM, Progress in male gamete ultrastructure and phylogeny. In: Adiyodi KG, RG, (ed) Reproductive biology of invertebrates, vol 8. Oxford & IBH Publishing Co. PVT LTD, Queensland, pp 311–388

Alberti G, Michalik P (2004) Feinstrukturelle Aspekte der Fortpflanzungssysteme von Spinnentieren (Arachnida). Denisia 12:1–62

Alberti G, Weinmann C (1985) Fine structure of spermatozoa of some labidognath spiders (Filistatidae, Segestriidae, Dysderidae, Oonopidae, Scytodidae, Pholcidae; Araneae; Arachnida) with remarks on spermiogenesis. J Morphol 185:1–35

Austad SN (1984) Evolution of sperm priority patterns in spiders. In: Smith RL (ed) Sperm competition and the evolution of animal mating systems. Academic, New York, pp 223–249

Berendonck B, Greven H (2005) Genital structures in the entelegyne widow spider *Latrodectus revivensis* (Arachnida; Araneae; Theridiidae) indicate a low ability for cryptic female choice by sperm manipulation. J Morphol 263:118–132

Brignoli PM (1978) Some remarks on the relationships between the Haplogynae, the Semientelegynae and the Cribellatae (Araneae). Symp Zool Soc Lond 42:285–292

Burger M, Nentwig W, Kropf C (2003) Complex genital structures indicate cryptic female choice in a haplogyne spider (Arachnida, Araneae, Oonopidae, Gamasomorphinae). J Morphol 255:80–93

Burger M, Michalik P, Graber W, Jacob A, Nentwig W, Kropf C (2006a) Complex genital system of a haplogyne spider (Arachnida, Araneae, Tetrablemmidae) indicates internal fertilization and full female control over transferred sperm. J Morphol 267:166–186

Burger M, Graber W, Michalik P, Kropf C (2006b) *Silhouettella loricatula* (Arachnida, Araneae, Oonopidae): a haplogyne spider with complex female genitalia. J Morphol 267:663–677

Coddington JA, Levi HW (1991) Systematics and evolution of spiders (Araneae). Annu Rev Ecol Syst 22:565–592

Cooke JAL (1966) Synopsis of the structure and function of the genitalia in *Dysdera crocata* (Araneae, Dysderidae). Senckenbergiana 47:35–43

Eberhard WG (1996) Female control: sexual selection by cryptic female choice. Princeton University Press, Princeton

Forster RR, Platnick NI (1985) A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. Bull Am Mus Nat Hist 181:1–230

Galis F (1996) The application of functional morphology to evolutionary studies. Trends Ecol Evol 11:124–129

Gerhardt U (1927) Neue biologische Untersuchungen an einheimischen und ausländischen Spinnen. Z Morphol Ökol Tiere 8:96–186

Gerhardt U (1933) Neue Untersuchungen zur Sexualbiologie der Spinnen, insbesondere an Arten der Mittelmeerländer und der Tropen. Z Morphol Ökol Tiere 27:1–75

Gruber J (1990) Fatherless spiders. Newsl Br Arachnol Soc 58:3

Hellriegel B, Ward PI (1998) Complex female reproductive tract morphology: its possible use in postcopulatory female choice. J Theor Biol 190:179–186

Huber BA (1994) Genital morphology, copulatory mechanism and reproductive biology in *Psilochorus simoni* (Berland, 1911) (Pholcidae; Araneae). Neth J Zool 44:85–99

Huber BA (1995) Copulatory mechanism in *Holocnemus pluchei* and *Pholcus opilionoides*, with notes on male cheliceral apophyses and stridulatory organs in Pholcidae (Araneae). Acta Zool 76:291–300

Huber BA (2002) Functional morphology of the genitalia in the spider *Spermophora senoculata* (Pholcidae, Araneae). Zool Anz 241:105–116

Michalik P, Dallai R, Giusti F, Alberti G (2004) The ultrastructure of the peculiar synspermia of some Dysderidae (Araneae, Arachnida). Tissue Cell 36:447–460

Michalik P, Reiher W, Suhm-Tintelnot M, Coyle FA, Alberti G (2005) The female genital system of the folding-trapdoor spider *Antrodiaetus unicolor* (Hentz, 1842) (Antrodiaetidae, Araneae)—an ultrastructural study of form and function with notes on reproductive biology of spiders. J Morphol 263:284–309

Quicke DLJ (1997) Parasitic wasps. Chapman & Hall, London, p 470

Schult J (1980) Die Genitalstrukturen haplogyner Araneae unter phylogenetischem Aspekt (Arachnida). Doctoral thesis, University of Hamburg

Uhl G (1994a) Genital morphology and sperm storage in *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae; Araneae). Acta Zool Stockh 75:1–12

Uhl G (1994b) Ultrastructure of the accessory glands in female genitalia of *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae; Araneae). Acta Zool Stockh 75:13–25

Uhl G (1996) Sperm storage secretion of female cellar spiders (*Pholcus phalangioides*; Araneae): a gel-electrophoretic analysis. J Zool 240:153–161

Uhl G (2000) Two distinctly different sperm storage organs in female *Dysdera erythrina* (Araneae: Dysderidae). Arthropod Struct Dev 29:163–169

Uhl G (2002) Female genital morphology and sperm priority patterns in spiders (Araneae). In: Toft S, Scharff N (eds) European arachnology 2000. Aarhus University Press, Aarhus, pp 145–156

Wiehle H (1953) Spinnentiere oder Arachnoidea (Araneae). IX: Orthognatha-cribellatae—haplogynae, entelegynae. In: Dahl F (ed) Tierwelt Deutschlands, vol. 42. Gustav Fischer Verlag, Jena

Wiehle H (1967) *Meta*, -eine semientelegyne Gattung der Araneae (Arach.). Senckenbergiana 48:183–196